# Appendix I

*Updated* Draft Housing Element Update (October 2021)

The *Updated* Draft Housing Element Update (October 2021) is available to download using the following link:
https://cityclerk.lacity.org/lacityclerkconnect/index.cfm?fa=ccfi.viewrecord&cfnumber=21-1230

# Appendix J

*Updated* Draft Safety Element Update (October 2021)

The *Updated* Draft Safety Element Update (October 2021) is available to download using the following link:

https://cityclerk.lacity.org/lacityclerkconnect/index.cfm?fa=ccfi.viewrecord&cfnumber=20-1213

# Appendix K

Listing of Amendments to the Plan for a Healthy Los Angeles (October 2021)

The Listing of Amendments to the Plan for a Healthy Los Angeles is available to download using the following link:

https://cityclerk.lacity.org/lacityclerkconnect/index.cfm?fa=ccfi.viewrecord&cfnumber=15-0103-S3

# Appendix L

Bracketed Public Comments Received for the Draft EIR

# Agencies Comments

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# Fwd: Draft Housing Element

**Cally Hardy** <cally.hardy@lacity.org> Mon, Aug 16, 2021 at 9:15 AM
To: Housing Element <housingelement@lacity.org>

---------- Forwarded message ---------
From: **Matthew Glesne** <matthew.glesne@lacity.org>
Date: Fri, Aug 13, 2021 at 4:19 PM
Subject: Fwd: Draft Housing Element
To: Ari Briski <ari.briski@lacity.org>, Betty Barberena <betty.barberena@lacity.org>, Blair Smith <blair.smith@lacity.org>, Cally Hardy <cally.hardy@lacity.org>, Pallini, Conni <conni.pallini-tipton@lacity.org>, Wajiha Ibrahim <wajiha.ibrahim@lacity.org>

FYI

---------- Forwarded message ---------
From: **Vince Bertoni** <vince.bertoni@lacity.org>
Date: Fri, Aug 13, 2021 at 4:09 PM
Subject: Fwd: Draft Housing Element
To: Arthi Varma <arthi.varma@lacity.org>, Matthew Glesne <matthew.glesne@lacity.org>, Yeghig Keshishian <yeghig.keshishian@lacity.org>

FYI

LOS ANGELES CITY PLANNING

**Vincent P. Bertoni, AICP**
Pronouns: He, His, Him
Director of Planning
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
Los Angeles, CA 90012
Planning4LA.org
T: (213) 978-1271 | F: (213) 978-1275
E: vince.bertoni@lacity.org

E-NEWS

---------- Forwarded message ---------
From: **Councilmember Martinez** <councilmember.martinez@lacity.org>
Date: Fri, Aug 13, 2021 at 2:53 PM
Subject: Draft Housing Element
To: Vince Bertoni <vince.bertoni@lacity.org>, Ann Sewill <Ann.sewill@lacity.org>
Cc: Max Podemski <max.podemski@lacity.org>

Dear Mr. Bertoni and Ms. Sewill,

Please find the attached letter regarding the Draft Housing Element.

If you have any questions you can contact my staff member, Max Podemski, at max.podemski@lacity.org.

Sincerely,

NURY MARTINEZ
LA City Council President
Councilwoman, 6th District
--

**Matthew Glesne**
Preferred Pronouns: He, Him, His
Senior City Planner
**Los Angeles City Planning**
200 N. Spring St., Room 750
Los Angeles, CA 90012
Planning4LA.org
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E-NEWS

--

**Cally Hardy** (she/her/hers)
City Planning Associate
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E-NEWS

**8.13.21 Housing Element Letter_vF.pdf**
431K

CITY HALL
LOS ANGELES, CALIFORNIA 90012

August 13th, 2021

Letter A-1

Mr. Vince Bertoni, Director of Planning
Los Angeles Department of City Planning
200 North Spring Street
Los Angeles, CA 90012

CC: Ann Sewill, General Manager HCIDLA

**RE: Draft Housing Element**

Dear Mr. Bertoni,

For decades, the City of Los Angeles, the surrounding region, and the State as a whole have critically underbuilt housing. This shortage has led to some of the highest rents and home prices in the nation. The biggest impact is on working class families of all backgrounds, rendering the American Dream of homeownership and upward mobility out of reach. A direct consequence of this lack of housing is evident through the increasing numbers of families and individuals experiencing displacement, gentrification, and, for our most vulnerable, homelessness.

Systemic inequity in our planning and land use policies has fostered our current housing crisis, with Los Angeles, like cities across the country, still reeling from the racist practice of redlining. This federal policy segregated urban areas into zones based on their demographic and physical characteristics. The result was generational and systematic disinvestment in many neighborhoods which continues to deny generations of black and brown families the ability to build wealth through homeownership. 1

While redlining has officially been abolished, its impact is still evident in the scope, quality and production of housing, public transit access, open space, and jobs-production throughout the city. Affluent neighborhoods have been largely insulated from the demands for growth while communities of color have become dumping grounds for facilities not wanted anywhere else, such as freeways, airports and landfills. However, the biggest ramification of redlining is on housing. A majority of the land in the City is today subject to overlapping restrictions created piece by piece over time that work together to constrain housing supply, particularly affordable housing.

The housing crisis is Los Angeles' number one issue. It compromises our economic strength when a company's employees cannot afford to live here. It limits our ability to address our climate and sustainability goals if we cannot create areas that support transit. It threatens families with displacement and homelessness.

However, with the new Housing Element, and the reforms called for in CF: 20-1042 (Martinez), we have an opportunity to assist in solving these issues by fixing our broken land use system. The City can become more affordable and equitable by creating vibrant and walkable communities near jobs and transit while respecting the character of our single family neighborhoods. This will allow Los Angeles to go from redlining to green and prosperous neighborhoods.

The City has made great strides in trying to tackle the affordable housing crisis through recent policies. This includes making it easier to build Accessory Dwelling Units (ADUs), affordable housing incentive programs, and Measure HHH among others. It also should be noted that the City's housing crisis is partially the result of State policies. This includes environmental reviews that make housing more expensive, Costa Hawkins and the Ellis Act which make it difficult to protect tenants, and the dissolution of Redevelopment Agencies which resulted in a dramatic cut in funding for affordable housing.

The Department of City Planning should be applauded for the incredible undertaking on the Housing Element up to this point. The Department has conducted a rigorous analysis of the City's existing capacity and outlined important programs for achieving our Regional Housing Needs Assessment (RHNA) target. It is a progressive first step and has been cited as being one of the best Draft Housing Elements in the State. However, the crisis facing Los Angeles requires bold action and this document can be further strengthened so that we can make Los Angeles a home for all. 1 cont.

**Incentive Program**

Los Angeles has an abundance of land on commercial corridors where much of the city's new housing can be accommodated without disrupting existing single family neighborhoods. These streets are often served by rapid transit yet are composed of single story buildings or large parking lots, with severe height, density and Floor Area restrictions. In these areas it's not enough to simply add base incentives on existing zoning citywide. The Housing Element must identify these constrained zones and ensure that they have underlying capacity to support the mid-rise, mixed use corridors the City needs to create walkable and vibrant neighborhoods.

Program 48 in the Draft Housing Element calls for expanding the city's existing incentive programs such as Density Bonus and Transit Oriented Communities (TOC). These programs have resulted in many market rate and affordable housing units being built. The report on CF: 19-0416 (Cedillo) states that nearly 80% of all affordable units in high income areas were produced through these incentive programs.

However, the incentive programs have not had an equal impact on all neighborhoods. These programs should be modified so that they are tailored to the demographics and market conditions of the communities it is expanded in. In certain areas, affordable housing requirements should exceed the current TOC program standards. The type of affordable housing should also reflect

the need in that area. For example, in certain areas developments utilizing TOC have resulted in a net loss of affordable and larger size units.

The city also has a critical shortage of housing for families, seniors and the disabled population, new incentives should be included to build housing for these populations. The incentive concept should be further expanded to include upgrading infrastructure in neighborhoods where projects are built. This should include funding for first last mile improvements, streetscape infrastructure, transit demand management programs, open space, and overall mobility improvements.

The rezoning program should expand these incentive programs in the high and highest opportunity areas as defined by the California Tax Credit Allocation Committee (TCAC). This is an index and opportunity mapping tool to identify areas of high opportunity (labeled "Highest Resource" and "High Resource") as well as areas of high segregation and poverty (labeled "High Segregation and Poverty areas"). It should also be expanded in other areas of the city, particularly along commercial corridors and areas that do not pose a displacement risk for existing tenants.

**Rezoning Program**

Program 121 in the Draft Housing Element calls for a 219,732 unit rezoning program to accommodate our RHNA allocation of 456,643 units by 2029. However, Los Angeles's housing deficit, particularly for affordable units, is estimated to be much higher than this number. The Draft Housing Element is also based on a rate of ADU production and completion of private development projects the city has not historically achieved. In order to ensure that Program 121 actually results in enough new construction to meet our RHNA allocation, we encourage Planning to adopt a rezoning target of 300,000 homes by 2029. 1 cont.

The rezoning program should focus on commercial cores and boulevards to ensure it does not impact existing neighborhoods and low income tenants in particular. The current rezoning analysis includes parcels that are currently occupied with housing covered under the Rent Stabilization Ordinance (RSO). Los Angeles desperately needs to create more housing, but this should not be done at the expense of low income Angelenos. We encourage Planning to incorporate the recommendations in CF: 21-0035 (Martinez) to ensure that if RSO buildings are redeveloped, each unit is replaced and the tenants are given the right to return. The Housing and Community Investment Department (HCID) and the Housing Authority of the City of Los Angeles (HACLA) should also seek to acquire RSO housing to bring it off the speculative market and ensure it stays affordable as called for in CF: 21-0046 (Martinez).

**Removing Barriers to Housing Production**

Program 54 of the Draft Housing Element recommends modifying site plan review for 100% affordable projects. This could be further expanded to offer additional ministerial review processes for projects that include a minimum percentage of affordable units or ownership opportunities for low to moderate-income households.

Another major barrier to building housing are P, or Parking Zones. These zones have been declared antiquated by the Department yet they are still abundant along commercial corridors where new growth should be focused. Many of these streets have good transit access and are otherwise primed for appropriate redevelopment, such as Van Nuys Boulevard which will soon have a new light rail line. However, in many places the P Zones enshrine existing low density

land uses composed of single story shopping centers surrounded by a sea of surface parking Program 48 calls for allowing housing in P Zones through a new incentive program. P Zones should also be eliminated through Program 121 and have those zones permit uses consistent with the multi-family or commercial zone in proximity to the P-zoned lot, while still ensuring an appropriate buffer between abutting sensitive uses such as single family homes.

**Expediting Affordable Housing:**
We strongly support expediting affordable and permanent supportive housing. One of the largest barriers for these projects is navigating between multiple city departments to gain approvals. The city must strengthen the communication and coordination between these departments and create an internal citywide system to expedite affordable and permanent supportive housing projects, such as those approved under CF: 21-0054 (de León).

Program 54 calls for expediting affordable housing projects. This program should also look at prioritizing the production of affordable housing on publicly-owned land particularly in high opportunity neighborhoods. It should also consider an affordable housing zoning overlay that would provide incentives for the creation of housing with a high level of affordability. This program should incorporate the goals of CF: 21-0658 (Raman). It should also incorporate the goals of CF: 21-0054 (Price) to create a tiered structure of processing, and expedite processing overall, for projects that create the largest amount of affordable or permanent supportive housing.

**Missing Middle:**
Missing Middle housing is referenced in several work programs listed in the Draft Housing Element including Programs 59 and 64. This term does not refer to specific affordability requirements, but modest three to eight unit buildings. This type of housing is an important tool in building naturally affordable housing due to the fact that they are built on the same sized lot as a single family home allowing land costs to be distributed efficiently across multiple units. Historically, missing middle housing types such as bungalow courts provided affordable accommodations in neighborhoods across the city. Today, these structures are cherished for their charming architecture and human scale.

1 cont.

Missing Middle housing should become its own work program in the Housing Element. It should be a critical tool in the program to provide more housing in a way that is sensitive to neighborhood character. Since it is difficult to include onsite affordable housing in small scale developments, Planning should incorporate CF: 21-0037 (Martinez) to create an incentive program where these buildings pay into a rental assistance program on an annual basis through a covenant. The Program should also create pre-approved standard ADU, small-scale “missing middle” multifamily and small lot subdivision housing plans, allowing more family owned and small builders to receive a permit quickly if they use a pre-approved design which was called for by CF: 21-0061 (Blumenfield/de León). This program should also explore strategies for incentivizing homeownership for low and moderate-income families in these buildings.

**Community Plan Updates:**
In the 20th century, land-use policies were introduced across the nation to facilitate the dispersal of households from crowded cities and encourage more property ownership. Underlying many of these laws, however, was a concerted effort to segregate households by race and ethnicity.

Historically redlined neighborhoods and the contours of segregation in our country remain as entrenched today as they were a hundred years ago. It is essential that the Planning Department

explore a new methodology as part of the Housing element update that ensures that equity is at the core of future land use considerations including the Citywide Community Plan Update Program to counter past injustices created by planning practices.

One way this new methodology can ensure that our land use planning creates opportunities for all Angeleno's is by ensuring that a diverse array of housing types and affordability levels are built in each neighborhood. Programs 49, 50, and 60 seek to create citywide growth targets and distribute them by Community Plan Areas. We are in strong support of Program 50 which calls for updating the Citywide Growth Strategy as part of an update to the Land Use Element to ensure that the growth and land use distribution strategy aligns with citywide goals around equity and sustainability.

These programs should enforce the Measure JJJ requirement that community plan updates do not reduce the capacity for creation and preservation of affordable housing or undermine California Government Code Section 65915 or any other affordable housing incentive program by requiring that all increases in allowable density and FAR be aligned with on-site affordable housing standards that meet or exceed TOC. The Community Housing Needs Assessment Process should be based upon citywide housing production goals and utilize a methodology that balances traditional factors such as job and transit access with a new prioritization for high opportunity areas, anti-displacement, healthy and affordable housing, and achieving housing opportunities at the deepest affordability levels. 1 cont.

We commend the work the Planning Department has done so far on the Draft Housing Element. We strongly recommend including these recommendations to create an even stronger plan for housing all Angelenos.

Sincerely,

NURY MARTINEZ
Councilmember, 6th District

MARQUEECE HARRIS-DAWSON
Councilmember, 8th District

GILBERT A. CEDILLO
Councilmember, 1st District

BOB BLUMENFIELD
Councilmember, 3rd District

CURREN D. PRICE
Councilmember, 9th District

KEVIN DE LEON
Councilmember, 14th District

NITHYA RAMAN
Councilmember, 4th District

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# SCH # 2021010130, Los Angeles Citywide Housing Element 2021-2029 Update and Safety Element Update

3 messages

**Gibson, Emily@DOT** <Emily.Gibson@dot.ca.gov> Wed, Sep 1, 2021 at 11:23 AM
To: OPR State Clearinghouse <State.Clearinghouse@opr.ca.gov>
Cc: "housingelement@lacity.org" <housingelement@lacity.org>

Hello,

For your records, the attached letter is Caltrans District 7's response to the following project: **SCH # 2021010130, Los Angeles Citywide Housing Element 2021-2029 Update and Safety Element Update**. The Lead Agency under CEQA, which is the City of Los Angeles, is CC'ed on this email.

Please let me know if you have any questions or need anything else from me.

Best regards,


## Emily Gibson

Associate Transportation Planner, Local Development-Intergovernmental Review

Caltrans District 7, Los Angeles

Emily.Gibson@dot.ca.gov

Work Cell Phone: 213-266-3562


*Note: Due to COVID-19, I am teleworking.*

**Response Letter_GTS # 07-LA-2021-03661.pdf**
130K

**OPR State Clearinghouse** <State.Clearinghouse@opr.ca.gov> Wed, Sep 1, 2021 at 11:40 AM
To: "Gibson, Emily@DOT" <Emily.Gibson@dot.ca.gov>
Cc: "housingelement@lacity.org" <housingelement@lacity.org>

Hello,

Thank you for your submittal – the State Clearinghouse has received your comment.

**Olivia Naves** |she/her|

Assistant Planner – State Clearinghouse Unit

Governor's Office of Planning and Research

1400 Tenth Street

Sacramento, CA 95814

[Quoted text hidden]

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**Housing Element** <housingelement@lacity.org> Wed, Sep 1, 2021 at 2:31 PM
To: OPR State Clearinghouse <State.Clearinghouse@opr.ca.gov>
Cc: "Gibson, Emily@DOT" <Emily.Gibson@dot.ca.gov>

Hello,

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

**DEPARTMENT OF TRANSPORTATION**
DISTRICT 7 – Office of Regional Planning
100 S. MAIN STREET, MS 16
LOS ANGELES, CA 90012
PHONE (213) 266-3562
FAX (213) 897-1337
TTY 711
www.dot.ca.gov

*Making Conservation a California Way of Life.*

Letter A-2

September 1, 2021

Cally Hardy
City of Los Angeles
Department of City Planning
200 North Spring Street, Room 750
Los Angeles, CA 90012

RE: Los Angeles Citywide Housing Element 2021-2029 Update and Safety Element Update – Draft Environmental Impact Report (DEIR)
SCH # 2021010130
GTS # 07-LA-2021-03661

Dear Cally Hardy:

Thank you for including the California Department of Transportation (Caltrans) in the environmental review process for the above referenced DEIR. The project involves updates to the City of Los Angeles General Plan Housing Element and Safety Element, and a Rezoning Program for the creation of additional housing units. The Housing Element Update will further the goal of meeting the existing and projected housing needs of all family income levels of the community through the construction and operation of 420,327 housing units; provide evidence of the City's ability to accommodate the Regional Housing Needs Assessment (RHNA) Allocation of 456,643 housing units through the year 2029; and identify a Rezoning Program that will create at least 219,732 housing units of new capacity by October 2024. This will accommodate both the City's RHNA Allocation and target capacity of 486,379 housing units. The Safety Element Update will formally integrate related long-range planning efforts to ensure compliance with State law, including additions to goals, policies, and objectives to better address climate change; integration of updated background information and mapping; and incorporation and update of various programs. The project also involves a targeted update to the Plan for a Healthy Los Angeles to clarify that it is the City's General Plan Element containing environmental justice goals and policies for the City, in compliance with Senate Bill 1000. The City of Los Angeles is the Lead Agency under the California Environmental Quality Act (CEQA). 1

The project covers the City of Los Angeles, which includes several state facilities, such as the Interstate (I) 210, United States 101, State Route (SR) 134, SR-118, SR-170, I-405, I-10, I-110, I-105, I-5, and I-710. From reviewing the DEIR, Caltrans has the following comments.

The DEIR states that the VMT impacts of the new Housing Element and Safety Element, as well as the Rezoning Program, should be less than significant, but that future individual housing developments might result in significant Vehicle Miles Traveled (VMT). For these individual projects, Transportation Demand Management (TDM) programs may be used to reduce their VMT impacts to less than significant levels. Caltrans supports the use of TDM measures to decrease VMT. Implementing TDM strategies aligns with Caltrans's mission is to provide a safe, sustainable, integrated and efficient transportation system to enhance California's economy and livability. Caltrans looks forward to reviewing the CEQA documents of future housing developments that emerge from these plan and program updates, and collaborating with 2

the City of Los Angeles on identifying TDM strategies to limit VMT from these future projects. 2 cont.

The DEIR also states that the Rezoning Program component of the project will prioritize opportunities for rezoning and development incentives in areas that are in Transit Priority Areas, near major job centers, and in higher resource areas. We also support this kind of prioritization, as it will result in limited project VMT. 3

In addition, the DEIR states that build out of the RHNA may contribute to queuing on freeway off-ramps that lead to unsafe speed differentials. Since the Housing Element Update is programmatic and there is currently no specific information on where safety impacts may occur as a result of freeway off-ramp queuing, it is not possible to identify appropriate mitigation measures. Therefore, impacts related to highway safety would be significant and unavoidable. Caltrans agrees with this assessment, and the idea that the LADOT and Caltrans can identify specific queueing impacts and solutions on a case-by-case basis during individual housing project reviews. Potential solutions include additional TDM strategies and changes to the ramp terminal such as traffic signalization, signal phasing, or timing modifications. Thus, like our previous statement, Caltrans looks forward to coordinating with the City of Los Angeles during the CEQA review process on identifying strategies to limit queueing and safety issues from future housing developments that emerge from these plan and program updates. 4

If you have any questions about these comments, please contact Emily Gibson, the project coordinator, at Emily.Gibson@dot.ca.gov, and refer to GTS # 07-LA-2021-03661.

Sincerely,

Miya Edmonson

MIYA EDMONSON
IGR/CEQA Branch Chief

cc: Scott Morgan, State Clearinghouse

# Organization Comments

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# LA City Housing Element - Comment Letter

**Housing Element** <housingelement@lacity.org> Wed, Aug 18, 2021 at 5:35 PM
To: Anthony Dedousis <anthony@abundanthousingla.org>

Anthony,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
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T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

On Wed, Jul 28, 2021 at 9:33 AM Anthony Dedousis <anthony@abundanthousingla.org> wrote:

> Dear Mr. Bertoni and colleagues,
>
> Hope your week is going well. I'm reaching out to share a letter from Abundant Housing LA and YIMBY Law regarding the City of Los Angeles' draft housing element.
>
> We are supportive of the draft housing element's sophisticated, data-driven site inventory analysis, the detailed and objective assessment of fair housing issues in Los Angeles, and the recognition that significant upzoning will be needed to achieve the RHNA target. However, we wish to draw your attention to issues in the draft housing element's site inventory methodology, and to the lack of specificity in the proposed zoning and land use reform plan.
>
> The attached letter contains a detailed explanation of where we view the City as having fallen short of HCD's standards and state law. Please let us know when you are available to discuss these concerns, and thank you for your consideration.
>
> Regards,
>
> Anthony
>
> --
> **Anthony Dedousis**
> Director, Policy and Research
> Abundant Housing LA
> 515 S Flower Street, 18th Floor
> Los Angeles, CA 90071
> 516-660-7402

July 27, 2021

Letter O-1

Mr. Vince Bertoni
Director of Planning
Los Angeles Department of City Planning
200 North Spring Street
Los Angeles, CA 90012

Dear Mr. Bertoni,

Thank you for the opportunity to comment on the process of updating the housing element of the City of Los Angeles' general plan. We are writing on behalf of **Abundant Housing LA** and **YIMBY Law** regarding the 6th Cycle housing element update. **Abundant Housing LA** is a pro-housing, nonprofit advocacy organization working to help solve Southern California's housing crisis, and **YIMBY Law**'s mission is to make housing in California more accessible and affordable through enforcement of state housing law. We support more housing at all levels of affordability and reforms to land use and zoning codes, which are needed in order to make housing more affordable, improve access to jobs and transit, promote greater environmental sustainability, and advance racial and economic equity. 1

**That's why we've called for a housing element update that distributes the citywide 456,000-home RHNA goal, including 184,000 that are affordable to lower-income households, to each of Los Angeles' community plan areas in a fair, equitable way.** This requires high-opportunity neighborhoods to accommodate more housing opportunities, including those that have historically blocked new housing through exclusionary zoning. Additionally, as we plan for housing growth, there must be no conversion of wildlife habitat to housing.

Our organizations, together with a broad coalition of groups representing the policy, academic, environmental, business, social justice, and affordable housing communities, have engaged with the City on the housing element update through the process' inception in early 2020: 2

- In January 2021, we wrote to recommend that, as part of the housing element update process and RHNA rezoning, the City set housing growth targets for each CPA, based on objective, quantifiable criteria like housing costs, median income, access to transit, proximity to job centers, access to parks and schools, patterns of historical exclusion and segregation, and environmental quality.
- In February, we wrote to express our concern that early drafts of the housing element update did not incorporate an equitable distribution approach to promoting housing growth.
- In April, the California Department of Housing and Community Development (HCD) issued detailed guidelines that clearly require cities to promote lower-income housing opportunities in high-opportunity neighborhoods, and defines quantitative benchmarks for assessing cities' AFFH compliance. This indicates that HCD intends to set the bar

high on AFFH compliance in housing element updates, as required under Assembly Bill 686.

- In June, we wrote to express support for the Report Relative to Citywide Equitable Distribution of Affordable Housing (CF 19-0416) and the Report Relative to a City Zoning Code Update (CF 20-1042), and encouraged the City Council to incorporate major reforms into the housing element update.

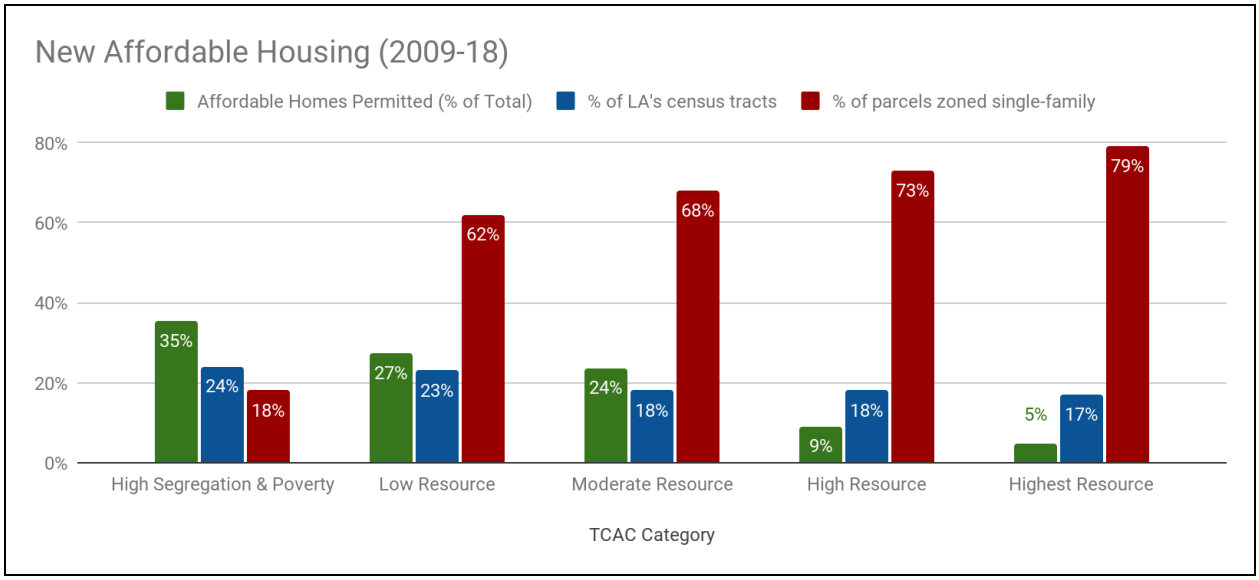
2 cont.

We have reviewed the City's draft Housing Element, as well as the Citywide Equitable Distribution of Affordable Housing and City Zoning Code Update Reports ("Fair Share Reports"), and **we are encouraged that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. In particular:**

- **The econometric approach to estimating the site capacity is outstanding.** The City's collaboration with Terner Center economists and subject matter experts resulted in a rigorous, high-quality quantitative model that predicts each parcel's likelihood of redevelopment, using a decade of parcel-level redevelopment data. This provides a fair estimate of the City's current realistic capacity for new housing, demonstrating that Los Angeles will only build 10% of its RHNA target, or about 45,000 homes, in a "business as usual" scenario. This also recognizes that Assembly Bill 1397 (2017) requires cities to discount sites' capacity by the sites' probability of development during the planning period, as argued by experts in housing element law.
- **The draft housing element provides a thorough, data-driven AFFH analysis of the site inventory.** This analysis, undertaken at the census tract level, assessed the likely neighborhood-level impacts of the site inventory. This demonstrated that, due to the geographic patterns of where today's zoning allows (and forbids) multifamily housing, the site inventory's development potential would not reduce (and might even increase) the concentration of lower-income households in low-resource areas, a clear AFFH violation. This analysis strengthens the case for focusing zoning and land use reforms in high-resource areas, to ensure that the housing element update reduces the citywide concentration of lower-income households in disadvantaged neighborhoods.
- **The Fair Share Reports provide data-driven evidence that Los Angeles' zoning and land use regulations are a root cause of housing scarcity and high costs.** Using neighborhood and census tract level data, Planning and HCID illustrate that restrictive zoning, especially apartment bans, have discouraged housing production (both market-rate and subsidized) in Los Angeles' higher-cost, supply-constrained neighborhoods. This has worsened patterns of income and racial segregation, and pushed low- and moderate-income households out of Los Angeles, with an especially negative impact on Los Angeles' communities of color.
    - For example, between 2009 and 2018, just 14% of new affordable homes were permitted in high- and highest-resource census tracts, even though these areas make up 35% of the City's total census tracts. This is because apartments are banned on 76% of the residential parcels in these well-resourced areas, a

3

function of exclusionary zoning. By contrast, 35% of new affordable homes that were permitted during that time were located in census tracts with high segregation and poverty. These areas allow apartments on 82% of their residential parcels.[1]




- **The draft housing element proposes to accommodate 220,000 more homes (almost 50% of the total RHNA goal) by 2029 through rezoning and land use reform.** Both the draft housing element and Fair Share reports propose bold policy reforms that encourage equitable citywide housing supply growth, including:
    - An equitable distribution approach to the housing element's rezoning program, where the bulk of new housing opportunities, including affordable housing opportunities, would be promoted in high- and moderate-resource areas.
    - An expansion and possible merger of the City's Transit-Oriented Communities (TOC) and Density Bonus programs.
    - A Citywide Housing Needs Allocation Process/Targeted Fair Share Zoning Allocation formula that would guide a future Framework Element update and community plan updates.

3 cont.

**We thank the hardworking staff at Planning and HCID for taking these important steps towards a successful housing element update that provides long-awaited solutions to Los Angeles' housing shortage.**

**However, we still have serious concerns about the City's plan to meet its state-mandated RHNA targets.** Portions of the draft housing element contain major inconsistencies with HCD's instructions and the requirement that housing element updates affirmatively further fair housing under Assembly Bill 686, and does not provide a detailed, specific, and credible plan for

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[1] Report Relative to Citywide Equitable Distribution of Affordable Housing, May 2021, p. 12 and p. 14

implementation of a successful rezoning and land use reform program, as required under Government Code Section 65583(c).

**The following issues are of particular concern to us:**

***1. Portions of the Adequate Sites Inventory methodology are over-optimistic about the City's likely housing development potential without rezoning or major land use reforms. As a result, the housing element only proposes to accommodate 220,000 homes through rezoning, which would likely leave the City short of its RHNA goal.***

The draft housing element's analysis of the Adequate Site Inventory finds that the City's total development potential during the 6th cycle is 266,647 homes.[2] While the forecasts for Expected Unit Potential (44,832 homes), Public Land (7,314 homes), Warner Center Specific Plan (10,491 homes), and Project Homekey (4,600 homes) are well-grounded, the forecasts for Private Development Project completion, ADU production, and Public Land Programs are over-optimistic and likely to fall short in reality. Additionally, the proposed No Net Loss buffer is insufficient, and the Adequate Site Inventory includes parcels containing rent-stabilized units as potential redevelopment sites.

The Adequate Site Inventory therefore forecasts that an annual average of 33,331 homes will be permitted throughout the 6th cycle, **almost double the average number of homes permitted between 2017 and 2020 (about 17,800 homes).**[3] This suggests that many of the Adequate Site Inventory's assumptions are over-aggressive, and should be revised downwards. 4 cont.

**A. A buffer of at least 15-30% extra capacity for the lower-income RHNA targets is not included in the housing element site inventory.**

The No Net Loss law established by SB 166 (2017) requires adequate sites to be maintained at all times throughout the planning period to accommodate the remaining RHNA target **by each income category**.[4] If a jurisdiction approves a development on a parcel listed in the site inventory that will have fewer units (either in total or at a given income level) than the number of units (either in total or at a given income level) anticipated in the site inventory, then the jurisdiction must identify and make available enough sites to accommodate the remaining unmet RHNA target for each income category.[5]

If additional sites with adequate zoned capacity don't exist, then the jurisdiction must rezone enough sites to accommodate the remaining unmet RHNA target within 180 days. If the jurisdiction fails to accomplish this rezoning in the required period, then the consequences will include decertification of the housing element and potential state legal action. HCD

[2] Draft Housing Element, City of Los Angeles, pg. 4-6
[3] HCD APR Dashboard, Units Permitted by Structure per Year, 2017-20
[4] HCD No Net Loss Law Memo, pg. 1
[5] HCD Site Inventory Guidebook, pg. 22

recommends that “the jurisdiction create a buffer in the housing element inventory of at leas 15-30% more capacity than required, especially for capacity to accommodate the lower income RHNA.”[6] **This is important because it ensures that adequate affordable housing capacity exists in the housing element through the 6th Cycle.**

The draft housing element claims to identify capacity for 486,379 housing units, only 7% higher than the RHNA goal of 456,643 homes. While this includes a 15% moderate-income buffer, only a 10% buffer is provided for the very low- and low-income RHNA targets. **This does not fulfill HCD’s recommendation to maintain a 15-30% capacity buffer <u>at each income level,</u>** giving the City inadequate margin in the event that a site intended for subsidized housing is developed with market-rate housing**.**

**Draft Housing Element No Net Loss Buffers**

| Income Category | RHNA Target | Target Capacity | Buffer |
|---|---|---|---|
| Very Low Income | 115,978 | 127,576 | 10% |
| Low Income | 68,743 | 75,617 | 10% |
| Moderate Income | 75,091 | 86,355 | 15% |
| Above Moderate Income | 196,831 | 196,831 | 0% |
| **Total** | **456,643** | **486,379** | **7%** |

The January 2021 initial study **targeted a citywide capacity increase of 501,642 homes**, including an appropriate 25% buffer for the very low- and low-income RHNA targets (although no buffer was included for the moderate-income target). No explanation was provided for the draft housing element’s use of a 10% buffer for the very low- and low-income RHNA targets.

The housing element **should increase its very low- and low-income buffers back to 25%**, as provided for in the January initial study, while maintaining the proposed 15% moderate-income buffer. **This would result in a targeted citywide capacity increase of 514,088 homes, or a 13% overall buffer.** This is necessary to avoid violating the No Net Loss requirement and mid-cycle rezoning, a costly process in terms of time, money, and political will.

**Recommended No Net Loss Buffers**

| Income Category | RHNA Target | Target Capacity | Buffer |
|---|---|---|---|
| Very Low Income | 115,978 | 144,973 | 25% |
| Low Income | 68,743 | 85,929 | 25% |

4 cont.

[6] HCD Site Inventory Guidebook, pg. 22

| | | | |
|---|---|---|---|
| Moderate Income | 75,091 | 86,355 | 15% |
| Above Moderate Income | 196,831 | 196,831 | 0% |
| **Total** | **456,643** | **514,088** | **13%** |

**B. The housing element's estimate of the likelihood that in-pipeline projects will be completed during the 6th cycle, based on historical data, is over-optimistic.**

HCD allows cities to count permitted or entitled units towards its 6th Cycle RHNA goals, on the grounds that some of these projects will be built during the 6th Cycle. However, the city must **realistically** estimate how many of these units will ultimately be built during the 6th Cycle, based on recent historical data. This is necessary because not every pending project gets approved, and not every approved project gets built.

The draft housing element forecasts that in-pipeline projects will **produce 144,070 homes during the 6th cycle.** This forecast multiplied the completion rates of pipeline development projects **since 2015** by the number of proposed units currently in-pipeline.[7]

4 cont.

**Draft Housing Element Pipeline Forecast**

| **Category** | **Units Proposed** | **% Units Expected to be Completed** (based on 2015-19 data) | **# Units Expected to be Completed** |
|---|---|---|---|
| Active Planning Entitlements | 175,907 | 53% | 93,231 |
| Approved Planning Entitlements with No Building Permit | 72,537 | 58% | 42,071 |
| By-Right Building Permit Applications (Permit not Issued) | 3,713 | 95% | 3,527 |
| Approved Building Permits with No Certificate of Occupancy | 5,516 | 95% | 5,240 |
| **Total** | **257,673** | **56%** | **144,070** |

However, this reflects a more aggressive set of assumptions relative to the January 2021 initial study, which used the completion rates of pipeline development projects **during 2018-19**.[8] No

[7] Draft Housing Element, City of Los Angeles, pg. 4-20
[8] Initial Study, City of Los Angeles, pg. 16

clear justification was provided for using a five-year lookback period, rather than the initial approach of using the two-year lookback period, which likely better reflects current development conditions. Using the more current completion data, we forecast that 105,019 in-pipeline units, or 39,051 fewer than the housing element's forecast, will be built during the 6th cycle.

**Recommended Housing Element Pipeline Forecast**

| Category | Units Proposed | % Units Expected to be Completed (based on 2018-19 data) | # Units Expected to be Completed |
|---|---|---|---|
| Active Planning Entitlements | 175,907 | 37% | 65,086 |
| Approved Planning Entitlements with No Building Permit | 72,537 | 45% | 32,642 |
| By-Right Building Permit Applications (Permit not Issued) | 3,713 | 79% | 2,933 |
| Approved Building Permits with No Certificate of Occupancy | 5,516 | 79% | 4,358 |
| **Total** | **257,673** | **41%** | **105,019** |

4 cont.

**The City should explain its rationale for using more aggressive assumptions to forecast in-pipeline production, or should update its pipeline analysis to align with the methodology in the January 2021 Initial Study.**

**C. The housing element did not use an HCD-recommended safe harbor methodology for forecasting future ADU production, nor does it provide for mid-cycle adjustments if ADU production falls short of projections.**

HCD has established two safe harbors for forecasting ADU production during the 6th Cycle[9]. One option ("Option #1") is to project forward the local trend in ADU construction since January 2018**.** The other, for use when no other data is available ("Option #2"), assumes ADU production at five times the local rate of production prior to 2018. This ensures that ADU development estimates reflect actual on-the-ground conditions, maximizing the likelihood that ADUs will be built to the level forecasted in the housing element update.

[9] HCD Site Inventory Guidebook, pg. 31

The City issued permits for 4,646 ADUs in 2018, 4,766 ADUs in 2019, and 4,190 ADUs in 202[illegible]. Under HCD's "Option #1", the City would take the average of the ADU permitting trend between 2018 and 2020, and forecast that 4,534 ADUs will be permitted per year during the 6th Cycle. **This would allow for a total 6th cycle forecast of 36,272 ADUs.**

**The draft housing element counts 45,344 ADUs, or 5,668 ADUs per year, towards the City's RHNA target**. The City argues that "based on current interest and demand for ADUs, and ongoing and planned future programs to promote ADU development in the City", ADU permitting will increase 25% above the current annual average throughout the 6th cycle.[10] However, this contention is not supported by real-world data or other convincing evidence, and it seems unlikely that providing these relatively minor incentives will yield the forecasted outcome.

**The City must correct its calculation of the ADU safe harbor, and simply apply the average of annual ADU permits issued between 2018 and 2020, per HCD's guidelines.**

**D. The site inventory counts 10,000 units of "equitable housing on public land" to be built by 2026, without adequately identifying funding sources and public resources to maximize the likelihood that these projects are actually built.**

Under state law, a housing element must affirmatively "[a]ssist in the development of adequate housing to meet the needs of extremely low, very low, low, and moderate-income households" (Gov't Code 65583(c)(2)). Additionally, HCD's AFFH Guidance Memo states that "The schedule of actions generally must (1) enhance the mobility of low-income and minority communities, (2) encourage the development of new affordable housing in high-opportunity areas, (3) protect existing residents from displacement, and (4) invest in disadvantaged places."

4 cont.

Housing elements should use available public resources, including real estate transfer taxes and publicly owned land, in order to fund and encourage the preservation of existing affordable housing, potentially through a local Tenant Opportunity to Purchase Act, community land trusts, land banks, or assisting mission-driven nonprofits with acquisition of housing whose affordability covenants are close to expiration. This is important to ensure that lower-income households are able to maintain access to quality affordable housing options.

The draft housing element counts 10,000 units of "equitable housing" on 300 acres of public land towards the city's Adequate Sites Inventory, explaining that the City recently received a Local Early Action Planning grant to support a program that would "streamline and scale up the production of affordable housing on public land" by 2027.[11]

However, acquiring and/or building 10,000 units of subsidized housing is an ambitious and expensive effort, and the LEAP grant alone is unlikely to provide enough funding to achieve this goal by the end of the 6th cycle, let alone 2027. By the City's own admission, "The program is

[10] Draft Housing Element, City of Los Angeles, pg. 4-23
[11] Draft Housing Element, City of Los Angeles, pg. 4-25

currently in the planning process, and no sites have been secured at this time."[12] Additionally, similar recent efforts by the City have not delivered affordable units quickly, on budget, and at scale. Proposition HHH, which generated $1.2 billion for supportive housing production in 2016, has suffered from significant cost overruns and delays. As a result, it has only delivered a handful of completed housing units, nearly five years after the approval of the bond.

While it's certainly possible that the City's equitable housing initiative will succeed, this outcome should not be treated as a sure thing. **Therefore, the City must exclude these units from the Adequate Sites Inventory.**

**E. The analysis of expected unit potential appears to include parcels containing rent-stabilized housing units.**

The draft housing element's econometric analysis of expected unit potential estimated the redevelopment potential of nearly all parcels in the City. "An indicator for existing structures subject to the Los Angeles' Rent Stabilization Ordinance" was included as an independent variable in the model[13], suggesting that parcels containing rent-stabilized housing units were included in the analysis of the City's current redevelopment potential.

4 cont.

We are concerned that including parcels containing rent-stabilized housing units will lead to the demolition of rent-stabilized buildings, causing displacement of lower-income renters. The realistic capacity anticipated on these sites should instead be achieved through rezoning of parcels that do not host rent-stabilized buildings.

**The econometric analysis should be updated to omit parcels containing rent-restricted and de facto affordable housing units, and the new forecast of expected unit potential be reported in the final version of the housing element.** This would be in keeping with Planning's modifications to the original econometric analysis, which removed vacant parcels located in a Very High Fire Hazard Severity Zone and parcels containing restricted affordable units that are subject to a land use covenant.[14]

**Recommendation:**

We urge the City to update the Adequate Sites Inventory methodology to include more realistic assumptions about the City's likely housing development potential without major land use reforms. **This would reduce the Adequate Sites Inventory's realistic capacity from about 267,000 homes to roughly 208,000 homes, necessitating a new rezoning target of roughly 306,000 homes, in order to achieve a citywide target capacity increase of 514,000 homes.**

[12] Draft Housing Element, City of Los Angeles, pg. 4-25
[13] Draft Housing Element, Appendix 4.6, pg. 14
[14] Draft Housing Element, Appendix 4.6, pg. 29

**Recommended updates to ASI methodology**

| | ASI Capacity | Rezoning | Total Target Capacity |
|---|---|---|---|
| **Draft Housing Element Target Capacity** | **267,000** | **219,000** | **486,000** |
| Increase to NNL buffer | | +28,000 | +28,000 |
| Adjustment to pipeline forecast | -40,000 | +40,000 | |
| Adjustment to ADU forecast | -9,000 | +9,000 | |
| Omission of equitable housing proposal | -10,000 | +10,000 | |
| **Recommended Target Capacity** | **208,000** | **306,000** | **514,000** |

4 cont.

***2. The City's proposal for zoning and land use reform lack specificity and detail, as well as a clear, rapid path to implementation. Without a firm, credible plan, the housing element will fail to adequately address the City's housing shortage and fall short on AFFH compliance.***

AB 686 (2018) requires housing element updates to "affirmatively further fair housing", which is defined as "taking meaningful actions, in addition to combating discrimination, that overcome patterns of segregation and fosters inclusive communities free from barriers that restrict access to opportunity based on protected characteristics." The City must address the issue of residential segregation by accommodating the lower-income RHNA targets in a way that conforms with AFFH requirements.

In April 2021, HCD issued an AFFH Guidance Memo, which establishes a number of important principles for promoting fair housing, including:

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- A city's AFFH analysis should reveal "current and historical spatial patterns of subsidized housing within and surrounding the jurisdiction, including emergency shelters, subsidized affordable housing, supportive housing, and usage of housing choice vouchers."[15]
- The distribution of housing-element inventory sites with lower or moderate income capacity must not be skewed toward lower-income neighborhoods. To demonstrate that the site inventory furthers fair housing, the city must calculate the percentage of households at lower, moderate, and above-moderate income levels in each census tract or "block group" in the city, and then do the same for the lower, moderate, and above-moderate-income RHNA units assigned to the tract or block group. The share of lower-income RHNA units assigned to tracts (or block groups) with a higher-than-average share of lower-income households should be less than the current share of lower-income households in those tracts.[16]
- The housing element must benchmark the citywide distribution of household incomes against the distribution in the county or region, and state. The AFFH program of a city

[15] AFFH Guidance Memo, p. 46
[16] AFFH Guidance Memo, p. 47

with an above-average median income must break down barriers that keep lower incom and minority households from accessing housing in the city.[17]

- "Goals, policies, and actions" to further fair housing must be "aggressively set to overcome ... contributing factors [to fair housing problems, and thus] to meet the 'meaningful impact' requirement in statute."[18] The list of actions shall include concrete timeframes for implementation, measurable outcomes, explicit prioritization ("high," "medium," or "low"), and "must be created with the intention to have a significant impact, well beyond a continuation of past actions."[19]
- "The schedule of actions generally must (1) enhance the mobility of low-income and minority communities, (2) encourage the development of new affordable housing in high-opportunity areas, (3) protect existing residents from displacement, and (4) invest in disadvantaged places."[20]

**The draft housing element is therefore obligated to promote fair housing opportunities and undo patterns of segregation.** The City must follow HCD's recommendation that cities distribute lower-income housing opportunities throughout the city, and recommends that cities first identify development potential for lower-income housing in high-opportunity neighborhoods.[21] **This would mean rezoning more parcels, including residential parcels currently zoned single-family only, to encourage enough housing growth to achieve the RHNA target.** 5 cont.

The City is also obligated to provide meaningful AFFH analysis, including evidence that its proposed distribution of lower-income housing opportunities would reduce the concentration of lower-income households in locations with an existing concentration of low- and moderate-income households. **HCD's recent AFFH guidance makes it abundantly clear that this benchmark will be used to help determine AFFH compliance.[22]**

**Additionally, Government Code Section 65583(c) requires housing elements to include programs with concrete action steps to facilitate housing production.[23]** Per HCD's Housing Elements Building Blocks, "Programs must include specific action steps the locality will take to implement its policies and achieve its goals and objectives. Programs must also include a specific timeframe for implementation, identify the agencies or officials responsible for implementation, describe the jurisdiction's specific role in implementation, and (whenever possible) identify specific, measurable outcomes." Building Blocks lists definite time frames for implementation, demonstration of a firm commitment to implement the program, description of the local government's specific role in program implementation, description of the specific action

[17] AFFH Guidance Memo, pp. 15, 32-34, 77
[18] AFFH Guidance Memo, p. 52
[19] AFFH Guidance Memo pp. 52, 71
[20] AFFH Guidance Memo, p. 54
[21] HCD Site Inventory Guidebook, pg. 3
[22] AFFH Guidance Memo, p. 47
[23] "The element shall contain all of the following: A program [or programs] that sets forth a schedule of actions during the planning period, each with a timeline for implementation, that may recognize that certain programs are ongoing, such that there will be beneficial impacts of the programs within the planning period, that the local government is undertaking or intends to undertake to implement the policies and achieve the goals and objectives of the housing element through the administration of land use and development controls, the provision of regulatory concessions and incentives…"

steps to implement the program, and proposed measurable outcomes (e.g., the number of units created, completion of a study, development of a homeless shelter, initiation of a rezone program, preservation of at-risk units, etc.) as appropriate examples of concrete action steps.

The draft housing element and Fair Share Reports appropriately identify major governmental constraints that perpetuate housing scarcity, provide convincing evidence that restrictive zoning and land use rules are associated with a lack of affordable housing opportunities in high-resource neighborhoods, and propose a reasonable set of high-level policy solutions. **However, the draft housing element doesn't provide an appropriately specific rezoning, constraint removal, and overall land use reform program, nor is there a firm commitment to implementing specific policy measures to encourage strong housing growth citywide, particularly in high-resource neighborhoods.** The Goals section of the draft housing element frequently uses words like "plan", "explore", "consider", "examine", but contains very few firm commitments to action or implementation. 5 cont.

**Without a more detailed plan and a credible path to implementation by October 2024, the City will not achieve its RHNA target.** Additionally, the draft housing element's lack of specificity on a land use reform program makes it impossible to assess whether it, or the draft housing element altogether, complies with state AFFH law.

**We urge the City to provide a thorough, detailed plan for rezoning, constraint removal, and overall land use reform as part of the final version of the housing element update, including details on implementation.**

**<u>A credible plan for equitably achieving the RHNA goal would include:</u>**

**A. Committing to the creation of 306,000 new homes by 2029 through the housing element's rezoning and land use reform programs.**

The draft housing element's contention that the RHNA target can be achieved by only rezoning for 220,000 new homes is based on an overly optimistic assessment of the Adequate Sites Inventory. Committing to land use reforms that target the creation of 306,000 more homes by 2029 is necessary in order to meet the RHNA target. 6

This must include a firm commitment to increase Los Angeles' **realistic capacity** by 306,000 homes (i.e. increasing the city's zoned capacity enough to result in the production of 306,000 homes), not simply increasing the **theoretical zoned capacity** by 306,000 units. A parcel's maximum theoretical capacity is not the same as its realistic capacity. To draw a parallel to college admissions, when UCLA wants 2,000 students in its incoming class, they admit 4,000 students. Similarly, to achieve housing production targets, jurisdictions must increase zoned capacity well above the target number of new homes.

State housing element law requires cities to target realistic capacity growth, not theoretical zoned capacity, in its rezoning program, just as it does for assessment of the site inventory.[24] Similarly, HCD instructs cities to "accommodate 100 percent of the shortfall of sites necessary to accommodate the remaining housing need for housing for very low- and low-income households during the planning period…" and that "Those sites must meet the adequate sites requirements in terms of the suitability and availability outlined above."[25] This also would be in keeping with the draft housing element's excellent model for assessing the City's Expected Unit Potential, which recognizes that parcel-level estimates of likelihood of redevelopment are critical for accurately forecasting future housing production.

**B. Implementation of a comprehensive Fair Share approach to the RHNA rezoning program, which would define "opportunity" holistically.**

CPA and/or neighborhood-level RHNA targets, including affordable housing growth RHNA targets, should be based on a formula that includes the following objective, numerical criteria:

- Housing costs
- Median income
- Access to transit
- Proximity to job centers
- Access to public resources (e.g. parks, schools)
- Patterns of historical exclusion and segregation
- Environmental quality

6 cont.

This would essentially merge the proposed Equitable RHNA Rezoning Program and Citywide Housing Needs Allocation Process/Targeted Fair Share Zoning Allocations methodologies, ensuring that a consistent set of standards would guide RHNA rezoning, a Framework Element update, expansion of TOC and the city Density Bonus program, and all future community plan updates. This would also ensure that a majority of new lower-income housing opportunities are accommodated in moderate-, high-, and highest-resource census tracts.

**C. Increase affordable housing opportunities in high-opportunity neighborhoods.**

In order to meet HCD's AFFH standards, the City's housing element must reverse historic patterns of socioeconomic segregation by dismantling the barriers to housing opportunities for low- and moderate-income households in high-income neighborhoods. **Policies that would promote this outcome include:**

[24] **Gov't Code 65583(c)(1):** "The housing element program "shall … (1) Identify actions that will be taken to make sites available during the planning period with appropriate zoning and development standards and with services and facilities to accommodate that portion of the city's or county's share of the regional housing need for each income level that could not be accommodated on sites identified in the inventory completed pursuant to paragraph (3) of subdivision (a) without rezoning..." It is noteworthy that the same term, "accommodate," is used in the statute to describe both what's learned from the site capacity analysis, and what will be done through the rezoning.

[25] HCD Site Inventory Guidebook, pg. 33

- **Rezoning parcels located near transit, job centers, schools, and parks in order to expand the supply of housing in the City's highest-opportunity areas. This should include R1 zoned parcels where single-family detached homes are currently mandated by law.**
- **Significantly reducing the concentration of lower-income households in neighborhoods with high concentrations of low- and moderate-income households, in neighborhoods with high exposure to pollution, and in R/ECAPs.**
- **Identifying new funding sources and public resources to encourage the production of affordable housing, such a real estate transfer tax or congestion pricing.**
- **Exempting parcels containing rent-restricted and de facto affordable housing units from rezoning, in order to prevent lower-income renter displacement.**
- **Ensuring that "no net loss" provisions apply to parcels in the site inventory and rezoning program with a monitoring and implementation program.**
- **Prioritizing the production of affordable housing on publicly-owned land.**
- **Creating a 100% affordable housing zoning overlay that encompasses high-opportunity neighborhoods, including R1 zoned parcels.**
- **Implementation of stronger tenant protection policies, including expanded affordable unit replacement requirements ("no net loss") for redevelopment of existing rental properties, a "right of return" after redevelopment at the same rent as before, and rental assistance during redevelopment.**

6 cont.

**D. Avoid relying on Community Plan updates for implementation of the RHNA rezoning program.**

Program 121 in the draft Housing Element states that "The Rezoning Program is anticipated to be implemented through a number of work efforts including updates to up to 16 Community Plans (four West LA plans and six SE/SW Valley plans, two Downtown plans, Boyle Heights, Hollywood, Harbor-Gateway and Wilmington), two Specific Plans (CASP and Slauson TNP) as well as at least one citywide ordinance that will create additional zoning capacity through an expansion of affordable housing incentive programs (Density Bonus Update)."

It is concerning that the City proposes to rely on Community Plan updates to achieve a significant portion of the RHNA rezoning program, since the Community Plan update process has a very poor track record of delivering strong housing growth. Recent Community Plan updates have suffered from years-long delays to develop and implement, often due to nuisance lawsuits from housing opponents (the Hollywood Community Plan update is a particularly salient example). Additionally, these updates often reflect the policy preferences of vocal housing opponents (e.g. the Westside Community Plan), rather than the broader community, which is why they generally do not meaningfully increase new housing opportunities. **Relying on a fundamentally broken process to achieve a rezoning program that must be implemented by October 2024 is a recipe for failure.**

The final Housing Element should report the increase in realistic capacity for housing (see Recommendation A) that would be created via the Downtown and Hollywood Community Plan updates, and should commit to achieving the remainder of the rezoning target through policy reforms that apply citywide (see Recommendations B, C, E, and G for examples).

**E. Expand and merge TOC and the city Density Bonus program.**

The City's successful TOC program has led to the production or proposal of over 30,000 housing units, of which 21% are affordable to lower-income households. Expanding it to cover more transit-rich locations and locations with access to high-quality resources, jobs, and amenities would create even more affordable housing units in high-income neighborhoods. We are encouraged by the Housing Element and Fair Share Reports' support for expanding TOC and combining it with the City's Density Bonus Program.

Crucially, this expansion must include locations where apartments are currently banned, since TOC incentives currently do not apply to parcels where fewer than five units may be built. This significantly limits the effectiveness of the TOC program, and helps to explain why relatively few TOC units have been produced in the Westside and San Fernando Valley, where R1 zoning is particularly widespread.

**F. Update the Framework Element by 2024, in parallel with the RHNA rezoning, or consider abolishing the Framework Element altogether.**

The Framework Element, a strategy for long-term growth that influences future community plan and citywide element updates, is decades out of date. By relying on flawed and outdated forecasts of future neighborhood population growth, it effectively sets artificial caps on housing production in many neighborhoods, acting as a significant barrier to an equitable distribution of new housing opportunities citywide.

While the Housing Element and Fair Share Reports recognize the need for an updated Framework Element, they don't commit to a date by which to achieve this effort. Updating the Framework Element by 2024 is a necessary step towards implementation of a high-quality, comprehensive Fair Share approach to the RHNA rezoning program. Alternatively, the City should consider abolishing the Framework Element altogether, since it is optional and not required under state law.

**G. Implement a strong constraint removal program that would apply citywide.**

While the Housing Element and Fair Share Reports discuss at length the many governmental constraints that restrict housing production and foster housing scarcity and unaffordability, they lack a detailed, credible plan for constraint removal that would apply citywide, as required under California housing element law. **Policies that would promote constraint removal, housing supply growth, and greater housing affordability include:**

6 cont.

- **End exclusionary zoning by legalizing 8 housing units on all residentially-zoned parcels, and by legalizing mid-rise and high-rise housing production on parcels near transit in high-resource areas where apartments are banned today.**
    - Legalizing denser housing on owner-occupied R1 parcels is especially important, given that the draft Housing Element's rezoning program appears over-reliant on multifamily residential and commercial parcels that likely host rent-stabilized units ("More than 50% of lower income rezoning will occur on sites with exclusively residential uses or allowing 100% residential uses.")[26] Senate Bill 10, if passed, would help to facilitate this local reform.
- **Eliminate on-site parking requirements, instead allowing property owners to decide how much on-site parking is necessary.**
- **Reduce restrictions on maximum height, floor-area ratio, unit size, and lot coverage.**
- **Raise the Site Plan Review threshold to 250 homes, and establish a fast by-right review process for all new multifamily and mixed-use buildings which meet the zoning law and the General Plan.**
- **Pre-approve standard ADU, small-scale "missing middle" multifamily and small lot subdivision housing plans, allowing developers to receive a permit quickly if they use a pre-approved design.**

6 cont.

**H. Include a full list of parcels where the rezoning program will apply in the final version of the Housing Element update.**

The City's final Housing Element should provide a full parcel-level dataset explaining where the proposed rezoning program would and would not apply, as well as summary statistics breaking out the number of homes in each income bucket accommodated in each neighborhood and by TCAC category of census tracts. This level of transparency is necessary to demonstrate that the City's rezoning program appropriately meets the state's AFFH requirements. This would also be in keeping with Los Angeles County's housing element, which provided a complete list of parcels that would be rezoned in order to implement its rezoning program.

***

The City of Los Angeles has a legal obligation to sufficiently plan to meet current and future residents' housing needs, in a way that guarantees access to opportunity for Californians of all racial and ethnic backgrounds. The issues that we've highlighted above suggest that the City has not yet offered a credible plan for fulfilling this legal obligation. We urge you to actively embrace this opportunity to provide a variety of attainable housing options for the residents and workers of Los Angeles.

7

[26] Draft Housing Element, pg. 6-84 and 6-85

Finally, state law imposes penalties on jurisdictions that fail to adopt a compliant 6th Cycle housing element update by October 15, 2021. On that date, noncompliant jurisdictions will forfeit the right to deny residential projects on the basis of local zoning, so long as projects include at least a 20% set-aside for below market-rate units or are 100% moderate-rate projects.[27] Noncompliant jurisdictions may also lose the ability to issue building permits, including permits for kitchen and bath renovations. Jurisdictions that want to maintain local control over new development should therefore plan to adopt a compliant housing element update on time.

In May, HCD declined to certify San Diego's 6th Cycle housing element, on the grounds that it did not adequately meet the legal requirements to affirmatively further fair housing, and to demonstrate the likelihood of redevelopment of non-vacant sites. If San Diego does not meet these requirements by June 16, 2021, HCD will find the housing element out of compliance. This suggests that HCD will be bold in enforcing housing element law, and that the City risks rejection of its 6th Cycle housing element and decertification if it continues down this path.

7 cont.

We request the opportunity to meet with you and your colleagues to address the concerns raised in this letter. Thank you for your time and consideration.

Sincerely,

| | |
|---|---|
| Leonora Camner | Sonja Trauss |
| Executive Director | Executive Director |
| Abundant Housing LA | YIMBY Law |

CC: Jason Elliott, Senior Counselor to Governor Gavin Newsom
Megan Kirkeby, Deputy Director, Housing Policy Development, HCD
Melinda Coy, Land Use and Planning Manager, HCD
Tyrone Buckley, Assistant Deputy Director of Fair Housing, HCD
Paul McDougall, Housing Policy Development Manager, HCD

[27] California Government Code 65589.5(d)(5).

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# Fwd: Updated Housing Elements and Zoning Codes

**Housing Element** <housingelement@lacity.org> Wed, Aug 18, 2021 at 5:29 PM
To: info@thetwohundred.org

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
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T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

---------- Forwarded message ---------
From: <info@thetwohundred.org>
Date: Fri, Aug 6, 2021 at 4:50 PM
Subject: Updated Housing Elements and Zoning Codes
To: <mayor.helpdesk@lacity.org>, <vince.bertoni@lacity.org>

Hello,

Please see attached correspondence from The 200, a civil rights homeownership advocacy group. Replies and future correspondence can be directed to our Vice-Chair, Robert Apodaca, at robert@thetwohundred.org.

Respectfully,

The 200 Coalition

The Two Hundred

Letter O-2

August 6, 2021

Mayor Eric Garcetti
The City of Los Angeles
Delivered via email to mayor.helpdesk@lacity.org

Mr. Vince Bertoni
Director of Planning
The City of Los Angeles
Delivered via email to vince.bertoni@lacity.org

Re: Updated Housing Elements and Zoning Codes Must Meet Regional Housing Needs Allocation (RHNA) Targets **and Comply with Federal and State Housing Laws Including** Attainable Homeownership, Authorizing Housing That is Affordable by Design Without Reliance on Lottery Outcomes and Taxpayer Subsidies, Affirmatively Further Fair Housing, and Ending Residential Racial Segregation

Dear Mayor Garcetti and Mr. Bertoni,

The Two Hundred is a civil rights homeownership advocacy group that was founded and remains comprised of veteran civil rights leaders, former legislators and cabinet secretaries, retired judges, and other diverse housing advocacy leaders. Many of us worked for our entire careers to enact federal and state fair housing laws to end agency "redlining" practices such as denying communities of color access to insured home mortgages and veterans' loans, and promoting residential racial segregation through razing historic minority neighborhoods through "redevelopment" and siting freeways to protect "public harmony" by dividing our communities. 1

California's severe housing shortage, and astronomical (and still-rising) housing prices, have undone decades of civil rights progress. As confirmed by scholars at UC Berkeley, residential racial segregation is worse in the Bay Area than it was before the enactment of civil rights reforms in the 1960s – a pattern repeated in wealthier counties statewide. https://belonging.berkeley.edu/segregationinthebay As we explain in our *Redlining* video, minority homeownership rates, which in the early part of this century had finally started to attain parity with white families who had access to government programs like federally-insured low cost mortgages, plummeted during the Great Recession of 2009. With the full support of regulatory agencies, as of 2010 lenders engaged in more than a decade of predatory loans and foreclosures that wiped out trillions of dollars of the multi-generational wealth that our communities had finally accumulated through homeownership. Our communities now stagger from housing costs that are so high the US Census Bureau has confirmed that our state has the highest poverty rate in the country! When added to the other high costs of living in California, including the highest electricity and gasoline prices of any state other than California, almost 2

40% of our residents cannot reliably pay routine monthly expenses even after receiving public assistance to help buy food and medical care. United Ways of California - The Real Cost Measure in California 2019 (unitedwaysca.org) California leaders should not brag about creating Silicon Valley billionaires without also recognizing the crushing burdens of decades of hostility to starter homes and other housing needed by our communities, nor can California's leaders lawfully hide behind unfunded rhetorical commitments to fund 100% "affordable" rental housing and again force our communities into segregated rental housing "projects." 2 cont.

We write because you have been entrusted with the decade's most important housing task, which is assuring that your agency complies with civil rights housing laws and updates your General Plan and Zoning Code to accommodate your community's share of new homes in compliance with your Regional Housing Needs Assessment (RHNA).

Both federal and state civil rights laws, as well as United States Supreme Court decisions, have long prohibited agencies from directing new "affordable" housing for lower income residents to a limited geographic subarea, and instead require the dispersal of new housing at all affordability levels throughout the community. In 2018, the California Legislature strengthened this longstanding civil rights requirement in AB 686 (effective January 1, 2019) which requires all public agencies to "affirmatively further fair housing" (AFFH) in California. As explained by the Housing and Community Development (HCD) agency, quoting from the new law, **"[p]ublic agencies must now examine existing and future policies, plans, programs, rules, practices, and related activities and make proactive changes to promote more inclusive communities**." AFFH / Fair Housing (ca.gov) 3

Before the AFFH was enacted in 2018, and based on a complex set of planning, zoning, and environmental laws, policies and principles, most California cities and counties did in fact adopt "policies, plans, programs, rules, practices and related activities" that constrain housing supplies, and raise housing prices so high that our hard working families – the majority of which now include members in our communities of color – can no longer afford to buy, and in many neighborhoods cannot even afford to rent, a home. These status quo housing policies result in unlawful racial segregation, and violate the affirmatively furthering fair housing laws. Our families, many of which are led by the essential workers each community relies on such as teachers, first responders, workers in construction, health care, hospitality, small business employees, and laborers – cannot and should not be asked to wait to have their name drawn in an "affordable" housing lottery, or wait for "magic money" to appear from the repeal of Proposition 13 (or capitalism). State and local agency actions violate civil rights laws, including California's new AFFH, must stop – and housing production, of market-rate housing that can be purchased by median income families, must increase more than tenfold under the current RHNA cycle.

We hereby formally and respectfully request that these civil rights housing legal violations be corrected in your General Plan Housing Element and Zoning Code updates which feasibly, based on your median income families and your available funding resources today, plan for housing typologies and locations that meet your assigned RHNA targets. We identify below the worst offenders, and practical solutions, to assure that you do not adopt General Plan and Zoning Code updates that violate civil rights housing laws.

1. **Charging Country Club Initiation Fees for New Housing is Racist and Exclusionary**
Country clubs often charge initiation fees of $50,000 or more, with the express intent to select wealthier members and exclude "those people" who cannot afford steep fees. Many local agencies have imposed fees on new housing that wildly exceed even $50,000, such as San Francisco which has charged fees of $165,000 per apartment! While we appreciate that new homes need to pay for their "hard" infrastructure needs like water and sewage services, too many jurisdictions have allowed well-meaning special interests seeking additional funds for important local priorities like art, affordable housing, and recreational programs to pile these fees onto new housing rather than obtain funding (as or if needed by special assessments or taxes approved by existing residents) equitably, which means paid for equitably by the city's existing (not just future) residents. As documented by UCB, excessive and wildly different housing development fees increase housing costs and decrease housing production and affordability – and these fees are passed along to new residents. Development_Fees_Report_Final_2.pdf (berkeley.edu) Most cities and counties defend high fees on new housing with "nexus" studies, based on made-as-instructed reports prepared by consultants paid by cities. "Nexus" may pass constitutional muster, but violates civil rights housing laws by excluding housing – and "those people" (us) from your community.

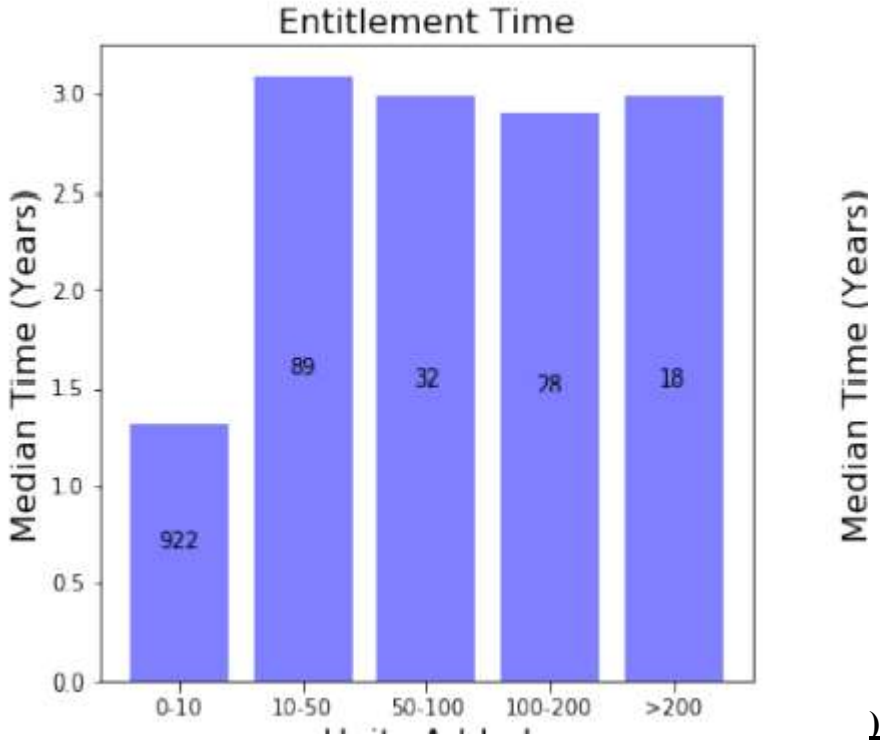
***Civil Rights Compliant Solution to Exclusionary Fees:*** *Residents of new housing should pay no more in fees than existing taxpayers. For example, if a city has 50,000 existing homes and a RHNA obligation to produce 5,000 more homes, housing fees should be capped at the levels paid by taxpayers. If existing city residential households subsidize arts program with $500,000, residents of new housing should pay no more than the same share ($100 per new home). If existing city residents contribute nothing to build affordable housing, then neither should residents of new housing: existing policies created the affordable housing shortage and crisis, and solving this problem on the backs of those shut out of the housing market creates an unfair, unlawful and racially discriminatory burden on new residents. Stop imposing discriminatory fees on new residents.*

2. **Housing Delayed is Housing Denied**. While some jurisdictions have streamlined the housing project review and approval process, most have not. The two most commonly-identified delay factors in the housing project approval process are multi-step, multi-department review processes with no intra-agency deadlines or housing accountability production metrics, and the California Environmental Quality Act (CEQA) review process. As shown in Figure 1, in one recent study of the San Francisco entitlement process, all but the smallest (less than 10 units) took about three years to complete this combined bureaucratic and CEQA process.

3 cont.

**Figure 1: Housing Project Entitlement/CEQA Process Time in San Francisco (by Project Size/Unit Count)**

Measuring the Housing Permitting Process in San Francisco - Terner Center (berkeley.edu)

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3 cont.

**A**. **End Bureaucratic Delays to Housing Approvals**. Also as explained by UCB, "[t]he most significant and pointless factor driving up production costs was the length of time it takes to for a project to get through the city permitting and development process" which in turn caused even higher costs as projects stuck in bureaucratic review proceedings were required to repeatedly modify their projects to deal with the "additional hoops and requirements" that "pop up" at various stages of the permitting and development process. San_Francisco_Construction_Cost_Brief_-_Terner_Center_January_2018.pdf (berkeley.edu), p. 2.

> ***Civil Rights Compliant Solution to Housing Delays Caused by Bureaucrats***. *This too has a simple solution: prescribe, disclose, enforce, and publish outcomes of housing review and approval deadlines on every city department (and responsible unit within each department), and hold responsible managers in each department accountable in performance evaluations and promotion decisions to meeting (or beating) deadlines. This is a housing production accountability metric that should be expressly added to General Plan Housing Element implementation mandates.*

B. **End Anti-Housing CEQA Abuse.** Before a misguided appellate court decision, issued without Legislative direction in 1984, CEQA did not apply to city and county approvals of housing that complied with General Plan and zoning ordinances. For several decades, however, increasingly fussy academics and planners insisted that zoning codes require a "conditional use

permit" (CUPs) even for code-compliant housing, to allow local agencies to apply a "we know it when we see it" open-ended level of discretion to allow, deny, or condition housing approvals – the same standard the Supreme Court applies to obscenity. In 1984, this CUP process – brought to us all by the same generation of planners that (obscenely) insisted on single-family only residential zoning and outlawed even duplexes that had previously been allowed and common throughout California – unleashed the full force of CEQA delays and lawsuits even on fully compliant housing in "infill" neighborhoods. Friends of Westwood, Inc. v. City of Los Angeles (1987) :: :: California Court of Appeal Decisions :: California Case Law :: California Law :: US Law :: Justia By 2008, housing had become the most frequent target of CEQA lawsuits – and the tool of choice for both those seeking to block housing and those seeking financial and other payoffs for threatening CEQA lawsuits. In one study of all anti-housing CEQA lawsuits in the Los Angeles region, for example, 14,000 housing units were targeted in CEQA lawsuits – 99% of which were located in existing urbanized areas (not "greenfields), 70% of which were located within ½ mile of transit, and 78% of which were located in the region's whiter, wealthier, and environmentally healthier communities. In the Name of the Environment Update: CEQA Litigation Update for SCAG Region (2013-2015) | Insights | Holland & Knight (hklaw.com) Instead of facilitating housing near jobs and transit, CEQA had been distorted into this generation's anti-housing, anti-"those people" (us) redlining tool of choice.

***Civil Rights Compliant Solution to Anti-Housing CEQA Abuse***. *Under the Housing Accountability Act, cities and counties no longer have the discretion to disallow housing, require fewer units, or impose fees and exactions that make housing projects infeasible. Local control determines the allowable location and density of housing, but these cannot be "paper housing" that is never actually approved (or approved with feasible conditions). Only housing that causes a demonstrable and specific significant adverse consequence to human health or safety can be downsized, delayed, or conditioned with costly obligations.* Housing Accountability Act Technical Assistance Advisory Housing Element implementation procedures should expressly acknowledge this state law as a prohibition on the local agency's exercise of its discretion on any issue other than a demonstrable and specific adverse health or safety risk caused by the proposed housing project, and eliminate or limit subsequent CEQA review under conforming zoning requirements to prescribed objective health and safety standards specifically caused by the proposed housing project. As determined recently by the California Supreme Court, local government may still preserve exterior architecture and design review processes that do not create discretionary authority to add new conditions addressing CEQA topics. McCorkle Eastside Neighborhood Group v. City of St. Helena :: 2019 :: California Courts of Appeal Decisions :: California Case Law :: California Law :: US Law :: Justia. Local General Plan and zoning codes following this recommendation avoid mandatory CEQA processing and litigation risks, and are a mandate – especially in the whiter, wealthier and healthier communities such as most of Marin County that have elevated their "no growth" environmentalism into open and flagrant racist conduct such as intentionally segregating its public schools by race. First desegregation order in 50 years hits Marin schools - Los Angeles Times (latimes.com)

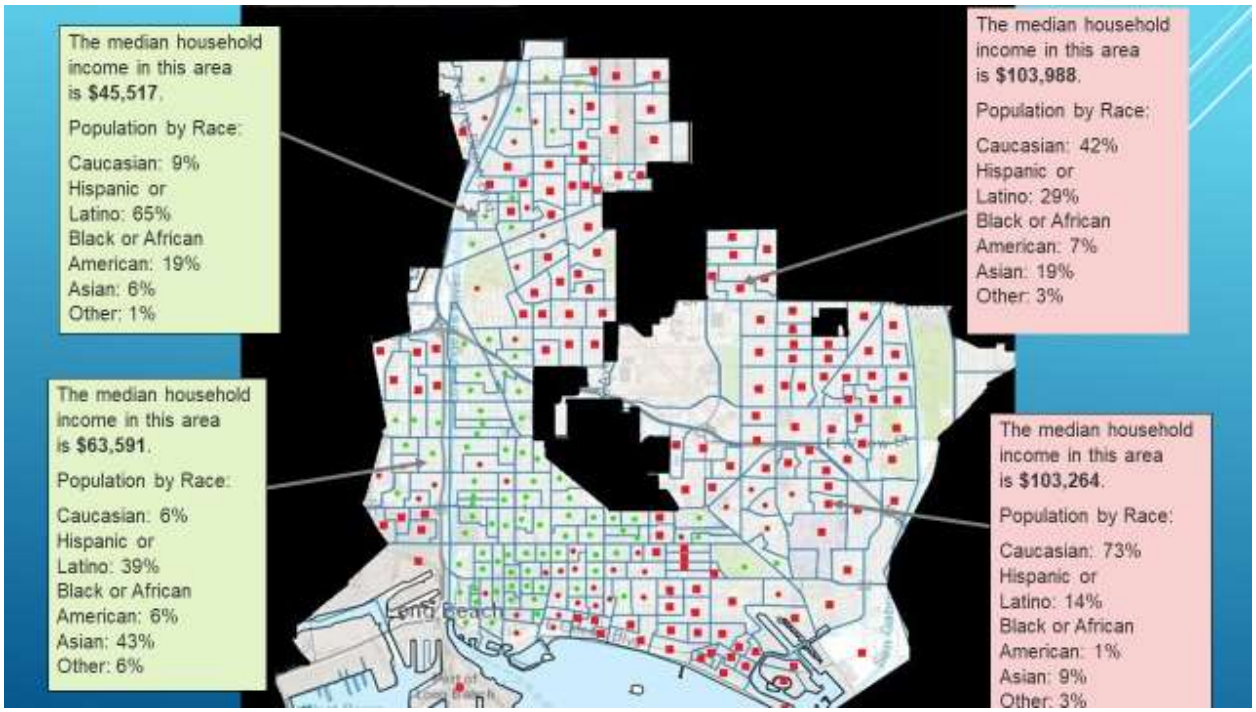
3 cont.

3. **Avoid Exacerbating Racial Segregation with Special Interest Demands that Retard Housing Production and Increase Housing Costs**. Increased production of housing that is affordable that working families can purchase has been repeatedly blocked by many California's environmental organizations and their state agency allies. We and our families experience, and agree we should reduce, pollution – and we too enjoy and want to protect California's spectacular natural resources. We also support California's climate leadership, but do not agree that our working families and poor should be collateral damage in the state's war on climate. Much as California led the nation in past decades in the involuntarily sterilization aimed primarily at women of color in the name of discredited "science," and unleashed civic "redevelopment" schemes that wiped out once-thriving (and now forgotten) Black and Latino communities in the name of discredited economic theories, we now face demands that new housing consist of small rental apartments located near non-operating bus stops with rental rates of more than $4000 per month to reduce "Vehicle Miles Travelled" (VMT). California leads the nation in buying, supporting, and ultimately mandating electric vehicles – but VMT housing policy is redlining, pure and simple.

The Southern California Association of Governments (SCAG), which includes 197 cities an 6 counties where collectively the majority of Californians live, was on the verge in 2020 of adopting a VMT-centric regional housing plan that prioritized agency-decreed VMT reductions above all other laws, including federal and state anti-discrimination and housing laws. Under this plan, which conflicted with and undermined almost all city and county General Plans by assuming the massive demolition of existing residential and commercial neighborhoods and replacement with high density apartment housing near planned bus routes, historical and existing residential racial discrimination was intentionally worsened. Figure 2, for example, shows where new housing in Long Beach should be located – noted with green dots in polygons called "Traffic Analysis Zones" (TAZ), which includes many of the most densely-populated, poorest neighborhoods in Long Beach – communities of color highly vulnerable to displacement and gentrification. The TAZ maps showing "red" dots or squares are dominated by single family residences, where even "infill" housing such as townhomes on former strip malls is excluded from SCAG's VMT-reduction housing plan. The "no new housing" neighborhoods are far whiter, and far wealthier, than the neighborhoods slated to receive many thousands of new housing units in a haunting repeat of the "slum clearance" schemes that wiped out minority neighborhoods in years past.

3 cont.

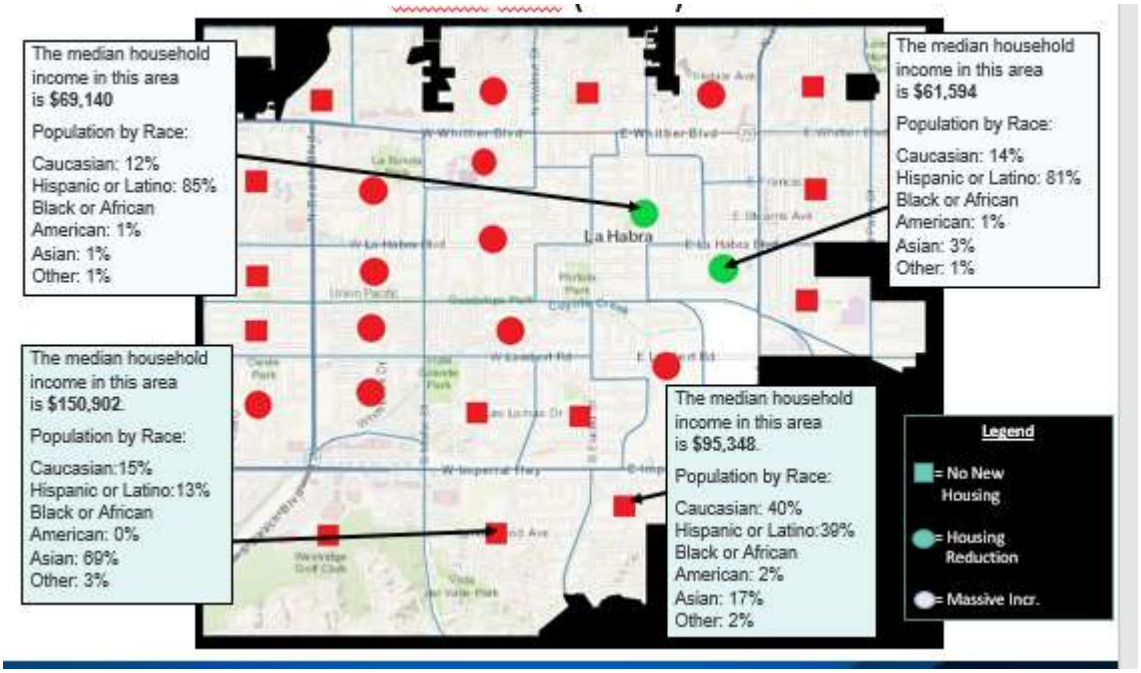
**Figure 2: Long Beach VMT Reduction Housing Plan (SCAG 2020)**




3 cont.

When applied to smaller communities, such as the small town of La Habra in Orange County, SCAG's VMT-reducing housing scheme was even more blatantly racist. As shown in Figure 3, SCAG decreed that housing belonged in the city's two poorest TAZ zone neighborhoods – majority Latino – and excluded from the adjacent "nice" homes in nearby hills occupied primarily by Whites and Asians.

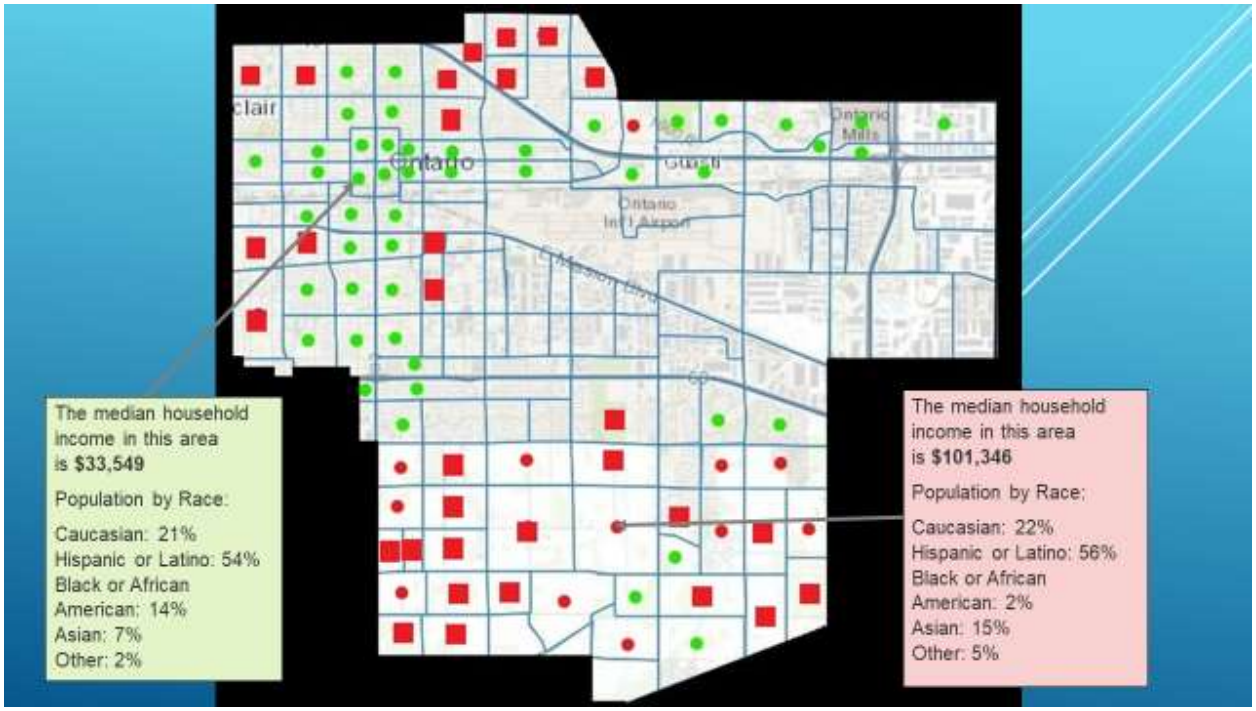
**Figure 3: La Habra VMT Reduction Housing Plan (SCAG 2020)**




SCAG's VMT-based housing plan would also have created new obstacles under CEQA even to the buildout of approved housing. Figure 4 shows Ontario, with new housing planned along a heavily-commercial freeway corridor (Interstate-10) that also has an express bus route, and along another bus route through existing poorer parts of the city that are also near a bus route. (The bus was not operating in 2020, during COVID, and had consistently low ridership even pre-COVID.) The SCAG VMT-based housing plan wanted no more housing built in southern Ontario, which is actually the best selling new community in all of California – with an affordable price for new homes, and a majority Latino and other minority new home purchasers.

3 cont.

**Figure 4: Ontario VMT Reduction Housing Plan (SCAG 2020)**



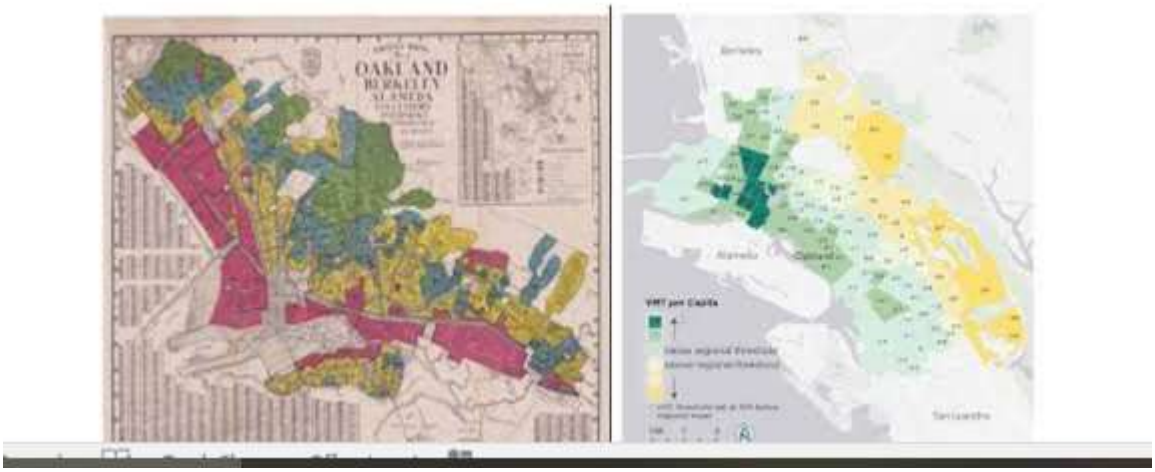

3 cont.

To its credit, when SCAG realized the redlining consequences of its VMT-reduction housing plan, it disavowed the plan and forbade its use in any context (including RHNA and CEQA) in a Regional Council approval Resolution that recognized the "conflict" between California's housing and climate goals. We can achieve climate goals without worsening racial segregation, demolishing disadvantaged communities (again), and ending attainable homeownership even within existing cities for the majority-minority families that have been shut out of the California homeownership market by catastrophic planning and policy decisions (many brought to us by the same advocates and bureaucrats who invented reducing VMT for electric cars as a "necessary" climate mandate) over the past two decades. In fact, the California Legislature has repeatedly declined to mandate reductions in VMT – and has repeatedly found that the housing crisis harms both existing California residents and exacerbates climate change by driving Californians to worse climate states like Texas to find a house they can afford to buy.

Although the VMT data is most accessible in the SCAG region of Southern California, it is critical that your agency recognize that this same discriminatory outcome occurs everywhere. In Figure 5, for example, we compare Oakland's historic "redlining" maps where federal bureaucrats refused to approve low cost loans in Black neighborhoods and other communities of color (colored red) with the majority white communities where low cost mortgages were available (colored green and yellow). Oakland's "low VMT" map (where housing is demanded by today's special interests based on claimed climate "science") is the redlined area of Oakland that has already lost much of its historic Black residents, businesses, and civic institutions – the remainder of which would be

wiped out by high density, transit-oriented housing near BART and bus lines. Oakland's "high VMT" map, where housing should not be built, is those lush, wealthy, white, and historically segregated hills.

**Figure 5: Oakland Redlining and VMT Map Comparison**




Both the future of work, and the future of transportation, are in flux. Even before COVID, however, more people were working from home in the SCAG region than riding fixed-route public transit – with bus ridership suffering the most substantial declines. Fixed-route transit ridership plunged during COVID, and has not recovered. VMT has increased over the past month with the re-opening of the state, although peak hour volumes (and trip durations) have diminished. From remote work, to the explosion of new electric technologies for short-distance localized trips, to the massive expansion of app-based rides and carpools, it's important to know what we don't know – which is the future – and what we do know, which as UCLA's transportation experts repeatedly confirmed, is that low income workers rely on low cost used personal vehicles instead of the bus: people can perform multiple trips (drop kids of at school before, carpool kids to soccer after school), and can reliably access more than twice as many jobs in less than half as much time. https://www.its.ucla.edu/publication/transit-blues-in-the-golden-state-analyzing-recent-california-ridership-trends/ 3 cont.

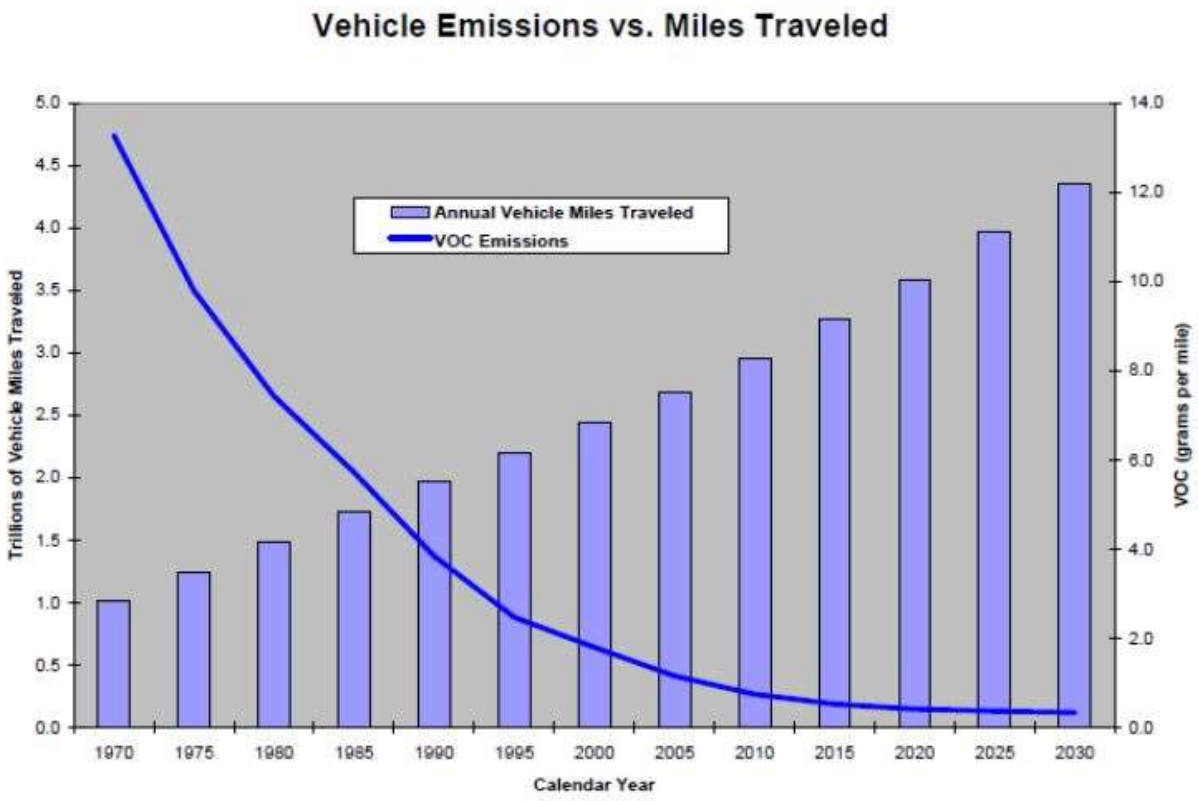
There are two other inconvenient truth about this VMT-based housing policy civil rights violation.

First, there are no proven, or effective, ways of "mitigating" VMT to "below the level of significance" demanded by the state's CEQA lead agency, the Office of Planning & Research (OPR), for unsubsidized housing bigger than about 10 units that is located in a suburban scale existing community not served by high frequency transit. Using the methodology demanded by OPR, San Diego County calculated that the majority of the housing they have approved over the past decade – which helped meet their RHNA housing goals, and had been approved by state climate agencies – would have had significant unmitigated VMT impacts. Again using OPR-endorsed "mitigation" methodologies, for which there is insufficient evidence of effectiveness, San Diego County determined that VMT mitigation fees alone would add $50,000 - $690,000 ***per housing unit***. San Diego County further acknowledged that it could not meet its RHNA

obligation if this VMT scheme was enforced as proposed by OPR.
https://bosagenda.sandiegocounty.gov/cob/cosd/cob/doc?id=0901127e80d032bb

Second, although the purported purpose of this VMT policy is to reduce greenhouse gases, there are many – many – alternatives to imposing a massive car tax on new housing that are more effective at reducing GHG without engaging in racially discriminatory housing policies. When smog was first identified as a problem in Los Angeles during World War II, initially scientists speculated it was a poison gas attack by the Japanese – only to later learn that smog was domestically produced by our own activities. When the Clean Air Act was passed in 1972, the same no growth special interests initially demanded that that cars and other smog sources be banned, but as shown in Figure 6 we instead banned lead in gas, and used catalytic converters and now clean engine/fuel mandates to cut vehicular emissions by more than 98% while VMT – cars driven by actual people to actual jobs etc. – rose steadily alongside population and employment, as reported by President Obama in 2016:

**Figure 6: Reduction in Tailpipe Emissions from Vehicles (line) v. Increase in Vehicle Miles Travelled from Population/Job Growth (bar columns)**




***Civil Rights Solution to Special Interest Exclusionary Housing VMT Scheme: Comply with Civil Rights Housing Laws including Affirmatively Furthering Fair Housing.*** *The current housing emergency, which disproportionately harms our communities, is not the appropriate forum to "experiment" with a housing density scheme dependent on fixed-route bus ridership and high density, high cost rental housing. Housing locations,*

3 cont.

*densities, and typologies need to match the needs of our communities, including respecting – not just paying lip service – to racial equity and housing civil rights laws we helped enact to create equitable access to the American Dream of homeownership. We have sued the state agencies responsible for this VMT scheme, and the state has been unsuccessful in dismissing our civil rights claims – while engaging in years-long stall tactics like forcing us to file a Public Records Act lawsuit for VMT documents they attempted to hide (a lawsuit we won). VMT is simply a measure of the transportation options – even of 100% clean vehicles – available in a community. It must now be studied under CEQA (at least until our lawsuit is resolved), but it should not distort your Housing Update to worsen residential racial segregation, shield majority-white wealthy neighborhoods from housing in violation of the AFFH laws, and again wipe out our communities in unfunded displacement schemes.*

4. **Paper Zoning for Economically Infeasible Housing is Illegal and Racist.** Partly in response to no growth anti-homeownership schemes like VMT, and partly because existing laws requiring that housing meet the actual needs of actual Californians alive today have become as routinely ignored by academics and bureaucrats as civil rights laws, some cities may be tempted to "solve" for RHNA allocations by assuming that mid-rise and high rise apartments costing in excess of $4000 in monthly rent for even for one-bedroom units are lawful housing compliance pathways under RHNA. In fact, because that rental rate – and other real life obstacles to lower cost condo development – are entirely unaffordable to median income households, a Housing Element update that assume high cost higher density product types that cost more than 2.5 times more to build than single family homes, duplexes and townhomes as even admitted by an overly-optimistic UCB study that demanded an "all-infill" higher density housing future for California is a violation of housing civil rights law. (https://www.next10.org/publications/right-housing ) The same study also acknowledged that to accommodate what has only grown to ever more severe housing unit shortfalls, "tens or even hundreds of thousands of single family homes" would need to be demolished to make way for the new high density units. We have seen these academic conclusions before, and we have seen the horrendous outcome of targeting the least expensive – aka neighborhoods housing people of color – and thus least costly/most profitable housing demolition/expensive new housing scheme. What is astounding is how often, whether in the name of openly racist segregation goals, or veiled "public harmony" goals, or "urban revitalization" double-speak, and now special interest NIMBY environmentalism, overwhelmingly white academics, bureaucrats, and hired gun consultant "experts," keep finding new ways to destroy our communities and deprive our people of the right to achieve the American Dream of homeownership.

3 cont.

These same "experts" have now inserted yet another poison pill into state housing law, which is that when property designated in a General Plan for housing includes economically infeasible higher densities – which in most communities includes even mid-rise six story structures over podium parking – is approved for lower density economically feasible housing types like townhomes, local governments must transfer the unbuilt infeasible units to a different property that must accept even higher densities than included in the General Plan Housing Element update. Because the impacts of that receiving site's additional spillover housing itself triggers CEQA, an applicant for an economically feasible housing project must also assume the cost, schedule, and litigation burdens of CEQA compliance for whatever unrelated receiving housing site is designated by the city – at an unknown point in the process – to add more density than

allowed in the General Plan Housing Element. Housing Elements that assume non-existent conditions (e.g., repeal of Proposition 13, end of capitalism, vast new tax revenues dedicated to missing middle housing to fund the millions of additional housing units, etc.) are illegal, as are Housing Elements that prescribe economically infeasible higher density housing and fail to plan for the vast majority of "missing middle" and "affordable" housing required by RHNA, are illegal. The San Francisco Bay Area has led the state in assuming that $4000 per month high rise apartments will be financially feasible in suburbs where median incomes can pay $1500 for housing – or $2000 per month for a mortgage. This "paper zoning" of high rise transit-oriented neighborhoods at every bus stop has resulted in a massive out-migration of higher paid Bay Area workers to Stockton and the Central Valley, Salinas and the South Bay, and Sacramento and beyond – which in turn results in unattainable housing prices for those with local jobs in those areas. This paper zoning academic fiction, pursued for more than two decades by some "woke" Bay Area "experts" alongside "urban limit lines" and "ecosystem service taxes" paid by urban residents to non-profit "stewards" of natural lands, is the modern day form of Jim Crow strategies to deprive the hard working families in our communities access to attainable homeownership.

> ***Civil Rights Solution to Paper Zoning for Infeasible Housing.*** *Just don't do it. Townhomes, stacked flats, quadplexes, garden clusters, and small lot homes are just some of the many examples of lower cost housing that once dominated the "starter" housing market before academics, planners, and special interest no-growthers decided they could intentionally create a housing crisis and nobody would notice because the people most harmed don't earn enough to donate to political campaigns. Housing densities, and locations, need to be designed for the people who need housing. "Move-up" housing for higher income families forced to rent or spend four times more for a home than they would spend in a neighboring state is also needed. General Plan Housing Element updates should include in the disadvantaged community/environmental justice analysis housing affordability criteria to designate housing typologies, densities, and locations, as well as expedited approval processes, to make new housing needed to meet RHNA targets "affordable by design" so that median income families without taxpayer subsidies or winning lottery tickets can buy a home. As recognized by the Legislature itself, solving the housing crisis will help achieve California's climate targets by keeping our families here, in new housing that is hugely more energy efficient, and climate friendly, than existing housing or housing built in our competitor states like Texas, Arizona and Nevada. The more new housing (and people) your agency plans for, the lower your per capita greenhouse gas emissions – a feasible, just, and civil rights compliant outcome that will actually help achieve California (and global) climate goals.*

3 cont.

When longtime civil rights champion Amos Brown was recently asked whether "the Bay Area is a safe haven for Black people and other people of color" he was unambiguous: "No. . . Since 1970, we have lost Black people who were pushed out of this city. The 70's Black population was between 15-16%. Well now it's down to about 4%. That didn't happen by accident and it wasn't just economics. This happened because of public policy."
https://www.sfchronicle.com/lift-every-voice/article/Amos-Brown-16219697.php

Beyond the COVID pandemic, 2020 brought us yet another year of race riots and yet another round of rhetoric about the need to "address" the new race avoidance buzzwords of

diversity and inclusion. The time for rhetoric around housing justice should have ended before it started, and we thought for sure was made illegal with the 1960s civil rights laws. We were wrong: as Mr. Brown reports, "public policy" keeps shoving our communities out of neighborhoods that become desirable to white families. Stop it. Just stop it. Comply with civil rights laws, comply with RHNA, and plan for housing that can be purchased by median income households – not just for low income and homeless families, and not just for the wealthy. Housing experts like to call us the "missing middle" – we aren't missing at all. We just aren't being seen by housing "experts" and bureaucrats and special interests who get paid by the wealthy to advocate full-time while members of our communities hold down the essential jobs that make communities work. In fact, some sneeringly dismiss us entirely by concluding the "ship has sailed" on homeownership – and yep, communities of color weren't allowed on the ship, and then got tossed off it with predatory foreclosures, but that's just too bad we should wait for our lottery ticket to come in and move back into the projects if or when they are ever built.

3 cont.

**Systemic discrimination doesn't happen by accident – it happens because of bad policy**

Come to your senses. Plan housing for people. Welcome us to your communities, not just to work but to live. Let's restore our common love for California and build those diverse and inclusive communities your agency, and its advisors and consultants, have been talking about since our country's racial reckoning last year. Do the right thing, and adopt the right Housing Element and Zoning Code updates.

4

Please contact me at robert@thetwohundred.org if you'd like to discuss any of this further. We can sue – and we have and will continue to sue to enforce civil rights housing laws – but doing right is by far the cheaper, faster, easier, and just pathway to doing your share to solve the housing crisis.

We look forward to hearing back from you at your earliest convenience.

Respectfully,

Robert Apodaca
Vice-Chair and Director of Public Policy
The Two Hundred
www.thetwohundred.org

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# Regarding City of LA Rezoning Program (CF: 20-1042) - Letter from ACT-LA

**Laura Raymond** <lraymond@allianceforcommunitytransit.org> Thu, Aug 19, 2021 at 1:25 PM
To: vince.bertoni@lacity.org, Matthew Glesne <matthew.glesne@lacity.org>, Housing Element <housingelement@lacity.org>, ann.sewill@lacity.org
Cc: "Alfonso Directo Jr." <adirecto@allianceforcommunitytransit.org>

Dear Vince, Matt, Ann and the Housing Element team,

Good afternoon, I hope this finds you well.

We continue to appreciate the opportunity to engage in the Housing Element update and will be sending further comments on the full draft Housing Element in the coming weeks.

Given City Council's action this week on the Rezoning Program, our coalition is submitting the attached letter first, with initial recommendations regarding this Program. We hope to further engage as this Program is developed.

Best,

Laura

--

**Laura Raymond** (she/her)
Director | Alliance for Community Transit - Los Angeles
cell: (646) 344-0381
website: www.allianceforcommunitytransit.org

**ACT-LA Letter on LA City's Rezoning Program - 2021-0819.pdf**
168K

act·LA
Housing Jobs & Transit for All

August 19, 2021

Letter O-3

Vince Bertoni, Director
Los Angeles City Planning
200 North Spring Street
Los Angeles, CA 90012

**RE: Rezoning Program in the draft Housing Element (CF: 20-1042)**

Dear Director Bertoni,

The Alliance for Community Transit - Los Angeles (ACT-LA) is a county-wide coalition of 41 organizations working on the forefront of racial, environmental, and economic justice. Our coalition members include tenants' rights organizations, affordable housing developers, workers' centers, public interest law firms, and public health advocates, among many others. Thanks to our coalition's diversity, we view housing policy through an intersectional lens. Our mission is to uplift communities—through affordable housing opportunities, good jobs and access to high quality public transit—as the Southland transforms into a more sustainable region. Given our commitment to equity, we believe that low-income communities and communities of color must be centered in decisions that seek to transform our neighborhoods. 1

Communities that we represent have borne the heaviest toll from generations of failed land use policy and environmental injustice, including redlining and exclusionary zoning. We feel housing justice for our communities means that your department should engage with our communities in a way that centers their concerns with the draft Housing Element and the Rezoning Program as these new policies and programs are revised, finalized, and implemented. In addition, the Rezoning Program should also materially benefit our communities by resulting in more and better housing opportunities from our community's point of view.

We appreciate Council President Martinez's letter (dated August 13, 2021), which was co-authored with six of her Councilmember colleagues and issued to your department, detailing their commitment to equitable distribution of housing throughout LA. We appreciate that many of our coalition's recommendations were included in the Council President's letter, but we write to emphasize the ongoing need to tie on-site affordable housing requirements to rezoning. This fundamental approach would help our city meet the scale of affordable housing needed at this moment in our city's history. Our coalition's top three recommendations to the Rezoning Program are as follows. 2

1. Design the Housing Element's Rezoning Program to include on-site affordable housing requirements that exceed TOC program standards on every site that is rezoned, and include displacement avoidance and protection measures such as excluding tenant-occupied sites from rezoning. The Rezoning Program should require progressive

tiers of affordability for increasingly higher density development. The Rezoning Program should be limited to high and highest opportunity areas of Los Angeles. The City should simultaneously invest public dollars in community-led planning, affordable housing opportunities and housing stability programs, and other community-serving, health-promoting strategies to protect and uplift residents living in historically disinvested areas and areas that are susceptible to gentrification.

2. Expand the City's affordable housing incentive programs to create mixed-income and 100% affordable housing in communities in the California Tax Credit Allocation Committee (TCAC) high and highest opportunity areas, while subtracting census tracts that have a displacement risk.

3. Enforce the Measure JJJ requirement that community plan updates do not reduce the capacity for creation and preservation of affordable housing or undermine California Government Code Section 65915 or any other affordable housing incentive program by requiring that all increases in allowable density and FAR be aligned with on-site affordable housing standards that meet or exceed TOC. The Community Housing Needs Assessment Process should be based upon citywide housing production goals and utilize a methodology that balances traditional factors such as job and transit access with a new prioritization for high opportunity areas, anti-displacement, healthy and affordable housing, and achieving housing opportunities at the deepest affordability levels.

2 cont.

We appreciate your consideration and are looking forward to ongoing engagement with your department as our city's Rezoning Program and Housing Element is finalized and implemented.

Sincerely,

The ACT-LA Coalition

CC:

Ann Sewill, General Manager, HCIDLA

Housing Element Team Email: HousingElement@lacity.org

Matt Glesne, Senior City Planner, LA City Planinng

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# 2021 - 2029 Housing Element Update

**President of RVNC** <rampartvillage@gmail.com> Fri, Aug 20, 2021 at 2:26 PM
To: Vince Bertoni <vince.bertoni@lacity.org>
Cc: housingelement@lacity.org, craig.bullock@lacity.org, Ronald Reece <roneereecervnc@gmail.com>, David Rockello <rockello@gmail.com>

Vincent P. Bertoni, AICP, Director
Los Angeles Department of City Planning

Dear Mr. Bertoni:

Please find attached for your consideration the Rampart Village Neighborhood Council's comments on the 2021 - 2029 Housing Element Update.

Thank you.

*Diversity Is Our Strength!*

*Philip Armstrong, President*
*Rampart Village Neighborhood Council*
*155 N. Occidental Blvd. Suite 236*
*Los Angeles, CA 90026*
*(o) 213.568.3086*
*(c) 213.275.9322*
*www.RVNC.org*
*f: realRVNC*

- Immediate life threatening police, fire or medical emergency: **9-1-1**
- Parking enforcement (blocked driveway, parking violation, locate impounded vehicle): **213-485-4184**
- Police non-emergency: **877-ASK-LAPD (877-275-5273)**
- Sanitation (missed trash pick-up, broken container): **800-773-2489**
- Traffic control (signal light out): **213-485-4184**
- Dept. of Water & Power: **800-342-5397**
- Other City issues: **3-1-1**

**8.17.2021RVNCComments.pdf**
744K

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**Housing Element <housingelement@lacity.org>**

# 2021 - 2029 Housing Element Update

**Housing Element** <housingelement@lacity.org> Fri, Aug 20, 2021 at 3:18 PM
To: President of RVNC <rampartvillage@gmail.com>

Thank you for sharing your thoughts on the draft plan. Your comments will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Letter O-4

# Comments on 2021 - 2029 Housing Element Update

Philip Armstrong, President | Ronee Reece, Vice President
Lara Morrison, Treasurer | Rachel Day, Secretary
Raquel Valencia, At-Large Rep | Quazi Huda, Community Interest Rep
Vacant, Community Based Org Rep | Rick Shumacher, Business Rep
Charlie Cea, Student Youth Rep

Date: August 17, 2021

To: Vincent P. Bertoni, AICP, Director
Los Angeles Department of City Planning

From: Rampart Village Neighborhood Council

Subject: 2021 - 2029 Housing Element Update

The Rampart Village Neighborhood Council (RVNC), at its duly noticed General Board meeting on August 17, 2021, considered on its agenda, Item VII(I):

- Propose changing the draft 2021 – 2029 Housing Element Update to incorporate the goal of 100 percent retention of affordable housing units showing as expiring.
- In Chapter 6 of the draft Housing Element, consider proposal to revise Policy 4, Shared Equity Models for Goal 2 and 4, on page 6-16, so that instead of “study barriers to the greater utilization of shared ownership models,” the objective would be to “implement the greater utilization of shared ownership models” since ample evidence is available to support the use of shared ownership models.

In considering these proposals, the RVNC relied on the following information:

- The Housing Element Update is the vehicle for the City to set targets over an 8-year period for construction of new housing, including affordable housing (for very low income, low income, and moderate income levels) and market rate or "above moderate income level” housing as well as to document the preservation of existing affordable housing.
- In the prior 8-year period (2013 - 2021), as of the 2020 Annual Element Progress Report, the City of Los Angeles achieved 34% of the RHNA (Regional Housing Needs Assessment) for very low income, 30% of the RHNA for low income, 6% of the RHNA for moderate income, and 298% of the RHNA for above moderate income (market rate) housing based on information provided in the 2020 Annual Element Progress Report.
- As for the next 8 years (2021 - 2029), the following information is provided on pages 20 and 21 of the Executive Summary of the Draft Housing Element: “While the RHNA allocation suggests that almost 260,000 units affordable to households earning less than 120% AMI will be needed, it is anticipated that approximately 51,000 affordable units may be constructed within the eight year RHNA period at this range (about 20% of the target). This is a reflection that total housing needs for lower and moderate income households greatly exceeds the ability to meet those needs with existing financial resources and incentive programs.”

1

- Between October 1, 2011 and September 30, 2021, there were 4,406 housing units located in 225 projects whose affordability restrictions expired or were terminated ("Units Expired in the Last 10 Years" on page 3 of Appendix 2.2). Table 2.2.2 in Appendix 2.2 of the draft Housing Element Update provides information on the cost to preserve at risk units. Table 2.2.1 in Appendix 2.2 puts the cost of acquisition and rehabilitation of existing affordable units at $465,000 per unit compared to the cost of new construction at $571,000 per unit.

On July 25, 2021, at a duly noticed meeting of the RVNC Public Safety, Housing & Transportation Committee, after consideration and having provided an opportunity for public comment, the Committee voted (3-0 with one absent) in favor of agendizing to propose changing the draft 2021 – 2029 Housing Element Update to incorporate the goal of 100 percent retention of affordable housing units showing as expiring.

1 cont.

After consideration and having provided an opportunity for public comment, the RVNC General Board voted in favor of the motion (6-1 with one absent) to *support:*

- Incorporating the goal of 100 percent retention of affordable housing units showing as expiring; and
- Implementing the greater utilization of shared ownership models.

Please notify the RVNC of any future meetings and/or hearings on this item.

Sincerely,

Rampart Village Neighborhood Council

Cc: Housing Element Team (housingelement@lacity.org)
Craig Bullock, CD13 Planning Director
Los Angeles Neighborhood Council Coalition

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# letter from del rey homeowenrs association

2 messages

**President DRRA** <president@delreyresidentsassn.org> Wed, Sep 1, 2021 at 10:31 AM
To: HousingElement@lacity.org

please confirm receipt of email.

--

Elizabeth Layne, President

Del Rey Residents Association Since 1972

**DRRA Housing_Safety Comment Letter 08262021.pdf**
1278K

**Housing Element** <housingelement@lacity.org> Wed, Sep 1, 2021 at 2:40 PM
To: President DRRA <president@delreyresidentsassn.org>

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

EMAIL TO: HousingElement@lacity.org

USPS TO: Cally Hardy, City Planning Associate
City of Los Angeles Department of City Planning
200 North Spring Street, Room 75
Los Angeles, CA 90012

8/26/2021

Re: ENV-2020-6762-EIR
Draft Environmental Impact Report for the
Updates to the Housing Element and the Safety Element

Dear Ms. Hardy:

The Del Rey Residents Association (DRRA) is a 501(c)(4) social welfare organization that represents the interests of the residents of Del Rey. Thank you for the opportunity to comment on the Housing and Safety Elements.

BACKGROUND

Del Rey has about 35,000 residents in an area of Los Angeles bounded by Lincoln Blvd., Washington Blvd., Culver City and Jefferson Blvd. It is transected by THREE creeks: Ballona Creek, Centinela Creek and the Sepulveda Channel. 1

The federal Army Corps of Engineers, the Los Angeles County Dept of Public Works and the City of Los Angeles all have different responsibilities for the creeks.

SAFETY ELEMENT

The Safety Element must address the evacuation problems we face during power failures or as a result of floods, fires or earthquakes.

Del Rey is in a flood plain.

In earlier years—long before modern development and density—LA experienced catastrophic floods. The year 1862 was the largest flood in recorded history for the area.[1] 2

In the 1938 flood, the Los Angeles River was flowing at about 99,000 cubic feet per second. Our Ballona Creek is a tributary. It is unlikely that the levees will withstand a major flood.

---

1

The Great Flood of 1862 was caused by a series of powerful storms that began over the Pacific Ocean. These storms were so strong because local temperatures were higher than normal—the winter of 1862 was unusually warm in California. ... The higher temperatures caused more ocean water to evaporate into the air. -- Regents University of California

We wrote about our flood concerns in our Ballona Comment letter during the process of the State's proposed restoration of the Ballona Creek Wetlands.

The 2018 Local Hazard Mitigation Plan (LHMP) does not include a flood map (Figure 10-7 on page 10-14 is missing). It lists nineteen flood-related issues on page 10-40 (see attached). What is the current status of each of these flood-related issues? Have any of them been satisfactorily addressed? Does the City's Flood Map include Del Rey and the Ballona Wetlands?

Del Rey lies within a Tsunami Zone.

Because of the creeks (Centinela Creek enters Ballona Creek at the peninsula known as Bird Island) Del Rey has a number of cul-de-sac streets. As a result, there are few north-south or east-west traffic corridors. We are left to count on the 405 freeway to accommodate an evacuation. What safety plans are in place to accommodate such an evacuation, and how are they communicated to local residents? 2 cont.

Del Rey adjoins the gas storage fields and related facilities in the Ballona Wetlands.

Our gas storage concerns have been previously documented in our Ballona Comment letter.

It has been six years since the Aliso Canyon gas incident. What is the plan for ensuring the safety of our community and preventing a similar incident? How will the community be kept informed during a disaster, and educated in advance? Which pages in the 2018 LHMP address the specific concerns related to gas storage in the Ballona Wetlands?

HOUSING ELEMENT

The housing element must face the reality that up-zoning and density building will not alleviate homelessness. It is a specious theory for many reasons, and one this group has written about many times.

We agree with funding permanent supportive housing and programs that keep people from falling into homelessness. We disagree that up-zoning/increased density is the way to accomplish this goal. 3

In the Housing Element and the Safety Element, please include the comments and concerns specified in our Comment Letter on the Community Plan dated September 14, 2020.

TIMING

The Housing Element Update is required to be adopted by October 15, 2021, and to remain in effect through October 2029; the draft EIR Inventory of Properties has yet to specify the parcels for rezoning. 4

This Housing update is being reviewed before the Planning Department has even completed its update of the Palms/Mar Vista/Del Rey Community Plan.

There remain many issues of unintended consequences that should be addressed in the Housing Element, including the effects of COVID-19 on housing needs,

infrastructure adequacy, existing zoning and allotment of new units, traffic, parking, overcrowding, and general quality of life. 4 cont.

CALCULATION OF REQUIRED HOUSING UNITS

The Housing Element should include an assessment of the number of units already allowed by the City's existing zoning. Rezoning a site does not mean it will be built; instead, it may encourage developers to wait for the next Housing Element when the State may allow projects with ever increasing height and density. The existing 'allowance' from prior re-zoning should be available to offset the 'shortfall' from prior years. 5

Per the Initial Study, the current calculation of the required RHNA includes not only the current eight-year projection (as in prior cycles) but also 100% of the cumulative shortfall from prior years. This is the first Housing Element that this calculation is in effect; instead of putting 100% of the shortfall into this cycle, the shortfall should be spread over several cycles.

Please contact us if there are any questions about our comments. This process will have a critical and ongoing impact on our community.

Our Land Use committee drafted this letter, and it was approved by our Board at its meeting on Monday, August 30, 2021.

Regards,

Elizabeth Campos Layne
President, Del Rey Residents Association

cc:
Representative Karen Bass
Representative Ted Lieu Lieu.staff@mail.house.gov
State Senator Ben Allen
State Assemblymember Autumn Burke
State Assemblymember Isaac Bryan
County Supervisor Holly Mitchell asargsyan@bos.lacounty.gov
Councilmember Mike Bonin councilmember.bonin@lacity.org
Vishesh Anand vishesh.anand@lacity.org
Del Rey Neighborhood Council board@delreync.org

Post Office Box 661450 – Los Angeles, CA 90066
www.delreyhome.org

September 14, 2020

VIA E-MAIL and U.S.P.S.
planning.thewestside@lacity.org

Westside Community Plans
Los Angeles City Planning
200 N. Spring St., Room 750
Los Angeles, CA 90012

To the Westside Community Planning Group:

Thank you for this opportunity to comment on the Draft Land Use Concepts for the Mar Vista/Palms/Del Rey Westside Community Plan (Draft Concepts).

The Del Rey Residents Association (DRRA) is a 501(c)(4) social welfare organization that represents the interests of the residents of Del Rey. Our comments follow.

General Comments

1. Many aspects of these Draft Concepts were developed before the COVID-19 pandemic began. We believe that the pandemic will continue to impact people's willingness to live and work in enclosed spaces. The current Draft Concepts are based upon an underlying belief that increasing density in a community is a good thing that will result in lower housing prices. We disagree, and believe that the update of the Community Plan needs to be prepared with the following points in mind:

    a. As more people work at home, there will be greater demand for housing that includes a yard or easy access to a park or recreation center that is not being used as a homeless shelter.

6

b. If people are less willing to use public transit because it may expose them to infection, the idea of allowing higher densities near transit lines that operate every 15 minutes makes less sense.
c. Del Rey is only 2.45 square miles in size, and we do not want tall buildings to be built along all of our major streets (Lincoln Blvd., Washington Blvd., Sepulveda Blvd., Jefferson Blvd., Centinela Avenue, Inglewood Blvd). It will segment the community and make us feel as if we are being boxed-in.
d. Any planned density increases need to be planned in conjunction with the City's Infrastructure Plan (which is more than a decade out of date), the Housing Element (which is currently being updated), and the Regional Housing Needs Assessment (which calls for housing construction that could occur with no need for a change in our current zoning).
e. Pushing new, multi-family housing into already built-out neighborhoods near transit without (1) providing additional open space and recreational opportunities, (2) addressing climate issues such as heat islands created when buildings replace trees, and (3) ensuring sufficient infrastructure will exacerbate inequities in quality of life issues for new and existing residents. Additional residential densification in Del Rey must be very limited.

6 cont.

2. We agree that the Del Rey community needs to have housing that is accessible for low income residents, but we believe that using "density bonuses" for the construction of affordable units is the wrong way to achieve that goal. It has been our experience that developers take advantage of "density bonuses" to break through height and setback requirements without addressing the infrastructure needs that result from increased density (roads, parking, parks, libraries, utilities, etc.) The addition to a development of "affordable housing" units, through State mandates and incentives, must not result in building heights that would be overly tall for the existing community. This requires a reduction of the proposed height limits so that even with affordable housing, the final height and shape of each project will not be out of character for the neighborhood.

3. We also recognize that slums are created when all of the low income housing is built in one area. Del Rey is fortunate to have a number of 100% affordable complexes - Mar Vista Gardens, two complexes built by Thomas A. Safran and Associates, a PATH building, at least five buildings operated by Venice Community Housing Corporation - dispersed throughout the area. We also have numerous "community care facilities" and "co-living" projects that affect the community's infrastructure needs, but these pockets of residential density are not shown anywhere in the Draft Plan and need to be identified in that draft.

4. In June 2011, the Planning Department participated in a "visioning session" concerning Del Rey's "Area H" (between Ballona Creek and Jefferson Blvd.). The top responses to the Questionnaire at that time were as follows:

    a. What is your vision for your neighborhood? Greater sense of community/community identity; More "walkable"/pedestrian friendly.
    b. What do you consider to be the biggest land use challenge(s) in your neighborhood? Playa Vista and associated density/traffic; traffic and congestion.
    c. What do you consider the biggest strength(s) of your neighborhood? Neighborhood unity/sense of community; Proximity to LAX/beaches/freeways, etc.
    d. Do you have any specific suggestions for improving your neighborhood? Increase "walkability."
    e. Please provide us with some specific examples of areas, projects, resources that you consider a real strength/asset in your community that you would like to see preserved, maintained or further improved. Ballona corridor/wetlands.
    f. What city services...would you like to see provided and/or policies and programs promoted in your neighborhood that you think are currently missing? Develop parks/community gardens.

    It is clear from these responses that "walkability" is important, and yet most of the new projects in Del Rey, particularly in the Glencoe-Maxella area, have been designed to be inward-facing, providing almost no interface with the neighborhood and failing to foster a sense of community outside of each project.

5. The Community Plan also needs to acknowledge and accept the importance of "Location, Location, Location." Del Rey is desirable because it is close to the ocean, and it is criss-crossed by three creeks -- Ballona Creek, Centinela Creek, the Sepulveda Channel. That desirability means that housing in Del Rey is going to be less affordable than in other communities, and Del Rey is never going to be the same as a community in the San Fernando Valley or the Inland Empire. The Community Plan should reflect Del Rey's uniqueness.

6. The three creeks also create challenges when it comes to emergency preparedness. If Del Rey were to experience a major flood, earthquake, or manmade disaster, it would be difficult for Del Reyans to evacuate. The Community Plan and the Mobility Plan have been developed separately, but they need to be considered together. When the Community Plan allocates additional density to an area, it

6 cont.

needs to consider how those residents are going to enter and leave the area, particularly in an emergency.

7. The key to any Community Plan is that it will be enacted as a City ordinance, and it must be enforceable. The amount of discretion granted to the Planning Department must be tightly circumscribed so there is no perception that developers can obtain variances if they are willing to pay the right price.

Concept Plan Elements

1. Marina Marketplace:
   The Concept Plan sanctions a project (Paseo Marina; Case No. ENV-2016-3343-EIR) that potentially allows development of a project that has been overwhelmingly rejected by the community due to its height, residential density, reduced commercial space, lack of automobile parking, and lack of open space.

   It is already difficult for Del Reyans to cross Lincoln Blvd. to access the amenities in Marina del Rey, and the proposed Paseo Marina project would make it even more difficult for residents to move back and forth between Marina del Rey and Del Rey.

   The community is adamant about retaining Marina Marketplace primarily as a neighborhood-friendly retail commercial center with added open space that provides pathways for the public throughout and integrates the project with the neighborhood. To retain the local character, the height must be limited to no higher than that of currently existing adjacent properties, not including the Stella apartment building. The Stella development was granted a 'Zone change' to exceed the allowable height by at least 20 feet. It also includes a Q condition that restricts any further development on the remaining portion of that parcel. This exception to the pre-existing height limit must not be used to justify any future height limits. We also request that the Q condition be integrated into the Community Plan. The Concept Plan picture shows a project that would cut off the project from the neighborhood. The DRRA asks that the Marina Marketplace redevelopment be required to provide at least as much ground level local retail commercial space as currently exists and require public pathways and open space.

2. New Low and Medium Residential:
   Several neighborhoods in Del Rey are proposed for Low or Medium Residential designation, allowing for duplexes, triplexes, fourplexes, courtyard apartments, bungalow courts, townhomes and even large scale multi-family buildings. The proposed neighborhoods currently are predominantly single family residential. Most of the lot sizes are 5,000 sq.ft. or smaller and simply cannot support

6 cont.

increased density. Moreover, because these lots are small, increasing building footprints will mean that trees will be removed. Studies show that a smaller tree canopy leads to higher temperatures, with known health and environmental risks. Allowing multiple units will encourage developers to acquire multiple lots and drastically change the character of these neighborhoods. New multi-unit buildings will dwarf the existing small, mostly single-story bungalow homes and will deprive them of light, air and open space. Moreover, these streets cannot accommodate more parking. A large number of residents already use garage space for storage or other non-car uses and park their cars on the street, or they drive work trucks or sport utility vehicles that do not fit into existing garage spaces. Further, the retail businesses and restaurants on Washington Blvd. and Centinela Avenue do not have sufficient parking, and the overflow goes to the very blocks that are proposed for Low Residential. Residents have already obtained restricted parking on many of these streets. Though these blocks are close to bus lines, the vast majority of residents have private cars. Increased density will exacerbate the problem.

3. Centinela and Inglewood Neighborhood Villages:
   We support the establishment of neighborhood villages on Centinela Avenue and Inglewood Blvd. as depicted in the plan. We agree with the plan's goal of establishing maximum commercial tenant sizes to encourage small independent businesses, and prohibiting uses that do not support walkability. We object to allowing development with heights over 2 stories, however. We are seeking to transform Centinela Ave into the Heart of Del Rey via the Great Streets program. This area should reflect our unique identity and stand as a special place to be protected as a community resource. We would like to create design guidelines to guide development and preservation activities within the Centinela Ave and the Inglewood Blvd areas.

4. Traffic:
   The impacts of private car transportation on the environment and housing needs are all very significant, valid concerns, but the burden cannot be placed on a few who happen to live within a block of a bus line. Many of the residents of the Low Residential blocks have lived in their homes for decades. Their small homes have a lower environmental footprint than large homes on large lots that consume more energy, water for lawns and pools and furniture to fill the rooms. The very small benefit of crowding more residences into these areas and hoping that some of the

6 cont.

residents will use a bus for most of their transportation is far outweighed by the harm it will cause to the people living there.

In addition, plans for "transit-oriented development" fail to accommodate the residents who live within one-half mile of a street served by transit, but who cannot use public transit because the routes do not take them where they need to go, or they need to transport goods or people who are mobility-challenged and unable to use public transit.

5. Lincoln Boulevard:
   Lincoln Boulevard north of the Ballona Wetlands should **not** be designated a Regional Center, and there should **not** be a Regional Center located in or adjacent to the protected wetlands. As a main north-south vehicle route through the westside and Santa Monica to LAX, Lincoln Boulevard is already beyond its vehicle capacity. Traffic congestion is a nightmare, particularly during the summer tourist season (before COVID-19). Soon, the redeveloped Cedars Sinai Hospital will begin to draw more patients and visitors. Redevelopment of large-scale residential projects in the Glencoe-Maxella Specific Plan area and Marina del Rey without traffic mitigation continue to exacerbate the dire traffic conditions. A Regional Center would make traveling along Lincoln Boulevard intolerable and should not be part of the Community Plan until a breakthrough traffic reduction system, such as a center lane light rail route, is in place.

6. Ballona Wetlands Ecological Buffer:
   The DRRA agrees with the proposal to apply specific design standards and buffer zones for properties adjacent to the Ballona Creek Bike Path and the Ecological Reserve. We recognize the need for cyclists and pedestrians to connect from Sepulveda Blvd. along Centinela Avenue and Inglewood Blvd. to the Ballona Bike Path, and from the Ballona Bike Path north to UCLA and Santa Monica, perhaps along McLaughlin Avenue and Beethoven Avenue. However, we do not support expanded access to the ecological reserve itself. The reserve should be maintained as open space for non-human species with as little human activity as possible.

7. Mar Vista Gardens:
   The DRRA supports preserving Mar Vista Gardens as legacy garden style apartments for low income housing. However, this property is not considered architecturally or historically significant nor a prime example of Planning for its period. Therefore, the preservation of the buildings as they are designed should

6 cont.

not be required or even encouraged.

8. Open Space / Public Space:
   Del Rey lacks a public meeting space. There are very few government/public or civic buildings, and those that exist (schools and LAPD Pacific Division) do not provide easy access for indoor community meetings or nighttime gatherings. Ideally, the City would acquire property (or use a portion of the LAPD lot) to develop a large public meeting space that is accessible directly from a public way, has adequate parking for meeting attendees and which enhances the neighborhood character and usability. Additionally, Marina Marketplace must incorporate such a space.

   The entire length of the Culver Boulevard Bike Path should be called out in the Community Plan as important open space for the community.

   Area C of the Ballona Wetlands and the Tule Wetlands should be zoned Open Space, not agricultural.

9. Hybrid Industrial Live/Work - Area H:
   Area H was one of few light industrial areas on the Westside. Like the others, it has been slowly changing character, and now includes schools, residences, several medical facilities, office and storage buildings. Each non-industrial development begets more. It will not be long until there are no industrial businesses left if the area is designated Hybrid Industrial Live/Work. In addition, the multiple cul-de-sacs and Ballona Creek are barriers that must be considered when planning for this area. Further, building heights should be determined by the Floor-to-Area Ratios and not the heights of nearby buildings.

10. Del Rey Beethoven Island:
    Del Rey Beethoven Island, known in the community as Bird Island, is a vital stopover for creek birds and supports the open vista corridor of the Ballona Creek environment. Because it is so small, any development is problematic, even with additional ecological design standards. This property should revert to its previous zoning as open space.

11. Hybrid Industrial (Jobs Emphasis) - Mesmer Triangle:
    The DRRA supports retaining the Mesmer Triangle as an industrial hub but opposes heights ranging from 6-8 stories. The area of mostly one or two-story local businesses is unique on the westside of Los Angeles. The small-size, older

6 cont.

buildings provide space for small, local businesses. Allowing mid-high rises will completely change the character of the area and likely push out these businesses. Densification in this area should be prohibited. Restoration and reuse of existing buildings should be required.

12. Neighborhood Villages:
    The DRRA supports neighborhood villages and suggests that more be added to the plan in existing commercial and mixed-use locations; these must be subject to height limits as stated above.

Missing Information

1. The available draft does **not** include sufficient information on:
    a. The expected impact of additional development on traffic and related parking.
    b. Additional open space in the form of parks available to all residents (that is, not including 'open space' available only to residents of a particular development).
    c. Projections for student population and school requirements.
    d. Expected housing requirements for specific areas. The only information available was for the City of Los Angeles in its entirety.
    e. For Development guidelines, the Concepts contain height information but not density/other limits.
    f. Future changes in demand for particular types of housing and working locations as a result of COVID.
    g. Projected needs for electricity and internet connectivity as we transition away from fossil fuels.

2. The draft does not provide a tactical plan to eliminate homelessness while maintaining the quality of life for the non-homeless residents.

6 cont.

Sincerely,

*Maureen Madison*

Maureen Madison, President
Del Rey Residents Association

Westside Community Planning Group
DRRA Comments re Draft Concepts
September 14, 2020

Cc via email:
Diego Janacua
Kinikia Gardner
Mike Bonin
Len Nguyen
Vishesh Anand
Del Rey Neighborhood Council Board

Housing Element <housingelement@lacity.org>

# Brentwood Community Council Public Impact Statement

2 messages

**Bisnoff Email** <bisnoff@gmail.com> Mon, Sep 6, 2021 at 8:00 PM
To: Len Nguyen <len.nguyen@lacity.org>, cpc@lacity.org, Housing Element <housingelement@lacity.org>

Dear City Planning, Housing Element and CD11 Staff:

Please find the attached Housing Element public comment from the Brentwood Community Council regarding the City's Draft Housing Element and EIR for 2022-2029.

While we discuss in detail all related issues in the attached letter, the summary comments are as follows:

***The Housing Element Update, and the Draft EIR, need to be amended, in particular: (i) incorporate the 2020 census data, (ii) reflect the allocated upzoning locations, and (iii) address associated environmental impacts with this information reflected in each of the 35 separate Community Plan areas, with the public being offered the opportunity to make comment once there is information available that provides an accurate picture of the impacts of the Housing Element Update by each Community Plan area.***

***We further request that the City prioritize the implementation of surplus City property in facilitating the absorption of the additional housing inventory projected to be needed under RHNA prior to allocating additional housing units to private property. This use of surplus City property is particularly important in addressing the more affordable forms of housing, as the costs of real estate present its own challenge in developing affordable housing, while the City has the luxury of being able to assist in achieving affordability.***

Many thanks
Michelle Bisnoff

*Michelle A. Bisnoff*
*Chair, BCC*
*Commissioner, City of Los Angeles Innovation and Performance Commission & Chair, Fund Committee*
*Board Member, Los Angeles County Animal Care Foundation*

**Housing Element Update Draft EIR Comment Letter-FIle Submitted Letter BCC Executed.pdf**
162K

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:41 PM
To: Bisnoff Email <bisnoff@gmail.com>

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

BRENTWOOD COMMUNITY COUNCIL

September 6, 2021

Letter O-6

**VIA E-MAIL**

housing.element@lacity.org.
Attention: Cally Hardy, City Planning Associate

City Planning Commission
cpc@lacity.org

len.nguyen@lacity.org
CD11 Planning

*RE: Comments to the Draft Housing Element 2021-2029 Update ("**Draft HE**") and the Draft EIR prepared by City of Los Angeles Department of City Planning 200 North Spring Street, Room 750 Los Angeles, California 90012 prepared with the assistance of Rincon Consultants, Inc. 250 East 1st Street, Suite 1400 Los Angeles, California 90012 July 2021 (the "**Draft EIR**")*

Members of the Housing Element and City Planning Staffs::

The Brentwood Community Council ("**BCC**") is the broadest-based Brentwood community organization, representing approximately 36,000 stakeholders of the community, including homeowner associations, multi-family residential dwellers, business organizations, schools, religious groups, volunteer service groups, public safety, and environmental organizations. The BCC wishes to submit the following comments concerning the Draft EIR for the Draft HE and Safety Element Update, as well as the Draft HE and the Safety Element Updates. These comments are based upon a review by the BCC Land Use Committee (Committee), other interested members of the BCC and members of the Brentwood community at large. 1

*The Draft EIR is deficient as the Draft Housing Element Update is Missing Critical Data*

Without certain missing information sufficiently in advance of the deadline for comments, the process relating to the Housing Element Update is fatally flawed and adoption of the Update would be unlawful. The current draft Housing Element Update, as posted on the City of Los Angeles Department of Planning website, is still missing Appendix 4.7, the list of Candidate Sites for upzoning. The EIR is necessarily and fatally deficient in that it is unable to examine environmental impacts in response to the actual allocation of the 219,732 additional residential units among the various neighborhoods of Los Angeles. While in the abstract one can likely conclude that, within the City of Los Angeles, 219,732 additional residential units could be absorbed City-wide, it is an equally likely conclusion that all additional units could not be located in any one specific neighborhood, and answers will vary as additional units are assigned to specific areas. Accordingly, we object to the current Draft EIR and ask that the City ensure that the Draft EIR be revised once the allocation of the additional residential units is made. 2

In addition, both the draft Housing Element Update and the Draft EIR are missing 2020 census data information. The housing needs are based on projections missing critical data that would allow for a more accurate analysis as to projected needs. Population increase is assumed, while we saw a decrease in population and the loss of a Congressional seat. While the Draft EIR, working with artificially high numbers, may provide a conservative review of environmental impacts in the aggregate, the Draft Housing Element is providing for an housing increase, and related upzoning, that may be entirely unnecessary. Moreover, when we both don't have the information as to where upzoning will occur, we combine it with upzoning beyond what is required, and we have no control over what "upzoned" properties are actually developed, the Draft Housing Element may be creating a situation where one or another community ends up bearing an unreasonable share of increased density, with the Draft EIR not addressing the impacts of the upzoning by Community Plan, and the Draft EIR's mitigation measures only applying to those developments requiring discretionary approvals, which do not apply once a property is upzoned. At a minimum, the application of the Draft EIR mitigation measures need to apply not just where discretionary approvals are required, but need to apply on each parcel that is upzoned to accommodate the RHNA allocation, as, but for the upzoning, any project using the density afforded by upzoning would have previously been a project requiring discretionary approvals. 3

*The Housing Element Update should be adjusted to account for actual additional residential units needed.*

The Housing Element Update works off an assumed number of needed additional units as mandated by the State of California, and then unnecessarily increases that number. The Housing Element Update indicates that, to ensure that sufficient capacity exists in the Housing Element to accommodate the RHNA throughout the planning period, the draft plan sets a target capacity (or buffer) that is 10% higher than the RHNA for lower income units, and 15% higher than the RHNA for moderate income units. This results in a target capacity for the Adequate Sites Inventory and Rezoning Program of 486,379 units. Conversely, most local jurisdictions challenged the State's target numbers and worked to reduce their required zoning increase. For all the same reasons and concerns that the EIR is being prepared, because an increase in residential units of this magnitude will have environmental impacts, the City of Los Angeles should be working off the actual allocation of 456,643, rather than the 486,643. The analysis demonstrates that, during the 6th cycle, the City has an anticipated unit potential of 266,647 units. As a result, the Plan identifies a need for a Rezoning Program to accommodate 219,732 units. When reduced by the potential additional capacity already existing, the additional housing unit capacity to be created would only be 189,996. 4

As mentioned above, we believe the number of additional units that must be added to by way of upzoning is artificially high. In addition, we note that the Housing Element did not count any existing undeveloped site in a VHFHSZ as a potential site for any by-right development. [We do not necessarily oppose existing by-right development, particularly replacement of single family housing that was lost/damaged due to a fire, that complies with all necessary mitigation measures when developing in VHFHSZs. Counting such units in the mix may increase the amount of potentially available sites for housing, thereby reducing the number of units needed to be made available through upzoning.][Alternative: We note this approach because we believe there is a critical thought process 5

underlying the assumption.] What is absolutely critical is that no increased density be assigned to any parcels located in VHFHSZs as part of the Zoning program to accommodate the additional housing capacity]\. We believe that such a policy would be a natural extrapolation of the City's approach to the Housing Element Update by not counting any existing vacant parcel of land in a VHFHSZ. The Housing Element Update should be modified to make clear that no upzoning will occur in VHFHSZs

5 cont.

Regardless of the correct number, the timeline as laid out in the Executive Summary of the Housing Element Update indicates that: the "shortfall must be accommodated by a Rezoning Program, which must be adopted by October 2024." As stated in the prior section, the EIR is wholly inadequate if it is analyzing an increase in zoning (and impact on an area) without having the actual upzoning data.

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With respect to the Draft EIR Sections, we offer the following comments, concerns and observations:

Draft EIR Elements:

4.9 Land Use and Planning – As we had commented in our comments to the Initial Study ("IS") outlining the scope of the EIR, we believe it is imperative that this section analyze the impacts of the Housing Element Update upon each of the City's 35 separate Community Plan areas. However, the draft EIR analyzes the impact of the Housing Element Update only upon the General Plan itself, and concludes there are no significant impacts. City-wide, that is likely a rational conclusion; but the impact of the Housing Element Update will be based squarely upon where increased density is assigned in each separate Community Plan Area, which plan areas vary quite significantly from one another. Moreover, and as noted at the outset of this comment letter, the absence of the specific allocation of the additional housing units renders the Draft EIR and its conclusion meaningless.

7

In addition, the Draft EIR assumes that "the Rezoning Program would be subject to applicable City regulations, environmental review processes, and RCM." (Draft EIR at 4.9-29). However, if the increased density is accomplished by way of upzoning specific parcels, no EIR will be required when those parcels are developed, as the increased density was awarded "by right" with the upzoning. This assumption in the Draft EIR needs to be clarified and explained if there is subsequent CEQA protection available to the community, or the statement needs to be stricken with the effect of upzoning specifically and objectively analyzed.

8

4.10 Noise – The Draft EIR does analyze the impact of construction noise resulting from development of projects that are authorized through the Housing Element Update, and offers mitigation measures for projects requiring discretionary approval (4.10-35). Again, this application of mitigation measures begs the question as to how this will be implemented when the increased zoning is assigned – once specific parcels are upzoned to allow for increased housing units, how will the mitigation measures apply, as it is found that there is an impact requiring mitigation, but the consequence of upzoning is that the project is "by right," and not "discretionary." The Draft EIR needs to address not just
discretionary" projects, but all projects that result or benefit from the assignment of increased housing capacity.

9

The Draft EIR assumes that the increased housing density will be in areas with rich transportation offerings, and therefore there is no analysis of the noise impact related to increased traffic. However

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without the actual allocation of the housing units, and transportation rich areas being only one of several preferred areas for increased density, it is not reasonable to assume that noise resulting from increased traffic need not be analyzed. 10 cont.

4.11. Population and Housing – The Draft EIR and the Housing Element Update are both admittedly working with inaccurate population data as they state that the 2020 census information is not yet available. However, it seems that such data is available, and the Draft EIR should be updated and re-circulated as a draft for public comment with such data. In that regard, this referenced section of the Draft EIR could objectively and thoroughly assess the issues by being updated with more relevant and specific data. That data, once obtained, needs to be further analyzed by each separate Community Plan area as previously noted in our comment letter to the IS. Further, the application of the Housing Element Update to each Community Plan area must be done so on a consistent basis for all Community Plan areas – the process must not proceed differently in different Communities merely because the City has chosen to update the Community Plans of certain areas prior to the Community Plans of other areas. 11

4.12. Public Services –

Fire – Without the allocation of increased housing, and therefore potential development, within each Community Plan Area, and with the single most important aspect of delivery on fire protection is the proximity of the responding fire station to the fire in question, the Draft EIR is not able to provide meaningful analysis of the increased burden on existing fire safety measures or on sufficient mitigation measures in terms of needs of actual fire response units and locations. Further, the City's adoption of the Housing Element Update and the Safety Element Update cannot proceed without the Reports called for by City Council's adoption of the Motion in CF 20-1213 relating to the inter-relationship of evacuation routes and increased development. 12

Police – the Draft EIR concludes that, even with mitigation efforts, there will be significant adverse impacts on police protection. The Draft EIR then goes on to indicate that individual projects could have various safety measures required by Building and Safety, but actual mitigation measures are only offered for projects involving more than 10 acres or 300 units (these projects will be the exception, with the norm being small urban infill projects based on development opportunities). The Draft EIR needs to re-analyze the issue of police protection and offer mitigation measures on a per project basis, rather than assume that in issuing building permits, safety concerns will be taken into account and addressed in the permitting process. A listing of safety measures should be developed and offered as a mitigation measure. 13

Schools – The Draft EIR briefly analyzes the impact of construction of additional school facilities that may be required as a result of the increased density that will be created by construction of additional single and multi-family housing, and concludes that such school construction will not result in significant impacts. However, the Draft EIR does not address the differing impacts within our City of the ability of schools to handle increased enrollment, particularly by Community Plan area. Construction takes time, and may lag well behind enrollment demand. There is no analysis offered as to potential existing capacity, or room for growth within a campus. The EIR must analyze and disclose not only the impact of additional school construction, but also the impact on the education system if housing and population in 14

an area significantly precedes in time the likely construction of additional school facilities in a reasonable time. 14 cont.

4.13. Recreation

The Draft EIR's conclusion is that there will be significant and unavoidable impacts on the City's park system, with overuse and degradation of existing parks due to increased housing creating increased demand on an already overtaxed parks system. The City has previously altered and expanded the radius in which Quimby funds can be deployed, resulting in the potential for funds to be used at a great distance from where the increased density is occurring. The Draft EIR should consider, as a mitigating measure, whether decreasing the radius for the deployment of Quimby funds would be a helpful mitigation measure. 15

4.14. Transportation –

The Draft EIR's analysis respecting the impact of the Housing Element Update on transportation relies upon the following:

> "A large portion of the anticipated housing capacity is expected to be located within Transit Oriented Communities Areas, which are defined as the half-mile radius around a Major Transit Stop. Based on the estimated capacity of 266,647 units, and the total target capacity of 486,379 units, the Housing Element finds a need for a Rezoning Program for the creation of 220,000 additional units of capacity. The Rezoning Program, which would need to be completed by 2024, will likely be accomplished through updates to the City's Community Plans (Land Use Element), an update to the City's Density Bonus program, targeted zone changes, updates to specific plans and overlays, or other zoning ordinances. These programs would likely identify opportunities for rezoning or development incentives in areas that are located in a Transit Priority Area, near major job centers, neighborhood services and amenities, and particularly in higher resource areas shown in Figure 3-5 to provide the most equitable distribution of housing opportunities." (Draft EIR at 4.14.-52). 16

The Housing Element Update needs to identify the precise locations for upzoning, and the Draft EIR updated, to react to and address the actual impacts based on the facts, rather than assuming the "likely" scenarios.

As elsewhere throughout the EIR, the mitigation measures are suggested (i) for addressing the temporary impacts of construction, which is helpful, but does not address the permanent impacts of increased construction, and (ii) for "discretionary" projects only, which misses the point that the Housing Element Update will upzone properties, making such projects be "by right," and not subject to the mitigation measures, even though it is the project(s) creating the need for the mitigation measures. 17

The Draft EIR does not address transportations issues that would be exacerbated in communities with pre-existing intersections with "D" or "F" ratings, as for which no mitigation measures would be sufficient. The Draft EIR needs to identify those neighborhoods whose traffic conditions are already at 18

unacceptable levels of service and address how those neighborhoods are to accommodate increased density when they are not accommodating existing density. At a minimum, the EIR must analyze and disclose those intersections that would become "F" rated as a result of upzoning, particularly during peak traffic hours. For example, if much of the City's roads and traffic intersections came to a gridlocked standstill as a result of increasing housing, the conclusion cannot be that the housing must be created – no matter what. There must be some point where the City becomes unlivable according to generally accepted standards.

18 cont.

4.16 Utilities and Service Systems -

The Draft EIR does not address the quality of the utility infrastructure system within the City of Los Angeles, or identify those areas within the City of Los Angeles where the infrastructure is not accommodating its existing usage and experiences regular lapses in service, whether from water main breaks or power outages. Nor does the Draft EIR study utility infrastructure by Community Plan area. These deficiencies must be corrected in the Draft EIR so that there is meaningful information to utilize in the determination of the locations for upzoning – or a plan on the part of the City to upgrade such utilities and service systems prior to any such upzoning.

19

4.17. Wildfire –

We appreciate the Draft EIR recognized comments received with respect to the IS and addressed wildfire to the extent it did. We also note that the Draft EIR states that "Under the Housing Element Update, the Rezoning Program will prioritize areas near transit, jobs, and in High and Very High Resource Areas; however, no rezones within environmentally sensitive areas such as the SRA and VHFHSZs are proposed." (Draft EIR4.17-36) We concur that it would be problematic to have any upzoning occur in VHFHS zones or in SRAs. We have not been able to identify the specific language in the Housing Element Update that ensures no rezones within SRAs or VHFHSZs will occur. If the statements are within the Housing Element update, then it is critical that this aspect of the Draft Housing Element remain the same, and that no upzoning is assigned to any property within the City of Los Angeles located in any of these areas. If the concept is not expressly articulated in the Housing Element Update, it should be. Should any increased density be assigned to a property in a VHFHS zone or in an SRA through the zoning program, then the Draft EIR would have to re-analyze wildfire in that context.

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With respect to the Safety Element update, it mentions several fire safety hazards but applies no safety related restrictions to mitigate these hazards. Due to the lack of evacuation routes, additional density in fire zone areas with only 1 route of egress has been life threatening for many California communities. A responsible policy prohibiting further density in State designated VHFHSZ (fire zone) areas, including ADU's, should be enacted, excluding by right zoning. Due to the high fire potential of adding frequent traffic to State-designated VHFHSZ, non-residential development should be specifically prohibited in such fire zone areas unless it is by right zoning as of August 31, 2021.

21

We further note these issues:

a. 50% of the land mass in Brentwood is located in a Very High Fire Hazard Severity Zone
b. Brentwood is subject to recurrent wildfires

22

c. Steep canyon and hillside areas in Brentwood make fighting fires dangerous and/or difficult from the ground and in winds over 40 miles per hour, inaccessible by fixed wing and rotary firefighting aircraft
d. High above-ground power lines and narrow evacuation routes in Brentwood increase the dangers associated with wildfires
e. In an area with significant levels of construction, the danger of construction-related fire is likely to increase, amplified by the increase of associated traffic that limits both the effectiveness of firefighting and the availability of evacuation routes
f. Long Emergency Response Vehicle Times
g. Densification of residential parcels only would increase the dangers listed above

22 cont.

6. ALTERNATIVES

The Draft EIR did not, as one of its alternatives, discuss how preparing the Draft EIR by Community Plan Area would lead to different, and we believe, better informed results. The Draft EIR also did not address how the preparation of the Draft EIR would lead to different, and we believe, better informed results if the preparers had the actual upzoning information available to factor into their analysis.

23

In addition, we are concerned that neither the Draft EIR, nor the Draft Housing Element Update, address the sequence of the completion of the Housing Element in 2021 while the Draft EIR and Draft Housing Element both presently have missing materials and are necessarily deficient; the preparation and completion of a rezoning program is required by 2024, which would be implemented through the Community Plan Update process, some of which Community Plans are well on their way to completion, while others have not started, and the Housing Element Update intends to provide for upzoning for in excess of what is required, which no means to facilitate actual usage in any area – so some areas may be exceptionally burdened if upzoning (including the "buffer amount") is acted upon in certain areas, but not in others.

24

***In conclusion, the Housing Element Update, and the Draft EIR, need to be amended as described above, including, in particular, to: (i) incorporate the 2020 census data, (ii) reflect the allocated upzoning locations, and (iii) address associated environmental impacts with this information reflected in each of the 35 separate Community Plan areas, with the public being offered the opportunity to make comment once there is information available that provides an accurate picture of the impacts of the Housing Element Update by each Community Plan area. We further request that the City prioritize the implementation of surplus City property in facilitating the absorption of the additional housing inventory projected to be needed under RHNA prior to allocating additional housing units to private property. This use of surplus City property is particularly important in addressing the more affordable forms of housing, as the costs of real estate present its own challenge in developing affordable housing, while the City has the luxury of being able to assist in achieving affordability.***

25

Respectfully submitted,

*Michelle A. Bisnoff*

Michelle Bisnoff
Chairperson
Brentwood Community Council

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# Fwd: Comment Letter: Draft Housing Element 2021-2029 update & Draft EIR

2 messages

**info@pacpalicc.org** <info@pacpalicc.org> Tue, Sep 7, 2021 at 11:33 AM
To: housingelement@lacity.org

Please see message below and attached letter.

Best regards,

Christina Spitz
Secretary
Pacific Palisades Community Council
www.pacpalicc.org

**From:** <info@pacpalicc.org>
**To:** <housing.element@lacity.org>, <cally.hardy@lacity.org>, <cpc@lacity.org>
**Cc:** <davidcard22@gmail.com>, <dkaplan6@gmail.com>, <rgcohen@aol.com>, <johnpadden@kw.com>, Joanna Spak <jlspak@yahoo.com>, <ppfriends3@hotmail.com>
**Sent:** 9/7/2021 11:28 AM
**Subject:** Comment Letter: Draft Housing Element 2021-2029 update & Draft EIR

> To: Dept. of City Planning/attn. Cally Hardy
> and City Planning Commission:
>
> Please see attached comment letter from Pacific Palisades Community Council regarding the above matter.
>
> Thank you.
>
> Best regards,
>
> Christina Spitz
> Secretary
> Pacific Palisades Community Council
> www.pacpalicc.org

**PPCC Comment Letter Housing Element DEIR.pdf**
310K

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 4:45 PM
To: info@pacpalicc.org

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012

LOS ANGELES CITY PLANNING

Planning4LA.org
T: (213) 978-1302

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

# PACIFIC PALISADES COMMUNITY COUNCIL

September 7, 2021

City of Los Angeles, Department of City Planning (DCP)
Attention: Cally Hardy, City Planning Associate
Via email to: housing.element@lacity.org

and

Los Angeles City Planning Commission
Via email to: cpc@lacity.org

Letter O-7

*Re: Comments on the Draft Housing Element 2021-2029 Update ("Draft HE") and the Draft EIR prepared by City of Los Angeles Department of City Planning with the assistance of Rincon Consultants, Inc. July 2021 (the "Draft EIR")*

DCP and Planning Commission:

Pacific Palisades Community Council ("PPCC") is the broadest-based Palisades community organization, representing approximately 25,000 stakeholders. PPCC submits the following comments concerning the Draft EIR for the Draft HE and Safety Element Update, as well as the Draft HE and the Safety Element Updates. These comments are based upon a review of the documents by the PPCC Executive Committee and by the concerns and positions stated in PPCC's February 12, 2021 comment letter.[1] 1

Our comments are also based on the letter submitted on September 6, 2021 in this matter by Brentwood Community Council (BCC) (9/6 BCC Letter).[2] Brentwood is a community to the immediate east of Pacific Palisades. We share a community plan – the Brentwood-Pacific Palisades Community Plan (BPPCP) – and we also share common concerns related to wildfire and evacuation hazards.

Specifically, PPCC shares the following concerns and comments as expressed in the 9/6 BCC letter: 2

- The concerns expressed in the comments under the heading *"The Draft EIR is deficient as the Draft Housing Element Update is Missing Critical Data."*
- The concerns expressed under the heading "Draft EIR Elements: 4.9. Land Use and Planning."

We note that the BPPCP has not been scheduled for an update yet; we are still completely unaware of the City's land use and zoning plans for our area. 3

- The concerns expressed under the heading "Draft EIR Elements: 4.11. Population and Housing." 4
- The concerns expressed under the heading "Draft EIR Elements: 4.12. Public Services – Fire."
- The concerns expressed under the heading "Draft EIR Elements: 4.17. Wildfire."

In this regard, we appreciate that the Draft EIR expressly recognizes comments previously submitted by PPCC with respect to wildfire impacts. We also appreciate the following statement: "Environmentally sensitive areas, 5

[1] http://pacpalicc.org/wp-content/uploads/2021/02/PPCCHousing-Element-Comment-Letter.pdf.
[2] https://drive.google.com/drive/folders/1FW1Zq_nSUl1c3MGqUh3AhKJuwoFO3uTr

including Very High Fire Hazard Severity Zones (VHFHSZ) and areas vulnerable to sea level rise, will be excluded from the Rezoning Program, even if they have overlap with the above-described growth areas and higher resource areas."

5 cont.

We reiterate that 100% of Pacific Palisades is within the Very High Fire Hazard Severity Zone (VHFHSZ). Pacific Palisades otherwise shares the same conditions noted in issues b) – g) under the heading "4.17. Wildfire" of the 9/6 BCC Letter.

We further agree with the concluding sentences of the 9/6/21 BCC Letter, regarding prioritizing the use of surplus City property for affordable housing,

6

For all of these reasons, we respectfully submit that Pacific Palisades should be excluded from the Rezoning Program.

7

Thank you for your consideration and attention to our comments and concerns.

Sincerely,

Executive Committee, Pacific Palisades Community Council

| | |
|---|---|
| David Card, Chair | Christina Spitz, Secretary |
| David Kaplan, Vice-Chair | John Padden, Organization Representative (P.R.I.D.E.) |
| Richard G. Cohen, Treasurer | Joanna Spak, Elected Representative (Area 1; Castellammare, Paseo Miramar) |

Connect Create Collaborate

Letter O-8

**Housing Element <housingelement@lacity.org>**

# Re: "The Livable Communities Initiative" - Submission for Public Comment - 2021-29 Los Angeles Housing Element

3 messages

**Matthew Glesne** <matthew.glesne@lacity.org> Tue, Sep 7, 2021 at 2:56 PM
To: Tony Gittelson <tonygittelson@gmail.com>, Housing Element <housingelement@lacity.org>
Cc: Blair Smith <blair.smith@lacity.org>, Lindsay Sturman <lindsay.sturman@gmail.com>, Jennifer Levin <jentwelve@gmail.com>, helen eigenberg <hm.eigenberg@gmail.com>

Thank you Tony. I am CCing this to our official Housing Element comment email (housingelement@lacity.org) to make sure it is reflected in the record. Really appreciate the thoughts and work reflected here.

Matt

On Tue, Sep 7, 2021 at 1:03 PM Tony Gittelson <tonygittelson@gmail.com> wrote:

> Sept. 7, 2021
>
> Mr. Matthew Glesne,
> Senior City Planner
> Mr. Matthew Glesne,
> Senior City Planner
> Ms. Blair Smith,
> City Planner
> Citywide Policy Planning Department
>
> Dear Matthew Glesne and Blair Smith,
>
> Pursuant to our conversation with you, we wish to submit, for public comment, the attached proposal, **The Livable Communities Initiative**, that we urge be included as a Program in the **2021-29 Housing Element.**
>
> We are affiliated with a coalition of approximately 2,700 concerned homeowners, renters and Los Angelenos deeply engaged in local, grassroots community organizing. The name of our coalition is **Hang Out, Do Good**. As part of our work, our Housing Committee is extremely focused on the lack of sufficient, equitable affordable housing in our own communities, and throughout Los Angeles (city and county).
>
> To address this urgent crisis, we have engaged in lengthy conversations with our own members, and with our neighbors, and with a vast array of housing experts, academics, city planners and affordable housing developers, to craft **The Livable Communities Initiative (LCI)**.
>
> The Livable Communities Initiative (LCI) is a combination of existing LA City goals and programs, explicitly stated throughout the 2021-2029 Housing Element, but one that holistically addresses equitable and affordable housing, mobility and transit justice, and climate, as one idea, rather than piecemeal. LCI grew out of a collaboration between housing activists and mobility, bike, and transit activists; we found that by linking the issues of housing equity and mobility together, we created a virtuous cycle in which the collective vision had much greater impact than each component part--at the same time, we have crafted a comprehensive approach to equitable affordable housing, based on the **City's Equitable Distribution Plan** (May 21, 2021) that Affirmatively Furthers Fair Housing (AFFH), ensuring that high-opportunity neighborhoods provide a fair share of affordable housing. By adding affordable housing in job-rich, transit-rich and amenity-rich neighborhoods, Los Angeles can reverse the pressures that create displacement and gentrification in under-resourced communities.
>
> The core of the LCI is to address our housing crisis by upzoning under-utilized commercial arterials to 3-5 stories while simultaneously transforming the street: slowing the cars, adding wide sidewalks, a tree canopy, al fresco dining, bike lanes, and fast and frequent transit -- making it a "Complete Street." By

1

combining affordable housing and equitable distribution -- with mobility, safe bike lanes, and a low car/slow car streets -- we can create a linear version of what is called the "15 Minute City": smaller, livable communities where everything an individual needs--access to jobs, schools and amenities--is no more than 15 minutes away, by bike, walking, or mass transit. A city that can and should be accessed, and enjoyed, by Los Angelenos of *all* income levels.

Los Angeles has hundreds of miles of down-zoned commercial arterials -- Pico, Venice, Western, Westwood Blvd, to name just a few. By creating **LCI Zones**, allowing for streamlined "gentle density" development, the LCI will give all Angelenos, at all socioeconomic income levels, a safe and dignified way to live in LA without requiring a car. We believe there is a huge untapped demand for beautiful low-car streets with affordable, equitable housing, bike lanes, fast transit and amenities.

1 cont.

As the City of LA embarks on a three-year re-zoning for 300,000 new units of housing, the LCI would give *every* Angeleno the option to live affordably and sustainably, with safe and convenient transportation options, in *every* neighborhood in Los Angeles.

The draft language of the **Livable Communities Initiative** is attached. We urge that it be included as its own Program in the **2021-2029 Los Angeles City Housing Element**.

Thank you so much,

Lindsay Sturman & Tony Gittelson
The Livable Communities Initiative

Jennifer Levin & Helen Eigenberg
Co-Founders
**Hang Out, Do Good**

Louis Abramson
Chair, Homelessness Committee
Central Hollywood Neighborhood Council
(Signing on behalf of himself)

Gerhard Mayer
GGLO
Architect and Urbanist

Patricia Bijvoet
Landscape Architect and Urban Planner
UPLA Studio

Terenig Topjian
Founder, Have A Go
haveago.city

--

LOS ANGELES CITY PLANNING

**Matthew Glesne**
Preferred Pronouns: He, Him, His
Senior City Planner
**Los Angeles City Planning**
200 N. Spring St., Room 750
Los Angeles, CA 90012
Planning4LA.org
T: (213) 978-2666
E-NEWS

**Tony Gittelson** <tonygittelson@gmail.com> Tue, Sep 7, 2021 at 4:19 PM
To: Matthew Glesne <matthew.glesne@lacity.org>
Cc: Housing Element <housingelement@lacity.org>, Blair Smith <blair.smith@lacity.org>, Lindsay Sturman <lindsay.sturman@gmail.com>, Jennifer Levin <jentwelve@gmail.com>, helen eigenberg <hm.eigenberg@gmail.com>

Thank you so much, Matt!

We look forward to continuing the conversation, and thank you for your guidance on this.

All best,

Tony

Tony Gittelson
Los Angeles, CA
Tel. (323) 938-5535
Cell (213) 400-1494
TonyGittelson@gmail.com

[Quoted text hidden]

---

**Matthew Glesne** <matthew.glesne@lacity.org> Tue, Sep 7, 2021 at 4:51 PM
To: Housing Element <housingelement@lacity.org>

[Quoted text hidden]

**Livable Communities Initiative (LCI) - DRAFT - Sept. 7 2021.pdf**
63K

**Housing Element Program Proposal: "Livable Communities Initiative"**

**129. The Livable Communities Initiative (NEW)**

**Goal #: 3, 2, 1, 4, 5**

**Lead Agencies: DCP, HACLA, LAHD, LAHSA, LA METRO, LA DOT**

**Funding Source: General Fund, Addtl Funding From Existing Programs Falling Within the Scope of the "Livable Communities Initiative"**

**Objective:** Falling within the purview of Program 121 (RHNA Re-Zoning) and Program 123 (Assessment of Fair Housing), the **Livable Communities Initiative** (**LCI**) will create a Program to advance a holistic concept of livable, healthy, and sustainable communities along the City's transit-rich corridors. Expanding the successful TOC model, under the additional RHNA Re-Zoning Plan (2021-24), LCI creates a program, primarily along commercial and underdeveloped industrial corridors in High Opportunity areas, that utilizes higher-density mixed-use, mixed-income housing and a variety housing typologies, including: microunits, row houses, perimeter housing block surrounding green space, shared housing models (including boarding house and dorm-style living), and other contextual Los Angeles typologies for a diverse, mixed socio-economic status community which includes 20% - 100% affordable housing.



**TEXT**

Falling within the purview of Program 121 (RHNA Re-Zoning) and Program 123 (Assessment of Fair Housing), the **Livable Communities Initiative** (**LCI**) will create a Program to advance a holistic concept of livable, healthy, and sustainable communities along the City's transit-rich corridors. Expanding the successful TOC model, under the additional RHNA Re-Zoning Plan (2021-24), LCI creates a program, primarily along commercial and under-developed industrial corridors in High Opportunity areas, that utilizes higher-density mixed-use, mixed-income housing and a variety housing typologies, including: microunits, row houses, perimeter housing block surrounding green space, shared housing models (including boarding house and dorm-style living), and other contextual Los Angeles typologies for a diverse, mixed socio-economic status community which includes 20% - 100% affordable housing.

The goal of the Livable Communities Initiative (LCI) is to develop a variety of innovative Affordable Housing models--creating smaller holistic communities within the larger City--that will promote gentle-density, sustainable, livable, walkable and

bikeable neighborhoods, with access to transit, jobs and amenities, including: tree-lined, shaded streets and small public spaces; reduced car traffic; safe protected bike lanes; and increased bus frequency (where applicable). These contained, well-planned holistic communities address every policy goal in the Housing Element: facilitating housing production that results in more equitable and affordable options by creating both affordable rental units, and affordable homeownership models, across all levels of affordability (Goal 1,2 and 4); creating healthy, livable, sustainable communities that improve the lives of all Angelenos (Goal 3); fostering racially and socially inclusive neighborhoods that correct the harms of historic racial, ethnic and social dicrimination; Affirmatively Furthering Fair Housing (AFFH), especially in High Opportunity Areas; creating Affordable Homeownership opportunities as a strategy to increase wealth building for communities of color (Goals 1, 2 and 4); and, as LCI is scaled-up, it will add significantly to the permanent housing stock, relying in large part on private funding (for low-income and moderately low-income groups), which frees up public resources for Permanent Supportive Housing, proven strategies for reducing homelessness (Goal 5).

To facilitate the Livable Communities Initiative (LCI), within all LCI-designated zones, the TOC program will be expanded to provide zoning bonuses and increased density (for multi-family housing); streamlined permitting, "zero fee permitting" (where possible), and ministerial approval for housing that is from 20-100% affordable; eliminate parking requirements and utilize parking maximums (with exceptions, including ADA); and utilize as necessary deed-restricted covenants to insure sufficient affordable housing is created across all four levels of affordability (Extremely Low Income, Very Low Income, Low Income, and Moderate AMI). LCI will promote both affordable rental housing, as well as an affordable homeownership model, under Policy Objective 2.2.1 and 2.2.3 and Housing Element Programs 1, 2, 4, and 90. The location and size of the zones will be determined by data collection from partner organizations in order to serve all households who wish to participate.

2 cont.

The LCI will be a collaboration between housing and transportation agencies, including LADOT, Metro, StreetsLA, and DCP to create safe bikeable, walkable neighborhoods, using data and proven models, such as the five principles of the CROW Design Manual for Bicycle Traffic (Cohesion, Directness, Safety, Comfort, Attractiveness). StreetsLA will oversee the urban and landscape design for sustainable, livable, healthy streets and housing - including shade trees, low-car streets to alleviate air pollution, noise pollution, and create safety for vulnerable populations from fast moving vehicles (seniors, ADA, hearing and vision impaired, children), community-enhancing spaces such as al fresco dining and parklets, interior courtyards that have been shown to improve mental health outcomes and foster community (Goal 2, 3 and 4). Under Programs 12, 16, 58, 59, 62 and 78, the

Mayor's Office and LACP, HCID, HACLA, and related agencies, will create and implement design standards to enhance the quality of housing (Goal 2).

All of the policy objectives described in the Livable Communities Initiative derive entirely from Programs contained in the current Housing Element. LCI falls primarily under the scope of three *new* Program Elements: **Program 121 - The RHNA Re-Zoning** (which has a three-year horizon); **Program 124 - Affirmatively Furthering Fair Housing**; and **Program 125** that expands **Transit Oriented Communities**. Together these three plans, and the related Housing Programs cited below, describe the scope of LCI and address every housing creation policy goal contained in the 2021-2029 Housing Element, including:

Affordable housing production; zoning reform; the expansion of TOC's; density bonuses and other innovative and adaptive housing models; integrating RHNA targets into local Community Plans; developing commercial corridors and residential areas off commercial corridors; rapidly accelerating affordable housing production via permitting streamlining; design innovation; creating livable, sustainable and healthy communities; and affirmatively furthering fair housing (AFFH) and housing equity across all of Los Angeles.

Other specific Housing Programs (listed below), all contribute to the Livable Communities Initiative, under the following headings:

2 cont.

Affordable Housing Creation: Program 4,6,7,10 (seniors), 14, 15, 16, 18, 20, 24, 30, 46, 48, 49, 50, 60, 61, 65, 66, 80, 81, 107, 115, 125, 126

Funding Programs: Program 4,6,10 (linkage fee-*new*),18,20,30,41, 66, 126

Re-Zoning, Density Bonuses, TOC expansion: Program 7, 48, 49, 50, 60, 61, 62, 81, 115, **124, 125,** 126

Streamlining: Program 16, 37, 54, 55, 57, 60, 62, 115

Parking Requirements: 21, 65

Urban Design & Innovation: 12, 13, 16, 21, 58, 59, 62, 78

Sustainability and Livability: Program 9, 14, 24, 59, 65, 73, 78, 79, 124

Affordable Homeownership Models & CLT's: Program 1, 2, 4, 90

Monitoring: Program 47

Education: Program 67, 120

"No Net Loss" Programs: 28, 29, 124

AFFH and Housing Equity: Program 7, 10(seniors), 15, 24, 30, 41, 48, 90, 92, 99, 107, 124, 126

Reducing Homelessness*****: Program 92, 99, 107

***** The intent of LCI is to significantly increase affordable housing production across LA, and in so doing, directly reduce homelessness--these highlighted programs in the Housing Element specifically address housing and homelessness.

2
cont.

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# Fwd: Comments on City of LA's Housing and Safety Element Update DEIR

2 messages

**Flora Melendez** <flora.melendez@lacity.org> Wed, Sep 8, 2021 at 8:17 AM
To: Housing Element <housingelement@lacity.org>, Matthew Glesne <matthew.glesne@lacity.org>, Blair Smith <blair.smith@lacity.org>, Cally Hardy <cally.hardy@lacity.org>
Cc: Arthi Varma <arthi.varma@lacity.org>, Nicholas Maricich <nicholas.maricich@lacity.org>

Hello.

I'm forwarding an email received by Vince.

Thank you.

~ Angie

LOS ANGELES CITY PLANNING

**Flora (Angie) Melendez**
Pronouns: she/hers/her
Executive Administrative Assistant III
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
Los Angeles, CA 90012
Planning4LA.org
T: (213) 978-1271 | F: (213) 978-1275
E: flora.melendez@lacity.org

E-NEWS

---------- Forwarded message ---------
From: **Elizabeth Reid-Wainscoat** <ereidwainscoat@biologicaldiversity.org>
Date: Tue, Sep 7, 2021 at 4:37 PM
Subject: Comments on City of LA's Housing and Safety Element Update DEIR
To: Vince Bertoni <vince.bertoni@lacity.org>
Cc: mayor.helpdesk@lacity.org <mayor.helpdesk@lacity.org>, councilmember.buscaino@lacity.org <councilmember.buscaino@lacity.org>, councilmember.blumenfield@lacity.org <councilmember.blumenfield@lacity.org>, councilmember.bonin@lacity.org <councilmember.bonin@lacity.org>, gilbert.Cedillo@lacity.org <gilbert.Cedillo@lacity.org>, councilmember.harris-dawson@lacity.org <councilmember.harris-dawson@lacity.org>, councilmember.Krekorian@lacity.org <councilmember.Krekorian@lacity.org>, paul.koretz@lacity.org <paul.koretz@lacity.org>, councilmember.lee@lacity.org <councilmember.lee@lacity.org>, councilmember.martinez@lacity.org <councilmember.martinez@lacity.org>, councilmember.ofarrell@lacity.org <councilmember.ofarrell@lacity.org>, councilmember.price@lacity.org <councilmember.price@lacity.org>, councilmember.rodriguez@lacity.org <councilmember.rodriguez@lacity.org>, councilmember.raman@lacity.org <councilmember.raman@lacity.org>, councilmember.wesson@lacity.org <councilmember.wesson@lacity.org>, Councilmember.kevindeleon@lacity.org <Councilmember.kevindeleon@lacity.org>, lauren.faber@lacity.org <lauren.faber@lacity.org>

Dear Mr. Bertoni,

On behalf of the Center for Biological Diversity, I am submitting these comments on the Draft Program Environmental Impact Report for the City of Los Angeles' Housing and Safety Element Updates.

You can access our references via this folder.

Please confirm that you have received our comments and are able to access the references at the link provided.

Thank you for the opportunity to submit comments. Please add the Center to your notice list for all future actions associated with the Update and do not hesitate to contact us if you have any questions.

Sincerely,

Elizabeth

Elizabeth Reid-Wainscoat (she/her)

Urban Wildlands Campaigner

CENTER *for* BIOLOGICAL DIVERSITY

660 S. Figueroa Street #1000

Los Angeles, CA 90017

Cell: (831) 428-3312

ereidwainscoat@biologicaldiversity.org

**CommentLetter_City of LA Housing Element_2021-09-07.pdf**
397K

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**Housing Element** <housingelement@lacity.org> Wed, Sep 8, 2021 at 9:04 AM
To: ereidwainscoat@biologicaldiversity.org

Thank you for your email. Your comments and attachments have been received and filed.

Regards,
The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Letter O-9

CENTER for BIOLOGICAL DIVERSITY Because life is good.

September 7, 2021

***Sent via email***

Mr. Vince Bertoni
Director of Planning
Los Angeles Department of City Planning
200 North Spring Street
Los Angeles, CA 90012
vince.bertoni@lacity.org

**Re: City of Los Angeles' General Plan Housing Element 2021-2029 and Safety Element Updates**

Dear Mr. Bertoni,

These comments are submitted on behalf of the Center for Biological Diversity ("Center") regarding the Housing Element 2021-2029 and Safety Element Updates' ("Update") Draft Environmental Impact Report (DEIR). We have reviewed the DEIR and Update and provide these comments for consideration to the City of Los Angeles Planning Department ("Planning").

We support all the goals of the Update. We understand that solving the affordable housing crisis will require innovative solutions that provide a wide range of housing types to meet the needs of current and future residents, including extremely low, very low, and low income households. Ensuring those most at risk are given options within their means is critical to tackling the affordable housing crisis. We also strongly support initiatives that build communities with equitable access to employment opportunities, services, and amenities. Too often, ostensibly affordable housing is provided outside the urban core. This results in unequitable access to public services, as well as the personal expenses required to commute to job centers and schools. Furthermore, these housing options are often near known pollution sources like freeways, or vulnerable to other hazards like wildfire.

1

While we are happy to see that the Rezoning Program excludes areas "within environmentally sensitive areas such as the SRA and VHFHSZs," we would like to encourage the City to use this Update as an opportunity to ensure *all* future developments reflect these smart growth principles. Beyond the human impact, sprawl development significantly impacts native biodiversity and destroys our natural lands. Mayor Eric Garcetti's Green New Deal envisions a more sustainable city that protects the environment, reduces greenhouse gas emissions, and provides equal access for all communities to open space. As the City works towards ensuring affordability and protecting communities against displacement, the Center

urges for a more comprehensive approach to growth that addresses community health as well as the needs of wildlife and habitats that are removed, fragmented, and degraded by sprawl development.

1 cont.

Overall, the Center's comments can be summarized by the following:

- In alignment with the **General Plans' Policy 1.1.5** ("Reduce potential risk hazards due to natural disaster to the greatest extent feasible") as well as the **Update's Policy 3.3.2** ("Establish plans, incentives, and development standards that eliminate or minimize disaster risk and promote positive health outcomes for communities most at risk") and the **Update's Program #53**, Disaster Resilience and Recovery ("Explore ways to amend codes in very high fire hazard severity zones and other hazard areas to better protect life and safety")
    - The Update should prohibit or limit new residential development in very high and high wildfire hazard severity zones
    - The Update should require developers to provide proof of the availability of private insurance for the prospective property for all hazards, including wildfire, before a permit to build is approved
    - The Update should include programs for home-hardening against wildfire
- In addition, to align with the **Update's Program #73, Housing and Ecology** ("Develop and implement design standards that foster ecological diversity in the City's hillsides, riverine and coastal areas, open spaces and Significant Ecological Areas through programs including the Wildlife Pilot Study and Ridgeline Protection Ordinance")
    - The Update should also require adoption of the Wildlife Ordinance by the end of 2021.
- For the **Update's Program #121, RHNA Re-zoning**, we support ***Livable Communities Initiative***'s proposal to "up-zone under-utilized commercial arterials to 3-5 stories while simultaneously transforming the street--slowing the cars, adding wide sidewalks, al fresco dining, bike lanes, and fast and frequent transit -- making it a Complete Street."
- We strongly oppose the **Update's Program #55 Implement CEQA Streamlining Measures** ("Create necessary policies and procedures to facilitate streamlining efforts. Develop templates for such streamlining tools as SCEAs and SCPEs. Aim to make more projects that achieve Citywide Housing Priorities to be exempt from or receive CEQA streamlining")

2

More detailed comments are provided below.

## I. Wildfire poses a significant threat to the region and the City's stated commitments to addressing the climate crises, protecting habitat, safeguarding human health and increasing access to open space.

3

According to a report from Governor Gavin Newsom's Office, construction of more homes in the wildland-urban interface is one of the main factors that "magnify the wildfire threat and place substantially more people and property at risk than ever before" (Governor Newsom's Strike Force, 2019). Syphard et al. (2019) found that housing and human infrastructure in fire-prone wildlands are the main drivers of fire ignitions and structure loss. This is not new

information; scientists have been reporting it for many years in scientific, peer-reviewed journals, and firefighters have observed it.

As outlined in the Center's recent report, *Built to Burn*[1], increasing housing development in high fire-risk wildlands is putting more people in harm's way and contributing to a dramatic increase in costs associated with fire suppression and damages. Next 10 and UC Berkeley's recent report, *Rebuilding for a Resilient Recovery: Planning in California's Wildland Urban Interface*[2], likewise found that state and local land use policies are increasing the economic and human cost of wildfire by encouraging rebuilding in the high risk-wildland urban interface instead of focusing development away from fire-prone areas. Sprawl developments with low/intermediate densities extending into habitats that are prone to fire have led to more frequent wildfires caused by human ignitions, like power lines, arson, improperly disposed cigarette butts, debris burning, fireworks, campfires, or sparks from cars or equipment (Balch et al., 2017; Bistinas et al., 2013; Keeley et al., 1999; Keeley & Fotheringham, 2003; Keeley & Syphard, 2018; Radeloff et al., 2018; Syphard et al., 2007, 2012, 2019). Human-caused fires account for 95-97% of all fires in Southern California's Mediterranean habitats (Balch et al., 2017; Syphard et al., 2007). In some Southern California counties, Keeley and Syphard (2018) found that human ignitions were responsible for 98-100% of fires between 1919-2016. Leapfrog developments in high fire-prone areas have the highest predicted fire risk (Syphard et al. 2013), and multiple studies indicate that developments with low/intermediate-density clusters surrounded by fire-dependent vegetation (*i.e.*, grasslands, chaparral, scrub) in areas with a history of fires have the highest chances of burning (Bistinas et al., 2013; Syphard et al., 2012, 2013, 2019). The Update, as currently drafted, could result in the placement of more homes, infrastructure, roads, and communities in high fire-prone areas that have burned in the past and will inevitably burn again.

By placing people in fire-prone areas, the induced sprawl perpetuated by the Update would increase the number of potential ignition sources, and therefore the risk of wildfires occurring. In addition, power lines and electrical equipment are a significant source of human-caused ignitions (Keeley & Syphard, 2018). The 2017 Thomas Fire, 2017 Tubbs Fire, 2018 Camp Fire, and 2018 Woolsey Fire were found to have been caused by electrical transmission lines and electrical equipment, and the 2019 Kincade Fire is suspected to have been caused by power lines as well. Placing homes and people in high fire-prone areas would only increase the potential likelihood of these ignition sources, as has been documented in multiple scientific studies (Balch et al., 2017; Bistinas et al., 2013; Keeley et al., 1999; Keeley & Fotheringham, 2003; Keeley & Syphard, 2018; Radeloff et al., 2018; Syphard et al., 2007, 2012, 2019).

Although public utilities companies (*i.e.*, PG&E and Southern California Edison) are altering operations in the form of power outages and blackouts during extreme weather conditions (Callahan et al., 2019; Fry, Dolan, et al., 2019; Krishnakumar et al., 2019), wildfires can still spark and spread quickly towards homes, as evidenced by the wildfires in Moraga

3 cont.

[1] Tiffany Yap, et al, *Built to Burn: California's Wildlands Developments Are Playing With Fire* (Feb. 2021), available at https://www.biologicaldiversity.org/programs/urban/pdfs/Built-to-Burn-California-Wildfire-Report-Center-Biological-Diversity.pdf.

[2] Next 10 and UC Berkeley, *Rebuilding for a Resilient Recovery: Planning in California's Wildland Urban Interface* (June 2021), available at https://www.next10.org/sites/default/files/2021-06/Next10-Rebuilding-Resilient-Final.pdf.

(Hernández et al., 2019) and Saddleridge/Sylmar (Fry, Miller, et al., 2019). And the power outages themselves disproportionately burden our most vulnerable communities, including the elderly, poor, and disabled (Chabria & Luna, 2019), and can cause traffic jams and collisions (CBS San Francisco, 2019). Michael Wara, Director of the Climate and Energy Policy Program and a senior research scholar at the Stanford Woods Institute for the Environment, estimated that PG&E's power outage in Northern and Central California could have an economic impact of $2.5 billion in losses, with most of the burden on businesses (Callahan et al., 2019). It is clear that placing more homes in known fire-prone areas and wind corridors is irresponsible and can lead to deadly and costly consequences.

In addition, such sprawl developments disrupt the natural fire regime and lead to a dangerous feedback loop of deadly fires and habitat destruction. Native California habitats are adapted to infrequent (every 30 to 150 years or more), large, high-intensity crown fire regimes (Keeley & Fotheringham, 2001). However, if these regimes are disrupted, the habitats become degraded (Keeley, 2005, 2006; Syphard et al., 2018). When fires occur too frequently, type conversion occurs and the native shrublands are replaced by non-native grasses and forbs that burn more frequently and more easily, ultimately eliminating native habitats and biodiversity while increasing fire threat over time (Keeley, 2005, 2006; Safford & Van de Water, 2014; Syphard et al., 2009, 2018). This could have serious consequences for special-status species in the region that rely on these native habitats for survival, like California red-legged frogs and Least Bell's vireos. In addition, large-scale landscape changes due to vegetation-type conversion from shifts in natural fire regimes could impact wide-ranging species like mountain lions (Jennings, 2018), whose populations are already struggling in the area due to lack of connectivity and genetic isolation (Dellinger, 2019; Gustafson et al., 2018).

3 cont.

Furthermore, this increase in wildfire results in higher frequency and toxicity of smoke exposure to communities in and downwind of the fires. This can lead to harmful public health impacts due to increased air pollution not only from burned vegetation, but also from burned homes, commercial buildings, cars, etc. Buildings and structures often contain plastic materials, metals, and various stored chemicals that release toxic chemicals when burned, such as pesticides, solvents, paints, and cleaning solutions (Weinhold, 2011).

Increased fire frequency due to human activity and ill-placed developments lead to increased occurrences of poor outdoor and indoor air quality from smoke (*e.g.*, Phuleria et al. 2005), which can have public health effects. Hospital visits for respiratory symptoms (*e.g.*, asthma, acute bronchitis, pneumonia, or chronic obstructive pulmonary disease) and cardiovascular symptoms have been shown to increase during and/or after fire events (Delfino et al., 2009; Künzli et al., 2006; Liu et al., 2015; Rappold et al., 2012; Reid et al., 2016; Viswanathan et al., 2006). Children, elderly, and those with underlying chronic disease are the most vulnerable to the harmful health effects of increases in wildfire smoke. The EIR does not include sufficient analysis of the RTP/SCS's potential impacts of increased smoke exposure due to increased human-caused ignitions.

4

Finally, the DEIR does not adequately consider the impacts on firefighters and first responders of the growth induced by the Update in high fire-prone natural areas subject to intermittent wildfires. Adding more development to these wild areas will necessitate significant

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firefighting costs from both state and local authorities. Cal Fire is primarily responsible for addressing wildfires when they occur, and its costs have continued to increase as wildfires in the wildland urban interface have grown more destructive. During the 2017-2018 and the 2018-2019 fiscal years, Cal Fire's fire suppression costs were $773 million and an estimated $635 million, respectively (Cal Fire, 2019). Note that this does not include the cost of lives lost, property damage, or clean up during these years, which is estimated to be billions of dollars. The vast majority of wildfires in southern California are caused by humans (Balch et al., 2017; Keeley & Syphard, 2018), and inducing sprawl development in high fire hazard areas will increase the frequency and likelihood of such fires (Radeloff et al., 2018; Syphard et al., 2012, 2013, 2019). The City of LA should not be approving an Update that will induce unsustainable sprawl in high fire-prone areas and burden future generations of California with the costs of defending and recovering even more cities from dangerous blazes.

According to Captain Michael Feyh of the Sacramento Fire Department, California no longer has a fire season (Simon, 2018); wildfires in California are now year-round because of increased human ignitions in fire-prone areas. Emergency calls to fire departments have tripled since the 1980s (Gutierrez & Cassidy, 2018), and firefighters (and equipment) are being spread thin throughout the state. Firefighters often work 24- to 36-hour shifts for extended periods of time (often weeks at a time), and they are being kept away from their homes and families for more and more days out of the year (Ashton et al., 2018; Bransford et al., 2018; Del Real & Kang, 2018; Gutierrez, 2018; Simon, 2018). In addition, the firefighting force often must rely on volunteers to battle fires year-round.

5 cont.

The extended fire season is taking a toll on the physical, mental, and emotional health of firefighters, as well as the emotional health of their families (Ashton et al., 2018; Del Real & Kang, 2018; Simon, 2018). The physical and mental fatigue of endlessly fighting fires and experiencing trauma can lead to exhaustion, which can cause mistakes in life-or-death situations while on duty, and the constant worry and aftermath that family members endure when their loved ones are away working in life-threatening conditions can be harrowing (Ashton et al., 2018). According to psychologist Dr. Nancy Bohl-Penrod, the strain of fighting fires without having sufficient breaks can impact firefighters' interactions with their families, their emotions, and their personalities (Bransford et al., 2018). There have also been reports that suicide rates and substance abuse have been increasing among firefighters (Greene, 2018; Simon, 2018). This is not sustainable.

Given the well-known impacts of siting new development in fire-prone areas, the Update's Policy 3.3.2 ("Establish plans, incentives, and development standards that eliminate or minimize disaster risk and promote positive health outcomes for communities most at risk") should include a policy prohibiting new discretionary residential development in very high and high fire hazard severity zones or state responsibilities areas. At a minimum, to preserve public health and the environment and consistent with the principles in the CEQA Guidelines, Policy 3.3.2 should prohibit such development if there is substantial evidence in the record that the development will:

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a. expose people or structures, including existing and nearby communities, either directly or indirectly, to a significant risk of loss, injury or death involving wildland fires;
b. substantially impair an adopted emergency response plan or emergency evacuation plan;
c. due to slope, prevailing winds, and other factors, exacerbate wildfire risks, including risk of ignition and/or spread, and thereby expose project occupants to, pollutant concentrations from a wildfire or the uncontrolled spread of a wildfire;
d. require the installation or maintenance of associated infrastructure (such as roads, fuel breaks, emergency water sources, power lines or other utilities) that may exacerbate fire risk or that may result in temporary or ongoing impacts to the environment; or
e. expose people or structures to significant risks, including downslope or downstream flooding or landslides, as a result of runoff, post-fire slope instability, or drainage changes.

6 cont.

Moreover, Policy 3.3.2 should require that during the entitlement process for a new development of 5 units or more in a very high or high fire hazard severity zone or state responsibility area, the applicant must provide sufficient documentation that (1) private insurance currently exists that will insure the proposed homes for all hazards, including wildfire; or (2) the applicant must provide a plan and adequate funding to self-insure them.

Any new development in a very high or high fire hazard severity zone has the potential to cause a significant impact, as described in the numerous scientific studies referenced in the Wildfire Report. In addition, as the Wildfire Report notes, even homes built to current standards still are not fireproof, and more human activities and infrastructure have the potential to cause additional unintentional ignitions. Therefore, it is imperative that **this Update include restrictions for new development in these wildfire hazard severity zones, and at a minimum, ensure that these new properties will be able to obtain insurance on the private market before they are built because homeowners deserve this security in their investment**.

## II. Home-hardening existing communities should be a central component of the Update's Objective 3.3 "Promote disaster and climate resilience in citywide housing efforts"

For homes already in high fire-risk areas, home-hardening is important to minimize the chances of human ignitions and fire spread. It is estimated that more than 2 million homes are located in high fire-risk areas (Verisk, 2020). Investing resources primarily in fire suppression without adequately addressing the human-related cause of the fires will not reduce wildfire losses (Stephens et al., 2009). State funds must be equitably distributed to retrofit existing communities in fire-prone areas to reduce the chances of unintentional ignitions and minimize spread should a fire ignite.

7

**The Update's proposed policy 3.3.5**, which would identifying funding and other resources to support the retrofitting of existing buildings to improve resilience and health, **should provide a plan for specific retrofits including**:

1. Ember-resistant vents;
2. Fire-resistant roofs;
3. Irrigated defensible space within 100 feet of structures;
4. External sprinklers with an independent water source; and
5. Clean energy microgrids including rooftop solar

Although such features do not make homes fireproof, they have been shown to either reduce a community risk of ignition and/or improve the chances of structure survival in fires (Syphard et al., 2014, 2017). For example, external sprinklers with an independent water source have been proven to reduce flammability of structures (California Chaparral Institute, 2018). Although external sprinklers are not required by law, water-protected structures are much less likely to burn compared to dry structures, thus the Update should find funding streams for all development currently in wildfire zones and require implementation for all new development. In addition, local solar power paired with batteries could reduce power flow (and therefore reduce extreme temperatures) in electricity lines, which would reduce the need for power outages during extreme weather conditions and provide power for communities when outages are necessary (A. Lee, 2019). Michael Wara argues that solar power and batteries for homes and "microgrids" linking business districts would help make communities in high fire risk areas safer because it would provide backup power for medical devices, refrigerators, and the internet to run while allowing the main power grid to get shut down (Wara, 2018). 7 cont.

The city must also engage, prepare and train homeowners to harden their homes, reduce the risk of fire ignitions and spread, and be ready to safely defend their homes or evacuate early when needed (Stephens et al., 2009). As communities rebuild from recent wildfire destruction, now is the time to instill a culture of coexistence with wildfire. The City of LA can help our region meet this crucial challenge. Strong land use policies that consider the city's diverse fire history and ecology will help improve our relationship with wildfire and ensure a safer and healthier future for both humans and wildlife.

## III. Protecting wildlife connectivity in the region is essential to preserving native biodiversity, mitigating against the climate crisis and prioritizing human health.

Roads and development create barriers that lead to habitat loss and fragmentation, which harms native wildlife, plants, and people. As barriers to wildlife movement, poorly-planned development and roads can affect an animal's behavior, movement patterns, reproductive success, and physiological state, which can lead to significant impacts on individual wildlife, populations, communities, landscapes, and ecosystem function (Brehme et al., 2013; Ceia-Hasse et al., 2018; Haddad et al., 2015; Marsh & Jaeger, 2015; Mitsch & Wilson, 1996; Trombulak & Frissell, 2000; van der Ree et al., 2011). For example, as noted above, habitat fragmentation from roads and development has been shown to cause mortalities and harmful genetic isolation in mountain lions in southern California (Ernest et al., 2014; Riley et al., 2014; Vickers et al., 2015), increase local extinction risk in amphibians and reptiles (Brehme et al., 2018; Cushman, 2006), cause high levels of avoidance behavior and mortality in birds and insects (Benítez-López 8

et al., 2010; Kantola et al., 2019; Loss et al., 2014), and alter pollinator behavior and degrade habitats (Aguilar et al., 2008; Goverde et al., 2002; Trombulak & Frissell, 2000). Habitat fragmentation also severely impacts plant communities. An 18-year study found that reconnected landscapes had nearly 14% more plant species compared to fragmented habitats, and that number is likely to continue to rise as time passes (Damschen et al., 2019). The authors conclude that efforts to preserve and enhance connectivity will pay off over the long-term (Damschen et al., 2019). In addition, connectivity between high quality habitat areas in heterogeneous landscapes is important to allow for range shifts and species migrations as climate changes (Cushman et al., 2013; Heller & Zavaleta, 2009; Krosby et al., 2018). Loss of wildlife connectivity decreases biodiversity and degrades ecosystems. Unfortunately, it does not appear that the DEIR includes any such analysis.

Edge effects of development in and adjacent to open space will likely impact key, wide-ranging predators, such as mountain lions and bobcats (Crooks, 2002; Delaney et al., 2010; J. S. Lee et al., 2012; Riley et al., 2006; Smith et al., 2015, 2017; Vickers et al., 2015; Wang et al., 2017), as well as smaller species with poor dispersal abilities, such as song birds, small mammals, and herpetofauna (Benítez-López et al., 2010; Cushman, 2006; Kociolek et al., 2011; Slabbekoorn & Ripmeester, 2008). Limiting movement and dispersal can affect species' ability to find food, shelter, mates, and refugia after disturbances like fires or floods. Individuals can die off, populations can become isolated, sensitive species can become locally extinct, and important ecological processes like plant pollination and nutrient cycling can be lost. Negative edge effects from human activity, such as traffic, lighting, noise, domestic pets, pollutants, invasive weeds, and increased fire frequency, have been found to be biologically significant up to 300 meters (~1000 feet) away from anthropogenic features in terrestrial systems (Environmental Law Institute, 2003)

8 cont.

The EIR must also consider corridor redundancy (*i.e*. the availability of alternative pathways for movement) because it allows for improved functional connectivity and resilience. Compared to a single pathway, multiple connections between habitat patches increase the probability of movement across landscapes by a wider variety of species, and they provide more habitat for low-mobility species while still allowing for their dispersal (Mcrae et al., 2012; Olson & Burnett, 2008; Pinto & Keitt, 2008). In addition, corridor redundancy provides resilience to uncertainty, impacts of climate change, and extreme events, like flooding or wildfires, by providing alternate escape routes or refugia for animals seeking safety (Cushman et al., 2013; Mcrae et al., 2008; Mcrae et al., 2012; Olson & Burnett, 2008; Pinto & Keitt, 2008).

Corridor redundancy is critical when considering the impacts of climate change on wildlife movement and habitat connectivity. Climate change is increasing stress on species and ecosystems, causing changes in distribution, phenology, physiology, vital rates, genetics, ecosystem structure and processes, and increasing species extinction risk (Warren et al., 2010). A 2016 analysis found that climate-related local extinctions are already widespread and have occurred in hundreds of species, including almost half of the 976 species surveyed (Wiens, 2016). A separate study estimated that nearly half of terrestrial non-flying threatened mammals and nearly one-quarter of threatened birds may have already been negatively impacted by climate change in at least part of their distribution (Pacifici et al., 2017). A 2016 meta-analysis reported that climate change is already impacting 82 percent of key ecological processes that

form the foundation of healthy ecosystems and on which humans depend for basic needs (Scheffers et al., 2016). Genes are changing, species' physiology and physical features such as body size are changing, species are moving to try to keep pace with suitable climate space, species are shifting their timing of breeding and migration, and entire ecosystems are under stress (Cahill et al., 2012; Chen et al., 2011; Maclean & Wilson, 2011; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Warren et al., 2010).

In addition, riparian ecosystems have long been recognized as biodiversity hotspots performing important ecological functions in a transition zone between freshwater systems and upland habitats. Many species that rely on these aquatic habitats also rely on the adjacent upland habitats (*e.g.*, riparian areas along streams, and grassland habitat adjacent to wetlands). In fact, 60% of amphibian species, 16% of reptiles, 34% of birds and 12% of mammals in the Pacific Coast ecoregion depend on riparian-stream systems for survival (Kelsey and West 1998). Many other species, including mountain lions and bobcats, often use riparian areas and natural ridgelines as migration corridors or foraging habitat (Dickson et al, 2005; Hilty & Merenlender, 2004; Jennings & Lewison, 2013; Jennings & Zeller, 2017). Additionally, fish rely on healthy upland areas to influence suitable spawning habitat (Lohse et al. 2008), and agricultural encroachment on these habitats and over-aggressive removal of riparian areas have been identified as a major driver of declines in freshwater and anadromous fish (e.g., Stillwater Sciences 2002; Lohse et al. 2008; Moyle et al. 2011). Therefore, buffers that allow for connectivity between the aquatic resource and upland habitat is vital for many species to persist.

It is estimated that 90-95% of historic riparian habitat in the state has been lost (Bowler, 1989; Riparian Habitat Joint Venture, 2009). Using 2002 land cover data from CalFire, the Riparian Habitat Joint Venture estimated that riparian vegetation makes up less than 0.5% of California's total land area at about 360,000 acres (Riparian Habitat Joint Venture, 2004). This is alarming because riparian habitats perform a number of biological and physical functions that benefit wildlife, plants, and humans, and loss of what little is left will have severe, harmful impacts on special-status species, overall biodiversity, and ecosystem function. California cannot afford to lose more riparian corridors.

8 cont.

A literature review found that recommended buffers for wildlife often far exceeded 100 meters (~325 feet), well beyond the largest buffers implemented in practice (Robins, 2002). For example, Kilgo et al. (1998) recommend more than 1,600 feet of riparian buffer to sustain bird diversity. In addition, amphibians, which are considered environmental health indicators, have been found to migrate over 1,000 feet between aquatic and terrestrial habitats through multiple life stages (Cushman, 2006; Fellers & Kleeman, 2007; Semlitsch & Bodie, 2003; Trenham & Shaffer, 2005). Accommodating the more long-range dispersers is vital for continued survival of species populations and/or recolonization following a local extinction (Cushman, 2006; Semlitsch & Bodie, 2003). In addition, more extensive buffers provide resiliency in the face of climate change-driven alterations to these habitats, which will cause shifts in species ranges and distributions (Cushman et al., 2013; Heller & Zavaleta, 2009; Warren et al., 2011). This emphasizes the need for sizeable riparian and upland buffers around streams and wetlands in and adjacent to any project included in the Update, as well as connectivity corridors between heterogeneous habitats. The EIR must adequately assess and mitigate impacts to local, regional, and global wildlife movement and habitat connectivity.

In short, the DEIR's biological resources section fails to offer any real protections for wildlife connectivity. **The Center urges the City to revise the Update and DEIR to include a goal to develop and adopt the Wildlife Ordinance by the end of 2021. A draft of the ordinance has already been prepared by Planning, and a strong final ordinance must be adopted as soon as possible.**

8 cont.

In addition to the scientific evidence provided above, the City has a legal obligation under state law to protect endangered or threatened animal populations, and not approve projects or plans that may jeopardize the survival of such populations. The mountain lions of the Santa Monica mountains and San Gabriel mountains are provisionally listed under the California Endangered Species Act and are presently at risk of extinction, primarily due to loss of habitat connectivity and open space caused by poorly sited development and lack of wildlife crossings (Gustafson et al. 2018; Benson et al. 2016; Benson et al. 2019). The City has an obligation not to push this population closer to extinction by allowing further degradation of existing wildlife corridors through poorly planned development. Because the Update provides a plan to accommodate new development in mountain lion habitat and connectivity areas, it must analyze and fully mitigate the impacts of such development.

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## IV. Re-zoning should be transit-oriented and invest in "Complete Streets" as outlined by the Livable Communities Initiative

The Livable Communities Initiative (LCI) is a combination of existing LA City programs that equitably address housing, mobility, and climate simultaneously. It grew out of a collaboration between housing activists and mobility, bike, and transit activists that found by addressing the two issues of housing and mobility together, the result had a broader appeal, including with groups who have historically fought housing.

The core of the LCI is to address our affordable housing crisis by up-zoning under-utilized commercial arterials to 3-5 stories while simultaneously transforming the street—slowing the cars, adding wide sidewalks, al fresco dining, bike lanes, and fast and frequent transit—making it a Complete Street. By combining affordable housing with mobility, safe bike lanes, and a low car/slow car street, we can create a linear version of the 15 Minute Cities.[3] LA has hundreds of miles of downzoned commercial arterials including Pico, Venice andWestwood Blvd. The LCI will give Angelenos a safe and dignified way to live in LA without a car. A car-free livable street is not for everyone, but as one survey showed, 50% of Americans want to live in a walkable neighborhood and 63% of Millennials would prefer to live where they don't need a car. We believe there is a huge untapped demand for beautiful low-car streets with affordable housing, bike lanes, fast transit and lots of amenities. This is especially true in job-rich, transit-rich, amenity-rich neighborhoods which have historically prevented the construction of affordable housing, leading to gentrification and displacement in low-income communities and communities of color. As the city of LA embarks on re-zoning for 220,000 new units of

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[3] Congress for the New Urbanism (CNU). "Defining the 15-minute city." Accessed September 7, 2021. https://www.cnu.org/publicsquare/2021/02/08/defining-15-minute-city

housing, the LCI would give every Angeleno the option to live affordably and sustainably with safe and convenient transportation options. 10 cont.

## V. CEQA streamlining harms communities and perpetuates historical discriminatory planning practices

The Update's Program #55 aims to "create necessary policies and procedures to facilitate streamlining efforts" and "develop templates for such streamlining tools as SCEAs and SCPEs to make more projects that achieve Citywide Housing Priorities be exempt from or receive CEQA streamlining." As outline in the California Environmental Justice Alliance's "Environmental & Housing Justice Policy Platform,"[4] historic and present-day discriminatory planning decisions perpetuate inappropriate land use patterns and have led to higher concentrations of toxic and polluting land uses in and near low-income communities and communities of color. Poor planning decisions are further exacerbated by the fact that municipal codes, permit conditions, and other land use standards are not routinely or equitably enforced for these communities. In addition, state agencies and local entities responsible for cleaning up and remediating toxic sites have a well-documented history of failing to fulfill their duty to protect communities from hazardous waste. CEQA is one of the few tools that disadvantaged communities have to be aware of and fight back against housing being located next to polluting developments, such as light and heavy industrial facilities, oil and gas operations, recycling and manufacturing facilities, and warehouses with heavy truck traffic. The law's robust environmental review process can require site specific analysis and additional soil sampling to verify site safety. It is also critical that housing is built on sites that are healthy and suitable for housing development. Exempting projects from CEQA without adequate safeguards could allow homes to be built on toxic and polluted land without appropriate public participation, impact analysis and disclosure, and mitigation. **We therefore strongly oppose the Update's Program #55, Implement CEQA Streamlining Measures, and recommend that it be removed from the Update.** 11

[4] California Environmental Justice Alliance. "Environmental & Housing Justice Policy Platform." Accessed September 7, 2021. https://calgreenzones.org/platform-for-environmental-housing-justice/

## VI. Conclusion

The Center urges the Update to include policies that restrict new development in wildfire hazard severity zones as well as adopt the Wildlife Ordinance by the end of 2021. In addition, the EIR must include an assessment of the significant impact of wildfire to human health and wildlife and include science-based mitigation efforts to minimize this threat. Prohibiting new development in wildfire zones would prioritize human health and safety as well as the protection of the City's biodiversity. 12

Thank you for your consideration of these comments.

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Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# Housing Element DEIR Comment Letter

2 messages

**Kimberly Christensen** <kimwncseat4@gmail.com> Tue, Sep 7, 2021 at 5:01 PM
To: HousingElement@lacity.org
Cc: Terri Tippit <westsidenc@ca.rr.com>

Please find attached the Westside Neighborhood Council's letter on the Housing Element Update.

Please confirm receipt.

Kimberly Christensen, AICP
Westside Neighborhood Council

**WNC letter Housing Element 2021 Udpate and Safet Element Update DEIR commens.09.7.2021.signed.doc.pdf**
397K

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 5:06 PM
To: Kimberly Christensen <kimwncseat4@gmail.com>
Cc: Terri Tippit <westsidenc@ca.rr.com>

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
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E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Letter O-10

WESTSIDE NEIGHBORHOOD COUNCIL
P.O. Box 64370 Los Angeles CA 90064
www.wncla.org (310) 474-2326

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September 7, 2021

City of Los Angeles Department of City Planning
Attn: Cally Hardy, City Planning Associate
221 North Spring Street, Room 750
Los Angeles, CA 90012
Via email: HousingElement@lacity.org

**RE: Los Angeles Citywide Housing Element 2021-2029 Update and Safety Element Update – Draft EIR**

**Case Nos. ENV-2020-6762-EIR;**
**CPC-2020-1365-GPA; and**
**CPC-2021-5499-GPA**

**State Clearinghouse No. 2021010130**

Dear Ms. Hardy:

The Westside Neighborhood Council (WNC) reviewed and considered the Draft Environmental Impact Report (DEIR) for the DEIR for the Citywide Housing Element 2021-2029 Update and Safety Element Update. The WNC's comments are provided below

We request that the following issue areas as discussed below be addressed further in the DEIR. Additionally, we have the following general concerns about the Housing Element Update process and preparation of the DEIR. 1

We believe that the entire Housing Element and draft EIR process has been grossly out of compliance with State laws (both CEQA and Planning laws relating to General Plans). The process has not been transparent with the public and City stakeholders. We have repeatedly asked for information from the City regarding population projections, housing demand, and the candidate sites information through the course of the Housing Element Update process. The WNC adopted a motion at its August 12, 2021 meeting asking for the missing sections of the Housing Element (including the Candidate Sites maps) and for the City to ask the

State to extend the deadline for the Housing Element Update process to allow adequate time to complete the draft Housing Element and Safety Element Updates, Draft EIR, and to allow appropriate pubic participation in the process. CEQA is integral to agency decision making as discussed in Public Resources Code Section 21006. When the Housing Element Updates is not released in its entirety and with one of the most significant pieces of information relevant to the CEQA process and adequate review of all required issue areas. We believe that recirculation of the DEIR will be required because additional analysis will be required.

The draft Housing Element was released on July 1, 2021. However, Appendix 4.1 (Housing Sites Adequacy analysis) and Appendix Section 4.7 (Candidate Sites Map) were missing when it was released. Appendix 4.1 it was incomplete when it was released. The EIR was released on July 22, 2021 with the public comment period closing on September 7, 2021. How can the Draft EIR possibly be complete, thorough and accurate in its analysis when the Candidate Sites Map information has not been released yet? It was not available before the Draft EIR was completed and released to the public. Appendix 4.1 regarding the adequacy of housing sites analysis was not prepared and released publicly before the Draft EIR was completed and released to the public for comment. The required 45-day public comment period is closing before the Appendix 4.7 Candidates Sites information is even released. The comment period for the DEIR should be extended and the DEIR should be recirculated because it analyzed a document (the Housing Element) that was not even complete.

1 cont.

Additionally, it came to our attention on September 4, 2021 that Appendix 4.1 had finally been added and the posted Housing Element had been modified. We received notice from the City that the public comment period for the Housing Element was being extended from September 9 2021 to September 22, 2021 in fact because there had been changes to the Housing Element.

No summary of the changes to the Housing Element have been provided to the public. The notice indicated that two public hearings would be held on September 21, 2021 (the day before written public comments are due) and on September 22, 2021 (just hours before written public comments are due). Additionally, the notice indicated that the first part of each hearing would be to explain the changes to the Housing Element to the public. If the public is not provided the information and not told what the changes are until the meeting, how is that due process and how is the public supposed to have the time to evaluate the new information and provide comment within a matter of hours?

2

This violates the entire purpose of the requirements to provide adequate opportunity for the public to participate in the General Plan Update process. While California Government Code Section 65355 requires that a legislative body hold at least one public hearing prior to adopting an amendment to a General Plan, the purpose of the public hearing is to allow the pubic to participate and provide informed input to the

deliberations on the proposed amendment to the General Plan. The City has failed that test when the entire document is still not even available for review. 2 cont.

**General Comments**

Page 4-2 refers to a 1-10 units as a single-family residential project. One unit is a single-family residential use. Two to ten units are a multi-family residential project. This discussion should be revised and clarified as the wording is confusing. 3

What was the criteria used in selecting the 54 sample projects.to be used in the EIR analysis? How did you determine that these projects would be a representative sample? They seem to be primarily located in Downtown Los Angeles. 4

**Aesthetics**

The Aesthetics Section does not discuss or analyze impacts based upon goals, policies and objectives of all he Community Plans and requirements of the Neighborhood Oriented Districts such as those on Pico and Westwood. These should be included in the EIR analysis. The EIR should be evaluating impacts based upon all Community Plans and not just the Downtown Plan. 5

**Air Quality Impacts**

The threshold of significance of 462 of single-family residential units 612 multi-family residential units, or some combination before mitigation is required per Air Quality mitigation measure 4.2-2(b) is incredibly high before mitigation is required to implement TDM measures in housing development projects. The City should require TDM measures such as bike sharing and electrical vehicle charging station infrastructure among other at a much lower threshold to reduce Air Quality impacts and GHG impacts. Waiting to exceed air quality attainment levels in the SCAQMD basin when there are already existing air quality issues is bad public policy regardless of the CEQA impact threshold levels. 6

**Cultural Resources**

The City of Los Angeles has very limited protections of historic resources even in HPOZ's. Housing development "by right" should not destroy, remove or compromise the historic integrity of a historic resource. Additional mitigation measures can and should be added that require protections of designated historic resources. 7

**Land Use**

4.1-12 does not address NOD's and that they have provisions for ground floor level retail. 8

The EIR does not address heightened impacts if housing is concentrated 9

only in certain parts of the City (High and Very High Resource Areas (HRA's and VHRA's)) and are not distributed throughout the City. 9 cont.

How will Objective 4.3 be met to conserve the scale and character of residential neighborhoods and make the compatible to the surrounding area in High and VHRA's? (see discussion on page 4.9-20). 10

How can adequate mitigation measures be developed for impacted areas without analyzing the candidate site maps? 11

**Recreation**

The DEIR concludes that the impacts to recreation are significant and unavoidable. It is true that the City is woefully deficient in meeting all the minimum thresholds for acreage per thousand residents whether it be community parks, regional parks, local parks or pocket parks. Deficiencies are further exacerbated by heavy concentration of the City's recreation resources primarily in the less densely populated areas of the City such as the Santa Monica Mountains and northern part of the City (e.g. the San Fernando Valley) and the greatest deficiencies in the western, central and eastern part of the City where much of he High and Very High Resource Areas are proposed. The significant and unavoidable impacts should not be made worse by not including meaningful mitigation in the DEIR that can be incorporated as requirements for housing development. First, further development of housing should not eliminate existing parks. Second, incorporation of recreational amenities should be encouraged on-site for smaller housing projects and required for larger housing projects to lessen the impacts to existing parks and recreation facilities. This should be separate from development impact/Quimby fees. LAMC Section 21.10.3 requirement of a construction parks fee per dwelling unit of $200 per residential unit is woefully inadequate to provide any meaningful amount of recreation/open space per resident. 12

**Transportation**

Threshold Impact 4.14-4 (see page 4.14-74) only addresses impacts to emergency access during construction. No analysis has been provided regarding permanent operational impacts for emergency access. Mitigation Measure MM4.14-1 does not address operational impacts to inadequate emergency access. An assessment needs to be conducted regarding operational impacts to emergency access. We believe that if housing is concentrated solely in High or Very High Resource Areas that there may be significant impacts to emergency access during operational conditions. Many areas of Los Angeles including the Westside of Los Angeles have streets that have limited accessibility because of at-grade transit (light rail) line crossings with streets and restricted intersection turning movements for vehicles that impact access by police and fire services. Examples in West Los Angeles include at-grade crossings of the Exposition line with streets at Barrington, Military, Westwood and Overland Avenues. An example of restricted vehicle turning movements occur at Exposition and Westwood Boulevards. There are many other 13

locations on other light rail lines as well throughout the City of Los Angeles. This needs to be studied in the Draft EIR. 13 cont.

**Utilities and Service Systems**

We have concerns that demands on water could exceed the supply considering the unusually high and repeated levels of drought that California and other Western states have been experiencing. The historically low levels of Lake Mead and the Colorado River and other water sources are real. The projected demands and supply per the city's Urban Water Management Plan do not seem to account for these unprecedented reductions to water supply based upon climate change. We believe that more conservative analysis is required. The DEIR states that the impact is less than significant. However, we believe that the water supply will be impacted at a greater level than analyzed with continued extreme drought conditions. Furthermore, the water quality is more impacted the lower the reservoirs become. This issue should have further analysis. 14

**Other CEQA Considerations**

On Page 5-2, the DEIR asserts that new technologies or systems will emerge that will further reduce the City's reliance on nonrenewable resources and then concludes that the Housing Element Update would not involve a wasteful or inefficient manner in use of natural resources even though consumption of natural resources in the City would increase due to development associated population increases. This is a false assumption as future possible advances in technology are not known at this time and cannot be assumed for this analysis. Even if some improvements in technology will be made in the future, the City of Los Angeles is still adding 375,431 new residents, 109,966 new households, 128,921 new jobs (per Table 4-3 of this DEIR) and 456,643 new residential units per the requirements of RHNA for the planning period ending in 2029 as specified on Page 4-16 of the DEIR. This analysis should be revised. 15

**Closing Comments**

We appreciate consideration and response to the comments raised in this letter relating to the sufficiency of the Draft EIR. We have additional comments that we were not able to complete prior to the September 7th deadline. We will submit an additional letter with those comments as the comment period for the DEIR should be extended considering the incompleteness of the draft Housing Element that was released. 16

Please keep us informed of future meetings and hearings associated with this matter during all phases of future consideration.

Please do not hesitate to contact us with any questions.

Sincerely,

*Terri Tippit*

_____
Terri Tippit, Chair
Westside Neighborhood Council

*Kimberly Christensen, AICP*

_____
Kimberly Christensen, Land Use Committee Co-Chair
Westside Neighborhood Council

Cc: Councilman Paul Koretz, CD5 (paul.koretz@lacity.org)
Daniel Skonick, Planning Deputy, CD5 (daniel.skolnick@lacity.org)
Angel Izard, District Deputy, CD5 (angel.izard@lacity.org)

# Individual Comments

Connect Create Collaborate

Housing Element <housingelement@lacity.org>

# Fw: [ANGELES-ENVIRO-JUSTICE] Fwd: Notice of Availability of Draft EIR for Updates to Housing Element and Safety Element / Aviso de Disponibilidad del borrador del Informe de Impacto Ambiental para las actualizaciones del Elemento de Vivienda y del Elemento de Seguridad

2 messages

[redacted] Thu, Jul 22, 2021 at 7:02 PM

Although reference is made to DEIR, the plan update linked to this page is not an EIR, draft or otherwise. Please provide the DEIR separate from the Updated Plan element - specifically Safety Element. 1

So initial comments is that the Safety Element DEIR is totally inadequate and incomplete. 2

Dr. Tom Williams

----- Forwarded Message -----
**From:** [redacted]
**To:** "angeles-enviro-justice@lists.sierraclub.org" <angeles-enviro-justice@lists.sierraclub.org>
**Sent:** Thursday, July 22, 2021, 05:27:36 PM PDT
**Subject:** [ANGELES-ENVIRO-JUSTICE] Fwd: Notice of Availability of Draft EIR for Updates to Housing Element and Safety Element / Aviso de Disponibilidad del borrador del Informe de Impacto Ambiental para las actualizaciones del Elemento de Vivienda y del Elemento de Seguridad

Hello everyone,

Here is the info on the Draft EIR Updates to the Housing Element and Safety Element for the City of Los Angeles.

The deadline to submit comments is 5:00 pm, Thursday, September 7.

Yvonne

Sent from my iPhone

Begin forwarded message:

> **From:** Los Angeles City Planning <housingelement@lacity.org>
> **Date:** July 22, 2021 at 8:50:32 AM PDT
> **To:** [redacted]
> **Subject: Notice of Availability of Draft EIR for Updates to Housing Element and Safety Element / Aviso de Disponibilidad del borrador del Informe de Impacto Ambiental para las actualizaciones del Elemento de Vivienda y del Elemento de Seguridad**
> **Reply-To:** housingelement@lacity.org

*Para español siga hacia abajo.*

## Interested Parties,

This email is to inform you of the Notice of Availability (NOA) for the Draft Environmental Impact Report (EIR) prepared for the Updates to the Housing Element and the Safety Element. These documents are being prepared by Los Angeles City Planning as part of the Plan to House LA and Safety Element Update.

The NOA and Draft EIR materials are now available on Los Angeles City Planning's website.

Beginning today, City Planning is accepting comments on the Draft EIR. **The Draft EIR comment period will close at 5:00 p.m. on Tuesday, September 7, 2021**.

If you wish to submit comments on the Draft EIR, please submit your written comments (including a name, contact information, and the following file number ENV-2020-6762-EIR) during the comment period, via mail or e-mail to the following addresses:

**Cally Hardy |** City Planning Associate
City of Los Angeles Department of City Planning
200 North Spring Street, Room 750
Los Angeles, CA 90012

**E-mail**
HousingElement@lacity.org

Beyond the DEIR comment period, general public comments on the plan drafts are also welcome until the Plan is adopted by City Council.

## Partes Interesadas,

Este correo electrónico es para informarle del Aviso de Disponibilidad (NOA por sus siglas en inglés) para el Borrador del Informe de Impacto Ambiental (EIR por sus siglas en inglés) preparado para las Actualizaciones del Elemento de Vivienda y del Elemento de Seguridad. Estos documentos están siendo preparados por el Departamento de

Planeación de la Ciudad de Los Ángeles como parte del Plan de Vivienda y Elemento de Seguridad.

Los materiales del NOA y el Borrador del EIR ya están disponibles en el sitio web del Departamento de Planeación de la Ciudad de Los Ángeles (en inglés). El Aviso de Disponibilidad (el NOA) está disponible en español.

Empezando hoy, el Departamento de Planeación está aceptando comentarios sobre el Borrador del EIR. **El período de comentarios del Borrador del EIR se cerrará a las 5:00 p.m. del martes 7 de septiembre de 2021**.

Si desea enviar comentarios sobre el Borrador del EIR, por favor envíe sus comentarios por escrito (incluyendo su nombre, información de contacto, y el siguiente número de archivo ENV-2020-6762-EIR) durante el período de comentarios, por correo o vía correo electrónico a las siguientes direcciones:

**Cally Hardy |** City Planning Associate
City of Los Angeles Department of City Planning
200 North Spring Street, Room 750
Los Angeles, CA 90012

**Correo Electrónico**
HousingElement@lacity.org

Comentarios públicos generales sobre los borradores de los planes también son bienvenidos hasta que sean adoptados por el Concejo de la Ciudad.

**LOS ANGELES CITY PLANNING**

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Planning4LA.com

Los Angeles City Planning | 200 N. Spring St, Room 525, Los Angeles, CA 90012

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Sent by housingelement@lacity.org powered by

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* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *

To unsubscribe from the ANGELES-ENVIRO-JUSTICE list, send any message to ANGELES-ENVIRO-JUSTICE-signoff-request@lists.sierraclub.org, or visit Listserv online. Listserv users can sign in online to manage subscriptions, personalize delivery options, and view message archives. To create an account or reset your password, click here. Listserv policies may apply.

**Housing Element** <housingelement@lacity.org> Fri, Jul 23, 2021 at 9:05 AM
To: [redacted]

Dr. Williams,

Yesterday's email includes a link to the webpage containing the DEIR materials. For your convenience, here is the link directly: https://planning.lacity.org/development-services/eir/Housing-Element_2021-2029_Update_Safety-Element_Update_deir

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Connect Create Collaborate

**Housing Element <housingelement@lacity.org>**

# Housing Element 2021-2029 Update, DEIR Comments, ENV-2020-6762-EIR

2 messages

[redacted] > Tue, Sep 7, 2021 at 9:41 AM
To: housingelement@lacity.org
[redacted]

Dear Ms. Hardy,

I'd like to submit the attached comments on the Housing Element Update DEIR.

Could you please send a brief response to confirm you received this?

Thanks,

Casey Maddren

**Housing Element EIR Comments Maddren FINAL COMPLETE.pdf**
1084K

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:56 PM
[redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

September 6, 2021

Cally Hardy, City Planning Associate
Department of City Planning
200 N. Spring Street, Room 750
Los Angeles, CA 90012

Re: Housing Element 2021-2029 Update, EIR Comments
Case Nos.: ENV-2020-6762-EIR; CPC-2020-1365-GPA; CPC-2021-5499-GPA

Dear Ms. Hardy,

I would like to submit the following comments on the EIR for the 2021-2029 Housing Element Update. I believe there are serious deficiencies in the EIR that must be addressed before it's adopted. Please see my detailed comments below.

Thanks for your help.

Sincerely,
[redacted]

## COMMENTS ON THE 2021-2029 HOUSING ELEMENT UPDATE E.I.R.

### UTILITIES AND SERVICE SYSTEMS

#### Wastewater & Stormwater

The EIR provides an overview of the city's wastewater treatment facilities, and concludes that the creation of over 400,000 new housing units would have no significant impact. However, in light of the recent crisis at the Hyperion Water Treatment Plant, it seems important to question the authors' claims.

On page 4.16-2, under Environmental Setting, Wastewater, we find the following description of the Hyperion Sanitary Sewer System:

*"The Hyperion Sanitary Sewer System is the largest of the City's three sanitary sewer systems. An average wastewater flow rate of approximately 300 million gallons per day (mgd) is treated by the system, which includes the Donald C. Tillman Water Reclamation Plant and the Los Angeles-Glendale Water Reclamation Plant and has a peak wet weather capacity of 800 mgd. The Donald C. Tillman Water Reclamation Plant services the area between Chatsworth and Van Nuys in the San Fernando Valley. The Los Angeles-Glendale Water Reclamation Plant is located in the San Fernando Valley and services the communities in east San Fernando Valley that are both within and outside of the City limits. Approximately 60 mgd is treated at Donald C. Tillman and Los-Angeles Glendale Water Reclamation Plants. All other flows in the system, and the biosolids from the Donald C. Tillman and Los-Angeles Glendale Water Reclamation Plants* 1

*which are returned to the collection system, are treated at the Hyperion Water Reclamation Plant (HWRP) located in Playa Del Rey (LADPW 2017a)."*

Without question Hyperion is the largest of the city's wastewater treatment systems, serving Central LA, South LA and the San Fernando Valley. For this reason it is deeply troubling that the Hyperion Treatment Plant in Playa Del Rey was recently overwhelmed with a massive flow of debris which left it severely damaged.

*L.A. water recycling imperiled after beach sewage spill, hurting drought conservation, LA Times, August 11, 2021*
*https://www.latimes.com/california/story/2021-08-11/water-recycling-impaired-by-hyperion-sewage-disaster*

*"Problems at a Los Angeles sewage treatment plant that caused a massive spill into Santa Monica Bay last month have severely reduced the region's water recycling ability, forcing officials to divert millions of gallons of clean drinking water at a time of worsening drought conditions, The Times has learned."*

It is disturbing enough that this calamity has drastically reduced the Hyperion Plant's recycling capability. It is even more disturbing that, in spite of the EIR's claims that there are 30 automatic "real time" flow monitors and 74 additional "near time" monitors located within the system, the Bureau of Sanitation apparently was unaware of the approach of this massive flow of debris. It gets worse. At the time of this writing, almost two months after the July 11, 2021 incident, the Bureau of Sanitation has been unable to explain what happened.

1 cont.

Given these facts, we must take another look at the thresholds of significance: Impacts would be significant if implementation of the Housing Element Update would:

- *Threshold 4.16-1: Require or result in the relocation or construction of new or expanded wastewater treatment facilities, the construction or relocation of which could cause significant environmental effects*
- *Threshold 4.16-2: Require or result in the relocation or construction of new or expanded stormwater drainage facilities, the construction or relocation of which could cause significant environmental effects*
- *Threshold 4.16-3: Result in a determination by the wastewater treatment provider which serves or may serve the project that it does not have adequate capacity to serve the project's projected demand in addition to the provider's existing commitments*

In asking whether the construction of over 400,000 new housing units would trigger these thresholds, we must keep in mind:

- *The Hyperion Plant is the terminus for the city's largest sewer system, serving Central LA, South LA and the San Fernando Valley.*
- *The Hyperion Plant has been severely damaged, and the City of LA has not given any timeline for restoring the Hyperion Plant to full capability.*
- *Almost two months after the event, the City of LA has been unable to provide an explanation as to how this massive flow of debris arrived at the Hyperion Plant.*

With these facts in mind, we must question the EIR's description of a highly sophisticated, carefully monitored system that is capable of handling all existing wastewater flows, plus the additional wastewater produced by over 400,000 new residential units.

In light of this recent, catastrophic event, which occurred after the preparation of the EIR, we must ask if the assertion that there would be no significant impacts with regard to wastewater is credible. The EIR should be revised to provide a more accurate picture of Hyperion's current and long-term treatment capabilities.

1 cont.

**Water Supply & Facilites**

With regard to water usage, the Initial Study asks:

*Would the project:*

*a) Require or result in the relocation or construction of new or expanded water, wastewater treatment or storm water drainage, electric power, natural gas, or telecommunications facilities, the construction or relocation of which could cause significant environmental effects?*

*b) Have sufficient water supplies available to serve the project and reasonably foreseeable future development during normal, dry and multiple dry years?*

*c) Result in a determination by the wastewater treatment provider which serves or may serve the project that it has adequate capacity to serve the project's projected demand in addition to the provider's existing commitments?*

While the EIR says that the Project could have potentially significant impacts in all three of these areas, the chapter Utilities & Service Systems ultimately finds that impacts in these areas would be less than significant. To reach this conclusion, the EIR references LA City's 2020 Urban Water Management Plan (UWMP).

2

Page 4.16-47 states that:

*To determine demand on water facilities and water supply for Thresholds 4.16-4 and 4.16-5, demand from build out of the RHNA is determined based on the physical connection of 420,327 housing units to the City's potable water supply system, and applicable utility rates per type of housing unit included in the LADWP 2020 UWMP. Long range water demand forecasts in the 2020 UWMP are based on SCAG growth projections for the 2020-2045 RTP/SCS, which projects increases in housing to address the housing shortage in Southern California and a related reduction in persons per household. Therefore, per the 2020 UWMP, per unit water demand is forecast to decline over time. This is consistent with RHNA assumptions, in which full build-out of the RHNA units would foreseeably reduce the average utility rate per housing unit. [Emphasis added.]*

The 2020 UWMP also says that its demographic projections are based on SCAG data. On page 1-6 it states:

*Demographic projections were provided for the LADWP service area by MWD, which received projected demographic data from Southern California Association of Governments (SCAG).*

What is bewildering is that the Housing Element states that RHNA Allocations are based on SCAG projections, and the 2020 UWMP states that its housing data is based on SCAG projections, but the results they come up with are wildly different.

In the chapter on Utilities & Service Systems, the EIR states that of the RHNA Allocation of 456,643 units, 420,327 units will be physically connected to the City's potable water supply system. But while the EIR references the City of LA's 2020 Urban Water Management Plan (UWMP), the City's RHNA Allocation is far beyond the housing projections given by the UWMP.

Under Demographics and Climate, on page ES-5 of the Executive Summary, the UWMP states:

*The total number of housing units increased from 1.10 million in 1980 to 1.44 million in 2020, representing an average annual growth rate of 0.8 percent.*

In Exhibit ES-C, Demographic Projections for LADWP Service Area, the UWMP makes the following projection for the year 2030:

| | *2030* |
|---|---|
| *Single-Family* | *639,280* |
| *Multi-Family* | *969,198* |
| ***Total*** | ***1,608,479 [sic]*** |

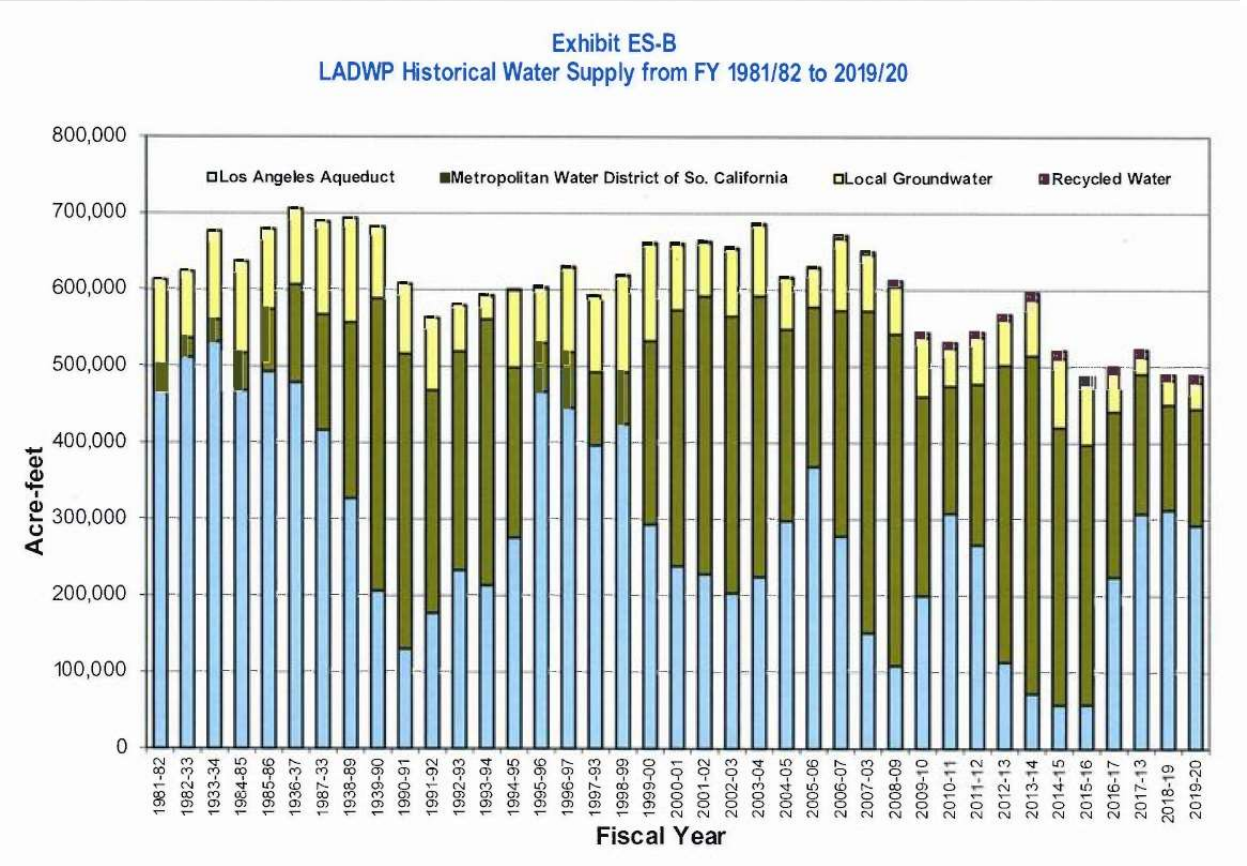
2 cont.

To find net growth projected by the UWMP, we subtract the estimate of 2020 housing units from the 2030 projection:

1,608,479
\- 1,440,000
**168,479** **Net growth in housing units per 2020 UWMP**

This shows that the growth projected for the year 2030 by the UWMP is far below the 420,327 units assessed by the Housing Element by 2029. **The UWMP's calculations regarding projected water usage by 2030 are based on a net gain of 168,479 new units. The Housing Element's 2029 projection is about 2.5 times that number.** Based on the UWMP's water supply projections, the Housing Element claims that there will be ample water to serve new customers even with the addition of new housing to comply with the RHNA Allocation. But the UWMP's projections are based on very optimistic assumptions regarding both future water deliveries, future conservation and future stormwater capture.

It's important to remember LA has limited groundwater resources, which are already compromised by contamination. The city imports most of its water from sources outside its boundaries, including the State Water Project, the LA Aqueduct and the Colorado River. On page ES-3 of the UWMP, Exhibit ES-B gives a breakdown of the resources we've drawn on since 1981.




The graph clearly shows that in recent years the city has relied heavily on deliveries from the LA Aqueduct, while percentages from groundwater and the MWD have been sharply reduced. However, based on current conditions and future projections, it's questionable whether the city can rely on similar deliveries from the LA Aqueduct.

For context, please see this excerpt from page 7 of the May 2021 report from the CA LAO's Office, What Can We Learn From How the State Responded to the Last Major Drought?

https://lao.ca.gov/reports/2021/4429/learn-from-last-drought-051321.pdf

2 cont.

***Update on Current Conditions***

***State Is Experiencing Another Multiyear Dry Period***

*California experienced below average precipitation in 2020—receiving only roughly 60 percent of the rain and snow that falls in a normal year. So far, 2021 is shaping up to be even drier. As of May 10, 2021, precipitation levels were tracking at 48 percent of average for the year in the Northern Sierra region, 49 percent in the mid-Sierra San Joaquin region, and 36 percent further south in the Tulare Basin region. At this point in the "water year" (which measures precipitation from October through September each year), 2020-21 represents the third driest year on record, with little chance of significant additional precipitation on the horizon until the fall. Current snowpack levels are roughly 9 percent of normal for this time of year for the Northern and Central Sierra regions, and only 4 percent of normal for the Southern Sierra. Moreover, all of*

3

*the major reservoirs across the state currently contain less water than historical average levels this date, with the two largest—Shasta and Oroville—at 56 percent and 50 percent of average levels, respectively. In many of the state's major rivers—including the Feather and American Rivers, and the inflow into Shasta Lake—current flow rates are currently tracking below the runoff levels for the same date in 2014 and 2015.*

Please also see this excerpt from the Union of Concerned Scientists Climate Hot Map.

Union of Concerned Scientists, Climate Hot Map
https://www.climatehotmap.org/global-warming-locations/hetch-hetchy-ca-usa.html

*Meeting California's growing demand for water from the Sierra Nevada mountains can be a challenge as global warming further reduces snowpack. That decline is likely to affect both the timing and availability of water for drinking, agriculture, and recreation.*

- *The Sierra snowpack provides natural water storage equal to about half the capacity of California's major human-made reservoirs. Earlier spring runoff typically means a longer dry season and reduced water resources in summer.*
- *By the 2020s, loss of snowpack in the Sierras and Colorado River basin is likely to threaten more than 40 percent of Southern California's water supply.*
- *If our heat-trapping emissions continue to rise unabated, California is projected to face critically dry years up to 50 percent more often, and decreases in water for crops and livestock of 40-50 percent.*

3 cont.

With Sierra Nevada snowpacks already in decline, and projected to decline further, it seems likely that the City will not be able to rely on deliveries from the LA Aqueduct to the same degree that it has in years past.

The UWMP's assessment of future water supplies is also undermined by unforeseen recent events that occurred after it was prepared. Water levels at Hoover Dam/Lake Mead have fallen faster than anyone expected, indicating that Southern California will be forced to accept a reduced allocation from the Colorado River. See this excerpt from the LA Times:

*'Unrecognizable.' Lake Mead, a lifeline for water in Los Angeles and the West, tips toward crisis, LA Times, July 11, 2021*
*https://www.latimes.com/world-nation/story/2021-07-11/lake-mead-hoover-dam-drought-nevada-arizona-california*

*"Next month, the federal government expects to declare its first-ever shortage on the lake, triggering cuts to water delivered to Arizona, Nevada and Mexico on Jan. 1. If the lake, currently at 1,068 feet, drops 28 more feet by next year, the spigot of water to California will start to tighten in 2023."*

Immediately following the declaration of a shortage by the Bureau of Reclamation, the MWD issued a water supply alert:

*Metropolitan Declares Water Supply Alert in Response To Severe Drought*
*https://www.mwdh2o.com/newsroom-press-releases/metropolitan-declares-water-supply-alert-in-response-to-severe-drought/*

And the recent calamity at the Hyperion Treatment Plant has sharply reduced its ability to provide recycled water.

*L.A. water recycling imperiled after beach sewage spill, hurting drought conservation, LA Times, August 11, 2021*
*https://www.latimes.com/california/story/2021-08-11/water-recycling-impaired-by-hyperion-sewage-disaster*

3 cont.

While the UWMP did assume reduced deliveries of water imports, it was prepared before recent developments at Lake Mead and the Hyperion Treatment Plant. The Housing Element EIR chapter Utilities & Service Systems relies heavily on the UWMP for its projections. Because the UWMP was prepared before these previously unforeseeable events and does not reflect their impact on water supply, the EIR's assumptions related to future water supplies cannot be considered reliable.

**Solid Waste**

It's not surprising that the EIR relegates the discussion of solid waste to the appendix containing the Initial Study. The City's record on solid waste is appalling. Worse, the City refuses to even acknowledge its failures in this area, and instead continues to make false claims based on old data to support its environmental assessments.

The Initial Study asks:

- *Would the project generate solid waste in excess of State or local standards, or in excess of the capacity of local infrastructure, or otherwise impair the attainment of solid waste reduction goals?*

- *Would the project comply with federal, state, and local management and reduction statutes and regulations related to solid waste?*

The EIR concludes that the construction of over 400,000 new units would have a less than significant impact. Unfortunately, the EIR's findings in this regard cannot be considered credible. On page 137 of the Initial Study, the authors state the following:

4

*The City has enacted numerous waste reduction and recycling programs in order to comply with the California Integrated Waste Management Act (AB 939), which require every city in California to divert at least 50 percent of its annual waste by the year 2000, and be consistent with AB 341, which sets a 75 percent recycling goal for California by 2020. As tracked by the City's Zero Waste Progress Report, the City achieved a landfill diversion rate of 76.4 percent as of 2012 (City of Los Angeles Sanitation 2013). The City of Los Angeles has also prepared a Solid Waste Integrated Resources Plan (SWIRP), which contains long-term goals, objectives and policies for solid waste management for the City. It specifies that the City's Zero Waste goal is to reduce, reuse, recycle, or convert the resources currently going to disposal so as to achieve an overall diversion rate of 90 percent or more by the year 2025 (LASAN 2013).*

One might first ask why the EIR cites data from 2012 to support its claims about diversion to recycling. The City is nowhere near the claimed 76.4% rate of diversion to recycling. It's likely that the reason the City uses data from nine years ago is that it actually has no idea how much solid waste is currently being diverted to recycling. In July of this year I submitted a PRA

request asking for data on the RecycLA program's rate of diversion to recycling for the years 2019 and 2020. *[See Exhibit A.]* I received the following response:

*City does not currently have the percentage of material diverted for 2019 or 2020.*

Since 2012, significant changes have occurred with regard to solid waste disposal. Up until 2018, the City had been shipping most of its recyclable materials to China, but China has largely closed its doors to imported waste. When exports to China ceased, this created a glut of recycling materials in California, driving down prices for recyclables and resulting in the closure of many recycling companies. Faced with this crisis, in 2019 the City amended the contracts it had entered into with waste haulers participating in the RecycLA program, reducing the targets for diversion to recycling. The details can be obtained by referring to the following contract amendment between the City and Athens Services.

*CONTRACT NO. C-128879-1*
*FIRST AMENDMENT TO PERSONAL SERVICES CONTRACT BETWEEN*
*THE CITY OF LOS ANGELES AND ARAKELIAN ENTERPRISES, INC. DBA ATHENS SERVICES*

On pages 14 and 15 the amendment states:

*For the first disposal reduction assessment period ending at 60 months following the START OF SERVICE only (January 31, 2023), the DISPOSAL TARGET percentage (as a percentage of annual disposal compared to adjusted baseline tonnage) for 2022 (as set forth in APPENDIX A) increased by ten percentage points or 65 percent, whichever is greater, shall be used to determine whether LIQUIDATED DAMAGES shall be assessed. Failure to meet the aforementioned Disposal Targets shall result in LIQUIDATED DAMAGES of $50,000 for the first 1,000 tons, and $5,000 for every 100 tons thereafter. For the second disposal reduction assessment period ending at 84 months following the START OF SERVICE (January 31, 2025), the DISPOSAL TARGET percentage (as a percentage of annual disposal compared to adjusted baseline tonnage) of 45 percent shall be used to determine whether LIQUIDATED DAMAGES shall be assessed.*

4 cont.

Similar language is included in all 2019 contract amendments signed with waste haulers participating in the RecycLA program.

In other words, the waste hauler agrees that it will not dispose of more than 65% of solid waste collected in landfills through 2023, and then agrees that it will not dispose more than 45% of solid waste collected in landfills through 2025. If the City were to achieve the goal of 45% solid waste disposal in landfills, it would be in compliance with AB 939. However, in light of the response to my PRA request, we must ask where this data will come from. Will the City be monitoring compliance? No, the waste haulers will be monitoring themselves. The following language appears on page 12 of the amendments:

*5.10.4 CONTRACTOR RESPONSIBLE FOR DISPOSAL*

*The CONTRACTOR shall track all materials that are collected, processed, and disposed throughout the term of the AGREEMENT including but not limited to enable measurement of diversion performance. The CONTRACTOR shall be responsible for monitoring the success of their Diversion Programs and the reduction of disposal tonnage throughout the term of the AGREEMENT.*

The City has no data on diversion to recycling because the City doesn't collect any data. They leave it to the private waste haulers, who face financial penalties for failing to meet targets, to monitor their own performance.

The EIR's claim that the City will achieve a rate of 90% diversion to recycling by 2025 is not credible. Furthermore, the City is currently NOT diverting 50% of solid waste to recycling and therefore, contrary to the EIR's assertion, not in compliance with the requirements of AB 939.

The vast majority of new multi-family units created pursuant to the RHNA Allocation will be served by RecycLA, which serves all commercial and large multi-family residential structures. Based on the above, it is clear that the EIR's claim that there will be no significant impact is not supported by substantial evidence. In fact, it's not supported by any evidence at all.

The City will claim that there is still no significant impact, since the City has adequate landfill capacity to handle the increase in solid waste. However, landfills are a significant source of GHG emissions. Please see the following section from the City's Solid Waste Integrated Resources Plan:

4 cont.

*1.2.2.2 Greenhouse Gas Emissions Reductions*

*The waste sector in the U.S. emitted approximately 100 million metric tons of carbon dioxide equivalent emissions in 2012, which represents the sixth-largest generator in the industry sector. [….] Landfills are the third-largest source of generated methane emissions in the U.S. and contributed approximately 17.5 percent of the total U.S. emissions of generated methane in 2011.*

Based on the evidence cited above, it is clear that the EIR fails to adequately assess the impacts of the Housing Element with regard to solid waste.

**EXHIBIT A**

**cmaddren@gmail.com**

**From:** publicrecords@lacity.org <support@nextrequest.com>
**Sent:** Tuesday, July 27, 2021 8:05 AM
**To:** [redacted]
**Subject:** [External Message Added] City of Los Angeles public records request #21-6204

-- Attach a non-image file and/or reply ABOVE THIS LINE with a message, and it will be sent to staff on this request. --

City of Los Angeles Public Records

# A message was sent to you regarding record request #21-6204:

**REQUEST FOR DOCUMENTS - UNDER THE PUBLIC RECORDS ACT**

In reply to your request of July 23, 2021, for Next Request # 21-6204.

LA Sanitation has information that is responsive to your request.

In 2019 there was 1,519,976 tons of solid waste collected for disposal through the recycLA program. In 2020 there was 1,298,289 tons of solid waste collected for disposal through the recycLA program. City does not currently have the percentage of material diverted for 2019 or 2020.

This request is now completed and will be closed.

Respectfully,

LA Sanitation and Environment

**View Request 21-6204**

https://lacity.nextrequest.com/requests/21-6204

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*Questions about your request?* Reply to this email or sign in to contact staff at City of Los Angeles.

*Technical support:* See our help page

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Letter I-3

**Housing Element <housingelement@lacity.org>**

# Plan to house LA

2 messages

**George Papanikolas** [redacted] Thu, Jul 22, 2021 at 9:30 AM
To: housingelement@lacity.org

I would like to see the city build a lot more housing, taller housing, there is no reason why everything should be limited to five stories. If we allow it more developments that are sky high skyscrapers then we can have more open space and parks. Please illuminate height restrictions so that we can build a lot more units on each property rather than being limited to 5-8 stories. 1

George Papanikolas
[redacted]

**Housing Element** <housingelement@lacity.org> Wed, Jul 28, 2021 at 8:42 AM
To: George Papanikolas [redacted]

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Letter I-4

**Housing Element <housingelement@lacity.org>**

# Resubmitting Comment on Housing Element Update

2 messages

[redacted] Thu, Jul 22, 2021 at 2:03 PM
To: HousingElement@lacity.org

To whom it concerns:

First, I want to say I applaud the City of LA for tackling this multi-faceted way of seeking to fulfill housing needs of Angelenos going forward, to create a more equitable and sustainable solution to housing.

Recently, I've read that in some communities there are development organizations buying up large numbers of properties sold at auction, by $1 "bidding up", thereby gaining ability to lot-split while also adversely influencing and depressing real estate values of neighboring properties. If this is taking place in Los Angeles, especially where seniors and/or persons of color have invested their lives and limited wealth, I am very concerned for how we are to preserve and protect such communities and homeowner/residents going forward.

The document titled "DRAFT 2021-2029 Housing Element" [accessed under link: "What does the plan do?"] includes under subsection "Key Objective and Policy Changes" of section "Preventing Displacement and Ensuring Housing Stability" the following statement:

" Protect communities, especially communities of color, from predatory lending, land acquisition, speculative real estate transactions (Policy 2.2.5)".

How might above-captioned Policy 2.2.5 be implemented/"enforced" to ensure this objective is met? Thank you.

1

Respectfully submitted,

Janis

Janis Hatlestad
[redacted]

Updated to add reference file number:
ENV-2020-6762-EIR

---

**Housing Element** <housingelement@lacity.org> Wed, Jul 28, 2021 at 8:37 AM
To: [redacted]

Thank you for this comment and question.

There are many ways we believe the plan addresses protecting the most vulnerable - please see the "Key Programs" in the section of the document you referenced, as well as under *Advancing Racial Equity & Access to Opportunity.*

Please also know that the next Draft in we will release in September will explicitly link each Policy to specific Programs to help readers better connect the dots.

Regards,

The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Connect Create Collaborate

Letter I-5

**Housing Element <housingelement@lacity.org>**

# Re: Notice of Availability of Draft EIR for Updates to Housing Element and Safety Element / Aviso de Disponibilidad del borrador del Informe de Impacto Ambiental para las actualizaciones del Elemento de Vivienda y del Elemento de Seguridad

**Housing Element** <housingelement@lacity.org> Wed, Jul 28, 2021 at 11:47 AM
To: [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

On Thu, Jul 22, 2021 at 2:14 PM <[redacted]> wrote:

> What's at stake? How can an ordinary Angeleno make sense of this?
>
> LIke for instance, can we raise our public voice to be clear that residents should not be
>
> able to purchase a $35 placard from LADOT that serves as an exclusive license to use the public road way.
>
> This planning element, that owners can purchase adjacent roadway for below market prices, thereby pushing Angelenos into a ticketing trap... is not equity oriented. It's appalling. For shame!
>
> I suggest that Seleta Reynolds hold a public hearing with Vince Bertoni on this subject, before EIR deadline in September. Thank you.
>
> Eric Preven

1

-----Original Message-----
From: Los Angeles City Planning <housingelement@lacity.org>
To: [redacted]
Sent: Thu, Jul 22, 2021 8:50 am
Subject: Notice of Availability of Draft EIR for Updates to Housing Element and Safety Element / Aviso de Disponibilidad del borrador del Informe de Impacto Ambiental para las actualizaciones del Elemento de Vivienda y del Elemento de Seguridad

*Para español siga hacia abajo.*

## Interested Parties,

This email is to inform you of the Notice of Availability (NOA) for the Draft Environmental Impact Report (EIR) prepared for the Updates to the Housing Element and the Safety Element. These documents are being prepared by Los Angeles City Planning as part of the Plan to House LA and Safety Element Update.

The NOA and Draft EIR materials are now available on Los Angeles City Planning's website.

Beginning today, City Planning is accepting comments on the Draft EIR. **The Draft EIR comment period will close at 5:00 p.m. on Tuesday, September 7, 2021**.

If you wish to submit comments on the Draft EIR, please submit your written comments (including a name, contact information, and the following file number ENV-2020-6762-EIR) during the comment period, via mail or e-mail to the following addresses:

**Cally Hardy |** City Planning Associate
City of Los Angeles Department of City Planning
200 North Spring Street, Room 750
Los Angeles, CA 90012

**E-mail**
HousingElement@lacity.org

Beyond the DEIR comment period, general public comments on the plan drafts are also welcome until the Plan is adopted by City Council.

## Partes Interesadas,

Este correo electrónico es para informarle del Aviso de Disponibilidad (NOA por sus siglas en inglés) para el Borrador del Informe de Impacto Ambiental (EIR por sus siglas en inglés) preparado para las Actualizaciones del Elemento de Vivienda y del Elemento de

Seguridad. Estos documentos están siendo preparados por el Departamento de Planeación de la Ciudad de Los Ángeles como parte del Plan de Vivienda y Elemento de Seguridad.

Los materiales del NOA y el Borrador del EIR ya están disponibles en el sitio web del Departamento de Planeación de la Ciudad de Los Ángeles (en inglés). El Aviso de Disponibilidad (el NOA) está disponible en español.

Empezando hoy, el Departamento de Planeación está aceptando comentarios sobre el Borrador del EIR. **El período de comentarios del Borrador del EIR se cerrará a las 5:00 p.m. del martes 7 de septiembre de 2021**.

Si desea enviar comentarios sobre el Borrador del EIR, por favor envíe sus comentarios por escrito (incluyendo su nombre, información de contacto, y el siguiente número de archivo ENV-2020-6762-EIR) durante el período de comentarios, por correo o vía correo electrónico a las siguientes direcciones:

**Cally Hardy |** City Planning Associate
City of Los Angeles Department of City Planning
200 North Spring Street, Room 750
Los Angeles, CA 90012

**Correo Electrónico**
HousingElement@lacity.org

Comentarios públicos generales sobre los borradores de los planes también son bienvenidos hasta que sean adoptados por el Concejo de la Ciudad.

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Letter I-6

**Housing Element <housingelement@lacity.org>**

# Wisdom From: Katrina Jenkins

2 messages

**Katrina Jenkins** Thu, Jul 22, 2021 at 9:13 PM
To: housingelement@lacity.org, mayor.garcetti@lacity.org

I wanted to comment of the LA City Planning Forum. Housing is one of the largest issues in LA County. I'm glad that I participated in the forum because it drew a light on the issues I wanted to address. Let me just say, you all are doing an awesome job with the limited area you are trying to establish.

My input would be to maximize the area that's being developed. The only way to do that is to build going up. Example: parking structure underneath, business structures at street level, housing units and then green deal projects on top ( community gardens/ roof top playgrounds). Projects on the roof tops should have conservation built in, Example: recycled parts in the construction and recycled water ways.

As for our homeless with mental health issues, they will need housing units with built in supports. They're should be a live-in Social Worker on these sites. They will need someone certified to juggle their individual needs. Community and Activity Rooms / Outdoor Exercise equipment and sitting areas, as they promote mental health wellbeing. Perhaps you can offer FREE housing to the Social Workers to draw them into these type of housing structures. Most importantly the zoning laws for assisting them will need to be re-written to allow the support first.

Truely we are our brothers keeper.❤😉

It can be done! Stay encouraged... This is a huge undertaking.

Katrina Jenkins 🙏

**Housing Element** <housingelement@lacity.org> Wed, Jul 28, 2021 at 8:55 AM
To: Katrina Jenkins Cc:
mayor.garcetti@lacity.org

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

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Letter I-7

**Housing Element <housingelement@lacity.org>**

# Hi from pb.....7/23 What happened to FEMA involvement..... Notice of A vailability of Draft EIR for Updates to Housing Element and Safety Ele ment / Aviso de Disponibilidad del borrador del Informe de Impacto Amb iental para las actualizaciones del Elemento de Vivienda y del Element o de Seguridad

2 messages

[redacted] Fri, Jul 23, 2021 at 12:08 PM
To: housingelement@lacity.org

in protecting LA river from FLOODING ? we were told "mandatory" flood insurance would be required for new home owners & tat FEMA was now in the insurance business....90039 my hood was one of the areas....big meetings, plans Brace & Boldt programs now nothing ???? typical of how LA drops the ball on PLANS!....and again WHAT ABOUT BOW TIE PARK the dump site that should be better planned, this has been going on for 20 years since I lived here . 1

---------- Original Message ----------
From: Los Angeles City Planning <housingelement@lacity.org>
To: [redacted]
Subject: Notice of Availability of Draft EIR for Updates to Housing Element and Safety Element / Aviso de Disponibilidad del borrador del Informe de Impacto Ambiental para las actualizaciones del Elemento de Vivienda y del Elemento de Seguridad
Date: Thu, 22 Jul 2021 11:50:24 -0400 (EDT)

*Para español siga hacia abajo.*

Interested Parties,

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The NOA and Draft EIR materials are now available on Los Angeles City Planning's website.

Beginning today, City Planning is accepting comments on the Draft EIR. **The Draft EIR comment period will close at 5:00 p.m. on Tuesday, September 7, 2021**.

If you wish to submit comments on the Draft EIR, please submit your written comments (including a name, contact information, and the following file number ENV-2020-6762-EIR) during the comment period, via mail or e-mail to the following addresses:

**Cally Hardy |** City Planning Associate
City of Los Angeles Department of City Planning
200 North Spring Street, Room 750
Los Angeles, CA 90012

**E-mail**
HousingElement@lacity.org

Beyond the DEIR comment period, general public comments on the plan drafts are also welcome until the Plan is adopted by City Council.

## Partes Interesadas,

Este correo electrónico es para informarle del Aviso de Disponibilidad (NOA por sus siglas en inglés) para el Borrador del Informe de Impacto Ambiental (EIR por sus siglas en inglés) preparado para las Actualizaciones del Elemento de Vivienda y del Elemento de Seguridad. Estos documentos están siendo preparados por el Departamento de Planeación de la Ciudad de Los Ángeles como parte del Plan de Vivienda y Elemento de Seguridad.

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**Cally Hardy |** City Planning Associate
City of Los Angeles Department of City Planning
200 North Spring Street, Room 750
Los Angeles, CA 90012

**Correo Electrónico**
HousingElement@lacity.org

Comentarios públicos generales sobre los borradores de los planes también son bienvenidos hasta que sean adoptados por el Concejo de la Ciudad.

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**Housing Element** <housingelement@lacity.org> Wed, Aug 18, 2021 at 6:08 PM
To: [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

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Letter I-8

**Housing Element <housingelement@lacity.org>**

# Housing Element Feedback (ENV-2020-6762-EIR)

**Housing Element** <housingelement@lacity.org> Wed, Jul 28, 2021 at 11:43 AM
To: Brian Trautman <[redacted]>

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

On Fri, Jul 23, 2021 at 8:10 PM Brian Trautman <[redacted]> wrote:

> ENV-2020-6762-EIR
>
> Hi!
>
> I'm heartened by the good work that LA County has done on their housing element. In order to assure affordable housing for everyone, we need to ensure adequate housing availability.
>
> We need to ensure our policies don't just serve people already lucky enough to own property in LA county, but renters and potential new residents as well.
>
> Thank you!
>
> Brian Trautman
> [redacted]

1

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Letter I-9

**Housing Element <housingelement@lacity.org>**

# Re: Notice of Availability of Draft EIR for Updates to Housing Element and Safety Element / Aviso de Disponibilidad del borrador del Informe de Impacto Ambiental para las actualizaciones del Elemento de Vivienda y del Elemento de Seguridad

[redacted] Wed, Jul 28, 2021 at 9:04 AM
Reply-To: [redacted]
To: "housingelement@lacity.org" <housingelement@lacity.org>

OK, great. When will Reynolds and Bertoni address the strategy of selling the public right of way to home owners at the cost of workers and visitors?

Please add this as well:
Bonin starts every meeting with Seleta Reynolds, the General Manager of the Los Angeles Department of Transportation (LADOT), by presenting a verbal report relative to the Department's on-going activities.

And he goes out of his way to offer recognition for Department employees for outstanding service ticketing the public.

The use of parking permit districts by municipalities have been upheld through the Supreme Court since 1977: Arlington County Board v. Richards.

Ripe for a challenge or settled law is always a tough call. One thing was very clear, Mike Bonin was a believer.

Despite no coherent strategy -- because if you push every car out of one neighborhood, it will obviously land in an adjacent one -- Bonin will be remembered as Field Marshal committed to bringing the relief. 1

Like a modern-day General Lucius Dubignon Clay, The Great **Uncompromiser --** a decedent of Henry Clay, the U.S. senator from Kentucky -- Bonin was beyond dedicated.

Clay orchestrated the Berlin Airlift (1948–1949) when the USSR blockaded West Berlin. Aircrews from the American, British, French, Canadian, Australian, New Zealand, and South African air forces flew over 200,000 sorties in one year, providing necessities such as fuel and an astonishingly high carbohydrate-loaded menu of relief food:

646 tons of flour and wheat, 3 tons of fresh yeast for baking, 180 tons of dehydrated potatoes,125 tons of cereal, with limited protein representing 109 tons of meat and fish, 64 tons of fat,10 tons of cheese.

A mere 11 tons of coffee, but airlifts can be really exhausting. It was a miraculous and filling accomplishment.

Bonin was bringing a different kind of relief.

He was bringing the diligent wiring up of every neighborhood in the city to prevent even the possibility of outsiders, no matter how need, from parking on the public roadway.

At City Council, Mike Bonin was advocating #DoNoHarm. But up in Transportation and Public Safety, they were banging out 50 to 55 smart boots a day and on one day applied 81 smart boots.

With the vigor of Dr. Fauci promoting vaccination, Mike Bonin pushed through 247 roadway closures often consisting of hundreds of spaces during 2017, 2018, and six months of 2019. . .that's 247 in 30 months = 8 per month or 2 per week.

As an example, the Preferential Parking District (PPD) No. 276 in the Studio City Area in Council District Two is comprised of about 30 blocks. A block is defined as a street segment between two intersecting streets. Between 300 and 600 spaces.

So if we take an average of 500 spaces x 247 restrictions* = 123,500 spaces!

The Bonin Carlift was a breathtaking nose to the grindstone campaign to rescue NIMBY residents from Angelenos desperate to park.

And why? "The increase goes from $78 to $250 for the first violation, $500 for a second violation within 12 months, and $1,000 for the third violation within 12 months, and increased late penalties."

Bonin was committed to bringing parking restrictions citywide, of every conceivable variety. . .along with Avak he would agendize dozens and dozens and dozens. . .relative to prohibiting the parking of vehicle, prohibit the stopping, standing, or parking vehicles that are in excess of 22 feet in length or over 7 feet in height, parking of vehicles advertising the private sale of those vehicles.

1 cont.

The people had never seen anything like it because they were mostly squirrelled away in committee.

During all of his relief work, Bonin still found time to falsely tag a civil rights advocate as a racist. . . offering ear plugs for public comments.

Check embarrassing video of Lady Gaga's "A Million Reasons" playing over the life in pictures that he tagged a racist, while his BFF from the StreetsBlogLA was reduced to tears.

The Mayor said and you can be sure that Mike Bonin concurs, "I didn’t declare wars that brought people back with PTSD; I haven’t been putting people into prisons for years; I didn’t declare the drug war; I haven’t been in charge of the foster care system.”

No, but you both made it harder for the folks who have it hardest.

Not everyone agrees, if one person is hurting. . .we are all hurting. Standing in solidarity, when one person is grieving, we're all grieving.

Bonin is "closing and fencing" but he's still way better than Buscaino!

[Quoted text hidden]

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Letter I-10

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Thomas Szelazek** [redacted] Wed, Jul 28, 2021 at 2:01 PM
Reply-To: [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

Now, additional bold action and specific implementation measures are needed to make the housing element update successful. I urge the City to:
-Target the creation of 300,000 new homes through rezoning and land use reforms.
-Implement a comprehensive Fair Share approach to the RHNA rezoning program, which would set specific housing growth targets for all neighborhoods.
-Increase affordable housing opportunities in high-opportunity neighborhoods.
-Expand and merge TOC and the city Density Bonus program, including parcels where apartments are currently banned.
-Exclude parcels that contain RSO housing units from the site inventory and rezoning plan, in order to prevent lower-income renter displacement.

The housing element update is our opportunity to build a Los Angeles with lower housing costs, a growing regional economy, greater access to opportunity, and greater socioeconomic diversity. I encourage you to incorporate the above policies into the housing element update so that we can create a prosperous, affordable Los Angeles where everyone is welcome.

Personally sent by Thomas Szelazek using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Thomas Szelazek
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:10 AM
[redacted]

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-11

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Brennan Lawson** [redacted] Wed, Jul 28, 2021 at 2:01 PM
Reply-To: [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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The housing element update is our opportunity to build a Los Angeles with lower housing costs, a growing regional economy, greater access to opportunity, and greater socioeconomic diversity. I encourage you to incorporate the above policies into the housing element update so that we can create a prosperous, affordable Los Angeles where everyone is welcome.

Personally sent by Brennan Lawson using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Brennan Lawson
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:11 AM
[redacted]

Dear Brennan,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
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[Quoted text hidden]

Connect Create Collaborate

Letter I-12

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Anthony Castelletto** [redacted] Wed, Jul 28, 2021 at 2:02 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

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Personally sent by Anthony Castelletto using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Anthony Castelletto
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:11 AM
[redacted]

Dear Anthony,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-13

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Chase Engelhardt** [redacted] Wed, Jul 28, 2021 at 2:02 PM
Reply-T[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Chase Engelhardt using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Chase Engelhardt
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:12 AM
[redacted]

Dear Chase,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

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Letter I-14

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Jennifer Martinez** [redacted] Wed, Jul 28, 2021 at 2:06 PM
Reply [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Jennifer Martinez using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Jennifer Martinez
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:12 AM
[redacted]

Dear Jennifer,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

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Letter I-15

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Colleen OBrien** [redacted] Wed, Jul 28, 2021 at 2:06 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Colleen OBrien using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Colleen OBrien
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:13 AM

[redacted]

Dear Colleen,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

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Letter I-16

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Mark S. and Marsha Novak** [redacted] Wed, Jul 28, 2021 at 2:08 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Mark S. and Marsha Novak using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Mark S. and Marsha Novak
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:13 AM

[redacted]

Dear Mark and Marsha,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

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Letter I-17

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Chad Stinson** [redacted] Wed, Jul 28, 2021 at 2:11 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Chad Stinson using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Chad Stinson
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:14 AM

[redacted]

Dear Chad,

Hope all is well.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-18

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Sarah Back** [redacted] Wed, Jul 28, 2021 at 2:16 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Sarah Back using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Sarah Back
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:53 AM

[redacted]

Hello Sarah,

Hope all is well.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-19

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Stanley Johnson** [redacted] Wed, Jul 28, 2021 at 2:20 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Stanley Johnson using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Stanley Johnson
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:53 AM

[redacted]

Hello Stanley,

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[Quoted text hidden]

Connect Create Collaborate

Letter I-20

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Golden Bachelder** [redacted] Wed, Jul 28, 2021 at 2:29 PM

To: vince.bertoni@lacity.org

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Personally sent by Golden Bachelder using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Golden Bachelder
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:52 AM

[redacted]

Hello Golden,

Hope all is well.

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Best,

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[Quoted text hidden]

Connect Create Collaborate

Letter I-21

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Andrew Silver** [redacted] Wed, Jul 28, 2021 at 2:40 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

Today the City Council approved revisions to LAMC 41.18. The city must now to the hard work of creating affordable housing.

Now, additional bold action and specific implementation measures are needed to make the housing element update successful. I urge the City to:
-Target the creation of 300,000 new homes through rezoning and land use reforms.
-Implement a comprehensive Fair Share approach to the RHNA rezoning program, which would set specific housing growth targets for all neighborhoods.
-Increase affordable housing opportunities in high-opportunity neighborhoods.
-Expand and merge TOC and the city Density Bonus program, including parcels where apartments are currently banned.
-Exclude parcels that contain RSO housing units from the site inventory and rezoning plan, in order to prevent lower-income renter displacement.

The housing element update is our opportunity to build a Los Angeles with lower housing costs, a growing regional economy, greater access to opportunity, and greater socioeconomic diversity. I encourage you to incorporate the above policies into the housing element update so that we can create a prosperous, affordable Los Angeles where everyone is welcome.

Personally sent by Andrew Silver using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Andrew Silver
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:51 AM
To: Andrew Silver[redacted]

Hello Andrew,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org

T: (213) 978-1302

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Connect Create Collaborate

Letter I-22

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Elizabeth Sroka** [redacted] Wed, Jul 28, 2021 at 2:44 PM
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Elizabeth Sroka using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Elizabeth Sroka
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:50 AM
To: [redacted]

Hello Elizabeth,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

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[Quoted text hidden]

Connect Create Collaborate

Letter I-23

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Rafael Sands** [redacted] Wed, Jul 28, 2021 at 2:48 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Rafael Sands using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Rafael Sands
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:50 AM

To: [redacted]

Hello Rafael,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-24

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Alec Mitchell** [redacted] Wed, Jul 28, 2021 at 2:52 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Alec Mitchell using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Alec Mitchell
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:49 AM

[redacted]

Hello Alec,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-25

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Chelsea Bangasser** [redacted] Wed, Jul 28, 2021 at 3:05 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Chelsea Bangasser using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Chelsea Bangasser
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:46 AM

[redacted]

Hello Chelsea,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Connect Create Collaborate

Letter I-26

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Chelsea Byers** [redacted] Wed, Jul 28, 2021 at 3:19 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Chelsea Byers using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Chelsea Byers
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:46 AM

[redacted]

Hello Chelsea,

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**Los Angeles City Planning**

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[Quoted text hidden]

Connect Create Collaborate

Letter I-27

Housing Element <housingelement@lacity.org>

# Please commit to reform housing now!

2 messages

**Greg Chasen** [redacted] Wed, Jul 28, 2021 at 3:36 PM
Reply-To: [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Greg Chasen using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Greg Chasen
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:45 AM
[redacted]

Hello Greg,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-28

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Marcus Owens** [redacted] Wed, Jul 28, 2021 at 4:03 PM
Reply-To: [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Marcus Owens using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Marcus Owens
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:45 AM
[redacted]

Hello Marcus,

Hope all is well.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-29

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Babak Mozaffari** [redacted] Wed, Jul 28, 2021 at 4:19 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Babak Mozaffari using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Babak Mozaffari
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:44 AM
To: Babak M [redacted]

Hello Babak,

Hope all is well.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-30

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Kyle Chrise** [redacted] Wed, Jul 28, 2021 at 4:37 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

More housing: Let's get this done!

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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-Target the creation of 300,000 new homes through rezoning and land use reforms.
-Implement a comprehensive Fair Share approach to the RHNA rezoning program, which would set specific housing growth targets for all neighborhoods.
-Increase affordable housing opportunities in high-opportunity neighborhoods.
-Expand and merge TOC and the city Density Bonus program, including parcels where apartments are currently banned.
-Exclude parcels that contain RSO housing units from the site inventory and rezoning plan, in order to prevent lower-income renter displacement.

The housing element update is our opportunity to build a Los Angeles with lower housing costs, a growing regional economy, greater access to opportunity, and greater socioeconomic diversity. I encourage you to incorporate the above policies into the housing element update so that we can create a prosperous, affordable Los Angeles where everyone is welcome.

Personally sent by Kyle Chrise using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Kyle Chrise
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:43 AM
[redacted]

Hi Kyle,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org

T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-31

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Bruce Van Voorhis** [redacted] Wed, Jul 28, 2021 at 5:36 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Bruce Van Voorhis using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Bruce Van Voorhis
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:28 AM

[redacted]

Hello Bruce,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-32

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Tom Vosburgh** [redacted] Wed, Jul 28, 2021 at 5:55 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Tom Vosburgh using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Tom Vosburgh
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:25 AM

[redacted]

Hello Tom,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-33

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Michael Hayes** [redacted] Wed, Jul 28, 2021 at 6:16 PM
Rep [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Michael Hayes using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Michael Hayes
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:24 AM
[redacted]

Hi Michael,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

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Letter I-34

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Mehnaaz Chowdhury** [redacted] Wed, Jul 28, 2021 at 6:25 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Mehnaaz Chowdhury using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Mehnaaz Chowdhury
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:23 AM
[redacted]

Hello Mehnaaz,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Connect Create Collaborate

Letter I-35

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Tanya Lebeck** [redacted] Wed, Jul 28, 2021 at 7:19 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles.

We need to fix our city's affordable housing shortage. To do this we need to create at least 456,000 new homes by 2029, including at least 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

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Personally sent by Tanya Lebeck using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Tanya Lebeck
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:22 AM

[redacted]

Hello Tanya,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

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[Quoted text hidden]

Connect Create Collaborate

Letter I-36

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Ben Creed** [redacted] Wed, Jul 28, 2021 at 8:15 PM
Reply-To: [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Ben Creed using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Ben Creed
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:20 AM
[redacted]

Hello Ben,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-37

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Eddie Isaacs** [redacted] Wed, Jul 28, 2021 at 9:19 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Eddie Isaacs using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Eddie Isaacs
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:12 AM

[redacted]

Hello Eddie,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-38

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Terence Heuston** [redacted] Thu, Jul 29, 2021 at 5:37 AM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Terence Heuston using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Terence Heuston
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:03 AM
[redacted]

Hello Terence,

Hope all is well.

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**Los Angeles City Planning**

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[Quoted text hidden]

Connect Create Collaborate

Letter I-39

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Mary Rose Fissinger** [redacted] Thu, Jul 29, 2021 at 7:21 AM
Reply-To: [redacted]
To: vince.bertoni@lacity.org

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Personally sent by Mary Rose Fissinger using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Mary Rose Fissinger
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:02 AM
[redacted]

Hello Mary,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-40

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Steven Guerry** [redacted] Thu, Jul 29, 2021 at 8:05 AM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I was a resident of Los Angeles from 2004 to 2020. I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

Now, additional bold action and specific implementation measures are needed to make the housing element update successful. I urge the City to:
-Target the creation of 300,000 new homes through rezoning and land use reforms.
-Implement a comprehensive Fair Share approach to the RHNA rezoning program, which would set specific housing growth targets for all neighborhoods.
-Increase affordable housing opportunities in high-opportunity neighborhoods.
-Expand and merge TOC and the city Density Bonus program, including parcels where apartments are currently banned.
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Personally sent by Steven Guerry using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Steven Guerry
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 11:00 AM

[redacted]

Hello Steven,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

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**Los Angeles City Planning**

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Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-41

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Carey Bennett** [redacted] Thu, Jul 29, 2021 at 8:40 AM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Carey Bennett using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Carey Bennett
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:58 AM
[redacted]

Hi Carey,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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**Los Angeles City Planning**

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Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-42

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Jessamyn Prince** [redacted] Thu, Jul 29, 2021 at 8:43 AM
Reply-To: [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Jessamyn Prince using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Jessamyn Prince
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:57 AM
[redacted]

Hello Jessamyn,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

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**Housing Element Staff**
**Los Angeles City Planning**

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Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-43

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

4 messages

**Nicholas Burns III** [redacted] Thu, Jul 29, 2021 at 9:32 AM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Nicholas Burns III using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Nicholas Burns III
[redacted]

**Vince Bertoni** <vince.bertoni@lacity.org> Thu, Jul 29, 2021 at 10:38 AM
To: Flora Melendez <flora.melendez@lacity.org>

[Quoted text hidden]
--

**Vincent P. Bertoni, AICP**
Pronouns: He, His, Him
Director of Planning
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
Los Angeles, CA 90012
Planning4LA.org
T: (213) 978-1271 | F: (213) 978-1275
E: vince.bertoni@lacity.org

LOS ANGELES CITY PLANNING

E-NEWS

**Flora Melendez** <flora.melendez@lacity.org> Thu, Jul 29, 2021 at 10:39 AM
To: Housing Element <housingelement@lacity.org>

---------- Forwarded message ---------
From: **Nicholas Burns III** <[redacted]
Date: Thu, Jul 29, 2021 at 9:32 AM
Subject: Please commit to reform housing now!
To: <vince.bertoni@lacity.org>

[Quoted text hidden]
--

~ Angie

LOS ANGELES CITY PLANNING

**Flora (Angie) Melendez**
Pronouns: she/hers/her
Executive Administrative Assistant III
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
Los Angeles, CA 90012
Planning4LA.org
T: (213) 978-1271 | F: (213) 978-1275
E: flora.melendez@lacity.org

E-NEWS

---

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:56 AM
[redacted]

Hello Nicholas,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

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[Quoted text hidden]

Connect Create Collaborate

Letter I-44

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Catherine Fabre** [redacted] Thu, Jul 29, 2021 at 10:48 AM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Catherine Fabre using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Catherine Fabre
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:56 AM
[redacted]

Hello Catherine,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

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**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-45

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

3 messages

**Aleli Valencia** [redacted] Thu, Jul 29, 2021 at 11:05 AM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Aleli Valencia using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Aleli Valencia
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:54 AM
[redacted]

Hi Aleli,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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**Los Angeles City Planning**

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Planning4LA.org
T: (213) 978-1302

E-NEWS

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[Quoted text hidden]

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**postmaster@lacounty.gov** <postmaster@lacounty.gov> Tue, Aug 3, 2021 at 10:54 AM
To: housingelement@lacity.org

## Delivery has failed to these recipients or groups:

[redacted]

A communication failure occurred during the delivery of this message. Please try resending the message later. If the problem continues, contact your helpdesk.

The following organization rejected your message: BL0GCC02FT004.mail.protection.outlook.com.

**Diagnostic information for administrators:**

Generating server: ITSSDDCHYB04.HOSTED.LAC.COM

[redacted]
BL0GCC02FT004.mail.protection.outlook.com
Remote Server returned '550 5.4.1 All recipient addresses rejected : Access denied. AS(201806271) [BL0GCC02FT004.eop-gcc02.prod.protection.outlook.com]'

Original message headers:

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 id 15.0.1497.2; Tue, 3 Aug 2021 10:54:44 -0700
Received: from esa17.hc4088-88.iphmx.com (10.49.240.15) by
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 id 15.0.1497.2 via Frontend Transport; Tue, 3 Aug 2021 10:54:44 -0700
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From: Housing Element <housingelement@lacity.org>
Date: Tue, 3 Aug 2021 10:54:30 -0700
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To: [redacted]
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---------- Forwarded message ----------
From: Housing Element <housingelement@lacity.org>
[redacted]
Cc:
Bcc:
Date: Tue, 3 Aug 2021 10:54:30 -0700
Subject: Re: Please commit to reform housing now!

CAUTION: External Email. Proceed Responsibly.

Hi Aleli,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

E-NEWS

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

On Thu, Jul 29, 2021 at 11:05 AM Aleli Valencia [redacted] wrote:

> Dear Director of City Planning Vince Bertoni,
>
> I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.
>
> It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.
>
> Now, additional bold action and specific implementation measures are needed to make the housing element update successful. I urge the City to:
> -Target the creation of 300,000 new homes through rezoning and land use reforms.
> -Implement a comprehensive Fair Share approach to the RHNA rezoning program, which would set specific housing growth targets for all neighborhoods.
> -Increase affordable housing opportunities in high-opportunity neighborhoods.
> -Expand and merge TOC and the city Density Bonus program, including parcels where apartments are currently banned.
> -Exclude parcels that contain RSO housing units from the site inventory and rezoning plan, in order to prevent lower-income renter displacement.
>
> The housing element update is our opportunity to build a Los Angeles with lower housing costs, a growing regional economy, greater access to opportunity, and greater socioeconomic diversity. I encourage you to incorporate the above policies into the housing element update so that we can create a prosperous, affordable Los Angeles where everyone is welcome.
>
> Personally sent by Aleli Valencia using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.
>
> Sincerely,
> Aleli Valencia
> [redacted]

Connect Create Collaborate

Letter I-46

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Bob C** [redacted] Thu, Jul 29, 2021 at 11:10 AM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

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Personally sent by Bob C using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Bob C
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:51 AM

[redacted]

Hello Bob,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

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Letter I-47

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Marek Slipski** [redacted] Thu, Jul 29, 2021 at 11:14 AM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Marek Slipski using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Marek Slipski
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:50 AM

[redacted]

Hi Marek,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Best,

LOS ANGELES CITY PLANNING

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**Los Angeles City Planning**

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[Quoted text hidden]

Connect Create Collaborate

Letter I-48

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Tommy Atlee** [redacted] Thu, Jul 29, 2021 at 11:33 AM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

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Personally sent by Tommy Atlee using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Tommy Atlee
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:48 AM

[redacted]

Hello Tommy,

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[Quoted text hidden]

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Letter I-49

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Elisa Visick** [redacted] Thu, Jul 29, 2021 at 11:52 AM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Elisa Visick using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Elisa Visick
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:47 AM

[redacted]

Hello Elisa,

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[Quoted text hidden]

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Letter I-50

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

3 messages

**Daniel Poineau** [redacted] Thu, Jul 29, 2021 at 1:06 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

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Personally sent by Daniel Poineau using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Daniel Poineau
[redacted]

**Vince Bertoni** <vince.bertoni@lacity.org> Thu, Jul 29, 2021 at 1:10 PM
To: Flora Melendez <flora.melendez@lacity.org>

LOS ANGELES CITY PLANNING

**Vincent P. Bertoni, AICP**
Pronouns: He, His, Him
Director of Planning
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
Los Angeles, CA 90012
Planning4LA.org
T: (213) 978-1271 | F: (213) 978-1275
E: vince.bertoni@lacity.org

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[Quoted text hidden]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:46 AM
To: [redacted]

Hello Daniel,

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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Thank you,

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Connect Create Collaborate

Letter I-51

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Kevin Zelaya** [redacted] Thu, Jul 29, 2021 at 1:11 PM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Kevin Zelaya using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Kevin Zelaya
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:46 AM

[redacted]

Hello Kevin,

Hope all is well.

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Thank you,

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**Los Angeles City Planning**

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T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-52

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Jeffrey White** [redacted] Thu, Jul 29, 2021 at 1:22 PM
Rep [redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

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Personally sent by Jeffrey White using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Jeffrey White
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:45 AM
[redacted]

Hello Jeffrey,

Hope all is well.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-53

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Sarah Kate Levy** [redacted] Thu, Jul 29, 2021 at 1:37 PM

To: vince.bertoni@lacity.org

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Personally sent by Sarah Kate Levy using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Sarah Kate Levy
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:42 AM

[redacted]

Hi Sarah,

Hope all is well.

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[Quoted text hidden]

Connect Create Collaborate

Letter I-54

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Mark Larson** [redacted] Fri, Jul 30, 2021 at 9:00 PM

To: vince.bertoni@lacity.org

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Personally sent by Mark Larson using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Mark Larson
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:38 AM

[redacted]

Hi Mark,

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[Quoted text hidden]

Connect Create Collaborate

Letter I-55

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

4 messages

**Ann Bickerton** [redacted] Fri, Jul 30, 2021 at 2:44 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

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Personally sent by Ann Bickerton using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Ann Bickerton
[redacted]

**Vince Bertoni** <vince.bertoni@lacity.org> Fri, Jul 30, 2021 at 2:51 PM
To: Flora Melendez <flora.melendez@lacity.org>

[Quoted text hidden]
--

LOS ANGELES CITY PLANNING

**Vincent P. Bertoni, AICP**
Pronouns: He, His, Him
Director of Planning
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
Los Angeles, CA 90012
Planning4LA.org
T: (213) 978-1271 | F: (213) 978-1275
E: vince.bertoni@lacity.org

E-NEWS

**Cally Hardy** <cally.hardy@lacity.org> Mon, Aug 9, 2021 at 9:13 AM
To: Housing Element <housingelement@lacity.org>

---------- Forwarded message ---------
From: **Susan Wong** <susan.s.wong@lacity.org>
Date: Wed, Aug 4, 2021 at 7:46 AM
Subject: Fwd: Please commit to reform housing now!
To: Cally Hardy <cally.hardy@lacity.org>

Hi Cally,

This comment was sent to us in error.

Susan

**Susan Wong**
City Planner
**Los Angeles City Planning**
200 N. Spring St., Room 667
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1472 | F: (213) 978-1477
E-NEWS

---------- Forwarded message ---------
From: **Flora Melendez** <flora.melendez@lacity.org>
Date: Fri, Jul 30, 2021 at 5:36 PM
Subject: Fwd: Please commit to reform housing now!
To: Planning Ridgelines <planning.ridgelines@lacity.org>

---------- Forwarded message ---------
From: **Ann Bickerton** <[redacted]
Date: Fri, Jul 30, 2021 at 2:45 PM
Subject: Please commit to reform housing now!
To: <vince.bertoni@lacity.org>

[Quoted text hidden]
--

~ Angie

**Flora (Angie) Melendez**
Pronouns: she/hers/her
Executive Administrative Assistant III
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
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T: (213) 978-1271 | F: (213) 978-1275
E: flora.melendez@lacity.org

E-NEWS

--

**Cally Hardy** (she/her/hers)

City Planning Associate
**Los Angeles City Planning**
200 N. Spring St., Room 750
Los Angeles, CA 90012
Planning4LA.org
(213) 978-1643

---

**Housing Element** <housingelement@lacity.org> Wed, Aug 18, 2021 at 4:17 PM
To: [redacted]

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Connect Create Collaborate

Letter I-56

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Verity Freebern** [redacted] Sat, Jul 31, 2021 at 9:28 AM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my outrage about the most recent city council decision to criminalize poverty. The council's majority vote to reinstate the no-lie law is shameful and inhumane. It must not be allowed to happen.

Additionally, I support a strong, transformative housing element update for LA.

I urge the City to:
-Target the creation of 300,000 new homes through rezoning and land use reforms.
-Implement a comprehensive Fair Share approach to the RHNA rezoning program, which would set specific housing growth targets for all neighborhoods.
-Increase affordable housing opportunities in high-opportunity neighborhoods.
-Expand and merge TOC and the city Density Bonus program, including parcels where apartments are currently banned.
-Exclude parcels that contain RSO housing units from the site inventory and rezoning plan, in order to prevent lower-income renter displacement.

The housing element update is our opportunity to build a Los Angeles with lower housing costs, a growing regional economy, greater access to opportunity, and greater socioeconomic diversity. I encourage you to incorporate the above policies into the housing element update so that we can create a prosperous, affordable Los Angeles where everyone is welcome.

Personally sent by Verity Freebern using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Verity Freebern
[redacted]

---

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:37 AM
[redacted]

Hello Verity,

Hope you're well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

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Letter I-57

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Zennon Ulyate-Crow** [redacted] Sat, Jul 31, 2021 at 10:47 AM

To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

Now, additional bold action and specific implementation measures are needed to make the housing element update successful. I urge the City to:
-Target the creation of 300,000 new homes through rezoning and land use reforms.
-Implement a comprehensive Fair Share approach to the RHNA rezoning program, which would set specific housing growth targets for all neighborhoods.
-Increase affordable housing opportunities in high-opportunity neighborhoods.
-Expand and merge TOC and the city Density Bonus program, including parcels where apartments are currently banned.
-Exclude parcels that contain RSO housing units from the site inventory and rezoning plan, in order to prevent lower-income renter displacement.

The housing element update is our opportunity to build a Los Angeles with lower housing costs, a growing regional economy, greater access to opportunity, and greater socioeconomic diversity. I encourage you to incorporate the above policies into the housing element update so that we can create a prosperous, affordable Los Angeles where everyone is welcome.

Personally sent by Zennon Ulyate-Crow using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Zennon Ulyate-Crow
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Aug 3, 2021 at 10:23 AM

[redacted]

Hi Zennon,

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

Best,

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

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Letter I-58

**Housing Element <housingelement@lacity.org>**

# Chapter 2 Constraints/Housing Element Suggestions

[redacted] Wed, Aug 4, 2021 at 6:47 PM
To: housingelement@lacity.org
Cc: matthew.glesne@lacity.org

Hi Housing Element Folks,

Constraints preventing expeditious housing development include the post-approval plan check, condition clearance, and covenant acquisition process. Chapter 2 of the draft Housing Element must better address removal of these constraints that result in months' long delays after a housing development project is approved. Some post-approval delays are a result of items, such as:

- Post-approval second guessing of entitlements/project details after approval. After approval, plan check staff will second guess and re-interpret zoning provisions applicable to projects that the Planning Department already approved; any interpretation of code provisions, compliance with requirements needs to happen during the entitlement process when the City processes the application. Aside from Housing Accountability Act requirements (for those projects subject to it) that prevent the City from identifying late inconsistencies, the late-hit review causes massive uncertainty, drives up costs, and takes a significant amount of time to resolve. This should be addressed. 1

- Post-approval covenant acquisition. We have run into issues with Recreation and Parks, in particular (but with an assist from the City Attorney's office), not issuing draft covenants for review and execution to effectuate park fee credits. I have one project where we are waiting more than eight months for RAP staff to even provide a draft of a required covenant for review. This is resulting in fees increasing substantially, creation of uncertainty, and massive delay – and we haven't even negotiated the covenant yet. There is no justification why the draft covenant and the terms going into the covenant cannot be prepared concurrent with the project approval instead of after the fact, especially since the open space areas were clearly and unambiguously identified during the entitlement process. This is a significant issue. Similarly, the HCID affordability covenant includes items not found in City codes and also is a late hit. There is no reason why many, if not, most of all the terms cannot be implemented via set ordinance or prepared concurrent with project approval instead of after the fact. These are two examples of real world constraints that impede the development of housing, increase costs, and create massive uncertainty. I imagine that land use professionals working in the City have many similar or other examples showing how the City's current post-approval covenant approval process majorly constrains housing development.

- City not accepting plan check drawings electronically or approving drawings electronically. Aside from bringing the City plan check process into the 21st Century more than twenty years late, this could save considerable time and expense by not having to produce paper, replicate and deliver paper copies.

I look forward to seeing the revised draft Housing Element addressing and helping to remove these constraints with real reform efforts so that the City can produce and lower the cost of housing.

Thank you,

**Ryan Leaderman** | [redacted]

[redacted]

Add to address book | View professional biography

[redacted]

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Letter I-59

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

2 messages

**Shenette Holman** [redacted] Sun, Aug 8, 2021 at 3:46 PM
Reply-[redacted]
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

Hello, my name is Shenette Holman and I'm urging you to please fix our city's affordable housing shortage. As a mother of four children my family and I had housing in the past. Now that my two oldest children are grown and are out in the world creating their own lives it's just my two youngest children and I.

My two youngest children have really been resilient by dealing with being homeless during this pandemic and school closures. I truly feel as if my children have suffered enough and deserve a home to continue to strive for excellence in.

My children are really good children that deserve more than I could ever give them. During the pandemic their grades did slip but that was due to not having housing, getting sufficient internet and computer access. I can't begin to explain how difficult it was to charge all these various electronics while the world was shutdown. Yet, I do cause I care about my children and their education. Now I'm pleading with you to please do your part and help not just my family but the many families who are in the same boat.

You do believe that all human beings deserve adequate housing right ? Especially our children. Below is the standard message that we are encouraged to send. You can choose to read it or not the choice is yours. With that being said when it comes to affordable housing you can chose to fix the city's lack of affordable housing issue or you could choose to not fix it and continue to let the homeless population grow and be criminalized.

Thank you,

Shenette H.

I'm writing to express my support for a strong, transformative housing element update in Los Angeles. To fix our city's affordable housing shortage, we need a high-quality plan to create 456,000 new homes by 2029, including 184,000 that are affordable to lower-income households. We can't miss this opportunity to promote greater affordability, equity, and sustainability, as well as a strong economic recovery from the COVID-19 pandemic.

It's encouraging that the City has incorporated a sophisticated, data-driven site inventory analysis in its draft housing element, as well as a detailed and objective assessment of fair housing issues in Los Angeles. By creating a thorough quantitative model that estimates sites' likelihood of redevelopment, Planning has provided a fair estimate of the City's current realistic capacity for new housing and acknowledged that Los Angeles will only achieve 10% of its RHNA target in a "business as usual" scenario. The draft housing element also proposes creating over 220,000 homes through rezoning and other land use reforms, particularly in high-resource areas that have accommodated little new housing in recent years. All of this represents significant progress.

Now, additional bold action and specific implementation measures are needed to make the housing element update successful. I urge the City to:
-Target the creation of 300,000 new homes through rezoning and land use reforms.
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Personally sent by Shenette Holman using Abundant Housing LA's Advocacy Tool. Abundant Housing LA is a grassroots pro-housing organization.

Sincerely,
Shenette Holman
[redacted]

1

**Housing Element** <housingelement@lacity.org> Wed, Aug 18, 2021 at 4:16 PM
[redacted]

Hope all is well.

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-60

**Housing Element <housingelement@lacity.org>**

# Please commit to reform housing now!

3 messages

**Joann Gioia** [redacted] Thu, Sep 2, 2021 at 1:10 PM
To: vince.bertoni@lacity.org

Dear Director of City Planning Vince Bertoni,

Hi:

I am writing to tell you to please ignore Abundant Housing's suggestions for the Los Angeles City Housing Element. Abundant Housing has no right to tell the City or the residents of Los Angeles how they should run or live in their City. There is no need to allow duplexes to be built on lots zoned single family. The Los Angeles City Council was correct in opposing SB 9 and SB 10. These bills will destroy Los Angeles. The City of Los Angeles needs to have a balance of single and multi family homes. Only the City of LA and residents of LA can decide where it is best to allow density. Please do not listen to the YIMBYS, they are pushing high density everywhere. If a person purchased a home that is zoned R1 that home should remain R1. It is illegal to change zoning after a purchase has been made without the approval of the residents that change will involve. Let's work on the housing element together and keep the YIMBYs (Abundant Housing ) out of it. 1

Sincerely,
Joann Gioia
[redacted]

**Vince Bertoni** <vince.bertoni@lacity.org> Thu, Sep 2, 2021 at 1:12 PM
To: Flora Melendez <flora.melendez@lacity.org>

LOS ANGELES CITY PLANNING

**Vincent P. Bertoni, AICP**
Pronouns: He, His, Him
Director of Planning
**Los Angeles City Planning**
200 N. Spring St., Suite 525C
Los Angeles, CA 90012
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E: vince.bertoni@lacity.org

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[Quoted text hidden]

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 2:20 PM
To: Joann Gioia [redacted]

Thank you for sharing your thoughts on the draft plan. Your comment will be added to our case file and taken into consideration as we update the Housing Element. Please note that the draft Housing Element is continuing to be refined based on the community feedback we've received to date. We will be sharing the revised draft this fall.

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**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-61

**Housing Element <housingelement@lacity.org>**

# ENV-2020-6762-EIR

2 messages

**Bill Cotter** [redacted] Sun, Sep 5, 2021 at 3:11 PM
To: housingelement@lacity.org

There are so many things wrong with this “plan” it’s hard to know where to start.

Let’s eliminate zoning, fill the city with apartment buildings even though we don’t have water or power for what we have today, then not require the homeless to do anything to address the core of their problems. We have EMPTY BEDS now because people CHOOSE to stay on the street. Get them help for their addictions and illnesses, please – covering the city in apartment houses is NOT going to address these issues. I’m sure it will enrich your developer buddies big time though. 1

For those considering this “plan” – are you ready to have the house next door torn down and be replaced by a multi-story building full of untreated addicts? That’s what this plan espouses.

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:08 PM
To: Bill Cotter [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

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Letter I-62

**Housing Element <housingelement@lacity.org>**

# File Number ENV-2020-6762-EIR

2 messages

**Anna Berberian** [redacted] Sun, Sep 5, 2021 at 3:33 PM
To: housingelement@lacity.org

Good afternoon,

My name is Anna Berberian and I am writing to you as a concerned citizen and taxpayer living in the City of L-A that is tired of being held hostage in her neighborhood by the homeless population that is comprised of criminals and drug addicts. Enough is enough.
What exactly is the reasoning beyond the harebrained idea of Housing First DOES NOT REQUIRE ENTERING A TREATMENT PROGRAM even though they will OFFER the services but addicts don't have to take them? Mayor Garcetti took over Petit Park Rec Center to house chronic homeless during covid which left us with “housing resistant” drug users, drug sellers, and unstable mentally ill people walking in our streets today.

When you help the ROOT CAUSES of substance abuse and severe mental health problems, many homeless can become welcome and productive members of society, and the community will feel supportive of helping. The community voted for Prop HHH because they wanted to help people but they need the right kind of help! Putting these individuals within residential communities without proper mental health care puts the community at risk just like allowing drunk drivers on the road.

Housing the homeless is important, but homeless people have different reasons for being homeless. Putting law-abiding individuals in low-income housing in the area is not a problem. But putting drug abusers and mentally ill who constantly disturb the community while leaving their taxpayer provided Housing First home is a big problem for nearby residents. This city has refused to address the root cause of many homeless.

It is irresponsible to leave UNTREATED individuals in Tiny Homes, apartments or on the streets in our communities. It threatens the well-being of the community. Long-term in-patient rehabilitation needs to occur away from residents-not at casual sober-living type homes where they allow people to wander away and continue to do drugs. Some people may need locked mental health treatment to keep them and the community safe. Los Angeles is terribly short on mental beds compared to other major cities.

In addition, zoning laws and regulations were made for good reason. The rules cannot be arbitrarily lifted to permit harm to society because LA politicians believe they cannot solve the massive addiction/mental illness crises. The general population would not have a NIMBY attitude if their safety and well-being were not threatened. Substance abuse, erratic behaviors, petty theft to support bad habits, public nuisance, and vandalism are crimes that add up to a poor quality of life. This does not bode well for a healthy society.

1

Thank you

Sent from my iPhone

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:12 PM
To: Anna Berberian [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org

T: (213) 978-1302

For more information on the Plan to HouseLA visit our website, and/or join our listserv (if you have not already), in order to stay abreast of any Plan updates.

[Quoted text hidden]

Connect Create Collaborate

Letter I-63

**Housing Element <housingelement@lacity.org>**

# ENV 2020-6762- EIR

2 messages

**Angiee Suarez** [redacted] Sun, Sep 5, 2021 at 5:34 PM
To: housingelement@lacity.org

Cally Hardy,
I am a resident in North Granada Hills and urge to please aid us with the homelessness issue here. Please do not put tiny homes, etc in this community where we have schools, parks, etc. Without addressing the mental Health Of the people experience in homelessness. We have been ravaged in this community by a sudden surge in population since the pandemic started. These individuals that were sent to our community from other areas have severe mental issues and drug issues that have not been resolved and therefore allowing them to be put into homes in our neighborhood close to churches schools etc. has already proven to be very ineffective and harmful to our children and the residents.

Please think of our children and what they have already seen. Naked women and men offering them sex while they walk to school, crack pipes and drug paraphernalia being thrown at them on sidewalks
To name a few.

-Angela M. Suarez

Sent from my iPhone

1

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:14 PM
To: Angiee Suarez [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Letter I-64

**Housing Element <housingelement@lacity.org>**

# ENV-2020-6762-EIR Comments

2 messages

**Lisa K.Carothers** [redacted] Sun, Sep 5, 2021 at 7:24 PM
To: "housingelement@lacity.org" <housingelement@lacity.org>

To: Cally Hardy

Regarding: ENV-2020-6762-EIR

From: Lisa Carothers
[redacted]

Please see my comments below. I am angry that a survey went and it's too late for me to respond and I barely received notice about the ability to add my comments to the city's plan to resolve the unhoused situation.

- Regarding Policy 5.1.5 - Reduce zoning and other regulatory barriers to the placement and operation of housing and services for the unhoused.

**NO! Not unless you make it mandatory for people to receive mental health treatment! We cannot have those who have erratic and often drug-seeking behaviors placed in our community! The citizens have a right to know who their neighbors are and not risk the often poor oversight that goes along with facilities.**

- Regarding Policy 5.1.4. - Implement a housing-first approach and coordinate service provision(Policy 5.1.4 )

**NO! Housing First isn't safe for the homeless who are mentally ill or on drugs nor is it safe for the community! We have too many housing-resistant who roam the streets stealing, throwing bottles at citizens, doing drugs in broad daylight, and dropping drug paraphernalia all over the place. We are tired of the rampant codependency by the LA City Government where these sick people are permitted to traumatize the neighborhoods instead of being placed in treatment facilities where they get immediate help for their drug problem.** 1

**Stop and look at the ROOT CAUSE! Stop asking the sick people if they want help and just make them take it! They aren't in their right minds due to drugs yet you expect a sane response from them? I'm angriest at the politicians and the City department heads who are so grossly irresponsible.**

**You don't allow often dangerous people to roam the streets looking for another fix when they should be inside seeing psychiatrists, social workers, and attending 12-step types of programs in addition to medication to stabilize moods and prevent psychosis.**

- Regarding Policy 5.1.4 - Identify and remove barriers to permitting, preserving, and expanding licensed community care facilities

**NO! Not unless you make it mandatory for people to receive mental health treatment! We cannot have those who have erratic and often drug-seeking behaviors placed in our**

**community! The citizens have a right to know who their neighbors are and not risk the often poor oversight that goes along with facilities. They need guarded facilities while detoxing to keep ALL citizens safe.**

- Regarding Program 116 - Adopt amendments to zoning code to remove restrictions for health-based residential facilities

**NO! Again, not unless you make it mandatory for people to receive mental health treatment! We cannot have those who have erratic and often drug-seeking behaviors placed in our community! The citizens have a right to know who their neighbors are and not risk the often poor oversight that goes along with facilities.**

1 cont.

- Regarding Program 115 - Adopt amendments to zoning code to facilitate by-right siting of shelter and transitional housing facilities

**NO! Again, not unless you make it mandatory for people to receive mental health treatment! We cannot have those who have erratic and often drug-seeking behaviors placed in our community! The citizens have a right to know who their neighbors are and not risk the often poor oversight that goes along with facilities.**

---

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:16 PM
To: "Lisa K.Carothers" [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Connect Create Collaborate

Letter I-65

**Housing Element <housingelement@lacity.org>**

# Comment on ENV-2020-6762-EIR

2 messages

**Ann Dorsey** [redacted] Sun, Sep 5, 2021 at 8:21 PM
To: "housingelement@lacity.org" <housingelement@lacity.org>

To Whom It May Concern:

I am writing to submit a comment on file number ENV-2020-6762-EIR.

Although there may be a need for increased housing at all income levels, Los Angeles has to find a way to meet AFORDABLE housing needs. This must be a priority, or the homelessness situation will only get worse. 1

Thank you,

Ann Dorsey
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:18 PM
To: Ann Dorsey [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
Los Angeles, CA. 90012
Planning4LA.org
T: (213) 978-1302

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[Quoted text hidden]

Letter I-66

**Housing Element <housingelement@lacity.org>**

# ENV-2020-6762-EIR

2 messages

**Winifred Powelllipton** [redacted] Mon, Sep 6, 2021 at 9:02 AM
To: housingelement@lacity.org

Housing first does not demand that a treatment program be entered, offering this service is not enough, addicts will refuse and have refused. Petit park is overrun with drug addicts and mentally unstable people who have made it dangerous to live around this park. Garcetti took over Petit Rec Center to house chronic homeless and left us with drug dealers, addicts and mentally unstable individuals who resist housing. Dealing with the root causes is vital and should putting those who are not in treatment into communities is putting us in danger. Low income housing for law abiding people is welcomed but not drug abusing individuals who will put the community at risk. Long term rehabilitation needs to occur away from family homes, where older families live or young people are living not at casual sober living houses in our communities where they are free to leave and continue to do drugs. The mentally ill need to be where they are treated and not a danger to themselves or the community. 1
Zoning laws and regulations were made with good reason. To arbitrarily lift them will cause harm to families who live in these areas and only benefits developers. Leave our zoning laws alone. Families have worked hard to afford the American dream and you want to wipe that away with new zoning laws, not to mention the extra power and water needed for apartment buildings when California is having great difficulty supplying those homes and apartments now. Parking and traffic on top of that. More buses is not the answer. Our quality of life is going down hill fast and it seems that our elected officials, at ever level, to not care.

Marie Lipton
[redacted]
ENV-2020-6762-EIR
Sent from my iPhone

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 3:20 PM
To: Winifred Powelllipton [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

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[Quoted text hidden]

Connect Create Collaborate

Letter I-67

**Housing Element <housingelement@lacity.org>**

# (no subject)

2 messages

**Jennifer Cox** [redacted] Tue, Sep 7, 2021 at 10:28 AM
To: housingelement@lacity.org

File Number: ENV-2020-6762-EIR
ATTN: Cally Hardy, CIty Planning Associate, City of Los Angeles Department of CIty Planning

In response to the survey regarding The Plan to House L.A., as a homeowner in the city I have substantial concerns and objections to this plan. Please do not change zoning for the operation of housing and services for the unhoused. My community is already suffering from increased crimes, violence and vandalism. 1

The unhoused that were brought to my community during the start of the COVID pandemic have been constantly using drugs in the open on our streets and in our parks, attacking residents and businesses, made the sidewalks impassable and have been terrorizing us.

Please provide long term care facilities, rehab and mental health.

Thank you,
Jennifer Cox, resident
[redacted]

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 4:40 PM
To: Jennifer Cox [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

LOS ANGELES CITY PLANNING

**Housing Element Staff**
**Los Angeles City Planning**

200 N. Spring St., Room 750
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[Quoted text hidden]

Connect Create Collaborate

Letter I-68

**Housing Element <housingelement@lacity.org>**

# file number ENV-2020-6762-EIR

2 messages

**Monica Dragavon** [redacted] Tue, Sep 7, 2021 at 4:53 PM
To: "housingelement@lacity.org" <housingelement@lacity.org>

TO:
Cally Hardy, City Planning Associate, City of Los Angeles Department of City Planning
file number ENV-2020-6762-EIR

Dear Ms. Hardy,

I am concerned with and oppose the components and explain reasons below:
●Reduce zoning and other regulatory barriers to the placement and operation of housing and services for the unhoused.(Policy 5.1.5 )
●Implement a housing-first approach and coordinate service provision(Policy 5.1.4 )
●Identify and remove barriers to permitting, preserving, and expanding licensed community care facilities(Policy 5.1.5)
●Adopt amendments to zoning code to remove restrictions for health-based residential facilities(Program 116)
●Adopt amendments to zoning code to facilitate by-right siting of shelter and transitional housing facilities(Program 115)

Housing First DOES NOT REQUIRE ENTERING A TREATMENT PROGRAM. Even though they may OFFER services, addicts don't have to take them. When Mayor Garcetti took over Petit Park Rec Center to house chronic homeless during covid, it left behind “housing resistant” drug users, drug sellers, and unstable mentally ill people who moved to the area and still continue to cause repeated problems. This particular group of tranisents has attracted gangs and drug users/sellers to the area. Housed or unhoused, nobody wants to live near this.

When you help the ROOT CAUSES of substance abuse and severe mental health problems, many homeless can become welcome and productive members of society, and the community will feel supportive of helping. The community voted for Prop HHH because they wanted to help people, but they need the right kind of help! Housing First was NOT written in measure HHH. People did not vote for that. Housing active substance abusers/chronic mentally ill individuals in residential communities without proper long-term rehab/mental health care beforehand, puts the entire community at risk. We do not allow drunk drivers on the road due to poor judgement so why place similar poor judgement individuals, due to illicit drug use/chronic mentally ill, to present poor judgment and harm to the community daily? 1

Don’t risk our quality of life by building housing for untreated individuals in residential/local business areas! If they choose to continue to use drugs and the State choses to enable them, do so without harming the rest of us. Data has shown that Housing First is more successful with housing individuals-NOT with treatment. I have gone as far as requesting data from the Mayor’s office, but they would not provide as “it was complicated.” What is not complicated, is the data I have found which shows there is no increase in addicts getting clean with Housing First. Don’t rezone; put Housing First for active abusers where it will not be a problem or health or safety risk to others.

Housing is important, but it is irresponsible to house UNTREATED individuals in Tiny Homes, apartments or on the streets in our communities. It threatens the well-being of any community. Long-term in-patient rehabilitation needs to occur away from residents-not at casual sober-living type homes where they allow people to wander away and continue to do drugs. Although some of these facilities are run well, unfortunately there has not been enough oversight at some of these money mills. Plus, when you allow business to purchase residential properties to use as money-making businesses, they can afford to purchase high which brings the comps and cost of housing high and out of reach to regular individuals looking to buy their first home, but now out of reach. Like Air BNB, your use of these half-way homes are part of the problem to affordable real estate.

In addition, some people may need lock-up mental health treatment to keep them and the community safe. Los Angeles is terribly short on mental beds compared to other major cities. Please open up a state run facility! Work of changing mental illness laws for the sake of those who have already refused the offered apartment and ended up dying on the streets. It was NOT a housing problem in Granada Hills, but mental illness that the individual did not realize they had and died on the sidewalk. To be clear: she was offered her own apartment, refused, died. Outreach had been by multiple times and offered her an apartment. Please add more beds to mental facilities so more people can be helped-LA is sorely lacking compared to other major cities.

In addition, zoning laws and regulations were made for good reason. The rules cannot be arbitrarily lifted to permit harm to society because LA politicians believe they cannot solve the massive addiction/mental illness crises. The general population would not have a NIMBY attitude if their safety and well-being were not threatened. Substance abuse, erratic behaviors, petty theft to support bad habits, public nuisance, and vandalism are crimes that add up to a poor quality of life. This does not bode well for a healthy society. The City should not be allowed to put society at risk. After treatment, let's hope they are ready to start over with community support!

To be clear, although I am opposed to any re-zoning, my comments above are not in reference to low income housing, but specifically to Housing First situations with untreated individuals detailed above. For low income housing, I believe this can be done by other means rather than changing rezoning codes and thus, the character of a neighborhood. Why change the essence of a community? We can create low income housing without the rezoning. Los Angeles is following San Francisco with the overpriced, unaffordable housing and it's not right. People of all income levels need to live in a safe and clean community. I have ideas if you care.

1 cont.

Monica Dragavon

[redacted]

file number ENV-2020-6762-EIR

---

**Housing Element** <housingelement@lacity.org> Tue, Sep 7, 2021 at 5:00 PM
To: Monica Dragavon [redacted]

Thank you for your email. Your comments and/or attachments have been received and filed.

Regards,
The Housing Element Team

**Housing Element Staff**
**Los Angeles City Planning**

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# Appendix M-1

Center for Biological Diversity References (Comment Letter O-9)

Molecular Ecology (2008) **17**, 5177–5188 doi: 10.1111/j.1365-294X.2008.03971.x

INVITED REVIEW

# Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches

RAMIRO AGUILAR,*† MAURICIO QUESADA,* LORENA ASHWORTH,† YVONNE HERRERIAS-DIEGO* and JORGE LOBO‡

*Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Campus Morelia, Apartado Postal 27-3 (Xangari), Morelia, 58089 Michoacán, México, †Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba – CONICET, CC 495, (5000) Córdoba, Argentina, ‡Universidad de Costa Rica, Escuela de Biología, 2060 San José, Costa Rica

**Abstract**

**Conservation of genetic diversity, one of the three main forms of biodiversity, is a fundamental concern in conservation biology as it provides the raw material for evolutionary change and thus the potential to adapt to changing environments. By means of meta-analyses, we tested the generality of the hypotheses that habitat fragmentation affects genetic diversity of plant populations and that certain life history and ecological traits of plants can determine differential susceptibility to genetic erosion in fragmented habitats. Additionally, we assessed whether certain methodological approaches used by authors influence the ability to detect fragmentation effects on plant genetic diversity. We found overall large and negative effects of fragmentation on genetic diversity and outcrossing rates but no effects on inbreeding coefficients. Significant increases in inbreeding coefficient in fragmented habitats were only observed in studies analyzing progenies. The mating system and the rarity status of plants explained the highest proportion of variation in the effect sizes among species. The age of the fragment was also decisive in explaining variability among effect sizes: the larger the number of generations elapsed in fragmentation conditions, the larger the negative magnitude of effect sizes on heterozygosity. Our results also suggest that fragmentation is shifting mating patterns towards increased selfing. We conclude that current conservation efforts in fragmented habitats should be focused on common or recently rare species and mainly outcrossing species and outline important issues that need to be addressed in future research on this area.**

*Keywords*: conservation genetics, habitat fragmentation, mating systems, meta-analysis, plant genetic diversity, rarity status

*Received 8 July 2008; revision received 5 September 2008 and 22 September 2008; accepted 24 September 2008*

## Introduction

The development of human civilization throughout the last two centuries has resulted in the transformation of vast natural areas into anthropogenic landscapes, resulting in a process of habitat fragmentation that alters the structure, distribution, and functioning of natural ecosystems (Saunders *et al*. 1991). Immediate consequences of this process include habitat loss, the formation of remnant habitat patches of varied forms and sizes, a reduction of population sizes, and an increase in the degree of isolation of the remaining populations immersed in an anthropogenic matrix (McGarigal & Cushman 2002; Fahrig 2003). These persistent phenomena are well recognized as the main current driving forces of biodiversity loss in terrestrial ecosystems across the planet (Sala *et al*. 2000).

Studies of fragmentation effects in plants have largely concentrated on population demographic processes,

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especially evaluating plant reproductive dynamics in fragmented habitats (Hobbs & Yates 2003; Ghazoul 2005; Honnay *et al*. 2005; Aguilar *et al*. 2006). However, within the last decade there has been an increased interest in assessing the genetic consequences of habitat fragmentation in plants as stated by initial and recent reviews on this subject (Young *et al*. 1996; Lowe *et al*. 2005; Ouborg *et al*. 2006; Honnay & Jacquemyn 2007). The expected genetic consequences of fragmentation, which creates small, discrete, and isolated populations, are based on traditional island biogeography and metapopulation theories (MacArthur & Wilson 1967; Levins 1969). Thus, habitat fragmentation is expected to erode genetic variability and to increase interpopulation genetic divergence of plant populations due to increased random genetic drift and inbreeding, and reductions in gene flow (e.g. Young *et al*. 1996; Sork *et al*. 1999; Lowe *et al*. 2005).

The most immediate effects of fragmentation on the genetic composition of plant populations depend on two factors: the effective population size within fragments and the patterns of genetic variability of the original populations previous to fragmentation (Nason *et al*. 1997; Hamrick 2004). Once a continuous forest is cleared and subdivided into small patches, from a metapopulation viewpoint, the distribution of genetic variability within and between the remaining populations in the landscape will depend on the spatial scale of fragmentation relative to the spatial scale of the pre-existent breeding neighbourhood (Nason *et al*. 1997; Hamrick 2004). Some hypotheses have been proposed to address the effects of habitat fragmentation on plant population genetics. As an immediate result, the genetic variation of populations is reduced due to genetic bottlenecks; specifically, a lower proportion of polymorphic loci and a reduction in the number of alleles per locus are expected within the fragments (Nei *et al*. 1975; Ellstrand & Elam 1993; Young *et al*. 1996). If fragmentation conditions persist over successive generations, decreased heterozygosity due to random drift and increased inbreeding are expected resulting in the accumulation of deleterious recessive alleles, lowering the fecundity of individuals, increasing seed/seedling mortality, and reducing the growth rate of individuals, eventually driving populations to extinction (e.g. Lande 1988; Young *et al*. 1996). The loss of genetic variation may reduce a population's ability to respond to future environmental change, such that the probability of extinction is increased or, at best, opportunities for evolution are limited (Caro & Laurenson 1994; Young *et al*. 1996; Nason *et al*. 1997; Booy *et al*. 2000).

The hypotheses concerning the negative impact of fragmentation on genetic diversity are the basis for the conservation genetic paradigm (Ouborg *et al*. 2006). The field of conservation genetics is relatively recent, and one of its main concerns is to develop basic and applied knowledge to create tools and strategies for conserving the genetic resources and the evolutionary potential of species (Amos & Balmford 2001; Ouborg *et al*. 2006; Pertoldi *et al*. 2007). In order to develop such tools for effective conservation efforts, it is crucial to arrive to generalizations of plant genetic response patterns of plant species to habitat fragmentation.

Nevertheless, the empirical evidence from the literature provides inconsistent results to support these hypotheses, implying that not all fragmentation episodes necessarily result in genetic erosion of plant populations (e.g. Young *et al*. 1996; Collevatti *et al*. 2001; Lowe *et al*. 2005; Kettle *et al*. 2007). In this regard, quantitative statistical approaches are especially useful tools to integrate and synthesize the body of evidence from published literature (Arnqvist & Wooster 1995). Quantitative reviews such as meta-analysis allow us to reach general conclusions about a domain of research despite the apparent contradictory response patterns of individual studies (Gurevitch & Hedges 2001). This is accomplished by treating individual published results as if they were subjected to sampling uncertainty; thus, we are able to obtain not only the magnitude and direction of each effect (regardless of their $P$ values), but also the variability of effects among individual studies (Hedges & Olkin 1985; Arnqvist & Wooster 1995; Gurevitch & Hedges 2001). Consequently, we can estimate the average magnitude of the effect across all studies, test whether the effect is significantly different from zero, and examine potentially causative differences in the effects among studies (Gurevitch & Hedges 2001).

Particular life-history traits of plants may confer different vulnerability to fragmentation effects. Because genetic erosion in fragmented habitats should be more pronounced after several generations, it is expected to find stronger negative effects on the adult generation of short-lived species compared to long-lived species (Young *et al*. 1996); or more precisely, in any plant population subjected to fragmentation conditions for several generations. Similarly, the ability of plants to reproduce clonally, via vegetative spread, may also buffer the genetic effects of fragmentation as a result of delaying the time between generations (Honnay & Bossuyt 2005). Also, the ploidy level of plants may influence the effects on genetic diversity due to fragmentation; as theory predicts, autotetraploids are less subject to the loss of genetic diversity by genetic drift than diploids (Bever & Felber 1992; Moody *et al*. 1993). Finally, the mating system of plants determines the spatial distribution of genetic variation within and among populations (Loveless & Hamrick 1984). Outcrossing plants typically show higher genetic variation within populations, whereas in selfing plants most of the genetic variation is found among populations (Loveless & Hamrick 1984; Hamrick & Godt 1989). Sudden decreases in effective population sizes due to habitat fragmentation would then have stronger negative effects on within-population genetic diversity of outcrossing

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species. The fewer individuals remaining after fragmentation, the more severe the genetic bottleneck, which will have particularly large effects on the maintenance of rare alleles (Nei *et al*. 1975).

Likewise, some ecological processes, especially pollination and seed dispersal of plants, can shape the level of demographic and genetic connectivity among populations in fragmented habitats (Nason *et al*. 1997; Nathan & Muller-Landau 2000; Tewksbury *et al*. 2002; Hamrick 2004). The ability of vectors to move pollen and seeds through the fragmented landscape will determine the potential of plant species to offset the effects of genetic drift. In animal-pollinated or animal seed-dispersed plants, the level of genetic connectivity among fragments will depend on vector distribution, abundance, composition, and behaviour (Nason *et al*. 1997), attributes of pollinators and seed dispersers that are usually affected by habitat fragmentation (Didham *et al*. 1996; Graham 2001; Aizen & Feinsinger 2003; Griscom *et al*. 2007). Therefore, animal-pollinated and animal seed-dispersed plant species are expected to show decreased genetic connectivity due to habitat fragmentation compared to abiotically pollinated and abiotically seed-dispersed plants (Nathan & Muller-Landau 2000; García *et al*. 2007). The rarity of species can also determine susceptibility to genetic erosion. Naturally rare species, defined by their narrow geographical range, restricted habitat specificity or small local population sizes (*sensu* Rabinowitz 1981) are usually genetically less diverse than more widespread or common species (Karron 1987; Hamrick & Godt 1989; Ellstrand & Elam 1993). Then, common species may be more susceptible to lose genetic variation due to habitat fragmentation compared to rare species. Including rarity in models is problematic because authors do not uniformly assess rarity; species categorized as rare are not always *naturally* rare, but rather *recently* rare as a consequence of anthropogenic disturbance and habitat fragmentation (Gitzendanner & Soltis 2000). Thus, this categorization usually overlaps with the conservation status of the species (i.e. recently rare species are typically threatened or endangered). Once common and now rare species are expected to show stronger effects on genetic diversity than naturally rare species, as the former have suffered recent (i.e. in non-*evolutionary time*) decreases in regional or local abundance of populations (Huenneke 1991; Gitzendanner & Soltis 2000).

Certain characteristics of published studies may also influence the sensibility to find fragmentation effects. The ability to find fragmentation effects on genetic parameters may be different when using allozymes vs. DNA-based genetic markers. Specifically, because DNA-based genetic markers such as microsatellites have higher mutation rates (and consequently higher levels of variation), they may have higher resolution to detect changes in inter- and intra-population genetic variation compared to allozymes. Also, fragmentation effects on genetic erosion may not be detected on adult individuals of long-lived woody species, but may be detected in their progeny. Thus, in species of long generational time, the type of tissue used by authors to measure genetic diversity (either from adult or progeny) may determine the magnitude of fragmentation effects. Finally, the time elapsed since fragmentation occurred should be an important factor to assess genetic erosion in plants. Effects are expected to be stronger in plant populations subjected to fragmentation conditions for larger periods of time, where a few or several generations have passed.

In this paper, we conduct a quantitative review to assess the overall effects of habitat fragmentation on plant population genetic parameters and test the predictions of the conservation genetic paradigm. Specifically, we determined (i) the overall magnitude and direction of fragmentation effects on the genetic variability of plant populations; (ii) whether longevity, ploidy level, mating system, clonal growth, type of pollen and seed dispersal vector, and rarity status of plants determine differential susceptibility to genetic erosion in fragmented habitats; (iii) whether different methodological approaches used by the authors determine the ability to find fragmentation effects; and (iv) whether there is a relationship between time elapsed in fragmentation conditions and the magnitude of fragmentation effects in genetic parameters.

## Methods

### *Literature search*

We surveyed the literature through different databases using a combination of 'fragment*' AND 'genet*' AND 'plant' as keywords. Searches were conducted in the Science Citation Index and Biological Abstracts databases and also in the main editorials (Blackwell Science, Springer-Verlag, and Elsevier) and scientific societies that group the most relevant indexed journals of ecological genetics and conservation biology. We obtained a large number of papers that were examined for suitability in the meta-analyses. Considering that habitat fragmentation produces three main outcomes in the landscape (namely habitat loss, decreased population sizes, and increased isolation among populations), we included studies using any of these measures of fragmentation, which were statistically compared to assess whether any one of them had particularly stronger effects on genetic parameters. Thus, we included studies conducted in real habitat fragments, in natural plant populations of different sizes and/or degrees of isolation. We also considered a few studies evaluating the effects of fragmentation due to selective logging on genetic parameters. This type of disturbance introduces changes in population density of adult trees, a measure of population size (Kunin 1997; Lowe

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*et al*. 2005), without necessarily creating habitat fragments. We excluded articles that exclusively analysed correlations among population size and genetic variability without any explicit mention to the effects of habitat fragmentation (see Leimu *et al*. 2006). We included only studies that correlated genetic variability with population size as an indirect assessment of habitat fragmentation effects.

As measures of genetic variability, we considered expected heterozygosity ($H_E$), percent polymorphic loci ($P$), number of alleles ($A$), and inbreeding coefficient ($F_{IS}$). In cases where heterozygosity was not given (typically in studies using random amplified polymorphic DNA or amplified fragment length polymorhphism), we used molecular variance or gene diversity and analysed these parameters together with expected heterozygosity. These four genetic parameters were not necessarily evaluated all together in each study, thus sample sizes for each meta-analysis differed. In several studies, we were able to calculate inbreeding coefficients from observed and expected heterozygosity values ($F_{IS} = H_E–H_O/H_E$). Whenever available, we also included measures of outcrossing rate ($OR$) in fragmented habitats.

For each plant species studied, we gathered information on several life-history traits and ecological aspects as well as on the methodology used by the authors of each study as potential predictors of the genetic responses to habitat fragmentation. We determined: (i) the longevity associated to the different life forms (woody long lived, herbaceous perennial or herbaceous short lived); (ii) whether vegetative reproduction occurred; (iii) the ploidy level (polyploid or diploid); (iv) the mating system, whether a species was mainly outcrossing (which included strictly self-incompatible species, as well as self-compatible species with a predominant outcrossing mating system) or selfing (including species with predominant selfing mating system and some self-compatible species with mixed mating system with clear capability of selfing) as explicitly declared by the authors; (v) pollen dispersal vector (biotic or wind); (vi) seed dispersal vector (biotic or abiotic); (vii) rarity (common, naturally rare or recently rare). We also evaluated the type of genetic marker (allozyme or DNA based) and the plant tissue used for each study (either from adult individuals or progenies). We further searched in each paper for information regarding the time elapsed in fragmentation conditions; this included rough estimates given by authors (expressed as a *few decades or centuries*, *more than* or *between* certain amount of time) and also more precise dates or time periods elapsed. With this information, we created three categories (less than 50 years, between 50 and 100 years, and more than 100 years) to compare the magnitude of effect sizes. Furthermore, within the group of publications where authors gave a more precise date of when fragmentation started, we searched for the approximate lifespan of each species. We found information on lifespans in the same or different publications for 35 out of 47 species. For some species, we used genus-level lifespan information. For the remaining 12 species, we conservatively assigned a tabulated lifespan for woody and non-woody perennials following Ehrlén & Lehtilä (2002). For these species, we calculated the number of generations under fragmentation conditions by dividing the time period of fragmentation by the lifespan of the species, and ran correlation analyses between the number of generations and the effect sizes for $H_E$ and $F_{IS}$. Based on theoretical grounds, these two genetic parameters are expected to be correlated with the number of generations under fragmentation conditions, showing stronger negative effects as more generations pass by. All the species' information was obtained from the same article, from other publications on the same species, or by contacting the authors. However, not every species' characteristic was available, thus predictor variables within a meta-analysis do not necessarily share the same sample size.

Seven articles evaluated the effects of fragmentation on genetic parameters in two species simultaneously and we included each of these species in the same analysis. Because the magnitude and sometimes direction of the responses of each species to habitat fragmentation within the same study were quite different, it is reasonable to assume that the effects are independent for each species (Gurevitch & Hedges 2001).

### *Data analysis*

We used a categorical meta-analytical approach due to the large majority of studies evaluating population genetic parameters of plants in contrasting conditions (i.e. fragmented vs. non-fragmented). We obtained the mean value ($\bar{X}$) and standard deviations (SD) of each genetic parameter ($H_E$, $A$, $P$, $OR$, and $F_{IS}$) from plant populations ($n$) in each of the two conditions (fragmented and continuous habitats) in each published study. These data were taken either from text, tables or graphs (data from graphs were scanned using Datathief II software available online).[1] For each study, the magnitude of the effect of fragmentation on each of the genetic parameters ($d_i$) was estimated as the unbiased standardized mean difference (Hedge's $d$) between the mean value of the genetic parameter in fragmented and continuous habitats:

$$d_i = \frac{\bar{x}^F - \bar{x}^C}{SD^{FC}} J$$

where $\bar{X}^F$ is the mean value of a given genetic parameter in fragmented habitats, $\bar{X}^C$ is the mean value of the same genetic parameter in continuous habitats, $SD^{FC}$ is the pooled standard deviation, of both groups and $J$ is a term

[1] http://www.nikhef.nl/~keeshu/datathief/

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that corrects for bias due to small sample size (see Gurevitch & Hedges 2001). The effect size $d$ can be interpreted as the difference between the genetic diversity of plants in fragmented habitats and continuous conditions, measured in units of standard deviations. Thus, large differences and low variability generate the largest effect sizes (Gurevitch & Hedges 2001). For each genetic parameter, the overall weighted mean effect size estimate ($d^*_{++}$) was calculated as:

$$d^*_{++} = \frac{\sum_{i=1}^{n} w_i d_i}{\sum_{i=1}^{n} w_i}$$

where $d_i$ is the effect size of the $i^{th}$ study and $w_i$ is the weight (reciprocal of the sampling variance) of the $i^{th}$ study.

Positive values of the effect size ($d$) for $H_E$, $A$, $P$, and $OR$, imply positive effects of habitat fragmentation on these parameters whereas negative $d$ values imply negative effects of fragmentation on these parameters. The interpretation of effect sizes for inbreeding coefficients is exactly the opposite: positive values of $d$ imply negative effects of habitat fragmentation (i.e. higher inbreeding) whereas negative $d$ values imply positive effects of fragmentation (i.e. lower inbreeding). For studies using correlational approaches to evaluate fragmentation effects (typically using population size as the independent variable), we calculated the mean value, standard deviation and sample size by pooling the data points for the lower-half (used as fragmented condition values) and higher-half values (used as non-fragmented condition values) of the continuous independent variable.

We used MetaWin 2.0 (Rosenberg *et al*. 2000) to run the analyses and bootstrap re-sampling procedures as described in Adams *et al*. (1997) to calculate confidence intervals of effect sizes. An effect of habitat fragmentation was considered significant if the 95% biased-corrected bootstrap confidence intervals (CI) of the effect size ($d$) did not overlap zero (Rosenberg *et al*. 2000). Confidence intervals based on bootstrapping methods are generally wider than standard CI, which implies that re-sampling estimates of CI are more conservative (Adams *et al*. 1997). Data were analysed using random-effect models (Raudenbush 1994). This model assumes that differences among studies are due to both sampling error and random variation, which is usually the rule in ecological data (Gurevitch & Hedges 2001). The heterogeneity among effect sizes was assessed with $Q$ statistics. Specifically, we examined the $P$ values associated with $Q_{between}$ statistics, which describe the variation in effect sizes that can be ascribed to differences between the categories of each predictor variable (i.e. species' life history and ecological traits, and studies' methodologies). We also used these statistics to compare the effect sizes between studies that used different factors of analyses (e.g. fragment size, logging, population size) to evaluate habitat fragmentation. Within the species used for the meta-analyses, we found few congeneric species (Table S1, Supporting information). We re-ran analyses using data pooled by congeneric species and found no difference in magnitude or direction of effects compared to the analyses performed using all the species as independent data points. We also tested for potential interactions among predictor variables by measuring their pairwise level of dependence with chi-squared tests.

Quantitative reviews of published studies have the intrinsic problem of potential publication bias. That is, studies showing significant results may have a greater probability of publication than those showing non-significant results. We explored this possibility graphically (weighted histograms and funnel plots), and by calculating weighted fail-safe numbers. If the fail-safe number is larger than $5n + 10$, where $n$ is the number of studies, then publication bias may be safely ignored (i.e. results are robust regardless of publication bias; Rosenberg 2005).

## Results

### *Sample of studies*

From the literature search, we obtained 101 publications from 28 international indexed journals throughout the period of 1989–2008 that evaluated the effects of habitat fragmentation on plant population genetic parameters (Appendix S1, Supporting information). These studies measured at least one parameter of genetic variability on 102 unique plant species to conduct the meta-analyses, which yielded 101 data points for expected heterozygosity ($H_E$), 77 data points for number of alleles ($A$), 57 data points for percent polymorphic loci ($P$), 18 data points for outcrossing rate ($OR$), and 62 data points for inbreeding coefficients ($F_{IS}$). Although the species included in this review comprise a wide sample of plants with different biological and ecological attributes, there is some bias in these characteristics and also in the approaches used by authors to study genetic consequences of habitat fragmentation. Herbaceous perennial and woody long lived (shrubs and trees) represent 53% and 40% of the studied species, respectively, while herbaceous short-lived species comprised only 7% of the studied species. There are larger proportions of insect pollinated species (72%) and abiotically seed-dispersed species (77%). Diploid species are also a majority (84%). Although self-compatible (54%) and self-incompatible (46%) plants are approximately equally represented in the sample, within self-compatible plants there is a high number of mainly outcrossing plants as declared by the authors. Hence, there is a higher proportion of mainly outcrossing species (75%) compared with selfing plants (25%). Species without the capability of vegetative reproduction are slightly

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more represented (61%). Common species represent 48%, whereas naturally and recently rare species represent 25% and 27% of the sample, respectively. We found no significant pairwise associations among any of these predictor variables (not shown), which indicate they can be considered statistically independent. Most of the studies evaluate the effects of habitat fragmentation on the genetic variability of adult individuals (72%), using mainly allozymes (60%) as genetic markers.

A comparison of the different factors of analysis used by the authors as measures of habitat fragmentation showed no significant differences in the effect sizes for $H_E$ ($Q_{between} = 1.35$; $P = 0.493$), $A$ ($Q_{between} = 1.68$; $P = 0.441$), $P$ ($Q_{between} = 2.05$; $P = 0.162$), and $F_{IS}$ ($Q_{between} = 0.76$; $P = 0.652$). That is, fragmentation effects on each of these genetic parameters are comparable whether considering fragment size, degree of isolation, habitat loss, population size, or density of conspecifics (i.e. logging) as factors of analysis.

Weighted histograms showed unimodal distributions with the highest frequency around zero (not shown) and funnel plots of effect sizes vs. sample sizes showed no skewness (not shown), which indicates no bias in reporting results (cf. Aguilar *et al*. 2006 for details of interpretation). Similarly, the calculated weighted fail-safe numbers for each meta-analysis were larger than $5n + 10$ [$H_E$: $2249.4 > (5 * 101) + 10 = 515$; $A$: $2805.4 > (5 * 78) + 10 = 400$; $P$: $1444.2 > (5 * 57) + 10 = 295$; $OR$: $168.3 > (5 * 18) + 10 = 100$; $F_{IS}$: $1306.6 > (5 * 62) + 10 = 320$], reinforcing the robustness of these results.

### *Habitat fragmentation and genetic variability*

Overall weighted-mean effect sizes of habitat fragmentation on $H_E$, $A$, and $P$ were negative and significantly different from zero (Fig. 1). The $OR$, which was only consistently assessed in 18 studies, also showed an overall negative weighted-mean effect size (Fig. 1). Habitat fragmentation showed non-significant overall effects on $F_{IS}$ (Fig. 1), despite the small positive value implying a slight trend of increasing inbreeding due to habitat fragmentation.

From the evaluation of all predictor variables associated with the species' life history and ecological attributes for each of the genetic parameters, we present only the results that showed significant $P$ ($< 0.05$) values of $Q_{between}$ statistics in text and figures. We found that fragmentation effects were significantly different for $H_E$ between common, naturally rare and recently rare species ($Q_{between} = 23.18$; $P < 0.001$). On average, common and recently rare species showed strong, negative and significant effects of fragmentation on $H_E$, whereas naturally rare species showed non-significant effects on $H_E$ (Fig. 2a). The same trend was found for $A$ and $P$, although the heterogeneity among effect sizes was only marginally significant (for $A$: $Q_{between}$

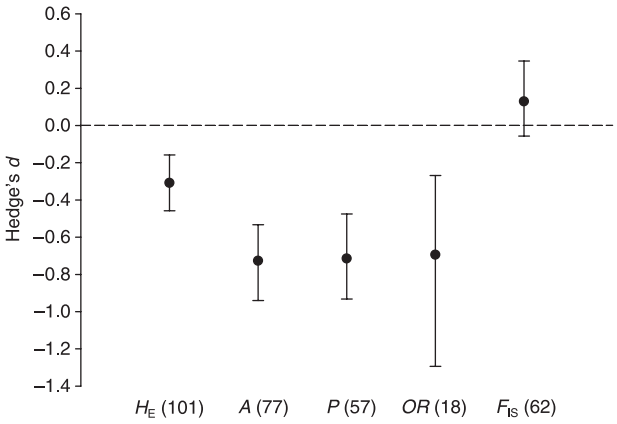


**Fig. 1** Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on expected heterozygosity ($H_E$), number of alleles ($A$), percent polymorphic loci ($P$), outcrossing rate (OR), and inbreeding coefficient ($F_{IS}$). Sample sizes for each meta-analysis are shown in parenthesis; dotted line indicates Hedge's $d = 0$.

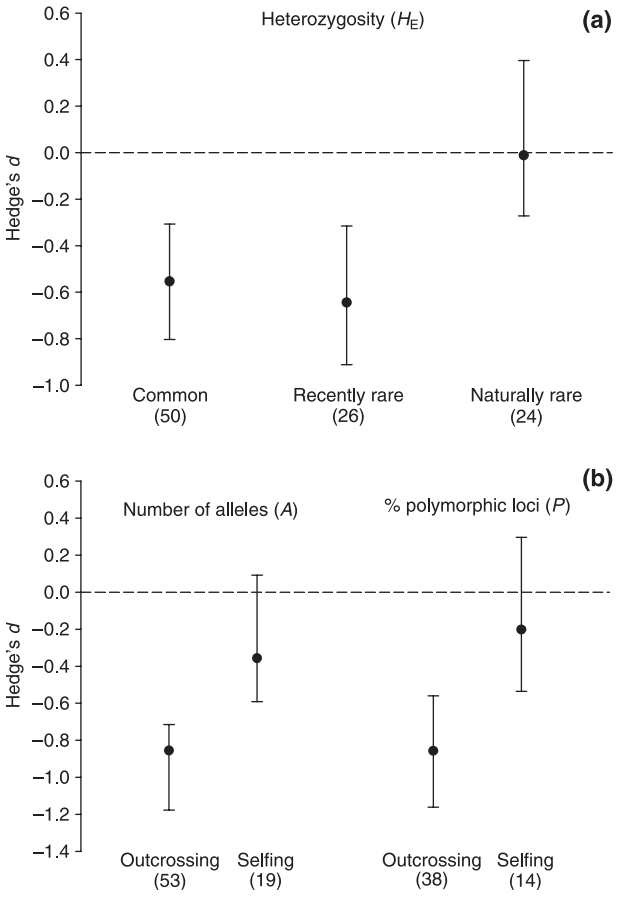


**Fig. 2** Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on (a) $H_E$ of plant species with different categories of rarity (common, recently rare, and naturally rare) and on (b) $A$ and $P$ of plants with different mating systems (outcrossing and non-outcrossing) showing statistically significant heterogeneity ($Q_{between}$). Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

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**Fig. 3** Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on inbreeding coefficient ($F_{IS}$) of studies evaluating adult and progeny tissues. Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

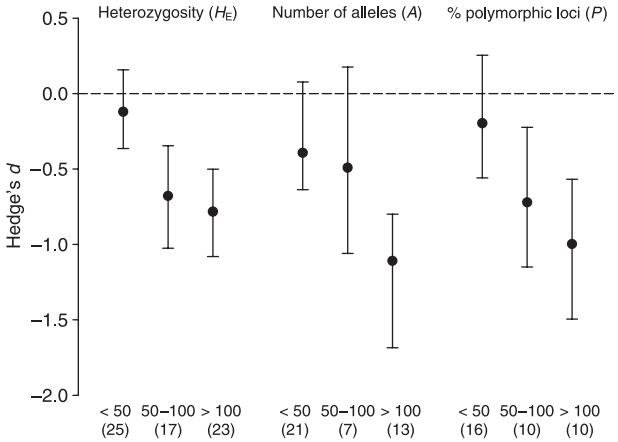


**Fig. 4** Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on $H_E$, $A$, and $P$ of plant populations subjected to different time periods in fragmentation conditions: less than 50 years (< 50), between 50–100 years (50–100), and more than 100 years (> 100). Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

= 4.72; $P = 0.094$; for $P$: $Q_{between} = 5.01$; $P = 0.081$). Furthermore, for $A$ and $P$, there were significant differences in mean effect sizes between outcrossing and selfing species ($Q_{between} = 14.96$; $P = 0.028$ and $Q_{between} = 9.17$; $P = 0.05$ for $A$ and $P$, respectively). Outcrossing species showed stronger negative effects of fragmentation on $A$ and $P$ compared to selfing species (Fig. 2b). A similar but marginally significant trend was observed for $H_E$, [$d_{outcrossing\ (n=69)} = -0.57$, $d_{selfing\ (n=24)} = -0.22$; $Q_{between} = 3.24$; $P = 0.071$]. In the case of inbreeding coefficients, none of these predictor variables showed significant heterogeneity, implying that fragmentation not only does not have an overall effect on inbreeding, but also no particular life-history trait is showing susceptibility to fragmentation (not shown). Surprisingly, fragmentation effects on inbreeding were only studied in one short-lived species, which precluded the formal comparison between short- and long-lived species. None of the other life history (life form, vegetative growth capability, and ploidy level) and ecological traits (pollination and seed dispersal vector types) evaluated as predictor variables showed significant heterogeneity in effect sizes of fragmentation on these genetic parameters (not shown).

The use of different genetic markers (allozymes vs. DNA based) did not significantly alter the magnitude of effect sizes for each of the genetic parameters evaluated in fragmented habitats (not shown). Furthermore, effect sizes of fragmentation on $H_E$, $A$, and $P$ were also homogeneous among studies sampling adult or progeny tissues (not shown). For inbreeding coefficients, on the contrary, there was a significant difference in mean effect sizes between studies evaluating adult and progeny tissues ($Q_{between} = 16.80$; $P = 0.012$; Fig. 3): progenies showed a significant positive overall mean effect size value while adults showed a non-significant mean effect size (Fig. 3). This result implies that progenies generated in fragmented habitats (which comprised mostly non-established seeds) presented higher inbreeding coefficients than progenies produced in continuous habitats; whereas for adult individuals no difference in mean $F_{IS}$ values were observed between fragmented and continuous habitats. Depending on the parameter evaluated, between 53% and 64% of the studies gave at least rough information on the time elapsed in fragmentation condition. Overall, species subjected for more than 100 years in fragmentation conditions had significantly stronger effects on $H_E$ ($Q_{between} = 17.72$; $P = 0.009$), $A$ ($Q_{between} = 6.68$; $P = 0.05$), and $P$ ($Q_{between} = 15.57$; $P = 0.018$; Fig. 4) compared to species evaluated in fragmented systems of less than 50 years, which showed non-significant mean effect sizes on these three genetic parameters (i.e. CI's overlapping zero value; Fig. 4).

Finally, we were able to estimate the number of generations elapsed in fragmentation conditions for 47 and 35 case studies evaluating $H_E$ and $F_{IS}$, respectively. We log-transformed the number of generations and ran correlations with the effect sizes of fragmentation on these two parameters. We found a significant negative correlation between the number of generations elapsed and the species' effect sizes for $H_E$ ($r = -0.36$, $P = 0.012$, Fig. 5). That is, the more generations elapsed in fragmentation conditions for any given plant population, the stronger negative magnitude of effect sizes on $H_E$. In the case of fragmentation effects on inbreeding coefficient, we found a non-significant positive correlation with the number of generations ($r = 0.29$, $P = 0.102$, $n = 35$), suggesting a trend of higher inbreeding as more generations pass by in fragmentation conditions.

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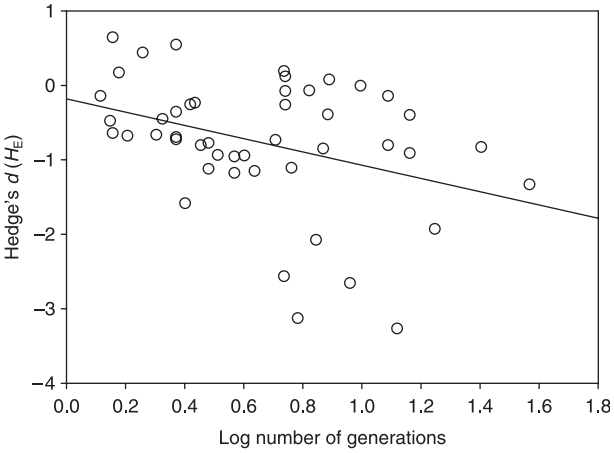


**Fig. 5** Correlation between the log-transformed number of generations of plant populations in fragmented habitats and the effect sizes of fragmentation on $H_E$ for 47 plant species. Correlation coefficient $r = –0.36$, $P = 0.012$.

## Discussion

Anthropogenic habitat fragmentation is a recent phenomenon in evolutionary time but a pervasive feature of modern landscapes (Fahrig 2003). Plant populations that remain in habitat fragments are confronted with modified environments of reduced area, increased isolation, and new ecological boundaries, potentially affecting their biotic and abiotic interactions (e.g. Fahrig 2003; Ewers & Didham 2006). The genetic consequences of fragmentation on plant populations have been studied for over two decades and no clear response patterns have emerged from the literature. Recently, two reviews have focused on the relationship between genetic diversity and population size (Leimu *et al*. 2006; Honnay & Jacquemyn 2007), one of the immediate possible demographic consequences of habitat fragmentation. Nevertheless, fragmentation is a complex process that involves several different factors simultaneously (McGarigal & Cushman 2002; Fahrig 2003; Ezard & Travis 2006; Leblois *et al*. 2006; Ouborg *et al*. 2006); thus analyzing solely reductions of population size may not fully reflect what is happening in real fragmented scenarios. Population size per se may not be very important for animal pollinators and seed dispersers, whereas the degree of population isolation or the matrix characteristics surrounding the fragments may have more influence on their foraging behaviour (Kunin 1997; Ricketts 2001), affecting their ability to maintain gene flow among fragmented populations. These different factors, which often interact in diverse ways, are difficult to separate in observational or non-experimental designs, the rule in fragmentation studies. Authors tend to focus on one factor and do not usually control for the others (Leblois *et al*. 2006; Ouborg *et al*. 2006; but see e.g. Prober & Brown 1994; Honnay *et al*. 2007). Thus, the cause of reduced genetic diversity in fragmented habitats should not be adjudicated to one single factor, but rather to the interacting effects of, at least, population size, degree of isolation and matrix characteristics (Ezard & Travis 2006).

In this review, we explicitly focused on fragmentation studies and arrived at a conclusive generalization: habitat fragmentation decreases the genetic diversity of plant populations. The vast majority of studies were conducted on adult populations of long-lived species in relatively recently fragmented systems, which indicates the effects observed on genetic diversity, especially on $A$ and $P$, are probably mainly the result of genetic bottlenecks, the most immediate consequence of fragmentation (e.g. Young *et al*. 1996; Nason *et al*. 1997; Oostermeijer *et al*. 2003; Lowe *et al*. 2005). These species and studies' characteristics may also be the reason for the absence of overall significant effects on inbreeding coefficients (i.e. most sampled adults have probably established before fragmentation took place) and the comparatively smaller mean effect size observed on $H_E$, which may be mostly due to the overall reduction in number and frequency of alleles (Barret & Kohn 1991; Nason *et al*. 1997). In a closer examination of the subset of studies that provided dates of fragmentation events, it was clearly observed that time and, more precisely, the number of generations elapsed under fragmentation conditions, are crucial in determining stronger genetic diversity reductions in plant populations, especially in heterozygosity, which may take a number of generations to become apparent (Young *et al*. 1996; Lowe *et al*. 2004, 2005). Studies conducted in more than 100-year-old fragmented systems presented significantly stronger negative effects on genetic diversity (Fig. 4). This notion was more specifically supported by the significant correlation between the estimated number of generations for a subset of species and the magnitude of negative fragmentation effects on $H_E$ (Fig. 5), primarily as a result of random genetic drift (e.g. Young *et al*. 1996; Young & Clarke 2000; Lowe *et al*. 2004).

### *Gene flow and mating patterns in fragmented habitats*

The amount of gene flow among remnant populations is a key element that will ultimately determine the genetic consequences of habitat fragmentation (Sork *et al*. 1999; Frankham *et al*. 2002; Hamrick 2004; Sork & Smouse 2006). Moderate or even relatively low levels of gene flow via pollen or seeds between fragmented populations can significantly alleviate the loss of genetic diversity by preventing the effects of genetic drift (e.g. Sork *et al*. 1999; Couvet 2002). In this regard, we found no evidence of any particular pollinator or seed dispersal vector type (either biotic or abiotic) to confer differential susceptibility to the loss of genetic diversity. Although this result does not give

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us information about the patterns of gene flow per se in fragmented habitats, it does indicate there is no obvious type of vector able to conduct consistently extensive gene flow between fragments within the studies analysed.

In the present review, we were not able to evaluate contemporary gene flow due to the current paucity of this kind of study and the difficulty of generating effect size measures from gene flow parameters. However, the results observed for outcrossing rates and inbreeding coefficients may indirectly support the possibility of disrupted gene flow and/or changes in mating patterns of fragmented plant populations. Outcrossing rates in fragmented populations showed a significant overall decrease compared to populations in continuous habitats (Fig. 1), suggesting that fragmented plant populations are suffering changes in mating patterns towards increased selfing. Moreover, inbreeding coefficients will increase immediately in the first generation of progenies if mating patterns are biased towards higher selfing or mating among related individuals (e.g. Young *et al*. 1996; Lowe *et al*. 2005; Kettle *et al*. 2007). Precisely, we found that progenies in fragmented habitats presented significant mean higher inbreeding coefficients than progenies in non-fragmented habitats (Fig. 3), indicating adult individuals in fragmented populations are mating more frequently among related individuals and/or through autogamous pollination.

In addition to reduced heterozygosity due to random genetic drift in populations that remain fragmented for several generations, heterozygosity erosion is more severe when inbreeding accompanies fragmentation (e.g. Young *et al*. 1996; Nason *et al*. 1997; Young & Clarke 2000). The few species subjected to fragmentation conditions for many generations presented quite strong negative effect sizes on $H_E$ (Fig. 5), probably as a result of both drift and increased inbreeding. In the hypothetical scenario of anthropogenic fragmentation ceasing and landscapes remaining as they are today, the effects on genetic diversity of plants will still be much stronger in the future than we have estimated here if mating patterns continue shifting towards selfing.

### *Mating systems*

Self-incompatible (SI) and mainly outcrossing self-compatible species, which contain most of their genetic variability within populations, suffered greater losses of alleles and polymorphic loci than non-outcrossing self-compatible and selfing species. For self-incompatible species in particular, this may result in the loss of low-frequency self-incompatibility alleles (S) (Wright 1965; Nei *et al*. 1975). In genetically controlled self-incompatibility systems, sharing of even a single S allele can prevent mating between individuals (De Nettancourt 2001). Thus, SI plants surviving in small, isolated populations may experience mate limitation due to reduced S allele diversity so that the effective population size is further reduced (Byers & Meagher 1992; Glémin *et al*. 2008). Such synergism between genetic and demographic processes has great potential to influence population viability of these species (Young & Clarke 2000; Glémin *et al*. 2008). In fact, animal-pollinated SI species are also strongly negatively affected in terms of effective pollination service and seed production by habitat fragmentation (Aguilar *et al*. 2006), thus these species are exceptionally vulnerable to fragmentation as a consequence of both, ecological and genetic mechanisms. These results represent a clear example of how genetic erosion can have short-term impacts on individual fitness and population viability (e.g. Cascante *et al*. 2002; Fuchs *et al*. 2003).

### *Rarity status*

Our results support the initial hypothesis regarding the rarity status of plants: because common species have comparatively higher levels of genetic variability than naturally rare species, they are expected to lose more diversity due to recent fragmentation processes. Whether rarity is a cause or a consequence of evolutionary and ecological processes is still an open question (Rabinowitz 1981; Gitzendanner & Soltis 2000). In this regard, naturally and recently rare species may represent different timescales and origins of disturbance, which affect the genetic characteristics they possess in the present (Karron 1987; Ellstrand & Elam 1993; Gitzendanner & Soltis 2000; Oostermeijer *et al*. 2003). If this is true, it would be important to distinguish in the system under study whether habitat fragmentation is a consequence of natural phenomena, and thus occurred through evolutionary time, or whether is the result of anthropogenic activity, occurring in recent ecological times. While evolutionary fragmentation may be a more gradual and slower process that may also 'have an end', ongoing ecological fragmentation is a much faster increasing, non-random process (Saunders *et al*. 1991; McGarigal & Cushman 2002; Fahrig 2003). Given the ubiquitous nature of anthropogenic habitat fragmentation in today's landscapes, the results presented here are important and of interest to conservation biology as they situate common species in potential risk of genetic erosion, which is counterintuitive to current conservation principles that almost exclusively emphasize efforts on rare or threatened species (Honnay & Jacquemyn 2007; Gaston & Fuller 2008).

### *Conservation implications and future directions*

Conservation of genetic diversity within populations has direct implications not only for ecosystem functioning but also for providing resilience in the face of environmental change (Luck *et al*. 2003; Reusch & Hughes 2006). The

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controversy about whether ecological and demographic factors are more important than genetic factors in driving species to extinction (Lande 1988; Frankham *et al*. 2002) has been recently quantitatively assessed: most taxa are not driven to extinction before genetic factors affect them adversely (Spielman *et al*. 2004), an assertion also supported by further research on plants in fragmented habitats (e.g. Endels *et al*. 2007). Thus, revealing which plant traits are more susceptible to suffer genetic erosion in fragmented habitats is crucial to detect lowered evolutionary potential, compromised reproductive fitness, and elevated extinction risks of wild populations, which should help generate criteria to prioritize conservation efforts (Young *et al*. 1996; Young & Clarke 2000; Amos & Balmford 2001; Lowe *et al*. 2005). Our results indicate that such efforts should be directed to common or recently rare species and mainly outcrossing species. Strictly self-incompatible, animal-pollinated species are at even greater risk due to their additional reproductive impairment in fragmented habitats (Aguilar *et al*. 2006).

Despite these unequivocal signals of susceptibility in plants, there is a clear gap in the literature of plant population genetics in fragmented habitats that precluded us making further generalizations. Such is the case of the poor representation of short-lived species as study targets and the dearth of studies evaluating contemporary gene flow via pollen and seeds on plant species with different life forms coupled with ecological information on the biotic dispersal vectors. Also, special attention should be given to the study of established progenies (seedlings and saplings) in fragmented habitats. Most of the progeny tissue evaluated up to now comes from non-established seeds (personal observation) and their genetic composition may differ markedly from that of the progeny that is actually being recruited in fragmentation conditions if they are subjected to selective pressures shaped by seed predators and herbivores (e.g. Cascante *et al*. 2002) and/or if they come from seed banks of previous reproductive episodes (Mandák *et al*. 2006; Honnay *et al*. 2008). Increasing these types of studies may allow us to determine whether gene flow mediated by animals is in fact changing and how changes in mating patterns will affect the genetic diversity of future generations of plant populations. Including precise measures and information on the history and characteristics of fragmented systems is particularly important, not only to determine timescales of fragmentation but also to test for possible fragmentation thresholds below which genetic variation is lost (e.g. Prober & Brown 1994; Ezard & Travis 2006). These approaches imply the merging of population genetics, plant–animal interaction ecology, and landscape ecology, a multidisciplinary endeavor that will provide knowledge-based tools for conserving the evolutionary potential of species and for managing ongoing anthropogenic modified landscapes.

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The authors share research interests in the ecology, evolution and genetics of plant reproductive dynamics. They have been evaluating the effects of forest fragmentation and other anthropogenic disturbances on pollinators, sexual reproduction and the genetic structure of flowering plants. They are interested in generating basic and applied knowledge in ecology and conservation biology of plant-animal interactions and their role in preserving the genetic diversity of plant populations in human-altered landscapes. Other research interests involve the study of hybridization processes between genetically modified plants with native relatives, the role of pollinators as ecological service providers for human well-being, and the conservation of tropical and subtropical dry forests.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Table S1** List of 102 unique plant species included in the meta-analyses. For each species, we provide the botanical family, the genetic parameters evaluated in the study, the molecular marker used, the compatibility system, mating system, pollination vector, seed dispersal vector, ploidy level, vegetative growth capability, life form, type of rarity, studied tissue, time elapsed in fragmentation conditions and the source publication where information was obtained.

**Appendix S1** List of complete references of the studies included in the analyses.

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THE SACRAMENTO BEE

## The State Worker

Chronicling civil-service life for California state workers

THE STATE WORKER

# 249 nights away at California fires: Firefighter families cope with a 'new normal'

BY ADAM ASHTON, RYAN LILLIS AND WILLIAM RAMIREZ
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REDDING — Melissa Morgado began 2018 trying to solve an arithmetic problem: How many nights did she and her firefighter husband spend apart because of work in the previous year?

He was gone for the hot summer months, of course, and again for most of October, and then 19 more days in December when deadly fires broke out on the Central Coast.

Her tally hit 249 nights, the most she and her husband spent apart in his 14 years at Cal Fire.

“I don’t like the term ‘fire season’ anymore. It’s a fire year,” said Morgado, 33, who wrote about their long separations in a popular blog post called “A Year in the Life of a Cal Fire Wife.”

The stress on her home and thousands of other firefighter families in California is another sign of the state’s “new normal” of severe, drawn-out wildfires that begin earlier in the year and run almost to the end of it.

Those expansive fires are leading emergency agencies to change their tactics, and they’re also prompting firefighters and their families to rethink how they manage the strains of long months in harm’s way.

Alarming reports of suicides, substance abuse and domestic violence persuaded Cal Fire Director Ken Pimlott to pour resources into firefighter support services.

“We’re responding to unprecedented kinds of fire. We’re doing everything we have to do, so how do we make sure we’re taking care of our employees?” he said.

An April study released by the nonprofit Ruderman Family Foundation reported that firefighters experience a higher suicide rate than the general American population, and that 103 firefighters killed themselves while 93 died on duty. The report followed a 2015 study that found firefighters experienced an “alarmingly high” rate of suicidal thoughts.

Some firefighters are turning to Cal Fire-sponsored support services that offer counseling in the field and at home fire stations. Others are using union-backed counselors to talk through some of the life-changing scenes firefighters are witnessing on the fire lines.

And some, like Morgado’s family, are making a point to schedule time off even in what used to be considered the peak of California’s fire season.

In the past, "you could assume you'd be home for the holidays. Not anymore," said Cal Fire Deputy Chief Michael Ming, 41, the incoming deputy chief of the department's employee support program.

He, too, has started scheduling vacation days in the late summer so he's ready for what might come in the fall, or later.

## Giving CPR to a baby

Ming is part of a seven-person team in a department-sponsored unit that aims to improve the emotional and psychological well-being of firefighters and their families. The program, called employee support services, dates back to the 1990s. It swelled to resemble its current state — with seven full-time staff members and trained liaisons throughout the state — about five years ago.

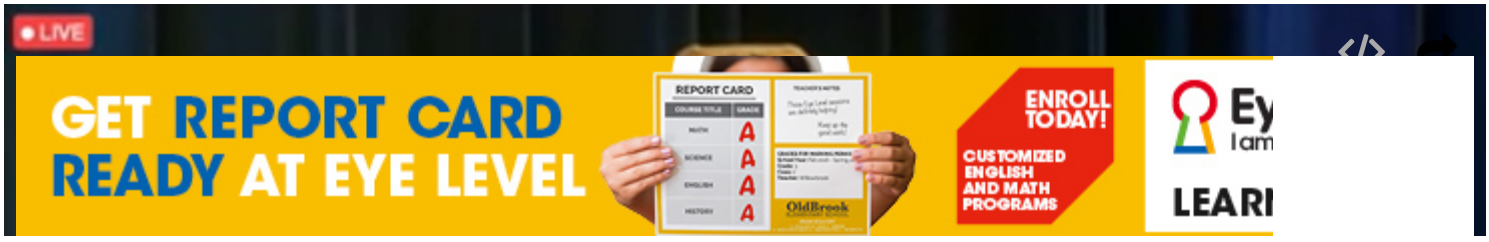
They visit the toughest fires and walk the lines with rank-and-file firefighters. They train firefighters to look for signs of post-traumatic stress in each other, and hold seminars for spouses.

Firefighter unions offer a parallel resource, sending peer counselors to traumatic events, like suicides and firefighter on-duty deaths. California Professional Firefighters, the umbrella organization that advocates for most California fire unions, has trained more than 200 of them.

"What you have to focus on is doing your job and being able to take that experience after it happened, and do some analysis with it," said California Professional Firefighters President Brian Rice, who can still vividly describe the first death he witnessed on duty in the 1980s.

Their efforts to raise awareness about mental health coincides with growing recognition that firefighters carry vivid memories of traumatic events long after their shifts end.

"This is all still groundbreaking," said Los Angeles County Fire Capt. Scott Ross, 53, a peer counselor for the International Association of Firefighters who spent the past week in Redding talking with firefighters battling the Carr Fire. "There are still departments that don't have peer training, but in the last few years, I've seen this trend of people understanding and departments understanding that we have to take care of our own."



A celebration of life was held for the Cal Fire bulldozer operator Braden Varney after he died fighting the Ferguson Fire earlier this month.

By Kayla Fitzgerald

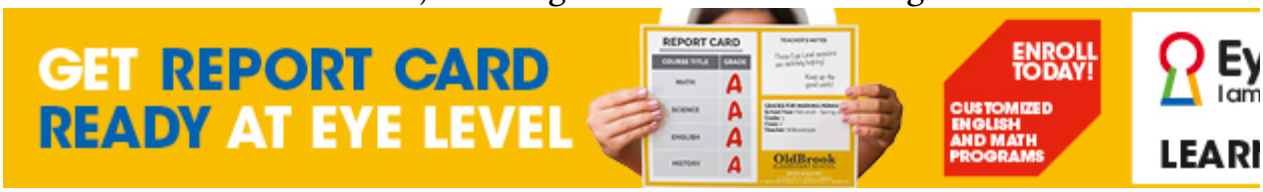
Counselors like Ross build connections with on-the-ground firefighters by listening, and by relating the moments that stayed with them for decades. They leave their phone numbers where they can, and follow up weeks and months later.

Ming, for instance, couldn't sleep at times because he worried an electrical fire would strike his house. His partner, Dattalion Chief Robert Ellis, for decades cried when he remembered the time he tried to resuscitate an infant who had died from sudden infant death syndrome. The baby reminded him of his own daughter.

"I thought I would lose it and end up in a straitjacket," Ellis, 65, said. "I couldn't handle the thought that I might go out of my mind. When I found out my mind was working in a normal way, I could handle that. I could handle being normal. It was the abnormal that scared me."

## 'We're stretched super thin'

This year is shaping up to be another intense one, with massive, deadly wildfires taking off from the North Coast to Yosemite, claiming the lives of three firefighters and a Cal Fire contractor.



“We’re stretched super thin,” Cal Fire firefighter Trevor Pappas said last week in downtown Lakeport, where Cal Fire and U.S. Forest Services battled to check fast-growing blazes. “We have crews everywhere.”

Across the state, firefighters are spending weeks in the field before returning to their homes. Some are confronting life-changing scenes, like the two-day effort to recover Cal Fire firefighter Braden Varney after he tumbled to his death into a steep Mariposa County canyon.

His friends and former colleagues stood watch over him until they could muster up a safe recovery plan that had them lifting his body hand by hand out of the canyon.

“Firefighters knew what was at stake. They knew it was dangerous. The fire was coming. But that’s what firefighters do, and Braden was brought to the road,” Cal Fire’s Nancy Koerperich, Varney’s unit chief, said at his memorial last month.

Exhaustion is setting in for some.

“People are definitely tired. People are working 24 hour shifts: 24 on, 24 off. You can work for 21 days then have two days off and go back out and have 21 days on again,” said Cal Fire spokesman Scott McLean.

Cal Fire last week received permission to hire 300 more seasonal firefighters, who will round out the department’s ranks and help ensure that firefighters can rest as the fires drag on.

“Right now what we’re working on is just trying to get these guys some relief because they’re going nonstop,” said Tim Edwards, the rank and file director for the union that represents Cal Fire firefighters. “These guys have no relief, and that’s what takes a toll, not just their bodies, but their families.”

## Taking time

Morgado, the Cal Fire wife, didn’t like what she saw when she realized that her husband was home for only 109 nights last year. Aside from the 249 he spent at fire stations and in the field, he had a week-long elk hunt that kept him away, too.

They have two children with a third on the way. She wanted her kids to have more time with their dad.

“He just missed out on the first year of his son’s life and almost all of our daughters “terrific 3’s.” He missed the ups and downs of our fast growing children. Next time you see a firefighter, know that they don’t just risk their lives for the lives of strangers. They also sacrifice being present with their families,” Morgado wrote on her blog.

They live in southern Idaho. He commutes for 72-hour shifts at a station in the northeast corner of California. It sounds like a long drive, but many Cal Fire firefighters have similar commutes when they move from station to station as they seek better jobs in the department.

This year, the couple decided they would be better off scheduling more vacation days. That can be complicated for firefighters. They often have to book vacations months, or a year, in advance. Firefighters with more seniority get more leeway.

Her husband has been gone since July 11, but she’s looking forward to a break they scheduled later this month.

“I know there’s a certain day; there’s a light of the end tunnel,” she said.

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# Human-started wildfires expand the fire niche across the United States

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Edited by Gregory P. Asner, Carnegie Institution for Science, Stanford, CA, and approved January 6, 2017 (received for review October 20, 2016)

**The economic and ecological costs of wildfire in the United States have risen substantially in recent decades. Although climate change has likely enabled a portion of the increase in wildfire activity, the direct role of people in increasing wildfire activity has been largely overlooked. We evaluate over 1.5 million government records of wildfires that had to be extinguished or managed by state or federal agencies from 1992 to 2012, and examined geographic and seasonal extents of human-ignited wildfires relative to lightning-ignited wildfires. Humans have vastly expanded the spatial and seasonal "fire niche" in the coterminous United States, accounting for 84% of all wildfires and 44% of total area burned. During the 21-y time period, the human-caused fire season was three times longer than the lightning-caused fire season and added an average of 40,000 wildfires per year across the United States. Human-started wildfires disproportionally occurred where fuel moisture was higher than lightning-started fires, thereby helping expand the geographic and seasonal niche of wildfire. Human-started wildfires were dominant (>80% of ignitions) in over 5.1 million km$^2$, the vast majority of the United States, whereas lightning-started fires were dominant in only 0.7 million km$^2$, primarily in sparsely populated areas of the mountainous western United States. Ignitions caused by human activities are a substantial driver of overall fire risk to ecosystems and economies. Actions to raise awareness and increase management in regions prone to human-started wildfires should be a focus of United States policy to reduce fire risk and associated hazards.**

anthropogenic wildfires | fire starts | ignitions | modern fire regimes | wildfire causes

The United States has experienced some of the largest wildfire years this decade, with over 36,000 km$^2$ burned in 2006, 2007, 2012, and 2015 (1). There is national and global concern over how fire regimes have changed in the past few decades and how they will change in the future (2–4). In the western United States, there is strong evidence that regional warming and drying, including that directly attributed to anthropogenic climate change, are linked to increased fire frequency and size and longer fire seasons (5–9). However, the role that humans play in starting these fires and the direct role of human-ignitions on recent increases in wildfire activity have been overlooked in public and scientific discourse because of the difficulty in ascribing a cause, either human- or lightning-started (10). Humans primarily alter fire regimes in three ways: changing the distribution and density of ignitions, shifting the seasonality of burning, or altering available fuels (2, 3). Geographic variability in regional and continental-scale fire activity in the United States is strongly tied to proxies for these human-caused changes, including population and road density, and different land-use and development patterns (10–15). Although changing climate and fuels also influence fire regimes across the United States (10, 16, 17), there can be no fire without an ignition source. Here, we explore the role that human-started wildfires play in modern United States fire regimes.

Ignitions are often presumed to be saturated (18, 19), and therefore have limited ability to predict fire activity. However, several studies suggest that humans play an important role in redistributing ignitions (20–22), particularly where lightning rarely occurs or where lightning is not concurrent with dry conditions (23). The human–fire connection in the modern era appears strongest at intermediate levels of development, as fires become less likely in the landscape beyond a certain population density, level of urbanization, or dependence on fossil fuels (11, 13, 24). Overall, humans expand the spatial and temporal "fire niche" by introducing ignitions into landscapes when fuels are sufficiently dry enough to ignite and carry fire, but when lightning is rare. Human ignitions are therefore a critical force acting to expand how the fire niche is realized across United States ecoregions.

National-scale analysis of human alteration of the fire niche is critical given that the annual expense of fighting wildfires has exceeded $2 billion in recent years, and the accrued direct and indirect impacts of wildfire on infrastructure and communities could be 30 times that amount (25). Policies that govern wildfire management and response are also directed at the national level, demanding analysis at a national scale (10, 22, 26). Although recent human influence on fire regimes has been studied at local (13) to regional scales (14), human influence nationally remains poorly understood (10). National policies can strongly influence fire regimes (27) and, with sufficient information on human ignitions, policy directives could target human behavior in ways that remediate increasing trends in wildfire risk.

Here, we ask how human ignitions have altered the spatial extents, seasonality, and temporal trends in wildfire across the coterminous United States. We analyze over 1.5 million records of both human- and lightning-started fires in the United States from

## Significance

**Fighting wildfires in the United States costs billions of dollars annually. Public dialog and ongoing research have focused on increasing wildfire risk because of climate warming, overlooking the direct role that people play in igniting wildfires and increasing fire activity. Our analysis of two decades of government agency wildfire records highlights the fundamental role of human ignitions. Human-started wildfires accounted for 84% of all wildfires, tripled the length of the fire season, dominated an area seven times greater than that affected by lightning fires, and were responsible for nearly half of all area burned. National and regional policy efforts to mitigate wildfire-related hazards would benefit from focusing on reducing the human expansion of the fire niche.**

Author contributions: J.K.B., B.A.B., and J.T.A. designed research; J.K.B., B.A.B., J.T.A., and R.C.N. performed research; J.K.B., B.A.B., J.T.A., and R.C.N. contributed new reagents/analytic tools; J.K.B., B.A.B., J.T.A., R.C.N., E.J.F., and A.L.M. analyzed data; and J.K.B., B.A.B., J.T.A., R.C.N., E.J.F., and A.L.M. wrote the paper.

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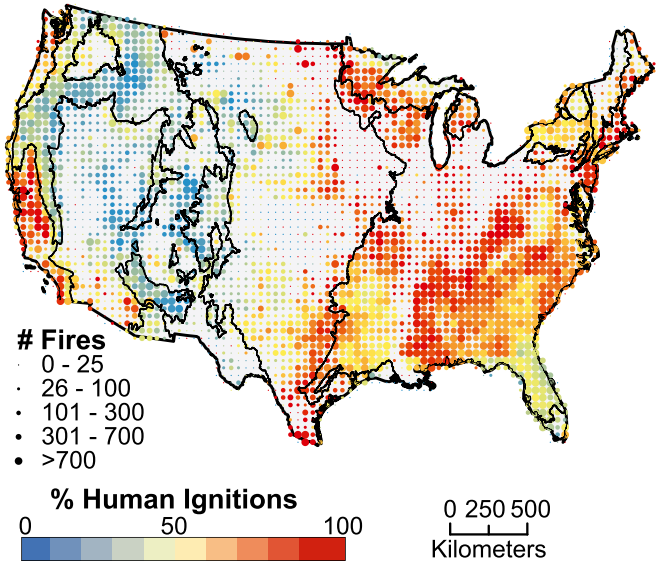


**Fig. 1.** The total number of wildfires (dot size) and the proportion started by humans (dot color: red indicating greater number of human started fires) within each 50 km × 50-km grid cell across the coterminous United States from 1992 to 2012. Black lines are ecoregion boundaries, as defined in the text.

1992 to 2012 (28). All of these wildfires necessitated an agency response to manage or suppress them, and therefore posed a threat to ecosystems or infrastructure; this record does not include intentionally set prescribed burns or managed agricultural fires. To our knowledge, this is the most comprehensive assessment of the role of human-started wildfires across the United States over the past two decades. We compare: (*i*) the spatial extents of human- vs. lightning-started wildfires, (*ii*) the seasonality of human vs. lightning wildfires, (*iii*) the climate niche for human- vs. lightning-started wildfires, and (*iv*) 21-y trends in large human vs. lightning wildfires. Our analysis documents the pronounced expansion of wildfire extent, seasonality of wildfires, and increasing numbers of large wildfires through time as a result of human-related ignitions across the United States.

## Human-Related Ignitions Vastly Expanded the Extent of Wildfire

Human-started wildfires represented 84% of the 1.5 million wildfires included in this analysis ($n$ = 245,446 lightning-started fires; $n$ = 1,272,076 human-started wildfires). The eastern United States and western coastal areas were dominated by human-started wildfires, whereas lightning-started fires dominated the mountainous regions of the western United States (Fig. 1, Table 1 and Table S1). Here we define a fire regime as dominated by either human or lighting ignitions when one cause accounts for more than 80% of the number of fires in a given 50 × 50-km grid cell. Based on this definition, 5.1 million km$^2$, or 60% of the total land area of the coterminous United States, was dominated by human-started wildfires, whereas only 0.7 million km$^2$, or 8% of the area, was dominated by lightning-started fires. In addition to expanding the numbers of fires, humans also expanded the total area burned. Human-started wildfires burned a total of 160,274 km$^2$, or ∼44% of the total area burned from 1992 to 2012 (Table 1).

## Human-Related Ignitions More Than Tripled the Length of the Wildfire Season

Human ignitions dramatically expanded the wildfire season in the United States, particularly during spring. The length of the human-started wildfire season [defined as the interquartile range (IQR) of human-ignited fires] was 154 d, more than triple that of the lightning wildfire season (IQR = 46 d) (Fig. 2 and Table 1). This national-scale expansion is driven by earlier (spring) human-started fires in eastern ecoregions coupled with later (late summer or fall) human-started fires in western ecoregions (Table S2). The median discovery date for human-started fires was over 2-mo (May 20th) earlier than lightning-started fires (July 25th). Summed across the 21-y record, the most common day for human-started fires by far was July 4th, US Independence Day, with 7,762 fires starting that day over the course of the record (Fig. 2), whereas, the most common day for lightning-started fires was July 22nd. Of all lightning-ignited fires, 78% occurred in the summer (June–August), 9% in the spring (March–May), and 12% in the fall (September–November). In contrast, human-ignited wildfires were more evenly distributed throughout the year, with 24% in summer, 38% in spring, 19% in fall, and 19% in winter. This pronounced expansion of the wildfire season was also evident spatially (Fig. 3), with human-ignited wildfires occurring predominantly in spring in the eastern United States and in the fall and winter in Texas and the Gulf states. See Table S1 for state-level analysis. When lightning-started fires were rare (<5% and >95% quantile; i.e., before May 13th or after September 16th), humans ignited 842,289 wildfires, effectively increasing the number of wildfires 35-fold compared with the 24,081 lightning-ignited wildfires during these spring, fall, and winter seasons.

**Table 1. The number of wildfires, total burned area (ha), and fire season length (IQR, in days), by ecoregion (ordered by percent human-caused fires) and within the coterminous United States from 1992 to 2012**

| | No. of fires | | | Area burned (ha) | | | Length (IQR, days) | | |
|---|---|---|---|---|---|---|---|---|---|
| Ecoregion | Human | Light | Human caused (%) | Human | Light | Human caused (%) | Human | Light | Human expansion (%) |
| MC | 87,274 | 2,855 | 97 | 2,143,282 | 253,210 | 89 | 85 | 45 | 189 |
| NF | 61,673 | 2,574 | 96 | 302,561 | 82,721 | 79 | 51 | 79 | N/A |
| ETF | 815,499 | 44,859 | 95 | 3,827,045 | 829,293 | 82 | 167 | 66 | 253 |
| MWCF | 14,586 | 925 | 94 | 19,251 | 27,291 | 41 | 67 | 52 | 129 |
| GP | 134,944 | 17,586 | 88 | 3,992,557 | 2,564,955 | 61 | 148 | 47 | 315 |
| SSH | 7,504 | 2,167 | 78 | 340,873 | 254,418 | 57 | 55 | 41 | 134 |
| TWF | 4,832 | 1,917 | 72 | 357,150 | 350,477 | 50 | 98 | 52 | 188 |
| NAD | 55,422 | 52,044 | 52 | 2,394,677 | 8,880,691 | 21 | 92 | 40 | 230 |
| NFM | 76,735 | 94,017 | 45 | 1,895,622 | 5,731,733 | 25 | 75 | 36 | 208 |
| TS | 13,607 | 26,502 | 34 | 754,393 | 1,152,064 | 40 | 85 | 39 | 218 |
| CONUS | 1,272,076 | 245,446 | 84 | 16,027,412 | 20,126,852 | 44 | 154 | 46 | 335 |

CONUS, Coterminous United States; ETF, Eastern Temperate Forests; GP, Great Plains; MC, Mediterranean California; MWCF, Marine West Coast Forests; NAD, North American Desert; NF, Northern Forests; NFM, Northwest Forested Mountains; SSH, Southern Semiarid Highlands; TWF, Tropical Wet Forests; TS, Temperate Sierras.

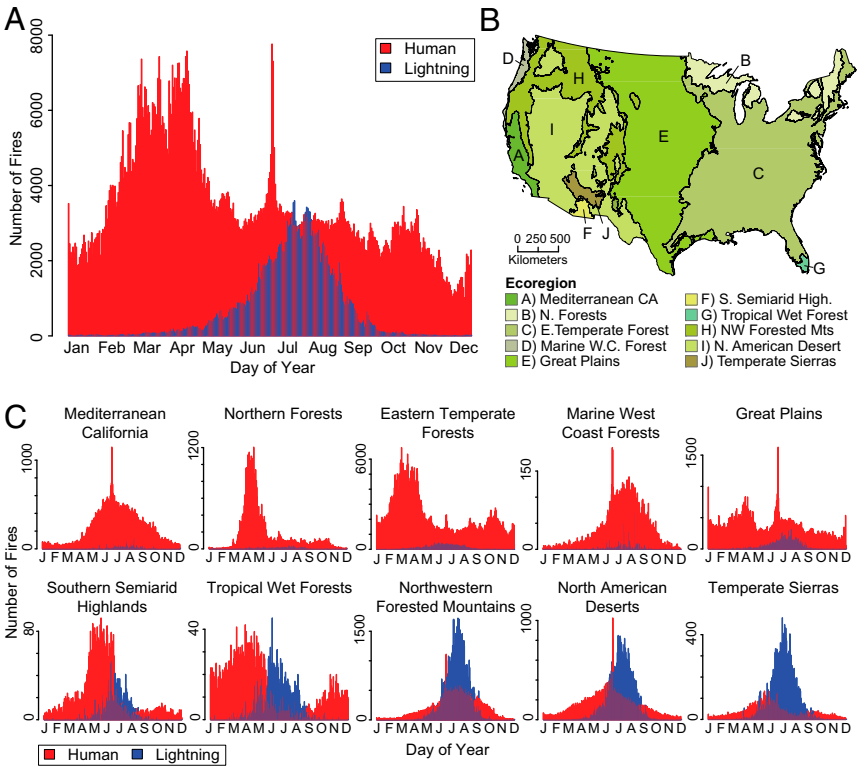


**Fig. 2.** Frequency distributions of human and lightning-caused wildfires by Julian day of year. (*A*) Frequency distribution of wildfires across the coterminous United States from 1992 to 2012 ($n$ = 1.5 million); (*B*) map of United States ecoregions; (*C*) frequency distributions of wildfires by ecoregions, ordered by decreasing human dominance.

## Human-Driven Expansion of the Fire Niche

Humans greatly expanded the natural fire niche (Fig. 4), which we calculated as the co-occurrence of the average monthly lightning density and 1,000-h dead fuel moisture. Regions and seasons of moderate to high lightning-started fire density (>0.4 fires per 1,000 km$^2$ per month) had a median lightning-strike density of 0.19 (IQR: 0.065–0.57) strikes per square kilometer per month and a median 1,000-h fuel moisture of 11.9% (IQR: 9.25–15.6%) (Fig. 4*A*). In contrast, regions and seasons of moderate to high human-started fire density (>0.4 fires per 1,000 km$^2$ per month) had a median lightning-strike density of only 0.11 (IQR: 0.025–0.39) strikes per square kilometer per month and a median 1,000-h fuel moisture of 17.8% (IQR: 15.95–19.25%) (Fig. 4*B*). The median fuel moisture and lightning conditions when human-started wildfires occurred were significantly different from those values for lightning-started fires ($P < 0.0001$). Areas and months of moderate to high human-caused fire density had approximately 40% fewer lightning strikes, and nearly 50% higher fuel moisture levels (based on median values) than for moderate to high lightning-caused fire density. Additional exploration of the fire niche for human-started and lightning-started fires relative to lightning density, fuel moisture, and net primary production (NPP), a proxy for fuels, is provided in Figs. S1 and S2.

## Increasing Trends in Large Human-Started Wildfires

During the 21-y time period, there were significant increasing trends in large wildfires ignited by both lightning ($n$ = 4,312; Theil-Sen estimated slope = 12.2; $P$ = 0.001) and humans ($n$ = 4,143; Theil-Sen estimated slope = 3.6; $P$ = 0.004) (Fig. S3). There was a strong dichotomy in human vs. lightning trends seasonally (Fig. 5). Overall trends in lightning-caused fires were primarily driven by increasing numbers of large summer fires (Fig. 5*B*), whereas overall trends in human-caused fires were primarily driven by increasing numbers of large spring fires (Fig. 5*D*). Spatially, lightning-caused fires increased the most in the Northwest Forested Mountains ecoregion (Fig. S4*A*), whereas human-caused wildfires increased the most in the Great Plains ecoregion (Fig. S4*B*).

## Discussion

Humans, the keystone fire species (29), play a primary role in spatially and temporally redistributing ignitions and resulting wildfires. We document that over 84% of the government-recorded

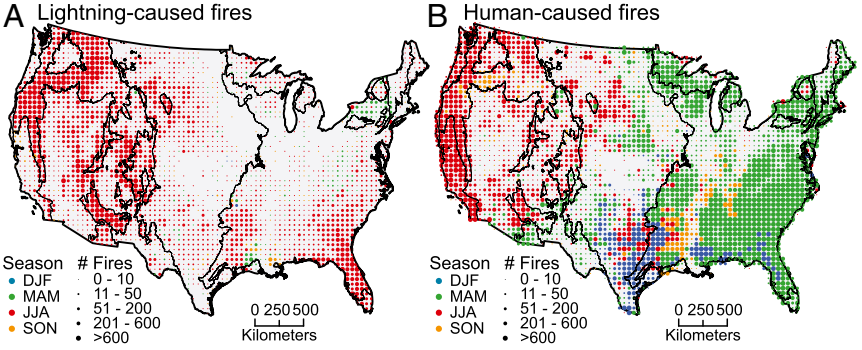


**Fig. 3.** Comparison of seasonality for (*A*) lightning- vs. (*B*) human-ignited wildfires. Human ignitions expand the seasonal fire niche considerably into spring and fall months. Colors show the season with the maximum ignitions caused by lightning and human within each 50 km × 50-km grid cell. Size of dot indicates the number of unique lightning and human fires between 1992 and 2012. Ecoregion boundaries are overlaid for visualization.

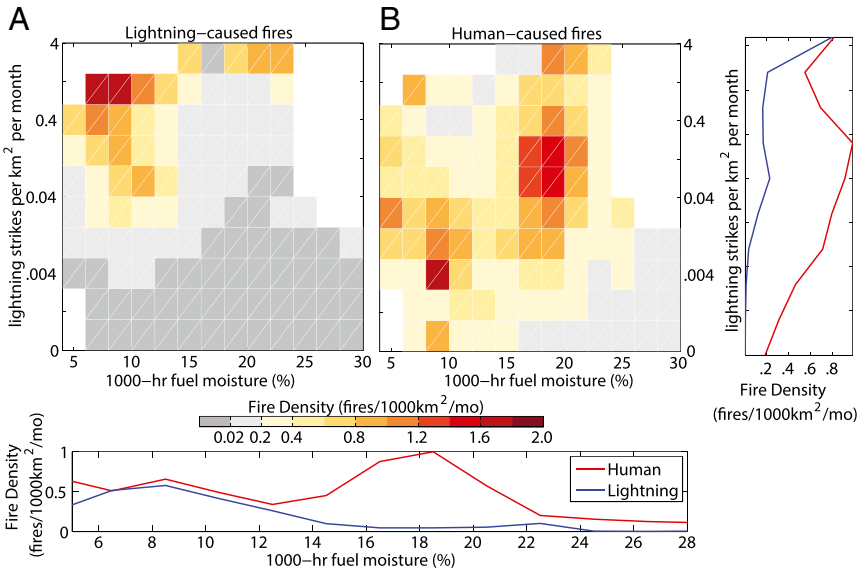


**Fig. 4.** Human vs. lightning fire niche relative to fuel moisture and lightning density, with greatest resulting wildfire density represented by dark red. (*A*) Lightning-started fires occur in areas with high lightning-strike density and dry fuels. (*B*) Human-started wildfires expand the fire niche to include areas with low lightning-strike density as well as areas with higher fuel moisture. Graphs on the bottom and far right show histograms of 1,000-h dead fuel moisture and lightning strikes, respectively, for human- and lightning-started fires.

wildfires were started by people from 1992 to 2012. Sixty percent of the total land area of the coterminous United States was dominated by human-started wildfires, whereas only 8% of the area was dominated by lightning fires. Humans tripled the length of the wildfire season, extending burning into the spring, fall, and winter months. During the spring, fall, and winter, people added more than 840,000 wildfires, a 35-fold increase over the number of lightning-started fires in those seasons. This expansion of the fire-niche was caused by human-related ignitions under higher fuel moisture conditions, compared with lightning-started fires. Moreover, during this 21-y record, large human-started wildfires increased significantly.

There was a strong national east–west dichotomy in the spatial distribution of human-started wildfires. Although human-started wildfires were pervasive across the United States (Fig. 1), the expansion of human-started wildfires relative to lightning-started fires was most dramatic in the eastern United States and central and southern California (Figs. 1 and 2*C*). Recent work for California confirms the important role of humans, with anthropogenic variables explaining half of the variability in fire probability over the past four decades (30). In contrast, lightning-started fires were found primarily in the intermountain west and Florida and occurred predominantly in the summer, reflecting national lightning strike patterns (31) (Fig. 2*C*). This finding supports other studies of human vs. lightning ignition sources that have found an important distinction between eastern and western United States fire patterns (10, 21) and drivers (32). Some explanations for this distinction include higher population and housing densities, lower proportions of public land, and more extensive land use and development in the eastern United States (33, 34), all of which could lead to more sources of anthropogenic ignitions. Synchrony between lightning activity and the seasonal nadir of fuel moisture in the western United States also likely contributes to these geographic differences. However, even with a projected increase in the number of lightning strikes as a result of anthropogenic climate change (50% by 2100) (35), humans would still remain the dominant ignition source across the majority of the United States land area. The majority of the wildfires requiring agency suppression in the east can be attributed to escaped fires from debris burning occurring in the spring months (or winter in Texas and the Gulf Coast) (Fig. 3). Between 1992 and 2012, wildfires caused by debris burning tended to be small (median

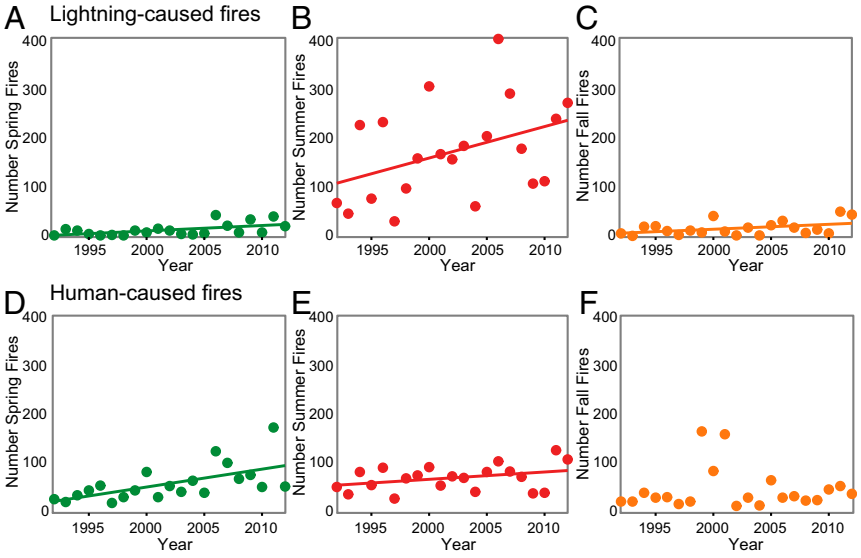


**Fig. 5.** Trends in the number of large wildfires verified by MTBS records from 1992 to 2012 for lightning-started fires (*A*–*C*) vs. human-started fires (*D*–*F*) in the spring (green: *A* and *D*), summer (red: *B* and *E*), and fall (orange: *C* and *F*). Where trend lines are shown, Theil-Sen estimated slopes are significantly different from zero ($P < 0.05$).

fire size 0.4 ha, IQR: 0.14–1.62 ha), but still an important source of risk to surrounding ecosystems. At finer scales, there are also notable patterns in human- vs. lightning-started wildfires (Fig. S5). Increased wildfires can follow road networks (36), the wildland–urban interface (13), and boundaries between agricultural and forested areas (37), highlighting just a few examples of how human activities and cultural drivers provide ignitions that substantially change the distribution of fire across the United States (38).

Our findings reinforce the strong imprint of people on fire regimes through changes in wildfire seasonality, which has been documented globally (39). In the past few decades, early onset of warmer and drier conditions has promoted greater fire activity across the western United States (6, 7, 40). However, our study highlights the equally important role of human ignitions in changing modern fire regimes by increasing the fire season length to encompass the entire year. The vast majority (78%) of lightning-started fires occurred during the summer months, whereas 76% of human-started fires occurred during the spring, fall, and winter months. Moreover, this trend varies substantially by ecoregion, reflecting again the principle dichotomy between the eastern and western United States (Fig. 3). Human-started fires extend the fire season earlier in the east, and later in the west (Fig. 3 and Table S2). Observations suggest that climate change has extended the duration of the fire weather season across most of the globe, including parts of the United States by a couple of weeks over the past three decades (5, 9), whereas we show that human ignitions in the United States increased the length of the fire season by more than three mo. There was also a notable mark of American culture on the distribution of wildfires, with the peak day of wildfires occurring on July 4th, concurrent with Independence Day fireworks displays (Fig. 2). Indeed, Americans start over twice as many wildfires on July 4th as any other summer day. A similar cultural mark has also been demonstrated globally with a marked decline in wildfires on Sunday compared with other weekdays (41).

Thus, at the national scale, human ignitions dramatically expand the spatial and seasonal niche of fire. The key components that define the fire niche are ignition sources, fuel mass, and desiccation. By exploring the fire niche along these axes, our results show that lightning fires are primarily constrained to areas with a lightning-strike density of greater than 100 strikes per grid cell per month (0.04 strikes/km$^2$ per month) and are concurrent with drier fuels (< 15% fuel moisture) (Fig. 4). Human ignitions expand fires into regions with higher fuel moisture (Fig. 4) and higher NPP (Figs. S1 and S2), suggesting that humans create sufficient ignition pressure for wetter fuels to burn. As a consequence, human ignitions have expanded the fire niche into areas with historically low lightning-strike density, such as Mediterranean California, or low concurrence of lightning and dry conditions, such as Eastern Temperate Forests (Fig. 1).

Over the past two decades, there was a significant increase across the United States for both human- and lightning-caused large fires (Fig. S3). The significant increase in large lightning fires is driven primarily by fires in summer months (Fig. 5) in the Northwest Forested Mountains ecoregion of the western United States (Fig. S4). This finding is consistent with other studies that have demonstrated an increase in large fires across the western United States (6, 7, 40), likely as a consequence of changes in climate and fuels rather than ignitions. In contrast, the significant trend in human-caused fires is primarily driven by an increase in large fires during spring months (Fig. 5) in the Great Plains ecoregion of the United States (Fig. S4). This increasing trend suggests that earlier springs as a result of climate change (42, 43) may be interacting with human ignition sources to increase the risk of large fires in the central United States.

The strong year-to-year variability in human ignitions (Fig. S3 and S4) may reflect the degree to which human choices can affect fire regimes. However, interannual climate variability also influences fuel moisture, NPP, and short-term weather conditions that enable the spread of human-ignited wildfires (44). There was a significant temporal correlation between large human- and lightning-started fires ($R$ = 0.75). This pattern has been observed previously in the western United States (23) and suggests that large-scale climate drivers affect the frequency of both human- and lightning-caused fires. It is unknown how human actions will be affected by hotter and drier conditions, potentially increasing or decreasing ignitions from land use, recreation, and other sources. Increased public awareness and focused policy and management, particularly in years with elevated fire risk associated with climatic anomalies, are needed to reduce the number of human-caused ignitions.

In conclusion, we demonstrate the remarkable influence that humans have on modern United States wildfire regimes through changes in the spatial and seasonal distribution of ignitions. Although considerable fire research in the United States has rightly focused on increased fire activity (e.g., larger fires and more area burned) because of climate change, we demonstrate that the expanded fire niche as a result of human-related ignitions is equally profound. Moreover, the convergence of warming trends and expanded ignition pressure from people is increasing the number of large human-caused wildfires (Fig. 5). Currently, humans are extending the fire niche into conditions that are less conducive to fire activity, including regions and seasons with wetter fuels and higher biomass (Figs. 3 and 4). Land-use practices, such as clearing and logging, may also be creating an abundance of drier fuels, potentially leading to larger fires even under historically wetter conditions. Additionally, projected climate warming is expected to lower fuel moisture and create more frequent weather conditions conducive to fire ignition and spread (45), and earlier springs attributed to climate change are leading to accelerated phenology (42). Although plant physiological responses to rising $CO_2$ may reduce some drought stress (46), climate change will likely lead to faster desiccation of fuels and increased risk in areas where human ignitions are prevalent.

Uncertainty remains regarding how anthropogenic climate change will alter wildfire activity geographically and seasonally (47, 48), particularly in areas where human-caused fires dominate. Moreover, the current wildland–urban interface, where houses intermingle with natural areas, constitutes 9% of the United States total land area (33) but is projected to double by 2030, predominantly in the intermountain West (49). This expected development expansion will increase not only ignition pressure, but also the vulnerability of new infrastructure. Human-driven expansion of the spatial and temporal distribution of ignitions makes national- and regional-scale policy interventions and increased public awareness critical for reducing national wildfire risk.

## Materials and Methods

For this analysis, we used the publically available US Forest Service Fire Program Analysis-Fire Occurrence Database (FPA-FOD) (28). This comprehensive dataset includes United States federal, state, and local records of wildfires (both on public and private lands) that were suppressed from 1992 to 2012, a total of ~1.6 million records. Previous studies have focused on the western United States (20), federal lands (22), or records from just one agency (21). Each entry includes at minimum the location, discovery date, and cause of the wildfire. We excluded 114,191 wildfires with an unknown cause and analyzed the spatial, seasonal, and temporal patterns of human- vs. lightning-started wildfires. In total, 1,517,522 wildfires were included in the analysis. Human-started wildfires were caused by a variety of sources, including the US Forest Service-designated categories of equipment use, smoking, campfire, railroad, arson, debris burning, children, fireworks, power line, structure, and miscellaneous fires (28). Spatially, we calculated the proportion of human- vs. lightning-caused wildfires within equal-area 50 × 50-km grid cells across the coterminous United States. This grid size corresponds roughly to the size of an average United States county. For each grid cell, we calculated the season (winter, spring, summer, or fall) when the majority of human-caused and lightning-caused wildfires were started. All spatial analyses were conducted in the Albers-Conical equal-area projection. To determine the seasonal distribution of wildfires, we plotted the distribution of human- and lightning-started fires by the day of year for the coterminous United States and for individual ecoregions. We used the level 1 ecological regions of North America, developed by the Commission for Environmental Cooperation (50). We calculated the length of the human- and lightning-caused fire seasons as the IQR of the Julian day of recorded fire ignition: that is, the difference between the first and third quartiles.

We determined how humans expanded the fire niche by comparing the lightning-strike density (i.e., natural ignition pressure) and fuel-moisture conditions under which actual human- and lightning-started fire events occurred. We obtained daily 1,000-h dead fuel moisture data from the surface meteorological data (51) on a 4-km grid from 1992 to 2012, and computed monthly averages across the 21-y study period. We obtained 4-km gridded monthly lightning-strike data from the Vaisala National Lightning Detection Network (https://www.ncdc.noaa.gov/data-access/severe-weather/lightning-products-and-services) and averaged the data over the 21-y study period. To account for fuel limitations, we also explored the fire niche as a function of fuel amount (approximated by NPP). We used MODIS mean annual NPP data (1-km resolution, from 2002 to 2015) (52) for this purpose. These three datasets were aggregated to the common 50 × 50-km grid cell. We calculated the number of human- and lightning-started fires by grid cell using the FPA-FOD dataset (28). We excluded any grid cells from subsequent analyses that did not report at least one lightning-caused or human-caused wildfire over the period of record. We tested whether fire niche expansion (as determined by fuel moisture and lightning-strike density) caused by human ignitions was significant based on Mann–Whitney tests between human- vs. lightning-started fires.

To assess trends in human- vs. lightning-caused wildfires through time, we used only large fires that were independently verified by the Monitoring Trends in Burn Severity (MTBS) project (53). We specifically focused on these large fires (>400 ha in the west, >200 ha in the east; $n$ = 8,455) for comparability with previous research, which has examined temporal trends in the western United States and the link to climate warming (6, 7, 40), but has not investigated the relative contribution of human-started fires at a national scale. In addition to overall temporal trends, we tested for significant trends by ignition source versus season (spring, summer, fall) and versus ecoregion based on the level I ecological regions of North America (50). We explored a similar analysis using all available FPA-FOD data, but changes in reporting frequency through time for some states precluded a robust temporal analysis. We tested for trends in wildfire numbers through time using the nonparametric Theil-Sen estimator (54) and tested for trend significance using nonparametric Mann–Kendall tests (55).

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Systematic review

# The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis

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ABSTRACT

Biodiversity is being lost at an increased rate as a result of human activities. One of the major threats to biodiversity is infrastructural development. We used meta-analyses to study the effects of infrastructure proximity on mammal and bird populations. Data were gathered from 49 studies on 234 mammal and bird species. The main response by mammals and birds in the vicinity of infrastructure was either avoidance or a reduced population density. The mean species abundance, relative to non-disturbed distances (MSA), was used as the effect size measure. The impact of infrastructure distance on MSA was studied using meta-analyses. Possible sources of heterogeneity in the results of the meta-analysis were explored with meta-regression.

Mammal and bird population densities declined with their proximity to infrastructure. The effect of infrastructure on bird populations extended over distances up to about 1 km, and for mammal populations up to about 5 km. Mammals and birds seemed to avoid infrastructure in open areas over larger distances compared to forested areas, which could be related to the reduced visibility of the infrastructure in forested areas. We did not find a significant effect of traffic intensity on the MSA of birds. Species varied in their response to infrastructure. Raptors were found to be more abundant in the proximity of infrastructure whereas other bird taxa tended to avoid it. Abundances were affected at variable distances from infrastructure: within a few meters for small-sized mammals and up to several hundred meters for large-sized mammals.

Our findings show the importance of minimizing infrastructure development for wildlife conservation in relatively undisturbed areas. By combining actual species distributions with the effect distance functions we developed, regions sensitive to infrastructure development may be identified. Additionally, the effect distance functions can be used in models in support of decision making on infrastructure planning.
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## 1. Introduction

Global biodiversity is changing at an unprecedented rate as a result of several human-induced changes in the global environment (Vitousek, 1994; Pimm et al., 1995; Sala et al., 2000; MEA, 2005). Biodiversity loss at the species level tends to result in the so-called homogenisation process (Lockwood and McKinney, 2001). This process is generally characterised by a decrease in the abundance of many species, culminating into an increase in the number of threatened species and the extinction of others, in combination with a simultaneous increase in the abundance of a few species. The main drivers of biodiversity change are land-use and land-cover change, climate change, pollution, fragmentation and infrastructure development (UNEP, 2001; Sala et al., 2000; Sanderson et al., 2002; Alkemade et al., 2009).

The ubiquity of road networks and the growing body of evidence of the negative impacts that roads and other linear infrastructure have on wildlife and ecosystems suggest that infrastructure represents a major driving factor of biodiversity loss. The most commonly reported impacts from roads and utility corridors include habitat loss, intrusion of edge effects in natural areas, isolation of populations, barrier effects, road mortality and increased human access (Andrews, 1990; Forman and Alexander, 1998; Spellerberg, 1998; Trombulak and Frissell, 2000; Forman et al., 2003). Road construction leads to habitat destruction and creates open spaces in otherwise closed forests (Gullison and Hardner, 1993; Reed et al., 1996; Santos and Tabarelli, 2002). The open spaces may fragment populations (barrier effect), attract light-demanding species and may be avoided by others (edge effect)

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(Kroodsma, 1984; Vos and Chardon, 1998; Bolger et al., 1997; Ortega and Capen, 1999). Additionally, the use of infrastructure by cars or trains increases the risk of collisions with wildlife and the stress on (breeding) individuals (due to noise and visual stimuli), both of these risks affecting animal populations (Van der Zande et al., 1980; Reijnen et al., 1996; Romin and Bissonette, 1996; Boarman and Sazaki, 2005; Parris and Schneider, 2009).

Besides roads, other types of infrastructure, such as railways, powerlines, pipelines, hydroelectric developments, oil wells, seismic lines and wind parks, have an impact on wildlife populations (Dunthorn and Errington, 1964; McLellan and Shackleton, 1989; Cameron et al., 1992; Van Dyke and Klein, 1996; Mahoney and Schaefer, 2002; Nellemann et al., 2003a; Barrios and Rodriguez, 2004). All these impacts may influence the long-term viability of populations and, eventually, biodiversity.

Qualitative reviews provide a broad understanding of the ecological effects of infrastructure that affect a range of taxa and ecosystems, but lack quantitative evidence (Trombulak and Frissell, 2000; Forman et al., 2003). However, the few attempts to quantify the effects of infrastructure (UNEP, 2001; Nellemann et al., 2003b; Fahrig and Rytwinski, 2009), or to model the vulnerability of animal populations to road effects (Jaeger et al., 2005), are not based on meta-analysis, which is the statistical procedure for combining the results of independent studies in a quantitative way (Arnqvist and Wooster, 1995). In this study, we aim at estimating the decline of animal populations in relation to proximity to infrastructure by using a meta-analytical approach.

Among all animal taxa, mammal and bird populations were chosen for our analysis since both have been widely reported to be declining in relation to their distance from infrastructure. However, large differences in disturbance sensitivity seem to exist between and within these groups. Bird populations seem to be affected within a few hundred metres from infrastructure, whereas a reduction in mammal populations has been found at distances of a few hundred metres up to several kilometres from infrastructure (McLellan and Shackleton, 1989; Cameron et al., 1992; Ortega and Capen, 1999; Nellemann et al., 2003a). Additionally, traffic intensity seems to play a role in the decline of both bird and mammal populations close to roads (Van der Zande et al., 1980; Reijnen et al., 1995, 1996; Dyer et al., 2001; Rheindt, 2003; Gagnon et al., 2007).

To quantify the patterns of reduced population densities in relation to infrastructural development, we searched the scientific and non-scientific literature for quantitative data on mammal and bird populations at varying distances from infrastructure. As the metric of effect size, we calculated the ratio between the species abundance at varying distances to infrastructure (Disturbance or Effect distance) relative to the species abundance at the largest (control) distance reported in the study. This ratio is a form of the biodiversity indicator mean species abundance (MSA) which represents the mean abundance of (remaining) original species in an area related to an undisturbed situation (Alkemade et al., 2009). Meta-analysis was used to combine the effect sizes (MSA values) across all studies for several distance intervals and test their level of significance. Furthermore, meta-regression was applied to model the relationship between distance to infrastructure and MSA for birds ($MSA_B$) and mammals ($MSA_M$) (infrastructure–distance effect), and to examine sources of heterogeneity in this relationship.

## 2. Methods

### 2.1. Search and selection of published studies on infrastructural effects

Relevant studies were searched by using the following electronic databases: Ebsco, ISI Web of Knowledge, JSTOR, Omega (Utrecht University Digital Publications Search Machine), Science Direct, Scopus, Springer Link and Wiley InterScience. The search terms were: road* AND impact* AND biodiversity OR mammal, bird; infrastructure AND impact* AND biodiversity OR mammal, bird; road* AND distance AND biodiversity OR mammal, bird; road-effect zone AND mammal abundance, bird abundance; road* AND disturbance* and biodiversity OR mammal, bird; powerline AND impact AND biodiversity OR mammal, bird; wind park AND biodiversity OR mammal, bird; road traffic* AND impact* AND biodiversity* OR mammal, bird; infrastructure AND disturbance AND biodiversity OR mammal, bird. An Internet search was also performed using the meta-search engine Google scholar. Bibliographies of articles viewed at full text were searched for relevant secondary articles. Authors and recognized experts in the field of infrastructure development, road establishment and effects on biodiversity (Christian Nellemann, UNEP-Grid Arendal, and Rien Reijnen, Alterra) were also contacted for further recommendations, and for provision of any unpublished material or missing data that may be relevant (grey literature). Foreign language searches were undertaken by using cross-reference.

### 2.2. Study inclusion criteria

From this bulk of literature we selected those studies of which title and keywords were associated to the objective of this review. Subsequently, information contained in the abstracts was examined to further narrow down the selection to those studies that met the following criteria:

- Relevant study objects: Populations of any mammal or bird species. Studies were included irrespective of habitat or spatial scale.
- Types of intervention: Disturbance distances or distances close to infrastructure at which mammal and bird populations might be reduced compared to larger distances or control distances (see Types of comparator).
- Types of outcome: Species abundance (density and/or counts) at varying distances to infrastructure.
- Types of comparator: Control distances or distances at which mammal and bird populations are unaffected by infrastructure and roads.

### 2.3. Data extraction

Finally, 49 studies met the selection criteria for data extraction, from which 90 datasets were extracted and stored in a database, resulting in 2107 data points. The data included the mean abundance at disturbance distances close to infrastructure and at a larger control distance; furthermore we recorded the sample size, the variance, and standard deviation or standard error, depending on the study. These data were used to estimate an effect size and its variance as required in meta-analysis (Osenberg et al., 1999). Additionally, we stored data on location, habitat, infrastructure type, taxon (order) and traffic intensity to explore sources of heterogeneity (see Table 2 in Supplementary material, available at http://www.environmentalevidence.org/SR68.html). These variables are considered biologically meaningful and could affect the way different taxa respond to infrastructure. Thus, we expected that different taxa would respond differently to different infrastructure types (linear and clustered) and in different habitat types according to varying visibility of infrastructure, while traffic intensity could affect the response due to the influence of noise and visual stimuli.

### 2.4. Effect size calculation: Mean Species Abundance (MSA)

For each study, individual effect sizes were calculated as the ratio between the abundance of each species close to the infrastructure

(Disturbance distance) and the abundance of the same species at the largest (control) distance, as reported in the study. Individual effect sizes were aggregated for each study and distance, resulting in an estimate of the mean species abundance (MSA), which is the metric of effect size for the meta-analysis (see Eq. (1))

$$\mathrm{MSA}_{sd} = \frac{\sum_i R_{isd}}{N_s}; \quad (1)$$

where $\mathrm{MSA}_{sd}$ is the relative mean species abundance estimated in study $s$ at a distance $d$; $R_{isd}$ is the ratio between the abundance or density of species $i$ at distance $d$ and the abundance or density of species $i$ at the control distance, calculated as: $A_{isd}/A_{isc}$ for $A_{isc} > 0$. $N_s$ is the number of species considered in study $s$. MSA values ranged from 0 to 1 and declined at shorter distances from infrastructure. For species with higher densities at short distances from infrastructure compared to the control distance, the MSA value was truncated to 1; therefore, if $A_{isd} > A_{isc}$, then $R_{isd} = 1$.

### 2.5. Estimation of variation in MSA values

The variance of the MSA value for each distance and study was estimated by calculating the variance of the external error (2), and of the internal error (3), which are both forms of the variance of a sample mean (Mood et al., 1973). The largest variance was used in the meta-analysis, thus taking into account the largest error associated with each data point (DerSimonian and Laird, 1986). For single species' studies, only the variance of the internal error could be calculated.

The variance of the external error was calculated as:

$$\sigma^2_{ext} = \frac{\sum (MSA_{sd} - R_{isd})^2}{N_s(N_s - 1)} \quad (2)$$

The variance of the internal error was calculated as:

$$\sigma^2_{int} = \frac{\sum \sigma^2_{R_{isd}}}{N_s^2}; \quad (3)$$

where $\sigma^2_{R_{isd}}$ is the individual variance for each ratio, which was calculated by using the Delta Method (4), a first-order approximation of the variance of a ratio of two random variables (Oehlert, 1992; Winzer, 2000).

$$\sigma^2_{R_{isd}} = \frac{A^2_{isd}}{A^2_{isc}}\left[\frac{A^2_{isd}}{\sigma^2_{A_{isd}}} + \frac{A^2_{isc}}{\sigma^2_{A_{isc}}} - \frac{2\rho \cdot \sigma_{A_{isd}} \cdot \sigma_{A_{isc}}}{A_{isd} \cdot A_{isc}}\right] \quad (4)$$

In this equation $\sigma^2_{A_{isd}}$ and $\sigma^2_{A_{isc}}$ are the variances of $A_{isd}$ and $A_{isc}$, respectively, and $\rho$ their correlation coefficient. We assume $A_{isd}$ and $A_{isc}$ to be independent and, therefore, the correlation coefficient $\rho$ to be zero. Variances of $A_{isd}$ and $A_{isc}$ were obtained from studies, when available; where this was not the case, the data was assumed to follow a Poisson distribution, in which $\mu = \sigma^2$ and, therefore, $A_{isd} = \sigma^2_{A_{isd}}$, and $A_{isc} = \sigma^2_{A_{isc}}$ (Sokal and Rohlf, 1981).

Finally, as some species had a density of zero at the disturbance distance ($A_{isd} = 0$), a continuity correction factor ($k = 1/2$) was added to the numerator and denominator of the ratio of all species, resulting in slightly higher variance estimates (Cox, 1970; Sweeting et al., 2004).

### 2.6. Study quality assessment

Study characteristics were summarized and experimental design (control and treatment plots) and data availability for extraction (means, standard errors and sample sizes) were used as criteria for determining study quality (low; medium–low; medium; medium–high; high) (Supplementary material available at http://www.environmentalevidence.org/SR68.html). A sensitivity analysis was done by removing studies scoring "medium–low" or "low".

### 2.7. Data analyses

Meta-analyses were performed separately for mammal and bird studies by using the package "metafor" in R 2.9.1 software (Viechtbauer, 2009). A random effects meta-analysis was done to derive a pooled effect size for all datasets allowing pseudoreplication. Additionally, meta-analyses were done per distance interval containing non-duplicated independent datasets.

Heterogeneity was assessed by inspection of Forest plots and formal tests of heterogeneity $Q$ and $I^2$ (Thompson and Sharp, 1999). Publication bias was also assessed using Funnel plots of asymmetry along with formal tests (Egger et al., 1997; Supplementary material available at http://www.environmentalevidence.org/SR68.html).

To explore factors introducing heterogeneity we built several Generalized Linear Mixed Models (GLMM), accounting for several alternative nested ecological hypotheses that included the following a priori selected explanatory variables: distance to infrastructure (DIST or LOGDIST when log-transformed), presence of forest cover (FOR), infrastructure type (INFTYP) and traffic intensity (TRAF). All GLMM were built in S-Plus 7.0 and fit by restricted penalised quasi-likelihood (Pinheiro and Bates, 2000). Each MSA value was weighed by its variance. Study was introduced as random effect since we expected similar but not identical effects of infrastructure across studies.

Models were compared and selected by means of information theoretic criteria, including Akaike's Information Criterion corrected for sample size (AICc) and Akaike weights. AIC corrected for overdispersion (QAIC) was not needed since the random effects of the GLMM accommodate any possible overdispersion in the data. This was *ad hoc* checked by calculating a scale parameter (sigma) for our models using package "lme4" in R 2.9.1. (Bates and Maechler, 2009). The model selected was that minimizing the loss of Kullback–Leibler information.

Additionally data was disaggregated and GLMM were built to examine differences in the relationship between MSA and distance for different habitats, for forested and non-forested habitats, for different infrastructure types (linear and clustered) and for different taxa.

## 3. Results

### 3.1. Data availability and selected studies: review statistics

More than 600 studies contained relevant titles and abstracts. Of these, 50 studies corresponded to the selected criteria for data extraction. Two studies referred to the same data and were treated as one (Noel et al., 2004; Joly et al., 2006), resulting in 49 studies used for the meta-analysis. Some geographical bias was found since most of the studies were from either North America (21) or Europe (23), while a few studies from Africa (3) and Oceania (2) were found.

Twenty-seven studies included 201 bird species, and 49 independent datasets were extracted for the meta-analysis. The other 22 studies included 33 mammal species, and 41 independent datasets were extracted. Some species were repeated more than once (Appendix 3, Supplementary material available at http://www.environmentalevidence.org/SR68.html). Of the 49 datasets for birds, 10 contained relevant information on traffic intensities. Of the 41 datasets for mammals, five included information on traffic intensity, which was considered insufficient for the inclusion of this variable in the analysis (Supplementary material available at http://www.environmentalevidence.org/SR68.html).

Bird datasets frequently included a large number of species (mean = 9.1 (1–54)), compared to mammal datasets, which (with some exceptions, e.g. Newmark et al., 1996; Goosem and Marsh, 1997; Yost and Wright, 2001) usually focused on a single species (mean = 3.7 (1–11)). The most represented habitat types within the bird datasets were grasslands and agricultural lands (each of them in 15 datasets), and the least represented was boreal forests (1 dataset). The most represented habitat type in the mammal datasets was arctic tundra (12 times) and the least represented habitat types were grasslands and semi-arid habitats (1 time each).

The most represented bird taxon was Passeriformes (21 datasets) and the least represented bird taxa were Coraciiformes, Psittaciformes and Trochiliformes (1 dataset each). The most represented mammal taxon was Artiodactyla (25 datasets) and the least represented mammal taxa were Lagomorpha and Perissodactyla (1 dataset each).

Reported distances in bird datasets were in the range of 0–2580 m whereas data points for mammals were obtained within a range of 0–17,000 m.

### 3.2. Meta-analysis

#### 3.2.1. Combination of all distances with pseudorreplication

The pooled effect size derived from an all-encompassing meta-analysis of MSA values for birds indicated that bird abundance declined within ca. 2600 m from infrastructure ($MSA_B$ = 0.678; 95% CI 0.636–0.720, $P < 0.0001$; Table 1). Likewise for mammals, $MSA_M$ decreased within 17,000 m from infrastructure ($MSA_M$ = 0.675; 95% CI 0.608–0.742, $P < 0.0001$). However, for both meta-analyses there was large heterogeneity and publication bias within the datasets ($Q_B$ = 16938.28, $P < 0.0001$; Egger $test_B$ = 5.785, $P < 0.0001$; $Q_M$ = 3466.80, $P < 0.0001$; Egger $test_M$ = 3.684, $P < 0.0001$; Tables 1 and 2). Fail-safe numbers indicated that a large number of studies reporting neutral or positive effects of the proximity of infrastructure on species abundance would be needed to overturn these results and so even with some publication bias, the results for mammals and birds can be considered a reliable estimate of the true effect (Rosenthal, 1979).

Sensitivity analyses were performed and the results remained similar after removing studies that scored "medium–low" in the study quality assessment. The pooled effect size for bird data increased slightly, heterogeneity was lower but still statistically significant and there was evidence of publication bias ($MSA_B$ = 0.683; 95% CI 0.627–0.740, $P < 0.0001$; $Q$ = 2653.70, $P < 0.0001$; Egger test = 4.699, $P < 0.0001$; Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html). For mammals the pooled effect size was similar, heterogeneity decreased slightly and there was publication bias ($MSA_M$ = 0.678; 95% CI 0.6086–0.7472, $P < 0.0001$; $Q$ = 3401.70, $P < 0.0001$; Egger test = 4.006, $P < 0.0001$; Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html).

#### 3.2.2. Effect size per distance interval

Pooled effect sizes calculated per distance interval for independent datasets were significant for mammal and bird data, but considerable heterogeneity and publication bias existed for most of the intervals. Lower MSA values were obtained at shorter distance intervals to infrastructure for both mammals and birds.

**Table 1**
Results of the meta-analysis for bird species at different distance intervals.

| Distance (m) | *n* | Effect size (MSA) | SE | CI (lb) | CI (ub) | *P* (e.size) | Q | *P*(Q) | $I^2$ (%) | Egger's test intercept | *P*(*t*) Egger | Fail-safe *N* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0–2580 | 288[a] | 0.6777 | 0.0215 | 0.6355 | 0.7200 | **<0.0001** | 16938.28 | **<0.0001** | 96.6 | 5.785 | **<0.0001** | **11,23,452** |
| <10 | 10 | 0.3983 | 0.1290 | 0.1455 | 0.6512 | **0.002** | 62.7322 | **<0.0001** | 94.4 | 2.625 | **0.0026** | **245** |
| 15–35 | 18 | 0.4855 | 0.0893 | 0.3105 | 0.6605 | **<0.0001** | 223.89 | **<0.0001** | 93.3 | 4.336 | **<0.0001** | **2233** |
| 38–65 | 20 | 0.5339 | 0.0905 | 0.3566 | 0.7112 | **<0.0001** | 370.28 | **<0.0001** | 95.2 | 3.639 | **<0.0001** | **1939** |
| 70–80 | 16 | 0.5923 | 0.0896 | 0.4165 | 0.7680 | **<0.0001** | 33.19 | **0.007** | 54.5 | 2.561 | **0.0002** | **689** |
| 90–100 | 16 | 0.6218 | 0.0722 | 0.4802 | 0.7634 | **<0.0001** | 38.42 | **0.0004** | 68.4 | 3.993 | **0.0003** | **1494** |
| 110–125 | 13 | 0.6673 | 0.1022 | 0.4671 | 0.8676 | **<0.0001** | 40.99 | **<0.0001** | 65.7 | 3.072 | **0.0001** | **577** |
| 130–140 | 5 | 0.7070 | 0.1592 | 0.3950 | 1.0190 | **<0.0001** | 45.79 | **<0.0001** | 85 | 4.981 | **0.0222** | **225** |
| 150–160 | 16 | 0.5978 | 0.0788 | 0.4434 | 0.7522 | **<0.0001** | 79.12 | **<0.0001** | 83.8 | 4.874 | **0.0002** | **1946** |
| 170–180 | 10 | Fisher scoring algorithm did not converge | | | | | | | | | | |
| 190–200 | 13 | 0.6292 | 0.0908 | 0.4512 | 0.8072 | **<0.0001** | 301.50 | **<0.0001** | 95.7 | 6.786 | **0.0015** | **2864** |
| 210–240 | 12 | 0.6734 | 0.1281 | 0.4223 | 0.9246 | **<0.0001** | 428.83 | **<0.0001** | 95.3 | 5.434 | **0.0124** | **1560** |
| 250–280 | 17 | 0.6676 | 0.0963 | 0.4789 | 0.8563 | **<0.0001** | 331.47 | **<0.0001** | 96.5 | 9.347 | **0.0122** | **9320** |
| 300–320 | 15 | 0.7454 | 0.1062 | 0.5374 | 0.9535 | **<0.0001** | 8769.78 | **<0.0001** | 99.4 | 15.540 | 0.202 | **20,053** |
| 340–375 | 10 | 0.6432 | 0.0943 | 0.4583 | 0.8281 | **<0.0001** | 34.74 | **0.0001** | 75.2 | 4.828 | **0.0161** | **851** |
| 380–480 | 16 | 0.7495 | 0.0888 | 0.5755 | 0.9236 | **<0.0001** | 1052.78 | **<0.0001** | 96.9 | 8.952 | **0.0003** | **7820** |
| 490–550 | 14 | 0.6946 | 0.1004 | 0.4978 | 0.8914 | **<0.0001** | 86.19 | **<0.0001** | 87 | 5.331 | **0.0073** | **2013** |
| 565–645 | 9 | 0.7182 | 0.0929 | 0.5361 | 0.9003 | **<0.0001** | 27.72 | **0.0005** | 75.8 | 6.594 | **0.0436** | **1294** |
| 650–785 | 11 | 0.7564 | 0.1203 | 0.5206 | 0.9921 | **<0.0001** | 581.18 | **<0.0001** | 94.1 | 5.980 | **0.0451** | **1588** |
| 800–860 | 3 | 0.6869 | 0.1968 | 0.3011 | 1.0728 | **<0.0001** | 12.75 | **<0.0001** | 81.1 | 4.640 | **0.0124** | **69** |
| 900–915 | 4 | 0.9152 | 0.1043 | 0.7108 | 1.1196 | **<0.0001** | 0.2687 | 0.9658 | 0 | 4.1168 | **0.0189** | **97** |
| 1000–1075 | 11 | 0.8363 | 0.0791 | 0.6812 | 0.9913 | **<0.0001** | 17.23 | 0.0695 | 46.7 | 4.585 | **0.0050** | **930** |
| 1100–1175 | 3 | 0.9696 | 0.1275 | 0.7198 | 1.2195 | **<0.0001** | 0.0722 | 0.9645 | 0 | 4.052 | 0.0780 | **52** |
| 1200–1290 | 4 | 0.8308 | 0.1097 | 0.6158 | 1.0459 | **<0.0001** | 5.011 | 0.171 | 47 | 5.426 | **0.0344** | **171** |
| 1300 | 1 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| 1400 | 2 | 0.9098 | 0.0515 | 0.8090 | 1.0107 | **<0.0001** | 0.0398 | 0.842 | 0 | 10.941 | 0.321 | **176** |
| 1500–1505 | 7 | 0.8511 | 0.0677 | 0.7183 | 0.9838 | **<0.0001** | 13.894 | **0.0308** | 71.7 | 10.572 | 0.0516 | **2018** |
| 1600 | 1 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| 1700–1750 | 4 | 0.9294 | 0.0992 | 0.7349 | 1.1239 | **<0.0001** | 0.5252 | 0.9133 | 0 | 4.4439 | **0.0148** | 113 |
| 1800–2000 | 4 | 1.0000 | 0.0483 | 0.9053 | 1.0947 | **0.0000** | 0 | 1.0000 | 0 | 7.868 | 0.136 | 362 |
| 2150 | 1 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| 2365 | 1 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| 2580 | 1 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |

[a] Total number of MSA values included in the meta-analysis for bird species. The total number of studies is 27, from which 49 datasets were extracted containing 288 MSA calculated values for different distances.

**Table 2**
Results of the meta-analysis for mammal species at different distance intervals.

| Distance (m) | *n* | Effect size (MSA) | SE | CI (lb) | CI (ub) | *P* (e.size) | *Q* | *P*(*Q*) | $I^2$ (%) | Egger's test intercept | *P*(*t*) Egger | Fail-safe *N* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0–17,000 | 151[a] | 0.6746 | 0.0342 | 0.6076 | 0.7415 | **<0.0001** | 3466.80 | **<0.0001** | 90.7 | 3.6843 | **<0.0001** | **114,151** |
| 1 | 6 | 0.1528 | 0.1005 | −0.0442 | 0.3498 | >0.1 | 12.74 | **0.0259** | 71.9 | 1.0862 | 0.0937 | 10 |
| 10–25 | 11 | 0.7110 | 0.0451 | 0.6227 | 0.7993 | **<0.0001** | 4.38 | 0.9284 | 0 | 4.300 | **<0.0001** | **816** |
| 30–50 | 16 | 0.5651 | 0.0726 | 0.4229 | 0.7073 | **<0.0001** | 28.65 | 0.0178 | 55.8 | 2.9972 | **<0.0001** | **834** |
| 75–100 | 7 | 0.3957 | 0.1831 | 0.0369 | 0.7545 | **<0.05** | 10.87 | 0.0925 | 47.7 | 1.4193 | **0.0016** | **362** |
| 110–180 | 16 | 0.8374 | 0.0520 | 0.7354 | 0.9394 | **<0.0001** | 7.42 | 0.9448 | 0 | 3.4069 | **<0.0001** | **1083** |
| 200 | 2 | 0.6104 | 0.2382 | 0.1435 | 1.0774 | **0.0104** | 0.02 | 0.878 | 0 | 1.464 | 0.402 | 2 |
| 250–300 | 9 | 0.8470 | 0.0627 | 0.7241 | 0.9698 | **<0.0001** | 7.78 | 0.4557 | 7.8 | 4.059 | **0.0037** | **485** |
| 350–600 | 19 | 0.6222 | 0.1115 | 0.4035 | 0.8408 | **<0.0001** | 206.68 | **<0.0001** | 91.9 | 3.3561 | **<0.0001** | **1485** |
| 750–1000 | 6 | 0.8669 | 0.1052 | 0.6608 | 1.0731 | **<0.0001** | 9.23 | 0.1002 | 50.2 | 4.8430 | **0.0036** | **307** |
| 1050–2200 | 20 | 0.5786 | 0.0806 | 0.4207 | 0.7366 | **<0.0001** | 75.49 | **<0.0001** | 74.1 | 3.0049 | **<0.0001** | **1316** |
| 2500 | 8 | 0.8233 | 0.2098 | 0.4121 | 1.2345 | **<0.0001** | 0.9453 | 0.9957 | 0 | 1.2516 | **0.0020** | 30 |
| 3500–4000 | 7 | 0.9807 | 0.1276 | 0.7307 | 1.2308 | **<0.0001** | 0.2907 | 0.9995 | 0 | 1.9095 | 0.0775 | **60** |
| 4500–5000 | 8 | 0.8666 | 0.1099 | 0.6512 | 1.0820 | **<0.0001** | 6.06 | 0.5323 | 30.8 | 3.395 | **0.0255** | **265** |
| 5500–7000 | 8 | 0.8049 | 0.1983 | 0.4163 | 1.1936 | **<0.0001** | 0.8083 | 0.9974 | 0 | 1.2467 | **0.0039** | 29 |
| 7500 | 2 | 0.8730 | 0.0118 | 0.8498 | 0.8962 | **<0.0001** | 0.0084 | 0.9272 | 0 | 37.35 | 0.494 | **2047** |
| 8500 | 1 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| 9500–11,000 | 4 | 1.0000 | 0.0131 | 0.9744 | 1.0256 | **<0.0001** | 0 | 1 | 0 | 76.122 | **<0.0001** | **2527** |
| 17,000 | 1 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |

[a] Total number of observations points or MSA values included in the meta-analysis for mammal species. The total number of studies is 22, from which 41 datasets were extracted containing 151 MSA calculated values for different distances.

The number of datasets per distance interval decreased as the distance from infrastructure increased (Tables 1 and 2).

Sensitivity analyses for mammal and bird data resulted in similar MSA values per distance interval with the exception of the distance intervals 300–320, 340–375 and 380–490 m for the bird data, which had larger MSA values (Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html). Heterogeneity was not statistically significant in these intervals, but there was publication bias.

### 3.2.3. Exploration of reasons for heterogeneity: meta-regression

The relationship between MSA and distance to infrastructure was positive for both mammals and birds (Fig. 1 and 2). When the data was subgrouped per habitat, all relationships were also positive except for temperate forests in the case of mammal species, and Mediterranean forests in the case of bird species (Tables 6 and 7). In forests both bird and mammal species abundances were affected in the proximity of infrastructure whereas in non-forested areas the effect extended over a larger distance (Tables 6 and 7). All relationships had lower AICc when "LOGDIST" was chosen as explanatory variable, except for Tundra.

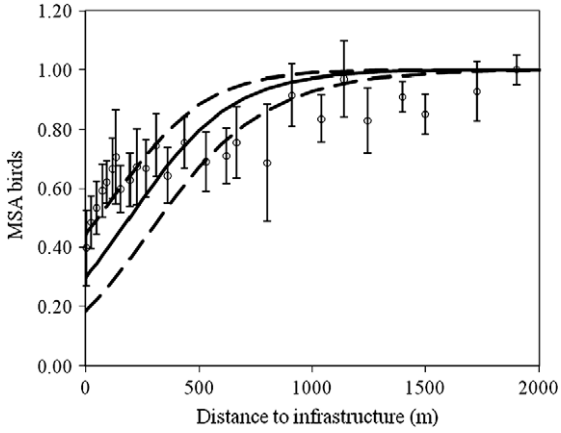


**Fig. 1.** Logistic regression between mean species abundance of birds and distance from infrastructure. Open dots represent the pooled results of the meta-analysis per distance interval ± S.E. The black line denotes the estimated curve for the decline of MSA, related to distance. Dashed lines are the 95% upper and lower limits of the confidence bands of the curve.

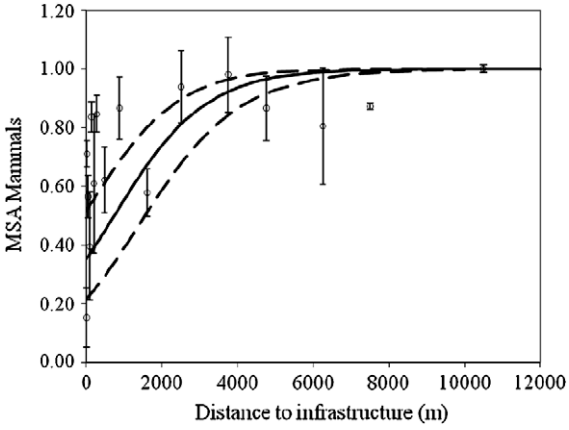


**Fig. 2.** Logistic regression between mean species abundance of mammals and distance from infrastructure. Open dots represent the pooled results of the meta-analysis per distance interval ± S.E. The black line denotes the estimated curve for the decline of MSA, related to distance. Dashed lines are the 95% upper and lower limits of the confidence bands of the curve.

There existed also differences in the relationship between MSA and distance to infrastructure for different taxa. Accitriformes and Falconiformes were the only bird taxa which were unaffected or positively affected by the presence of infrastructure, whereas for other bird taxa proximity to infrastructure seemed to exert a negative effect on species abundance, or the magnitude of the effect was unknown due to low sample size (Supplementary material available at http://www.environmentalevidence.org/SR68.html). From all mammal taxa, a positive relationship between MSA and distance to infrastructure could only be found for Artiodactyla and Rodentia, but abundances of the latter were only reduced at short distances from infrastructure while this effect extended over a large distance for the former.

Several *ad hoc* models were built to explore the high heterogeneity between effect sizes. We worked on several biological hypotheses to explain the variability in the relationship between MSA and distance to infrastructure. For bird species the most parsimonious model was that containing only the explanatory variable "LOGDIST" (Akaike weight: 0.78, Table 3). For mammal

**Table 3**
Models expressing different biological hypotheses on the influence of infrastructure distance, infrastructure type and infrastructure visibility (forest) on the mean species abundance of birds. The selected model appears in bold.

| Model (birds) | AICc | *K* | *n* | $\Delta_i$AICc | $w_i$ |
|---|---|---|---|---|---|
| LOGDIST + FOR + INFTYP + LOGDIST * INFTYP + LOGDIST * FOR + FOR * INFTYP + LOGDIST * INFTYP * FOR | No model convergence | | | | |
| LOGDIST + FOR + LOGDIST * FOR | 1630.78 | 6 | 288 | 3.04 | 0.17 |
| LOGDIST + INFTYP + LOGDIST * INFTYP | 1636.04 | 6 | 288 | 8.30 | 0.01 |
| LOGDIST + FOR | 1633.96 | 5 | 288 | 6.21 | 0.03 |
| LOGDIST + INFTYP | 1637.29 | 5 | 288 | 9.54 | 0.01 |
| LOGDIST | **1627.75** | **4** | **288** | **0.00** | **0.78** |
| FOR | 1647.18 | 4 | 288 | 19.43 | <0.01 |
| INFTYP | 1646.40 | 4 | 288 | 18.65 | <0.01 |
| DIST + FOR + DIST * FOR | 1762.19 | 6 | 288 | 134.45 | <0.01 |
| DIST + FOR | 1744.61 | 5 | 288 | 116.86 | <0.01 |
| DIST | 1739.98 | 4 | 288 | 112.23 | <0.01 |

AICc = Akaike Information Criterion corrected for sample size;
*K* = No. of estimable parameters: Intercept, log (effect distance), effect distance, forest, infra type, interaction term, study and error term;
*n* = No. of data points;
$\Delta_i$AICc = Delta AICc value;
$w_i$ = Akaike weight.

**Table 4**
Models expressing different biological hypotheses on the influence of infrastructure distance, infrastructure type and infrastructure visibility (forest) on the mean species abundance of mammals. The selected model appears in bold. See Table 3 for explanation of coefficients.

| Model (mammals) | AICc | *K* | *n* | $\Delta_i$AICc | $w_i$ |
|---|---|---|---|---|---|
| LOGDIST + FOR + INFTYP + LOGDIST * INFTYP + LOGDIST * FOR + FOR * INFTYP + LOGDIST * INFTYP * FOR | 889.18 | 10 | 151 | 3.59 | 0.14 |
| LOGDIST + INFTYP + LOGDIST * INFTYP | 963.06 | 6 | 151 | 77.50 | <0.01 |
| LOGDIST + FOR + LOGDIST * FOR | 900.02 | 6 | 151 | 14.46 | <0.01 |
| LOGDIST + LOGDIST | 919.67 | 5 | 151 | 34.12 | <0.01 |
| LOGDIST + FOR | 911.34 | 5 | 151 | 25.79 | <0.01 |
| LOGDIST | 923.42 | 4 | 151 | 37.87 | <0.01 |
| INFTYP | 896.93 | 4 | 151 | 11.38 | <0.01 |
| FOR | 899.30 | 4 | 151 | 13.75 | <0.01 |
| DIST + FOR + INFTYP + DIST * INFTYP + DIST * FOR + FOR * INFTYP + DIST * INFTYP * FOR | 1081.87 | 10 | 151 | 196.28 | <0.01 |
| DIST + FOR + DIST * FOR | 964.56 | 6 | 151 | 79.01 | <0.01 |
| DIST + INFTYP | 893.28 | 5 | 151 | 7.73 | 0.02 |
| DIST + FOR | **885.54** | **5** | **151** | **0.00** | 0.84 |
| DIST | 897.99 | 4 | 151 | 12.45 | <0.01 |

**Table 5**
Models expressing different biological hypotheses on the influence of infrastructure distance, traffic intensity (noise) and infrastructure visibility (forest) on the mean species abundance of birds. The selected model appears in bold. See Table 3 for explanation of coefficients.

| Model (birds) | AICc | *K* | *n* | $\Delta_i$AICc | $w_i$ |
|---|---|---|---|---|---|
| LOGDIST + FOR + TRAF + LOGDIST * TRAF + LOGDIST * FOR + FOR * TRAF + LOGDIST * TRAF * FOR | 583.52 | 10 | 87 | 10.87 | <0.01 |
| LOGDIST + TRAF + LOGDIST * TRAF | 512.30 | 6 | 87 | 31.65 | <0.01 |
| LOGDIST + TRAF | 503.06 | 5 | 87 | 22.40 | <0.01 |
| TRAF | 537.10 | 4 | 87 | 56.44 | <0.01 |
| LOGDIST | **480.66** | **4** | **87** | **0.00** | **0.99** |

species the most parsimonious model was that including the explanatory variables "DIST" and "FOR" (Akaike weight: 0.84, Table 4).

The most parsimonious model for the subset of bird data containing information on traffic intensity was that including only "LOGDIST" as explanatory variable (Akaike weight: 0.99, Table 5).

## 4. Discussion

### *4.1. Effect of distance from infrastructure on bird and mammal species abundance*

Our analyses suggest that infrastructure can have a negative impact on bird and mammal abundance and that this impact is more evident in the proximity of the infrastructure. Pooled results for pseudorreplicated data indicated a decline in species abundance of 28–36% and 25–38% for birds and mammals within 2.6 km and 17 km from infrastructure, respectively. Pooled results per distance interval showed that MSA of birds and of mammals became higher for distance intervals far away from infrastructure. The meta-regression also indicated a positive relationship between MSA of birds and mammals and distance to infrastructure. A second conclusion that can be obtained from these results is that bird populations are likely to be more affected at short distances from infrastructure while the effect on mammal populations seems to extend over larger distances. These results confirm the effect distances reported in other studies, which were larger for mammals (Cameron et al., 1992; Newmark et al., 1996; Nellemann et al., 2003a; Joly et al., 2006) than for birds (Van der Zande et al., 1980; Madsen, 1985; Reijnen et al., 1996; Rheindt, 2003). However, considerable heterogeneity was found in our results, especially for birds, and also publication bias, both limiting the robustness of these conclusions.

**Table 6**
Univariate meta-regression coefficients for the relationship between MSA and distance for bird species in different habitats. Models with log-transformed distance as explanatory variable are more parsimonious than without transformation for all habitats.

| Bird species | | | | | | | |
|---|---|---|---|---|---|---|---|
| Explanatory variable | Habitat | *b* | Intercept | *k* | *n* | *K* | AICc |
| LOGDIST | Agricultural lands | 1.523 | −7.933 | 15 | 109 | 4 | 626.29 |
| | Temperate forests | 0.761 | −2.868 | 8 | 35 | 4 | 192.57 |
| | Boreal forests | No model convergence | | 1 | 2 | | |
| | Mediterranean forests | 27.020 | −136.950 | 2 | 4 | 4 | −12.28 |
| | Grasslands | 1.014 | −5.193 | 15 | 97 | 4 | 417.24 |
| | Scrublands | 1.174 | −4.853 | 5 | 35 | 4 | 200.84 |
| | Tropical forests | 18.834 | −61.705 | 3 | 6 | 4 | 80.13 |
| | All forests | 0.826 | −2.770 | 14 | 47 | 4 | 263.04 |
| | Non-forested habitats | 1.333 | −6.712 | 35 | 241 | 4 | 1361.75 |
| DIST | Agricultural lands | 0.005 | −1.777 | 15 | 109 | 4 | 779.75 |
| | Temperate forests | No model convergence | | 8 | 35 | 4 | |
| | Boreal forests | No model convergence | | 1 | 2 | | |
| | Mediterranean forests | 0.046 | 3.222 | 2 | 4 | 4 | 0.45 |
| | Grasslands | 0.002 | −0.759 | 15 | 97 | 4 | 488.01 |
| | Scrublands | No model convergence | | 5 | 35 | 4 | |
| | Tropical forests | 0.522 | −17.254 | 3 | 6 | 4 | 97.57 |
| | Forests | 0.011 | −0.894 | 14 | 47 | 4 | 301.93 |
| | Non-forested habitats | 0.004 | −1.218 | 35 | 241 | 4 | 1478.68 |

**Table 7**
Univariate meta-regression coefficients for the relationship between MSA and distance for mammal species in different habitats. Models with log-transformed distance as explanatory variable are more parsimonious than without transformation for all habitats except for tundra.

| Mammal species | | | | | | | |
|---|---|---|---|---|---|---|---|
| Explanatory variable | Habitat | *b* | Intercept | *k* | *n* | *K* | AICc |
| LOGDIST | Agricultural lands | No model convergence | | 2 | 9 | | |
| | Temperate forests | 0.260 | 0.103 | 4 | 15 | 4 | 67.99 |
| | Boreal forests | 1.526 | −7.742 | 9 | 34 | 4 | 162.23 |
| | Grasslands | Only 1 dataset | | *1* | *5* | | |
| | Scrublands | 2.133 | −6.773 | 3 | 11 | 4 | 59.19 |
| | Tropical forests | 0.681 | −1.136 | 5 | 22 | 4 | 81.39 |
| | Semi-arid lands | Only 1 dataset | | *1* | *8* | | |
| | Arctic tundra | 2.854 | −21.429 | 12 | 52 | 4 | 364.50 |
| | All except for Tundra | 0.978 | −3.670 | 25 | 104 | 4 | 528.05 |
| | Forests | 0.860 | −3.151 | 18 | 71 | 4 | 313.90 |
| | Non-forested habitats | 1.142 | −7.089 | 19 | 85 | 4 | 548.28 |
| DIST | Agricultural lands | No model convergence | | 2 | 9 | | |
| | Temperate forests | 0.002 | 0.850 | 4 | 15 | 4 | 75.91 |
| | Boreal forests | No model convergence | | | | | |
| | Grasslands | Only 1 dataset | | *1* | *5* | | |
| | Scrublands | No model convergence | | 4 | | | |
| | Tropical forests | 0.003 | 0.592 | 5 | 22 | 4 | 107.21 |
| | Semi-arid lands | Only 1 dataset | | *1* | *8* | | |
| | Arctic tundra | 0.001 | −1.832 | 12 | 52 | 4 | 332.68 |
| | All except for Tundra | 0.004 | −0.478 | 25 | 104 | 4 | 614.09 |
| | Forests | 0.003 | −0.026 | 18 | 71 | 4 | 397.21 |
| | Non-forested habitats | 0.001 | −1.659 | 19 | 85 | 4 | 561.76 |

The sensitivity analyses resulted in a slightly (but not statistically significant) larger pooled effect size for pseudorreplicated data in the case of bird species. Sensitivity analyses per distance interval showed similar results to the full meta-analyses except for the distance intervals between 300 and 480 m from infrastructure, with larger effect sizes. Yet, fail-safe numbers indicate that a large number of non-significant studies would be needed to overturn the pooled effect sizes calculated for these distance intervals. Thus, we decided to maintain these studies in the meta-regression following Wolf and Guevara (2001), who advocate for the use of all available data when doing meta-analysis.

The high heterogeneity underlying the results of our meta-analysis indicates that infrastructure development can have negative impacts on bird and mammal abundance within a certain distance depending on a number of factors which we further explore in Section 4.2.

### 4.2. Exploration of sources of heterogeneity

Meta-regression helped us to elucidate that "LOGDIST" was the main explanatory variable for the decline in abundance of bird populations due to infrastructure. For mammals, "DIST" was the main variable but the variable "FOR" seemed to add important information to the model. Meta-regression on subgroups divided by habitat type and taxa indicated that in open habitats, both mammal and bird populations seem to avoid infrastructure over larger distances, compared to those in forested biomes, which could probably be related to reduced visibility of infrastructure. Forman and Deblinger (2000) showed similar results for breeding birds in open grasslands and in woodlands (data adapted from Reijnen et al. (1995, 1996)).

For the subset of bird data including information on traffic intensity, the most parsimonious model was that which contained

only "LOGDIST" as explanatory variable. Therefore it seems that traffic intensity has no effect on the reduction of bird populations nearby roads. These results are contrary to the findings of a number of authors that have highlighted the pernicious effects of traffic intensity and noise on bird populations (Reijnen and Foppen, 1994; Reijnen et al., 1995, 1996, 1997; Forman et al., 2002; Rheindt, 2003). However, there are other studies which found a decline in bird populations near roads with low traffic intensity (Räty, 1979; Madsen, 1985; Develey and Stouffer, 2001) and others which found no clear relationship (Peris and Pescador, 2004). Finally, some authors claim that there exists a trade-off between traffic intensity and velocity, with low traffic intensity being related to higher velocities (Martínez-Abraín, 1994; Drews, 1995). Yet, traffic velocity seems to be related to bird mortality, which occurs on the road itself. To the best of our knowledge, studies that deal with this topic usually do not report on bird densities at increasing distances from roads (or include a control distance for comparison). As none of the studies included in our analysis contained data on traffic velocity, the influence of this variable could not be evaluated.

Not all species showed a decline in abundance nearby infrastructure: species abundance of Accipitriformes and Falconiformes was larger in the proximity of infrastructure. This was not a surprising outcome since other studies have reported the presence of raptors nearby roads searching roadkill carrion (Forman and Alexander, 1998; Lambertucci et al., 2009) and hunting (Dónazar et al., 1993; Fajardo et al., 1998; Dean and Milton, 2003), with some exceptions during the breeding season (Martínez-Abraín et al., 2008).

In the case of mammals, we could detect that Rodentia populations were slightly affected within few meters from infrastructure. By contrast, Artiodactyla species were affected up to distances of several hundred meters. Within Artiodactyla wild reindeer (*Rangifer tarandus*) was one of the most studied and sensitive species, with their population abundance being reduced up to several kilometres from infrastructure (Nellemann and Cameron, 1996; Nellemann et al., 2001, 2003a,b). These outcomes are consistent with the fact that small-sized mammals usually have smaller home ranges and migration distances compared to medium- and large-sized mammals, the latter being more sensitive to infrastructure development and habitat fragmentation (Harestad and Bunnel, 1979; Buskirk, 2009).

### 4.3. Review limitations

Only some of the included studies used Before-After-Control-Impact (BACI) experimental designs, so we decided to use the largest reported distance in the study as control distance. Although the sensitivity analyses allowed us to remove some of the studies of lower quality and indeed the results did not vary in most of the cases, we acknowledge that our conclusions are restricted by the lack of proper comparators in some of the studies.

The identified publication bias is another of the weaknesses of our review. A few studies did not find negative effects of infrastructure on bird and mammal populations and were not included due to lack of proper data on the selected variables (e.g. Adams, 1984; Evans and Gates, 1997; Ballard et al., 2000); and there may exist many others that were never published due to non-significant results or that we were unable to obtain (grey literature). However, fail-safe numbers indicated that our results are sufficiently robust.

Many of the studies initially considered in our systematic review lacked suitable data for extraction and had to be left out of the analysis. Therefore we may have excluded potentially relevant studies and included lower quality studies due to availability of data on the selected variables.

The scope of the study was intended to be global and covered different types of biomes and habitats; nevertheless there is a geographical bias in the studies included in our review. Most studies were done in Europe and North America and therefore the applicability of the results to other geographic areas remains unknown.

### 4.4. Conclusions and management implications

Changes in wildlife populations in the proximity of infrastructure have been reported for decades in a number of studies (see Table 2 in Supplementary material, available at http://www.environmentalevidence.org/SR68.html), and have been pointed out in relevant authors' reviews (Spellerberg, 1998; Trombulak and Frissell, 2000; Forman et al., 2003). Additionally, there have been previous attempts to quantify wildlife population decline in relation to distance from infrastructure, either locally (Forman and Deblinger, 2000) or at the global scale (UNEP, 2001; Nellemann et al., 2003b; Fahrig and Rytwinski, 2009), but none of them followed the guidelines for systematic reviews (Pullin and Stewart, 2006) or summarized the information by means of a meta-analysis. Our study represents a step forward within the field of road ecology research that may contribute to the understanding of the magnitude of the pernicious effects of infrastructure development on animal populations. Reported effects for most bird populations extend over distances up to about 1 km, and for most mammal populations up to about 5 km, with variation according to taxa and habitat type (Fig. 1 and 2). However, the evidence shown by our results is somewhat hampered by the limitations mentioned in Section 4.3. We therefore encourage researchers to perform BACI studies whenever possible and make their data available for researchers pursuing a systematic review. Should new studies that include these recommendations be released in the future, the review can be updated by including the new available evidence.

Although the patterns found in our analysis are clear, we would like to emphasise that these only represent a partial estimate of the actual effect of infrastructure on wildlife. Therefore, we highlight the importance of broadening the analysis to other taxonomic groups, such as herpetofauna, plants and invertebrates (e.g. Przybylski, 1979; Angold, 1997; Auerbach et al., 1997; Haskell, 2000; Shine et al., 2004; Barrows et al., 2006). Further research on these taxonomic groups would add up to the current models presented in this study, contributing to eventually produce a model that would provide an accurate estimate of the effects of infrastructure development on biodiversity.

The results of our meta-analysis will be implemented in the next version of the GLOBIO3 model, which is used to estimate the biodiversity loss at global, regional and national level at current state and for possible future scenarios and policy options (Alkemade et al., 2009). The results of the GLOBIO3 model have been reported in global assessments such as the second Global Biodiversity Outlook and the fourth Global environmental Outlook and are aimed to support policy makers on the elaboration of biodiversity conservation policies (sCBD and MNP, 2007; UNEP, 2007). The method is also used at the regional level (Verboom et al., 2007) and at the country level (e.g. in Viet Nam, Ecuador and Nicaragua).

Our study shows the importance of minimizing infrastructure development for wildlife conservation in relatively undisturbed areas. By combining actual species distributions with the effect distance functions we developed as a form of dose–effect relationship, regions sensitive to infrastructure development may be identified. More specifically, the effect distance functions can be used in models in support of decision making on infrastructure planning. This would mean a substantial improvement of the current situation in which, in most cases, results of previous studies on ecological impacts are barely taken into account (OECD, 2002; Roedenbeck et al., 2007).

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## Supplementary material

Supplementary material available at http://www.environmentalevidence.org/SR68.html. Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.02.009.

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# Relationships between Human Population Density and Burned Area at Continental and Global Scales

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## Abstract

We explore the large spatial variation in the relationship between population density and burned area, using continental-scale Geographically Weighted Regression (GWR) based on 13 years of satellite-derived burned area maps from the global fire emissions database (GFED) and the human population density from the gridded population of the world (GPW 2005). Significant relationships are observed over 51.5% of the global land area, and the area affected varies from continent to continent: population density has a significant impact on fire over most of Asia and Africa but is important in explaining fire over < 22% of Europe and Australia. Increasing population density is associated with both increased and decreased in fire. The nature of the relationship depends on land-use: increasing population density is associated with increased burned are in rangelands but with decreased burned area in croplands. Overall, the relationship between population density and burned area is non-monotonic: burned area initially increases with population density and then decreases when population density exceeds a threshold. These thresholds vary regionally. Our study contributes to improved understanding of how human activities relate to burned area, and should contribute to a better estimate of atmospheric emissions from biomass burning.

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## Introduction

Fire is a natural process that has played a key role in the maintenance of natural ecosystems for millions of years, and regulates plant and animal population dynamics [1-3]. However, fire is also a tool used by people to transform the natural environment [4-6]. Humans are the dominant influence over most of the land surface today [7]. Prior to the industrial revolution only ca 5 % of the ice free land surface was used for agriculture and settlement. However, between 1700 and 2000 AD, the terrestrial biosphere transitioned from being mostly wild to mostly anthropogenic, passing the 50% threshold early in the 20th century [8]. This transformation makes it important to consider human influence on modern fire regimes [9].

Guyette et al. (2002) [9] identified four ways in which human influence the amount of land burnt (or the burned area fraction): anthropogenic ignitions, fuel production, fuel fragmentation and cultural behaviour. All these factors are linked to population density. Many regional studies show a single-peaked relationship between human population and fire extent and/or numbers of fires, with intermediate populations at the peak of this parabola, after which different land use activities and land cover types attenuate fire frequency and reduces burnt area fraction [10-13].

The objective of this study is to investigate the influence of population density on burnt area by exploring its spatial variability using Geographically Weighted Regression, and try to detect existence of critical thresholds in population density for fire behaviour using quantile regression. We then interpret the findings in the light of differences in major land use management classes.

## Data and Methods

### Data

Satellite-derived burned area maps covering 13 years (1997-2009) are available from the Global Fire Emissions Database version 3 (GFED3: [14]) at 0.5° cell resolution for the

whole globe (Fig. 1a), available at: http://www.globalfiredata.org/. This spatial resolution can reveal first-order global and continental-scale patterns in burnt area [15]. Giglio et al. (2010) [14] demonstrated that the GFED v3 data used in this study has improved accuracy over version 2 in Canada and the USA. Since active fire detection can capture mush smaller events (sub-pixel) than burned area products, GFED may indeed better represent area burned in small fires than products that do not rely on active fire data. For 0.5° spatial resolution burned area, GFED v3 uses either VIRS or ATSR world fire atlas fire counts [14]. The input data for a GWR are the centroids of the 0.5° cells. Cells that intersect water bodies, ice and artificial surfaces are considered to be non-combustible areas and were removed using a mask from the Global Land Cover 2000 database [16]. The global combustible area extent was calculated from the area of each cell using a latitude correction. The annual mean burned area ($km^2$) for the 13 years of observations was used as the response variable. Population density (persons per square kilometre: $p/km^2$) was obtained from the Gridded Population of the World version 3 [17] at 0.5° spatial resolution (Fig. 1b) available at: http://sedac.ciesin.columbia.edu/data/collection/gpw-v3, and is used as the predictor variable. As both burned area and population density are highly skewed toward small values, we applied a decimal logarithmic transformation to both variables.

To support the interpretation of our analyses of the human influence on burned area, we use the anthropogenic biomes (Anthromes) of the world [18] available at: http://ecotope.org/anthromes/v1/guide/. This dataset classifies terrestrial biomes based on the level of human influence, estimated as a function of population density, land use and land cover. The 21 anthromes are grouped into 6 major anthrome types in the original publication (Table 1; Figure 1c) and we use these major types here to simplify interpretation of the GWR results.

### Statistical Analyses

We initially computed the global linear relationship between burned area and population density using Ordinary Least Squares (OLS). The global OLS regression model assumes that the studied relationship is stationary, i.e. the estimated parameters do not vary spatially. To test the hypothesis that the relationship varies spatially, we use Geographically Weighted Regression (GWR). GWR estimates local parameter values as in (Eq. 1) [19,20].

$$y = \beta_o(\mu,\nu) + \sum_{j=1}^{p} \beta_j(\mu,\nu) X_j + \varepsilon \quad \textbf{(1)}$$

Where (μ,v) is the coordinate location and j is the number of the explanatory variables of the X matrix, β is a matrix with the regression coefficients and ε is a random error whose distribution is $N(0, \sigma^2 I)$ [20].

We initially ran the GWR at 0.5° spatial resolution, which is the original resolution of both the burned area and population data sets, but also the resolution used by several Dynamic Global Vegetation Models (DGVM). Other than such pragmatic criteria, the choice of an appropriate level of spatial aggregation for analyses of spatial relationships is essentially arbitrary [21]. The basic assumption of the GWR is that observations closer to a target point have more impact on the modelled relationship at that point than more distant observations. A distance decay function centered on each observation is used for this purpose, and this makes it important to choose an appropriate level of aggregation. The GWR procedure includes a step that assesses whether the selected scale is appropriate. However, to assess the sensitivity of the spatial relationship between population density and burned area to the choice of spatial resolution, we used Africa as a test case and re-ran the analyses for this continent using 0.25° and 1.0° cells. The distance-decay depends on the bandwidth of the spatial kernel used, which is the radius or the number of observations around each point [19]. Here, we used a continental space scale, defining the continents according to political borders (M. Charlton, personal communication). We used an adaptive Gaussian kernel, whose bandwidth varies according to the density of the data, an approach usually adopted when there is no prior knowledge of the studied relationship [19]. The optimal bandwidth for each continent was determined by minimizing the Akaike information criterion (AIC) [22,23]. Due to the different extent of land of each continent and the minimization of the AIC coefficient for the highest adjusted $R^2$, the bandwidth varies, but remains proportional at 5.1% of the total observations in all cases. The use of the AIC ensures that we use the appropriate level of spatial aggregation for each continent. The analysis is performed with GWR version 3.0. (see 20).

A Monte Carlo permutation test is used to test the significance of the spatial variability of local coefficient estimates. We only map the statistically significant values of the GWR output parameters (slope coefficients and intercept), as determined by a t-test. As multiple hypotheses tests are used, an alpha correction is employed to reduce type I errors [23]. The parameter coefficients were tested for significance according to the family-wise error rate $\xi_m$ by choosing

$$a = \frac{\xi_o}{1 + p_e - \frac{p_e}{np}} \quad \textbf{(2)}$$

where $p_e$ is the effective number of parameters, n is the total number of observations and p is the number of parameters in each model [23,24].

The relationship between population density and burned area is expected to be non-linear and non-monotonic. To examine whether there are abrupt changes in the nature of the relationship switches, we fit a linear "broken stick" version of quantile regression [25-28], using the package "quantreg" in R (http://cran.r-project.org/web/packages/quantreg/index.html). This technique makes no prior assumption of abruptness [29]. Since there could be more than a single slope in rate of change because of interactions between factors [30], we consider the $50^{th}$ and $90^{th}$ burned area percentiles, to explore the impact of human activities on area burnt.

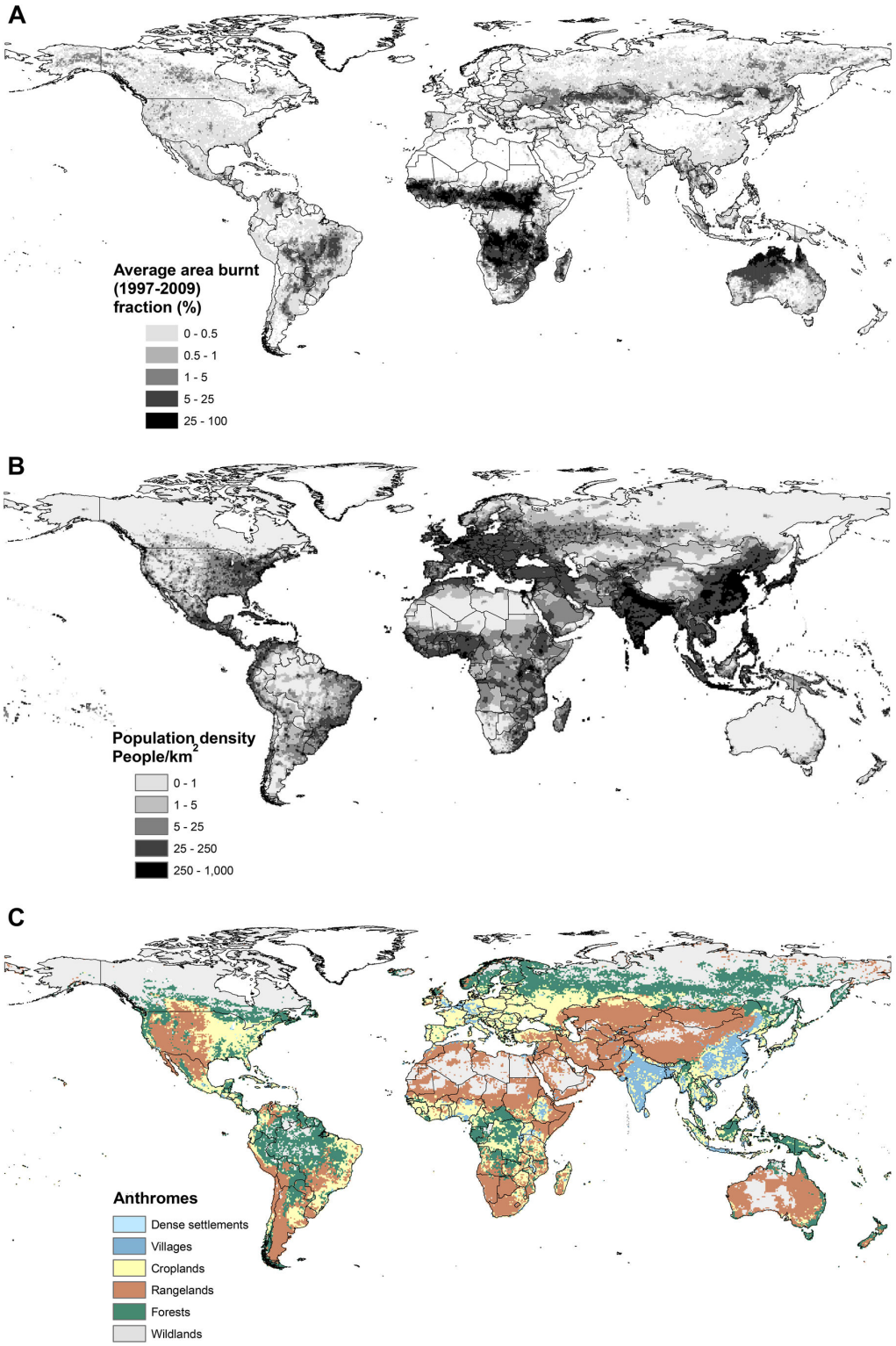


**Figure 1. Input data sets.** Average mean annual burned area (showed in cell area fraction instead of km$^2$ in order to help the interpretation), based on data from the Global Fire Emissions Database version 3 (GFED3: Giglio et al., 2010) for the period 1997-2009; (B) Population density (persons per square kilometre: p/km$^2$) from the Gridded Population of the World version 3 (Ciesin, 2005); and (C) The anthropogenic biomes (anthromes) of the world, mapped as the six major anthrome types (see Table 1) defined by Ellis and Ramankutty (2008).

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**Table 2.** Percentage of statistically significant values per continent, AIC coefficients and adjusted $R^2$ for the OLS and the GWR model.

| Continent | Number of observations | % significant slopes | % positive slopes | AIC (OLS) | AIC (GWR) | Adjusted $R^2$ (OLS) | Adjusted $R^2$ (GWR) |
|---|---|---|---|---|---|---|---|
| **Africa** | 10647 | 61.3 | 75.5 | 52871.22 | 39362.11 | 0.27 | 0.80 |
| **Asia** | 23799 | 65.7 | 78.3 | 115337.97 | 101721.13 | 0.04 | 0.46 |
| **N. America** | 17192 | 42.9 | 55.1 | 76372.24 | 67573.16 | 0.24 | 0.55 |
| **S. America** | 6551 | 46.8 | 81.8 | 31317.89 | 26493.67 | 0.07 | 0.56 |
| **Europe** | 6899 | 21.44 | 68 | 32402.14 | 27009.41 | 0.11 | 0.60 |
| **Australia** | 3038 | 20.51 | 76.4 | 14508.43 | 11947.93 | 0.001 | 0.58 |

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**Table 1.** Anthromes and major anthrome types defined by Ellis and Ramankutty (2008).

| Anthrome | Major anthrome type |
|---|---|
| Urban | Dense Settlement |
| Dense settlements | Dense Settlement |
| Rice villages | Villages |
| Irrigated villages | Villages |
| Cropped and pastoral villages | Villages |
| Pastoral villages | Villages |
| Rainfed villages | Villages |
| Rainfed mosaic villages | Villages |
| Residential irrigated cropland | Croplands |
| Residential rainfed mosaic cropland | Croplands |
| Populated irrigated cropland | Croplands |
| Populated rainfed cropland | Croplands |
| Remote croplands | Croplands |
| Residential rangelands | Rangelands |
| Populated rangelands | Rangelands |
| Remote rangelands | Rangelands |
| Populated forest | Forest |
| Remote forest | Forest |
| Wild forest | Wildlands |
| Sparse trees | Wildlands |
| Barren | Wildlands |

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## Results

### OLS versus GWR comparison

The relationship between log-transformed population density and burned area estimated using OLS is poor, with $R^2$ values varying from 0.001 (Australia) to a maximum of 0.27 (Africa). The relation between the log-transformed population density and burned area using the GWR models at 0.5° resolution is significant for all continents; the proportion of variability in burned area explained varies from 46% (Asia) to 80% (Africa). Thus, GWR performs much better than OLS for every continent. The GWR models also have lower AIC coefficients than OLS model and much higher adjusted $R^2$ values (Table 2), showing that the local model (GWR) is a significant improvement on the global (OLS) model for all continents.

The GWR analysis shows that there is no significant relationship between population density and burned area over 48.5% of the total area of the globe. A significant relationship between population density and burned area is found for ca 66% of the total area of Asia, ca 61% of Africa, ca 47% of South America and 43% of North America. Less than 22% of Europe and Australia are characterised by a significant relationship between burned area and population density.

### Spatial patterns

The relationship between population density and burned area is non-stationary and shows patterns that differ both in sign and magnitude (Figure 2a). The relationship can be positive or negative, where positive relationships indicate that human activities increase burned area and negative relationships indicate that human activities have negative influence on fire. The magnitudes of the slope coefficients are different in different continents, so we focus on the sign in regions showing significant relationships between population density and burned area. The intercept can be an estimate of the area burnt when population density is small (1 p/km$^2$), although absolute values are influenced by the slope coefficient. However, for regions displaying similar slopes, the intercept can be interpreted as a measure of the fire-proneness of the landscape, where positive intercepts indicate that the region is fire-prone and negative intercepts indicate that the region is less likely to burn.

### Africa

On average over the period 1997-2009, 69% of the global area burned is in Africa. This is comparable to Tansey et al.'s (2004) [31] estimate that Africa accounted for 64% of the total area burned in 2000. The relationship between population density and burned area is statistically significant over nearly 61% of the continental area, with positive relationships in the Maghreb, the Sahel, the Horn of Africa, central Africa, and south-western Africa (Figure 2a) and negative relationships in the Sudanian savannah region and parts of eastern Africa (Figure 2a). Over most of these areas, the slope coefficients are >1 (or < -1), indicating that the impact of people becomes progressively larger at higher population densities. Regions with positive relationships between burned area and population density generally occur in rangelands (Figure 1c), while the areas with negative relationships have a higher incidence in

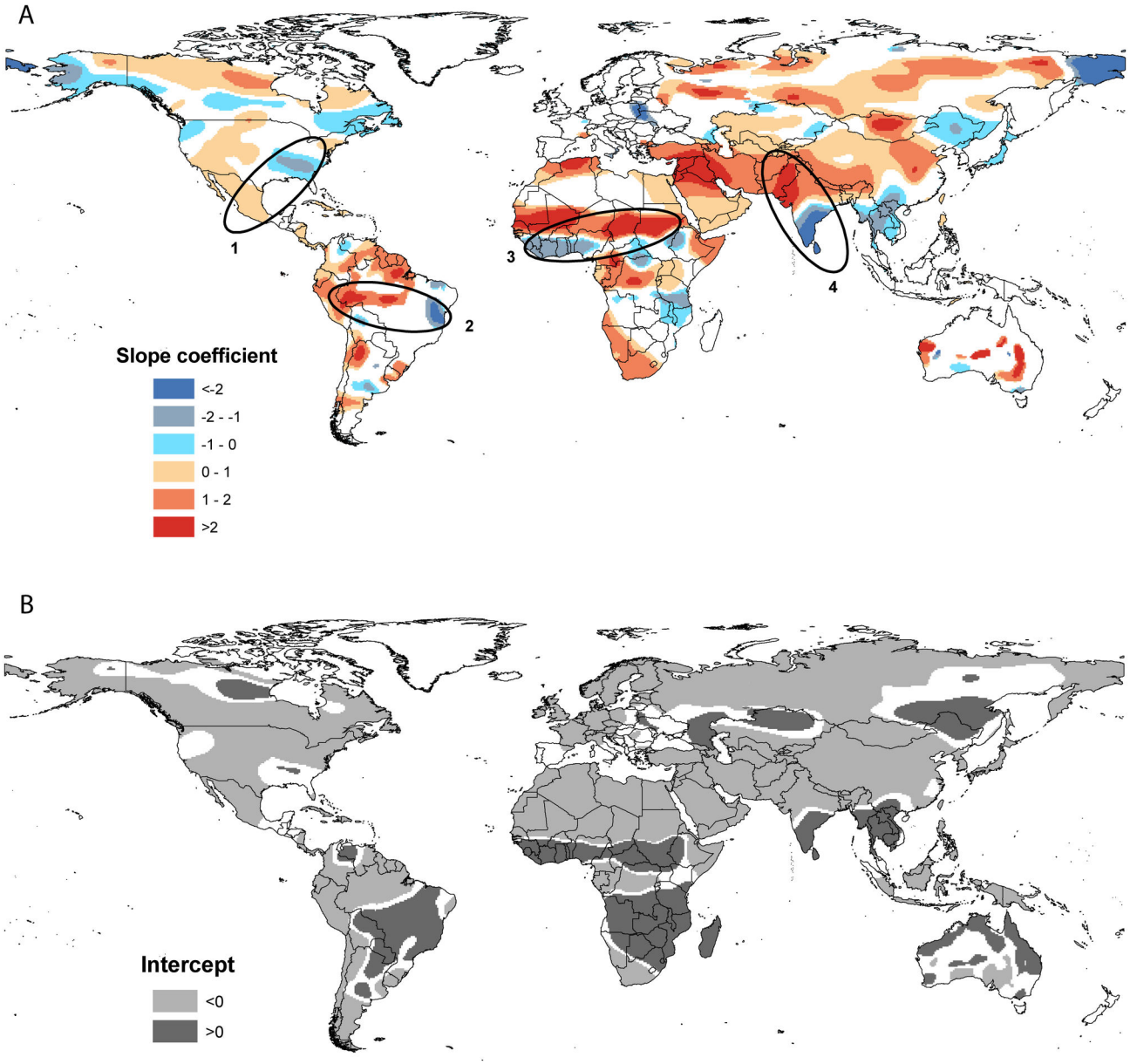


**Figure 2. Output parameters and local $R^2$.** The upper panel (A) shows results from the GWR analysis, showing the nature of the relationship between population density and burned area for those regions where the relationship is significant at the 95% level (red shows a positive relationship, blue shows a negative relationship). The slope coefficient classes are defined separately for each continent; (B) Mapped patterns in the sign and magnitude of the statistically significant intercept values from the GWR analysis of population density and burned area. Dark grey shows positive intercept values, where the area burned is large even at negligible population density (i.e. where the landscape is naturally fire-prone), while light grey shows negative intercept values where climatic or vegetation factors do not favour fire; (C) Showing the significant patterns for both intercept and slopes according to the sign of the relationship, thus the four combinations show both out being positive (red), positive slopes and negative intercept (green), negative slopes and positive intercept (yellow) and both being negative (blue) ;(D) Mapped patterns of the local $R^2$ for the regions where the relationship between population density and burned area is statistically significant.

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areas of croplands and villages, and in forests. Absence of fire (because of lack of fuel) explains the absence of significant relationships in the Sahara, but the absence of any significant relationship associated with the high burned area (Figure 1a) in the Angola-Congo-Zambia region is perhaps more surprising (Figure 2a), given the general view that Miombo woodlands are

highly susceptible to anthropogenic fires (e.g. 32) and has been identified as one of the highest fire incidence in the world [15]. Population density in this region is rather low (5-15 people per $km^2$) and shows little spatial variability. This could partly explain the lack of a significant relationship between burned area and population. However, the region is characterised by a mosaic of open, fire-prone savannah vegetation and it is likely that both the high incidence and variability of fire is mainly determined by variability in climate and vegetation.

About 40.1% of the regions showing a significant relationship between burned area and population density have positive values for the intercept (Figure 2b), most particularly the Sudanian savannah region and parts of eastern Africa, where the relationship between fire and population density is inverse (Figure 2a). The positive intercept values indicate that these regions are naturally fire-prone, and help to explain why increasing population density should lead to lower area burnt. In contrast, the regions with negative intercepts can be interpreted suggesting that low fuel loads would normally limit fire and human modification of the vegetation cover is responsible for the relatively high levels of fire in these regions. This is consistent with the finding that burned area increases strongly (values > 1) with population density, because landscape modification will also increase with population density.

### Asia

Asia is the continent with the largest area (over 49 million $km^2$) and the highest percentage (66%) of statistically significant slope values (Table 2). There are three regions that show a positive effect of population. The first extends from Turkey and Saudi Arabia through Iran and across to Afghanistan, Pakistan and northern India, the second is the rangelands of Mongolia and northern China, and the third occurs in the boreal parklands of Russia. Whereas the slope coefficients of the first two regions are always >1 (Figure 2a), a large part of the Russian parklands has slope coefficients <1, showing that the largest effects on fire occur for small population increments. Regions with significant negative slope coefficients occur in southern India, Southeast Asia and southern China, north-eastern China and Chukotka (north-eastern Siberia). As in the case of Africa, the regions showing positive relationships between burned area and population density tend to be predominantly characterised by rangelands. Regions characterised by villages and croplands, rangelands with extremely high population densities (e.g. in northern India and Pakistan, where populations densities are >250 p/$km^2$) and forested areas tend to show positive relationships between burned area and population density.

About 14% of the area of the total significant intercept values are positive (Figure 2b). Positive intercepts occur in southern India, Southeast Asia and north-eastern China – all areas where the relationship between burned area and population density is negative (i.e. an increase in population leads to suppression of fire). Areas with negative intercept values in the region stretching from Turkey through northern India to Mongolia show positive relationships between burned area and population density. The relationship in the boreal parklands is more complex, since although areas with positive slope coefficients mostly have negative intercept values, there are some limited areas with positive slope coefficients. However, the $R^2$ values (Figure 2d) in these regions are low (< 0.25), and the difference in the signals may not be robust. A different relationship occurs in Chukotka (and indeed in parts of Alaska), where negative relationships between burned area and population density are characterised by negative intercepts. Thus, in this not particularly fire-prone tundra region, increasing population density can significantly reduce fire incidence.

### North America

The relationship between population density and burned area is statistically significant for over 43% of the area of North America (Table 2a). Positive relationships are found in the semi-arid (and mostly rangeland areas) of northern Mexico and the Great Basin, and in the boreal parkland regions of Canada and north-eastern Alaska. Negative relationships are found in the forested and cropped landscapes of south-eastern U.S.A (Alabama, Georgia, South Carolina), the forested regions of the Pacific Northwest and southern Alaska, and the boreal forest zone of central and eastern Canada (Figure 2a). Across virtually all of North America, slope coefficients are between 1 and -1, a feature that is consistent with the high technological levels of agriculture and contrasts strongly with regions of more traditional agricultural practices, such as Africa.

Only 4.1% of the regions showing statistically significant intercept have positive values. Positive intercept values (Figure 2b) are found in the south-eastern U.S.A., where the relationship between burned area and population density is negative, and in the boreal parklands of northern Canada where the slope of the relationship is positive. Areas with negative intercepts are characteristic of the southern boreal forest in eastern Canada and southern Alaska, and the semi-arid rangelands of the Great Basin and northern Mexico. The relationship between slope and intercept in the rangeland areas (positive slope coefficients, negative intercepts) is consistent with what is observed in semi-arid rangelands in other parts of the world; the relationship in the southern boreal forests (negative slopes, negative intercepts) is distinctive.

### South America

The relationship between population density and burned area is statistically significant for 47% of the area of South America (Table 2). The relationship is positive around the margins of Amazonia, and in northern Argentina (Figure 2a). Negative relationships are found in the Bahia state in Brazil and, somewhat anomalously, in the rangeland area of central Argentina. The areas characterised by negative relationships between burned area and population density have positive intercepts (Figure 2b), i.e. these are fire-prone areas where increasing population leads to a reduction in fire. Most of the regions where the relationship between burned area and population density is positive are characterised by negative intercept values. However, in some parts of the so-called “arc of deforestation” on the southern side of the Amazon forest the positive relationship between fire and population density is associated with positive intercept values (Figure 2b), indicating

**Table 3.** Summary statistics of the GWR analysis for Africa, comparing the results obtained using 0.25°, 0.5° and 1.0° grid cell resolutions.

| Continent | Number of observations | % significant slopes | % positiveslopes | AIC (OLS) | AIC (GWR) | Adjusted $R^2$ (OLS) | Adjusted $R^2$ (GWR) |
|---|---|---|---|---|---|---|---|
| **Africa (0.25)** | 40864 | 67.7 | 65.5 | 189463.45 | 138841.26 | 0.21 | 0.77 |
| **Africa (0.5)** | 10647 | 61.3 | 75.5 | 52871.22 | 39362.11 | 0.27 | 0.80 |
| **Africa (1)** | 2557 | 52.4 | 97.8 | 12261.02 | 8188.66 | 0.36 | 0.87 |

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fire-prone landscapes where human activity is increasing the amount of burning.

### Europe and Australia

The relationship between population density and area burned is significant in < 22% of Europe and Australia (Table 2). In Europe, the only areas showing statistically significant negative relationships are in Poland, Ukraine and Belarus. However, intercept values in this region are positive, indicating some level of landscape susceptibility to fire. This feature most likely reflects a pattern dominated by the forested landscapes of e.g. the Carpathians, where natural forest fire regimes are suppressed with increasing population. Positive relationships between population density and burned area are found in some forested parts of north-western Russia; the intercept values are negative.

There are no significant relationships between area burned and population density in the savannah and rangeland areas of northern and western Australia characterised by the highest incidence of fire in the continent (Figure 1a). Areas showing a positive relationship between burned area and population density are in the rangelands of the Murray-Darling basin, on the northern margin of the Lake Eyre basin and to the south of the Hamersley Range in Western Australia. These regions are all associated with positive intercept values. Small areas showing a negative relationship between burned area and population density occur on rangelands of the Nullarbor Plain and in the densely-settled region (Figure 2a) around Melbourne in southern Victoria. The Nullarbor is characterised by negative intercept values (Figure 2b), presumably because of the very low vegetation cover and hence fuel loads in this region. In contrast, the area around Melbourne is characterised by positive intercept values – this is a fire-prone area where human activities work to suppress fire.

### Sensitivity to spatial resolution

As expected, the GWR is sensitive to the choice of spatial resolution (Table 3). The extent of the area with significant relationships decreases with spatial resolution, from 68% at 0.25° resolution to 52% at 1° resolution. Changing resolution does not affect the conclusion that most of the relationships between burned area and population density are positive, but the proportion of positive values increases with increasing resolution, reaching an unrealistically high value of 98% at 1° resolution. This presumably reflects the increasing homogenisation of grid cell values of burnt area and/or population density with increasing resolution. The geographical patterns of significant values, and positive and negative relationships, are not impacted by the change from 0.25° resolution to 0.5° resolution, although areas showing negative relationships between population density and burned area have virtually disappeared in the analyses at 1° resolution. These sensitivity tests suggest that the overall conclusions of our GWR analysis would not be affected by running at finer than 0.5° resolution, but clearly information is likely to be lost in analyses at coarser resolution.

### Impact of land-use on the relationship between burned area and population density

Both positive and negative relationships between burned area and population density are found in every type of anthrome (Figure 3). Wild lands represent a significant proportion of the regions where there is a significant correlation between burned area and population density, but nevertheless the proportion showing positive or negative correlations is about the same (29% of the total area showing positive, 31% showing negative correlations). However, croplands and rangelands are not equally represented in the two classes of relationship: 37% of the area where there is a negative relationship between burned area and population density is cropland and only 10% is rangelands. Conversely, rangelands account for nearly 40% of the area where there is a positive relationship between burned area and population density, while croplands account for only 11% of these regions.

### Quantile regression analysis

Although regions may show an overall positive or negative relationship between burned area and population density, the nature and strength of the relationship is not necessarily constant at different levels of population [33]. We examine whether there are critical thresholds in population density at which the relationship between population density and the burned area extent changes using quantile regression, focusing on four different regions in Africa, Asia and the Americas (Figure 2a). Each region is characterised by close bipolar patterns, thus displaying areas with both strongly positive and strongly negative slope coefficients (Figure 2a).

In Asia, the relationship between population density and burned area is monotonic (Figure 4, case 4): as population density increases the impact on fire, whether positive or negative, increases. This is true for regions with moderate levels (50%) and at higher levels of burned area. In Africa and South America, the relationship between population density and burned area is non-monotonic: burnt area increases up to

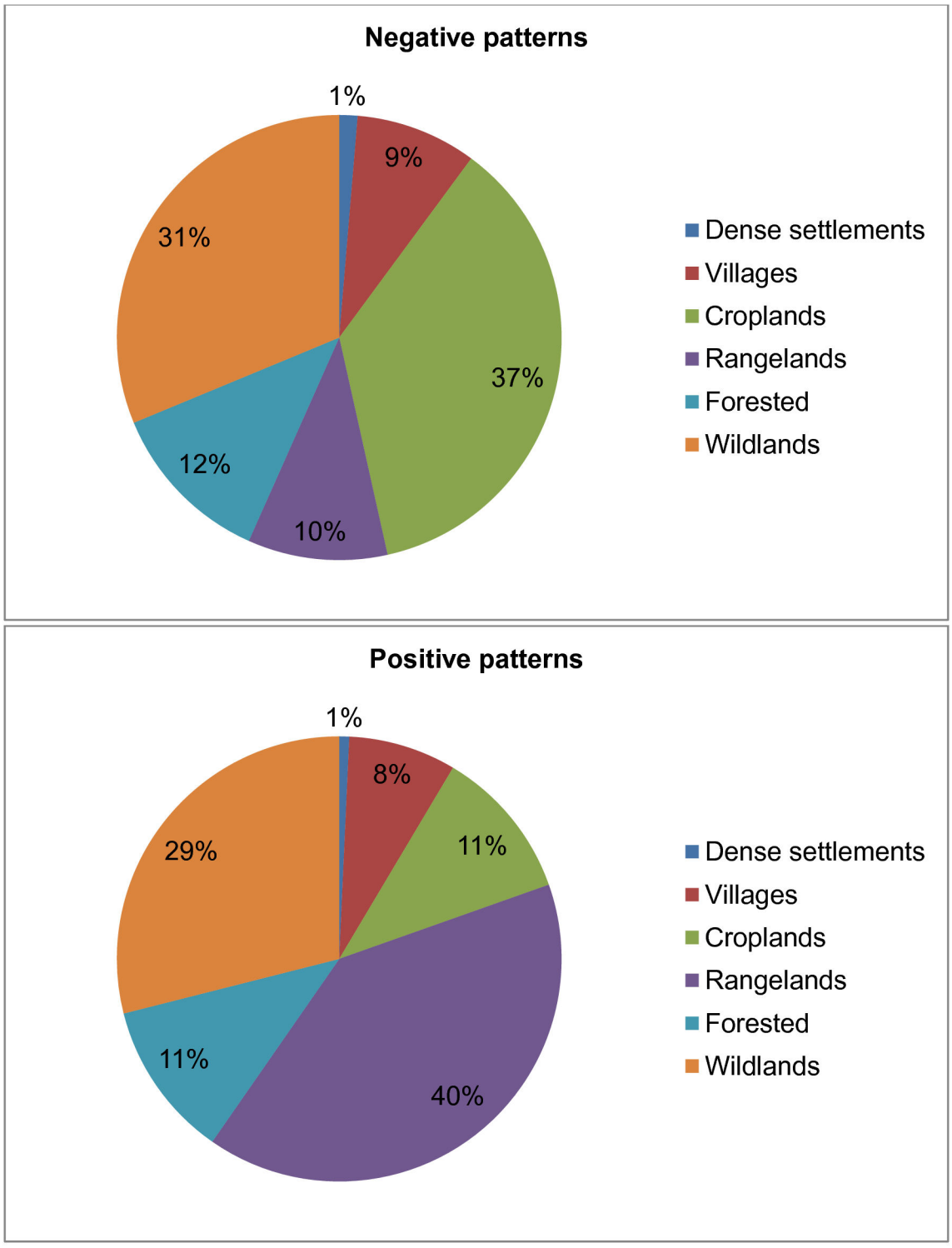


**Figure 3. Proportion of Anthromes showing negative and positive relationship.** Pie-charts showing the relative proportion of the total area showing (A) positive and (B) negative significant relationships between burned area and population density, classified according to the six major anthrome types defined by Ellis and Ramankutty (2008).

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a given threshold, reaches a peak and then declines (Figure 4, cases 2-3). In both regions, the change point in the nature of the relationship occurs at about 7 p/km$^2$ in both regions with moderate and high levels of fire. The impact of changes in population density on burned area becomes negligible at population densities greater than ca 10 p/km$^2$ in both regions. The relationship between burned area and population density in North America is also non-monotonic (Figure 4, case 1). In regions with only moderate levels of fire (as shown by the 50% quantile regression), the relationship is similar to that observed in South America and Africa: increasing population density leads to increasing impact on burned area up population densities of 7 p/km$^2$ and then becomes negative and the slope becomes more gentle at population densities of > 12 p/km$^2$. However, in regions with higher levels of fire (as shown by the 90% regressions), the negative relationship at population densities > 7 p/km$^2$ is reversed and becomes positive at population levels > 30 p/km$^2$.

## Discussion and Conclusions

This study quantifies the spatial variability in the relationship between human activities (as measure by population density) and fire (as measured by burned area). There is no statistically significant relationship between burned area and population density over more than 50% of the global land area. The univariate relationship between population density and area burnt is relatively unimportant in Australia and Europe: in the case of Australia this supports the idea of a strong climate control on fire regimes, while in Europe the lack of relationship most likely reflects the closely managed nature of the landscape. At a sub-continental scale, there are regions where population density has little or no impact on burned area. In Kazakhstan, for example, variability in burning shows no relationship with population density despite the fact that this is one of the biggest agricultural areas in the world [34] and the country that contributes with highest amount of area burnt in dry land ecosystems in central Asia [35]. A similar situation pertains in the Miombo woodlands region of Angola-Congo-Zambia, where variability in burned area is unrelated to population density. The absence of a relationship between population density and burned area over much of the globe does not imply that human activities have no influence on fire regimes. Several studies have shown, for example, that humans can alter the timing [36] or the number of fires [13,37]. However, since it is burned area (rather than timing or number) that is most important for the carbon cycle and pyrogenic emissions, the lack of a strong relationship between human activities and burned area over much of the globe, including areas characterised by high levels of burning, is noteworthy.

In areas where there is a statistically significant relationship, this relationship is positive (i.e. burned area increases with population density) over 73.3% of the global land area. However, there are substantial parts of the world, where the relationship between burned area and population density is negative (i.e. increasingly human activity leads to fire attenuation). The relative proportion of the land area showing positive/negative relationships varies from continent to continent. There has been considerable focus on the positive relationship between human activities and burned area, through using fire to clear land and as part of the agricultural regime [34,38]. The impact of landscape fragmentation on reducing fire in agricultural area has also been documented [16,39,40].

About 30% of the regions where a significant relationship between population density and burned area are classified as wild lands, but the relative proportion of wild lands in the areas showing positive or negative relationships between fire and human activity is approximately the same. This is not the case for all anthromes. Rangelands are over-represented in the regions showing positive relationships between fire and population, while croplands are over-represented in the regions showing negative relationships between fire and population. The distribution of rangelands is to some extent a reflection of climate controls, with most rangeland areas occurring in semi-arid regions and croplands occurring in more well-watered regions, nevertheless these tendencies suggest that land-use practices can have a significant impact of fire regimes.

The GWR analysis shows that, in general, regions which display a negative relationship between burned area and population density generally have positive intercept values, and vice versa. In other words, in regions where climate and/or vegetation create conditions where fires are likely (i.e. fire prone landscapes), people tend to supress fire whereas in regions that are less fire-prone because of e.g. lack of fuel, people tend to increase the area burned. However, there are regions where there is both a positive relationship between population and burned area and the intercept is also positive. One of these regions is the arc of deforestation on the southern border of Amazonia, suggesting that deforestation is exploiting a landscape that is already susceptible to the impact of fire. This is not a new suggestion; Le Page et al. (2010) [41] pointed out that this region experiences three to five months of low precipitation which facilitates extended periods of burning.

In most regions of the world, the nature of the relationship between population density and burned area is non-monotonic: increasing human activity (as measured by population density) initially lead to an increase in burned area but this peaks at intermediate levels of population density and then declines. The critical value in three of the case studies regions examine here is around 7 p/km$^2$ and above values of 12 p/km$^2$ there is no further impact of population density changes on fire. Our results for Africa support previous findings [13,42] that suggest that fire extent in this region displays a non-monotonic relationship with anthropogenic variables. However, in areas of North America characterised by high fire, there is a second threshold at ca > 30 p/km$^2$ where increasing population density leads to increasing burned area. The situation in Asia seems anomalous in that increasing population density always leads to an increased impact in burned area.

The GWR approach allows an appropriate spatial scale of comparison to be selected continent by continent through the choice of bandwidth combined with use of the AIC. Fotheringham et al. (2002) [20] showed that the GWR approach was more robust to the choice of spatial resolution than models that do not take spatial non-stationarity into

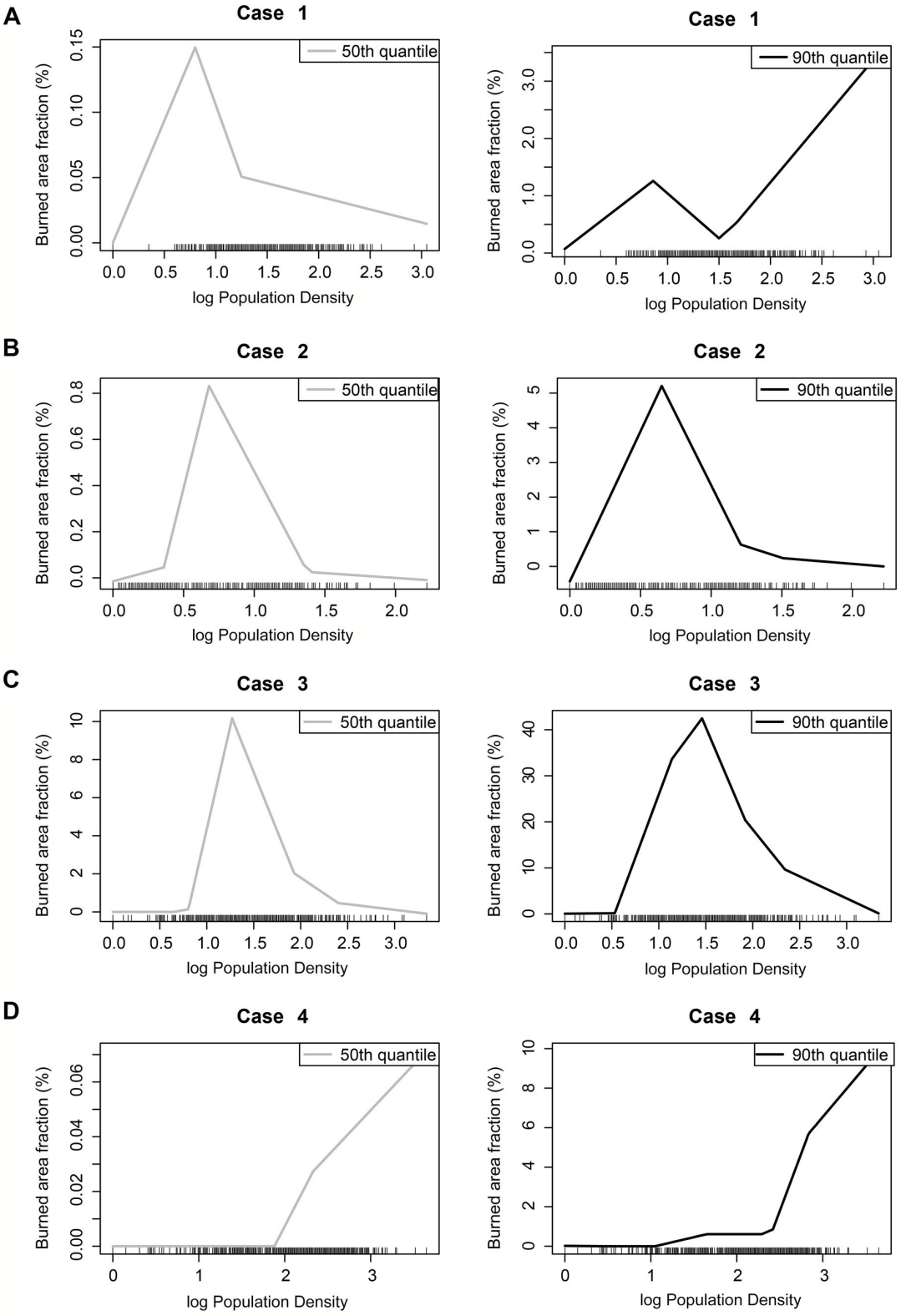


**Figure 4. The relationship between burned area and population density at different levels of burned area (50 and 90%) for the 4 case studies.** (A) Case 1 in North America. (B) Case 2 in South America. (C) Case 3 in Africa. (D) Case 4 in Asia.

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account. Nevertheless, we examined the impact of the choice of spatial resolution using Africa as a test case. The use of a higher resolution than our baseline of 0.5° produces no change in the geographic patterns of regions showing significant positive or negative relationships between population density and burnt area, although the percentage of grid cells showing positive values declines slightly (and the percentage showing negative values correspondingly increases). The overall impact of increasing the resolution is slight, and this suggests that our regional findings are robust. Most other studies of the controls on burnt area have used coarser spatial resolutions (e.g. 12,43). Our sensitivity analyses show that decreasing the resolution has a larger impact on the geographic patterns, and particularly on the recognition of areas where the relationship between population density and burnt area is negative. This suggests that these earlier studies may miss important aspects of the relationship between population density and burnt area because of their choice of spatial scale. The selection of spatial scale is can affect the conclusions about the nature of spatial relationships, making it important to use a technique (such as the AIC optimization) that allows this choice to be made objectively.

Understanding the complexity of the relationships between people and fire is important in a modelling context. Fire-enabled dynamic vegetation models can be used to predict the consequences of projected changes in climate on fire regimes (see e.g. 44-46). However, those models that explicitly include anthropogenic fire generally focus on human impacts on ignitions and furthermore employ either a universal population density value as a threshold for anthropogenic fire ignitions [47], or single-peaked global function of population density [48]. Other fire-enabled DGVMs (e.g. LPX: [49]) ignore anthropogenic ignitions, although they allow for human suppression of fire in agricultural areas. No extant model incorporates spatially varying relationships between burned area and population density that are dependent on vegetation types, land-use and cultural practices – which our analyses show a non-negligible influence on regional fire regimes. However, this study has not exhausted the analyses necessary to arrive at a complete understanding of the biogeography of fire.

## Author Contributions

Conceived and designed the experiments: IB DO ACLS JMCP. Performed the experiments: IB DO. Analyzed the data: IB DO ACLS SPH ICP JMCP. Contributed reagents/materials/analysis tools: IB DO ACLS JMCP. Wrote the manuscript: IB DO ACLS SPH ICP JMCP.

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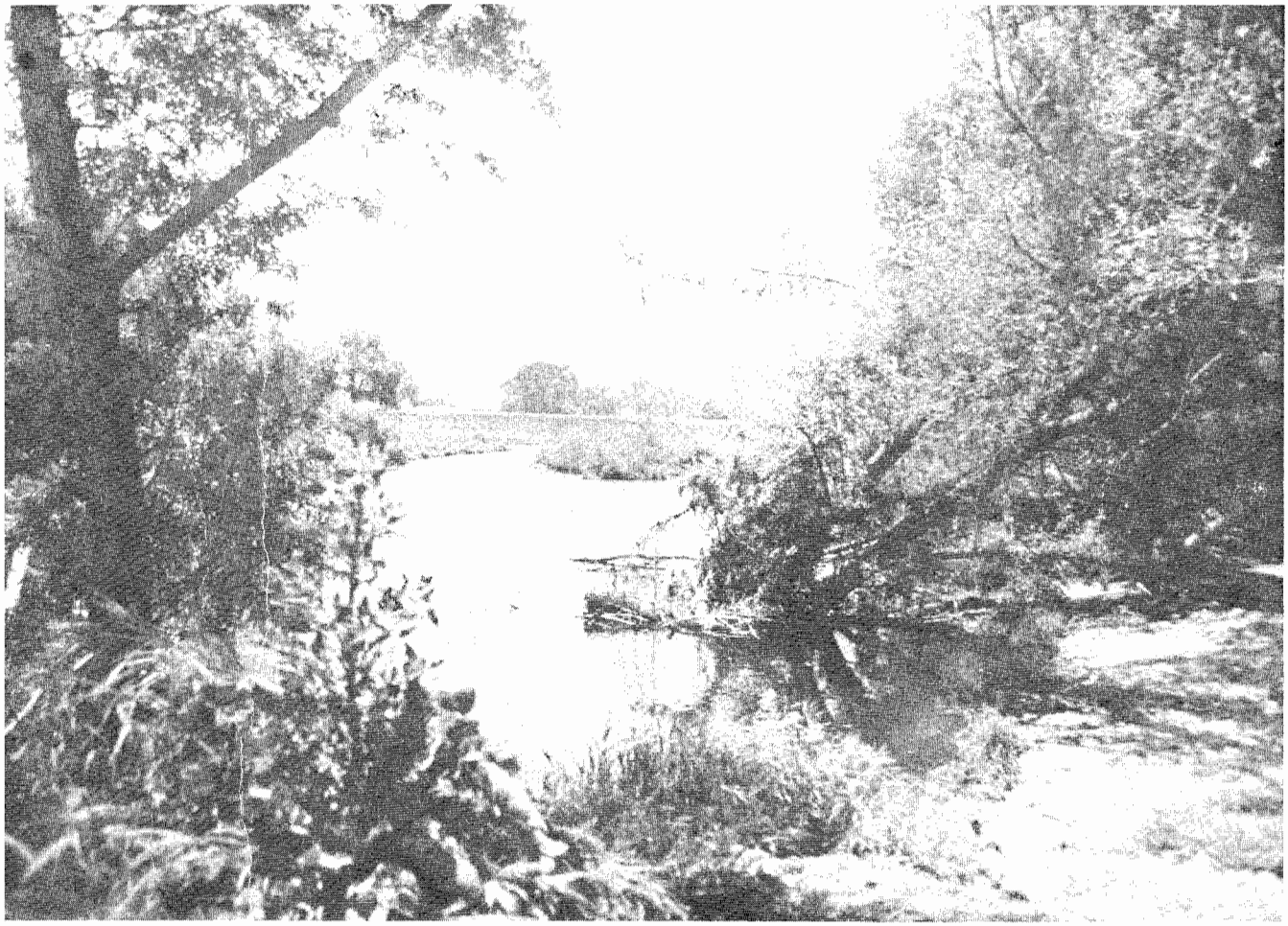
# ENDANGERED PLANT COMMUNITIES

# OF

# SOUTHERN CALIFORNIA



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# RIPARIAN WOODLAND: AN ENDANGERED HABITAT IN SOUTHERN CALIFORNIA

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## INTRODUCTION

There is no precise inventory of North American wetlands prior to European contact, but it has been estimated that wetland resources covered over 200 million acres (80 million ha) in the lower 48 states when European settlement began (Frayer, et. al., 1983). By the mid-1970s over half of the total had been eliminated, and only an estimated 99 million acres (40 million ha) remained. Destruction of wetlands over the previous two decades had proceeded at 400,000 to 500,000 acres (160-200 thousand ha) per year. By 1975 California had lost 91% of its wetland habitats (The Conservation Foundation, 1989). A dramatic example of riparian woodland loss occurred in the Sacramento Valley, where there were an estimated 800,000 acres (325,000 ha) of riparian habitat in 1850 (Roberts, Howe and Major, 1980). In 1952 this resource had shrunk to 20,000 acres (8000 ha) and by 1972 there were an estimated 12,000 acres (5000 ha) - or 1.5% of the original habitat - remaining. By 1980, the rate of national wetland "alteration" had slowed to an estimated average of 275,000 acres (111,000 ha) per year (Office of Technology Assessment, 1984), although in some areas, such as rapidly developing southern California, habitat loss continued at a high rate. Between the mid-1950s and mid-1970s an estimated 14,877,000 acres (6,023,000 ha) of freshwater wetlands were eliminated (Office of Technology Assessment and U.S.F.W.S. National Wetlands Trends Study, 1982). During this era, draining of wetlands for agricultural purposes dominated freshwater wetland habitat destruction of 11,720,000 acres (4,750,000 ha), or 79% of total losses - but rationales for converting wetlands to other land uses ranged from urban development of 925,000 acres (375,000 ha), or 6%, to flooding them behind hydroelectric projects, stream channelization, and filling them for agricultural use, among many others (Table 1). Current estimates of riparian habitat reduction in southern California floodplain areas have been as high as 95% -97% (Faber, et. al., 1989), a regional loss exceeding that of the endemic coastal sage scrub plant community. There is no question that riparian habitat in southern California is endangere. Global warming and a rising sea level in the next 150 years will claim another heavy toll for wetlands, particularly along the coasts. A few of the anticipated global warming impacts that will change riparian habitat distribution and perhaps even community structure to some extent, as summarized by Tonnessen (1988) and others, include:

- Air temperatures will be higher year-round which will increase evaporation and transpiration.

- It will be drier in the fall, drought will occur in the summer and there will be

Table 1.
Methods of altering wetlands (from The Conservation Foundation, 1989).

**Physical**

1. Filling:
   - adding any material to change the bottom level of a wetland or to replace the wetland with dry land;
2. Draining:
   - removing the water from a wetland by ditching, tiling, pumping, etc.;
3. Excavating:
   - dredging and removing soil and vegetation from a wetland;
4. Diverting water away:
   - preventing the flow of water into a wetland by removing water upstream, lowering lake levels, or lowering groundwater tables;
5. Clearing:
   - removing vegetation by burning, digging, application of herbicide, scraping, mowing or otherwise cutting;
6. Flooding:
   - raising water levels, either behind dams or by pumping or otherwise channeling water into a wetland;
7. Diverting or withholding sediment:
   - trapping sediment, through construction of dams, channelization or other types of projects; thereby inhibiting the regeneration of wetlands in natural areas of deposition, such as deltas;
8. Shading:
   - placing pile-supported platforms or bridges over wetlands, causing vegetation to die;
9. Conducting activities in adjacent areas:
   - disrupting the interactions between wetlands and adjacent land areas, or incidentally impacting wetlands through activities at adjoining sites;

**Chemical**

1. Changing nutrient levels:
   - increasing or decreasing levels of nutrients within the local water and/or soil system, forcing changes in the wetland plant community;
2. Introducing toxics:
   - adding toxic compounds to a wetland either intentionally (e.g. herbicide treatment to reduce vegetation) or unintentionally, adversely affecting wetland plants and animals;

Biological

1. Grazing:
   - consumption and compaction of vegetation by either domestic or wild animals;
2. Disrupting natural populations:
   - reducing populations of existing species, introducing exotic species or otherwise disturbing resident organisms.

**Selected riparian habitat alterations in southern California**
**(including most impacts reviewed in Faber, et.al., 1989).**

1. Channelization:
   - "... eliminates all riparian habitat and wildlife values" (Faber, et.al, 1989); breaks continuity and connectedness of riparian corridor, fragmenting riparian habitat within a watershed; eliminates the wildlife corridor function of stream courses - whether lined or unlined channelization is employed; reduces habitat diversity and distribution within watersheds;
2. Increased sediment loading:
   - caused by logging, clearing habitat for development, construction-related sediment generation, agriculture, road-building, overgrazing, and altering the fire cycle in natural upland vegetation, among other practices which generate sediment and increase vulnerability to erosion;

Table 1 (Continued)

3. Domestic or agricultural wells, ditching and draining of wetland sites:
   - lowers water table, reduces wetted areas available to riparian vegetation;
4. Man's recreational activities:
   - off-road vehicle (both motorcycle and four-wheel drive vehicle) and mountain bicycle use of streamchannels, riparian habitat and adjacent uplands as trails denudes habitat, increases erosion, and so forth; use of riparian trees and shrubs for firewood; camping and picnicing impacts; trash accumulation; graffiti and carvings on trees; shooting (glass, damaged vegetation); trails, roads, and human and pet waste in riparian habitat -among many other recreational impacts;
5. Gravel mining:
   - disrupts the streambed, increases downstream sediment loads, alters the water table, and requires roading through riparian habitat;
6. Proliferation of exotic species:
   - non-native plant species, such as castor bean, tamarisk, Indian tree tobacco, ice plant species, Pampas grass, and many other exotics are abundant in riparian settings (for example, there are 73 exotic plant species in the San Joaquin Marsh; also see Faber, et.al., 1989); non-native snails (Helix aspersa) consume vegetation;
7. Grazing:
   - eliminates riparian habitat, degrades aquatic ecosystem values, increases sedimentation and erosion, and so forth;
8. Altering natural flooding and flow regimes:
   - flood control, water storage, diurnal water level fluctuation impacts below hydroelectric facilities, and so forth (see Faber, et. al., 1989, for a discussion of flood-triggered seed production and dispersal);
9. Mitigation banking:
   - allows regional elimination of riparian habitat, simplifies regional habitat diversity, promotes "all your eggs in one basket" syndrome by allowing consolidated offsite mitigation (for example, see the U.S. Army Corps of Engineers, 1989, proposal to mitigation bank 27 riparian sites averaging 2 acres each at a single mitigation project on Aliso Creek); loss of diversity of riparian habitat by focusing on establishing target species (willow-woodland, for example); utilization of non-local genetic stock in plantings;
10. Failed attempts at mitigation:
    - lack of successful establishment of replacement communities, low species richness, lack of mitigation for wetland habitat altered to allow a site for target species (mitigation) plantings (for example, elimination of sedge or Baccharis for replacement with willow- woodland); long time spans between habitat destruction and functional replacement (see Kusler, 1989; 1990);
11. Impacts of lowered water quality:
    - though not clearly understood for all forms of pollution, "first flush" runoff from streets and freeways; herbicide, fungicide, pesticide and fertilizer laden runoff from golf courses, agricultural fields, nurseries, and to a lesser degree urban residential areas; industrial pollution; reclaimed sewage water (nutrient and salt rich) runoff from cities using it for city and large development landscape watering; chlorinated or chloraminated runoff; seepage from septic tanks or systems, all degrade water with varying potential impacts upon aquatic ecosystems and riparian communities (especially herbs and water quality-sensitive under story species). Synergistic and cumulative impacts as pollutants accumulate in sediments;
12. Urban development, creation of golf courses, flooding behind water storage or flood control projects, conversion to agricultural uses, freeway and other road building in riparian corridors all directly contribute to habitat loss and alteration (see the first portion of Table 1).

greater than average precipitation and runoff in the winter and spring.

- The Sierran snowline will be found at higher elevations and winter rain will be more frequent at intermediate elevations.

- There will be greater air pollution (ozone, acidic pollutants) transported to higher elevations.

- There will be a northward shift of storms, resulting in more monsoonal storms reaching into the southern Sierra during the summer.

- Major climatic zones could shift as much as 30-60 km northward and in mountainous areas the shift would be in elevation not latitude (see Ferren, 1989, and Byron, Jassby and Goldman, 1989, for numerous additional potential future influences on freshwater wetland systems and other references in this burgeoning area of research).

Increased need for water by agriculture and urban requirements will stress systems, and will make riparian habitat preservation planning extremely important. With lower water volumes pollution will be less diluted which will also cause an increased impact on riparian and aquatic habitat. As Ferren (1989) stated, "In urban areas, the likely increased need for water, increased levels of ozone, and the potential need to create new reservoirs in rivers and canyons all could contribute to the loss and degradation of riparian communities." In short, global warming is not good news for riparian habitats and will exacerbate the current situation.

## CHARACTERISTICS OF RIPARIAN ZONES

There are many anthropocentric as well as biocentric "benefits" afforded by wetland habitats (Table 2). Not the least of these is that nearly 35% of our endangered species depend upon wetland habitats although they comprise less than 5% of our lands (The Conservation Foundation, 1989).

Riparian zones usually have two essential characteristics: laterally flowing water that rises and falls at least once during the growing season, and a strong connectedness with other ecosystems (Ewel, 1978). They are buffers and filters between man's development and water resources. Riparian habitat is ecotonal in nature with an elongate shape and very high edge to area ratio (Odum, 1978). Riparian areas can range in width from less than a meter to hundreds of meters or more in a floodplain. Riparian habitat has a large energy, nutrient and biotic interchange with the aquatic systems on the one hand and with the upland terrestrial ecosystem on the outer margin. It exhibits the "edge effect"; the density and diversity of species tends to be higher at the land/water ecotone than in the adjacent uplands. Many animal species are riparian habitat obligates and large mammals that require access to water use the band of riparian habitat as a wildlife corridor. Hydroperiod and a natural hydrologic cycle are keys in determining vegetative composition and productivity. Riparian habitat when viewed at any point in a drainage is somewhat of an ecosystemic snapshot, and it's important to understand a site's context in terms of what lies below and above. Although botanists often don't think much about it, riparian vegetation in various stream sections in a watershed plays a large role in the energy flow in stream ecosystems (Figure 1). While this approach is diagrammatic, it is useful as long as one keeps in mind that these generalities

**Table 2. Wetlands functions, including biocentric and anthropocentric elements (from The Conservation Foundation, 1989, as adapted from Kusler, 1983)**

A. *Flood conveyance* - Riverine wetlands and adjacent floodplain lands often form natural floodways that convey flood waters from upstream to downstream points.

B *Barriers to waves and erosion* - Coastal wetlands and those inland wetlands adjoining larger lakes and rivers reduce the impact of storm tides and waves before they reach upland areas.

C. *Flood storage* - Inland wetlands may store water during floods and slowly release it to downstream areas, lowering flood peaks.

D. *Sediment control* - Wetlands reduce flood flows and the velocity of flood waters, reducing erosion and causing flood waters to release sediment.

E. *Fish and shellfish* - Wetlands are important spawning and nursery areas and provide sources of nutrients for commercial and recreational fin and shellfish industries, particularly in coastal areas.

F. *Habitat for waterfowl and other wildlife* - Both coastal and inland wetlands provide essential breeding, nesting, feeding, and predator escape habitats for many forms of waterfowl, other birds (see Zenbal's chapter), mammals, and reptiles.

G. *Habitat for rare and endangered species* - Almost 35 percent of all rare and endangered animal species are either located in wetland areas or are dependent on them, although wetlands constitute only about 5 percent of the nation's lands.

H. *Recreation* - Wetlands serve as recreation sites for fishing, hunting, and observing wildlife.

I. *Water supply* - Wetlands are increasingly important as a source of ground and surface water with the growth of urban centers and dwindling ground and surface water supplies.

J. *Food production* - Because of their high natural productivity, both tidal and inland wetlands have unrealized food production potential for harvesting of marsh vegetation and aqua-culture.

K. *Timber production* - Under proper management, forested wetlands are an important source of timber, despite the physical problems of timber removal.

L. *Historic, archaeological values* - Some wetlands are of archaeological interest. Indian settlements were located in coastal and inland wetlands, which serve as sources of fish and shellfish.

M. *Education and research* - Tidal, coastal, and inland wetlands provide educational opportunities for nature observation and scientific study.

N. *Open space and aesthetic values* - Both tidal and inland wetlands are areas of great diversity and beauty and provide open space for recreational and visual employment.

O. *Water quality* - Wetlands contribute to improving water quality by removing excess nutrients and many chemical contaminants. They are sometimes used in tertiary treatment of wastewater.

aren't hard and fast.

There are four primary factors governing stream ecosystems (modified from Cummins, 1979; Bowler, 1988):

- The annual hydrographic pattern (flooding cycles, low flow cycles, and seasonal variation), which determines scouring rate and the rate of hydrologic pruning, nutrient and sediment flow a riparian setting receives; hydroperiod determines the resilience of a riparian community.

- The geomorphic setting(the geology, gradient, and shape of the channel), which defines the slope and influences the non-sediment edaphic factors.

- The vegetative setting (riparian vegetation characteristics, particularly in the headwater reach), which can influence colonization rates, species diversity and the composition of communities which survive heavy seasonal floods and scouring.

- Stream order (the size of the stream).

In discussing riparian habitat it is useful to review briefly some of the characteristics of streams and drainages in headwater, mid-reach and lower river sections because it's important to realize that the often distinct settings in different reaches of a stream or river directly influence the kinds of riparian habitat found in each. Tables 3 and 4 show some of the characteristic plants from riparian woodlands in southern California and from Orange County, broken down into stream reaches. Faber, et. al. (1989) present examples of community dominants in riparian settings at various elevations at sites throughout southern California, though stream reaches are not identified.

The concept of the river as an energetic and ecosystemic continuum, as developed by Vannote, Cummins and others (Vannote, et. al., 1980; Knight and Bottorf, 1984), stresses the role that headwater vegetation plays in providing the coarse particulate organic matter which supports the predominantly heterotrophic community in the headwater reaches (Figure 1). Faber, et. al. (1989) presented an excellent synopsis of this relationship in southern Californian settings, although there is little data to fill out the broad ecosystemic functions known in other regions. As Faber, et. al. (1989) summarized, "Detritus provided by riparian vegetation is a source of up to 90 percent of the nutrients consumed by instream aquatic communities (Hubbard, 1977; Cummins, 1975; Merritt, 1978; Hart, 1975)." Furthermore, upland fire-adapted plant communities such as chaparral and coastal sage scrub may contribute nutrients to adjacent aquatic ecosystems through post-fire runoff (Faber, et. al., 1989).

The concept of connectedness (Ewel, 1978) plays a significant role in resilience, ensuring inflow of species after disturbance, but also exposes a system to the battering of impacts from above. In stream headwaters there is usually a heavy riparian cover, often with a closed canopy over the stream which limits the light reaching the streambed. This cover produces a heavy litter load and serves as the source for large quantities of coarse particulate organic matter, enhanced by deciduous trees and shrubs if the headwater elevation is great. The coarse particulate organic matter derived from riparian habitat becomes the primary foodsource for the predominantly heterotrophic community in light-limited, heavily shaded headwater situations. Headwater shading can also have a profound influence on water temperature. As is evident in Table 4, many of the

**TABLE 3.** Selected species occurring in Southern California riparian habitat in headwater, mid-drainage and floodplain settings. The abbreviations are keyed as follows: Deciduous = D; Evergreen = E; Headwater reach = HW; Mid-drainage = M; Floodplain = FP. (Adapted from Roberts, et.al., 1977 by Fred Roberts.)

1. Trees

A. Common:

| | | |
|---|---|---|
| Alnus rhombifolia | M (-FP) | D |
| Platanus racemosa | M - FP | D |
| Populus fremontii | FP | D |
| Quercus agrifolia | HW - M | E |
| Salix laevigata | FP | D |
| Salix lasiandra | FP | D |

B. Uncommon:

| | | |
|---|---|---|
| Acer macrphyllum | HW | D |
| Juglans californica | M | D |
| Populus trichocarpa | M - FP | D |
| Umbellularia californica | HW - M | E |

2. Shrubs

A. Common

| | | |
|---|---|---|
| Artemesia douglasiana | M - FP | E |
| Baccharis emoryi | FP | E |
| Baccharis glutinosa | M - FP | E |
| Baccharis pilularis subsp. consanguineus | | E |
| Cornus occidentalis | HW | D |
| Phoradendron tomentosum subsp. macrophyllum | M | |
| Rosa californica | M - FP | D |
| Salix hindsiana | FP | D |
| Salix lasiolepis | HW - FP | D |
| Sambucus mexicana | | D |

TABLE 4. Riparian communities in headwater, mid-drainage and floodplain settings in Orange County, California. The abbreviations are keyed as follows: E = Evergreen; D = Deciduous. These "communities" are not formally named, and are based on observation. (Compiled by Fred Roberts.)

1. **Headwater Settings, 800-1700 meters**
   **Montane Riparian Woodland**

| | |
|---|---|
| Acer macrophyllum | D |
| Quercus chrysolepis | E |
| Quercus agrifolia | E |
| Umbellularia californica | E |

2. **Midreach Settings, 180-800 meters**
   **Riparian Woodland**

| | |
|---|---|
| Quercus agrifolia | E |
| Alnus rhombifolia | D |
| Platanus racemosa | D |
| Salix lasiolepis | D |
| Populus trichocarpa | D |
| Fraxinus velutina | D |

3. **Floodplain Settings, 0-180 meters**
   **Sycamore Alluvial Woodland**

| | |
|---|---|
| Platanus racemosa (widely scattered) | D |
| Quercus agrifolia | E |
| Sambucas mexicana | D |

4. **Lowland Riparian Forest**

| | |
|---|---|
| Populus trichocarpa | D |
| Populus fremontii | D |
| Salix lasiolepsis | D |
| Salix laevigata | D |

Toxicodendron and Artemesia douglasiana are not uncommon, and less frequently Platanus racemosa and Quercus agrifolia.

5. **Willow Woodland**

| | |
|---|---|
| Salix lasiolepsis | D |
| Salix laevigata | D |
| Salix goodingii | D |

Mugwort often common in this communtiy as well.

6. **Mulefat Scrub**

| | |
|---|---|
| Baccharis glutinosa | E |

Often there is a little Salix lasiolepsis and Salix goodingii, but there isn't a real overstory development.

7. **Willow Scrub**

| | |
|---|---|
| Salix hindsiana | D |

Some other willows as well.

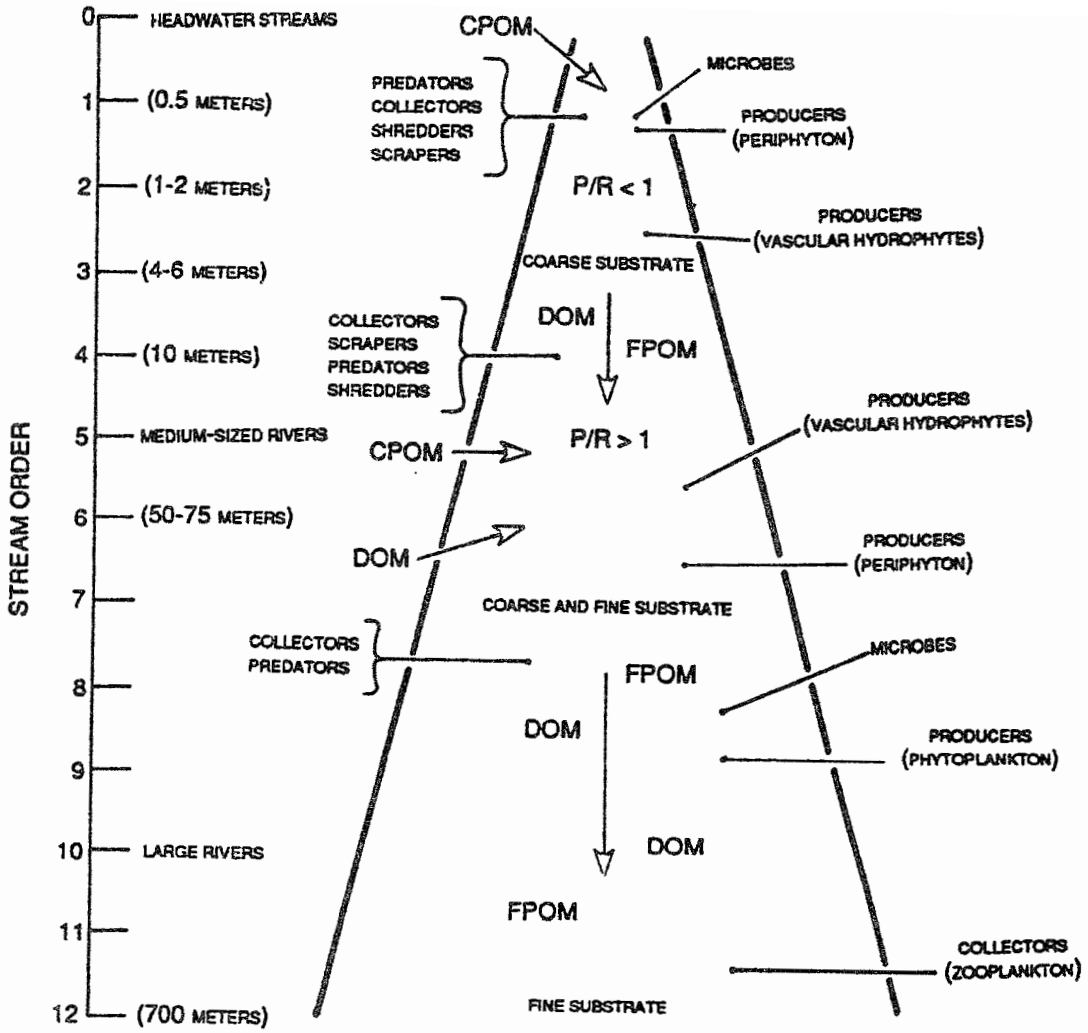


Figure 1. Schematic representation of a Sierran stream shown as an expanding continuum from headwaters (0.5-6m wide; order = 1) to a medium-sized river (50-75m wide; order = 4-6), to a large river (up to 700m wide; order = 12). Abbreviations: P/R = ratio of gross photosynthesis to community respiration; CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter; DOM = dissolved organic matter. Headwaters and large rivers are heterotrophic (P/R < 1), medium-sized rivers are shown as autotrophic (P/R > 1). (From Bowler, 1988, as adapted from Cummins, 1975, 1979; Knight and Bottorff, 1984; Vannote, et al, 1980.)

dominant woody species characteristic of headwater sites in Orange County are not deciduous, an interesting situation somewhat in contrast with other California settings.

In the mid-river reaches, the aquatic ecosystem shifts from a heterotrophic to an autotrophic community due, among other reasons, to a widening of the river valley and lack of a light-limited aquatic setting. There is usually relatively little shading by riparian vegetation in the middle sections of river systems, and there are higher nutrient and fine particulate organic matter levels from the upstream vegetation sources, which shifts the invertebrate community from shredders to grazers (Figure 1). The gradient is usually much flatter than headwaters and a well configured flood plain is often developed. The stereotypic "riparian forest" is often present in this section of the streamcourse.

The lower reaches of rivers near the mouth reflect a flat gradient with a broad floodplain. Under natural conditions this portion of a drainage would see seasonal flooding and blanketing with layers of soil and nutrients.

## HUMAN IMPACT ON RIPARIAN HABITAT

As anyone living in southern California is aware, humans have dramatically altered, if not mangled, nearly every watershed in our region (Figure 2). It has been said that the third largest perennial freshwater tributary entering the ocean in California and the largest in southern California is the Hyperion sewage treatment plant outfall. Water diversions reduce riparian potential and dams similarly alter natural drainage processes. In southern California, the Sweetwater River, Tijuana River and San Diego River were all perennial streams before water storage projects altered their natural hydrologic cycle.

By and large, dams produce half-lakes with depauperate terrestrial species diversity compared with free-flowing river reaches. As can be seen, for example, in San Diego County at Loveland Dam on the Sweetwater River near El Cajon, riparian vegetation is scoured out of the area below the dam. Residents familiar with the Sweetwater River in the reach below Loveland Dam recall white alder, Alnus rhombifolia, as a riparian community dominant, however, this species is now absent due to the altered stream flows caused by the water storage project (William Bretz, pers. comm.). Above the dam there is virtually no "riparian" vegetation, but a bathtub ring series of water level marks etched into a sterile hillside with emergent vegetation at the water's edge.

Though not a southern California situation, a site on the upper Middle Snake River in Idaho which my students and I studied, exhibited this phenomenon well (Jensen and Verhovek, 1980). In this study area within the Columbia Plateau and dominated by great basin sage associations and deciduous riparian forest along the river, we identified 158 vascular plant species, though only 78 species actually occurred within our transects. The Lower Salmon Falls Dam impoundment study site had a total of only 55 species, 34.5% of which were introduced. Along this impoundment there had been very little shoreline revegetation since the present water level was established around 40 years ago (the original riparian valley bottom was inundated in 1910 with a lower dam which was subsequently raised). The great basin sagebrush community came nearly to the water's edge and there was a discontinuous, thin band of a few meters

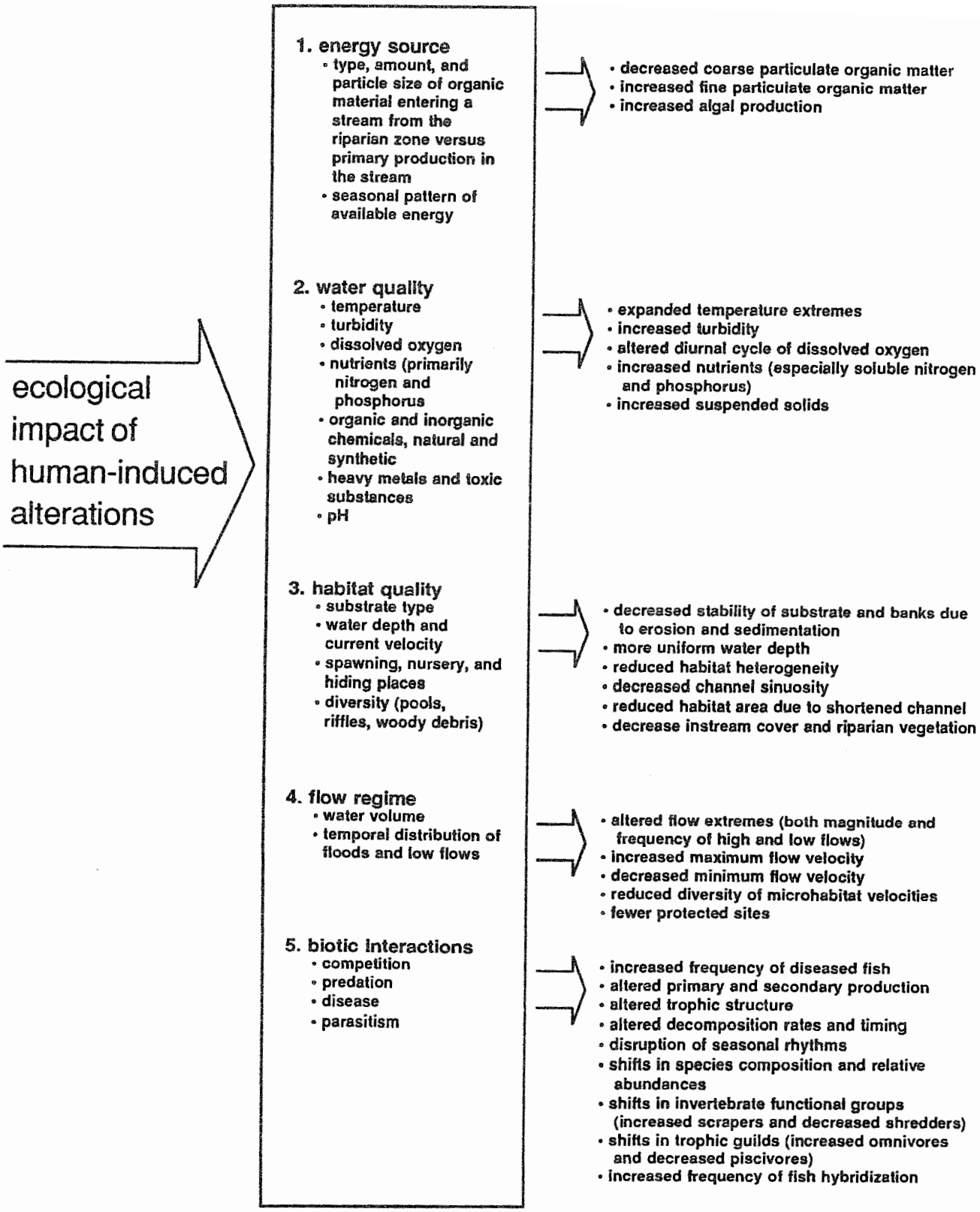


**Figure 2.** Five major classes of environmental factors that affect aquatic biota. The arrows indicate the kinds of effects that can be expected from human activities, in this case the alteration of headwater streams, excluding small impoundments (from Karr, et al., 1986, as modified from Karr, et al., 1983).

of low riparian vegetation. At three sample sites along the tailwaters below the dam, however, there was a very different species diversity and community composition, with 80 to 90 species present, a non-native percentage of 27%, and with large groves of hackberry (Celtis reticulata), river birch (Betula occidentalis), and squawbush (Rhus trilobata) - dominants of a rare deciduous riparian forest formation. In this study area riparian vegetation ranged between 0.5 and 75 meters from the water, and was typified by inconsistent distribution of species, mosaics of suitable habitat and many species which were infrequent or rare along the reach.

These results aren't surprising, since virtually all terrestrial, as well as aquatic, conditions are different before and after closing a water project. It's intuitively easy to see how eliminating habitat conditions along a natural streambed and raising the waterline to a height along a canyon wall normally dominated by sagebrush, chaparral or some other slope-inhabiting upland plant community, would produce a sterile shoreline.

Flood control projects - designed to capture water during flooding events and are therefore kept drained - are different in attendant vegetation from run-of-the-river hydroelectric impoundments, which are designed to store and release much smaller quantities of water. As Zembal documents elsewhere in this volume, the Prado Dam basin, designed as a storage facility for flood control, is a unique situation which has unintentionally created an interesting riparian situation with a simple community comprised of a few dominant species (Zembal, 1984a; see also Zembal, 1984b for data on the Santa Margarita River, still a natural riparian setting).

Another fundamental hydrologic character which has been transformed in southern California is that of the natural flooding cycle and the scouring effect experienced in mid-river and lower reach areas. While diversion of instream flow has reduced the quantity of water available for natural processes in a drainage, water storage has similarly altered the timing of waterflow in a stream - occasionally altering the seasonal streamflow regime to suit perennial percolation requirements and inadvertently providing a water supply more dependable during the dry season than would occur without dams and impoundments. In this context, a number of models have been designed to examine instream flow needs for aquatic ecosystems, but in reality not much is known about longterm impacts of altered instream flows upon riparian vegetation and terrestrial ecology.

A summary of data from California basins by the U.S.F.W.S. WELUT team indicated that:

- 10% of average annual streamflow is the absolute minimal to sustain short-term survival of most aquatic life forms.

- 40% of average annual streamflow is required as a base flow to sustain an adequate habitat for (aquatic) survival.

- 60% of average annual streamflow is required to provide excellent habitat protection for most aquatic life forms and the majority of recreational needs.

Even if this controversial and simplistic "rule of thumb" for aquatic habitat is accepted, there is little real idea of how reducing streamflow to these degrees would alter riparian habitat, but it would likely be profound.

While water storage and streamflow diversion cause changes, flood

control causes others. As is intuitively obvious, flooding impacts increase progressively down a drainage, and the successional aspect of riparian communities caused by streamside scouring, similarly, is often most conspicuous in the floodplain reaches below headwaters. Flood control projects capture runoff and hold back the scouring, sediment, and nutrient-transporting flows which normally would flush out stream channels and thin vegetation. In a sense, the lower areas of southern California drainages are more advanced and denser in riparian formation (as much as streamflow allows, so that these are like the riparian formations of smaller streams) than they would have been without flood interruption, when succession would have been a more rapid process. The historic canyons and floodplains are overfit for the reduced flows in them today. Channelization, another element of flood control, is habitat evisceration, leaving vegetation and stream ecology with segmented, sterile breaks in connectedness (see Faber, et. al., 1989, for an excellent treatment of this ubiquitous habitat gutting in southern California).

In this context, riparian vegetation can be characterized in areas of flooding as having many of the opportunistic features of plants entering disturbed areas - rapid colonization, high productivity, good dispersal, and so forth. Especially at lower elevations, if a reach is not flooded and scoured, species diversity drops and woody species, especially willows, become dominant. This is particularly true in urban or agricultural runoff situations, in which water is continuous during otherwise dry seasons for natural streams of comparable size. This "urban slobber" or "nuisance flow" has created a "new" category of riparian habitats, which are particularly important in southern California. Since the drainage capture of the Owens and Colorado Rivers, availability of water has resulted in runoff through drains, ditches and streamcourses which otherwise wouldn't occur. The U. S. Fish and Wildlife Service is in the process of inventorying California wetlands. The results of their survey will provide the first quantitative insight into the distribution and acreage of runoff-induced riparian habitat. In Orange County, the San Diego Creek and Laguna Lakes drainages are case histories that illustrate this phenomenon.

The San Diego Creek drainage as it exists today is an artifact of man's urban and agricultural needs. The broad contour of the drainage reflects an ancient and abandoned Santa Ana River channel; however, prior to the 1880s it was not a drainage emptying in the sense it does today into Upper Newport Bay. The end of the 1880s saw a gradual change from a pastoral land use to one more agriculturally based, rapidly leading to the need to drain and ditch the "Cienga de las Ranas," an extensive marshy wetland that formerly covered the Tustin Plain. The transition from range to fields occurred in a 20-year period, and the water table under the Tustin Plain, which had been ditched and drained beginning in 1906, dropped 10.2 meter between 1904 and 1928. Ditches became the watershed channels for storm flow, and by 1932 these channels connected with Upper Newport Bay. In 1942 the 47-acre (19 ha) Sand Canyon Reservoir was constructed and is currently owned and operated by the Irvine Ranch Water District. In the late 1960s San Diego Creek was channelized. The areas of the drainage that illustrate the effects of agricultural runoff and channelization particularly well are the sections below Sand Canyon Reservoir to MacArthur Bridge.

Over the past forty, but especially

during the last twenty years, the "stream" segment below Sand Canyon Reservoir has developed a lush closed-canopy willow habitat, which now extends all the way through Mason Regional Park to Culver Drive. Sunset Magazine recently touted the bicycle trail through the corridor as being one of the best touches of nature available to cyclists. While this is an excellent example of low elevation, willow-dominated habitat, it is actually a fairly simple community. The dominant willows are Salix goodingii, S. laevigata and S. lasiolepis. This cohort of willows has grown into trees of 5 or more meters in height. A few cottonwoods and a sycamore or two have been planted, so that the prospect is good for developing a multi-story habitat along the creek in future decades. Nonetheless, it is a skeleton, species-poor community compared with analogous elevational settings in natural streamcourses, such as the Santa Margarita River (Zembal, 1984b), though the scale in instream flow is significantly different between these sites.

The flood control channel between Campus Drive Bridge and MacArthur Bridge includes a sediment capture basin and the channelized creekbed with drop structures at both bridges. The sediment basin is cleared roughly each 5 years, and in the interim an interesting mosaic of plant communities develops. The flood control channel downstream of the sediment basin is also cleared, but less frequently. This site supports 59 species of plants, of which 59% are introduced. A majority of these species are rapid colonizers and are weedy.

Contrast this with the species-poor and simpler community in the Sand Canyon Wash above the "Christ College" reach. This riparian community is watered largely by agricultural runoff and has a poor herb and understory species representation - perhaps due to chemicals used on the fields. In these sites there is a climax willow situation, where the tall and dense stands of only a couple of Salix species become dominant. In a sense this is almost a senescent community, while the flood control channel supports a more diverse but early successional group of species.

The Laguna Canyon complex of vernal pools, lakes, perched drainage habitat and the riparian corridor provides a different insight to artificially enhanced watersheds. At this site a vernal pool has been severely degraded by cattle and the proliferation of Eucalyptus in the pool basin. Overflow of the lake receiving urban runoff from a portion of Leisure World (a local retirement community) enters a perched groundwater lens and supports a rich and diverse riparian community - primarily watered by subsurface sources. A channel on the opposite side of Laguna Canyon Road has a large willow corridor - not unlike that in Mason Park. In this mosaic of wetland communities there are approximately 75 species, 61% of which are native.

Data on Table 5 suggest how selected local habitats rank in terms of introductions and disturbance. Though Table 5 represents only a few sites, it's interesting to consider the degrees to which local communities have been invaded by non-native species. One could hypothesize from these data that local lightly to moderately disturbed coastal sage scrub and chaparral communities have somewhat fewer introductions (around 21-17%) than heavily grazed grasslands (around 40%), and that ruderal habitats could have the highest proportions of introduced species (58%). Riparian habitat seems variable, but supports a substantial suite of non-native species (between 28 and 38%). An advanced growth flood-control channel

Table 5. An analysis of some selected habitats (data are summarized from the University of California, Irvine, 1989 EIR record; Zembal, 1984a; Laguna Canyon EIR record; the Natural Reserve System database on the San Joaquin Marsh; and Jensen and Verhovek, 1980 for the Snake River sites).

| Site | Habitat Type | No. of Sp. | % Native | % Exotic |
|---|---|---|---|---|
| UCI | C. Sage Scrub | 120 | 68% | 32% |
| Lag. Canyon | C. Sage Scrub | 110 | 79% | 21% |
| Quail Hill | Grassland | 67 | 57% | 43% |
| Lag. Canyon | Grassland | 133 | 62% | 38% |
| Lag. Canyon | Chaparral | 93 | 79% | 21% |
| UCI SD CR. | Riparian | 59 | 41% | 59% |
| UCI | Riparian pockets | 26 | 62% | 28% |
| Lag. Canyon | Riparian/mixed Wetlands | 75 | 61% | 39% |
| Lag. Canyon | So. Oak Wdl. | 122 | 70% | 30% |
| Lag. Canyon | "Ruderal Habitats" | 91 | 42% | 58% |
| San Joaquin Freshwater Marsh | | 159 | 54% | 46% |
| Prado Dam Basin & Environs. | | 311 | 68% | 32% |
| Riparian/Dam Basin Only | | 143 | 63% | 37% |
| Snake River | | | | |
| Impoundment | Riparian | 55 | 65% | 35% |
| Freeflowing | Riparian | 155 | 73% | 27% |

had a percentage of around 59% non-natives, on a par with "ruderal habitats." If true, this could be because bulldozed "ruderal" area habitat is similar to the periodically pruned flood control channel in providing "habitat" most suitable to rapidly invading introduced weedy species.

Finally, any discussion of riparian habitat would not be complete without at least mentioning the impact of cattle upon western stream habitats. Grazing has been one of the most profound degraders of riparian habitat on public lands in the west, and the wreckage associated with cattle, such as trampling and subsequent increased runoff, destroys not only streamside vegetation but the instream ecology as well.

In conclusion, there is no question that riparian habitat is endangered in southern California. Wherever "natural" stands occur along historic watercourses they should be protected, and we should not be too proud as botanists to also demand "no net loss" standards for the fragments of habitat developing along

urban and agricultural runoff areas (See Kusler, 1989; 1990, for a thorough review of the successes and failures of the "no net loss" strategy of wetland preservation or replacement.

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The New York Times

# *As Carr Fire Kills 2 in California, Firefighters Reflect on a Job Now 'Twice as Violent'*

**By Scott Bransford, Jennifer Medina and Jose A. Del Real**

July 27, 2018

REDDING, Calif. — When Brian Rice fought wildfires in the 1990s, his time on the line was intense during the summer fire season, followed by months to recharge during the cooler winter. But fighting wildfires is no longer seasonal work in California.

"There used to be a rhythm to this, and you could at least count on that rhythm," he said. "It's a year-round cycle now."

Since 2012, according to state emergency management officials, there has not been a month without a wildfire burning — a stark contrast to previous decades, when fire officials saw the fall and winter as a time to plan and regroup. The recent historic drought and rising temperatures have heightened an already serious risk for widespread fires in the state.

Just this month, there have been three firefighters killed on the front lines, including two who died during a rapidly expanding wildfire in Northern California in the last two days. Dry conditions and triple-digit temperatures added fuel to that fast-moving blaze, known as the Carr Fire, as it marched eastward, swept over the Sacramento River and pushed into the outskirts of Redding, the largest city in the region. It continued to grow on Friday, burning dozens of buildings and prompting emergency officials to issue an urgent plea for people in parts of Redding and the surrounding areas to evacuate immediately.

"This fire is extremely dangerous and moving with no regard for what's in its path," said Bret Gouvea, the incident commander for the California Department of Forestry and Fire Protection.

Gov. Jerry Brown has called this the new normal and set aside more than $440 million in the state budget for emergency wildfires. But beyond the costs, the year-round fires have taken a heavy toll on thousands of firefighters in the state.

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[*Read more about why experts are saying this summer's destructive wildfire season is "the new normal."*]

In the town of Corning, about an hour south of Redding, the Rolling Hills Casino offered shelter to about 200 evacuees, opening its doors for people and animals fleeing flames for the second time this year. Evacuees slept in a ballroom off the main casino Friday, talking to family members on cellphones and watching for fire updates on a big-screen television.

For Michelle Hickok, 30, a graphic designer at the casino, the start of each fire brings the fear that her husband, a local firefighter, will be in harm's way. The longer fire seasons have exacerbated that worry, she said. "With summer being hotter and longer, you have tons of dry fuel up here," she said.

Firefighters had long looked at the area now burning and saw the dry vegetation as a disaster waiting to happen, she said. "They were afraid that when that day came it would be bad, and they were right," she said.

The fires in 2017 were among the most destructive in California's history, causing nearly $12 billion in damage and leaving 46 people dead.

"This job has gotten twice as busy and twice as violent," said Mr. Rice, who retired from fighting fires in 2011 and is based in Sacramento, and is now president of California Professional Firefighters, a statewide union. "I was down in Ventura and realized, holy smokes, we have firefighters on the fire line on Christmas Day. In my 30 years, I've never heard of that.

**COMMENT OF THE MOMENT**

K **Kathy Lollock** **Times Pick**
Santa Rosa, CA | July 27

This is a nightmarish replay of what my county went through last year. I pray for those people and their homes. How can there be any doubt of global warming and climate change? Over my long years of life here in CA, I have recently witnessed too many hot summers, fierce and destructive winds, and dry winters. Yet the powers that be deny us the means to at the very least assuage the wrath of Mother Nature. We can do something about this. But this administration sacrifices the many for the few who are parasites off the land in the name of greed.

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"This is the first year for me that I really feel like one fire season has connected itself to the next 12 months," he added. "Is that going to be the new normal or the new reality? I don't know."

In addition to the Carr Fire, wildfires are burning in Central and Southern California. The Ferguson Fire caused the largest closing of Yosemite National Park in 30 years, and the Cranston Fire is only 5 percent contained in the San Jacinto Mountains in Southern California. After evacuating thousands of tourists and residents near Yosemite earlier this week, officials on Friday were closely monitoring the flames as they crept toward groves of dry, dead trees.

"Now we really are having to look into a crystal ball, not only in terms of fires we're fighting already, but also fires that haven't even started yet," said Kelly Huston, a spokesman for California's Office of Emergency Services. "In the past there was some logic, some time to plan, but we don't have that time any more because these fires are so hot and so fast they are getting away from us more quicker than they used to."

A firefighter at a home that was destroyed in Redding, Calif., on Friday. Temperatures in the region were predicted to reach 110 degrees. Justin Sullivan/Getty Images

The constant fires have also made it more difficult to get enough firefighters up and down the state, with officials constantly scrambling to make sure there are enough people available, Mr. Huston said.

Often, the stretched resources have meant more firefighters working longer hours for longer stretches of time, leaving many of them exhausted. Experts and state officials said they all worry about short- and long-term fatigue, which can lead to mistakes.

"They still love it and they are still dedicated, but it takes a huge toll on them," said Nancy Bohl-Penrod, a psychologist who has worked with firefighters across the country for 30 years and who is currently supervising therapists working with firefighters in Yosemite. "When they get home, some of them don't talk to their families about it. Some it is just the mere fact that they are exhausted and that impacts their emotion and, their personality."

Dr. Penrod said far more fire departments are carrying out wellness and support programs and she has also seen a significant spike in the number of spouses and parents of firefighters attending workshops to learn how to cope with fires lasting for weeks on end.

Standing in a parking lot on the outskirts of Redding, where firefighters from multiple agencies had gathered, Anthony Romero, with the Kern County Fire Department, said the dynamics of present-day fire seasons also throws firefighters off by taking them further from their home bases, calling upon them to fight fires in parts of California where the terrain and weather patterns are unfamiliar. Mr. Romero, dripping with sweat and flecked in ash, noted that many firefighters from coastal California were not accustomed to Redding's notoriously intense sun, its parched and radiating grasslands, or its warm downslope winds.

"We can just stand here and we're dripping," Mr. Romero said. But, he added, "We still adapt to what's going on."

Scientists say that severe wildfire seasons in California may occur more frequently because of climate change. Since the 1970s, temperatures have risen by two degrees Fahrenheit in the western United States. And trees and grasses — the fuel of wildfires — are more dry and for longer periods of the year. That means fire season now lasts three months longer than it used to, starting earlier and often going on through the fall, said Jennifer Balch, a fire ecologist at the University of Colorado at Boulder.

"What's going on in the background is we've got warmer conditions. It's making our fuels drier earlier and for longer," Dr. Balch said. "Wildfires are a real in-your-face way we're seeing evidence of a warming climate."

California is feeling the brunt. Seven of the state's largest forest fires have come in the last decade, including one every year since 2012.

From Thursday night to Friday morning, the Carr Fire raged out of control and scorched an additional 16,000 acres, bringing the total area burned to more than 44,000 acres. By Friday night, an additional 4,000 acres had been burned. Firefighters struggled to contain its growth; the blaze was 5 percent contained on Friday night.

The weather was not expected to offer any relief through the weekend, according to the National Weather Service. The high temperature in Redding was in the hundreds on Friday and was expected to rise the next two days. Wind gusts could reach 25 miles an hour in areas where the fire continues to rage.

Fire officials said it was too early to account for the total damage caused by the Carr Fire, but said that at least 500 structures had been destroyed and additional 75 damaged. Nearly 5,000 structures in its path were threatened.

On Friday, the roads leading into downtown Redding, usually teeming with the traffic of summertime tourism, were largely deserted except for emergency vehicles.

Sundial Bridge, a popular stop for motorists on their way to Mount Shasta and points north, was closed because of the fire, and its parking lot, often filled close to capacity on weekend travel days, was mostly empty.

Flecks of ash checkered the blue uniform of Robert Valente, 61, a security guard for the facility, as he halted a stray group of tourists from the San Francisco area. Mr. Valente said it is frightening to see a fire this close to Redding. "You could lose everything," he said.

Erick Mattson, a captain with the Redding Fire Department, was battling out-of-control flames encroaching on homes in the Old Shasta community just outside Redding on Friday morning. Mr. Mattson, who has been a firefighter for over 20 years, said that his fire season used to end in October or November, but now stretches across the entire year.

"It's a situation where we just have to keep going. Those that have been in the fire service for a long time, they develop the skills necessary to cope with your body shutting down," he said. "That's kind of what we do. We encourage each other. We understand what the job is and what the end goal is. It's about serving the public and that's what pushes us, even when the fire seasons go longer."

Scott Bransford reported from Redding, Calif.; and Jennifer Medina and Jose A. Del Real from Los Angeles. Reporting was contributed by Matthew Haag, Somini Sengupta, Daniel Victor, Inyoung Kang and Terence McGinley in New York.

A version of this article appears in print on July 27, 2018, on Page A10 of the New York edition with the headline: Fire Kills Two In California, As It Reaches Urban Areas

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*Contributed Paper*

# Permeability of Roads to Movement of Scrubland Lizards and Small Mammals

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**Abstract:** *A primary objective of road ecology is to understand and predict how roads affect connectivity of wildlife populations. Road avoidance behavior can fragment populations, whereas lack of road avoidance can result in high mortality due to wildlife-vehicle collisions. Many small animal species focus their activities to particular microhabitats within their larger habitat. We sought to assess how different types of roads affect the movement of small vertebrates and to explore whether responses to roads may be predictable on the basis of animal life history or microhabitat preferences preferences. We tracked the movements of fluorescently marked animals at 24 sites distributed among 3 road types: low-use dirt, low-use secondary paved, and rural 2-lane highway. Most data we collected were on the San Diego pocket mouse (*Chaetodipus fallax*), cactus mouse (*Peromyscus eremicus*), western fence lizard (*Sceloporus occidentalis*), orange-throated whiptail (*Aspidoscelis hyperythra*), Dulzura kangaroo rat (*Dipodomys simulans*) (dirt, secondary paved), and deer mouse (*Peromyscus maniculatus*) (highway only). San Diego pocket mice and cactus mice moved onto dirt roads but not onto a low-use paved road of similar width or onto the highway, indicating they avoid paved road substrate. Both lizard species moved onto the dirt and secondary paved roads but avoided the rural 2-lane rural highway, indicating they may avoid noise, vibration, or visual disturbance from a steady flow of traffic. Kangaroo rats did not avoid the dirt or secondary paved roads. Overall, dirt and secondary roads were more permeable to species that prefer to forage or bask in open areas of their habitat, rather than under the cover of rocks or shrubs. However, all study species avoided the rural 2-lane highway. Our results suggest that microhabitat use preferences and road substrate help predict species responses to low-use roads, but roads with heavy traffic may deter movement of a much wider range of small animal species.*

**Keywords:** avoidance, connectivity, conservation planning, habitat fragmentation, heteromyid, reptiles, road ecology, urban ecology

**Resumen:** *Un objetivo principal de la ecología de caminos es entender y predecir como afectan los caminos la conectividad de las poblaciones silvestres. El comportamiento de evitación de caminos puede fragmentar poblaciones, mientras que la falta de evitación puede resultar en alta mortandad debido a colisiones. Muchas especies animales pequeñas enfocan sus actividades a microhábitats particulares dentro de su hábitat mayor. Buscamos estudiar como los diferentes tipos de caminos afectan el movimiento de pequeños vertebrados y conocer si ciertas respuestas hacia los caminos pueden ser predecibles basándose en la historia de vida del animal o el microhábitat. Rastreamos los movimientos de animales marcados con fluorescencia en 24 sitios distribuidos entre 3 tipos de caminos: tierra de bajo uso, camino secundario pavimentado de bajo uso, y carretera rural de 2 carriles. La mayoría de los datos que colectamos fueron sobre* Chaetodipus fallax, Peromyscus eremicus, Sceloporus occidentalis, Aspidoscelis hyperythra, Dipodomys simulans *(tierra, pavimentación secundaria), y* P. maniculatus *(solamente en carretera).* C. fallax *y* P. eremicus *se movían hacia los caminos de tierra pero no hacia una carretera de baja pavimentación de anchura similar o hacia la carretera, indicando que evitan los caminos con sustrato pavimentado.* S. occidentalis *y* A. hyperythra *se movían hacia la tierra y los caminos secundarios pavimentados pero evitaban la carretera rural de 2 carriles, indicando que pueden evitar el ruido, las vibraciones o el disturbio visual de un constante flujo de tráfico.* D. simulans *no evitaba el camino de tierra ni los caminos secundarios con pavimento. En general, el camino de tierra y los caminos*

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*secundarios fueron más permeables para las especies que prefieren forrajear o tomar el sol en áreas abiertas de su hábitat en lugar de bajo rocas o arbustos.* D. simulans *no evitó el camino de tierra ni los caminos secundarios pavimentados. Sin embargo todas las especies estudiadas evitaron la carretera de 2 carriles. Nuestros resultados sugieren que las preferencias de uso de microhábitat y sustrato de caminos ayudan a predecir las respuestas de las especies hacia caminos de bajo uso, pero los caminos con tráfico pesado pueden disuadir el movimiento de un rango mucho mayor de especies animales pequeñas.*

**Palabras Clave:** conectividad, ecología de caminos, ecología urbana, evitación, fragmentación de hábitat, heterómido, planificación de la conservación, reptiles

## Introduction

Terrestrial and aquatic areas have become increasingly permeated by roads. Roads affect movement patterns, demographics, and spatial distribution of local species. They can adversely affect wildlife by fragmenting habitats, creating population sinks, and acting as conduits for the spread of invasive species (e.g., Forman et al. 2003; Fahrig & Rytwinski 2009; Taylor & Goldingay 2010). They can positively affect wildlife by increasing connectivity between suitable habitat patches and food resources (e.g., Huey 1941; Getz et al. 1978; Forman et al. 2003).

A current need in the field of road ecology is to understand and predict how roads affect the probability wildlife populations will persist (Roedenbeck et al. 2007; Fahrig & Rytwinski 2009; Rytwinski & Fahrig 2012). This will likely require the development of demographic and spatial-movement models that incorporate behavioral responses to roads (e.g., Jaeger et al. 2005; Tracey 2006; Frair et al. 2008). Roads are highly variable, ranging from rarely traveled dirt roads to multilane highways with heavy traffic. Correspondingly, the responses of animals to different road types are expected to be highly variable.

To address variation in animal responses to different road attributes and traffic patterns, Jaeger et al. (2005) incorporated 3 types of road-specific avoidance behavior (road-surface avoidance related to road substrate and width, and, noise and car avoidance related to traffic) in their model for predicting when animal populations are at risk from roads. However, data to test these models are lacking because much of the current literature on road-related movement behavior typically focuses on either a single species or road type (e.g., Fahrig & Rytwinski 2009; Taylor & Goldingay 2010). There are also relatively few data available on reptiles, although this taxon is thought to be substantially and negatively affected by roads (Andrews et al. 2008). Finally, few researchers have incorporated both multiple road types and taxonomic classes in their studies to ascertain how animal communities respond to these linear features of the landscape.

Scrublands are distributed throughout mid-latitude deserts and areas with Mediterranean-type climates. Scrublands are characterized by low-growing shrubs adapted to arid conditions and range from open habitats with sparse vegetation cover to areas with dense vegetation (Kellman 1980). Our study area was in coastal sage scrubland of southern California (U.S.A.). Much of this area is fragmented by urbanization, disturbed, or permeated with highways, secondary roads, dirt roads, and trails (O'Leary 1995; Noss et al. 2000).

We sought to understand how roads affect habitat connectivity for small vertebrate populations within these scrublands. We assessed the movement patterns of 4 small-mammal species and 2 lizard species relative to 3 types of roads: low-use dirt roads, a secondary paved road, and a primary paved highway. We also examined whether animal responses to roads differed among species with different life-history strategies and whether species' microhabitat-use preferences could be used to predict their responses to roads.

## Methods

### Study Site

Our study area was in San Diego County, California, within the San Diego National Wildlife Refuge (Otay-Sweetwater Unit) and in Rancho Jamul, a 1915-ha ecological preserve managed by the California Department of Fish and Game. The coastal sage scrub (CSS) vegetation was dominated by California sagebrush (*Artemisia californica*), buckwheat (*Eriogonum fasciculatum*), and a variety of herbs and grasses. The region has a Mediterranean-type climate characterized by hot, dry summers and cool, wet winters. Average annual precipitation is 350 mm, and approximately 95% of the annual mean rainfall occurs from November through April. The CSS vegetation averaged 63% shrub cover, 30% grass and herb cover, and 28% open ground (total greater than 100% due to measures at multiple height categories [Brehme 2003]). There were 3 road types in the study area: 1.8 km of low-use unimproved dirt roads with an average width of 4.7 m (SD 1.3) and traffic volume of 0–20 vehicles/day; a 1.6-km low-use, secondary, 2-lane paved road (Millar Ranch Road) with an average width of 6.6 m (SD 0.2) and traffic volume of 200–500 vehicles/day (Traffic Section of San Diego County Public Works); and over 24 km of high-use, primary, 2-lane paved highway (State Highway 94) with an average width of 11.2 m (SD 0.9) and traffic volume of 7,400–18,000 vehicles/day

(California Department of Transportation). Road widths were measured as the width of grading for dirt roads and width of pavement for paved roads. Native soil or vegetation extended to the road edge for all unimproved and improved road types. During the study, there was no evidence of mowing or other vegetation-management activities.

### Data Collection

Eight linear trapping arrays were installed along the length of each of the 3 road types. We chose sites where CSS vegetation extended at least 50 m from both sides of the road to avoid confounding the presence of a road with any other edge. Linear trapping arrays consisted of 3, 9-L pitfall traps connected by a 15-m drift fence (7.5 m between each bucket), 4 Sherman live traps (along both sides of fence halfway between each bucket), and one funnel trap. We baited all traps with birdseed and rolled oats. Arrays were diagonal to the road to increase effectiveness of intercepting animals moving both parallel and perpendicular to the road. At one end of the array, the pitfall trap was 1 m from the road edge, and at the other end, the pitfall trap was 11 m from the road edge. The middle pitfall trap was 5 m from the road edge. Pitfall-array materials and installation procedures are described in Fisher et al. (2008). Trap arrays remained open during each trapping period and were checked every morning at sunrise. We conducted ten 3-night trapping sessions at each array from April to December of 2001.

We used fluorescent-powder tracking (Lemen & Freeman 1985; Fellers & Drost 1989) to track the movements of small mammals and reptiles captured in the trap arrays. The fluorescent powder (Radiant Color, Richmond, California, U.S.A.) is nontoxic and is a safe and effective means of tracking small-scale animal movements (Stapp et al. 1994). The powder-tracking technique allowed us to study species' direct responses to roads. Tracking movements over longer distances and periods of time (e.g., with radiotelemetry) would better document infrequent crossings, but the use of fluorescent dye allows for documentation of fine-scale movement activity that telemetry does not (Lemen & Freeman 1985).

To differentiate among individuals, we dusted each animal released from an array with 1 of 20 base colors or unique mixtures of base colors. We were careful to dust only the body and to avoid the head area to prevent the animal from breathing in the powder (Stapp et al. 1994). Prior to their natural activity period, we placed it on the lid of the center bucket 5 m from the road edge. This allowed for a standard release distance from the road for all animals without the drift fence acting as a barrier to movement in any direction. When releasing an animal, the handler crouched down parallel to the animal and the road, released the animal, slowly backed away staying parallel to the road, and then left the area. This release strategy was to prevent the handler from scaring the animal toward or away from the road. We traced the fluorescent powder tracks at night with a portable 12-watt long-wave ultraviolet lamp. We laid a 50-m measuring tape over the trail until the powder could no longer be traced. For each animal, we recorded the total distance of the fluorescent track and made a diagram of the animal's movements in relation to the road. We recorded locations of burrows where tracks ended at burrow entrances. We tracked the movement of most individuals only one time to avoid problems with pseudoreplication (Hurlbert 1984). We traced a small number of animals on several occasions to examine the variability of results for individuals. For these animals, only the result of their first tracking occasion was used in statistical analyses.

We categorized all movements as either road use or habitat use. Road use was when an animal moved over the road for any distance of the track length. Habitat use was when an animal stayed in the scrubland during the entire tracking period. We included in our analyses only animals tracked for a minimum of 10 m. For the Dulzura kangaroo rat (*Dipodomys simulans*), we included 2 movements of approximately 9.5 m because there were a low number of total tracks. Because all animals were released within 5 m of the road, this minimum track distance allowed us to document movements relative to the road or well away from the array in any direction. We calculated permeability as the number of animals that exhibited road use divided by the total numbers of animals tracked for each species and road type.

### Analyses

To test whether animals avoided or used the roads more than expected by chance, we compared observed species movement paths with paths simulated from species-specific correlated random walk (CRW) models. The CRW models represent predicted movement without any behavioral response to the roads. We parameterized CRW models with tracking data from at least 3 individuals of each species. We used only paths within the interior scrubland and well away from the road to represent typical movements within an animal's habitat. We used recorded spatial coordinates at 1.0-m intervals along the path to calculate move and turn angles. The move angle was the direction of movement, and the turn angle was the angle of the current move step minus the angle of the previous move step.

We parameterized the simulations in 2 stages. First, for each individual animal's movement path, we estimated the mean turn angle and concentration parameter that determined the dispersion of a von Mises distribution (Fisher 1993). Second, we fitted a von Mises distribution to the mean turn angles for all paths and a gamma distribution to the concentration parameter of the turn angles for all paths. When simulating a path, we randomly

drew a mean turn angle from the von Mises distribution and a concentration parameter from the gamma distribution. We added the turn angle to the move angle of the previous move step to obtain the move angle for the current move step. The move-step length was 1.0 m, and the total length was constrained to the average length of the observed paths for each species. We simulated 1000 paths for each species. To determine the expected number of animal movements onto roads if there was no barrier effect, we determined the number of CRW paths that transected a line 5 m from the start point. We parameterized and simulated all CRW models with a program written in R (R Development Core Team 2010). We compared the number of observed versus expected road movements with Fishers' exact tests. A significant result suggested the animals moved onto roads more or less than expected under the null hypothesis.

Individual animal movement behavior may be affected by population density (Swihart & Slade 1984; Hanski 1999). Therefore, we determined whether relative abundance differed among the roadside habitats with one-way analysis of variation for each species. For our index of species abundance, we used the minimum number of animals known alive. We calculated this index by removing all recaptures within each 3-day trapping session at each array. Although minimum number known alive can be biased as an abundance estimator, it is proportional to population sizes and is thus a reasonable index of abundance (Slade & Blair 2012).

## Results

We dusted 306 animals with fluorescent powder and released them 5 m from the road edge. One-third of the animals were not included in our analyses because their track lengths were <10 m. Most of the small mammals that were not used in the analyses were tracked to a nearby burrow on the side of the road on which they were released, and there were no obvious tracks coming out of the burrow. Small reptiles and those with smooth scales (many snakes, skinks, side-blotched lizards [*Uta stansburiana*], and whiptails [*Aspidoscelis* spp.]) did not retain the powder dye well; thus, many of their tracks were lost within several meters. Some species were excluded due to too few captures. The 181 individuals we used in the analyses (125 small mammals, 56 lizards) were followed an average of 20.7 m (SE 0.8).

We also tracked 19 animals on a second occasion to test the repeatability of individual results. All these animals repeated their initial movement types. Seventeen (12 mammals and 5 lizards) stayed within the scrubland on both tracking occasions, whereas 2 (1 mammal and 1 lizard) repeatedly crossed the road. We present the results for 4 small mammal species and 2 lizard species. These species represent movements of 54 San Diego pocket mice (*Chaetodipus fallax*), 57 cactus mice (*Peromyscus eremicus*), 6 Dulzura kangaroo rats (dirt and secondary paved road only), 8 deer mice (*Peromyscus maniculatus*) (highway only), 26 western fence lizards (*Sceloporus occidentalis*), and 30 orange-throated whiptail lizards (*Aspidoscelis hyperythra*) (secondary paved road and highway only).

### Small Mammals

San Diego pocket mice were tracked an average distance of 25.1 m (SE 1.6) from the point of release. Species-specific movement simulations predicted a permeability of 42% (percentage of animals moving onto road) if the roads had no effect on movement. Twenty-seven percent of San Diego pocket mice movements were tracked onto the dirt roads (Fisher's exact test, $n = 22$, $p = 0.194$). The majority of these movements (4 out of 5) were crossing events to the habitat on the other side of the road. The percentage of movements onto the secondary road was significantly lower than expected at 9.5% ($n = 21$, $p = 0.003$). The 2 movements onto the secondary road were not crossings, but along the edge of the road returning to the habitat on the same side of the road. There were no movements of San Diego pocket mice onto the primary highway ($n = 11$, $p = 0.004$) (Fig. 1). The relative abundance of pocket mice did not differ significantly among the 3 road types ($F_{2,21} = 1.493$, $p = 0.248$).

Cactus mice were tracked an average distance of 19.0 m (SE 1.2). Species-specific movement simulations predicted an expected road permeability of 30%. All the movements onto the dirt road were direct crossing events to the other side of the road (Fig. 2). Although 25% of the individuals went onto the dirt road (meaning there was no significant barrier effect [$n = 20$, $p = 0.626$]), no individuals were tracked onto the secondary paved road or primary highway ($n = 18$, $p = 0.003$ and $n = 19$, $p = 0.002$, respectively). Relative abundance of cactus mice did not differ significantly among the 3 road types ($F_{2,21} = 0.676$, $p = 0.522$).

Dulzura kangaroo rats were tracked an average of 14.6 m (SE 2.4). Movement simulations for this species predicted a road permeability of 41%. Although there were few animals tracked, most of them went onto the roadways. Of the 3 individuals tracked near the dirt road, all went onto the road ($n = 3$, $p = 0.070$), which indicates the road was more permeable to this species than the surrounding habitat. One individual's burrow entrance was in the middle of the roadway. Two out of 3 individuals tracked went onto the secondary paved road ($n = 3$, $p = 0.572$), which indicates this road was not a barrier to movement. One individual ran along the length of the road and the other crossed the road (Fig. 3).

Deer mice were tracked adjacent to the highway for an average length of 19.9 m (SE 2.3). Species-specific

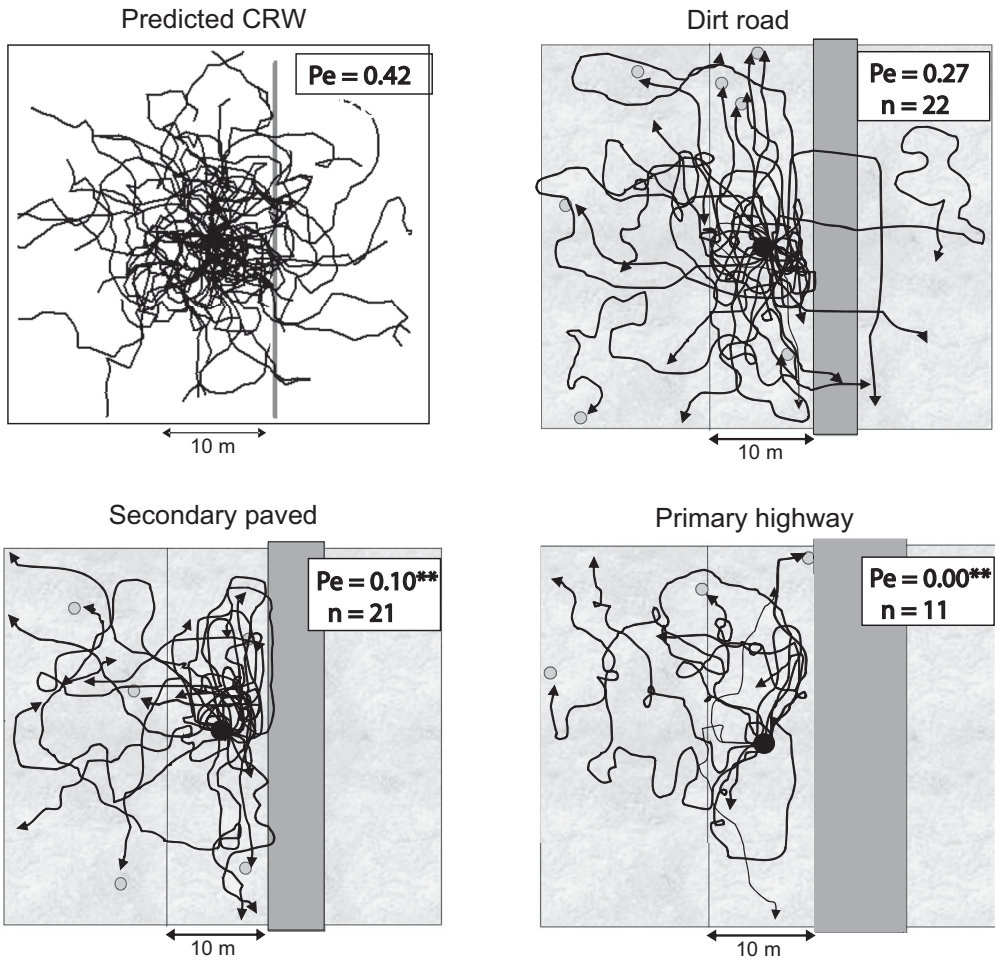


*Figure 1. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the San Diego pocket mouse (Chaetodipus fallax). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circles, burrows; $^{**}p < 0.01$).*

movement simulations predicted a road permeability of 37%. No deer mice went out onto the road, which indicates the rural highway was a significant barrier for this species ($n = 8, p = 0.030$). Many individuals were tracked to burrow entrances that were within a few meters of the road.

### Lizards

Western fence lizards were tracked an average distance of 17.4 m (SE 2.2) from point of release. Species-specific movement simulations predicted an expected road permeability of 31%. The permeability of the dirt roads to movement of western fence lizards was higher than expected; 66% of lizards went onto the dirt road ($n = 9$, $p = 0.030$). These were a mixture of crossing events and movement along the road. A high percentage (56%) of individuals also went onto the secondary paved road ($n = 9$, $p = 0.146$). These movements were all along the road and no crossing events were recorded. However, most of these tracks were lost on the pavement, so we could not determine which side of the road the animal went to. In comparison, not a single western fence lizard went onto the highway (Fig. 4). Although permeability between the expected and observed values for the highway was not significant ($n = 6, p = 0.186$), the permeability of the highway to fence lizard movements was significantly lower than permeability of the dirt ($p = 0.028$) and secondary paved roads ($p = 0.044$) to movements of fence lizards. Their relative abundance did not differ among road types ($F_{2,21} = 0.006, p = 0.994$).

Movement simulations predicted road permeability of 31% for orange-throated whiptail if the roads had no effect on movement behavior. The average track length was 17.0 m (SE 1.3) by the secondary and primary paved roads. Although 33.3% of orange-throated whiptails crossed the secondary paved road ($n = 6$, $p = 1.00$), none were tracked out onto the highway ($n = 24$, $p \leq 0.001$) (Fig. 5). Only one whiptail was captured by the dirt road, and its track length was <10 m. Whiptail abundance next to the paved road and highway did not differ significantly ($t_{14} = 1.612, p = 0.129$). However, the

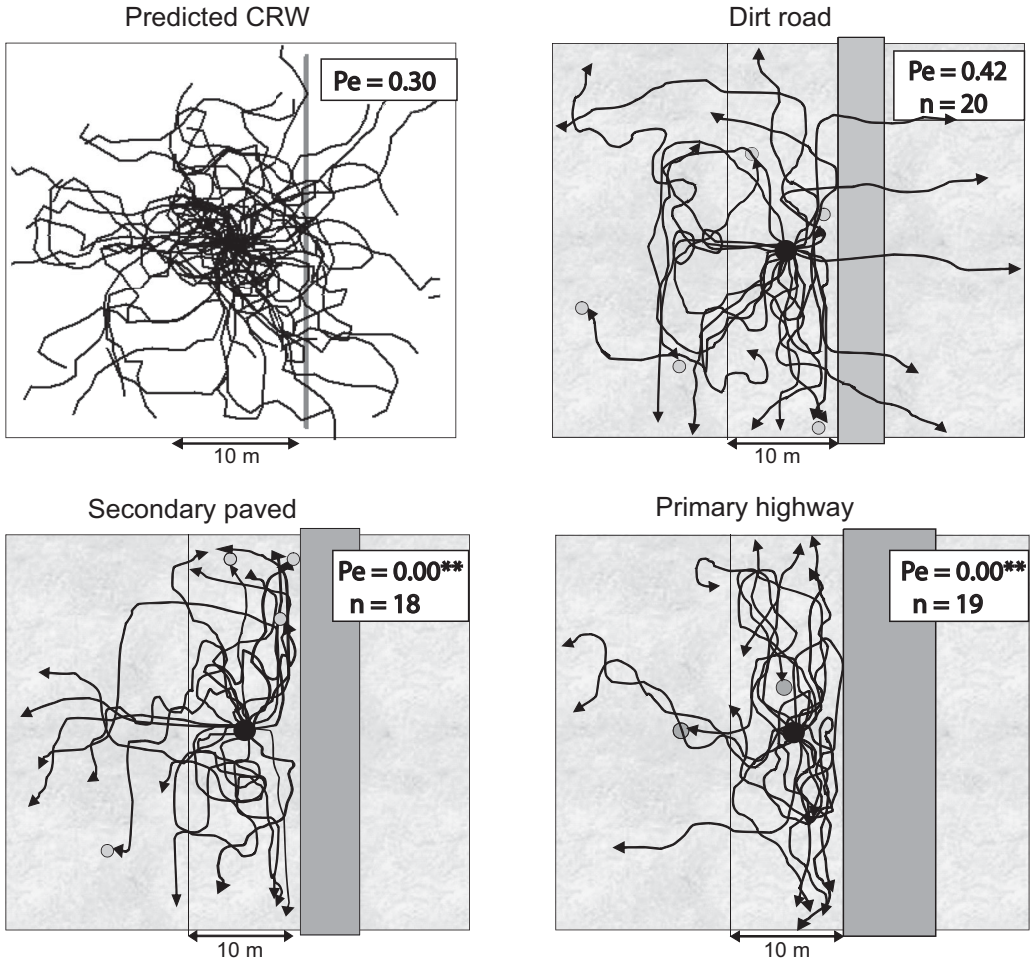


*Figure 2. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the cactus mouse (Peromyscus eremicus). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circles, burrows; $^{**}p < 0.01$).*

success rate in tracking the whiptail for distances >10 m was significantly greater by the highway (24/32) than by the paved road (6/20, $p = 0.002$).

## Discussion

Although they live in open scrub habitats, San Diego pocket mice and cactus mice prefer to move and forage under microhabitats of shrub and rock cover rather than open areas (Meserve 1976; Price & Kramer 1984). Thus, they may quickly pass through or avoid areas of open ground. This is consistent with their movements relative to the dirt road, which were primarily direct crossings to shrub and rock cover on the other side of the road. One cactus mouse crossed the dirt road on 2 occasions. This result indicates the dirt road was within its home range. In contrast to the dirt road, there were no documented movements of either species across the secondary paved road or highway even though the distances required to cross either road were well under the average tracked distances of the species. The secondary road differed from the dirt roads by an average added width of 1.9 m, the addition of pavement, and an increased traffic volume averaging one vehicle every 5 minutes. It is unknown which of these factors or combination thereof resulted in their avoidance of this road. However, because of the low traffic volume and little difference in width, it is likely that these species were avoiding the road substrate. White-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) avoid crossing paved roads regardless of traffic volume (McGregor et al. 2008). By comparing roads with different substrates and traffic volumes, our results support the hypothesis that many small mammal species avoid paved road substrates. The reasons for this are not understood and deserve further study. However, mammals are particularly sensitive to odors in their environment. Road pavement surfaces, such as asphalt and coal tar, contain complex mixtures of volatile and non-volatile compounds. Even very minute concentrations of smells and chemicals that mimic pheromones may elicit instinctive behavioral

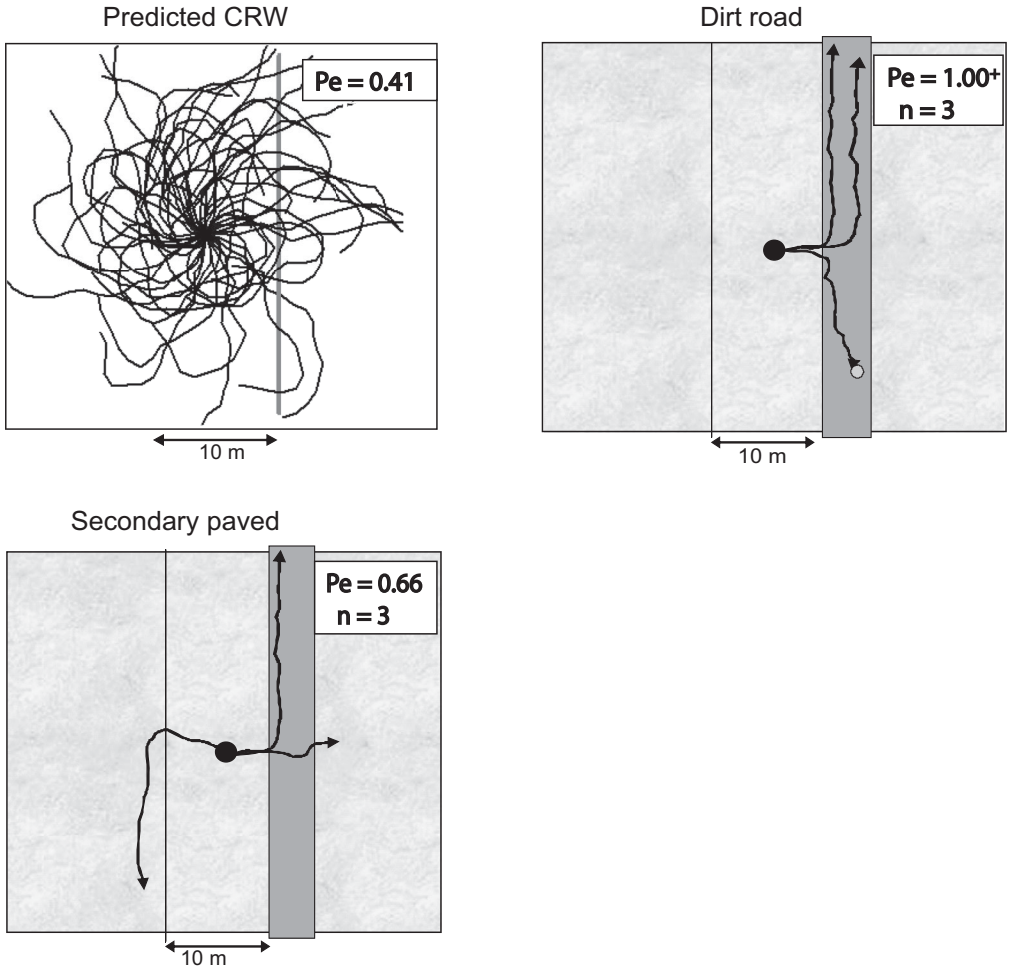


*Figure 3. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of Dulzura kangaroo rat (Dipodomys simulans). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circle, burrows; +$p < 0.10$).*

responses in some species (e.g., Leinders-Zufall et al. 2000).

However, the avoidance of pavement is not generalizable to all species of small mammals. The yellow-necked mouse (*Apodemus flavicollis*) regularly crossed both dirt and paved roads of similar width (Rico et al. 2007). In our study, 2 out of 3 Dulzura kangaroo rats went out onto the secondary paved road. Although we did not capture any Dulzura kangaroo rats by the highway, this species accounted for the majority of dead animals we observed on the highway (3 out of 7) (Brehme 2003), which indicates the highway was also somewhat permeable to movement for this species. The higher than expected permeability of dirt roads to movements of the Dulzura kangaroo rat is consistent with results of a previous study on the Stephens' kangaroo rat (*D. stephensi*) (Brock & Kelt 2004). Kangaroo rats may preferentially use dirt roads for movement within their habitat. These bipedal heteromyids prefer to move and forage within open-ground areas of scrub habitats and respond positively to disturbances such as fire (e.g., Meserve 1976; Price & Kramer 1984; Brehme et al. 2011). In areas with denser vegetation, low-use dirt roads and trails may provide an increased opportunity for kangaroo rats to disperse to open scrub habitats. Alternately, we would expect negative effects from high-traffic roads on kangaroo rats. Traffic noise can disrupt communication in kangaroo rats (Shier et al. 2012) and nonavoidance of these roads would very likely result in increased mortality rates from vehicular traffic.

Because many reptiles may be attracted to open spaces and paved surfaces for thermoregulatory purposes, it is often hypothesized that these animals do not avoid roads (e.g., Klauber 1939; Jochimsen et al. 2004; Andrews et al. 2008). The dirt and secondary paved roads in our study were highly permeable to movement of western fence lizards (67% and 56%, respectively). Their movements on the dirt roads consisted of crossings and movements along the road; thus, the road was in part used as a conduit for movement. In contrast, their

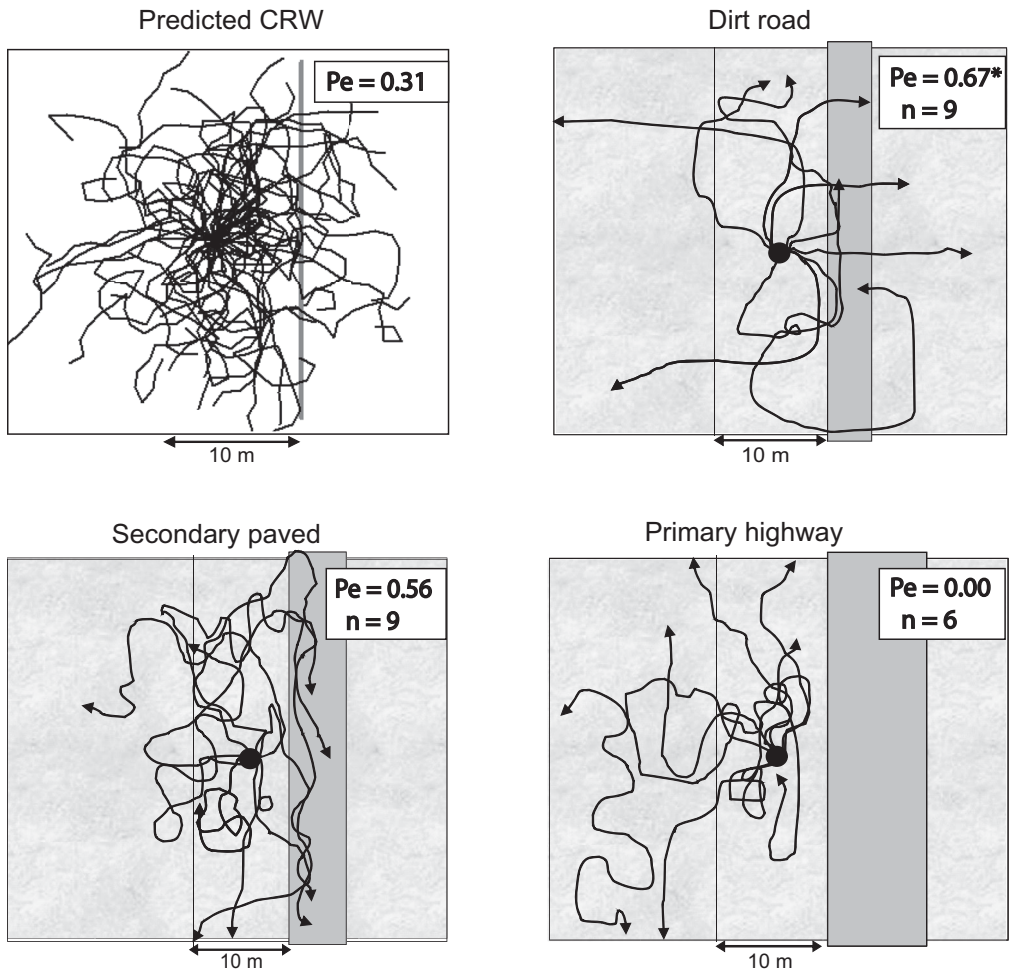


*Figure 4. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the western fence lizard (Sceloporus occidentalis). Each drawing represents movements tracked at multiple independent release sites that are superimposed onto a single frame ($^*p < 0.05$).*

movements on the secondary road were often erratic and irregular along the road edge. This suggests the paved road was used for basking which was regularly observed during the study. The complete absence of movements onto the highway was in stark contrast to their response to the dirt and secondary paved roads. Similarly, although the secondary road was permeable to movement of the orange-throated whiptail, this species also completely avoided the highway.

Delaney et al (2010) found that genetic diversity is lower in populations of western fence lizards that are separated by a highway than in populations in continuous habitat. Because of the high permeability of the secondary paved road to these 2 species, we think it is unlikely that the additional width of the highway (4.6 m) alone adequately explains their marked avoidance of the highway. However, the level of traffic (average 1 vehicle/7 seconds) was 40-fold higher on the highway than on the secondary paved road; thus, the constant stream of vehicular traffic and corresponding noise and vibration may have been sufficient to deter use of the highway. On the basis of our own literature search and recent reviews on responses of reptiles to roads (Andrews et al. 2008; Rytwinski & Fahrig 2012), we believe ours is the first study to document behavioral road avoidance in lizards.

All the study species exhibited increased road avoidance and thus experienced decreased connectivity as road improvement and traffic increased. By studying both small mammals and reptiles we were able to make direct comparisons of behavior between taxa with different microhabitat preferences and life-history strategies. Species microhabitat-use preferences within their habitat may be an important predictive factor for road permeability (Fig. 6). Animals that are more likely to focus their activities in open areas within their habitat were more likely to venture out onto low-use roads. In our study, the 3 species (Dulzura kangaroo rat, western fence lizard, orange-throated whiptail) that use open areas for foraging

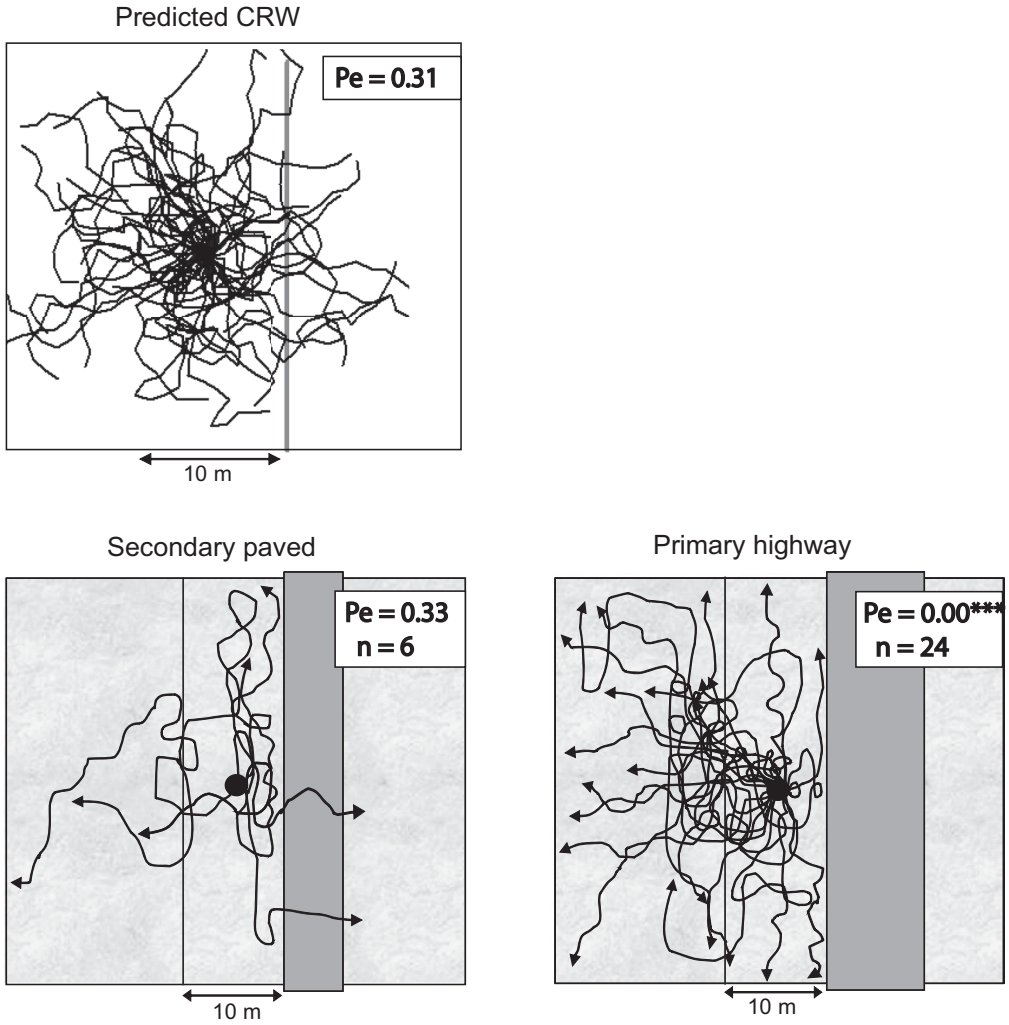


*Figure 5. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of orange-throated whiptail lizard (Aspedoscelis hyperythra). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (***$p < 0.001$).*

or thermoregulation ventured onto dirt and secondary paved roads more than the species (San Diego pocket mouse, cactus mouse) that prefer to forage within or under the cover of rocks and shrubs.

Thus, one would predict that the populations of small animals with closed microhabitat preferences would be in most danger of becoming fragmented by any type of road. For instance, small mammal and reptile species that avoid open ground, such as the cotton rat (*Sigmodon hispidus*), prairie vole (*Microtus ochrogaster*), Eastern massasauga rattlesnake (*Sistrurus c. catenus*), rosy boa (*Lichanura trivirgata*), and many rainforest species, avoid crossing even narrow dirt roads (Swihart & Slade 1984; Weatherhead & Prior 1992; Goosem 2001; Rochester et al. 2005). Whereas generalist species and those with open microhabitat preferences would be more likely to cross roads, use roads for activity, and as conduits for movement. However, even these species may avoid roads with heavy traffic due to the constant disturbance from noise, vibrations, and lights. Therefore, roads with moderate traffic would be expected to pose the greatest risk of vehicular mortality for generalists and open microhabitat specialists due to the use of roads by both animals and vehicles (Seiler 2003). Our results pertain to small mammals and lizards with home ranges that are small relative to the road matrices within the study area. It is expected that movements onto roads would be more common for animals that make long migratory movements or that have large home ranges relative to the road matrices within their habitat.

Our results show that a 2-lane rural highway through open scrubland can create a significant movement barrier for species of small mammals and reptiles. Behavioral mechanisms appear to be road surface avoidance for some small mammal species and traffic avoidance for lizard species. Avoidance of improved roads may be a beneficial response in that mortality from vehicular traffic is avoided or minimized. However, networks of

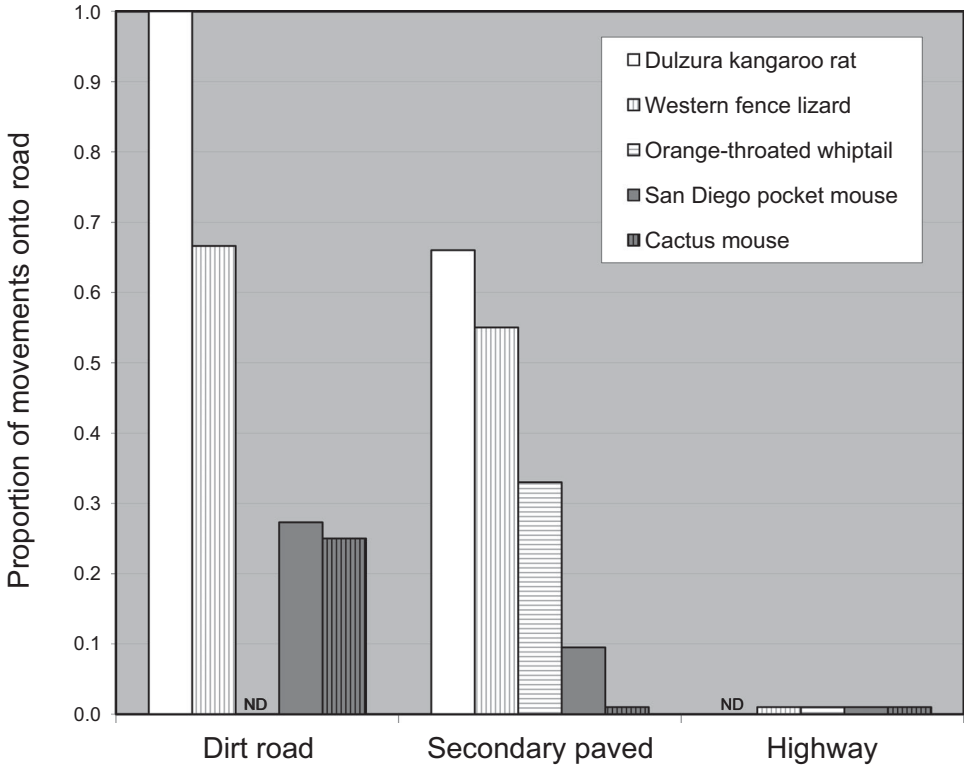


*Figure 6. Road permeability relative to species microhabitat-use preferences (white bars, species that typically forage in and use open areas of their habitat; gray bars, species that primarily forage under vegetation cover; ND, no data for species at specific road type). Expected permeability range 0.30–0.41 with no road response.*

roads throughout a landscape may divide habitat into fragments that are too small to sustain some populations over the long term. Barrier fencing and safe-crossing structures may reduce the effects of habitat fragmentation for species that avoid roads and reduce road mortality for species that do not avoid roads (e.g., Boarman & Sazaki 1996; Dodd et al. 2004).

More research is needed to determine whether road response patterns are consistent across other habitats and small animal species, whether microhabitat-use preferences can also help predict the use of road-crossing structures, and to further understand the population-level effects of movement-behavior decisions (Fahrig 2007; Rytwinski & Fahrig 2012). If generalizations are found, they will help us to identify vulnerable species and potentially detrimental roads within their habitat, inform population and spatial-movement models, and inform management decisions and mitigation measures for both studied and unstudied species.

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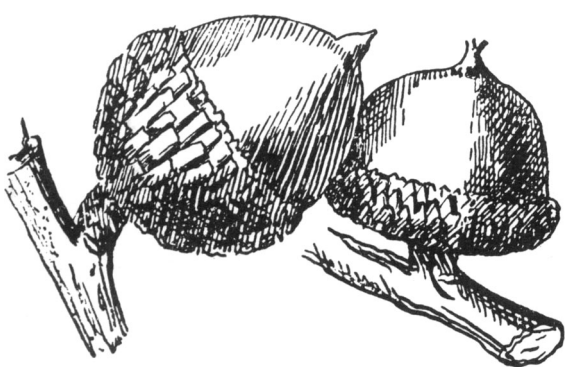

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RESEARCH ARTICLE

# An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California

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**Abstract**
*Context* Transportation and wildlife agencies may consider the need for barrier structures and safe wildlife road-crossings to maintain the long-term viability of wildlife populations. In order to prioritize these efforts, it is important to identify species that are most at risk of extirpation from road-related impacts.
*Purpose* Our goal was to identify reptiles and amphibians in California most susceptible to road mortality and fragmentation. With over 160 species and a lack of species-specific research data, we developed an objective risk assessment method based upon road ecology science.
*Methods* Risk scoring was based upon a suite of life history and space-use characteristics associated with negative road effects applied in a hierarchical manner from individuals to species. We evaluated risk to both aquatic and terrestrial connectivity and calculated buffer distances to encompass 95% of population-level movements. We ranked species into five relative categories of road-related risk (very-high to very-low) based upon 20% increments of all species scores.
*Results* All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species in California were ranked at high or very-high risk from negative road impacts. Results were largely consistent with local and global scientific literature in identifying high risk species and groups.
*Conclusions* This comparative risk assessment method provides a science-based framework to identify species most susceptible to negative road impacts. The results can inform regional-scale road mitigation planning and prioritization efforts and threat assessments for special-status species. We believe this approach is applicable to numerous landscapes and taxonomic groups.

**Keywords** Reptile · Amphibian · Road mortality · Habitat fragmentation · Road ecology · Risk assessment · Road

## Introduction

There have been many attempts to better characterize and quantify threat criteria in order to classify species at higher risk of extinction at state, national, and global levels (Congress 1973 (U.S. Endangered Species Act); Mace et al. 2008; Hobday et al. 2011; Thomson et al. 2016; IUCN 2017). Roads are a significant threat to wildlife populations (e.g., Forman et al. 2003;

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Andrews et al. 2015a; van der Ree et al. 2015), causing both barrier (habitat fragmentation) and depletion (road mortality) effects. Barrier effects occur when animals avoid crossing roads, in which case roads essentially fragment species habitat. Barrier effects include reduced size and quality of available habitat, reduced effective population size, reduced ability to find mates and resources, increased genetic structuring, and increased probability of local extirpation (e.g., Forman et al. 2003; Fahrig and Rytwinski 2009; D'Amico et al. 2016). Depletion effects occur when animals attempt to cross roads and are killed by vehicles. Depletion effects include all of the risks from barrier effects as well as reduced survivorship, making high road mortality an even greater concern (Jackson and Fahrig 2011). Among other stressors, such as habitat loss and fragmentation, invasive species, pesticide use, changing climate, and disease, the negative impacts from roads may independently or cumulatively threaten the persistence of populations and even species.

Amphibians and reptiles have been identified as being particularly susceptible to the negative effects of roads within their habitat (e.g., Klauber 1931; Forman et al. 2003; Rytwinski and Fahrig 2012; Andrews et al. 2015a, b; D'Amico et al. 2015). Many are slow moving, do not avoid roads, and are simply too small for drivers to see and avoid. During rains many amphibians make long linear terrestrial movements regardless of the presence of intersecting roadways (Glista et al. 2008), and because paved roads typically absorb and retain more heat than the surrounding habitat, snakes and lizards are often attracted to roads for thermoregulation (Case and Fisher 2001; Jochimsen et al. 2004). In fact, road surveys are one of the most common methods for surveying these reptiles (e.g., Sullivan 2012). Many herpetofauna species utilize both aquatic and terrestrial habitat for breeding, development, foraging, and overwintering and therefore require connectivity within and between both aquatic and terrestrial habitats to support basic life history requirements.

The primary goal of this study was to provide information to transportation and other planning agencies in California to assist them in prioritizing road mitigation efforts for amphibian and reptile species. Although there is still a lot to learn about the effectiveness of different designs of road mitigation systems, the use of barrier systems, underpasses, and overpasses can reduce road mortality and help to maintain connectivity and safe passage across roads for herpetofauna and other wildlife (Jochimsen et al. 2004; Colino-Rabanal and Lizana 2012; Langton 2015; Langen et al. 2015b). Because it is currently unrealistic and cost prohibitive to mitigate all roadways for all species, it is vital to identify species most susceptible to road-related impacts. Within species ranges, risks to populations and need for mitigation can then be evaluated based upon local road densities and matrix, road-types, traffic, and road locations in relation to species habitat and movement corridors (e.g., Jaeger 2000; Litvaitis and Tash 2008; Langen et al. 2015b; Zimmermann Teixeira et al. 2017).

Here we describe a road risk assessment methodology applied to native amphibian and reptile species in California, a global biodiversity hotspot (Myers et al. 2000). We also included analysis of subspecies if they had special federal or state protection status. This includes 166 species and subspecies of frogs, toads, salamanders, snakes, lizards, turtles, and tortoise. Rankings and prioritizations such as these can be very subjective. In order to avoid including low risk species that may be favored by the assessors or to unintentionally overlook species that are at high risk, it was important for this be done in an objective manner informed by current road ecology literature.

Very few quantitative data are available on the impact of roads on population persistence. Jaeger et al. (2005) were the first to develop a relative ranking system to compare the impact of roads on wildlife populations. Their ranking system was largely based upon behavioral responses of animal species to the road surface, road size, traffic noise, and vehicles with varying road sizes and traffic volumes. However, knowledge of these detailed behavioral responses to ranges in road and traffic characteristics is rarely found in literature and the link between individual behavior and population-level effects has not been clearly established (Rytwinski and Fahrig 2012, 2013).

Rytwinski and Fahrig (2012) performed a meta-analysis of wildlife groups to test whether certain life history characteristics were related to negative responses to roads. High reproductive rate (fecundity) was negatively associated with the magnitude of population-level effects for amphibians. No associations were significant in reptiles, although there were

few studies to inform this analysis. However, a strong link was shown between body size, greater mobility, lower reproductive rates and the magnitude of negative road effects in mammals, the most studied wildlife group. Conversely, simulations predicted populations of species with small home ranges and high reproductive rates were the least likely to be affected by roads (Rytwinski and Fahrig 2013).

We used these findings as a basis for creating a multi-tiered system to rank and identify reptile and amphibian species that may be most susceptible to road impacts. We based our ranking upon a suite of species life history and space-use characteristics associated with negative road effects, as well as including species distribution and conservation status. We evaluated risk to both aquatic and terrestrial connectivity and include buffer distances that were calculated to encompass 95% of population movements. Relative confidence in these distances is given for each species based upon the amount of support from scientific studies. We solely focused on the direct effects of roads as barriers and sources of road mortality and not impacts from road construction and maintenance or indirect effects from increased human use of the landscape once a road is in place (see review by Langen et al. 2015a).

Because we based the risk assessment solely upon space-use and life history characteristics, this represents a species relative susceptibility to road impacts. It is understood that circumstances associated with particular populations (e.g., local road types, locations, densities) may elevate or reduce the risk for certain populations and species.

## Methods

### Road risk assessment (overview)

We assessed the relative risk of California herpetofauna species to negative road-related impacts at three scales in a hierarchical fashion. We first assessed risk at the scale of an individual animal and then expanded the risk to the population and then to species (Fig. 1).

At the individual-level, we based road risk primarily upon the likelihood that an individual would encounter one or more roads. We considered this a product of movement distance (home range, seasonal migrations) and movement frequency (e.g., active foragers, seasonal migrants, sit-and-wait predators vs. sedentary species) (e.g., Bonnet et al. 1999; Carr and Fahrig 2001). Because many species are semi-aquatic, movement distance and frequency were scored separately for both aquatic and terrestrial habitats.

There is a theorized higher risk associated with depletion effects (i.e., road mortality) in comparison to barrier effects (Fahrig and Rytwinski 2009; Jackson and Fahrig 2011). Therefore, we gave additional weight to those species more likely to go out onto a road surface and be killed by vehicular traffic. For this we considered factors of habitat preference (e.g., open vs. closed), roads as potential attractants (e.g., for basking), and movement speed (e.g., slow vs. fast). However, individuals within and among species may respond differently to roads (attraction vs. avoidance) based upon local landscape features, road width, traffic volume, and perceived danger (Forman et al. 2003; Andrews 2005; Brehme et al. 2013; Jacobson et al. 2016). Because a state-wide analysis encompasses extreme variation in landscape and road characteristics, the extent to which roads act as barriers or sources of direct mortality within a species range is unknown. The risk disparity between depletion and barrier effects could also be highly variable. Therefore, we limited the additional weight for potential depletion effects to twenty percent of the individual risk score.

We assessed population-level road risk by multiplying individual risk with scores representing: (1) the relative proportion of the population at risk; and (2) the species ability to sustain higher rates of mortality. For instance, the proportion of the population at risk was expected to be higher for migratory species than for territorial species. Highly fecund species were expected to better withstand (or more quickly recover from) higher mortality in comparison to those with few annual offspring.

Finally, we assessed species-level road risk by multiplying population road risk with scores for range size (both within and outside of California) and conservation status according to the U.S. Fish and Wildlife Service (USFWS 2016) and the California Department of Fish and Wildlife (CDFW 2016a; Thomson et al. 2016). Species with smaller ranges typically have fewer populations and are thus less resilient to population-level stressors. Endangered, threatened, and special concern species have already been designated at risk of extirpation, often due to

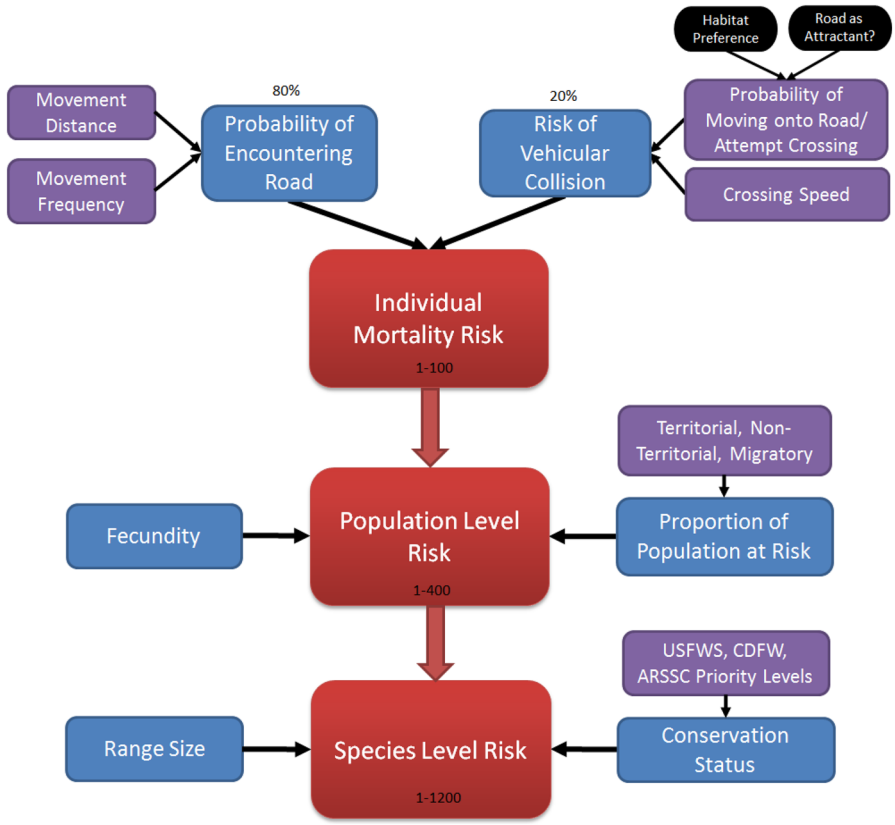


**Fig. 1** California reptile and amphibian road risk assessment conceptual model (*ARSSC* Amphibian and Reptile Species of Special Concern (Thomson et al. 2016))

multiple stressors, and are thus thought to be less likely to be resilient to additional road impacts.

Although we present both aquatic and terrestrial risk scores for semi-aquatic species, we used the higher of the two scores for the overall risk ranking.

## Literature review

Species life history data were primarily taken from and cross-checked among the following species account review sources;

1. U.S. Fish and Wildlife Service (USFWS) Recovery Plans and 5-year Reviews https://www.fws.gov/endangered/.
2. California Amphibian and Reptile Species of Special Concern (ARSSC; Thomson et al. 2016).
3. A Field Guide to Amphibians and Reptiles of California (Stebbins and McGinnis 2012)
4. Amphibian declines: the conservation status of United States species (Lannoo 2005).
5. Conservation Status of Amphibians and Reptiles on USDA National Forests, Pacific Southwest Region, 2012 (Evelyn and Sweet 2012).
6. Natureserve Explorer (natureserve.org): Species Accounts largely authored by G. Hammerson (2003–2016).

When these reviews were lacking life history information needed for the road risk assessment, we then searched for supplementary peer-reviewed literature using the Google Scholar search engine. Because movement distances (terrestrial, aquatic, home range, migratory) were so important for the risk assessment, we acquired referenced articles from the species accounts and independently searched the literature to acquire these data. Search terms included the species common name, scientific name, or genus and terms such as “movement”, “home-range”, “spatial”, and “telemetry”. We also reviewed articles for citations of other studies to find more recent information on movement. This literature included published articles,

book chapters, M.S. Theses, Ph.D. dissertations, agency reports, and consultant reports. In the case that specific life history or movement information was not found for a species, we chose a surrogate species based upon phylogeny, habitat, and body size. We first looked for the closest related species within the genus or family and chose a closely related surrogate based upon similar habitat and body size. If surrogates were used, these are clearly reported.

## Road risk metrics

The following section describes in detail the rank scoring used for Individual-level Road Risk, Population-level Road Risk, and Species-level Road Risk. All rank values are meant to represent the relative contribution of each attribute to either additive or multiplicative road risk.

### *Individual-level risk (100 points possible)*

Out of a total of 100 points for individual road mortality risk, we attributed up to 80 points (80%) to the risk of encountering a road and up to 20 points (20%) for the risk of an individual moving onto a road and being killed by a motor vehicle.

The risk of encountering a road was based on a combination of movement distance and general movement frequency. Movement distance was ranked 1–40 based upon home range movement distances (diameter) for non-migrants or migration distances for seasonal migrants that spanned from 0 to > 1200 m (Table 1). The scores are linearly correlated with increasing movement distance.

For species that use both terrestrial and wetland/stream/riverine habitats, such as frogs, toads, aquatic snakes and turtles, we scored aquatic and terrestrial movement distances and frequencies separately. This was necessary as some species move much larger distances and at different frequencies in one habitat versus the other. This also informs the type(s) of mitigation structures that may be warranted based upon habitat type, buffer distances and risk scores for each species. Aquatic movement distances were not calculated for pond-breeding amphibians. Ponds are typically small ephemeral bodies of water and terrestrial movements of amphibians to and among ponds account for the majority of movement for these species.

**Table 1** Individual-level Road Risk (IRR): Score criteria for risk of individuals encountering a road

| Risk of individuals encountering a road = Movement distance × frequency | | | |
|---|---|---|---|
| Movement distance (m) | Score | Frequency | Score |
| > 1200 | 40 | Active throughout home range | 2 |
| 901–1200 | 32 | Migratory (2–4 × per year)/ non-migratory sit and wait foragers | 1.5 |
| 601–900 | 24 | Sedentary, confined to specialized habitat | 1 |
| 451–600 | 16 | | |
| 301–450 | 12 | | |
| 201–300 | 8 | | |
| 101–200 | 5 | | |
| 51–100 | 3 | | |
| 0–50 | 1 | | |

The calculations and rankings for movement distances were well considered and deserve further explanation. Our original thinking was that maximum distances should reflect relative movement distances across species and these data were commonly reported in species accounts. However, it became increasingly difficult to determine whether maximum distances reported were seasonal migration movements, home range movements or rarer dispersal events. We believed this assessment should reflect annual movement distances and not rare dispersal events. We considered using average/median movement distances; however, these often underestimate the movement of seasonal migrants because in many cases a sizeable portion of the population may remain close to a breeding site, while another sizable portion make longer distance migrations causing an average or median to be uninformative. Therefore, we decided to use a buffer distance that incorporates the movement distances of 95% of the population studied. A 95% population movement distance is commonly accepted for the delineation of terrestrial buffer zones for amphibians (i.e., Semlitsch 1998; Semlitsch and Bodie 2003) and we believe it was the most biologically

meaningful and useful measure for this study. This measure, which we will refer to as Maximum Population Movement Distance (MPMD), should include almost all population movements, such as seasonal migration distances and annual home ranges (diameter), but not rare dispersal events. The MPMD should also be useful for local risk assessments as these distances can be used to aide in mapping and mitigation decisions.

The calculation we used for MPMD is commonly known as the 95% upper tolerance interval (Vangel 2015). A tolerance interval is an interval that is meant to contain a specified percentage of individual population measurements. This should not be confused with a confidence interval, which is an interval that is meant to contain the population mean. We chose a 50% confidence level for the upper 95% confidence limit of movement distances which is equal to the 95% prediction interval for future observations and is the mean + 1.645 × standard deviation. In cases where a standard deviation was not reported, we back calculated standard deviation from the standard error and sample size, calculated it from the individual data, or estimated it based on the methods recommended by Hozo et al. (2005). Although non-parametric tolerance intervals would be more appropriate for non-normally distributed movement data, the data required to calculate these is rarely reported in the published literature. In the case of non-normally distributed data where medians, sample sizes and ranges are reported, Hozo et al. (2005) methods allow for approximation of means and standard deviations with no assumption of the underlying data distribution. We found the resulting MPMDs to be reasonable in excluding large outliers but including multiple long distance movements below the maximum movement distance.

We recognize that for any species there can be substantial variability in movement distances that depend upon varying local, landscape, and climatic factors. This was often reflected in studies with sometimes widely varying estimates of home range and migration distances. We attempted to be conservative by using the study data for calculation of MPMD in which the largest population movement distances were observed. For studies where movement distance significantly varied between females and males, we used the information from the wider ranging sex. For migratory distances, we did not use distances from extreme environments, such as Canada, where suitable overwintering sites are typically much farther away from breeding and summer activity areas than in milder California climates (e.g., Gregory 1984). We did use study data from adjacent states or lower estimates of migration distances from those reported in Midwestern states. In some cases where little information was available, we made an educated guess based upon limited study data and/or closely related species and noted these in the tables. For all MPMDs, we report a relative confidence level based upon the number and quality of studies, sample sizes, and locations in or adjacent to California. It is intended that the scores be adjusted as new information becomes available.

To compute the risk of encountering a road, the MPMD was multiplied by a relative index of the expected frequency of longer distance movements (1–2 points; Table 1). We defined three frequency categories largely based upon annual migratory movements or foraging strategies for non-migratory species. The highest category included actively foraging predators which are characterized by frequent wandering movements throughout their home range (Pianka 1966). Less frequent movers included seasonal migrants traveling among breeding, summer foraging, and/or overwintering sites and non-migratory 'sit-and-wait' predators that remain still for long periods of time to ambush prey (Pianka 1966). Finally, low frequency included highly sedentary species with high site fidelity, particularly specialized rock, crevice, soil, or tree dwellers that may rarely traverse terrestrial or aquatic habitats.

The risk of an individual moving onto a road and being killed by a moving vehicle was ranked by attributes of habitat preference, road use, and movement speed (Table 2). Habitat preference represents the degree to which an individual is expected to go out onto or avoid an open road as predicted from their habitat and microhabitat preferences. Open habitat specialists and generalists were expected to more readily move onto a road than species that prefer cover (e.g., Forman et al. 2003; Brehme et al. 2013). Although many amphibians are closed habitat specialists, most readily move through open habitats during rain events, when most overland migratory movements tend to occur (Glista et al. 2008). Therefore, amphibians were considered open habitat specialists for this ranking. An additional factor that may increase road use is for thermoregulation for lizards

**Table 2** Individual-level Road Risk (IRR): Score criteria for risk of road mortality

| Risk of road mortality = Habitat preference + road use + movement speed | | | | | |
|---|---|---|---|---|---|
| Habitat preference | Score | Road use | Score | Movement speed | Score |
| Open habitat specialist/amphibians | 10 | Thermoregulation (snakes/lizards) | 4 | Slow (< 0.6 m/s) | 6 |
| Generalist | 8 | Other | 0 | Medium (0.6–2.0 m/s) | 3 |
| Edge specialist | 4 | | | Fast (> 2.0 m/s) | 0 |
| Closed habitat or aquatic specialist | 0 | | | | |

**Table 3** Population-level Road Risk (PRR): Score criteria for population level road risk

| PRR = IRR × (Fecundity + Proportion of population at risk) | | | | |
|---|---|---|---|---|
| Fecundity | Ave. potential offspring/year | Score | Proportion of population at risk | Score |
| Low | 0–10 | 2 | Seasonal migrants (Migratory) | 2 |
| Med | 11–25 | 1.5 | Wandering | 1.5 |
| High | 26–100 | 1 | Territorial | 1 |
| Very high | > 100 | 0 | | |

and snakes, as roads often retain more heat than the surrounding environment (Colino-Rabanal and Lizana 2012; Mccardle and Fontenot 2016). Finally, there is an increased risk of road mortality for slow versus fast moving species (see Andrews and Gibbons 2005; Mazerolle et al. 2005; Andrews et al. 2015b).

*Population-level Road Risk (400 points possible)*

To assess the risk of negative road impacts on the persistence of a population we incorporated scores for population-level movement behavior and fecundity (Table 3). For the proportion of a population expected to encounter a road, we scored the greatest risk to species that seasonally migrate to overwintering and breeding areas (Jackson et al. 2015). For those that do not migrate, we expected higher proportions of non-territorial or loosely territorial species ("wandering") to encounter roads than species that defend distinct territories.

Species with low fecundity are less resilient to road mortality impacts than highly fecund species (Rytwinski and Fahrig 2013). Relative fecundity was simply calculated from the average number of potential offspring per year whether the animals were oviparous or live-bearing. For egg-laying species, the number of potential offspring was calculated by multiplying the average clutch size by the average number of clutches per year.

Individual mortality risk (1–100 points) was multiplied by the sum of these population-level factors (1–4 points) to calculate population-level road risk.

*Species-level road risk (1200 points possible)*

In comparison to population-level risk, we considered the overall risk of roads to species to be negatively associated with species range and conservation status. Although some populations may be at high risk, species with a wide distribution and many populations should be more resilient to localized declines and extirpations. Therefore, we assigned a range isolation score ranging from 0 to 1 that considered species distributions range-wide (North America) and within California (CA) (Table 4). Range-wide distribution varied from "CA only" to "widespread" (> 4 states). If the species range extended into Mexico and/or Canada, these countries were counted as another state for calculation of the index. California-wide distribution was calculated based upon the number of CA geographic regions occupied out of twelve regions defined by Hickman (1993) and used in Stebbins and

**Table 4** Species-level Road Risk (SRR): Score criteria for species-level road risk

| SRR[a] = PRR × ((Range isolation score + Conservation status score)/2) | |
|---|---|
| (a) Range isolation score = (North America range + CA range)/2 | |
| North America range | Rank/score |
| CA only | 1.00 |
| 2 states (very restricted distribution) | 1.00 |
| 2 states (restricted) | 0.67 |
| 2–3 states | 0.33 |
| Widespread (4 + states) | 0.00 |
| California range (No. of geographic regions occupied) | Rank/score |
| 1 | 0.92 |
| 2 | 0.83 |
| 3 | 0.75 |
| 4 | 0.67 |
| 5 | 0.58 |
| 6 | 0.50 |
| 7 | 0.42 |
| 8 | 0.33 |
| 9 | 0.25 |
| 10 | 0.17 |
| 11 | 0.08 |
| 12 | 0.00 |
| (b) Conservation status score | |
| Conservation status | Rank/score[a] |
| CA or federal threatened/endangered | 1.00 |
| SSC priority 1 | 0.75 |
| SSC priority 2 | 0.50 |
| SSC priority 3 | 0.25 |
| None | 0.00 |

[a]Population-level risk > 80 only

McGinnis (2012). These two scores (Range-wide isolation, CA isolation) were summed and divided by two in order to normalize the overall range isolation score to a 0 to 1 scale.

At the species-level, we also incorporated conservation status (Table 4). Some species are declining and are at higher risk of extinction often due to multiple stressors. Federal and State Threatened and Endangered Species were given the highest score (1.0). In California, forty-five species are designated "Species of Special Concern (SSC)" with a ranking of 1, 2, or 3 based upon severity and immediacy of threats affecting each taxon (Thomson et al. 2016). SSC species were given a conservation status score ranging from 0.25 to 0.75 based upon their SSC ranking. Population-level Road Risk (score range 1–400) was multiplied by (1 + Range Isolation Score + Conservation Status Score; score range 1–3) to calculate the final Species-level Road Risk.

Range and conservation status were only used as a multiplier for species-level road risk if the population-level road risk was greater than 80 (20% of possible population score). This helped to prevent false inflation of the road risk metrics for low road susceptible species.

Because all members of the genus *Batrachoseps* (slender salamanders) are similar in body size, range size and general life history characteristics, we scored

**Table 5** Species-level frequency distributions and road risk rankings

| Percentile | Scores | Relative ranks |
|---|---|---|
| 81–100 | 322–710 | Very high |
| 61–80 | 213–321 | High |
| 41–60 | 63–212 | Medium |
| 21–40 | 53–62 | Low |
| 1–20 | 0–52 | Very Low |

the genus as whole with the most conservative estimates and conservation status but included all 20 species in the final count and calculations.

Once all 166 species (including subspecies with conservation status) were scored for species-level road risk within both terrestrial and aquatic habitats, we took the maximum score for each species and sorted them from the highest to lowest scores. We grouped species into categories of risk (Very high, high, medium, low, and very low) based upon ranges of values that represented frequency distributions in 20% increments of all species scores (Table 5, Fig. 2).

As a way to support the results of our ranking model with species literature, we focused on special status species. We reviewed recovery plans and 5-year reviews for federally listed species and state species accounts for California listed species and species of special concern (collectively referred to as special status species). For each rank group (i.e., "very low" to "very high"), we calculated the percentage of special status species where roads were specifically listed as a threat. Similarly, we tallied the number of species identified in a recent California preliminary road risk assessment (Levine 2013, Amy Golden pers. comm.) and compared the number of species that fell within each of our road risk categories.

## Results

All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species were ranked as high or very high risk from negative road impacts. (Table 6, Fig. 3).

Review of species accounts, recovery plans, and 5-year reviews for all special status species showed

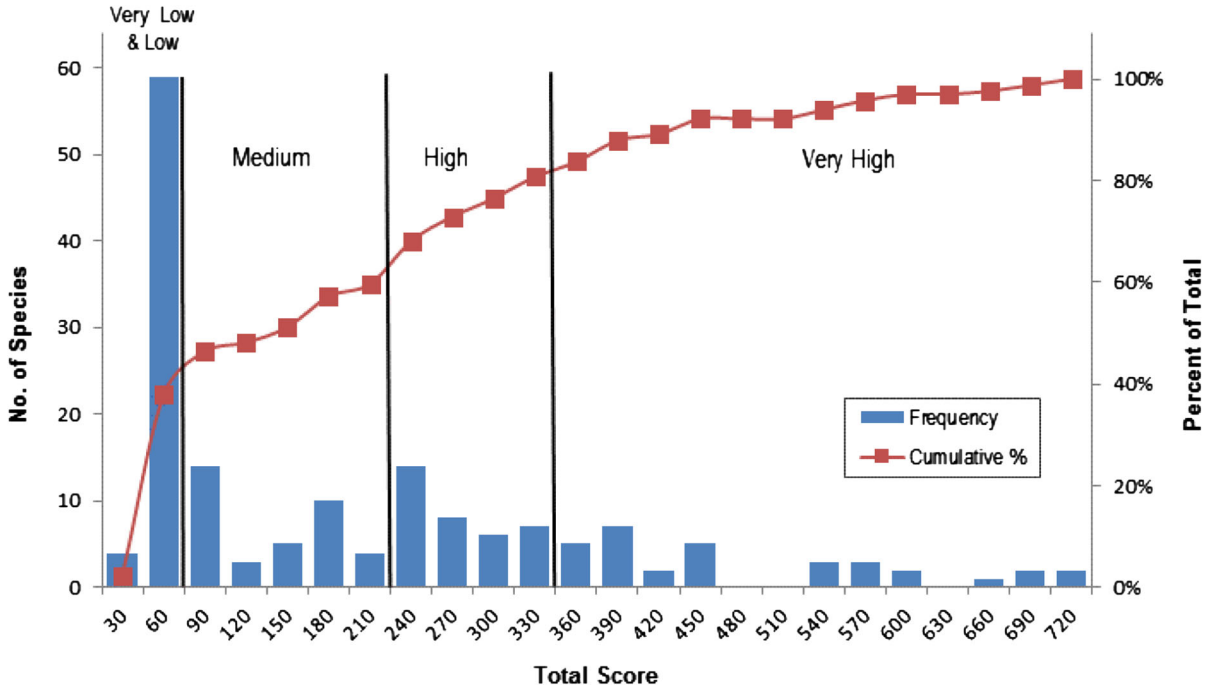


**Fig. 2** Histogram of species-level scores and approximate 20 percentile road risk categories

**Table 6** Numbers of species by taxa within each risk category

| Species group | Species-level rankings | | | | |
|---|---|---|---|---|---|
| | Very high | High | Med | Low | Very low |
| Salamander | 4 | 4 | 3 | 26 | 9 |
| Lizard | 5 | 3 | 8 | 7 | 21 |
| Anuran | 5 | 6 | 6 | 4 | 1 |
| Snake | 15 | 21 | 13 | 0 | 1 |
| Tortoise | 1 | 0 | 0 | 0 | 0 |
| Turtle | 3 | 0 | 0 | 0 | 0 |

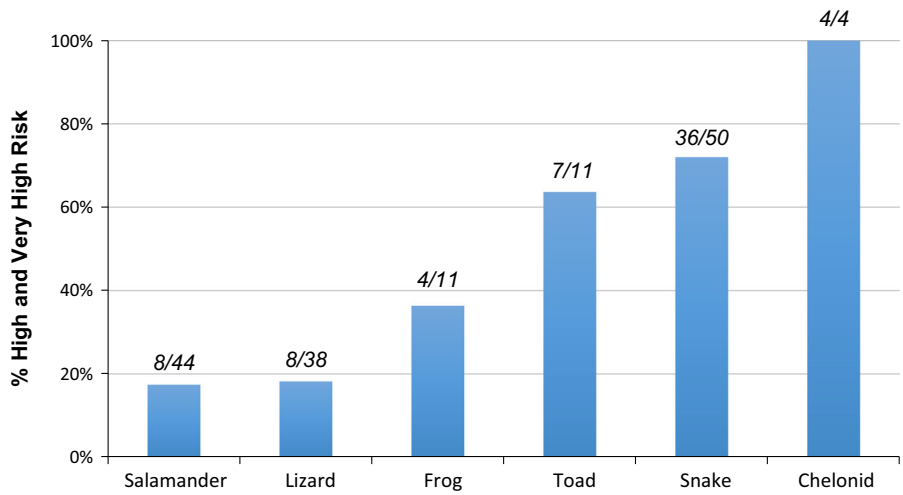


**Fig. 3** Percentages of species by taxa in high and very high road risk categories

that 94% (17/18) of species accounts that referenced roads as a threat to the species were ranked as "high" or "very high" in our risk assessment (Table 7). Of the special status species that ranked 'high' and 'very high', close to fifty percent (17/35) had road-related threats referenced in their listing literature. In comparison, only 4% (1/27) of 'medium' to 'very low' risk special status species accounts mentioned roads as a potential threat. In addition, 79% (15/19) of species of concern recommended in a recent Caltrans preliminary road risk assessment scored as 'high' or 'very high' risk in our analysis (Levine 2013, Amy Golden pers. comm.).

**Table 7** Comparison of road risk results and number of special status species with roads listed as threat

| Road risk level | Special status species | | | Caltrans PI[a] |
|---|---|---|---|---|
| | No. species in road risk level | No. species with roads listed as threat | % of Total | No. Spp in road risk level |
| Very high | 25 | 14 | 56 | 11 |
| High | 11 | 3 | 27 | 4 |
| Medium | 5 | 1 | 20 | 3 |
| Low | 10 | 0 | 0 | 1 |
| Very low | 7 | 0 | 0 | 0 |

[a]Caltrans PI are Caltrans identified sensitive species

**Table 8** Amphibian and reptile road risk assessment: very high risk species (80–100% percentile), high risk species (60–80% percentile), medium risk species (40–60% percentile range), low risk species (20–40% percentile) and very low risk species (0–20% percentile)

| | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| Risk Level-Species | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| Very High | Snake | Giant Gartersnake | *Thamnophis gigas* | 710 | 44 | 710 | THR | Yes | Yes |
| | Turtle | Southern Western Pond Turtle | *Actinemys pallida* | 707 | 283 | 707 | 1 | | Yes |
| | Snake | San Joaquin Coachwhip | *Masticophis flagellum ruddocki* | 689 | 689 | - | 2 | Yes | |
| | Snake | San Francisco Gartersnake | *Thamnophis sirtalis tetrataenia* | 663 | 238 | 663 | END | | Yes |
| | Snake | Alameda Striped Racer | *Masticophis lateralis euryxanthus* | 652 | 652 | - | THR | Yes | |
| | Snake | California Red-sided Gartersnake | *Thamnophis sirtalis infernalis* | 588 | 211 | 588 | 1 | | |
| | Tortoise | Mohave Desert Tortoise | *Gopherus agassizii* | 580 | 580 | - | THR | Yes | Yes |
| | Salamander | Red-bellied Newt | *Taricha rivularis* | 561 | 561 | 72 | 2 | Yes | Yes |
| | Turtle | Northern Western Pond Turtle | *Actinemys marmorata* | 547 | 219 | 547 | 3 | | Yes |
| | Snake | Two-striped Gartersnake | *Thamnophis hammondii* | 541 | 195 | 541 | 2 | | |
| | Snake | Baja California Coachwhip | *Masticophis fuliginosus* | 534 | 534 | - | 3 | Yes | |
| | Snake | Coast Patch-nosed Snake | *Salvadora hexalepis virgultea* | 533 | 533 | - | 2 | Yes | |
| | Salamander | California Newt | *Taricha torosa* | 532 | 532 | 72 | 2 | Yes | Yes |
| | Lizard | Banded Gila Monster | *Heloderma suspectum cinctum* | 446 | 446 | - | | | |
| | Salamander | California Tiger Salamander | *Ambystoma californiense* | 437 | 437 | - | THR | Yes | Yes |
| | Salamander | Sierra Newt | *Taricha sierrae* | 437 | 437 | 72 | | | |
| | Snake | Striped Whipsnake | *Masticophis taeniatus* | 425 | 425 | - | | | |
| | Lizard | Flat-tail Horned Lizard | *Phrynosoma mcallii* | 425 | 425 | - | 2 | Yes | |
| | Turtle | Sonoran Mud Turtle | *Kinosternon sonoriense* | 399 | 37 | 399 | 1 | | |
| | Lizard | Blunt-nosed Leopard Lizard | *Gambelia sila* | 393 | 393 | - | END | Yes | Yes |
| | Snake | Baja California Ratsnake | *Bogertophis rosaliae* | 387 | 387 | - | | | |
| | Snake | Panamint Rattlesnake | *Crotalus stephensi* | 387 | 387 | - | | | |
| | Frog | California Red-legged Frog | *Rana draytonii* | 380 | 380 | 300 | THR | Yes | Yes |
| | Toad | Yosemite Toad | *Anaxyrus canorus* | 379 | 379 | 284 | THR | Yes | |
| | Toad | Black Toad | *Anaxyrus exsul* | 379 | 379 | 284 | THR | | |
| | Lizard | Cope's Leopard Lizard | *Gambelia copeii* | 372 | 372 | - | 2 | | |
| | Toad | Sonoran Desert Toad | *Incilius alvarius (Possibly extinct in CA)* | 361 | 361 | 285 | 1 | | |
| | Lizard | Desert Horned Lizard | *Phrynosoma platyrhinos* | 356 | 356 | - | | | |
| | Snake | California Glossy Snake | *Arizona elegans occidentalis* | 340 | 340 | - | 1 | | |
| | Snake | North American Racer | *Coluber constrictor* | 334 | 334 | - | | | |
| | Snake | Coachwhip | *Masticophis flagellum* | 333 | 333 | - | | | |
| | Toad | Arroyo Toad | *Anaxyrus californicus* | 331 | 331 | 248 | END | Yes | Yes |
| | Snake | Striped Racer | *Masticophis lateralis* | 322 | 322 | - | | | |

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

Risk scores and relative rankings for California reptile and amphibian species in both terrestrial and aquatic habitats are presented in Tables 8. Terrestrial and Aquatic rankings are provided separately in Tables 9 and 10 and also include population-level risk scores, 95% population buffer distances, confidence levels, and identification of any surrogate species used for the distance calculations. Species scores for all ranking criteria and life history and movement references are provided in Appendices 1 and 2.

## Discussion

To our knowledge, this is the first attempt to objectively assess the relative risk of roads at a species level using a logical and scientifically based framework and apply it across a large array of species and habitats. We believe this approach could be useful for assessing and comparing susceptibility of species to negative road impacts within and among all taxonomic groups. To date, such risk assessments have been based largely upon expert opinion, limited information available on

**Table 8** continued

| | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| Risk Level-Species | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| High | Snake | Red Diamond Rattlesnake | *Crotalus ruber* | 321 | 321 | - | 3 | Yes | |
| | Snake | Speckled Rattlesnake | *Crotalus mitchellii* | 317 | 317 | - | | | |
| | Frog | Oregon Spotted Frog | *Rana pretiosa (Possibly extinct in CA)* | 315 | 41 | 315 | THR | | |
| | Salamander | Santa Cruz Long-toed Salamander | *Ambystoma macrodactylum croceum* | 308 | 308 | - | END | Yes | Yes |
| | Salamander | Rough-skinned Newt | *Taricha granulosa* | 304 | 304 | 72 | | | |
| | Snake | Sierra Gartersnake | *Thamnophis couchii* | 304 | 44 | 304 | | | |
| | Snake | Regal Ring-necked Snake | *Diadophis punctatus regalis* | 298 | 298 | - | 2 | | Yes |
| | Snake | California Lyresnake | *Trimorphodon lyrophanes* | 293 | 293 | - | | | |
| | Frog | Northern Red-legged Frog | *Rana aurora* | 291 | 291 | 230 | 2 | | Yes |
| | Snake | Mojave Rattlesnake | *Crotalus scutulatus* | 276 | 276 | - | | | |
| | Snake | Western Patch-nosed Snake | *Salvadora hexalepis* | 276 | 276 | - | | | |
| | Snake | Common Gartersnake | *Thamnophis sirtalis* | 271 | 165 | 271 | | | |
| | Snake | Aquatic Gartersnake | *Thamnophis atratus* | 266 | 40 | 266 | 0 | | |
| | Snake | Sidewinder | *Crotalus cerastes* | 263 | 263 | - | | | |
| | Salamander | California Giant Salamander | *Dicamptodon ensatus* | 260 | 260 | 72 | 3 | Yes | |
| | Snake | Sonoran Lyresnake | *Trimorphodon lambda* | 260 | 260 | - | | | |
| | Snake | Western Rattlesnake | *Crotalus oreganus* | 250 | 250 | - | | | |
| | Snake | Northwestern Gartersnake | *Thamnophis ordinoides* | 245 | 138 | 245 | | | |
| | Snake | Desert Nightsnake | *Hypsiglena chlorophaea* | 241 | 241 | - | | | |
| | Snake | Western Terrestrial Gartersnake | *Thamnophis elegans* | 240 | 75 | 240 | | | |
| | Lizard | Switak's Banded Gecko | *Coleonyx switaki* | 236 | 236 | - | THR | | |
| | Toad | Western Spadefoot | *Spea hammondii* | 234 | 234 | - | 1 | | Yes |
| | Snake | Coast Nightsnake | *Hypsiglena ochrorhyncha* | 233 | 233 | - | | | |
| | Lizard | Long-nosed Leopard Lizard | *Gambelia wislizenii* | 226 | 226 | - | | | |
| | Toad | Great Plains Toad | *Anaxyrus cognatus* | 222 | 222 | 175 | | | |
| | Toad | Woodhouse's Toad | *Anaxyrus woodhousii* | 222 | 222 | 175 | | | |
| | Lizard | Coastal Whiptail | *Aspidoscelis tigris stejnegeri* | 219 | 219 | - | 2 | | |
| | Snake | Western Shovel-nosed Snake | *Chionactis occipitalis* | 218 | 218 | - | | | |
| | Snake | Spotted Leaf-nosed Snake | *Phyllorhynchus decurtatus* | 218 | 218 | - | | | |
| | Salamander | Southern Long-toed Salamander | *Ambystoma macrodactylum sigillatum* | 217 | 217 | - | 2 | | |
| | Frog | Cascades Frog | *Rana cascadae* | 217 | 217 | 72 | 2 | | |
| | Snake | Western Diamond-backed Rattlesnake | *Crotalus atrox* | 214 | 214 | - | | | |
| | Snake | Western Groundsnake | *Sonora semiannulata* | 212 | 212 | - | | | |

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking
[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species
[d] California Amphibian and Reptile Crossing Preliminary Investigation

road mortality, and even less information available on population or species-level road effects (Levine 2013; Rytwinski and Fahrig 2015).

Overall, this is meant to be a first step in highlighting reptile and amphibian species that may be at highest risk from roads transecting their habitat. These species may deserve consideration for further study and for implementing mitigation solutions to reduce mortality and to maintain or enhance connectivity. The risk assessment was done for both terrestrial and aquatic habitats to further inform mitigation. Some aquatic species may greatly benefit from fish passages while others may better benefit from terrestrial barriers and wildlife crossings or both.

Although data are currently lacking to validate completely the scoring and results of the risk assessment, our review of species accounts, recovery plans, 5-year reviews for federal and state-listed species and California species of special concern show a strong association between elevated road risk from our

**Table 8** continued

| | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| Risk Level-Species | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| Medium | Snake | Checkered Gartersnake | *Thamnophis marcianus* | 210 | 69 | 210 | | | |
| | Lizard | Blainville's Horned Lizard | *Phrynosoma blainvillii* | 209 | 209 | - | 2 | | Yes |
| | Frog | Foothill Yellow-legged Frog | *Rana boylii* | 199 | 26 | 199 | 1 | | |
| | Snake | Gopher Snake | *Pituophis catenifer* | 189 | 189 | - | | | |
| | Snake | California Mountain Kingsnake | *Lampropeltis zonata* | 184 | 184 | - | | | Yes |
| | Snake | Glossy Snake | *Arizona elegans* | 180 | 180 | - | | | |
| | Lizard | Pygmy Short-horned Lizard | *Phrynosoma douglasii* | 179 | 179 | - | | | |
| | Toad | Couch's Spadefoot | *Scaphiopus couchii* | 178 | 178 | - | 3 | | |
| | Snake | California Kingsnake | *Lampropeltis californiae* | 175 | 175 | - | | | |
| | Snake | Long-nosed Snake | *Rhinocheilus lecontei* | 165 | 165 | - | | | |
| | Toad | Western Toad | *Anaxyrus boreas* | 165 | 165 | 130 | | | |
| | Snake | Ring-necked Snake | *Diadophis punctatus* | 164 | 164 | - | | | Yes |
| | Lizard | San Diego Banded Gecko | *Coleonyx variegatus abbotti* | 158 | 158 | - | 3 | Yes | |
| | Salamander | Northwestern Salamander | *Ambystoma gracile* | 152 | 152 | - | | | |
| | Toad | Great Basin Spadefoot | *Spea intermontana* | 152 | 152 | - | | | |
| | Toad | Red-spotted Toad | *Anaxyrus punctatus* | 147 | 147 | 72 | | | |
| | Salamander | Long-toed Salamander | *Ambystoma macrodactylum* | 143 | 143 | - | | | |
| | Lizard | Orange-throated Whiptail | *Aspidoscelis hyperythra* | 137 | 137 | - | | | |
| | Snake | Smith's Black-headed Snake | *Tantilla hobartsmithi* | 136 | 136 | - | | | |
| | Snake | California Black-headed Snake | *Tantilla planiceps* | 133 | 133 | - | | | |
| | Lizard | Western Whiptail | *Aspidoscelis tigris* | 118 | 118 | - | | | |
| | Salamander | Coastal Giant Salamander | *Dicamptodon tenebrosus* | 117 | 117 | 48 | | | |
| | Lizard | Western Banded Gecko | *Coleonyx variegatus* | 105 | 105 | - | | | |
| | Lizard | Common Chuckwalla | *Sauromalus ater* | 78 | 78 | - | | | |
| | Snake | Northern Rubber Boa | *Charina bottae* | 77 | 77 | - | | | |
| | Snake | Southern Rubber Boa | *Charina umbratica* | 77 | 77 | - | THR | | |
| | Snake | Northern Three-lined Boa | *Lichanura orcutti* | 77 | 77 | - | | | |
| | Lizard | Desert Iguana | *Dipsosaurus dorsalis* | 72 | 72 | - | | | |
| | Snake | Forest Sharp-tailed Snake | *Contia longicauda* | 70 | 70 | - | | | |
| | Snake | Common Sharp-tailed Snake | *Contia tenuis* | 70 | 70 | - | | | |
| | Frog | Pacific Treefrog | *Pseudacris regilla* | 68 | 68 | 36 | | | |

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

objective analysis and the probability that roads are listed as a potential threat to the species in the species listing literature.

Although more than 40% of special status species are semi-aquatic, roads were rarely considered a threat to aquatic connectivity in the species literature. This may be accurate if bridges or large culverts currently exist for water flow that also provide permeability to aquatic movement. Bridges are generally considered to be completely passable by all aquatic species. Bridges are more likely to be constructed adjacent to or over large water bodies and rivers, presumably resulting in less risk to aquatic movement of populations that inhabit lake and river systems. However, culverts that are more commonly constructed under roads in streams and wetlands vary in passability depending on factors such as diameter, length, slope, outlet configuration, and other characteristics (Furniss et al. 1991; Clarkin et al. 2005; Kemp and O'Hanley 2010). In fact, Januchowski-Hartley et al. (2013) found that only 36% of road crossings were fully passable to fish in the Great Lakes basin. In addition, many low water crossings in arid regions of the state are simply a dip in the road that allows water to flow

**Table 8** continued

| | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| Risk Level-Species | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| Low | Salamander | Scott Bar Salamander | *Plethodon asupak* | **62** | 62 | - | THR | | |
| | Salamander | Dunn's Salamander | *Plethodon dunni* | **62** | 62 | - | | | |
| | Salamander | Del Norte Salamander | *Plethodon elongatus* | **62** | 62 | - | | | |
| | Salamander | Siskiyou Mountains Salamander | *Plethodon stormi* | **62** | 62 | - | THR | | |
| | Frog | California Treefrog | *Pseudacris cadaverina* | **61** | 61 | 26 | | | |
| | Salamander | Southern Torrent Salamander | *Rhyacotriton variegatus* | **61** | 61 | 5 | 1 | | |
| | Lizard | Peninsula Leaf-toed Gecko | *Phyllodactylus nocticolus* | **60** | 60 | - | | | |
| | Lizard | Northern Alligator Lizard | *Elgaria coerulea* | **60** | 60 | - | | | |
| | Frog | Coastal Tailed Frog | *Ascaphus truei* | **59** | 59 | 30 | 2 | | Yes |
| | Lizard | Common Side-blotched Lizard | *Uta stansburiana* | **59** | 59 | - | | | |
| | Lizard | Coachella Fringe-toed Lizard | *Uma inornata* | **56** | 56 | - | THR | | |
| | Lizard | Colorado Desert Fringe-toed Lizard | *Uma notata* | **56** | 56 | - | 2 | | |
| | Lizard | Mohave Fringe-toed Lizard | *Uma scoparia* | **56** | 56 | - | 3 | | |
| | Frog | Lowland Leopard Frog | *Lithobates yavapaiensis (Possibly extinct in CA)* | **54** | 31 | 54 | 1 | | |
| | Frog | Southern Mountain Yellow-legged Frog | *Rana muscosa* | **54** | 26 | 54 | END | | |
| | Lizard | Zebra-tailed Lizard | *Callisaurus draconoides* | **54** | 54 | - | | | |
| | Salamander | Wandering Salamander | *Aneides vagrans* | **53** | 53 | - | | | |
| | Salamander | Slender Salamanders | *Batrachoseps (genus: 20 spp.)* | **53** | 53 | - | END[e] | | |
| Very Low | Salamander | Ensatina | *Ensatina eschscholtzii* | **51** | 51 | - | | | |
| | Salamander | Yellow-blotched Ensatina | *Ensatina eschscholtzii croceater* | **51** | 51 | - | | | |
| | Salamander | Large-blotched Ensatina | *Ensatina eschscholtzii klauberi* | **51** | 51 | - | | | |
| | Lizard | Southern Alligator Lizard | *Elgaria multicarinata* | **51** | 51 | - | | | |
| | Lizard | Panamint Alligator Lizard | *Elgaria panamintina* | **51** | 51 | - | 3 | | |
| | Frog | Sierra Nevada Yellow-legged Frog | *Rana sierrae* | **51** | 51 | 36 | THR | | |
| | Lizard | Western Fence Lizard | *Sceloporus occidentalis* | **49** | 49 | - | | | |
| | Salamander | Limestone Salamander | *Hydromantes brunus* | **48** | 48 | - | THR | | |
| | Salamander | Mount Lyell Salamander | *Hydromantes platycephalus* | **48** | 48 | - | | | |
| | Salamander | Clouded Salamander | *Aneides ferreus* | **44** | 44 | - | | | |
| | Salamander | Arboreal Salamander | *Aneides lugubris* | **44** | 44 | - | | | |
| | Lizard | Granite Spiny Lizard | *Sceloporus orcutti* | **43** | 43 | - | | | |
| | Snake | Western Blind Snake | *Rena humilis* | **42** | 42 | - | | | |
| | Lizard | Desert Spiny Lizard | *Sceloporus magister* | **41** | 41 | - | | | |
| | Lizard | Common Sagebrush Lizard | *Sceloporus graciosus* | **39** | 41 | - | | | |
| | Lizard | Gilbert's Skink | *Plestiodon gilberti* | **39** | 39 | - | | | |
| | Lizard | Western Skink | *Plestiodon skiltonianus* | **39** | 39 | - | | | |
| | Lizard | California Legless Lizard | *Anniella pulchra* | **35** | 39 | - | 2 | | |
| | Salamander | Black Salamander | *Aneides flavipunctatus* | **35** | 35 | - | | | |
| | Salamander | Santa Cruz Black Salamander | *Aneides flavipunctatus niger* | **35** | 35 | - | | | |
| | Lizard | Baja California Collared Lizard | *Crotaphytus vestigium* | **35** | 35 | - | | | |
| | Lizard | Sandstone Night Lizard | *Xantusia gracilis* | **33** | 33 | - | 3 | | |
| | Lizard | Granite Night Lizard | *Xantusia henshawi* | **33** | 33 | - | | | |
| | Lizard | Island Night Lizard | *Xantusia riversiana* | **33** | 33 | - | THR | | |
| | Lizard | Sierra Night Lizard | *Xantusia sierrae* | **33** | 33 | - | 1 | | |
| | Lizard | Desert Night Lizard | *Xantusia vigilis* | **33** | 33 | - | | | |
| | Lizard | Wiggins' Night Lizard | *Xantusia wigginsi* | **33** | 33 | - | | | |
| | Lizard | Long-tailed Brush Lizard | *Urosaurus graciosus* | **27** | 27 | - | | | |
| | Lizard | Baja California Brush Lizard | *Urosaurus nigricaudus* | **27** | 27 | - | | | |
| | Lizard | Ornate Tree Lizard | *Urosaurus ornatus* | **27** | 27 | - | | | |
| | Lizard | Mearns' Rock Lizard | *Petrosaurus mearnsi* | **21** | 21 | - | | | |

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking
[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species
[d] California Amphibian and Reptile Crossing Preliminary Investigation
[e] 4 Batrachoseps species with conservation status

**Table 9** Terrestrial risk ranking and population buffer distances

| Risk Level (Terrestrial) | | Species | | | Risk Scores (Terrestrial) | | Movement Distances (Terrestrial) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Very High | Very High | Snake | San Joaquin Coachwhip | *Masticophis flagellum ruddocki* | 689 | 285 | 1618 | High | *M. fulginosus* |
| | Very High | Snake | Alameda Striped Racer | *Masticophis lateralis euryxanthus* | 652 | 221 | 631 | Med/High | |
| | Very High | Tortoise | Mohave Desert Tortoise | *Gopherus agassizii* | 580 | 240 | 1155 | High | |
| | Very High | Salamander | Red-bellied Newt | *Taricha rivularis* | 561 | 228 | 1600 | High | |
| | Very High | Snake | Baja California Coachwhip | *Masticophis fuliginosus* | 534 | 285 | 1904 | High | |
| | Very High | Snake | Coast Patch-nosed Snake | *Salvadora hexalepis virgultea* | 533 | 221 | 631 | Low | *M. lateralis* |
| | Very High | Salamander | California Newt | *Taricha torosa* | 532 | 228 | 2500 | Med/High | |
| | Very High | Lizard | Banded Gila Monster | *Heloderma suspectum cinctum* | 446 | 210 | 1250 | High | |
| | High | Salamander | California Tiger Salamander | *Ambystoma californiense* | 437 | 152 | 1849 | Med/High | |
| | Very High | Salamander | Sierra Newt | *Taricha sierrae* | 437 | 228 | 2050 | Med | *T. torosa, T. rivularis* |
| | Very High | Snake | Striped Whipsnake | *Masticophis taeniatus* | 425 | 300 | 2380 | Med | |
| | Very High | Lizard | Flat-tail Horned Lizard | *Phrynosoma mcallii* | 425 | 217 | 788 | Med/High | |
| | High | Lizard | Blunt-nosed Leopard Lizard | *Gambelia sila* | 393 | 133 | 510 | High | |
| | Very High | Snake | Baja California Ratsnake | *Bogertophis rosaliae* | 387 | 238 | 780 | Low | *Elaphe obsoleta* |
| | Very High | Snake | Panamint Rattlesnake | *Crotalus stephensi* | 387 | 238 | 938 | Med | *C. mitchelli* |
| | High | Frog | California Red-legged Frog | *Rana draytonii* | 380 | 152 | 2360 | High | |
| | High | Toad | Yosemite Toad | *Anaxyrus canorus* | 379 | 128 | 1152 | Med/High | |
| | High | Toad | Black Toad | *Anaxyrus exsul* | 379 | 128 | 951 | Low | *A. canorus, A. punctatus* |
| | High | Lizard | Cope's Leopard Lizard | *Gambelia copeii* | 372 | 175 | 643 | Low/Med | *G. wislenzii* |
| | High | Toad | Sonoran Desert Toad | *Incilius alvarius (Possibly extinct in CA)* | 361 | 152 | 1400 | Low/Med | *A. cognatus* |
| | Very High | Lizard | Desert Horned Lizard | *Phrynosoma platyrhinos* | 356 | 259 | 1308 | Med/High | |
| | High | Snake | California Glossy Snake | *Arizona elegans occidentalis* | 340 | 154 | 316 | Low | *R. lecontii* |
| | Very High | Snake | North American Racer | *Coluber constrictor* | 334 | 308 | 1800 | Med | |
| | Very High | Snake | Coachwhip | *Masticophis flagellum* | 333 | 285 | 1618 | High | *M. fulginosus* |
| | High | Toad | Arroyo Toad | *Anaxyrus californicus* | 331 | 128 | 1082 | Med/High | |
| | Very High | Snake | Striped Racer | *Masticophis lateralis* | 322 | 221 | 631 | Med | |
| High | High | Snake | Red Diamond Rattlesnake | *Crotalus ruber* | 321 | 175 | 853 | High | |
| | Very High | Snake | Speckled Rattlesnake | *Crotalus mitchellii* | 317 | 238 | 938 | High | |
| | Med | Salamander | Santa Cruz Long-toed Salamander | *Ambystoma macrodactylum croceum* | 308 | 104 | 700 | High | |
| | Very High | Salamander | Rough-skinned Newt | *Taricha granulosa* | 304 | 228 | 2050 | Med | *T. torosa, T. rivularis* |
| | High | Snake | Regal Ring-necked Snake | *Diadophis punctatus regalis* | 298 | 152 | 566 | Low/Med | |
| | Very High | Snake | California Lyresnake | *Trimorphodon lyrophanes* | 293 | 195 | 800 | Low | |
| | High | Frog | Northern Red-legged Frog | *Rana aurora* | 291 | 152 | 2360 | Med | *R. draytonii* |
| | High | Turtle | Southern Western Pond Turtle | *Actinemys pallida* | 283 | 128 | 309 | Med-High | |
| | High | Snake | Mojave Rattlesnake | *Crotalus scutulatus* | 276 | 189 | 815 | Med/High | |
| | Very High | Snake | Western Patch-nosed Snake | *Salvadora hexalepis* | 276 | 221 | 631 | Low | *M. lateralis* |
| | High | Snake | Sidewinder | *Crotalus cerastes* | 263 | 186 | 767 | High | |
| | Med | Salamander | California Giant Salamander | *Dicamptodon ensatus* | 260 | 120 | 600 | Low | *D. tenebrosus* |
| | Very High | Snake | Sonoran Lyresnake | *Trimorphodon lambda* | 260 | 195 | 800 | Low | |
| | Very High | Snake | Western Rattlesnake | *Crotalus oreganus* | 250 | 231 | 1096 | Med/High | |
| | High | Snake | Desert Nightsnake | *Hypsiglena chlorophaea* | 241 | 175 | 566 | Low | *D. punctatus* |
| | Med | Snake | San Francisco Gartersnake | *Thamnophis sirtalis tetrataenia* | 238 | 81 | 300 | Med | |
| | Med | Lizard | Switak's Banded Gecko | *Coleonyx switaki* | 236 | 90 | 200 | Low | *C. variegatus (AZ)* |
| | Med | Toad | Western Spadefoot | *Spea hammondii* | 234 | 104 | 670 | Med | |
| | High | Snake | Coast Nightsnake | *Hypsiglena ochrorhyncha* | 233 | 175 | 566 | Low | *D. punctatus* |
| | High | Lizard | Long-nosed Leopard Lizard | *Gambelia wislizenii* | 226 | 175 | 643 | Med/High | |
| | High | Toad | Great Plains Toad | *Anaxyrus cognatus* | 222 | 152 | 1400 | Med/High | |
| | High | Toad | Woodhouse's Toad | *Anaxyrus woodhousii* | 222 | 152 | 1400 | Low | *A. cognatus* |
| | Med | Lizard | Coastal Whiptail | *Aspidoscelis tigris stejnegeri* | 219 | 105 | 300 | Low | *A. hyperythra (multiplied by 2 for body size)* |
| | High | Turtle | Northern Western Pond Turtle | *Actinemys marmorata* | 219 | 128 | 448 | Med | |
| | High | Snake | Western Shovel-nosed Snake | *Chionactis occipitalis* | 218 | 154 | 400 | Low | |
| | High | Snake | Spotted Leaf-nosed Snake | *Phyllorhynchus decurtatus* | 218 | 154 | 400 | Low | *C. occipitalis, M. taeniatus* |
| | Med | Salamander | Southern Long-toed Salamander | *Ambystoma macrodactylum sigillatum* | 217 | 104 | 700 | Med | |
| | Med | Frog | Cascades Frog | *Rana cascadae* | 217 | 104 | 759 | High | |
| | High | Snake | Western Diamond-backed Rattlesnake | *Crotalus atrox* | 214 | 147 | 484 | Med | |
| | High | Snake | Western Groundsnake | *Sonora semiannulata* | 212 | 154 | 400 | Low | *C. occipitalis* |
| | Med | Snake | California Red-sided Gartersnake | *Thamnophis sirtalis infernalis* | 211 | 81 | 300 | Low/Med | *T.s. tetrataenia* |

**Table 9** continued

| Risk Level (Terrestrial) | | Species | | | Risk Scores (Terrestrial) | | Movement Distances (Terrestrial) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Medium | Med | Lizard | Blainville's Horned Lizard | *Phrynosoma blainvillii* | 209 | 114 | 495 | Med | |
| | Med | Snake | Two-striped Gartersnake | *Thamnophis hammondii* | 195 | 81 | 239 | Low/Med | |
| | High | Snake | Gopher Snake | *Pituophis catenifer* | 189 | 189 | 820 | Med/High | |
| | High | Snake | California Mountain Kingsnake | *Lampropeltis zonata* | 184 | 147 | 501 | Low/Med | *L. getula, L. triangulum* |
| | High | Snake | Glossy Snake | *Arizona elegans* | 180 | 154 | 316 | Low | *R. leconтii* |
| | Med | Lizard | Pygmy Short-horned Lizard | *Phrynosoma douglasii* | 179 | 123 | 400 | Low | *P. mccallii (reduced 0.5 for body size)* |
| | Med | Toad | Couch's Spadefoot | *Scaphiopus couchii* | 178 | 104 | 670 | Med | |
| | High | Snake | California Kingsnake | *Lampropeltis californiae* | 175 | 175 | 501 | Med/High | |
| | High | Snake | Long-nosed Snake | *Rhinocheilus lecontei* | 165 | 132 | 337 | Low/Med | |
| | High | Snake | Common Gartersnake | *Thamnophis sirtalis* | 165 | 137 | 532 | Low/Med | |
| | High | Toad | Western Toad | *Anaxyrus boreas* | 165 | 152 | 2144 | Med/High | |
| | High | Snake | Ring-necked Snake | *Diadophis punctatus* | 164 | 136 | 566 | Low/Med | |
| | Med | Lizard | San Diego Banded Gecko | *Coleonyx variegatus abbotti* | 158 | 84 | 200 | Low/Med | *C. variegatus (AZ)* |
| | Med | Salamander | Northwestern Salamander | *Ambystoma gracile* | 152 | 104 | 700 | Low | *A. macrodactylum croceum* |
| | Med | Toad | Great Basin Spadefoot | *Spea intermontana* | 152 | 104 | 670 | Med | |
| | Med | Toad | Red-spotted Toad | *Anaxyrus punctatus* | 147 | 104 | 750 | Low | |
| | Med | Salamander | Long-toed Salamander | *Ambystoma macrodactylum* | 143 | 104 | 700 | Med | |
| | Med | Snake | Northwestern Gartersnake | *Thamnophis ordinoides* | 138 | 95 | 239 | Low | *T. hammondii* |
| | Med | Lizard | Orange-throated Whiptail | *Aspidoscelis hyperythra* | 137 | 84 | 150 | Low/Med | |
| | Med | Snake | Smith's Black-headed Snake | *Tantilla hobartsmithi* | 136 | 105 | 150 | Low | |
| | Med | Snake | California Black-headed Snake | *Tantilla planiceps* | 133 | 84 | 150 | Low | |
| | Med | Lizard | Western Whiptail | *Aspidoscelis tigris* | 118 | 105 | 300 | Low | *A. hyperythra (multiplied by 2 for body size)* |
| | Med | Salamander | Coastal Giant Salamander | *Dicamptodon tenebrosus* | 117 | 80 | 600 | Low/Med | |
| | Med | Lizard | Western Banded Gecko | *Coleonyx variegatus* | 105 | 84 | 200 | Low/Med | *C. variegatus (AZ)* |
| | Med | Lizard | Common Chuckwalla | *Sauromalus ater* | 78 | 78 | 296 | Med | |
| | Med | Snake | Northern Rubber Boa | *Charina bottae* | 77 | 77 | 230 | Low/Med | *L. trivirgata* |
| | Med | Snake | Southern Rubber Boa | *Charina umbratica* | 77 | 77 | 230 | Low/Med | *L. trivirgata* |
| | Med | Snake | Northern Three-lined Boa | *Lichanura orcutti* | 77 | 77 | 230 | Med/High | |
| | Med | Snake | Western Terrestrial Gartersnake | *Thamnophis elegans* | 75 | 75 | 104 | Low/Med | *T.gigas (-40% for size diff)* |
| | Med | Lizard | Desert Iguana | *Dipsosaurus dorsalis* | 72 | 72 | 150 | Low/Med | |
| | Med | Snake | Forest Sharp-tailed Snake | *Contia longicauda* | 70 | 70 | 150 | Low | |
| | Med | Snake | Common Sharp-tailed Snake | *Contia tenuis* | 70 | 70 | 150 | Low | |
| | Med | Snake | Checkered Gartersnake | *Thamnophis marcianus* | 69 | 69 | 239 | Low | *T. hammondii* |
| | Med | Frog | Pacific Treefrog | *Pseudacris regilla* | 68 | 68 | 400 | Low/Med | |
| Low | Low | Salamander | Scott Bar Salamander | *Plethodon asupak* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Salamander | Dunn's Salamander | *Plethodon dunni* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Salamander | Del Norte Salamander | *Plethodon elongatus* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Salamander | Siskiyou Mountains Salamander | *Plethodon stormi* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Frog | California Treefrog | *Pseudacris cadaverina* | 61 | 61 | 50 | Low/Med | |
| | Low | Salamander | Southern Torrent Salamander | *Rhyacotriton variegatus* | 61 | 61 | 50 | Low | *R. cascadae* |
| | Low | Lizard | Peninsula Leaf-toed Gecko | *Phyllodactylus nocticolus* | 60 | 60 | 200 | Low | *C. variegatus (AZ)* |
| | Low | Lizard | Northern Alligator Lizard | *Elgaria coerulea* | 60 | 60 | 106 | Med | |
| | Low | Frog | Coastal Tailed Frog | *Ascaphus truei* | 59 | 59 | 150 | Med/High | |
| | Low | Lizard | Common Side-blotched Lizard | *Uta stansburiana* | 59 | 59 | 152 | Med/High | |
| | Low | Lizard | Coachella Fringe-toed Lizard | *Uma inornata* | 56 | 56 | 52 | Med/High | |
| | Low | Lizard | Colorado Desert Fringe-toed Lizard | *Uma notata* | 56 | 56 | 75 | Med/High | |
| | Low | Lizard | Mohave Fringe-toed Lizard | *Uma scoparia* | 56 | 56 | 64 | Med | *U. notata, U. inornata* |
| | Low | Lizard | Zebra-tailed Lizard | *Callisaurus draconoides* | 54 | 54 | 150 | Med | |
| | Low | Salamander | Wandering Salamander | *Aneides vagrans* | 53 | 53 | 39 | Med/High | |
| | Low | Salamander | Slender Salamanders (20 species) | *Batrachoseps (genus)* | 53 | 53 | 50 | Low/Med | *B. pacificus* |

**Table 9** continued

| Risk Level (Terrestrial) | | Species | | | Risk Scores (Terrestrial) | | Movement Distances (Terrestrial) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Very Low | Very Low | Salamander | Ensatina | *Ensatina eschscholtzii* | 51 | 51 | 75 | Med | |
| | Very Low | Salamander | Yellow-blotched Ensatina | *Ensatina eschscholtzii croceater* | 51 | 51 | 75 | Med | |
| | Very Low | Salamander | Large-blotched Ensatina | *Ensatina eschscholtzii klauberi* | 51 | 51 | 75 | Med | *E. eschscholtzii croceater* |
| | Very Low | Lizard | Southern Alligator Lizard | *Elgaria multicarinata* | 51 | 51 | 106 | Low/Med | *E. coerulea* |
| | Very Low | Lizard | Panamint Alligator Lizard | *Elgaria panamintina* | 51 | 51 | 106 | Low/Med | *E. coerulea* |
| | Very Low | Frog | Sierra Nevada Yellow-legged Frog | *Rana sierrae* | 51 | 51 | 420 | Med | |
| | Very Low | Lizard | Western Fence Lizard | *Sceloporus occidentalis* | 49 | 49 | 160 | Med | |
| | Very Low | Salamander | Limestone Salamander | *Hydromantes brunus* | 48 | 48 | 80 | Low | |
| | Very Low | Salamander | Mount Lyell Salamander | *Hydromantes platycephalus* | 48 | 48 | 80 | Low | |
| | Very Low | Salamander | Clouded Salamander | *Aneides ferreus* | 44 | 44 | 39 | Med | *A. vagrans* |
| | Very Low | Salamander | Arboreal Salamander | *Aneides lugubris* | 44 | 44 | 39 | Med | *A. vagrans* |
| | Very Low | Snake | Giant Gartersnake | *Thamnophis gigas* | 44 | 44 | 174 | High | |
| | Very Low | Snake | Sierra Gartersnake | *Thamnophis couchii* | 44 | 44 | 115 | Low/Med | *T.gigas (-34% for size diff)* |
| | Very Low | Lizard | Granite Spiny Lizard | *Sceloporus orcutti* | 43 | 43 | 91 | Low/Med | |
| | Very Low | Snake | Western Blind Snake | *Rena humilis* | 42 | 42 | 50 | Low | |
| | Very Low | Lizard | Desert Spiny Lizard | *Sceloporus magister* | 41 | 41 | 91 | Low | |
| | Very Low | Frog | Oregon Spotted Frog | *Rana pretiosa (Possibly extinct in CA)* | 41 | 41 | 100 | Low | |
| | Very Low | Lizard | Common Sagebrush Lizard | *Sceloporus graciosus* | 41 | 41 | 41 | Med/High | |
| | Very Low | Snake | Aquatic Gartersnake | *Thamnophis atratus* | 40 | 40 | 99 | Low/Med | *T.gigas (-43% for size diff)* |
| | Very Low | Lizard | Gilbert's Skink | *Plestiodon gilberti* | 39 | 39 | 93 | Low/Med | *P. skiltonianus, P. fasciatus, S. laterale* |
| | Very Low | Lizard | Western Skink | *Plestiodon skiltonianus* | 39 | 39 | 93 | Low/Med | |
| | Very Low | Lizard | California Legless Lizard | *Anniella pulchra* | 39 | 39 | 15 | High | |
| | Very Low | Turtle | Sonoran Mud Turtle | *Kinosternon sonoriense* | 37 | 37 | 60 | Med | |
| | Very Low | Salamander | Black Salamander | *Aneides flavipunctatus* | 35 | 35 | 39 | Med | *A. vagrans* |
| | Very Low | Salamander | Santa Cruz Black Salamander | *Aneides flavipunctatus niger* | 35 | 35 | 39 | Med | *A. vagrans* |
| | Very Low | Lizard | Great Basin Collared Lizard | *Crotaphytus bicinctores* | 35 | 35 | 150 | Low/Med | *C. collaris* |
| | Very Low | Lizard | Baja California Collared Lizard | *Crotaphytus vestigium* | 35 | 35 | 150 | Low/Med | *C. collaris* |
| | Very Low | Lizard | Sandstone Night Lizard | *Xantusia gracilis* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Granite Night Lizard | *Xantusia henshawi* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Island Night Lizard | *Xantusia riversiana* | 33 | 33 | 14 | High | |
| | Very Low | Lizard | Sierra Night Lizard | *Xantusia sierrae* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Desert Night Lizard | *Xantusia vigilis* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Wiggins' Night Lizard | *Xantusia wigginsi* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Frog | Lowland Leopard Frog | *Lithobates yavapaiensis (Possibly extinct in CA)* | 31 | 31 | 100 | Low | |
| | Very Low | Lizard | Long-tailed Brush Lizard | *Urosaurus graciosus* | 27 | 27 | 130 | Low/Med | *S. occidentalis, S. graciosus* |
| | Very Low | Lizard | Baja California Brush Lizard | *Urosaurus nigricaudus* | 27 | 27 | 130 | Low/Med | *S. occidentalis, S. graciosus* |
| | Very Low | Lizard | Ornate Tree Lizard | *Urosaurus ornatus* | 27 | 27 | 130 | Low/Med | *S. occidentalis, S. graciosus* |
| | Very Low | Frog | Foothill Yellow-legged Frog | *Rana boylii* | 26 | 26 | 40 | Med/High | |
| | Very Low | Frog | Southern Mountain Yellow-legged Frog | *Rana muscosa* | 26 | 26 | 40 | Med | *R. boylii* |
| | Very Low | Lizard | Mearns' Rock Lizard | *Petrosaurus mearnsi* | 21 | 21 | 80 | Low/Med | |
| | Very Low | Lizard | Mearns' Rock Lizard | *Petrosaurus mearnsi* | 21 | 21 | 80 | Low/Med | |

over the surface during high flow events. These may be used as road crossings by species traveling along ephemeral stream corridors with or without water flow. Given these potential vulnerabilities, we believe that road impacts to aquatic connectivity of herpetofauna deserve greater consideration.

Across broad taxonomic groups, chelonids (tortoises/turtles) and snakes had the greatest percentages of species at 'high' or 'very high' risk from roads. They are similar in that many move long distances (home range and/or migratory), tend not to avoid roads (or are attracted to them for thermoregulation), are long lived, and have relatively low fecundity in comparison to other herpetofaunal groups. Because of these traits, chelonids and snakes have been identified elsewhere as being particularly susceptible to negative population effects from roads (Gibbs and Shriver 2002; Andrews et al. 2015b; Jackson et al. 2015).

There are only four species of chelonids in California, (desert tortoise (*Gopherus agazzii*),

Northwestern pond turtle (*Actinemys marmorata*), Southwestern pond turtle (*Actinemys pallida*), and the Sonoran mud turtle (*Kinosternon sonoriense*)). There has been a high level of attention to road impacts on the desert tortoise (*Gopherus agazzii*) as numerous studies have documented not only high road mortality, but measurable road effect zones, and mostly positive responses to barriers and underpasses (e.g., Boarman and Sazaki 1996, 2006; Peaden et al. 2016; but see Peadon et al. 2017). Although not listed as a primary threat to pond turtle populations in California (Thomson et al. 2016), road mortality is a major concern for western pond turtle populations in Oregon (Rosenberg et al. 2009). Pond turtles travel kilometers within perennial waters and from pool to pool in intermittent aquatic habitats to forage and find mates (Goodman and Stewart 2000). In addition, females nest and lay eggs in terrestrial habitats up to 0.5 km away from water which make roads that parallel aquatic habitat a threat to both females and hatchlings (Reese and Welsh 1997; Rathbun et al. 2002; Pilliod et al. 2013). In fact, road mortality of females has been identified as a cause for male-biased sex ratios in some populations of pond turtles and other freshwater turtle species (Steen et al. 2006; Rosenberg et al. 2009; Reid and Peery 2014). Therefore, this species requires consideration of both aquatic and terrestrial connectivity to satisfy their annual resource requirements. Sonoran mud turtles also travel long distances within intermittent streams and thus may be at risk of roads that transect their aquatic habitat (Hensley et al. 2010).

Larger colubrid snakes (Family Colubridae; many genera) and rattlesnakes (genus *Crotalus*) were ranked among the highest risk from negative road effects. In addition to being attracted to paved road surfaces for thermoregulation, many large snakes have wide home-ranges or may move large distances between winter hibernacula and summer foraging areas. In contrast to smaller species, larger snakes are also less likely to avoid roads (Rosen and Lowe 1994; Andrews and Gibbons 2005; Andrews et al. 2008; Siers et al. 2016). High road mortality (e.g., Klauber 1931; Rosen and Lowe 1994; Jones et al. 2011), reduced abundance near roads (Rudolph et al. 1999; Jones et al. 2011), increased extinction risk (Row et al. 2007), and decreased genetic diversity (Clark et al. 2010; Hermann et al. 2017) have been documented for numerous snake species; as have positive responses to barriers and underpasses (Dodd et al. 2004; Colley et al. 2017). In our statewide risk analysis, coachwhips (genus *Masticophis/Coluber*) were amongst the highest risk groups at both the population and species-levels. These are particularly wide-ranging and very active foragers in comparison to other snake genera (Stebbins and McGinnis 2012). The coachwhip (*Masticophis flagellum)* was found to be ninefold more likely to be extirpated from habitats that were fragmented by roads and urbanization, contributing to their decline throughout California (Case and Fisher 2001; Mitrovich 2006). Similarly, habitat fragmentation from roads and urbanization were identified as primary threats to the Alameda whipsnake (*Masticophis lateralis euryxanthus* USFWS 2011). Although road use and mortality have been documented for many other terrestrial California snake species on road-riding surveys (e.g., Klauber 1931; Jones et al. 2011; Shilling and Waetjen 2017), there is a paucity of studies examining population-level effects of roads on California snake species. We could find only one such study, where presence of a highway was shown to reduce gene flow in the Western diamond-backed rattlesnake (*Crotalus atrox)* in the Sonoran Desert, AZ (Hermann et al. 2017).

Long foraging movements within aquatic habitats also contributed to the majority of garter snakes (genus: *Thamnophis*) falling within the highest road risk categories. Maintaining aquatic and wetland connectivity is of primary concern for these species. Garter snakes also use terrestrial habitats for overwintering, reproduction, and for moving among wetland or aquatic patches. Some migrate long distances to winter hibernacula, making them also susceptible to roads within adjacent terrestrial habitats (Roe et al. 2006; Jackson et al. 2015). The highly aquatic giant garter snake (*Thamnophis gigas*) had the highest aquatic road risk score. Because it moves only short distances on land (Halstead et al. 2015), mitigation may best focus on functional aquatic passages with lengths of adjacent road barriers based upon their terrestrial movement distances.

Toads were the third highest ranking group with 64% ranked in the highest risk categories. In particular, Bufonid toads (family Bufonidae) may move large distances ($>$ 1 km) in both aquatic and terrestrial habitats to satisfy their annual resource requirements; thus 5 of 7 bufonid species ranked high or very high risk from roads. Consistent with our risk assessment

**Table 10** Aquatic risk ranking and population buffer distances

| Risk Level (Aquatic) | | Species | | | Risk Scores (Aquatic) | | Movement Distances (Aquatic) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Very High | Very High | Snake | Giant Gartersnake | *Thamnophis gigas* | 710 | 240 | 1556 | Med/High | |
| | Very High | Turtle | Southern Western Pond Turtle | *Actinemys pallida* | 707 | 320 | 3145 | High | |
| | Very High | Snake | San Francisco Gartersnake | *Thamnophis sirtalis tetrataenia* | 663 | 224 | 1146 | Med | *T. sirtalis* |
| | Very High | Snake | California Red-sided Gartersnake | *Thamnophis sirtalis infernalis* | 588 | 224 | 1146 | Med | *T. sirtalis* |
| | Very High | Turtle | Northern Western Pond Turtle | *Actinemys marmorata* | 547 | 320 | 3145 | High | *A. pallida* |
| | Very High | Snake | Two-striped Gartersnake | *Thamnophis hammondii* | 541 | 224 | 979 | Low | *T.gigas (-37% for size diff)* |
| | High | Turtle | Sonoran Mud Turtle | *Kinosternon sonoriense* | 399 | 168 | 1000 | Med | |
| High | Med | Frog | Oregon Spotted Frog | *Rana pretiosa (Possibly extinct in CA)* | 315 | 120 | 1300 | Low | |
| | Very High | Snake | Sierra Gartersnake | *Thamnophis couchii* | 304 | 192 | 1021 | Low | *T.gigas (-34% for size diff)* |
| | Med | Frog | California Red-legged Frog | *Rana draytonii* | 300 | 120 | 1864 | High | |
| | Med | Toad | Sonoran Desert Toad | *Incilius alvarius (Possibly extinct in CA)* | 285 | 120 | 1400 | Low/Med | *A. cognatus* |
| | Med | Toad | Yosemite Toad | *Anaxyrus canorus* | 284 | 96 | 1152 | Med/High | |
| | Med | Toad | Black Toad | *Anaxyrus exsul* | 284 | 96 | 951 | Low/Med | *A. canorus, A. punctatus* |
| | Very High | Snake | Common Gartersnake | *Thamnophis sirtalis* | 271 | 224 | 1146 | Med | |
| | High | Snake | Aquatic Gartersnake | *Thamnophis atratus* | 266 | 168 | 889 | Low | *T.gigas (-43% for size diff)* |
| | Med | Toad | Arroyo Toad | *Anaxyrus californicus* | 248 | 96 | 1000 | Med/High | |
| | High | Snake | Northwestern Gartersnake | *Thamnophis ordinoides* | 245 | 168 | 775 | Low | *T.gigas (-50% for size diff)* |
| | Very High | Snake | Western Terrestrial Gartersnake | *Thamnophis elegans* | 240 | 192 | 931 | Low | *T.gigas (-40% for size diff)* |
| | Med | Frog | Northern Red-legged Frog | *Rana aurora* | 230 | 120 | 1864 | Med | *R. draytonii* |
| Medium | High | Snake | Checkered Gartersnake | *Thamnophis marcianus* | 210 | 144 | 835 | Low | *T.gigas (-46% for size diff)* |
| | Med | Frog | Foothill Yellow-legged Frog | *Rana boylii* | 199 | 90 | 2420 | Med/High | |
| | Med | Toad | Great Plains Toad | *Anaxyrus cognatus* | 175 | 120 | 1400 | Med/High | |
| | Med | Toad | Woodhouse's Toad | *Anaxyrus woodhousii* | 175 | 120 | 1400 | Low/Med | *A. cognatus* |
| | Med | Toad | Western Toad | *Anaxyrus boreas* | 130 | 120 | 1274 | Low/Med | |
| | Med | Salamander | Red-bellied Newt | *Taricha rivularis* | 72 | 72 | 600 | High | |
| | Med | Salamander | California Newt | *Taricha torosa* | 72 | 72 | 600 | Med/High | *T. rivularis* |
| | Med | Salamander | Sierra Newt | *Taricha sierrae* | 72 | 72 | 600 | Med | *T. rivularis* |
| | Med | Salamander | Rough-skinned Newt | *Taricha granulosa* | 72 | 72 | 600 | Med | *T. rivularis* |
| | Med | Salamander | California Giant Salamander | *Dicamptodon ensatus* | 72 | 72 | 600 | Low | *Educated guess* |
| | Med | Frog | Cascades Frog | *Rana cascadae* | 72 | 72 | 759 | High | |
| | Med | Toad | Red-spotted Toad | *Anaxyrus punctatus* | 72 | 72 | 750 | Med | |
| Low | Low | Frog | Lowland Leopard Frog | *Lithobates yavapaiensis (Possibly extinct in CA)* | 54 | 54 | 900 | Low | |
| | Low | Frog | Southern Mountain Yellow-legged Frog | *Rana muscosa* | 54 | 54 | 665 | Med | |
| Very Low | Very Low | Salamander | Coastal Giant Salamander | *Dicamptodon tenebrosus* | 48 | 48 | 600 | Low | *Educated guess* |
| | Very Low | Frog | Pacific Treefrog | *Pseudacris regilla* | 36 | 36 | 400 | Low | *Educated guess* |
| | Very Low | Frog | Sierra Nevada Yellow-legged Frog | *Rana sierrae* | 36 | 36 | 525 | Med/High | |
| | Very Low | Frog | Coastal Tailed Frog | *Ascaphus truei* | 30 | 30 | 266 | Med/High | |
| | Very Low | Frog | California Treefrog | *Pseudacris cadaverina* | 26 | 26 | 200 | Low/Med | |
| | Very Low | Salamander | Southern Torrent Salamander | *Rhyacotriton variegatus* | 5 | 5 | 50 | Low/Med | *R. cascadae* |

results, there is evidence that bufonid toads are particularly susceptible to negative impacts from roads elsewhere (Trenham et al. 2003; Orłowski 2007; Eigenbrod et al. 2008).

Roads and traffic have been associated with reduced abundance and species richness of frog populations (e.g., Fahrig et al. 1995; Houlahan and Findlay 2003). However, approximately half of California species are small, primarily aquatic, highly fecund, with relatively limited movements and thus ranked low for road impacts. Four of 11 species ranked within the highest risk groupings; California red-legged frog (*Rana draytonii*), Oregon spotted frog (*R. pretiosa*), Northern red-legged frog (*R. aurora*), and Cascades frog (*R. cascadae*). The Oregon spotted frog (*R. pretiosa*) is known to move large distances within aquatic habitats (Bourque 2008; USFWS 2009). Construction of a highway that bisected the

Yellowstone population of Oregon spotted frogs was one important factor that reduced the population dramatically in the 1950s (see discussion in Watson et al. 2003). Although portions of the populations show high site fidelity, California red-legged frog and Northern red-legged frog migrants can move large distances (> 1 km) across both aquatic and terrestrial habitats (Bulger et al. 2003; Fellers and Kleeman 2007; Hayes et al. 2007). Road mortality or habitat fragmentation from roads and urbanization were listed as primary threats to these species elsewhere (USFWS 2002; COSEWIC 2015).

Lizards had relatively low percentages of species in the high risk groupings. Many lizard species are small, non-migratory, territorial, have small home ranges and are thus at low risk of negative road effects. Similar to snakes, lizards can also be attracted to road surfaces for thermoregulation. A few wide ranging species scored in the highest risk categories including the Gila monster (*Heloderma suspectum*), leopard lizards (genus *Gambelia*) and two horned lizard species (genus *Phrynosoma*). The Gila monster has been negatively associated with urbanization, where larger home ranges and greater movement rates result in higher mortality for males (Kwiatkowski et al. 2008). Sensitive to habitat fragmentation, the blunt-nosed leopard lizard (*Gambelia sila*) was found to be largely absent from habitat patches less than 250 ha (Bailey and Germano 2015). Flat-tailed horned lizards (*Phrynosoma mccallii*) are also susceptible to habitat fragmentation with very large home ranges for their size, particularly in wet years (Young and Young 2000). In fact, road mortality is a well-known threat for this species (see review by CDFW 2016b). Horned lizards are also particularly vulnerable to being killed on roads due to their tendency to flatten and remain motionless while being approached (Young and Young 2000).

Salamanders also had relatively low percentages of species in the high risk grouping. Over 75% (35/46) of the California salamanders are lungless salamanders (Plethodontidae) and Torrent salamanders (Rhyacotritonidae). These species are mostly small, sedentary, non-migratory, closed habitat specialists with limited movement distances and these traits have resulted in a high level of speciation. This is exemplified by there being at least 20 species of slender salamanders (genus *Batrachoseps*) in California alone (Martinez-Solano et al. 2007; Vences and Wake 2007). However, within the salamander group, newts and several other migratory salamander species were ranked within the highest risk categories from negative road effects. There is substantial evidence that habitat fragmentation and mortality due to roads negatively affect many of these species. For instance, newts regularly migrate long distances over land from and to breeding ponds, and to terrestrial foraging habitats (> 2 km; Trenham 1998). Large numbers are found dead on roads during dispersal periods and newt species are often the first to disappear in fragmented landscapes (Gibbs 1998; Trenham 1998, Shields pers. comm.). Similarly, road mortality and habitat fragmentation are primary threats to the California tiger salamander and other Ambystomid salamanders because terrestrial habitat is used for interpond migration and overwintering (Semlitsch 1998; Trenham et al. 2001; Bolster 2010).

Because this assessment covers a wide array of species and habitats, the risk to particular species populations must be re-assessed on a local level. This includes consideration of the locations, types, and densities of roads in relation to population and species ranges along with goals for functional, meta-population, and genetic connectivity (e.g., Marsh and Jaeger 2015). Due to very low road densities in their limited ranges, some species and populations may be at lower risk. For instance the Gila monster, Oregon spotted frog, Sonoran mud turtle, Sonoran desert toad (*Incilius alvarius*) and Yosemite toad (*Anaxyrus canorus*) scored high due to life history and space-use characteristics, however their limited ranges are largely in protected or low road density areas in the state. Thus roads may not be a significant threat to these species in California. In contrast, high road densities may increase the risk for species within coastal regions such as remaining populations of Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*), Alameda striped racer (*Masticophis lateralis euryxanthus*), and San Francisco garter snake (*Thamnophis sirtalis tetrataenia*). However, most species consist of numerous populations with a myriad of differing road-related threat levels. Although detailed species ranges and occupancy within ranges are well known for some species with very limited ranges, for most species range-wide surveys have not been conducted. Therefore, only general range boundaries are available that encompass large portions of the state and availability of species distribution models of habitat suitability and occupancy within their ranges is rare. This lack of detailed spatial information on species distribution

further limits the potential to incorporate road locations, types, and densities in a state and species-wide assessment.

We also note that relative risk to negative road impacts is provided for both populations and species. Risk was elevated for species with small and isolated ranges and that are facing a myriad of other threats. Because of this, a few common widespread species scored high at the population-level but not at the species-level. This included gopher snakes (*Pituophis catenifer*) and western toads (*Anaxyrus boreas*) where road mortality has been identified as a threat to the persistence of local populations (e.g., COSEWIC 2012; Jochimsen et al. 2014).

To potentially aid in local assessments, we have provided distance estimates or "buffer zones" that contain estimates for 95% of population-level movements for all species (e.g., Semlitsch and Bodie 2003). We provide all references evaluated for distance estimates in Appendix 2. Meta-population movements can be very important to the stability of pond-breeding amphibians (e.g., Semlitsch 2008; Jackson et al. 2015) and are included in many of the buffer zone calculations. However, we note that buffer zones may not include meta-population-level movements if the rate of these dispersal movements was less than 5% in the studies we used for our analyses.

This should be considered an initial assessment of susceptibility to negative road impacts in a hierarchical framework (e.g., see Level 2; Hobday et al. 2011). Therefore, as previously stated it will be important to re-assess the risk of specific populations to roads within their habitat and to evaluate and compare alternatives at the local scale (e.g., Suter 2016). This may include more detailed information on specific road attributes (e.g., density, type, location), as well as species behavior (Jaeger et al. 2005; Rouse et al. 2011; Rytwinski and Fahrig 2013; Jacobson et al. 2016). Age structured and spatially explicit population viability models are valuable tools to predict long-term population responses to roads and to compare outcomes of multiple mitigation scenarios (e.g., Gibbs and Shriver 2005; Borda-de-Água et al. 2014; Polak et al. 2014; Crawford 2015). Need and placement of mitigation structures can be guided by local population or meta-population dynamics, landscape attributes, movement routes, and road mortality hot spots (e.g., Bissonette and Adair 2008; Langen et al. 2009, 2015b; D'Amico et al. 2016; Loraamm and Downs 2016).

The quantity and quality of life history information, particularly movement data, are highly variable among species (see confidence levels; Tables 9 and 10). Therefore it is important to re-assess risk as new information becomes available. Finally, this is a structured assessment of comparative risk across a range of target species; therefore specific values for high risk have not been established. The ranking or assessment methodology should be adaptive and updated with advancements of road ecology science (e.g., Linkov et al. 2006).

## Conclusion

Although roads are a significant cause of mortality and habitat fragmentation for many wildlife populations, road-related risk rankings have been based largely on expert opinion due to a scarcity of literature on road effects for most species. Therefore, we developed an objective and scientifically-based comparative risk approach to assess the potential threat from negative road impacts using species life history and movement data. After applying it to over 160 herpetofaunal species (and subspecies) in the state of California, the results are consistent with road ecology literature in identifying known high risk species, and call attention to some species not previously identified. Overall, we found that snakes and chelonids had the largest proportion of species at high risk for negative road impacts due to longer movement distances (home range and/or migratory), lack of road avoidance, and relatively low fecundity in comparison to other herpetofaunal groups. Results also indicated that consideration of aquatic connectivity appears to be under-represented for semi-aquatic herpetofauna that use both terrestrial and stream, riverine, or wetland habitats.

In addition to informing transportation planning and mitigation considerations for California herpetofauna, we believe this approach may be useful for comparing the risk of road-related fragmentation and mortality for species elsewhere and for other taxonomic groups. The results can help to inform multi-criteria threat assessments for special status species or those in consideration for listing. Finally, this serves to highlight species that may deserve further study and consideration for aquatic and terrestrial road mitigation to reduce mortality and to maintain population-level connectivity.

This risk assessment approach compares the susceptibility of species to negative road impacts. Commonly, there are numerous populations within a species range that occupy areas with greatly differing road pressures. Therefore, the actual risk to specific species populations will depend upon local road densities, road-types, traffic, and road locations in relation to species habitat and movement corridors.

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# Research to Inform Caltrans Best Management Practices for Reptile and Amphibian Road Crossings

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# Chapter 1. Executive Summary

## Introduction

In October of 2014, the U.S. Geological Survey (USGS) began a 5-year project to conduct research to inform Best Management Practices (BMPs) for amphibian and reptile crossing and barrier systems in California. To inform future conservation and transportation planning, this project involved identification of species at highest risk of negative road impacts, creation of geodatabase and spatial mapping tools that crosswalk with California Essential Habitat Connectivity Planning, and field research to address information gaps in the efficacy of reptile and amphibian passage and barrier systems.

Per the agreement with California Department of Transportation (Caltrans; agreement 65A0553), this project was part of a broader collaborative effort between the Western Transportation Institute (WTI) of Montana State University and USGS Western Ecological Research Center (WERC). As part of this broader project, WTI conducted a worldwide literature review and gap analysis and produced a BMP manual for herpetofauna in California (Langton and Clevenger 2020). WTI and USGS were contracted separately although we worked closely together throughout this broader effort and each brought particular expertise to the project. WTI has expertise in highways, the attributes of the highway environment, and broad international experience with road ecology and herpetofauna connectivity systems worldwide. USGS WERC has expertise with California amphibian and reptile species and their ecology, study design and implementation, and landscape connectivity and road ecology.

## Overall Program Objectives and Tasks

To meet the objectives in the contract, the project was composed of six major tasks:

1) Meet with Caltrans and other California herpetologists to establish collaborative networks with California herpetologists and inform them about the Caltrans amphibian and reptile highway crossing design project.

2) Perform a risk analysis based on an evaluation of California amphibian and reptile species ranges, life histories, population locations, habitat needs, and movement patterns to identify road sensitive species and/or confirm road sensitive species previously identified by Caltrans.

3) Create spatial data and maps to crosswalk with the California Essential Connectivity Map (Caltrans/California Department of Fish and Wildlife (CDFW) / U.S. Department of Transportation (DOT)) and Amphibian and Reptile Species of Special Concern Maps (CDFW) for species evaluated in Task 2 and identify primary roadways that transect habitats for these sensitive species. This was done in consultation with the WTI research team, Caltrans, wildlife agencies (U.S. Fish and Wildlife Service (USFWS) and CDFW) and species experts.

4) Assist WTI in the synthesis of the state of the practice in reptile and amphibian highway crossings by compiling and reviewing literature on amphibians and reptiles and mitigation measures to reduce road impacts, including identifying research gaps and future research needs.

5) Using expertise from within WERC and input on roadways and animal crossings from WTI, develop and design a plan for field research to evaluate key design and environmental attributes of functional passage structures for select amphibian and reptile species. Select sensitive amphibian and reptile species from the prioritized list developed in Task 2. Conduct field studies at existing (and new if possible) crossing structures to determine effective means for enhancing the ability of the selected species to cross highways. Give preference to multiple replicated sites that allow for simple experimental manipulations.

6) Provide expertise on California amphibians and reptiles to the WTI research team for the preparation of the Best Management Practices (BMPs) manual. Prepare report of Tasks 1-5 and a manuscript for presentation and/or publication.

## Establishing Collaborative Networks (Task 1)

We began the first task by holding a special session at the California-Nevada Amphibian Populations Task Force (APTF) in Calabasas, CA on January 8-10, 2015. The session was entitled "Amphibian (and Amphibious Reptile) Road Ecology" and hosted by USGS with guest speakers Tony Clevenger (WTI), Tom Langton (Herpetofauna C I Ltd), Sally Brown (USFWS), Michael Westphal (U.S. Bureau of Land Management), Michael Hobbs (San Jose State University) and Chris Brown (USGS). We used this venue to highlight the project and to begin collaborative networking. Collaborations continued throughout the contract period through many meetings and communications with WTI, California scientists and herpetologists, Caltrans state and district biologists, USFWS, CDFW, U.S. Forest Service (USFS), and other scientists and herpetologists throughout the state. We also attended and presented at multiple conferences and meetings such as the Desert Tortoise Council Symposium (2016), annual APTF meetings (2015-16, 2018-2019), Western Section of the Wildlife Society (2019), USGS Amphibian Research Monitoring Initiative (ARMI 2015-2019), and the International Conference of Ecology and Transportation (2015, 2019).

Tasks 2 through 5 are individually summarized in the following subsections of Chapter 1 of this report along with summaries of findings, relevance of findings to informing the BMPs, and suggestions for future studies. Individual comprehensive reports for the risk analysis (task 2), geodatabase (task 3), and field research (task 5) are presented in subsequent Chapters.

## Risk Assessment (Task 2)

Caltrans considers the need for barrier structures and safe wildlife road-crossings important to maintain the long-term viability of wildlife populations (Caltrans 2019). To prioritize these efforts for herpetofauna, we identified species that are most at risk of extirpation from road-related impacts. With over 160 California species and a lack of species-specific research data, we developed an objective risk assessment method based upon road ecology science. Risk scores were based upon a suite of life history, movement, and space-use characteristics associated with negative road effects that were applied in a hierarchical manner from individuals to species (Figure 1). Considerations included movement distances, movement frequency, speed, habitat preferences, movement behavior (territorial, non-territorial, vs. migratory), fecundity, range size and conservation status. All California herpetofauna species (and some subspecies) were ranked into five relative categories of road-related risk to both aquatic and terrestrial connectivity (very-high to very-low) based upon 20% increments of all species scores.

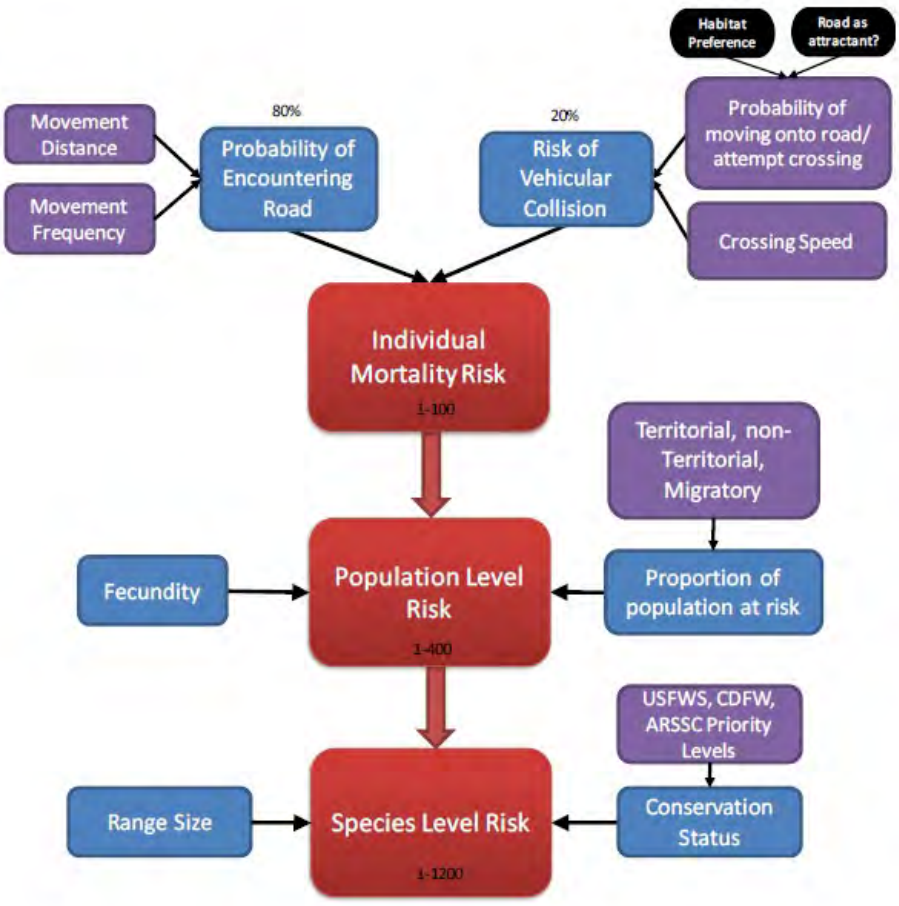


Figure 1. California Reptile and Amphibian Road Risk Assessment Conceptual Model.

All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species in California were ranked at high or very-high risk from negative road impacts. Results were largely consistent with local and global scientific literature in identifying high risk species and groups.

Overall, snakes and chelonids had the largest proportion of species at high risk for negative road impacts due to longer movement distances (home range and/or migratory), lack of road avoidance, and relatively low fecundity in comparison to other herpetofaunal groups. This includes the desert tortoise, that has been shown to suffer from high road mortality negatively affecting population abundance in the Mojave Desert, and pond turtles, that travel kilometers within perennial waters and intermittent aquatic habitats to forage and find mates. In addition, female pond turtles migrate from their aquatic habitat to terrestrial habitats to nest and lay eggs, which make roads that parallel aquatic habitat a threat to both females and hatchlings.

Many large colubrid snakes and rattlesnakes ranked high. They are not only attracted to paved road surfaces for thermoregulation but have wide home ranges or move large distances between winter hibernacula and summer foraging areas. Long foraging movements within aquatic habitats also contributed to many garter snakes falling within the highest road risk categories.

Approximately half of California anuran species were ranked at high risk of negative road effects. These include Bufonid toads and red-legged frogs that may move large distances in both aquatic and terrestrial habitats to satisfy their annual resource requirements. Newts and several Ambystomid salamander species whose populations annually migrate between aquatic and upland habitats also ranked as high risk. Only a few wide-ranging lizard species scored in the highest risk categories including the Gila monster, leopard lizards, and two horned lizard species.

This risk assessment approach compared the susceptibility of species to negative road impacts. Commonly, there are numerous populations that occupy areas with greatly differing road pressures within a single species range. The actual risk to specific populations will depend upon local road densities, road types, traffic, and road locations in relation to species habitat and movement corridors. Therefore, it will be important to reassess the risk of roads to specific populations and to evaluate and compare alternatives at the local scale.

To help inform transportation planning and for evaluating the suitability of different best management practices, the risk of roads to both terrestrial and aquatic connectivity was assessed. Thus, semi-aquatic species have two risk scores. Some scored high in both habitats, while others scored high in only one. This is important when evaluating the need for underpasses and other terrestrial crossings versus bridges and fish passages. For example, underpasses, barriers and other structures may be suitable for species with high terrestrial risk scores; such as tortoises, colubrid snakes, rattlesnakes, and Ambystomid salamanders. Conversely, the use of fish passages and bridges could also be considered for species with high aquatic risk scores; such as the giant gartersnake, California red-sided gartersnake, two-striped gartersnake, and Sonoran mud turtle. Both terrestrial and aquatic passages may be needed for species groups that ranked high in both categories; such as pond turtles, Bufonid toads, newts and red-legged frogs. Along with this, buffer distances for terrestrial and aquatic habitats were calculated to encompass 95% of population level movements of all species. This provides information to agencies deciding whether a population is

close enough to a road (within buffer distance) to warrant mitigation, the need for a barrier, and whether a goal should be to provide population-level connectivity or allow for occasional dispersal to provide long-term genetic connectivity.

A simplified list of high and very-high risk species is provided in Table 1. This work has been published (Brehme et al. 2018). The journal article with all California species rankings and buffer distances is included as Chapter 2 and is available at *https://link.springer.com/article/10.1007/s10980-018-0640-1*.

Table 1. California Amphibians and Reptiles Ranked at High and Very-high Risk of Negative Road-related Impacts.

| GROUP | VERY-HIGH RISK | HIGH RISK |
|---|---|---|
| Terrestrial Snakes | Alameda Striped Racer<br>Baja California Coachwhip<br>Baja California Ratsnake<br>California Glossy Snake<br>Coachwhip<br>Coast Patch-nosed Snake<br>North American Racer<br>Panamint Rattlesnake<br>San Joaquin Coachwhip<br>Striped Racer | California Lyresnake<br>Desert Nightsnake<br>Mojave Rattlesnake<br>Nightsnake<br>Red Diamond Rattlesnake<br>Regal Ring-necked Snake<br>Sidewinder<br>Sonoran Lyresnake<br>Speckled Rattlesnake<br>Spotted Leaf-nosed Snake<br>Western Groundsnake<br>Western Diamond-backed Rattlesnake<br>Western Patch-nosed Snake<br>Western Shovel-nosed Snake<br>Western Rattlesnake |
| Aquatic Snakes | California Red-sided Gartersnake<br>Giant Gartersnake<br>San Francisco Gartersnake<br>Two-striped Gartersnake | Aquatic Gartersnake<br>Common Gartersnake<br>Northwestern Gartersnake<br>Sierra Gartersnake<br>Western Terrestrial Gartersnake |
| Freshwater Turtles | Northern Western Pond Turtle<br>Southern Western Pond Turtle<br>Sonora Mud Turtle | |
| Tortoises | Mohave Desert Tortoise | |
| Toads | Arroyo Toad<br>Black Toad<br>Sonoran Desert Toad<br>Yosemite Toad | Great Plains Toad<br>Western Spadefoot<br>Woodhouse's Toad |
| Frogs | California Red-legged Frog | Cascades Frog<br>Northern Red-legged Frog<br>Oregon Spotted Frog |
| Lizards | Banded Gila Monster<br>Blunt-nosed Leopard Lizard<br>Cope's Leopard Lizard<br>Desert Horned Lizard<br>Flat-tailed Horned Lizard | Long-nosed Leopard Lizard<br>San Diegan Tiger Whiptail<br>Switak's Banded Gecko |
| Salamanders | California Newt<br>Callifornia Tiger Salamander<br>Red-bellied Newt<br>Sierra Newt | California Giant Salamander<br>Rough-skinned Newt<br>Santa-Cruz Long-toed Salamander<br>Southern Long-toed Salamander |

## Spatial Mapping (Task 3)

Caltrans and CDFW commissioned the California Essential Habitat Connectivity (CEHC) Project because they consider a functional network of connected wildlands essential to the continued support of California's diverse natural communities in the face of human development and climate change (Spencer et al. 2010). CEHC maps and spatial layers depict large, relatively natural habitat blocks greater than 809 ha (2000 acres) that support native biodiversity and areas deemed essential for regional scale animal and plant connectivity. These maps were intended to make transportation and land-use planning more efficient and less costly, while helping to reduce wildlife-vehicle collisions. They are available on the CDFW Biogeographic Information and Observation System (BIOS) website *https://wildlife.ca.gov/Data/BIOS*.

Essential Connectivity Areas (ECA), Natural Landscape Blocks (NLB), and Natural Areas_small (NA) from the Essential Connectivity Map geodatabase were provided by CDFW. Although habitat blocks greater than 809 ha are appropriate for planning connectivity for large mammals, small animals can persist on smaller size patches. Therefore, we merged ECA, NLB, and NA areas 10 ha or greater. The resulting layer was then dissolved into a single polygon feature class with a buffer of 100 meters added to it. This connected many of the smaller polygons and better represented natural areas large enough to support sensitive amphibian and reptile populations. We then prepared a spatial geodatabase that intersects the modified CEHC map, State Highways and high-risk species ranges from the California amphibian and reptile road risk assessment (Brehme et al. 2018). This geodatabase was designed to be a useful planning tool for Caltrans to quickly identify road segments which may warrant planning for increased connectivity of high-risk amphibian and reptile species.

The spatial geodatabase (CalTrans_SpeciesRoadRisk_Map.mpk) includes:

1) CEHC lands merged with smaller habitat blocks (>10 ha).
2) Ranges of high and very-high risk amphibian and reptile species.
3) California highway segments that intersect habitat ranges of high and very-high risk amphibian and reptile species.
3) California highway segments that intersect habitat ranges of high and very-high risk amphibian and reptile species and CEHC lands.
4) The total number of high and very-high risk species habitat ranges that intersect the highway segments and CEHC lands.

Here we show an example of a high-risk species density map for the state (Figure 2) and an individual species map (Figure 3), where the species habitat range intersects CEHC lands and state highway systems. Note that the accuracy of each species road risk map is dependent upon the accuracy of its most recent range map, which varies by species (see Chapter 3 for sources). Because many species are patchily distributed throughout their ranges, species may not be

occupying habitat along all intersecting highway segments. Therefore, highlighted road segments indicate the possibility of species occupancy as well as known occupancy.

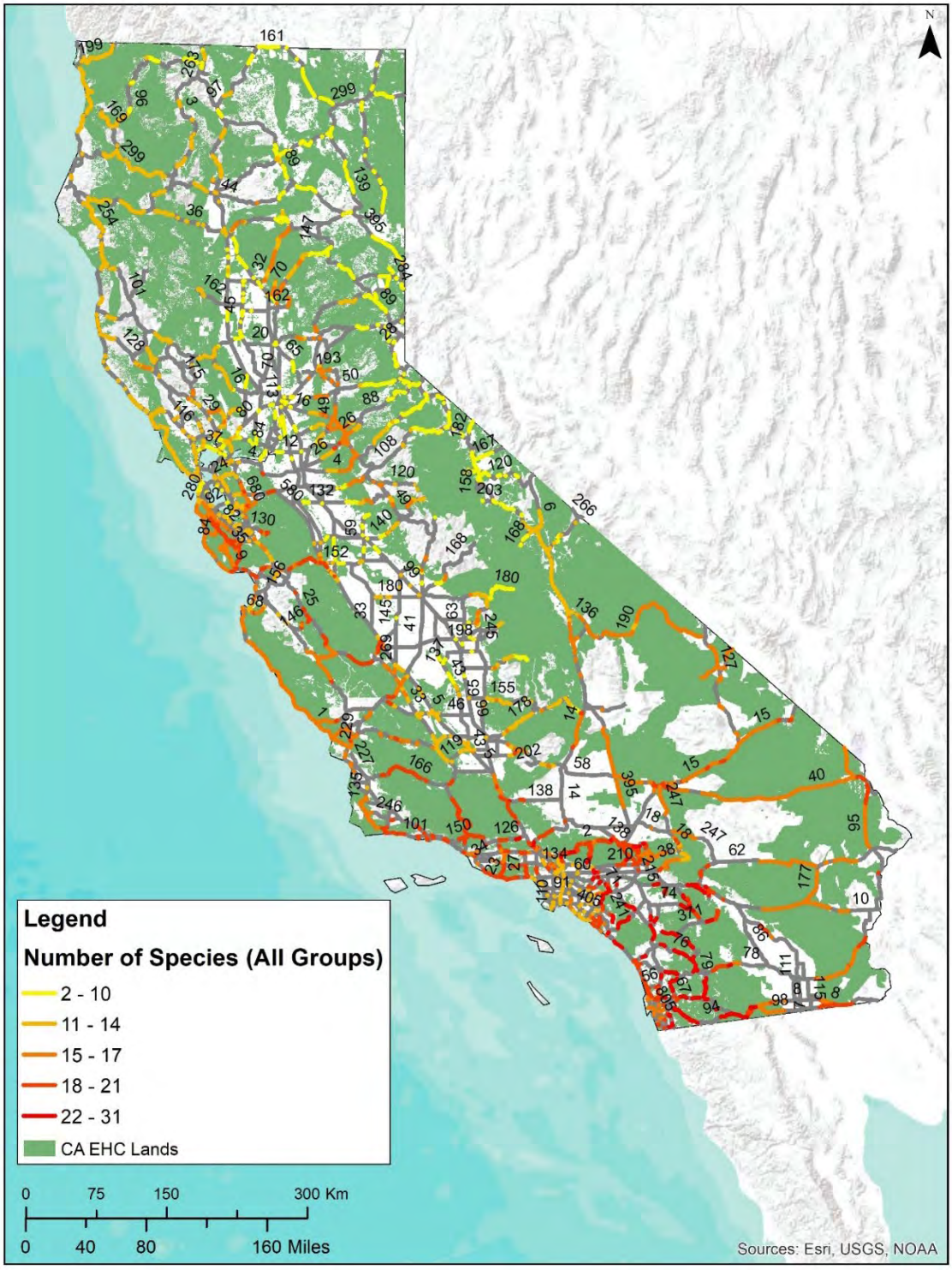


Figure 2. Density of High and Very-High Risk Reptile and Amphibian Species across the State Highway System (Elise Watson, USGS). Note: California Highway Numbers are in Black.

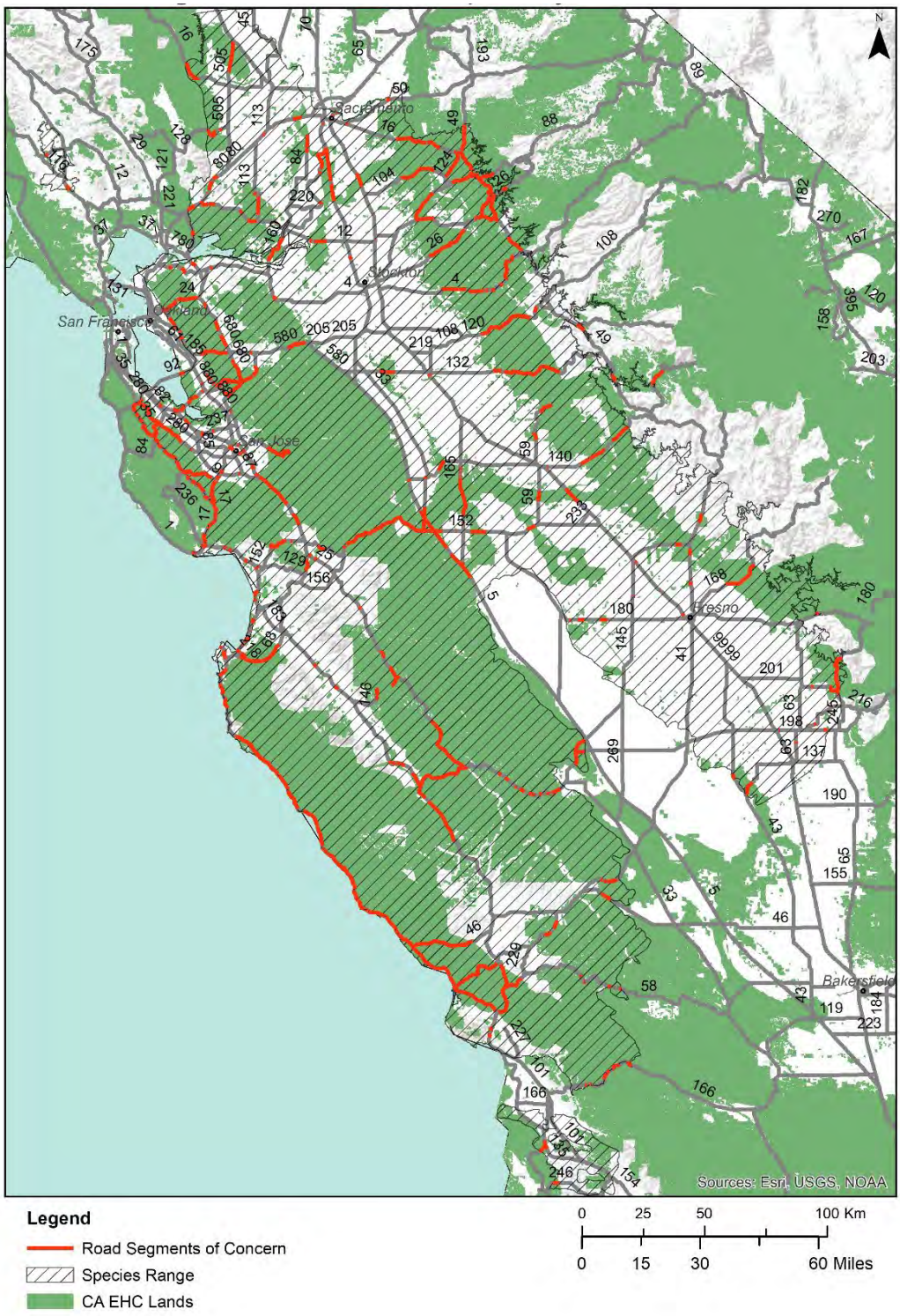


Figure 3. Overlay of Single Very-High Risk Species Range (*Ambystoma californiense*), CEHC Lands and the State Highway System (Elise Watson, USGS). Note: California Highway Numbers are in Black.

## Literature Review and Gap Analysis (Task 4)

To synthesize what was currently known about reptile and amphibian crossing systems in California and throughout the world and to identify primary information gaps in scientific and practical knowledge to inform these crossing systems, WTI conducted a detailed literature review and synthesis with input from USGS (Langton and Clevenger 2017). The authors reviewed 52 studies on crossing systems with 125 individual taxa (75 reptile and 50 amphibian species or sub-species) throughout Europe, North America, South America and Australasia. Of these, 45% were for reptiles and 55% amphibians. Information from each paper was summarized into three study or 'knowledge area' categories: passage construction and use, passage environmental variables and barrier construction and use.

Langton and Clevenger (2017) concluded than in most cases road mitigation was installed primarily to reduce road mortality versus to maintain connectivity. However, large passages tended to be more permeable to amphibian and reptile crossings than smaller passages. They determined that the literature reflected a widely spread and low-inference scientific knowledge base regarding the efficacy of amphibian and reptile passages and barrier systems, although the body of literature has been growing in recent years with specific species and systems. They also found little information on the role of existing infrastructure and drainage culverts in helping to maintain genetic and population connectivity for herpetofauna.

Therefore, Langton and Clevenger (2017) concluded there was a need for more properly designed studies to evaluate the effectiveness of purpose-built (engineered) and non-engineered passages and barriers. Research studies (controlled experimental or field settings) were needed to directly measure, test and compare results among mitigation structures, their structural and environmental characteristics, and permeability to species and species groups. Information and knowledge gaps identified from this analysis included the following:

- Use of existing highway structures by herpetofauna.
- Relative permeability of most commonly built structures to different herpetofauna groups.
- Relationship between use and openness ratio and length and width of passage.
- Whether populations could benefit from addition of barrier fencing to existing structures.
- The most effective ways to simulate natural and artificial light, temperature and moisture within underpasses.
- The influence of fence material and opacity on barrier effectiveness and passage use.
- Effectiveness of turnarounds at fence ends.
- The best designs to extend barriers along road access points.

This review and synthesis, along with the risk assessment, was used to help guide field research and for developing California Best Management Practices (BMPs) for sensitive amphibian and reptile highway crossings (Langton and Clevenger 2020).

## Research Questions and Field Studies (Task 5)

Based on the literature review and gap analysis, we devised a list of 9 research studies along with research objectives, target species/groups, general study designs, relative costs, and how each of these studies would inform Best Management Practices (BMPs) for Caltrans reptile and amphibian crossings. Representatives from Caltrans (Simon Bisrat, James Henke, Amy Golden, Amy Bailey), Western Transportation Institute (Tony Clevenger, Tom Langton), and USGS (Robert Fisher, Cheryl Brehme) met in September of 2017 to review the study options and select the studies that would be pursued as part of this project.

After reviewing and discussing each of the studies, the following studies were identified as being the most cost effective while providing valuable information for the BMPs. Below are the primary research questions, target species and locations chosen for these studies.

1. What is the maximum distance between passages to maintain permeability for migratory herpetofauna (pond breeding amphibians)?
    a. Target Species/Groups: California tiger salamander, Yosemite toad
    b. Locations: Stanford, Sierra National Forest.

2. How does fence material (transparency) influence species movement along barriers?
    a. Target Species/Groups: reptiles and amphibians, California tiger salamander, Yosemite toad
    b. Locations: San Diego, Stanford, Sierra National Forest

3. Fence ends: How effective are fence-end turnarounds?
    a. Target Species/Groups: reptiles and amphibians
    b. Location: San Diego, Stanford, Sierra National Forest

4. What designs of jump-outs are effective for herpetofauna and other small animals?
    a. Target Species/Groups: reptiles and amphibians
    b. Location: San Diego

Additionally, we included two extra questions in our studies as they developed.

5. What is the relative permeability of a special built passage system for California tiger salamanders (Type 5: Micro-underpass)?
    a. Target Species/Groups: California tiger salamander
    b. Location: Stanford

6. Is there an alternative to the tunnel passage system design for migratory amphibians and other high risk herpetofauna? Evaluation of a novel elevated road segment passage.
    a. Target Species/Groups: Yosemite toad
    b. Location: Sierra National Forest.

Individual reports of all field studies are provided in Chapters 4 through 7.

# Summary of Research Findings and Relevance to Caltrans BMP's (Task 6)

The results of our field studies inform the Caltrans Best Management Practices for amphibian and reptile crossing systems regarding passage spacing for migratory amphibians, barrier fencing materials, and the effectiveness of turnarounds and jump-outs. We also evaluated the permeability of an existing amphibian tunnel system and a novel pilot elevated road segment passage.

## Movement Distances along Barriers to Inform Passage Spacing for Migratory Amphibians *(Question 1 above)*

Our results from studies of California tiger salamanders (CTS) in Stanford, CA and Yosemite toads in the Sierra National Forest showed that many of these amphibians migrating between wetland and upland habitats were unlikely to reach the road passage systems if they encountered the barrier fencing away from the passage. CTS moved an average distance of 40 m and Yosemite toads moved an average distance of 52 m along barrier fencing before "giving up," and their probability of making it to a crossing decreased rapidly with increasing distance. In addition to distance moved, the direction the salamanders and toads turned when reaching the barrier fencing was a factor in whether they reached a passage. Individuals that reached the barrier fencing and then travelled in the wrong direction (away from the passage) were significantly less likely to reach the crossing than those that made the correct initial direction choice. The average distance moved by these amphibians indicates that approximately half of the individuals moved greater distances and half moved shorter distances before "giving up." We estimated a distance between passages of less than 12.5 m (CTS) and 20 m (Yosemite toads) would be needed along migratory pathways to maintain a high level of permeability.

Therefore, the likelihood by distance that animals reach a passage can inform the planning and spacing of crossing systems for migratory amphibians and other migratory species. Without considering this, amphibian road crossing systems composed of barrier fencing and underpasses have the potential to become a greater barrier to movement. This is particularly relevant when high connectivity is important for the sustainability of the population, such as for migratory amphibian species that must make population level movements between upland and breeding habitats. With non-migratory species, less frequent cross-road movements could be acceptable if roads do not transect seasonal habitats or vital resources. In these cases, occasional crossings to enable reproductive and genetic connectivity may be sufficient to maintain long term population persistence.

## Barrier Fencing Materials *(Question 2 above)*

Three of our studies were relevant to herpetofaunal responses to fencing materials of various transparencies. One was the fence trial behavioral study of reptiles in Rancho Jamul, one was our CTS study at Stanford, and the third was our Yosemite toad study in the Sierra Nevada.

The results from our behavioral studies show that herpetofauna are more likely to interact with the transparent and semi-transparent fences by poking at them with their noses, pacing back and forth, and attempting to climb. The transparent (hardware cloth) and semi-transparent fencing (polymer matrix "mesh") used in our studies were not only see-through, but permeable to the movement of air in comparison to plastic solid fencing. Because sight and chemoreception senses are typically well developed in reptiles, it is not clear to what extent these different senses are driving fence interaction behaviors. However, it is clear from our observations that animals exhibiting these behaviors appeared to be trying to find a way through the fence to the other side.

Although fence interaction behaviors have been documented elsewhere in comparing hardware cloth and solid fencing (Ruby et al. 1994, Milburn-Rodríguez et al. 2016), our trial behavioral studies showed a clear gradation of response from solid to semi-transparent to transparent fencing in all taxa studied. In addition, our studies showed that these behavioral responses typically resulted in animals moving slower, or spending more time, along transparent/permeable fencing in comparison to solid fencing. This may not be a large concern when the purpose of the fence is primarily to exclude animals. However, it may be an important consideration when a dual objective is to lead species toward a road crossing structure, particularly when high permeability and population connectivity across the structure is desired.

In our migratory amphibian studies, the transparency of fencing (mesh vs. solid) did not significantly affect the movement distances of CTS or Yosemite toads or their probability of making it to the underpass system, although the estimated probabilities of reaching underpasses were slightly lower for the semi-transparent fencing. With preliminary data, the speed and time of travel for Yosemite toads were not significantly different by fence type. However, for CTS, the speed and time of travel varied significantly by fence type. CTS moving along solid fencing moved at almost twice the average speed and were 3 times less likely to turn around and repeatedly move back and forth. Therefore, CTS moving along fencing that they could see through resulted in them expending a higher amount of time and energy to make it to the crossing.

There are many reasons why different fencing types (hardware cloth, mesh, or solid) may be used in particular landscapes, habitats, and climates with considerations that include heat, rain and wind, permeability, durability, and aesthetics (see Langton and Clevenger 2020). Our behavioral study was the first to show that addition of a simple visual barrier (6 in./153 mm in our study) from the ground upwards, at the base of transparent and semi-transparent fencing, can reduce fence interaction behaviors and increase rates of movement. In fact, for most measures, herpetofauna responses to mesh and hardware cloth fencing with a visual barrier were not significantly different than to the solid barrier. This could allow for more flexibility in the decision-making and planning processes for barrier systems for herpetofauna.

**Turnarounds** *(Question 3 above)*

Three studies were relevant to the efficacy of turnarounds. One was done in Rancho Jamul, one was our CTS study at Stanford, and the third was our Yosemite toad study in the Sierra Nevada. A general graphic of the turn-around design used is depicted in Figure 4.

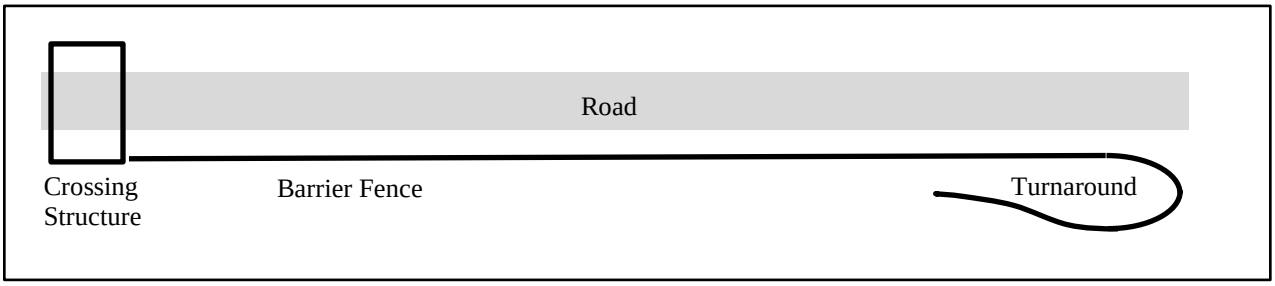


Figure 4. Diagram of Turn-around at Barrier Fence End

Our Rancho Jamul study was the first to show that small turnarounds at fence ends can be effective in changing the trajectory of movement for herpetofauna and small mammals. The turnarounds in our studies were approximately 1.5 m long and 1 m wide at the widest point with the turnaround ending approximately 0.4 m from the original fence line and extending another 0.4 m parallel to the fence. Turnarounds at fence ends were made of hardware cloth, mesh, or solid fencing (2 each). We documented that over 90% of herpetofauna (lizards, snakes and toads) and 69% of small mammals changed course after leaving a turnaround. Of those that changed their trajectory, 67% of herpetofauna and 43% of small mammals moved back along the original fence line while the remainder turned away from the fence line toward the habitat. We previously observed that animals spend more time interacting (e.g. poking, back and forth movements, climbing) with fencing that they can see and smell through (Question 2, Chapter 6). Animals also generally spent increased amounts of time in transparent/permeable and semi-transparent/permeable turnarounds than solid impermeable turnarounds.

Our results also suggest the use of transparent or semi-transparent fencing for turnarounds may increase their effectiveness for some species groups (Chapter 7). These results could be related to animals interacting with the fencing and spending more time in transparent turnarounds, so that they were less likely to remember and continue on their original trajectory. The results may also be related to the different types of spatial learning and memory used for navigation when animals are subjected to solid barriers (egocentric) in comparison to transparent barriers (allocentric) as has been shown in maze-food trials with rodents (Violle et al. 2009, Vorhees and Williams 2014). Validation of these findings in other locations and possibly more specific research studies addressing spatial learning and movement responses in reptiles, amphibians, and small mammals in their natural environments would be needed to further our understanding of these results.

We did not compare different sizes or shapes of turnarounds in our study; however, we hypothesize that having the end of the turnaround close to the original fence line may help to steer

animals back along the original barrier in the direction of original origin. Longer or larger turnarounds encompassing smaller turnarounds have been proposed to increase the probability that animals do not go out onto the roadways if they turn away from the fence and into habitat on leaving the turn around (Langton and Clevenger 2020).

In this study, we only documented animal movement for up to 1 m (3.4 feet) after leaving the turnaround. It is entirely possible that animals changed course again after they left the field of view of the video camera. In our Stanford and Sierra movement studies (Chapters 3 and 4), two out of three CTS that presumably reached a turnaround at the fence end were subsequently documented on another camera 25-125 m away moving back along the fence line. Preliminary results suggest seven out of 10 Yosemite toads changed course at a turnaround, while three continued in the direction past the fence ends. Of the seven toads that changed course, four were subsequently documented on another camera 40-80 m away moving back along the fence line toward the passage. Further studies using more cameras and/or tracking methods are needed to better understand how turnarounds affect movement of animals over a longer distances and time frames. Higher mortality of herpetofauna has been well documented at fence ends even with turnarounds (Gunson et al. 2014, Langton and Clevenger 2017, Helldin and Petrovan 2019). However, the high proportion of herpetofauna that changed directions in our study supports the use of turnarounds in attempts to reduce the chances that small animals go out onto the roadway at fence ends and potentially to help 'steer' them back toward to a crossing structure.

**Jump-outs** *(Question 4 above)*

Animals can get trapped within the roadway if they get through an opening in the fencing or overshoot the end of the fencing. Jump-outs provide a way for animals that get trapped within a roadway surrounded by vertical barrier fencing to safely get back into the habitat on the other side of the fence. Although jump-outs are commonly built structures along wildlife fencing for large mammals, they have not been incorporated into transportation planning for reptile and amphibian barriers. However, short curved or sloped fencing has been designed for amphibians that angles toward the habitat to allow movement over the top in one direction.

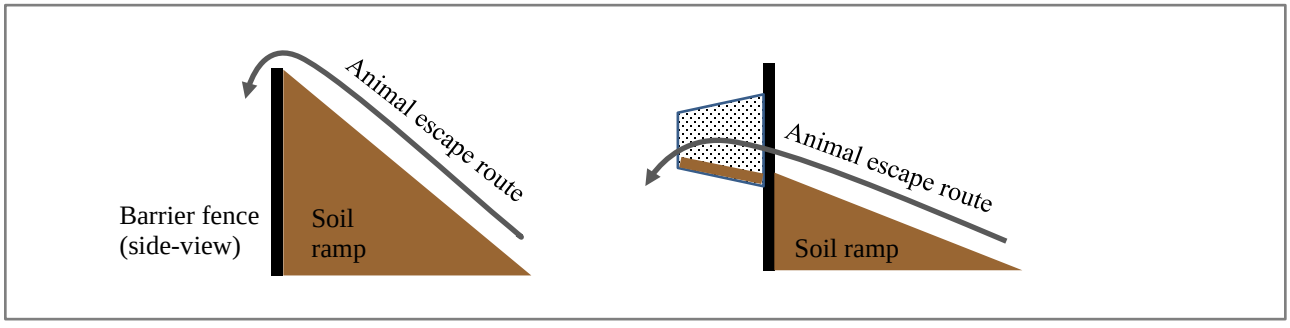


Figure 5. Diagram of Jump-out Configurations a) Over Fence and b) Through Fence.

Our experimental behavioral study showed that two jump-out configurations (Figure 5) were largely effective in allowing animals trapped on the 'wrong' side of a vertical fence to escape back into the habitat. One was simply a soil ramp to the top of the exclusion fencing (Figure 5a: 50 cm. in height) and the other was a polymer box funnel placed at a height of 25 cm above the ground within the exclusion fencing with a small soil ramp leading up to it (Figure 5b). A total of 75% of lizards, 95% of snakes, and 1 of 2 toads used a jump-out to escape the enclosure. There was little difference between the use of the high ramp and low funnel jump-outs by lizards or snakes. We observed that lizards often sat on top of the 50 cm high ramp for long periods of time before jumping to the ground, whereas there was little hesitation with the lower 25 cm jump-outs.

We suggest jump-outs be provided at regular intervals along vertical barriers in the form of a ramp leading to the top of the barrier or leading to a funnel type structure that opens to the habitat. It is also important that any jump-out design for herpetofauna consider the safety of other wildlife. This includes minimizing the size difference of the entrance and exit of box funnel designs so that larger animals do not get stuck in the funnel. Rectangular or cylindrical shapes with the same entry and exit size could be considered. For short barrier fencing, most other wildlife can simply step, climb, or jump over the barrier. For taller barrier fences, escape routes may include jump-outs of several sizes to accommodate a wider variety of species.

### Effectiveness of Crossing Structures: Amphibian Tunnels and a Novel Elevated Road Segment *(Questions 5 and 6 above)*

Many small animals, especially amphibian populations that must migrate between aquatic and terrestrial habitats, are susceptible to negative impacts from roads within their habitat (e.g. Hamer et al. 2008, Semlitsch 2008, Brehme et al. 2018). In the winter breeding seasons of 2018 and 2019, we studied the movement of CTS across three existing micro-passage amphibian tunnels spaced approximately 5 m apart from one another along Junipero Serra Blvd in Stanford, CA. The road bisects a historic CTS breeding pond and upland CTS habitat. CTS that did reach the opening of the passage system had a very high probability (87%) of making a complete crossing to the other side. The passages are made of inert materials (polymer concrete) and incorporate a slotted ceiling at the road surface to allow natural light, moisture and rainfall to permeate the length of the passage. These passages have been shown to be permeable to amphibian movement in North America and Europe (Jackson and Tyning 1989, Pagnucco et al. 2012, Langton and Clevenger 2017). Although they have not been used for amphibian passage on the state highway system to date, these results are promising for possible use of these and/or similarly designed passages by Caltrans.

Although micro-passage tunnels are a standard mitigation solution to reduce amphibian road mortality, there is evidence that these systems may filter movements of populations that disperse over large areas, particularly if passages are placed too far apart from one another across the migratory pathways (e.g. Allaback and Laabs 2002, Pagnucco et al. 2012, Ottburg and van der Grift 2019). In 2018 we tested a new and novel passage elevated road segment (ERS) prototype, an eight-in. high elevated road segment using road mats designed for use by heavy equipment at

construction sites. The ERS was installed on top of a USFS road along a Yosemite toad mortality "hotspot" with directional barrier fencing. The ERS provides a safe crossing nearly 100 ft wide while allowing both light and rain to pass through. We monitored Yosemite toad and other herpetofaunal activity along fencing and under the passage using specialized cameras. Initial results show that toads and other herpetofauna as well as small mammals used the passage and mortality was greatly reduced. Although the prototype was a 100-ft wide passage, theoretically they could be made to any length. This ERS prototype offers a new concept design to increase permeability of roads to migratory amphibians and other species. There is currently an effort underway by DOT and other transportation engineers to adapt this concept design to more permanent highway applications.

## Considerations for Future Studies

To further inform the design of effective barrier and passage systems for herpetofauna, we suggest consideration of the following research:

1. Continue study of Yosemite toads in Sierra National Forest to increase sample size and confidence in model predictions on passage spacing, fence opacity, and the permeability of the ERS crossing system.

2. Include one or more new study locations and species to better predict underpass spacing needs for high-risk migratory amphibian species. This would address the question of whether movement distances along barrier fencing are predictable among species groups and size classes.

3. Continue California tiger salamander and Yosemite toad studies to explore modifications to increase effectiveness of passages. Address the following questions:
    a. Will affixing a visual barrier to transparent or semi-transparent fencing change CTS behavior so that it more closely resembles the reaction to solid fencing? This is useful because in some areas, mesh fencing may be preferred for water/wind permeability, etc.
    b. Would more turnarounds along the length of barrier fencing help to increase the probability of success for animals that start out moving away from tunnels?

4. Continue research to assess the effectiveness of fence end treatments by studying the effect of turnaround length, materials and configuration on amphibian and reptile turnaround rates. Monitor animal movements over longer distances after exiting turnaround.

5. Work with engineers familiar with Caltrans materials and specifications to design (and test if possible) new options to add to existing BMP elements for increasing effectiveness of road crossings for herpetofauna such as:
    a. Elevated road segment (ERS) concept designs for primary roadways.
    b. Artificial lighting in tunnels that best simulates natural lighting for diurnal species. This is mainly for long underpasses where grated skylights in the shoulders and median are not feasible or sufficient to illuminate a passage .
    c. Drip or other drainage systems that deposit a path of moisture in otherwise dry underpasses during rain events.
    d. Design modifications to decrease the temperature differential between tunnel interiors and the surrounding environment.
    e. Design modifications to incorporate cover and ledges for herpetofauna within larger passages.

6. Design and implement studies to better understand if herpetofauna use existing passages and culverts for movement across roads.
    a. If so, what is the relative permeability of the most commonly built structures to different herpetofauna groups?
    b. Is the probability of use related to size of passage? If so, for which species groups?
    c. How is use of passages related to length and openness ratio?
    d. Would barrier fencing increase the use of non-engineered structures (i.e. culverts)?

These proposed studies will allow Caltrans to better evaluate the effectiveness of existing barrier and road crossing systems, to increase the 'toolbox' of innovative solutions, to increase the effectiveness of crossing systems for reptiles and amphibians in California, and to make more informed decisions on underpass spacing for high-risk migratory species.

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*Note: more extensive citations are included in individual study chapters*


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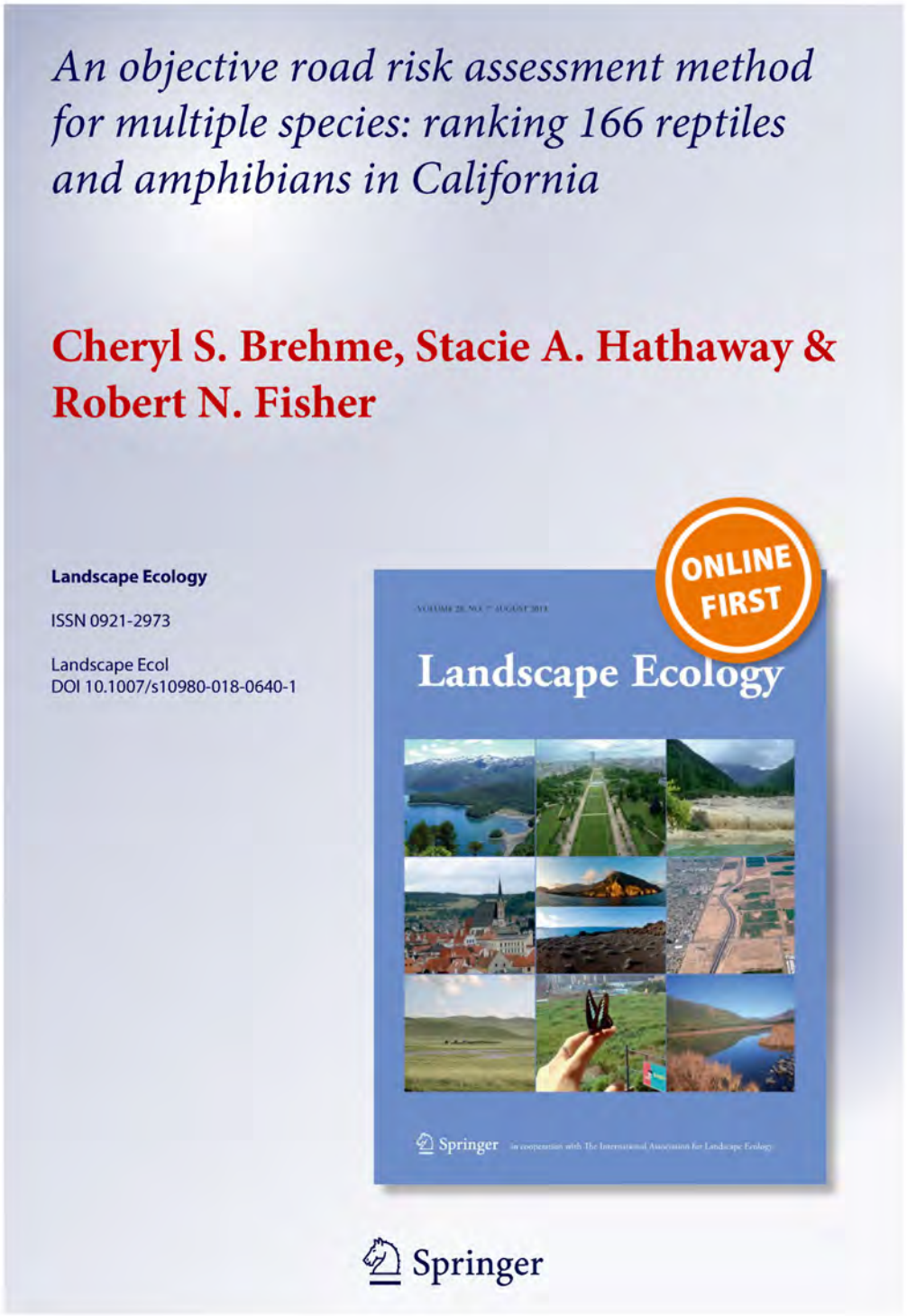
## Chapter 2. California Road Risk Analysis for Herpetofauna (Reprinted with permission)



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RESEARCH ARTICLE

# An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California

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**Abstract**
*Context* Transportation and wildlife agencies may consider the need for barrier structures and safe wildlife road-crossings to maintain the long-term viability of wildlife populations. In order to prioritize these efforts, it is important to identify species that are most at risk of extirpation from road-related impacts.
*Purpose* Our goal was to identify reptiles and amphibians in California most susceptible to road mortality and fragmentation. With over 160 species and a lack of species-specific research data, we developed an objective risk assessment method based upon road ecology science.
*Methods* Risk scoring was based upon a suite of life history and space-use characteristics associated with negative road effects applied in a hierarchical manner from individuals to species. We evaluated risk to both aquatic and terrestrial connectivity and calculated buffer distances to encompass 95% of population-level movements. We ranked species into five relative categories of road-related risk (very-high to very-low) based upon 20% increments of all species scores.
*Results* All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species in California were ranked at high or very-high risk from negative road impacts. Results were largely consistent with local and global scientific literature in identifying high risk species and groups.
*Conclusions* This comparative risk assessment method provides a science-based framework to identify species most susceptible to negative road impacts. The results can inform regional-scale road mitigation planning and prioritization efforts and threat assessments for special-status species. We believe this approach is applicable to numerous landscapes and taxonomic groups.

**Keywords** Reptile · Amphibian · Road mortality · Habitat fragmentation · Road ecology · Risk assessment · Road

## Introduction

There have been many attempts to better characterize and quantify threat criteria in order to classify species at higher risk of extinction at state, national, and global levels (Congress 1973 (U.S. Endangered Species Act); Mace et al. 2008; Hobday et al. 2011; Thomson et al. 2016; IUCN 2017). Roads are a significant threat to wildlife populations (e.g., Forman et al. 2003;

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Andrews et al. 2015a; van der Ree et al. 2015), causing both barrier (habitat fragmentation) and depletion (road mortality) effects. Barrier effects occur when animals avoid crossing roads, in which case roads essentially fragment species habitat. Barrier effects include reduced size and quality of available habitat, reduced effective population size, reduced ability to find mates and resources, increased genetic structuring, and increased probability of local extirpation (e.g., Forman et al. 2003; Fahrig and Rytwinski 2009; D'Amico et al. 2016). Depletion effects occur when animals attempt to cross roads and are killed by vehicles. Depletion effects include all of the risks from barrier effects as well as reduced survivorship, making high road mortality an even greater concern (Jackson and Fahrig 2011). Among other stressors, such as habitat loss and fragmentation, invasive species, pesticide use, changing climate, and disease, the negative impacts from roads may independently or cumulatively threaten the persistence of populations and even species.

Amphibians and reptiles have been identified as being particularly susceptible to the negative effects of roads within their habitat (e.g., Klauber 1931; Forman et al. 2003; Rytwinski and Fahrig 2012; Andrews et al. 2015a, b; D'Amico et al. 2015). Many are slow moving, do not avoid roads, and are simply too small for drivers to see and avoid. During rains many amphibians make long linear terrestrial movements regardless of the presence of intersecting roadways (Glista et al. 2008), and because paved roads typically absorb and retain more heat than the surrounding habitat, snakes and lizards are often attracted to roads for thermoregulation (Case and Fisher 2001; Jochimsen et al. 2004). In fact, road surveys are one of the most common methods for surveying these reptiles (e.g., Sullivan 2012). Many herpetofauna species utilize both aquatic and terrestrial habitat for breeding, development, foraging, and overwintering and therefore require connectivity within and between both aquatic and terrestrial habitats to support basic life history requirements.

The primary goal of this study was to provide information to transportation and other planning agencies in California to assist them in prioritizing road mitigation efforts for amphibian and reptile species. Although there is still a lot to learn about the effectiveness of different designs of road mitigation systems, the use of barrier systems, underpasses, and overpasses can reduce road mortality and help to maintain connectivity and safe passage across roads for herpetofauna and other wildlife (Jochimsen et al. 2004; Colino-Rabanal and Lizana 2012; Langton 2015; Langen et al. 2015b). Because it is currently unrealistic and cost prohibitive to mitigate all roadways for all species, it is vital to identify species most susceptible to road-related impacts. Within species ranges, risks to populations and need for mitigation can then be evaluated based upon local road densities and matrix, road-types, traffic, and road locations in relation to species habitat and movement corridors (e.g., Jaeger 2000; Litvaitis and Tash 2008; Langen et al. 2015b; Zimmermann Teixeira et al. 2017).

Here we describe a road risk assessment methodology applied to native amphibian and reptile species in California, a global biodiversity hotspot (Myers et al. 2000). We also included analysis of subspecies if they had special federal or state protection status. This includes 166 species and subspecies of frogs, toads, salamanders, snakes, lizards, turtles, and tortoise. Rankings and prioritizations such as these can be very subjective. In order to avoid including low risk species that may be favored by the assessors or to unintentionally overlook species that are at high risk, it was important for this be done in an objective manner informed by current road ecology literature.

Very few quantitative data are available on the impact of roads on population persistence. Jaeger et al. (2005) were the first to develop a relative ranking system to compare the impact of roads on wildlife populations. Their ranking system was largely based upon behavioral responses of animal species to the road surface, road size, traffic noise, and vehicles with varying road sizes and traffic volumes. However, knowledge of these detailed behavioral responses to ranges in road and traffic characteristics is rarely found in literature and the link between individual behavior and population-level effects has not been clearly established (Rytwinski and Fahrig 2012, 2013).

Rytwinski and Fahrig (2012) performed a meta-analysis of wildlife groups to test whether certain life history characteristics were related to negative responses to roads. High reproductive rate (fecundity) was negatively associated with the magnitude of population-level effects for amphibians. No associations were significant in reptiles, although there were

few studies to inform this analysis. However, a strong link was shown between body size, greater mobility, lower reproductive rates and the magnitude of negative road effects in mammals, the most studied wildlife group. Conversely, simulations predicted populations of species with small home ranges and high reproductive rates were the least likely to be affected by roads (Rytwinski and Fahrig 2013).

We used these findings as a basis for creating a multi-tiered system to rank and identify reptile and amphibian species that may be most susceptible to road impacts. We based our ranking upon a suite of species life history and space-use characteristics associated with negative road effects, as well as including species distribution and conservation status. We evaluated risk to both aquatic and terrestrial connectivity and include buffer distances that were calculated to encompass 95% of population movements. Relative confidence in these distances is given for each species based upon the amount of support from scientific studies. We solely focused on the direct effects of roads as barriers and sources of road mortality and not impacts from road construction and maintenance or indirect effects from increased human use of the landscape once a road is in place (see review by Langen et al. 2015a).

Because we based the risk assessment solely upon space-use and life history characteristics, this represents a species relative susceptibility to road impacts. It is understood that circumstances associated with particular populations (e.g., local road types, locations, densities) may elevate or reduce the risk for certain populations and species.

## Methods

### Road risk assessment (overview)

We assessed the relative risk of California herpetofauna species to negative road-related impacts at three scales in a hierarchical fashion. We first assessed risk at the scale of an individual animal and then expanded the risk to the population and then to species (Fig. 1).

At the individual-level, we based road risk primarily upon the likelihood that an individual would encounter one or more roads. We considered this a product of movement distance (home range, seasonal migrations) and movement frequency (e.g., active foragers, seasonal migrants, sit-and-wait predators vs. sedentary species) (e.g., Bonnet et al. 1999; Carr and Fahrig 2001). Because many species are semi-aquatic, movement distance and frequency were scored separately for both aquatic and terrestrial habitats.

There is a theorized higher risk associated with depletion effects (i.e., road mortality) in comparison to barrier effects (Fahrig and Rytwinski 2009; Jackson and Fahrig 2011). Therefore, we gave additional weight to those species more likely to go out onto a road surface and be killed by vehicular traffic. For this we considered factors of habitat preference (e.g., open vs. closed), roads as potential attractants (e.g., for basking), and movement speed (e.g., slow vs. fast). However, individuals within and among species may respond differently to roads (attraction vs. avoidance) based upon local landscape features, road width, traffic volume, and perceived danger (Forman et al. 2003; Andrews 2005; Brehme et al. 2013; Jacobson et al. 2016). Because a state-wide analysis encompasses extreme variation in landscape and road characteristics, the extent to which roads act as barriers or sources of direct mortality within a species range is unknown. The risk disparity between depletion and barrier effects could also be highly variable. Therefore, we limited the additional weight for potential depletion effects to twenty percent of the individual risk score.

We assessed population-level road risk by multiplying individual risk with scores representing: (1) the relative proportion of the population at risk; and (2) the species ability to sustain higher rates of mortality. For instance, the proportion of the population at risk was expected to be higher for migratory species than for territorial species. Highly fecund species were expected to better withstand (or more quickly recover from) higher mortality in comparison to those with few annual offspring.

Finally, we assessed species-level road risk by multiplying population road risk with scores for range size (both within and outside of California) and conservation status according to the U.S. Fish and Wildlife Service (USFWS 2016) and the California Department of Fish and Wildlife (CDFW 2016a; Thomson et al. 2016). Species with smaller ranges typically have fewer populations and are thus less resilient to population-level stressors. Endangered, threatened, and special concern species have already been designated at risk of extirpation, often due to

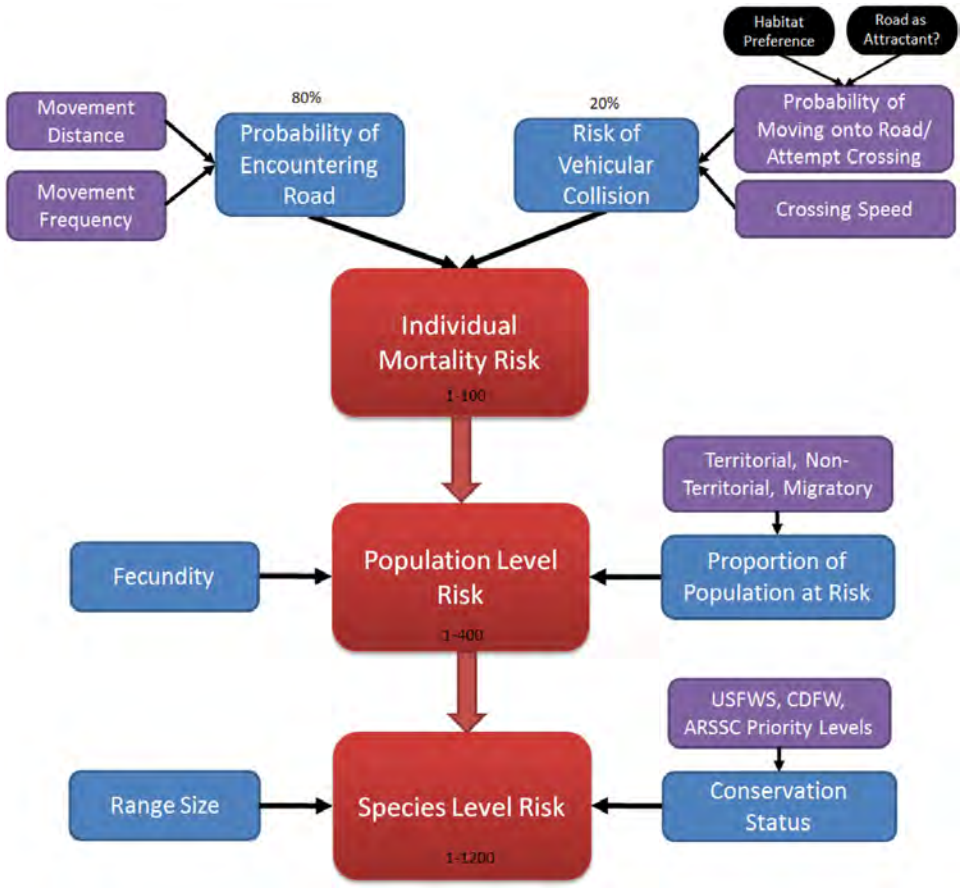


**Fig. 1** California reptile and amphibian road risk assessment conceptual model (*ARSSC* Amphibian and Reptile Species of Special Concern (Thomson et al. 2016))

multiple stressors, and are thus thought to be less likely to be resilient to additional road impacts.

Although we present both aquatic and terrestrial risk scores for semi-aquatic species, we used the higher of the two scores for the overall risk ranking.

## Literature review

Species life history data were primarily taken from and cross-checked among the following species account review sources;

1. U.S. Fish and Wildlife Service (USFWS) Recovery Plans and 5-year Reviews https://www.fws.gov/endangered/.
2. California Amphibian and Reptile Species of Special Concern (ARSSC; Thomson et al. 2016).
3. A Field Guide to Amphibians and Reptiles of California (Stebbins and McGinnis 2012)
4. Amphibian declines: the conservation status of United States species (Lannoo 2005).
5. Conservation Status of Amphibians and Reptiles on USDA National Forests, Pacific Southwest Region, 2012 (Evelyn and Sweet 2012).
6. Natureserve Explorer (natureserve.org): Species Accounts largely authored by G. Hammerson (2003–2016).

When these reviews were lacking life history information needed for the road risk assessment, we then searched for supplementary peer-reviewed literature using the Google Scholar search engine. Because movement distances (terrestrial, aquatic, home range, migratory) were so important for the risk assessment, we acquired referenced articles from the species accounts and independently searched the literature to acquire these data. Search terms included the species common name, scientific name, or genus and terms such as “movement”, “home-range”, “spatial”, and “telemetry”. We also reviewed articles for citations of other studies to find more recent information on movement. This literature included published articles,

book chapters, M.S. Theses, Ph.D. dissertations, agency reports, and consultant reports. In the case that specific life history or movement information was not found for a species, we chose a surrogate species based upon phylogeny, habitat, and body size. We first looked for the closest related species within the genus or family and chose a closely related surrogate based upon similar habitat and body size. If surrogates were used, these are clearly reported.

## Road risk metrics

The following section describes in detail the rank scoring used for Individual-level Road Risk, Population-level Road Risk, and Species-level Road Risk. All rank values are meant to represent the relative contribution of each attribute to either additive or multiplicative road risk.

### *Individual-level risk (100 points possible)*

Out of a total of 100 points for individual road mortality risk, we attributed up to 80 points (80%) to the risk of encountering a road and up to 20 points (20%) for the risk of an individual moving onto a road and being killed by a motor vehicle.

The risk of encountering a road was based on a combination of movement distance and general movement frequency. Movement distance was ranked 1–40 based upon home range movement distances (diameter) for non-migrants or migration distances for seasonal migrants that spanned from 0 to > 1200 m (Table 1). The scores are linearly correlated with increasing movement distance.

For species that use both terrestrial and wetland/stream/riverine habitats, such as frogs, toads, aquatic snakes and turtles, we scored aquatic and terrestrial movement distances and frequencies separately. This was necessary as some species move much larger distances and at different frequencies in one habitat versus the other. This also informs the type(s) of mitigation structures that may be warranted based upon habitat type, buffer distances and risk scores for each species. Aquatic movement distances were not calculated for pond-breeding amphibians. Ponds are typically small ephemeral bodies of water and terrestrial movements of amphibians to and among ponds account for the majority of movement for these species.

**Table 1** Individual-level Road Risk (IRR): Score criteria for risk of individuals encountering a road

| Risk of individuals encountering a road = Movement distance × frequency | | | |
|---|---|---|---|
| Movement distance (m) | Score | Frequency | Score |
| > 1200 | 40 | Active throughout home range | 2 |
| 901–1200 | 32 | Migratory (2–4 × per year)/ non-migratory sit and wait foragers | 1.5 |
| 601–900 | 24 | Sedentary, confined to specialized habitat | 1 |
| 451–600 | 16 | | |
| 301–450 | 12 | | |
| 201–300 | 8 | | |
| 101–200 | 5 | | |
| 51–100 | 3 | | |
| 0–50 | 1 | | |

The calculations and rankings for movement distances were well considered and deserve further explanation. Our original thinking was that maximum distances should reflect relative movement distances across species and these data were commonly reported in species accounts. However, it became increasingly difficult to determine whether maximum distances reported were seasonal migration movements, home range movements or rarer dispersal events. We believed this assessment should reflect annual movement distances and not rare dispersal events. We considered using average/median movement distances; however, these often underestimate the movement of seasonal migrants because in many cases a sizeable portion of the population may remain close to a breeding site, while another sizable portion make longer distance migrations causing an average or median to be uninformative. Therefore, we decided to use a buffer distance that incorporates the movement distances of 95% of the population studied. A 95% population movement distance is commonly accepted for the delineation of terrestrial buffer zones for amphibians (i.e., Semlitsch 1998; Semlitsch and Bodie 2003) and we believe it was the most biologically

meaningful and useful measure for this study. This measure, which we will refer to as Maximum Population Movement Distance (MPMD), should include almost all population movements, such as seasonal migration distances and annual home ranges (diameter), but not rare dispersal events. The MPMD should also be useful for local risk assessments as these distances can be used to aide in mapping and mitigation decisions.

The calculation we used for MPMD is commonly known as the 95% upper tolerance interval (Vangel 2015). A tolerance interval is an interval that is meant to contain a specified percentage of individual population measurements. This should not be confused with a confidence interval, which is an interval that is meant to contain the population mean. We chose a 50% confidence level for the upper 95% confidence limit of movement distances which is equal to the 95% prediction interval for future observations and is the mean + 1.645 × standard deviation. In cases where a standard deviation was not reported, we back calculated standard deviation from the standard error and sample size, calculated it from the individual data, or estimated it based on the methods recommended by Hozo et al. (2005). Although non-parametric tolerance intervals would be more appropriate for non-normally distributed movement data, the data required to calculate these is rarely reported in the published literature. In the case of non-normally distributed data where medians, sample sizes and ranges are reported, Hozo et al. (2005) methods allow for approximation of means and standard deviations with no assumption of the underlying data distribution. We found the resulting MPMDs to be reasonable in excluding large outliers but including multiple long distance movements below the maximum movement distance.

We recognize that for any species there can be substantial variability in movement distances that depend upon varying local, landscape, and climatic factors. This was often reflected in studies with sometimes widely varying estimates of home range and migration distances. We attempted to be conservative by using the study data for calculation of MPMD in which the largest population movement distances were observed. For studies where movement distance significantly varied between females and males, we used the information from the wider ranging sex. For migratory distances, we did not use distances from extreme environments, such as Canada, where suitable overwintering sites are typically much farther away from breeding and summer activity areas than in milder California climates (e.g., Gregory 1984). We did use study data from adjacent states or lower estimates of migration distances from those reported in Midwestern states. In some cases where little information was available, we made an educated guess based upon limited study data and/or closely related species and noted these in the tables. For all MPMDs, we report a relative confidence level based upon the number and quality of studies, sample sizes, and locations in or adjacent to California. It is intended that the scores be adjusted as new information becomes available.

To compute the risk of encountering a road, the MPMD was multiplied by a relative index of the expected frequency of longer distance movements (1–2 points; Table 1). We defined three frequency categories largely based upon annual migratory movements or foraging strategies for non-migratory species. The highest category included actively foraging predators which are characterized by frequent wandering movements throughout their home range (Pianka 1966). Less frequent movers included seasonal migrants traveling among breeding, summer foraging, and/or overwintering sites and non-migratory 'sit-and-wait' predators that remain still for long periods of time to ambush prey (Pianka 1966). Finally, low frequency included highly sedentary species with high site fidelity, particularly specialized rock, crevice, soil, or tree dwellers that may rarely traverse terrestrial or aquatic habitats.

The risk of an individual moving onto a road and being killed by a moving vehicle was ranked by attributes of habitat preference, road use, and movement speed (Table 2). Habitat preference represents the degree to which an individual is expected to go out onto or avoid an open road as predicted from their habitat and microhabitat preferences. Open habitat specialists and generalists were expected to more readily move onto a road than species that prefer cover (e.g., Forman et al. 2003; Brehme et al. 2013). Although many amphibians are closed habitat specialists, most readily move through open habitats during rain events, when most overland migratory movements tend to occur (Glista et al. 2008). Therefore, amphibians were considered open habitat specialists for this ranking. An additional factor that may increase road use is for thermoregulation for lizards

**Table 2** Individual-level Road Risk (IRR): Score criteria for risk of road mortality

| Risk of road mortality = Habitat preference + road use + movement speed | | | | | |
|---|---|---|---|---|---|
| Habitat preference | Score | Road use | Score | Movement speed | Score |
| Open habitat specialist/amphibians | 10 | Thermoregulation (snakes/lizards) | 4 | Slow (< 0.6 m/s) | 6 |
| Generalist | 8 | Other | 0 | Medium (0.6–2.0 m/s) | 3 |
| Edge specialist | 4 | | | Fast (> 2.0 m/s) | 0 |
| Closed habitat or aquatic specialist | 0 | | | | |

**Table 3** Population-level Road Risk (PRR): Score criteria for population level road risk

| PRR = IRR × (Fecundity + Proportion of population at risk) | | | | |
|---|---|---|---|---|
| Fecundity | Ave. potential offspring/year | Score | Proportion of population at risk | Score |
| Low | 0–10 | 2 | Seasonal migrants (Migratory) | 2 |
| Med | 11–25 | 1.5 | Wandering | 1.5 |
| High | 26–100 | 1 | Territorial | 1 |
| Very high | > 100 | 0 | | |

and snakes, as roads often retain more heat than the surrounding environment (Colino-Rabanal and Lizana 2012; Mccardle and Fontenot 2016). Finally, there is an increased risk of road mortality for slow versus fast moving species (see Andrews and Gibbons 2005; Mazerolle et al. 2005; Andrews et al. 2015b).

*Population-level Road Risk (400 points possible)*

To assess the risk of negative road impacts on the persistence of a population we incorporated scores for population-level movement behavior and fecundity (Table 3). For the proportion of a population expected to encounter a road, we scored the greatest risk to species that seasonally migrate to overwintering and breeding areas (Jackson et al. 2015). For those that do not migrate, we expected higher proportions of non-territorial or loosely territorial species ("wandering") to encounter roads than species that defend distinct territories.

Species with low fecundity are less resilient to road mortality impacts than highly fecund species (Rytwinski and Fahrig 2013). Relative fecundity was simply calculated from the average number of potential offspring per year whether the animals were oviparous or live-bearing. For egg-laying species, the number of potential offspring was calculated by multiplying the average clutch size by the average number of clutches per year.

Individual mortality risk (1–100 points) was multiplied by the sum of these population-level factors (1–4 points) to calculate population-level road risk.

*Species-level road risk (1200 points possible)*

In comparison to population-level risk, we considered the overall risk of roads to species to be negatively associated with species range and conservation status. Although some populations may be at high risk, species with a wide distribution and many populations should be more resilient to localized declines and extirpations. Therefore, we assigned a range isolation score ranging from 0 to 1 that considered species distributions range-wide (North America) and within California (CA) (Table 4). Range-wide distribution varied from "CA only" to "widespread" (> 4 states). If the species range extended into Mexico and/or Canada, these countries were counted as another state for calculation of the index. California-wide distribution was calculated based upon the number of CA geographic regions occupied out of twelve regions defined by Hickman (1993) and used in Stebbins and

**Table 4** Species-level Road Risk (SRR): Score criteria for species-level road risk

| SRR[a] = PRR × ((Range isolation score + Conservation status score)/2) | |
|---|---|
| (a) Range isolation score = (North America range + CA range)/2 | |
| North America range | Rank/score |
| CA only | 1.00 |
| 2 states (very restricted distribution) | 1.00 |
| 2 states (restricted) | 0.67 |
| 2–3 states | 0.33 |
| Widespread (4 + states) | 0.00 |
| California range (No. of geographic regions occupied) | Rank/score |
| 1 | 0.92 |
| 2 | 0.83 |
| 3 | 0.75 |
| 4 | 0.67 |
| 5 | 0.58 |
| 6 | 0.50 |
| 7 | 0.42 |
| 8 | 0.33 |
| 9 | 0.25 |
| 10 | 0.17 |
| 11 | 0.08 |
| 12 | 0.00 |
| (b) Conservation status score | |
| Conservation status | Rank/score[a] |
| CA or federal threatened/endangered | 1.00 |
| SSC priority 1 | 0.75 |
| SSC priority 2 | 0.50 |
| SSC priority 3 | 0.25 |
| None | 0.00 |

[a]Population-level risk > 80 only

McGinnis (2012). These two scores (Range-wide isolation, CA isolation) were summed and divided by two in order to normalize the overall range isolation score to a 0 to 1 scale.

At the species-level, we also incorporated conservation status (Table 4). Some species are declining and are at higher risk of extinction often due to multiple stressors. Federal and State Threatened and Endangered Species were given the highest score (1.0). In California, forty-five species are designated "Species of Special Concern (SSC)" with a ranking of 1, 2, or 3 based upon severity and immediacy of threats affecting each taxon (Thomson et al. 2016). SSC species were given a conservation status score ranging from 0.25 to 0.75 based upon their SSC ranking. Population-level Road Risk (score range 1–400) was multiplied by (1 + Range Isolation Score + Conservation Status Score; score range 1–3) to calculate the final Species-level Road Risk.

Range and conservation status were only used as a multiplier for species-level road risk if the population-level road risk was greater than 80 (20% of possible population score). This helped to prevent false inflation of the road risk metrics for low road susceptible species.

Because all members of the genus *Batrachoseps* (slender salamanders) are similar in body size, range size and general life history characteristics, we scored

**Table 5** Species-level frequency distributions and road risk rankings

| Percentile | Scores | Relative ranks |
|---|---|---|
| 81–100 | 322–710 | Very high |
| 61–80 | 213–321 | High |
| 41–60 | 63–212 | Medium |
| 21–40 | 53–62 | Low |
| 1–20 | 0–52 | Very Low |

the genus as whole with the most conservative estimates and conservation status but included all 20 species in the final count and calculations.

Once all 166 species (including subspecies with conservation status) were scored for species-level road risk within both terrestrial and aquatic habitats, we took the maximum score for each species and sorted them from the highest to lowest scores. We grouped species into categories of risk (Very high, high, medium, low, and very low) based upon ranges of values that represented frequency distributions in 20% increments of all species scores (Table 5, Fig. 2).

As a way to support the results of our ranking model with species literature, we focused on special status species. We reviewed recovery plans and 5-year reviews for federally listed species and state species accounts for California listed species and species of special concern (collectively referred to as special status species). For each rank group (i.e., "very low" to "very high"), we calculated the percentage of special status species where roads were specifically listed as a threat. Similarly, we tallied the number of species identified in a recent California preliminary road risk assessment (Levine 2013, Amy Golden pers. comm.) and compared the number of species that fell within each of our road risk categories.

## Results

All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species were ranked as high or very high risk from negative road impacts. (Table 6, Fig. 3).

Review of species accounts, recovery plans, and 5-year reviews for all special status species showed

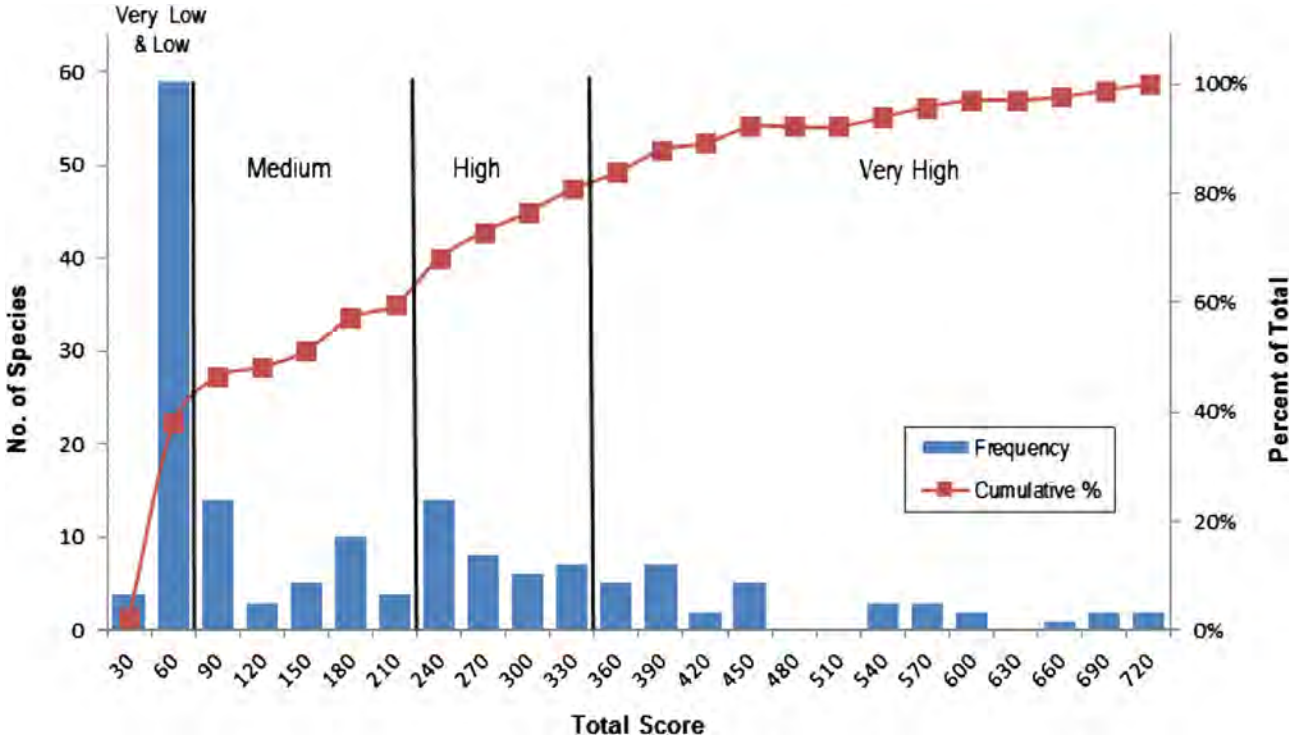


**Fig. 2** Histogram of species-level scores and approximate 20 percentile road risk categories

**Table 6** Numbers of species by taxa within each risk category

| Species group | Species-level rankings | | | | |
|---|---|---|---|---|---|
| | Very high | High | Med | Low | Very low |
| Salamander | 4 | 4 | 3 | 26 | 9 |
| Lizard | 5 | 3 | 8 | 7 | 21 |
| Anuran | 5 | 6 | 6 | 4 | 1 |
| Snake | 15 | 21 | 13 | 0 | 1 |
| Tortoise | 1 | 0 | 0 | 0 | 0 |
| Turtle | 3 | 0 | 0 | 0 | 0 |

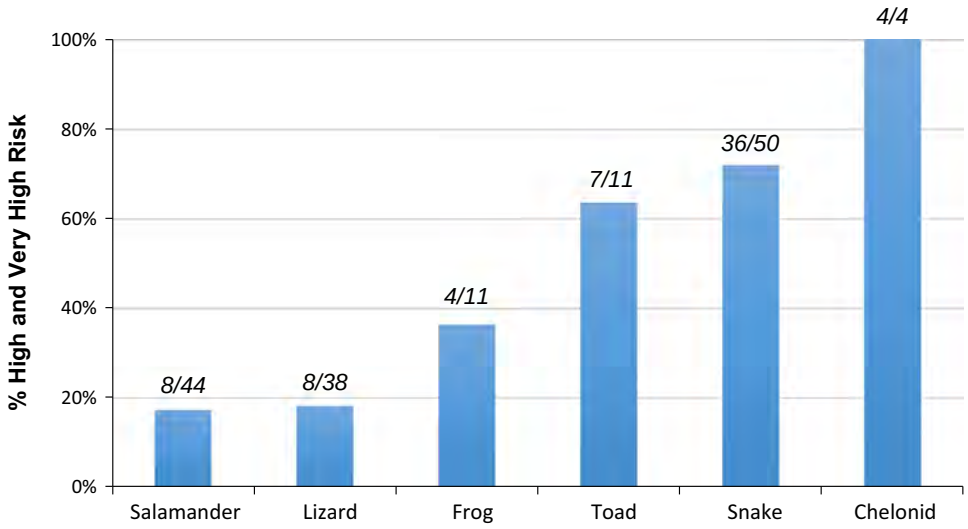


**Fig. 3** Percentages of species by taxa in high and very high road risk categories

that 94% (17/18) of species accounts that referenced roads as a threat to the species were ranked as "high" or "very high" in our risk assessment (Table 7). Of the special status species that ranked 'high' and 'very high', close to fifty percent (17/35) had road-related threats referenced in their listing literature. In comparison, only 4% (1/27) of 'medium' to 'very low' risk special status species accounts mentioned roads as a potential threat. In addition, 79% (15/19) of species of concern recommended in a recent Caltrans preliminary road risk assessment scored as 'high' or 'very high' risk in our analysis (Levine 2013, Amy Golden pers. comm.).

**Table 7** Comparison of road risk results and number of special status species with roads listed as threat

| Road risk level | Special status species | | | Caltrans PI[a] |
|---|---|---|---|---|
| | No. species in road risk level | No. species with roads listed as threat | % of Total | No. Spp in road risk level |
| Very high | 25 | 14 | 56 | 11 |
| High | 11 | 3 | 27 | 4 |
| Medium | 5 | 1 | 20 | 3 |
| Low | 10 | 0 | 0 | 1 |
| Very low | 7 | 0 | 0 | 0 |

[a]Caltrans PI are Caltrans identified sensitive species

**Table 8** Amphibian and reptile road risk assessment: very high risk species (80–100% percentile), high risk species (60–80% percentile), medium risk species (40–60% percentile range), low risk species (20–40% percentile) and very low risk species (0–20% percentile)

| | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| Risk Level-Species | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| Very High | Snake | Giant Gartersnake | *Thamnophis gigas* | 710 | 44 | 710 | THR | Yes | Yes |
| | Turtle | Southern Western Pond Turtle | *Actinemys pallida* | 707 | 283 | 707 | 1 | | Yes |
| | Snake | San Joaquin Coachwhip | *Masticophis flagellum ruddocki* | 689 | 689 | - | 2 | Yes | |
| | Snake | San Francisco Gartersnake | *Thamnophis sirtalis tetrataenia* | 663 | 238 | 663 | END | | Yes |
| | Snake | Alameda Striped Racer | *Masticophis lateralis euryxanthus* | 652 | 652 | - | THR | Yes | |
| | Snake | California Red-sided Gartersnake | *Thamnophis sirtalis infernalis* | 588 | 211 | 588 | 1 | | |
| | Tortoise | Mohave Desert Tortoise | *Gopherus agassizii* | 580 | 580 | - | THR | Yes | Yes |
| | Salamander | Red-bellied Newt | *Taricha rivularis* | 561 | 561 | 72 | 2 | Yes | Yes |
| | Turtle | Northern Western Pond Turtle | *Actinemys marmorata* | 547 | 219 | 547 | 3 | | Yes |
| | Snake | Two-striped Gartersnake | *Thamnophis hammondii* | 541 | 195 | 541 | 2 | | |
| | Snake | Baja California Coachwhip | *Masticophis fuliginosus* | 534 | 534 | - | 3 | Yes | |
| | Snake | Coast Patch-nosed Snake | *Salvadora hexalepis virgultea* | 533 | 533 | - | 2 | Yes | |
| | Salamander | California Newt | *Taricha torosa* | 532 | 532 | 72 | 2 | Yes | Yes |
| | Lizard | Banded Gila Monster | *Heloderma suspectum cinctum* | 446 | 446 | - | | | |
| | Salamander | California Tiger Salamander | *Ambystoma californiense* | 437 | 437 | - | THR | Yes | Yes |
| | Salamander | Sierra Newt | *Taricha sierrae* | 437 | 437 | 72 | | | |
| | Snake | Striped Whipsnake | *Masticophis taeniatus* | 425 | 425 | - | | | |
| | Lizard | Flat-tail Horned Lizard | *Phrynosoma mcallii* | 425 | 425 | - | 2 | Yes | |
| | Turtle | Sonoran Mud Turtle | *Kinosternon sonoriense* | 399 | 37 | 399 | 1 | | |
| | Lizard | Blunt-nosed Leopard Lizard | *Gambelia sila* | 393 | 393 | - | END | Yes | Yes |
| | Snake | Baja California Ratsnake | *Bogertophis rosaliae* | 387 | 387 | - | | | |
| | Snake | Panamint Rattlesnake | *Crotalus stephensi* | 387 | 387 | - | | | |
| | Frog | California Red-legged Frog | *Rana draytonii* | 380 | 380 | 300 | THR | Yes | Yes |
| | Toad | Yosemite Toad | *Anaxyrus canorus* | 379 | 379 | 284 | THR | Yes | |
| | Toad | Black Toad | *Anaxyrus exsul* | 379 | 379 | 284 | THR | | |
| | Lizard | Cope's Leopard Lizard | *Gambelia copeii* | 372 | 372 | - | 2 | | |
| | Toad | Sonoran Desert Toad | *Incilius alvarius (Possibly extinct in CA)* | 361 | 361 | 285 | 1 | | |
| | Lizard | Desert Horned Lizard | *Phrynosoma platyrhinos* | 356 | 356 | - | | | |
| | Snake | California Glossy Snake | *Arizona elegans occidentalis* | 340 | 340 | - | 1 | | |
| | Snake | North American Racer | *Coluber constrictor* | 334 | 334 | - | | | |
| | Snake | Coachwhip | *Masticophis flagellum* | 333 | 333 | - | | | |
| | Toad | Arroyo Toad | *Anaxyrus californicus* | 331 | 331 | 248 | END | Yes | Yes |
| | Snake | Striped Racer | *Masticophis lateralis* | 322 | 322 | - | | | |

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking
[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species
[d] California Amphibian and Reptile Crossing Preliminary Investigation

Risk scores and relative rankings for California reptile and amphibian species in both terrestrial and aquatic habitats are presented in Tables 8. Terrestrial and Aquatic rankings are provided separately in Tables 9 and 10 and also include population-level risk scores, 95% population buffer distances, confidence levels, and identification of any surrogate species used for the distance calculations. Species scores for all ranking criteria and life history and movement references are provided in Appendices 1 and 2.

## Discussion

To our knowledge, this is the first attempt to objectively assess the relative risk of roads at a species level using a logical and scientifically based framework and apply it across a large array of species and habitats. We believe this approach could be useful for assessing and comparing susceptibility of species to negative road impacts within and among all taxonomic groups. To date, such risk assessments have been based largely upon expert opinion, limited information available on

**Table 8** continued

| Risk Level-Species | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| High | Snake | Red Diamond Rattlesnake | *Crotalus ruber* | 321 | 321 | - | 3 | Yes | |
| | Snake | Speckled Rattlesnake | *Crotalus mitchellii* | 317 | 317 | - | | | |
| | Frog | Oregon Spotted Frog | *Rana pretiosa (Possibly extinct in CA)* | 315 | 41 | 315 | THR | | |
| | Salamander | Santa Cruz Long-toed Salamander | *Ambystoma macrodactylum croceum* | 308 | 308 | - | END | Yes | Yes |
| | Salamander | Rough-skinned Newt | *Taricha granulosa* | 304 | 304 | 72 | | | |
| | Snake | Sierra Gartersnake | *Thamnophis couchii* | 304 | 44 | 304 | | | |
| | Snake | Regal Ring-necked Snake | *Diadophis punctatus regalis* | 298 | 298 | - | 2 | | Yes |
| | Snake | California Lyresnake | *Trimorphodon lyrophanes* | 293 | 293 | - | | | |
| | Frog | Northern Red-legged Frog | *Rana aurora* | 291 | 291 | 230 | 2 | | Yes |
| | Snake | Mojave Rattlesnake | *Crotalus scutulatus* | 276 | 276 | - | | | |
| | Snake | Western Patch-nosed Snake | *Salvadora hexalepis* | 276 | 276 | - | | | |
| | Snake | Common Gartersnake | *Thamnophis sirtalis* | 271 | 165 | 271 | | | |
| | Snake | Aquatic Gartersnake | *Thamnophis atratus* | 266 | 40 | 266 | 0 | | |
| | Snake | Sidewinder | *Crotalus cerastes* | 263 | 263 | - | | | |
| | Salamander | California Giant Salamander | *Dicamptodon ensatus* | 260 | 260 | 72 | 3 | Yes | |
| | Snake | Sonoran Lyresnake | *Trimorphodon lambda* | 260 | 260 | - | | | |
| | Snake | Western Rattlesnake | *Crotalus oreganus* | 250 | 250 | - | | | |
| | Snake | Northwestern Gartersnake | *Thamnophis ordinoides* | 245 | 138 | 245 | | | |
| | Snake | Desert Nightsnake | *Hypsiglena chlorophaea* | 241 | 241 | - | | | |
| | Snake | Western Terrestrial Gartersnake | *Thamnophis elegans* | 240 | 75 | 240 | | | |
| | Lizard | Switak's Banded Gecko | *Coleonyx switaki* | 236 | 236 | - | THR | | |
| | Toad | Western Spadefoot | *Spea hammondii* | 234 | 234 | - | 1 | | Yes |
| | Snake | Coast Nightsnake | *Hypsiglena ochrorhyncha* | 233 | 233 | - | | | |
| | Lizard | Long-nosed Leopard Lizard | *Gambelia wislizenii* | 226 | 226 | - | | | |
| | Toad | Great Plains Toad | *Anaxyrus cognatus* | 222 | 222 | 175 | | | |
| | Toad | Woodhouse's Toad | *Anaxyrus woodhousii* | 222 | 222 | 175 | | | |
| | Lizard | Coastal Whiptail | *Aspidoscelis tigris stejnegeri* | 219 | 219 | - | 2 | | |
| | Snake | Western Shovel-nosed Snake | *Chionactis occipitalis* | 218 | 218 | - | | | |
| | Snake | Spotted Leaf-nosed Snake | *Phyllorhynchus decurtatus* | 218 | 218 | - | | | |
| | Salamander | Southern Long-toed Salamander | *Ambystoma macrodactylum sigillatum* | 217 | 217 | - | 2 | | |
| | Frog | Cascades Frog | *Rana cascadae* | 217 | 217 | 72 | 2 | | |
| | Snake | Western Diamond-backed Rattlesnake | *Crotalus atrox* | 214 | 214 | - | | | |
| | Snake | Western Groundsnake | *Sonora semiannulata* | 212 | 212 | - | | | |

[a] Maximum scores color-coded for toad risk type: terrestrial (gray), aquatic (blue), or both (gray/blue)
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking
[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species
[d] California Amphibian and Reptile Crossing Preliminary Investigation

road mortality, and even less information available on population or species-level road effects (Levine 2013; Rytwinski and Fahrig 2015).

Overall, this is meant to be a first step in highlighting reptile and amphibian species that may be at highest risk from roads transecting their habitat. These species may deserve consideration for further study and for implementing mitigation solutions to reduce mortality and to maintain or enhance connectivity. The risk assessment was done for both terrestrial and aquatic habitats to further inform mitigation. Some aquatic species may greatly benefit from fish passages while others may better benefit from terrestrial barriers and wildlife crossings or both.

Although data are currently lacking to validate completely the scoring and results of the risk assessment, our review of species accounts, recovery plans, 5-year reviews for federal and state-listed species and California species of special concern show a strong association between elevated road risk from our

**Table 8** continued

| | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| Risk Level-Species | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| Medium | Snake | Checkered Gartersnake | *Thamnophis marcianus* | 210 | 69 | 210 | | | |
| | Lizard | Blainville's Horned Lizard | *Phrynosoma blainvillii* | 209 | 209 | - | 2 | | Yes |
| | Frog | Foothill Yellow-legged Frog | *Rana boylii* | 199 | 26 | 199 | 1 | | |
| | Snake | Gopher Snake | *Pituophis catenifer* | 189 | 189 | - | | | |
| | Snake | California Mountain Kingsnake | *Lampropeltis zonata* | 184 | 184 | - | | | Yes |
| | Snake | Glossy Snake | *Arizona elegans* | 180 | 180 | - | | | |
| | Lizard | Pygmy Short-horned Lizard | *Phrynosoma douglasii* | 179 | 179 | - | | | |
| | Toad | Couch's Spadefoot | *Scaphiopus couchii* | 178 | 178 | - | 3 | | |
| | Snake | California Kingsnake | *Lampropeltis californiae* | 175 | 175 | - | | | |
| | Snake | Long-nosed Snake | *Rhinocheilus lecontei* | 165 | 165 | - | | | |
| | Toad | Western Toad | *Anaxyrus boreas* | 165 | 165 | 130 | | | |
| | Snake | Ring-necked Snake | *Diadophis punctatus* | 164 | 164 | - | | | Yes |
| | Lizard | San Diego Banded Gecko | *Coleonyx variegatus abbotti* | 158 | 158 | - | 3 | Yes | |
| | Salamander | Northwestern Salamander | *Ambystoma gracile* | 152 | 152 | - | | | |
| | Toad | Great Basin Spadefoot | *Spea intermontana* | 152 | 152 | - | | | |
| | Toad | Red-spotted Toad | *Anaxyrus punctatus* | 147 | 147 | 72 | | | |
| | Salamander | Long-toed Salamander | *Ambystoma macrodactylum* | 143 | 143 | - | | | |
| | Lizard | Orange-throated Whiptail | *Aspidoscelis hyperythra* | 137 | 137 | - | | | |
| | Snake | Smith's Black-headed Snake | *Tantilla hobartsmithi* | 136 | 136 | - | | | |
| | Snake | California Black-headed Snake | *Tantilla planiceps* | 133 | 133 | - | | | |
| | Lizard | Western Whiptail | *Aspidoscelis tigris* | 118 | 118 | - | | | |
| | Salamander | Coastal Giant Salamander | *Dicamptodon tenebrosus* | 117 | 117 | 48 | | | |
| | Lizard | Western Banded Gecko | *Coleonyx variegatus* | 105 | 105 | - | | | |
| | Lizard | Common Chuckwalla | *Sauromalus ater* | 78 | 78 | - | | | |
| | Snake | Northern Rubber Boa | *Charina bottae* | 77 | 77 | - | | | |
| | Snake | Southern Rubber Boa | *Charina umbratica* | 77 | 77 | - | THR | | |
| | Snake | Northern Three-lined Boa | *Lichanura orcutti* | 77 | 77 | - | | | |
| | Lizard | Desert Iguana | *Dipsosaurus dorsalis* | 72 | 72 | - | | | |
| | Snake | Forest Sharp-tailed Snake | *Contia longicauda* | 70 | 70 | - | | | |
| | Snake | Common Sharp-tailed Snake | *Contia tenuis* | 70 | 70 | - | | | |
| | Frog | Pacific Treefrog | *Pseudacris regilla* | 68 | 68 | 36 | | | |

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking
[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species
[d] California Amphibian and Reptile Crossing Preliminary Investigation

objective analysis and the probability that roads are listed as a potential threat to the species in the species listing literature.

Although more than 40% of special status species are semi-aquatic, roads were rarely considered a threat to aquatic connectivity in the species literature. This may be accurate if bridges or large culverts currently exist for water flow that also provide permeability to aquatic movement. Bridges are generally considered to be completely passable by all aquatic species. Bridges are more likely to be constructed adjacent to or over large water bodies and rivers, presumably resulting in less risk to aquatic movement of populations that inhabit lake and river systems. However, culverts that are more commonly constructed under roads in streams and wetlands vary in passability depending on factors such as diameter, length, slope, outlet configuration, and other characteristics (Furniss et al. 1991; Clarkin et al. 2005; Kemp and O'Hanley 2010). In fact, Januchowski-Hartley et al. (2013) found that only 36% of road crossings were fully passable to fish in the Great Lakes basin. In addition, many low water crossings in arid regions of the state are simply a dip in the road that allows water to flow

**Table 8** continued

| | Species | | | Road Risk Scores | | | Status | | |
|---|---|---|---|---|---|---|---|---|---|
| Risk Level-Species | Group | Common Name | Scientific name | Maximum (Aquatic & Terrestrial)[a] | Terrestrial | Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent) | Federal or State Listing/ ARSSC Priority Rank (1-3)[b] | Roads Listed as Potential Threat in Listing?[c] | Caltrans Identified Sensitive Species?[d] |
| Low | Salamander | Scott Bar Salamander | *Plethodon asupak* | 62 | 62 | - | THR | | |
| | Salamander | Dunn's Salamander | *Plethodon dunni* | 62 | 62 | - | | | |
| | Salamander | Del Norte Salamander | *Plethodon elongatus* | 62 | 62 | - | | | |
| | Salamander | Siskiyou Mountains Salamander | *Plethodon stormi* | 62 | 62 | - | THR | | |
| | Frog | California Treefrog | *Pseudacris cadaverina* | 61 | 61 | 26 | | | |
| | Salamander | Southern Torrent Salamander | *Rhyacotriton variegatus* | 61 | 61 | 5 | 1 | | |
| | Lizard | Peninsula Leaf-toed Gecko | *Phyllodactylus nocticolus* | 60 | 60 | - | | | |
| | Lizard | Northern Alligator Lizard | *Elgaria coerulea* | 60 | 60 | - | | | |
| | Frog | Coastal Tailed Frog | *Ascaphus truei* | 59 | 59 | 30 | 2 | | Yes |
| | Lizard | Common Side-blotched Lizard | *Uta stansburiana* | 59 | 59 | - | | | |
| | Lizard | Coachella Fringe-toed Lizard | *Uma inornata* | 56 | 56 | - | THR | | |
| | Lizard | Colorado Desert Fringe-toed Lizard | *Uma notata* | 56 | 56 | - | 2 | | |
| | Lizard | Mohave Fringe-toed Lizard | *Uma scoparia* | 56 | 56 | - | 3 | | |
| | Frog | Lowland Leopard Frog | *Lithobates yavapaiensis (Possibly extinct in CA)* | 54 | 31 | 54 | 1 | | |
| | Frog | Southern Mountain Yellow-legged Frog | *Rana muscosa* | 54 | 26 | 54 | END | | |
| | Lizard | Zebra-tailed Lizard | *Callisaurus draconoides* | 54 | 54 | - | | | |
| | Salamander | Wandering Salamander | *Aneides vagrans* | 53 | 53 | - | | | |
| | Salamander | Slender Salamanders | *Batrachoseps (genus: 20 spp.)* | 53 | 53 | - | END[e] | | |
| Very Low | Salamander | Ensatina | *Ensatina eschscholtzii* | 51 | 51 | - | | | |
| | Salamander | Yellow-blotched Ensatina | *Ensatina eschscholtzii croceater* | 51 | 51 | - | | | |
| | Salamander | Large-blotched Ensatina | *Ensatina eschscholtzii klauberi* | 51 | 51 | - | | | |
| | Lizard | Southern Alligator Lizard | *Elgaria multicarinata* | 51 | 51 | - | | | |
| | Lizard | Panamint Alligator Lizard | *Elgaria panamintina* | 51 | 51 | - | 3 | | |
| | Frog | Sierra Nevada Yellow-legged Frog | *Rana sierrae* | 51 | 51 | 36 | THR | | |
| | Lizard | Western Fence Lizard | *Sceloporus occidentalis* | 49 | 49 | - | | | |
| | Salamander | Limestone Salamander | *Hydromantes brunus* | 48 | 48 | - | THR | | |
| | Salamander | Mount Lyell Salamander | *Hydromantes platycephalus* | 48 | 48 | - | | | |
| | Salamander | Clouded Salamander | *Aneides ferreus* | 44 | 44 | - | | | |
| | Salamander | Arboreal Salamander | *Aneides lugubris* | 44 | 44 | - | | | |
| | Lizard | Granite Spiny Lizard | *Sceloporus orcutti* | 43 | 43 | - | | | |
| | Snake | Western Blind Snake | *Rena humilis* | 42 | 42 | - | | | |
| | Lizard | Desert Spiny Lizard | *Sceloporus magister* | 41 | 41 | - | | | |
| | Lizard | Common Sagebrush Lizard | *Sceloporus graciosus* | 39 | 41 | - | | | |
| | Lizard | Gilbert's Skink | *Plestiodon gilberti* | 39 | 39 | - | | | |
| | Lizard | Western Skink | *Plestiodon skiltonianus* | 39 | 39 | - | | | |
| | Lizard | California Legless Lizard | *Anniella pulchra* | 35 | 39 | - | 2 | | |
| | Salamander | Black Salamander | *Aneides flavipunctatus* | 35 | 35 | - | | | |
| | Salamander | Santa Cruz Black Salamander | *Aneides flavipunctatus niger* | 35 | 35 | - | | | |
| | Lizard | Baja California Collared Lizard | *Crotaphytus vestigium* | 35 | 35 | - | | | |
| | Lizard | Sandstone Night Lizard | *Xantusia gracilis* | 33 | 33 | - | 3 | | |
| | Lizard | Granite Night Lizard | *Xantusia henshawi* | 33 | 33 | - | | | |
| | Lizard | Island Night Lizard | *Xantusia riversiana* | 33 | 33 | - | THR | | |
| | Lizard | Sierra Night Lizard | *Xantusia sierrae* | 33 | 33 | - | 1 | | |
| | Lizard | Desert Night Lizard | *Xantusia vigilis* | 33 | 33 | - | | | |
| | Lizard | Wiggins' Night Lizard | *Xantusia wigginsi* | 33 | 33 | - | | | |
| | Lizard | Long-tailed Brush Lizard | *Urosaurus graciosus* | 27 | 27 | - | | | |
| | Lizard | Baja California Brush Lizard | *Urosaurus nigricaudus* | 27 | 27 | - | | | |
| | Lizard | Ornate Tree Lizard | *Urosaurus ornatus* | 27 | 27 | - | | | |
| | Lizard | Mearns' Rock Lizard | *Petrosaurus mearnsi* | 21 | 21 | - | | | |

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

[e] 4 Batrachoseps species with conservation status

**Table 9** Terrestrial risk ranking and population buffer distances

| Risk Level (Terrestrial) | | Species | | | Risk Scores (Terrestrial) | | Movement Distances (Terrestrial) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Very High | Very High | Snake | San Joaquin Coachwhip | *Masticophis flagellum ruddocki* | 689 | 285 | 1618 | High | *M. fulginosus* |
| | Very High | Snake | Alameda Striped Racer | *Masticophis lateralis euryxanthus* | 652 | 221 | 631 | Med/High | |
| | Very High | Tortoise | Mohave Desert Tortoise | *Gopherus agassizii* | 580 | 240 | 1155 | High | |
| | Very High | Salamander | Red-bellied Newt | *Taricha rivularis* | 561 | 228 | 1600 | High | |
| | Very High | Snake | Baja California Coachwhip | *Masticophis fuliginosus* | 534 | 285 | 1904 | High | |
| | Very High | Snake | Coast Patch-nosed Snake | *Salvadora hexalepis virgultea* | 533 | 221 | 631 | Low | *M. lateralis* |
| | Very High | Salamander | California Newt | *Taricha torosa* | 532 | 228 | 2500 | Med/High | |
| | Very High | Lizard | Banded Gila Monster | *Heloderma suspectum cinctum* | 446 | 210 | 1250 | High | |
| | High | Salamander | California Tiger Salamander | *Ambystoma californiense* | 437 | 152 | 1849 | Med/High | |
| | Very High | Salamander | Sierra Newt | *Taricha sierrae* | 437 | 228 | 2050 | Med | *T. torosa, T. rivularis* |
| | Very High | Snake | Striped Whipsnake | *Masticophis taeniatus* | 425 | 300 | 2380 | Med | |
| | Very High | Lizard | Flat-tail Horned Lizard | *Phrynosoma mcallii* | 425 | 217 | 788 | Med/High | |
| | High | Lizard | Blunt-nosed Leopard Lizard | *Gambelia sila* | 393 | 133 | 510 | High | |
| | Very High | Snake | Baja California Ratsnake | *Bogertophis rosaliae* | 387 | 238 | 780 | Low | *Elaphe obsoleta* |
| | Very High | Snake | Panamint Rattlesnake | *Crotalus stephensi* | 387 | 238 | 938 | Med | *C. mitchelli* |
| | High | Frog | California Red-legged Frog | *Rana draytonii* | 380 | 152 | 2360 | High | |
| | High | Toad | Yosemite Toad | *Anaxyrus canorus* | 379 | 128 | 1152 | Med/High | |
| | High | Toad | Black Toad | *Anaxyrus exsul* | 379 | 128 | 951 | Low | *A. canorus, A. punctatus* |
| | High | Lizard | Cope's Leopard Lizard | *Gambelia copeii* | 372 | 175 | 643 | Low/Med | *G. wislenzii* |
| | High | Toad | Sonoran Desert Toad | *Incilius alvarius (Possibly extinct in CA)* | 361 | 152 | 1400 | Low/Med | *A. cognatus* |
| | Very High | Lizard | Desert Horned Lizard | *Phrynosoma platyrhinos* | 356 | 259 | 1308 | Med/High | |
| | High | Snake | California Glossy Snake | *Arizona elegans occidentalis* | 340 | 154 | 316 | Low | *R. leconti* |
| | Very High | Snake | North American Racer | *Coluber constrictor* | 334 | 308 | 1800 | Med | |
| | Very High | Snake | Coachwhip | *Masticophis flagellum* | 333 | 285 | 1618 | High | *M. fulginosus* |
| | High | Toad | Arroyo Toad | *Anaxyrus californicus* | 331 | 128 | 1082 | Med/High | |
| | Very High | Snake | Striped Racer | *Masticophis lateralis* | 322 | 221 | 631 | Med | |
| High | High | Snake | Red Diamond Rattlesnake | *Crotalus ruber* | 321 | 175 | 853 | High | |
| | Very High | Snake | Speckled Rattlesnake | *Crotalus mitchellii* | 317 | 238 | 938 | High | |
| | Med | Salamander | Santa Cruz Long-toed Salamander | *Ambystoma macrodactylum croceum* | 308 | 104 | 700 | High | |
| | Very High | Salamander | Rough-skinned Newt | *Taricha granulosa* | 304 | 228 | 2050 | Med | *T. torosa, T. rivularis* |
| | High | Snake | Regal Ring-necked Snake | *Diadophis punctatus regalis* | 298 | 152 | 566 | Low/Med | |
| | Very High | Snake | California Lyresnake | *Trimorphodon lyrophanes* | 293 | 195 | 800 | Low | |
| | High | Frog | Northern Red-legged Frog | *Rana aurora* | 291 | 152 | 2360 | Med | *R. draytonii* |
| | High | Turtle | Southern Western Pond Turtle | *Actinemys pallida* | 283 | 128 | 309 | Med-High | |
| | High | Snake | Mojave Rattlesnake | *Crotalus scutulatus* | 276 | 189 | 815 | Med/High | |
| | Very High | Snake | Western Patch-nosed Snake | *Salvadora hexalepis* | 276 | 221 | 631 | Low | *M. lateralis* |
| | High | Snake | Sidewinder | *Crotalus cerastes* | 263 | 186 | 767 | High | |
| | Med | Salamander | California Giant Salamander | *Dicamptodon ensatus* | 260 | 120 | 600 | Low | *D. tenebrosus* |
| | Very High | Snake | Sonoran Lyresnake | *Trimorphodon lambda* | 260 | 195 | 800 | Low | |
| | Very High | Snake | Western Rattlesnake | *Crotalus oreganus* | 250 | 231 | 1096 | Med/High | |
| | High | Snake | Desert Nightsnake | *Hypsiglena chlorophaea* | 241 | 175 | 566 | Low | *D. punctatus* |
| | Med | Snake | San Francisco Gartersnake | *Thamnophis sirtalis tetrataenia* | 238 | 81 | 300 | Med | |
| | Med | Lizard | Switak's Banded Gecko | *Coleonyx switaki* | 236 | 90 | 200 | Low | *C. variegatus (AZ)* |
| | Med | Toad | Western Spadefoot | *Spea hammondii* | 234 | 104 | 670 | Med | |
| | High | Snake | Coast Nightsnake | *Hypsiglena ochrorhyncha* | 233 | 175 | 566 | Low | *D. punctatus* |
| | High | Lizard | Long-nosed Leopard Lizard | *Gambelia wislizenii* | 226 | 175 | 643 | Med/High | |
| | High | Toad | Great Plains Toad | *Anaxyrus cognatus* | 222 | 152 | 1400 | Med/High | |
| | High | Toad | Woodhouse's Toad | *Anaxyrus woodhousii* | 222 | 152 | 1400 | Low | *A. cognatus* |
| | Med | Lizard | Coastal Whiptail | *Aspidoscelis tigris stejnegeri* | 219 | 105 | 300 | Low | *A. hyperythra (multiplied by 2 for body size)* |
| | High | Turtle | Northern Western Pond Turtle | *Actinemys marmorata* | 219 | 128 | 448 | Med | |
| | High | Snake | Western Shovel-nosed Snake | *Chionactis occipitalis* | 218 | 154 | 400 | Low | |
| | High | Snake | Spotted Leaf-nosed Snake | *Phyllorhynchus decurtatus* | 218 | 154 | 400 | Low | *C. occipitalis, M. taeniatus* |
| | Med | Salamander | Southern Long-toed Salamander | *Ambystoma macrodactylum sigillatum* | 217 | 104 | 700 | Med | |
| | Med | Frog | Cascades Frog | *Rana cascadae* | 217 | 104 | 759 | High | |
| | High | Snake | Western Diamond-backed Rattlesnake | *Crotalus atrox* | 214 | 147 | 484 | Med | |
| | High | Snake | Western Groundsnake | *Sonora semiannulata* | 212 | 154 | 400 | Low | *C. occipitalis* |
| | Med | Snake | California Red-sided Gartersnake | *Thamnophis sirtalis infernalis* | 211 | 81 | 300 | Low/Med | *T.s. tetrataenia* |

**Table 9** continued

| Risk Level (Terrestrial) | | Species | | | Risk Scores (Terrestrial) | | Movement Distances (Terrestrial) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Medium | Med | Lizard | Blainville's Horned Lizard | *Phrynosoma blainvillii* | 209 | 114 | 495 | Med | |
| | Med | Snake | Two-striped Gartersnake | *Thamnophis hammondii* | 195 | 81 | 239 | Low/Med | |
| | High | Snake | Gopher Snake | *Pituophis catenifer* | 189 | 189 | 820 | Med/High | |
| | High | Snake | California Mountain Kingsnake | *Lampropeltis zonata* | 184 | 147 | 501 | Low/Med | *L. getula, L. triangulum* |
| | High | Snake | Glossy Snake | *Arizona elegans* | 180 | 154 | 316 | Low | *R. lecontii* |
| | Med | Lizard | Pygmy Short-horned Lizard | *Phrynosoma douglasii* | 179 | 123 | 400 | Low | *P. mccallii (reduced 0.5 for body size)* |
| | Med | Toad | Couch's Spadefoot | *Scaphiopus couchii* | 178 | 104 | 670 | Med | |
| | High | Snake | California Kingsnake | *Lampropeltis californiae* | 175 | 175 | 501 | Med/High | |
| | High | Snake | Long-nosed Snake | *Rhinocheilus lecontei* | 165 | 132 | 337 | Low/Med | |
| | High | Snake | Common Gartersnake | *Thamnophis sirtalis* | 165 | 137 | 532 | Low/Med | |
| | High | Toad | Western Toad | *Anaxyrus boreas* | 165 | 152 | 2144 | Med/High | |
| | High | Snake | Ring-necked Snake | *Diadophis punctatus* | 164 | 136 | 566 | Low/Med | |
| | Med | Lizard | San Diego Banded Gecko | *Coleonyx variegatus abbotti* | 158 | 84 | 200 | Low/Med | *C. variegatus (AZ)* |
| | Med | Salamander | Northwestern Salamander | *Ambystoma gracile* | 152 | 104 | 700 | Low | *A. macrodactylum croceum* |
| | Med | Toad | Great Basin Spadefoot | *Spea intermontana* | 152 | 104 | 670 | Med | |
| | Med | Toad | Red-spotted Toad | *Anaxyrus punctatus* | 147 | 104 | 750 | Low | |
| | Med | Salamander | Long-toed Salamander | *Ambystoma macrodactylum* | 143 | 104 | 700 | Med | |
| | Med | Snake | Northwestern Gartersnake | *Thamnophis ordinoides* | 138 | 95 | 239 | Low | *T. hammondii* |
| | Med | Lizard | Orange-throated Whiptail | *Aspidoscelis hyperythra* | 137 | 84 | 150 | Low/Med | |
| | Med | Snake | Smith's Black-headed Snake | *Tantilla hobartsmithi* | 136 | 105 | 150 | Low | |
| | Med | Snake | California Black-headed Snake | *Tantilla planiceps* | 133 | 84 | 150 | Low | |
| | Med | Lizard | Western Whiptail | *Aspidoscelis tigris* | 118 | 105 | 300 | Low | *A. hyperythra (multiplied by 2 for body size)* |
| | Med | Salamander | Coastal Giant Salamander | *Dicamptodon tenebrosus* | 117 | 80 | 600 | Low/Med | |
| | Med | Lizard | Western Banded Gecko | *Coleonyx variegatus* | 105 | 84 | 200 | Low/Med | *C. variegatus (AZ)* |
| | Med | Lizard | Common Chuckwalla | *Sauromalus ater* | 78 | 78 | 296 | Med | |
| | Med | Snake | Northern Rubber Boa | *Charina bottae* | 77 | 77 | 230 | Low/Med | *L. trivirgata* |
| | Med | Snake | Southern Rubber Boa | *Charina umbratica* | 77 | 77 | 230 | Low/Med | *L. trivirgata* |
| | Med | Snake | Northern Three-lined Boa | *Lichanura orcutti* | 77 | 77 | 230 | Med/High | |
| | Med | Snake | Western Terrestrial Gartersnake | *Thamnophis elegans* | 75 | 75 | 104 | Low/Med | *T.gigas (-40% for size diff)* |
| | Med | Lizard | Desert Iguana | *Dipsosaurus dorsalis* | 72 | 72 | 150 | Low/Med | |
| | Med | Snake | Forest Sharp-tailed Snake | *Contia longicauda* | 70 | 70 | 150 | Low | |
| | Med | Snake | Common Sharp-tailed Snake | *Contia tenuis* | 70 | 70 | 150 | Low | |
| | Med | Snake | Checkered Gartersnake | *Thamnophis marcianus* | 69 | 69 | 239 | Low | *T. hammondii* |
| | Med | Frog | Pacific Treefrog | *Pseudacris regilla* | 68 | 68 | 400 | Low/Med | |
| Low | Low | Salamander | Scott Bar Salamander | *Plethodon asupak* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Salamander | Dunn's Salamander | *Plethodon dunni* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Salamander | Del Norte Salamander | *Plethodon elongatus* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Salamander | Siskiyou Mountains Salamander | *Plethodon stormi* | 62 | 62 | 92 | Low | *P. glutinosus* |
| | Low | Frog | California Treefrog | *Pseudacris cadaverina* | 61 | 61 | 50 | Low/Med | |
| | Low | Salamander | Southern Torrent Salamander | *Rhyacotriton variegatus* | 61 | 61 | 50 | Low | *R. cascadae* |
| | Low | Lizard | Peninsula Leaf-toed Gecko | *Phyllodactylus nocticolus* | 60 | 60 | 200 | Low | *C. variegatus (AZ)* |
| | Low | Lizard | Northern Alligator Lizard | *Elgaria coerulea* | 60 | 60 | 106 | Med | |
| | Low | Frog | Coastal Tailed Frog | *Ascaphus truei* | 59 | 59 | 150 | Med/High | |
| | Low | Lizard | Common Side-blotched Lizard | *Uta stansburiana* | 59 | 59 | 152 | Med/High | |
| | Low | Lizard | Coachella Fringe-toed Lizard | *Uma inornata* | 56 | 56 | 52 | Med/High | |
| | Low | Lizard | Colorado Desert Fringe-toed Lizard | *Uma notata* | 56 | 56 | 75 | Med/High | |
| | Low | Lizard | Mohave Fringe-toed Lizard | *Uma scoparia* | 56 | 56 | 64 | Med | *U. notata, U. inornata* |
| | Low | Lizard | Zebra-tailed Lizard | *Callisaurus draconoides* | 54 | 54 | 150 | Med | |
| | Low | Salamander | Wandering Salamander | *Aneides vagrans* | 53 | 53 | 39 | Med/High | |
| | Low | Salamander | Slender Salamanders (20 species) | *Batrachoseps (genus)* | 53 | 53 | 50 | Low/Med | *B. pacificus* |

**Table 9** continued

| Risk Level (Terrestrial) | | Species | | | Risk Scores (Terrestrial) | | Movement Distances (Terrestrial) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Very Low | Very Low | Salamander | Ensatina | *Ensatina eschscholtzii* | 51 | 51 | 75 | Med | |
| | Very Low | Salamander | Yellow-blotched Ensatina | *Ensatina eschscholtzii croceater* | 51 | 51 | 75 | Med | |
| | Very Low | Salamander | Large-blotched Ensatina | *Ensatina eschscholtzii klauberi* | 51 | 51 | 75 | Med | *E. eschscholtzii croceater* |
| | Very Low | Lizard | Southern Alligator Lizard | *Elgaria multicarinata* | 51 | 51 | 106 | Low/Med | *E. coerulea* |
| | Very Low | Lizard | Panamint Alligator Lizard | *Elgaria panamintina* | 51 | 51 | 106 | Low/Med | *E. coerulea* |
| | Very Low | Frog | Sierra Nevada Yellow-legged Frog | *Rana sierrae* | 51 | 51 | 420 | Med | |
| | Very Low | Lizard | Western Fence Lizard | *Sceloporus occidentalis* | 49 | 49 | 160 | Med | |
| | Very Low | Salamander | Limestone Salamander | *Hydromantes brunus* | 48 | 48 | 80 | Low | |
| | Very Low | Salamander | Mount Lyell Salamander | *Hydromantes platycephalus* | 48 | 48 | 80 | Low | |
| | Very Low | Salamander | Clouded Salamander | *Aneides ferreus* | 44 | 44 | 39 | Med | *A. vagrans* |
| | Very Low | Salamander | Arboreal Salamander | *Aneides lugubris* | 44 | 44 | 39 | Med | *A. vagrans* |
| | Very Low | Snake | Giant Gartersnake | *Thamnophis gigas* | 44 | 44 | 174 | High | |
| | Very Low | Snake | Sierra Gartersnake | *Thamnophis couchii* | 44 | 44 | 115 | Low/Med | *T.gigas (~34% for size diff)* |
| | Very Low | Lizard | Granite Spiny Lizard | *Sceloporus orcutti* | 43 | 43 | 91 | Low/Med | |
| | Very Low | Snake | Western Blind Snake | *Rena humilis* | 42 | 42 | 50 | Low | |
| | Very Low | Lizard | Desert Spiny Lizard | *Sceloporus magister* | 41 | 41 | 91 | Low | |
| | Very Low | Frog | Oregon Spotted Frog | *Rana pretiosa (Possibly extinct in CA)* | 41 | 41 | 100 | Low | |
| | Very Low | Lizard | Common Sagebrush Lizard | *Sceloporus graciosus* | 41 | 41 | 41 | Med/High | |
| | Very Low | Snake | Aquatic Gartersnake | *Thamnophis atratus* | 40 | 40 | 99 | Low/Med | *T.gigas (~43% for size diff)* |
| | Very Low | Lizard | Gilbert's Skink | *Plestiodon gilberti* | 39 | 39 | 93 | Low/Med | *P. skiltonianus, P. fasciatus, S. laterale* |
| | Very Low | Lizard | Western Skink | *Plestiodon skiltonianus* | 39 | 39 | 93 | Low/Med | |
| | Very Low | Lizard | California Legless Lizard | *Anniella pulchra* | 39 | 39 | 15 | High | |
| | Very Low | Turtle | Sonoran Mud Turtle | *Kinosternon sonoriense* | 37 | 37 | 60 | Med | |
| | Very Low | Salamander | Black Salamander | *Aneides flavipunctatus* | 35 | 35 | 39 | Med | *A. vagrans* |
| | Very Low | Salamander | Santa Cruz Black Salamander | *Aneides flavipunctatus niger* | 35 | 35 | 39 | Med | *A. vagrans* |
| | Very Low | Lizard | Great Basin Collared Lizard | *Crotaphytus bicinctores* | 35 | 35 | 150 | Low/Med | *C. collaris* |
| | Very Low | Lizard | Baja California Collared Lizard | *Crotaphytus vestigium* | 35 | 35 | 150 | Low/Med | *C. collaris* |
| | Very Low | Lizard | Sandstone Night Lizard | *Xantusia gracilis* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Granite Night Lizard | *Xantusia henshawi* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Island Night Lizard | *Xantusia riversiana* | 33 | 33 | 14 | High | |
| | Very Low | Lizard | Sierra Night Lizard | *Xantusia sierrae* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Desert Night Lizard | *Xantusia vigilis* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Lizard | Wiggins' Night Lizard | *Xantusia wigginsi* | 33 | 33 | 14 | Med/High | *X. riversiana* |
| | Very Low | Frog | Lowland Leopard Frog | *Lithobates yavapaiensis (Possibly extinct in CA)* | 31 | 31 | 100 | Low | |
| | Very Low | Lizard | Long-tailed Brush Lizard | *Urosaurus graciosus* | 27 | 27 | 130 | Low/Med | *S. occidentalis, S. graciosus* |
| | Very Low | Lizard | Baja California Brush Lizard | *Urosaurus nigricaudus* | 27 | 27 | 130 | Low/Med | *S. occidentalis, S. graciosus* |
| | Very Low | Lizard | Ornate Tree Lizard | *Urosaurus ornatus* | 27 | 27 | 130 | Low/Med | *S. occidentalis, S. graciosus* |
| | Very Low | Frog | Foothill Yellow-legged Frog | *Rana boylii* | 26 | 26 | 40 | Med/High | |
| | Very Low | Frog | Southern Mountain Yellow-legged Frog | *Rana muscosa* | 26 | 26 | 40 | Med | *R. boylii* |
| | Very Low | Lizard | Mearns' Rock Lizard | *Petrosaurus mearnsi* | 21 | 21 | 80 | Low/Med | |
| | Very Low | Lizard | Mearns' Rock Lizard | *Petrosaurus mearnsi* | 21 | 21 | 80 | Low/Med | |

over the surface during high flow events. These may be used as road crossings by species traveling along ephemeral stream corridors with or without water flow. Given these potential vulnerabilities, we believe that road impacts to aquatic connectivity of herpetofauna deserve greater consideration.

Across broad taxonomic groups, chelonids (tortoises/turtles) and snakes had the greatest percentages of species at 'high' or 'very high' risk from roads. They are similar in that many move long distances (home range and/or migratory), tend not to avoid roads (or are attracted to them for thermoregulation), are long lived, and have relatively low fecundity in comparison to other herpetofaunal groups. Because of these traits, chelonids and snakes have been identified elsewhere as being particularly susceptible to negative population effects from roads (Gibbs and Shriver 2002; Andrews et al. 2015b; Jackson et al. 2015).

There are only four species of chelonids in California, (desert tortoise (*Gopherus agazzii*),

Northwestern pond turtle (*Actinemys marmorata*), Southwestern pond turtle (*Actinemys pallida*), and the Sonoran mud turtle (*Kinosternon sonoriense*)). There has been a high level of attention to road impacts on the desert tortoise (*Gopherus agazzii*) as numerous studies have documented not only high road mortality, but measurable road effect zones, and mostly positive responses to barriers and underpasses (e.g., Boarman and Sazaki 1996, 2006; Peaden et al. 2016; but see Peadon et al. 2017). Although not listed as a primary threat to pond turtle populations in California (Thomson et al. 2016), road mortality is a major concern for western pond turtle populations in Oregon (Rosenberg et al. 2009). Pond turtles travel kilometers within perennial waters and from pool to pool in intermittent aquatic habitats to forage and find mates (Goodman and Stewart 2000). In addition, females nest and lay eggs in terrestrial habitats up to 0.5 km away from water which make roads that parallel aquatic habitat a threat to both females and hatchlings (Reese and Welsh 1997; Rathbun et al. 2002; Pilliod et al. 2013). In fact, road mortality of females has been identified as a cause for male-biased sex ratios in some populations of pond turtles and other freshwater turtle species (Steen et al. 2006; Rosenberg et al. 2009; Reid and Peery 2014). Therefore, this species requires consideration of both aquatic and terrestrial connectivity to satisfy their annual resource requirements. Sonoran mud turtles also travel long distances within intermittent streams and thus may be at risk of roads that transect their aquatic habitat (Hensley et al. 2010).

Larger colubrid snakes (Family Colubridae; many genera) and rattlesnakes (genus *Crotalus*) were ranked among the highest risk from negative road effects. In addition to being attracted to paved road surfaces for thermoregulation, many large snakes have wide home-ranges or may move large distances between winter hibernacula and summer foraging areas. In contrast to smaller species, larger snakes are also less likely to avoid roads (Rosen and Lowe 1994; Andrews and Gibbons 2005; Andrews et al. 2008; Siers et al. 2016). High road mortality (e.g., Klauber 1931; Rosen and Lowe 1994; Jones et al. 2011), reduced abundance near roads (Rudolph et al. 1999; Jones et al. 2011), increased extinction risk (Row et al. 2007), and decreased genetic diversity (Clark et al. 2010; Hermann et al. 2017) have been documented for numerous snake species; as have positive responses to barriers and underpasses (Dodd et al. 2004; Colley et al. 2017). In our statewide risk analysis, coachwhips (genus *Masticophis/Coluber*) were amongst the highest risk groups at both the population and species-levels. These are particularly wide-ranging and very active foragers in comparison to other snake genera (Stebbins and McGinnis 2012). The coachwhip (*Masticophis flagellum)* was found to be ninefold more likely to be extirpated from habitats that were fragmented by roads and urbanization, contributing to their decline throughout California (Case and Fisher 2001; Mitrovich 2006). Similarly, habitat fragmentation from roads and urbanization were identified as primary threats to the Alameda whipsnake (*Masticophis lateralis euryxanthus* USFWS 2011). Although road use and mortality have been documented for many other terrestrial California snake species on road-riding surveys (e.g., Klauber 1931; Jones et al. 2011; Shilling and Waetjen 2017), there is a paucity of studies examining population-level effects of roads on California snake species. We could find only one such study, where presence of a highway was shown to reduce gene flow in the Western diamond-backed rattlesnake (*Crotalus atrox)* in the Sonoran Desert, AZ (Hermann et al. 2017).

Long foraging movements within aquatic habitats also contributed to the majority of garter snakes (genus: *Thamnophis*) falling within the highest road risk categories. Maintaining aquatic and wetland connectivity is of primary concern for these species. Garter snakes also use terrestrial habitats for overwintering, reproduction, and for moving among wetland or aquatic patches. Some migrate long distances to winter hibernacula, making them also susceptible to roads within adjacent terrestrial habitats (Roe et al. 2006; Jackson et al. 2015). The highly aquatic giant garter snake (*Thamnophis gigas*) had the highest aquatic road risk score. Because it moves only short distances on land (Halstead et al. 2015), mitigation may best focus on functional aquatic passages with lengths of adjacent road barriers based upon their terrestrial movement distances.

Toads were the third highest ranking group with 64% ranked in the highest risk categories. In particular, Bufonid toads (family Bufonidae) may move large distances (> 1 km) in both aquatic and terrestrial habitats to satisfy their annual resource requirements; thus 5 of 7 bufonid species ranked high or very high risk from roads. Consistent with our risk assessment

**Table 10** Aquatic risk ranking and population buffer distances

| Risk Level (Aquatic) | | Species | | | Risk Scores (Aquatic) | | Movement Distances (Aquatic) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Population | Group | Common Name | Scientific name | Road Risk: Species- Level | Road Risk: Population-Level | 95% Population Movement Distance (m) | Confidence in Distance Estimate | Surrogate Used |
| Very High | Very High | Snake | Giant Gartersnake | *Thamnophis gigas* | 710 | 240 | 1556 | Med/High | |
| | Very High | Turtle | Southern Western Pond Turtle | *Actinemys pallida* | 707 | 320 | 3145 | High | |
| | Very High | Snake | San Francisco Gartersnake | *Thamnophis sirtalis tetrataenia* | 663 | 224 | 1146 | Med | *T. sirtalis* |
| | Very High | Snake | California Red-sided Gartersnake | *Thamnophis sirtalis infernalis* | 588 | 224 | 1146 | Med | *T. sirtalis* |
| | Very High | Turtle | Northern Western Pond Turtle | *Actinemys marmorata* | 547 | 320 | 3145 | High | *A. pallida* |
| | Very High | Snake | Two-striped Gartersnake | *Thamnophis hammondii* | 541 | 224 | 979 | Low | *T.gigas (-37% for size diff)* |
| | High | Turtle | Sonoran Mud Turtle | *Kinosternon sonoriense* | 399 | 168 | 1000 | Med | |
| High | Med | Frog | Oregon Spotted Frog | *Rana pretiosa (Possibly extinct in CA)* | 315 | 120 | 1300 | Low | |
| | Very High | Snake | Sierra Gartersnake | *Thamnophis couchii* | 304 | 192 | 1021 | Low | *T.gigas (-34% for size diff)* |
| | Med | Frog | California Red-legged Frog | *Rana draytonii* | 300 | 120 | 1864 | High | |
| | Med | Toad | Sonoran Desert Toad | *Incilius alvarius (Possibly extinct in CA)* | 285 | 120 | 1400 | Low/Med | *A. cognatus* |
| | Med | Toad | Yosemite Toad | *Anaxyrus canorus* | 284 | 96 | 1152 | Med/High | |
| | Med | Toad | Black Toad | *Anaxyrus exsul* | 284 | 96 | 951 | Low/Med | *A. canorus, A. punctatus* |
| | Very High | Snake | Common Gartersnake | *Thamnophis sirtalis* | 271 | 224 | 1146 | Med | |
| | High | Snake | Aquatic Gartersnake | *Thamnophis atratus* | 266 | 168 | 889 | Low | *T.gigas (-43% for size diff)* |
| | Med | Toad | Arroyo Toad | *Anaxyrus californicus* | 248 | 96 | 1000 | Med/High | |
| | High | Snake | Northwestern Gartersnake | *Thamnophis ordinoides* | 245 | 168 | 775 | Low | *T.gigas (-50% for size diff)* |
| | Very High | Snake | Western Terrestrial Gartersnake | *Thamnophis elegans* | 240 | 192 | 931 | Low | *T.gigas (-40% for size diff)* |
| | Med | Frog | Northern Red-legged Frog | *Rana aurora* | 230 | 120 | 1864 | Med | *R. draytonii* |
| Medium | High | Snake | Checkered Gartersnake | *Thamnophis marcianus* | 210 | 144 | 835 | Low | *T.gigas (-46% for size diff)* |
| | Med | Frog | Foothill Yellow-legged Frog | *Rana boylii* | 199 | 90 | 2420 | Med/High | |
| | Med | Toad | Great Plains Toad | *Anaxyrus cognatus* | 175 | 120 | 1400 | Med/High | |
| | Med | Toad | Woodhouse's Toad | *Anaxyrus woodhousii* | 175 | 120 | 1400 | Low/Med | *A. cognatus* |
| | Med | Toad | Western Toad | *Anaxyrus boreas* | 130 | 120 | 1274 | Low/Med | |
| | Med | Salamander | Red-bellied Newt | *Taricha rivularis* | 72 | 72 | 600 | High | |
| | Med | Salamander | California Newt | *Taricha torosa* | 72 | 72 | 600 | Med/High | *T. rivularis* |
| | Med | Salamander | Sierra Newt | *Taricha sierrae* | 72 | 72 | 600 | Med | *T. rivularis* |
| | Med | Salamander | Rough-skinned Newt | *Taricha granulosa* | 72 | 72 | 600 | Med | *T. rivularis* |
| | Med | Salamander | California Giant Salamander | *Dicamptodon ensatus* | 72 | 72 | 600 | Low | *Educated guess* |
| | Med | Frog | Cascades Frog | *Rana cascadae* | 72 | 72 | 759 | High | |
| | Med | Toad | Red-spotted Toad | *Anaxyrus punctatus* | 72 | 72 | 750 | Med | |
| Low | Low | Frog | Lowland Leopard Frog | *Lithobates yavapaiensis (Possibly extinct in CA)* | 54 | 54 | 900 | Low | |
| | Low | Frog | Southern Mountain Yellow-legged Frog | *Rana muscosa* | 54 | 54 | 665 | Med | |
| Very Low | Very Low | Salamander | Coastal Giant Salamander | *Dicamptodon tenebrosus* | 48 | 48 | 600 | Low | *Educated guess* |
| | Very Low | Frog | Pacific Treefrog | *Pseudacris regilla* | 36 | 36 | 400 | Low | *Educated guess* |
| | Very Low | Frog | Sierra Nevada Yellow-legged Frog | *Rana sierrae* | 36 | 36 | 525 | Med/High | |
| | Very Low | Frog | Coastal Tailed Frog | *Ascaphus truei* | 30 | 30 | 266 | Med/High | |
| | Very Low | Frog | California Treefrog | *Pseudacris cadaverina* | 26 | 26 | 200 | Low/Med | |
| | Very Low | Salamander | Southern Torrent Salamander | *Rhyacotriton variegatus* | 5 | 5 | 50 | Low/Med | *R. cascadae* |

results, there is evidence that bufonid toads are particularly susceptible to negative impacts from roads elsewhere (Trenham et al. 2003; Orłowski 2007; Eigenbrod et al. 2008).

Roads and traffic have been associated with reduced abundance and species richness of frog populations (e.g., Fahrig et al. 1995; Houlahan and Findlay 2003). However, approximately half of California species are small, primarily aquatic, highly fecund, with relatively limited movements and thus ranked low for road impacts. Four of 11 species ranked within the highest risk groupings; California red-legged frog (*Rana draytonii*), Oregon spotted frog (*R. pretiosa*), Northern red-legged frog (*R. aurora*), and Cascades frog (*R. cascadae*). The Oregon spotted frog (*R. pretiosa*) is known to move large distances within aquatic habitats (Bourque 2008; USFWS 2009). Construction of a highway that bisected the

Yellowstone population of Oregon spotted frogs was one important factor that reduced the population dramatically in the 1950s (see discussion in Watson et al. 2003). Although portions of the populations show high site fidelity, California red-legged frog and Northern red-legged frog migrants can move large distances (> 1 km) across both aquatic and terrestrial habitats (Bulger et al. 2003; Fellers and Kleeman 2007; Hayes et al. 2007). Road mortality or habitat fragmentation from roads and urbanization were listed as primary threats to these species elsewhere (USFWS 2002; COSEWIC 2015).

Lizards had relatively low percentages of species in the high risk groupings. Many lizard species are small, non-migratory, territorial, have small home ranges and are thus at low risk of negative road effects. Similar to snakes, lizards can also be attracted to road surfaces for thermoregulation. A few wide ranging species scored in the highest risk categories including the Gila monster (*Heloderma suspectum*), leopard lizards (genus *Gambelia*) and two horned lizard species (genus *Phrynosoma*). The Gila monster has been negatively associated with urbanization, where larger home ranges and greater movement rates result in higher mortality for males (Kwiatkowski et al. 2008). Sensitive to habitat fragmentation, the blunt-nosed leopard lizard (*Gambelia sila*) was found to be largely absent from habitat patches less than 250 ha (Bailey and Germano 2015). Flat-tailed horned lizards (*Phrynosoma mccallii*) are also susceptible to habitat fragmentation with very large home ranges for their size, particularly in wet years (Young and Young 2000). In fact, road mortality is a well-known threat for this species (see review by CDFW 2016b). Horned lizards are also particularly vulnerable to being killed on roads due to their tendency to flatten and remain motionless while being approached (Young and Young 2000).

Salamanders also had relatively low percentages of species in the high risk grouping. Over 75% (35/46) of the California salamanders are lungless salamanders (Plethodontidae) and Torrent salamanders (Rhyacotritonidae). These species are mostly small, sedentary, non-migratory, closed habitat specialists with limited movement distances and these traits have resulted in a high level of speciation. This is exemplified by there being at least 20 species of slender salamanders (genus *Batrachoseps*) in California alone (Martinez-Solano et al. 2007; Vences and Wake 2007). However, within the salamander group, newts and several other migratory salamander species were ranked within the highest risk categories from negative road effects. There is substantial evidence that habitat fragmentation and mortality due to roads negatively affect many of these species. For instance, newts regularly migrate long distances over land from and to breeding ponds, and to terrestrial foraging habitats (> 2 km; Trenham 1998). Large numbers are found dead on roads during dispersal periods and newt species are often the first to disappear in fragmented landscapes (Gibbs 1998; Trenham 1998, Shields pers. comm.). Similarly, road mortality and habitat fragmentation are primary threats to the California tiger salamander and other Ambystomid salamanders because terrestrial habitat is used for interpond migration and overwintering (Semlitsch 1998; Trenham et al. 2001; Bolster 2010).

Because this assessment covers a wide array of species and habitats, the risk to particular species populations must be re-assessed on a local level. This includes consideration of the locations, types, and densities of roads in relation to population and species ranges along with goals for functional, meta-population, and genetic connectivity (e.g., Marsh and Jaeger 2015). Due to very low road densities in their limited ranges, some species and populations may be at lower risk. For instance the Gila monster, Oregon spotted frog, Sonoran mud turtle, Sonoran desert toad (*Incilius alvarius*) and Yosemite toad (*Anaxyrus canorus*) scored high due to life history and space-use characteristics, however their limited ranges are largely in protected or low road density areas in the state. Thus roads may not be a significant threat to these species in California. In contrast, high road densities may increase the risk for species within coastal regions such as remaining populations of Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*), Alameda striped racer (*Masticophis lateralis euryxanthus*), and San Francisco garter snake (*Thamnophis sirtalis tetrataenia*). However, most species consist of numerous populations with a myriad of differing road-related threat levels. Although detailed species ranges and occupancy within ranges are well known for some species with very limited ranges, for most species range-wide surveys have not been conducted. Therefore, only general range boundaries are available that encompass large portions of the state and availability of species distribution models of habitat suitability and occupancy within their ranges is rare. This lack of detailed spatial information on species distribution

further limits the potential to incorporate road locations, types, and densities in a state and species-wide assessment.

We also note that relative risk to negative road impacts is provided for both populations and species. Risk was elevated for species with small and isolated ranges and that are facing a myriad of other threats. Because of this, a few common widespread species scored high at the population-level but not at the species-level. This included gopher snakes (*Pituophis catenifer*) and western toads (*Anaxyrus boreas*) where road mortality has been identified as a threat to the persistence of local populations (e.g., COSEWIC 2012; Jochimsen et al. 2014).

To potentially aid in local assessments, we have provided distance estimates or "buffer zones" that contain estimates for 95% of population-level movements for all species (e.g., Semlitsch and Bodie 2003). We provide all references evaluated for distance estimates in Appendix 2. Meta-population movements can be very important to the stability of pond-breeding amphibians (e.g., Semlitsch 2008; Jackson et al. 2015) and are included in many of the buffer zone calculations. However, we note that buffer zones may not include meta-population-level movements if the rate of these dispersal movements was less than 5% in the studies we used for our analyses.

This should be considered an initial assessment of susceptibility to negative road impacts in a hierarchical framework (e.g., see Level 2; Hobday et al. 2011). Therefore, as previously stated it will be important to re-assess the risk of specific populations to roads within their habitat and to evaluate and compare alternatives at the local scale (e.g., Suter 2016). This may include more detailed information on specific road attributes (e.g., density, type, location), as well as species behavior (Jaeger et al. 2005; Rouse et al. 2011; Rytwinski and Fahrig 2013; Jacobson et al. 2016). Age structured and spatially explicit population viability models are valuable tools to predict long-term population responses to roads and to compare outcomes of multiple mitigation scenarios (e.g., Gibbs and Shriver 2005; Borda-de-Água et al. 2014; Polak et al. 2014; Crawford 2015). Need and placement of mitigation structures can be guided by local population or meta-population dynamics, landscape attributes, movement routes, and road mortality hot spots (e.g., Bissonette and Adair 2008; Langen et al. 2009, 2015b; D'Amico et al. 2016; Loraamm and Downs 2016).

The quantity and quality of life history information, particularly movement data, are highly variable among species (see confidence levels; Tables 9 and 10). Therefore it is important to re-assess risk as new information becomes available. Finally, this is a structured assessment of comparative risk across a range of target species; therefore specific values for high risk have not been established. The ranking or assessment methodology should be adaptive and updated with advancements of road ecology science (e.g., Linkov et al. 2006).

## Conclusion

Although roads are a significant cause of mortality and habitat fragmentation for many wildlife populations, road-related risk rankings have been based largely on expert opinion due to a scarcity of literature on road effects for most species. Therefore, we developed an objective and scientifically-based comparative risk approach to assess the potential threat from negative road impacts using species life history and movement data. After applying it to over 160 herpetofaunal species (and subspecies) in the state of California, the results are consistent with road ecology literature in identifying known high risk species, and call attention to some species not previously identified. Overall, we found that snakes and chelonids had the largest proportion of species at high risk for negative road impacts due to longer movement distances (home range and/or migratory), lack of road avoidance, and relatively low fecundity in comparison to other herpetofaunal groups. Results also indicated that consideration of aquatic connectivity appears to be under-represented for semi-aquatic herpetofauna that use both terrestrial and stream, riverine, or wetland habitats.

In addition to informing transportation planning and mitigation considerations for California herpetofauna, we believe this approach may be useful for comparing the risk of road-related fragmentation and mortality for species elsewhere and for other taxonomic groups. The results can help to inform multi-criteria threat assessments for special status species or those in consideration for listing. Finally, this serves to highlight species that may deserve further study and consideration for aquatic and terrestrial road mitigation to reduce mortality and to maintain population-level connectivity.

This risk assessment approach compares the susceptibility of species to negative road impacts. Commonly, there are numerous populations within a species range that occupy areas with greatly differing road pressures. Therefore, the actual risk to specific species populations will depend upon local road densities, road-types, traffic, and road locations in relation to species habitat and movement corridors.

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# Chapter 3. Spatial Mapping - California Essential Habitat Connectivity Lands, Highways, and High-Risk Species

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## Introduction

The California Department of Transportation (Caltrans) and California Department of Fish and Wildlife (CDFW) commissioned the California Essential Habitat Connectivity (CEHC) Project because a functional network of connected wildlands is essential to the continued support of California's diverse natural communities in the face of human development and climate change. This report is also intended to make transportation and land-use planning more efficient and less costly, while helping reduce dangerous wildlife-vehicle collisions (Spencer et al. 2010).

The statewide essential connectivity network consists of 850 relatively intact and well conserved Natural Landscape Blocks (ranging from 2,000 to about 3.7 million acres each) with over 1,000 potential connections among them. The 192 Essential Connectivity Areas represent principle connections between the Natural Landscape Blocks within which land conservation and management actions should be prioritized to maintain and enhance ecological connectivity (Spencer et al. 2010).

CEHC maps and spatial layers depict large, relatively natural habitat blocks that support native biodiversity and areas considered essential for regional large-scale connectivity. To better represent natural areas not included in the large-scale CEHC map but large enough to support sensitive amphibian and reptile populations in California, we also incorporated smaller natural areas between 25 to 2000 acres (10 to 809 ha) that were included in the CEHC map database for regional and local scale analyses. We then combined these into a spatial geodatabase to crosswalk the CEHC Map, State Highways, and the California amphibian and reptile road risk assessment (Brehme et al. 2018).

The spatial geodatabase includes:

1. CEHC natural habitat blocks greater than 10 ha (25 ac).
2. Range maps of high and very-high risk amphibian and reptile species.
3. California highway segments that intersect the ranges of high and very high-risk amphibian and reptile species.
4. California highway segments that intersect the ranges of high and very high-risk amphibian and reptile species and CEHC lands.
5. Postmile markers of all California highway segments that intersect the ranges of high and very high-risk amphibian and reptile species and CEHC lands.
6. The total number of high and very-high risk species ranges that intersect the highway segments and CEHC lands.

This geodatabase was designed to be a useful planning tool for Caltrans to quickly identify road segments that may warrant planning for increased connectivity of high-risk amphibian and reptile species.

## Methods

The GIS analyses were conducted using ArcGIS 10.5.1 software. Species range and highway layers were obtained from Caltrans and CDFW.

### *Species Range Layers*

Species ranges were obtained from the ARSSC_DFG_HerpRoadRiskRanges shapefile provided by Dr. Amber Wright (University of Hawaii), co-author of the California amphibian and reptile species of special concern (Thomson et al. 2016), and the California Wildlife Habitat Relationships (CWHR) GIS database (downloaded from the CDFW, *https://wildlife.ca.gov/Conservation/Planning/Data-and-Tools* on June 16, 2016). Updated range layers for 4 species were provided by email from CDFW in April 2020. All species range layers were merged into a single feature class, ARSSC_DFG_CWHR_SppRoadRiskRanges (CWHR). Table 1 lists the species that were included and the source of the GIS layers.

Table 1. List of High and Very-High Risk Species and GIS Source.

| Scientific Name | Common Name | Cons. Status[a] | Species Group | GIS Source |
|---|---|---|---|---|
| *Actinemys marmorata* | Northern Western Pond Turtle | ARSSC 3 | Turtle | ARSSC (2016) |
| *Actinemys pallida* | Southern Western Pond Turtle | ARSSC 1 | Turtle | CWHR (2020) |
| *Ambystoma californiense*[1] | California Tiger Salamander | THR$^{F,S}$, END$^{F}$ | Salamander | ARSSC (2016) |
| *Ambystoma macrodactylum croceum* | Santa Cruz Long-toed Salamander | END$^{F,S}$ | Salamander | ARSSC (2016) |
| *Ambystoma macrodactylum sigillatum* | Southern Long-toed Salamander | ARSSC 2 | Salamander | CWHR (2020) |
| *Anaxyrus californicus* | Arroyo Toad | END$^{F}$,ARSSC 1 | Toad | ARSSC (2016) |
| *Anaxyrus canorus* | Yosemite Toad | THR$^{F}$,ARSSC 1 | Toad | ARSSC (2016) |
| *Anaxyrus cognatus* | Great Plains Toad | | Toad | ARSSC (2016) |
| *Anaxyrus exsul* | Black Toad | THR$^{S}$ | Toad | ARSSC (2016) |
| *Anaxyrus woodhousii* | Woodhouse's Toad | | Toad | CWHR (2016) |
| *Arizona elegans occidentalis* | California Glossy Snake | ARSSC 1 | Snake-Terrestrial | ARSSC (2016) |
| *Aspidoscelis tigris stejnegeri*[2] | San Diegan Tiger Whiptail | ARSSC 2 | Lizard | CWHR (2016) |
| *Coleonyx switaki* | Switak's Banded Gecko | THR$^{S}$ | Lizard | CWHR (2016) |
| *Coluber constrictor* | North American racer | | Snake-Terrestrial | ARSSC (2016) |
| *Crotalus atrox* | Western Diamond-backed Rattlesnake | | Snake-Terrestrial | ARSSC (2016) |
| *Crotalus cerastes* | Sidewinder | | Snake-Terrestrial | CWHR (2016) |
| *Crotalus mitchellii* | Speckled Rattlesnake | | Snake-Terrestrial | ARSSC (2016) |
| *Crotalus oreganus* | Western Rattlesnake | | Snake-Terrestrial | ARSSC (2016) |
| *Crotalus ruber* | Red Diamond Rattlesnake | ARSSC 3 | Snake-Terrestrial | ARSSC (2016) |
| *Crotalus scutulatus* | Mojave Rattlesnake | | Snake-Terrestrial | CWHR (2016) |
| *Crotalus stephensi* | Panamint Rattlesnake | | Snake-Terrestrial | ARSSC (2016) |
| *Diadophis punctatus regalis* | Regal ring-necked Snake | ARSSC 2 | Snake-Terrestrial | ARSSC (2016) |
| *Dicamptodon ensatus* | California Giant Salamander | ARSSC 3 | Salamander | ARSSC (2016) |
| *Gambelia copeii* | Cope's Leopard Lizard | ARSSC | Lizard | ARSSC (2016) |
| *Gambelia sila* | Blunt-nosed Leopard Lizard | END$^{F}$ | Lizard | ARSSC (2016) |
| *Gambelia wislizenii* | Long-nosed Leopard Lizard | | Lizard | CWHR (2016) |
| *Gopherus agassizii* | Mohave Desert tortoise | THR$^{F,S}$ | Tortoise | ARSSC (2016) |

| Scientific Name | Common Name | Cons. Status[a] | Species Group | GIS Source |
|---|---|---|---|---|
| *Heloderma suspectum cinctum* | Banded Gila Monster | ARSSC | Lizard | ARSSC (2016) |
| *Hypsiglena chlorophaea* | Desert Nightsnake | | Snake-Terrestrial | CWHR (2016) |
| *Hypsiglena ochrorhyncha* | Nightsnake | | Snake-Terrestrial | ARSSC (2016) |
| *Incilius alvarius* | Sonoran Desert Toad | ARSSC 1 | Toad | ARSSC (2016) |
| *Kinosternon sonoriense*[3] | Sonora Mud turtle | ARSSC 1 | Turtle | ARSSC (2016) |
| *Phyllorhynchus decurtatus* | Spotted Leaf-nosed Snake | ARSSC 2 | Snake-Terrestrial | CWHR (2016) |
| *Masticophis flagellum* | Coachwhip | | Snake-Terrestrial | ARSSC (2016) |
| *Masticophis flagellum ruddocki* | San Joaquin Coachwhip | ARSSC 2 | Snake-Terrestrial | ARSSC (2016) |
| *Masticophis fuliginosus* | Baja California Coachwhip | ARSSC 3 | Snake-Terrestrial | ARSSC (2016) |
| *Masticophis lateralis* | Striped Racer | | Snake-Terrestrial | ARSSC (2016) |
| *Masticophis lateralis euryxanthus* | Alameda Striped Racer | $THR^{F,S}$ | Snake-Terrestrial | CWHR (2020) |
| *Masticophis taeniatus* | Striped Whipsnake | | Snake-Terrestrial | ARSSC (2016) |
| *Phrynosoma mcallii* | Flat-tailed Horned Lizard | $THR^{F}$, ARSSC 2 | Lizard | ARSSC (2016) |
| *Phrynosoma platyrhinos* | Desert Horned Lizard | | Lizard | ARSSC (2016) |
| *Rana aurora* | Northern Red-legged Frog | ARSSC 2 | Frog | ARSSC (2016) |
| *Rana cascadae* | Cascades Frog | ARSSC 2 | Frog | CWHR (2016) |
| *Rana draytonii* | California Red-legged Frog | $THR^{F}$, ARSSC 1 | Frog | ARSSC (2016) |
| *Rana pretiosa* | Oregon Spotted Frog | $THR^{F}$, ARSSC 1 | Frog | ARSSC (2016) |
| *Salvadora hexalepis* | Western Patch-nosed Snake | | Snake-Terrestrial | ARSSC (2016) |
| *Salvadora hexalepis virgultea* | Coast Patch-nosed Snake | ARSSC 2 | Snake-Terrestrial | ARSSC (2016) |
| *Sonora occipitalis* | Western Shovel-nosed Snake | | Snake-Terrestrial | CWHR (2016) |
| *Sonora semiannulata* | Western Groundsnake | | Snake-Terrestrial | CWHR (2016) |
| *Spea hammondii* | Western Spadefoot | ARSSC 1 | Toad | ARSSC (2016) |
| *Taricha granulosa* | Rough-skinned Newt | | Salamander | ARSSC (2016) |
| *Taricha rivularis* | Red-bellied Newt | ARSSC 2 | Salamander | ARSSC (2016) |
| *Taricha sierrae* | Sierra Newt | | Salamander | ARSSC (2016) |
| *Taricha torosa* | Coast Range Newt | ARSSC 2 | Salamander | ARSSC (2016) |
| *Thamnophis atratus* | Aquatic Gartersnake | | Snake-Aquatic | ARSSC (2016) |
| *Thamnophis couchii* | Sierra Gartersnake | | Snake-Aquatic | ARSSC (2016) |
| *Thamnophis elegans* | Terrestrial Gartersnake | | Snake-Aquatic | ARSSC (2016) |
| *Thamnophis gigas* | Giant Gartersnake | $THR^{F,S}$ | Snake-Aquatic | ARSSC (2016) |
| *Thamnophis hammondii* | Two-striped Gartersnake | ARSSC 2 | Snake-Aquatic | ARSSC (2016) |
| *Thamnophis ordinoides* | Northwestern Gartersnake | | Snake-Aquatic | ARSSC (2016) |
| *Thamnophis sirtalis infernalis*[4] | California Red-sided Gartersnake | ARSSC 1 | Snake-Aquatic | ARSSC (2016) |
| *Thamnophis sirtalis tetrataenia* | San Francisco Gartersnake | $END^{F,S}$ | Snake-Aquatic | CWHR (2020) |
| *Trimorphodon lambda* | Sonoran Lyresnake | | Snake-Terrestrial | ARSSC (2016) |
| *Trimorphodon lyrophanes* | California Lyresnake | | Snake-Terrestrial | ARSSC (2016) |

[a]Conservation Status: THR=Threatened, END= Endangered, Superscripts F and S are used to delineate State and Federal listing status, ARSSC= State Species of Special Concern with Priority Ranking 1-3.

[1]California tiger salamander Sonoma and Santa Barbara distinct population segments are federally endangered while central DPS is federally threatened.

[2]Species range layer for subspecies was not available so the species range for *Aspidoscelis tigris* was used.

[3]Species range does not contain any State highways

[4]Species range layer for subspecies was not available so the species range for *Thamnophis sirtalis spp*., and the South Coast Gartersnake, were used.

## *Connectivity Areas Layers*

Essential Connectivity Areas (ECA), Natural Landscape Blocks (NLB), and Natural Areas_small (NA; Natural areas smaller than 2,000 acres that otherwise meet NLB criteria) from the Essential Connectivity Map geodatabase were provided by CDFW. The ECA and NLB were

merged together with NA areas 10 hectares or greater. The resulting layer was then dissolved into a single polygon feature class with a buffer of 100 meters added to it. This connected many of the smaller polygons. This final layer was used to identify CEHC connectivity areas that overlapped with the target species ranges.

### *Roads Layers*

Road features were obtained from the Caltrans 2012 State Highway Network (SHN) geodatabase provided by Caltrans. The roads layer was clipped to the merged Essential Habitat Connectivity layer (Merged NLB_ECA_NA areas) to create a layer of highway segments that occur in essential habitat connectivity areas. This layer was then clipped to select target species ranges (Table 1). The resulting SHN_Lines_SpeciesRanges feature class represents potential highway segments of concern where species ranges at high risk of negative road impacts intersect with both California highways and California Essential Habitat Connectivity lands. Potential highway segments of concern maps for high risk species with conservation status (threatened, endangered, and species of special concern) are presented in Figures 1–35. Potential highway segments of concern maps for high risk species with no conservation status are not presented in this report. Some species range maps are based on greater knowledge and survey efforts than others. Also, most species are patchily distributed across their known ranges. In this feature class, highway segments of concern are based upon the intersection of broad species range maps, CEHC lands, and State highways. Thus, the segments of concern likely over-represent locations of many species in relation to highways. This feature class is meant to represent potential presence of high risk herpetofauna species. Local knowledge or surveys may be needed to verify their presence or absence adjacent to specific highway segments.

Using the SHN_Lines_SpeciesRanges feature class, start and end point vertices were generated for each road segment of concern for each species (PostMileMarkers_SpeciesRanges). The nearest postmile marker along the same route was identified using the Near Analysis. Postmile marker features were identified using a State Highway Postmile shapefile obtained from Caltrans (shn204v3_TenthPM.shp). The distance from the road start/end point to the postmile the Odometer (distance in miles from start of highway to postmile), post mile marker interval, and route identifier of the marker were included in the feature class.

### *Species Density Layers*

A hexagonal grid with an area of 15 $km^2$ per grid was generated for the entire state of California using the Generate Tessellation tool. This grid was then intersected with the species range layer (ARSSC_DFG_CWHR_SppRoadRiskRanges). The Summary Statistics tool was used to calculate the number of unique species whose ranges fell within each grid cell as well as number of species per group (frogs, toads, lizards, salamanders, terrestrial and aquatic snakes, turtles, and tortoise). This species density grid was intersected with the SHN lines feature class to create a species density overlay of the road network. These features overall and by group are included in a final map package provided to Caltrans. Densities of all high and very-high risk species across the state and associated highway segments are presented in Figures 36 and 37.

## Results: Maps High and Very-High Risk Species

Figure 1. Highway Segments of Concern: Northern Western Pond Turtle (*Actinemys marmorata*)

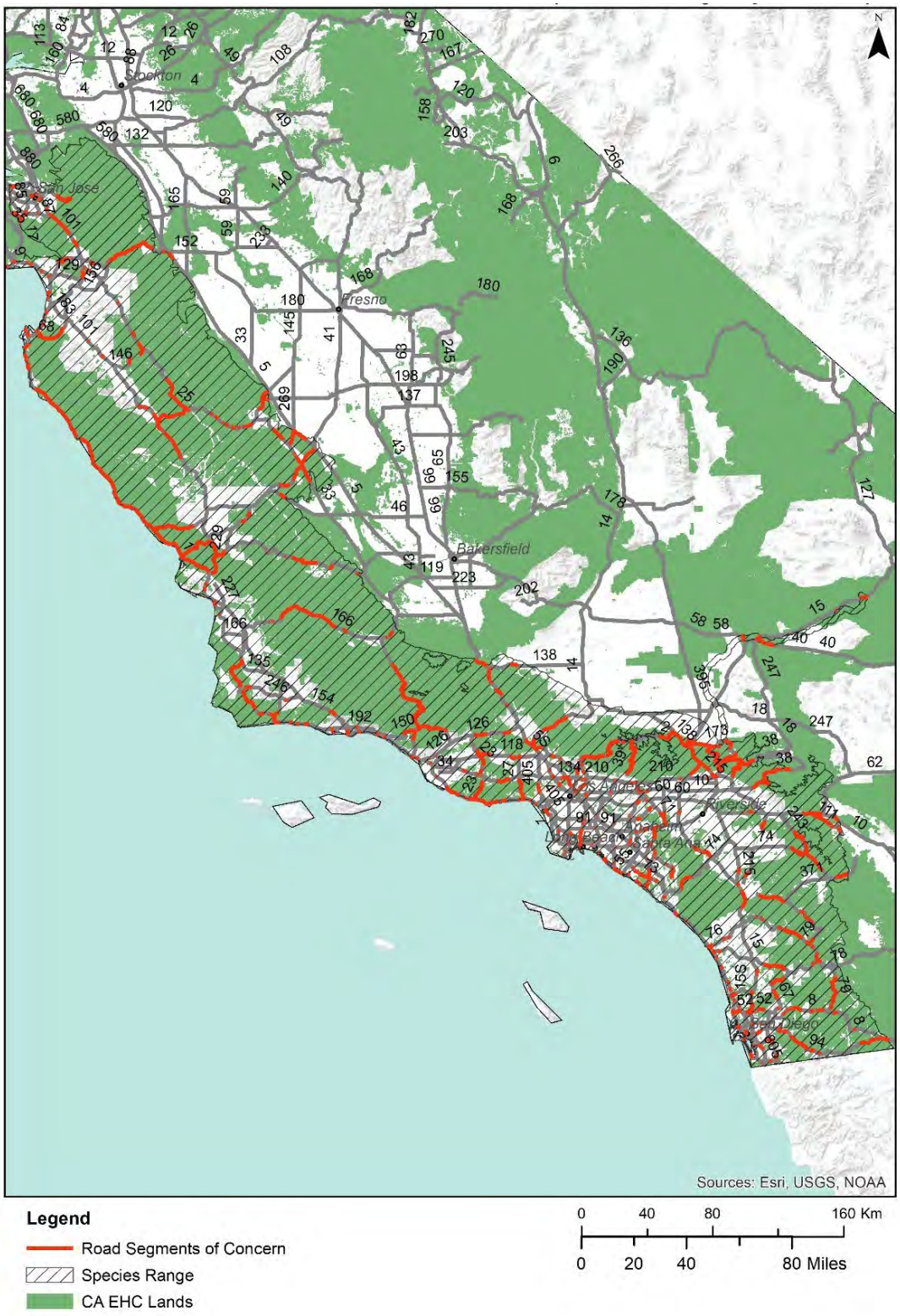


Figure 2. Highway Segments of Concern: Southern Western Pond Turtle (*Actinemys pallida*)

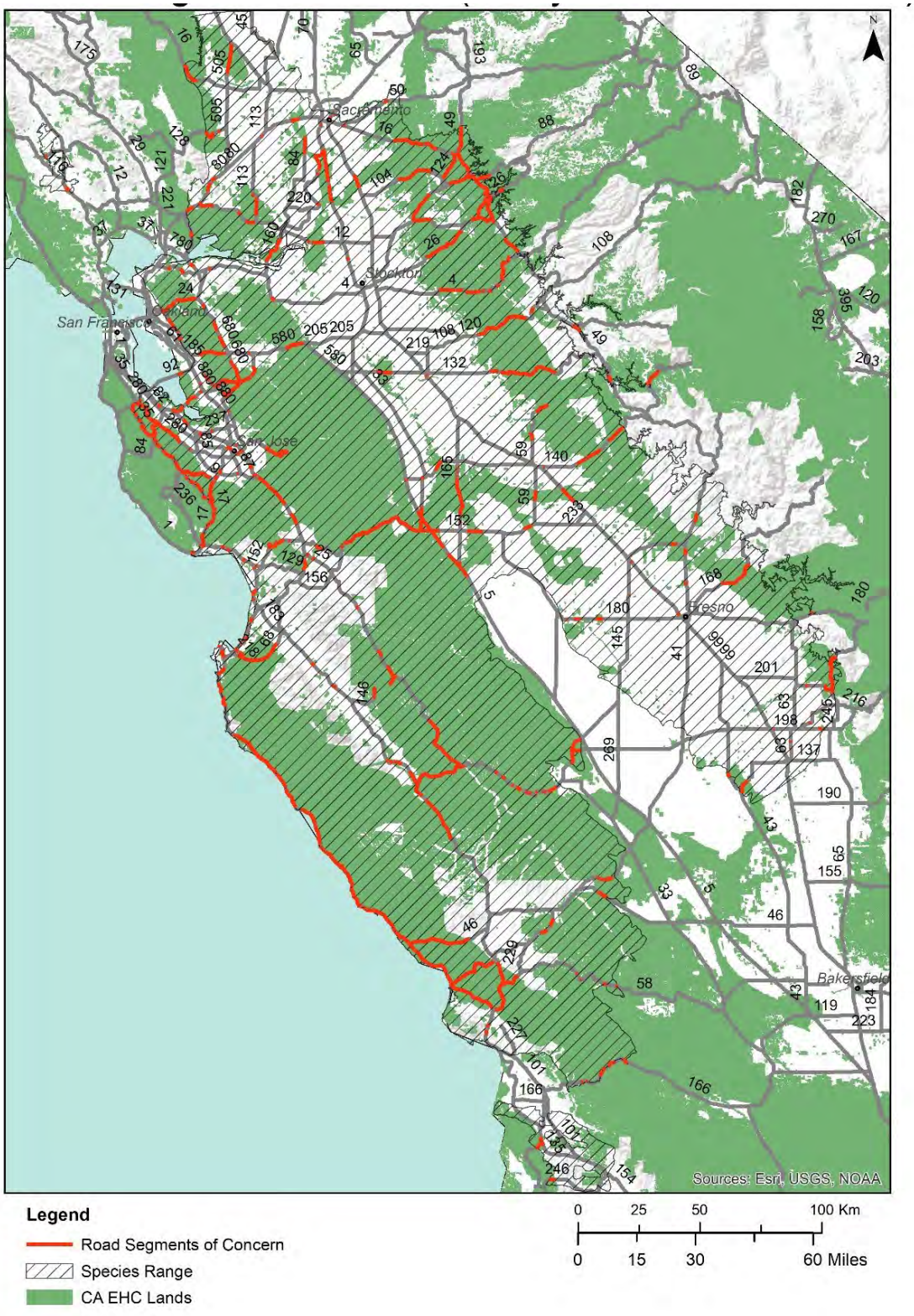


Figure 3. Highway Segments of Concern: California Tiger Salamander (*Ambystoma californiense*)

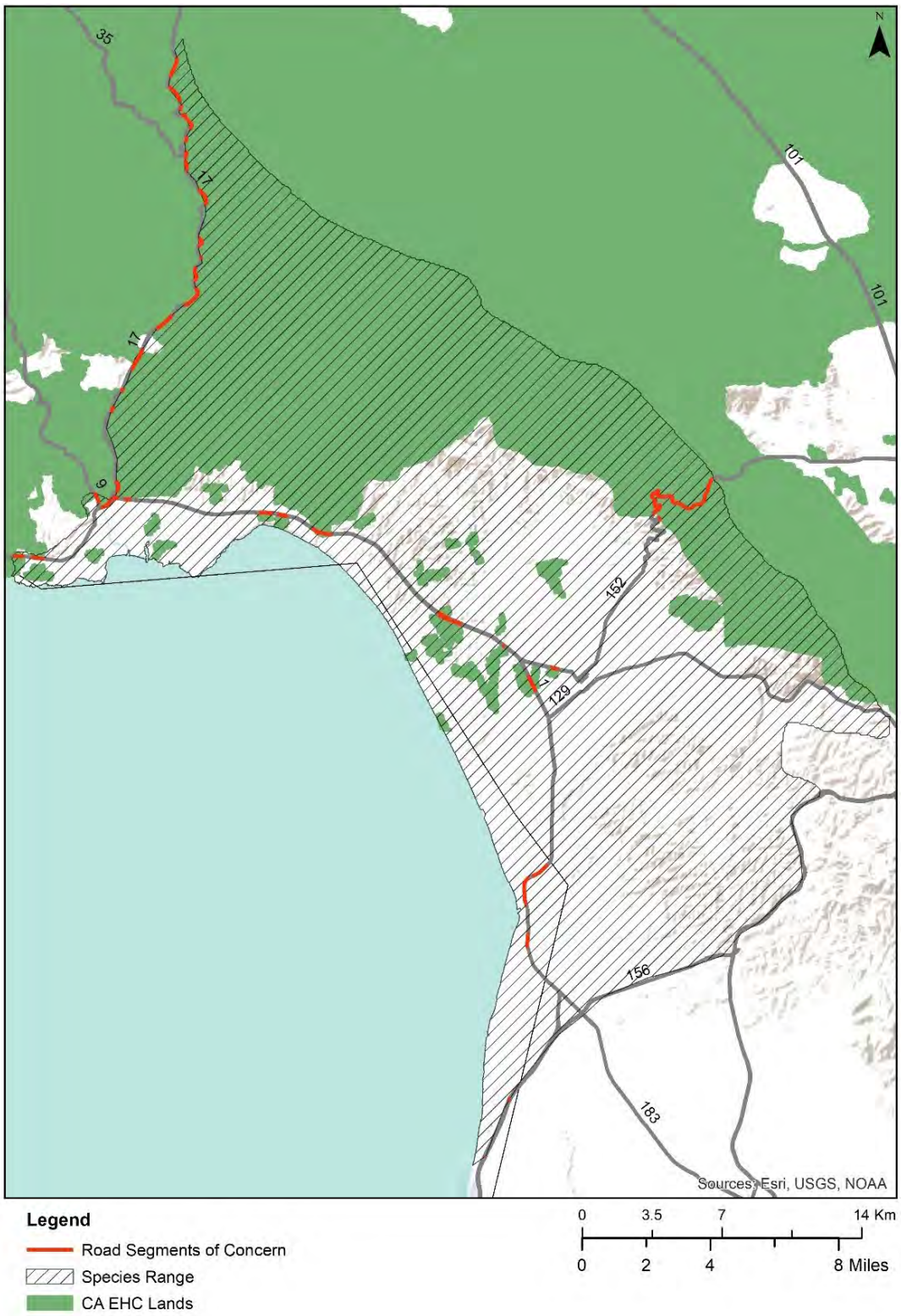


Figure 4. Highway Segments of Concern: Santa Cruz Long-toed Salamander (*Ambystoma macrodactylum croceum*)

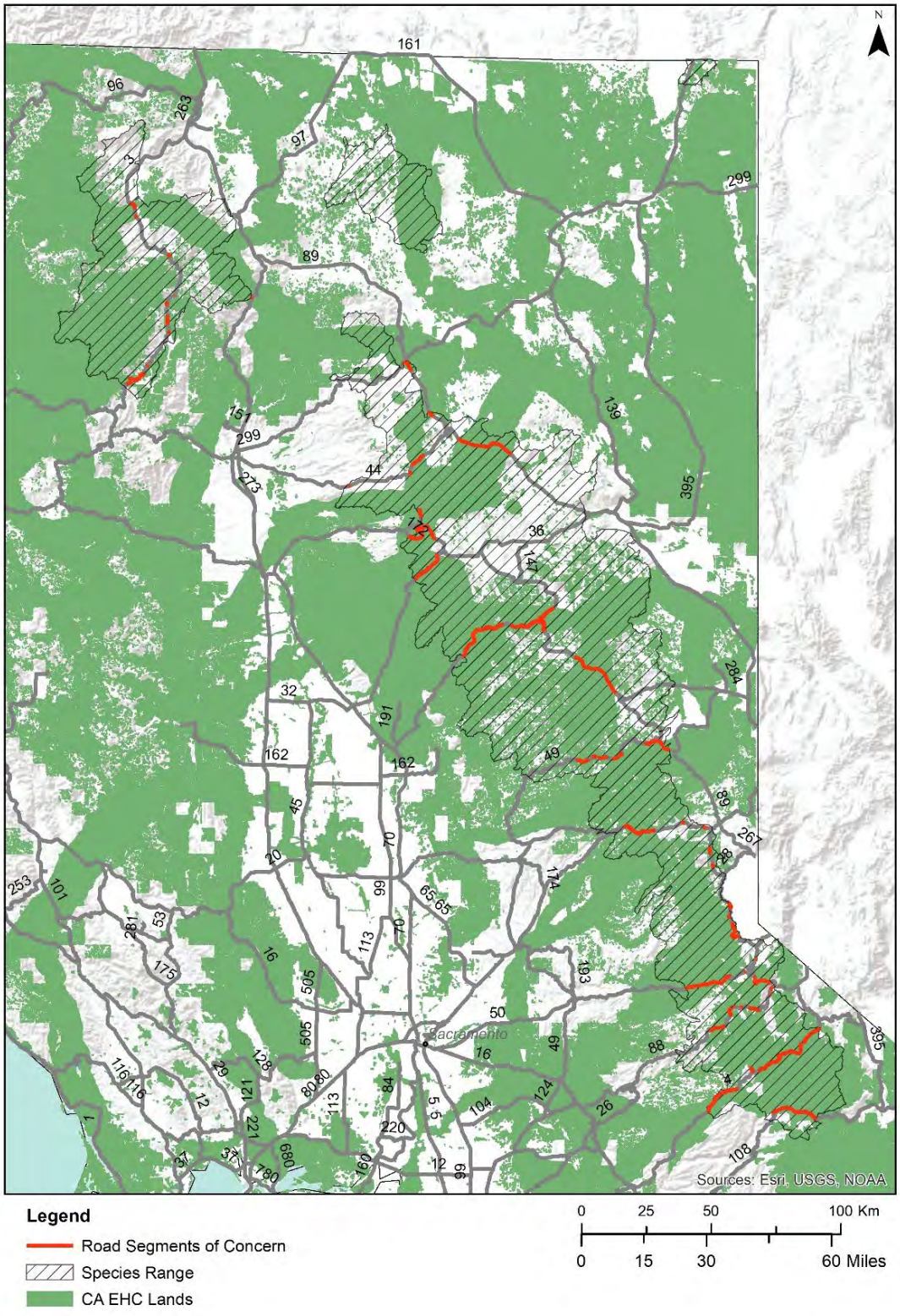


Figure 5. Highway Segments of Concern: Southern Long-toed Salamander (*Ambystoma macrodactylum sigillatum*)

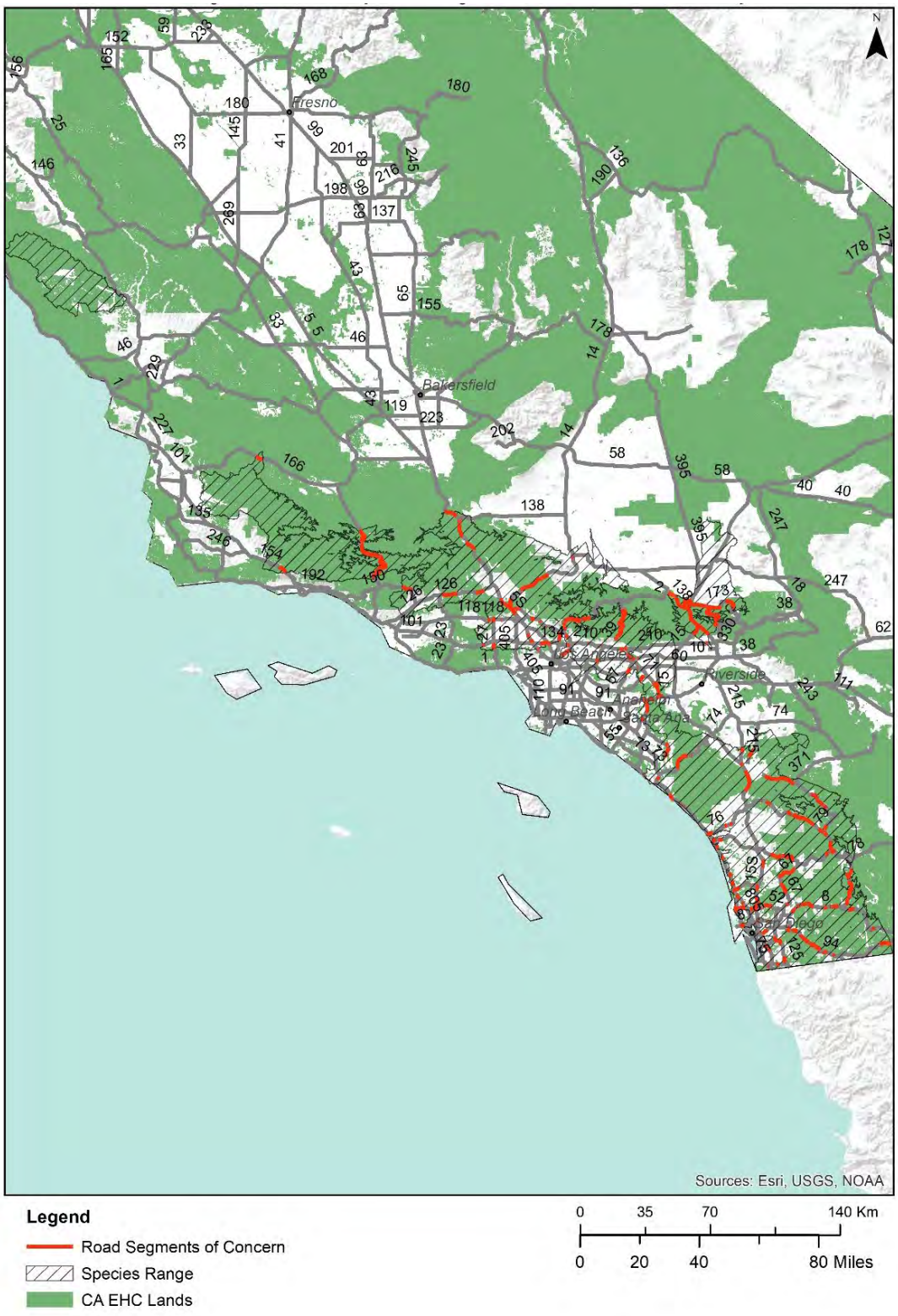


Figure 6. Highway Segments of Concern: Arroyo Toad (*Anaxyrus californicus*)

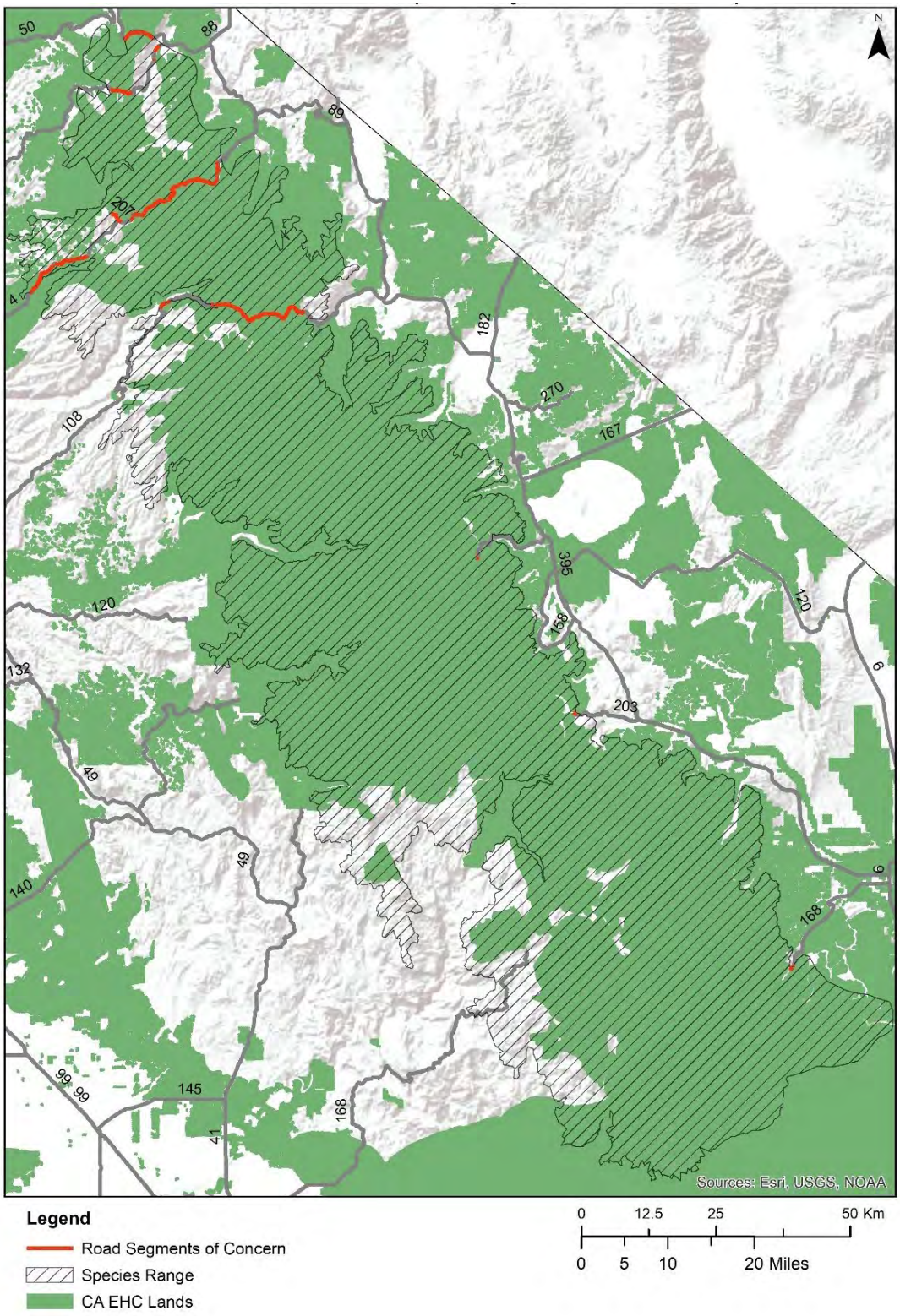


Figure 7. Highway Segments of Concern: Yosemite Toad (*Anaxyrus canorus*)

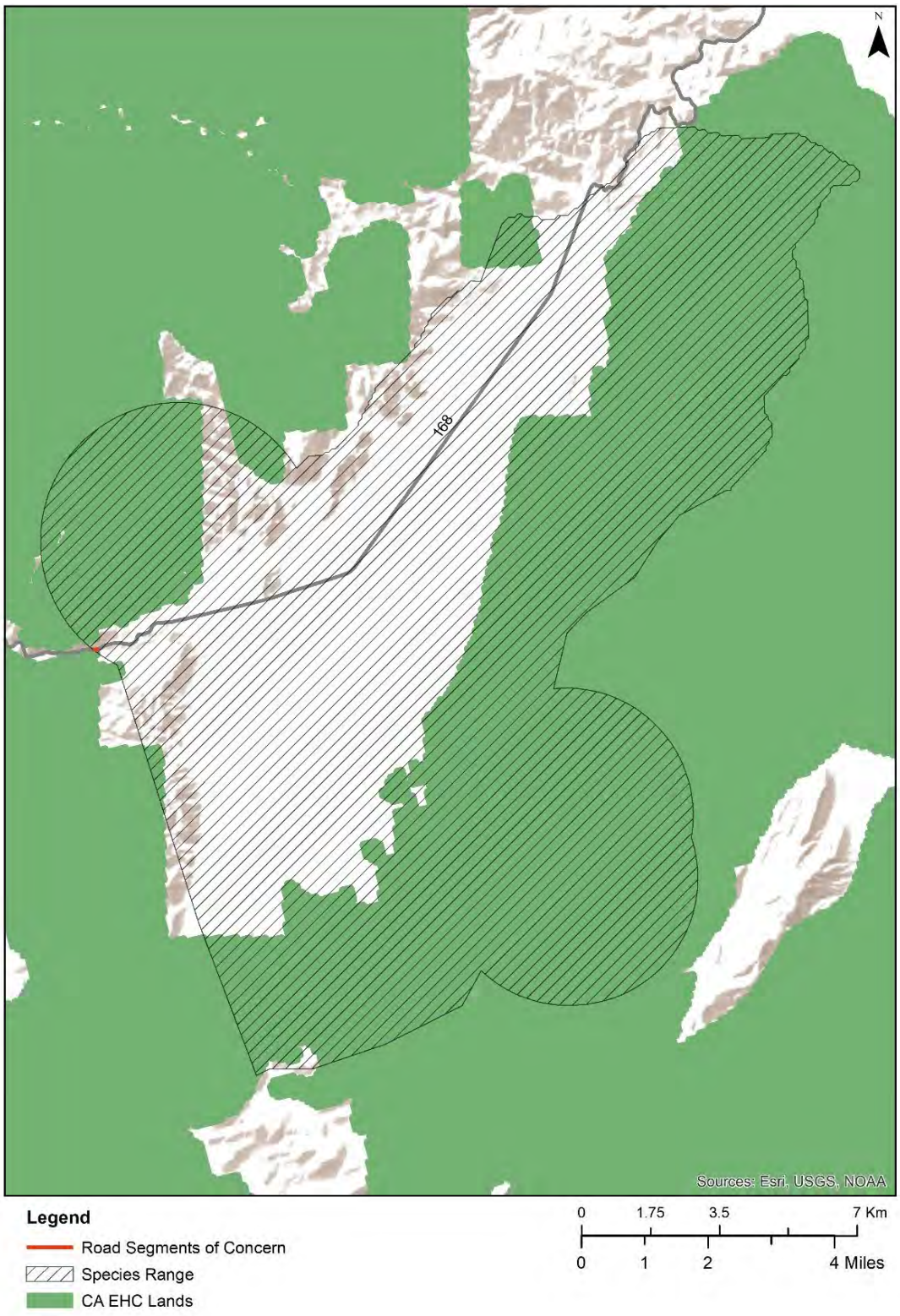


Figure 8. Highway Segments of Concern: Black Toad (*Anaxyrus exsul*)

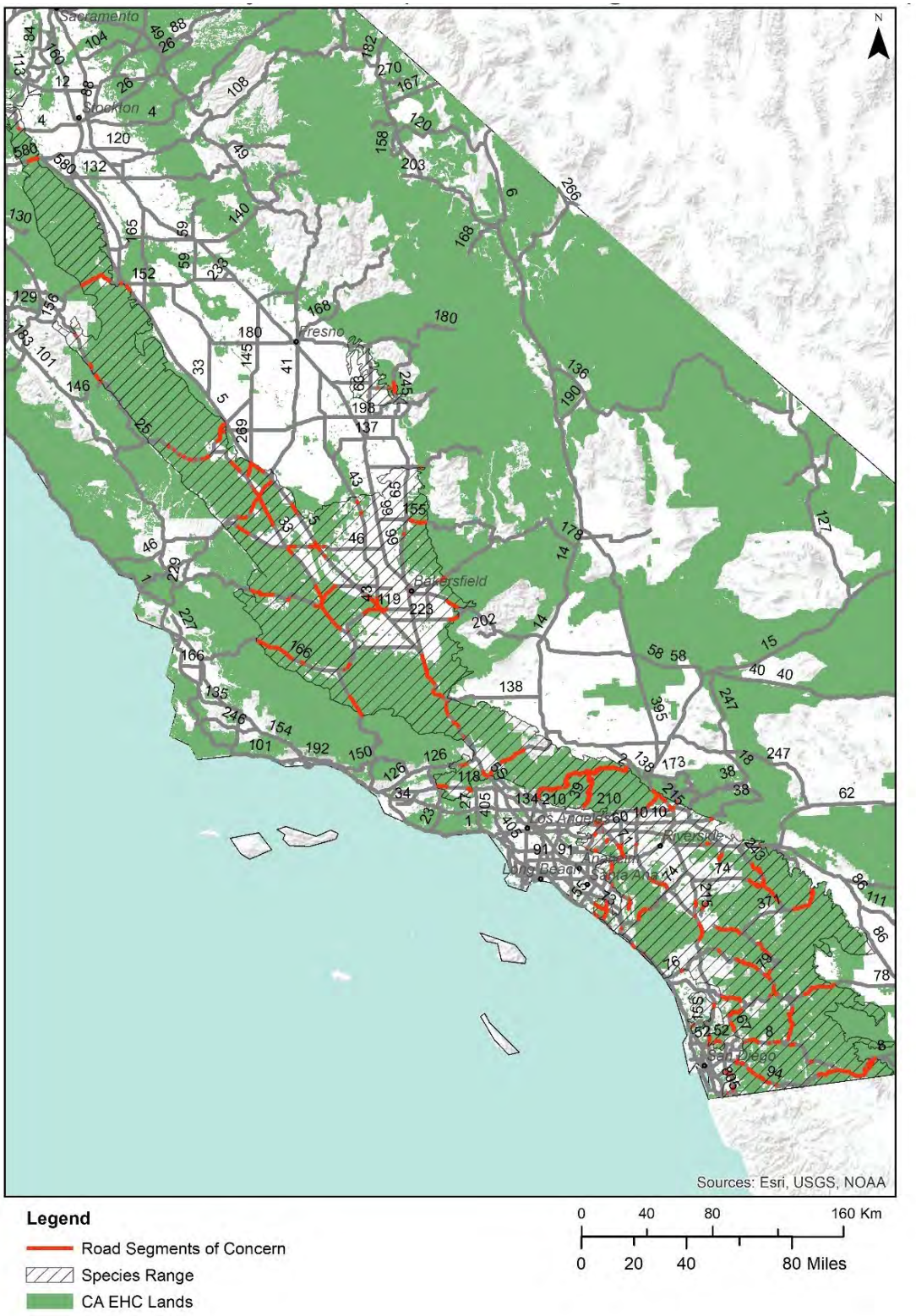


Figure 9. Highway Segments of Concern: California Glossy Snake (*Arizona elegans occidentalis*)

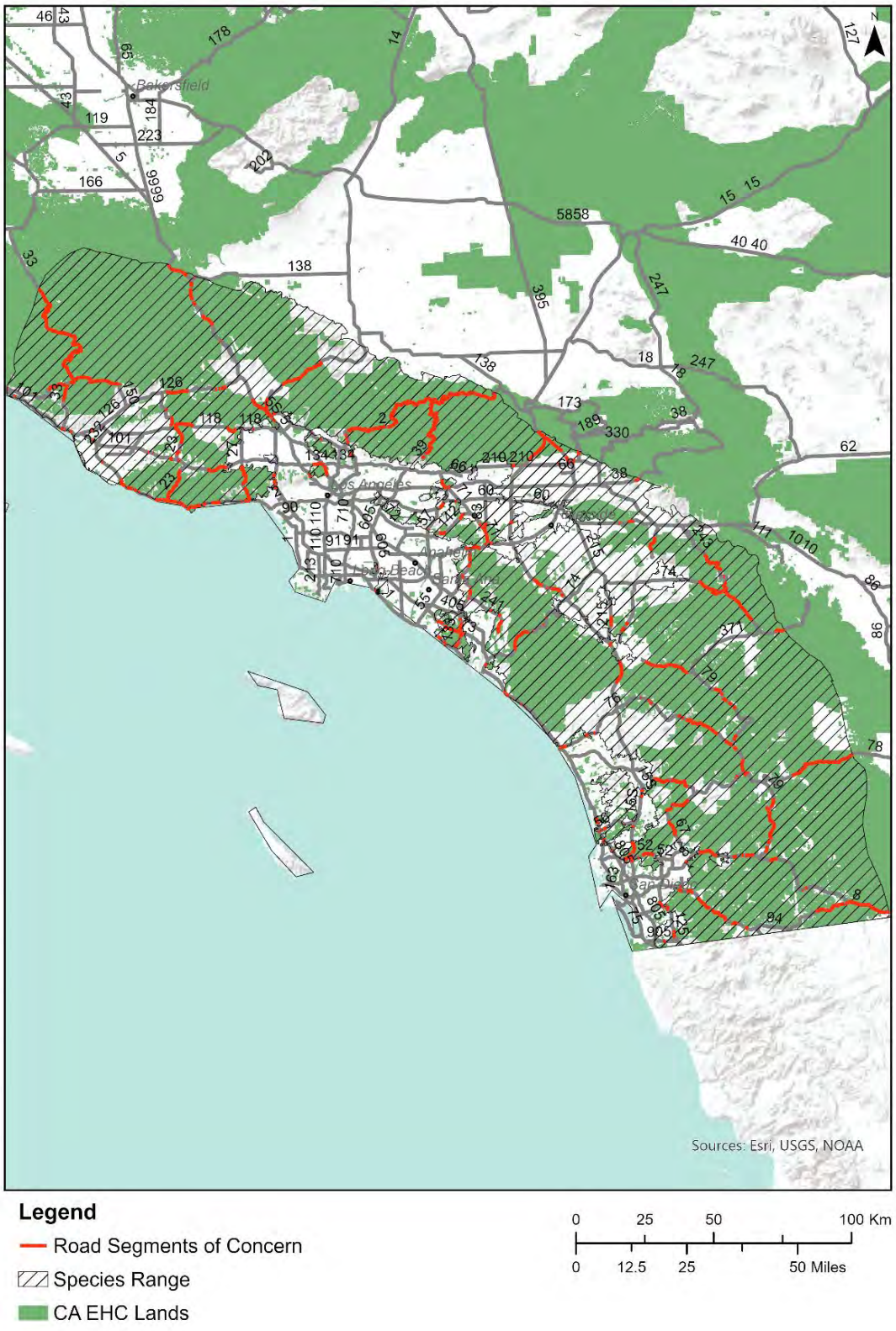


Figure 10. Highway Segments of Concern: San Diegan Tiger Whiptail (*Aspidoscelis tigris stejnegeri*)

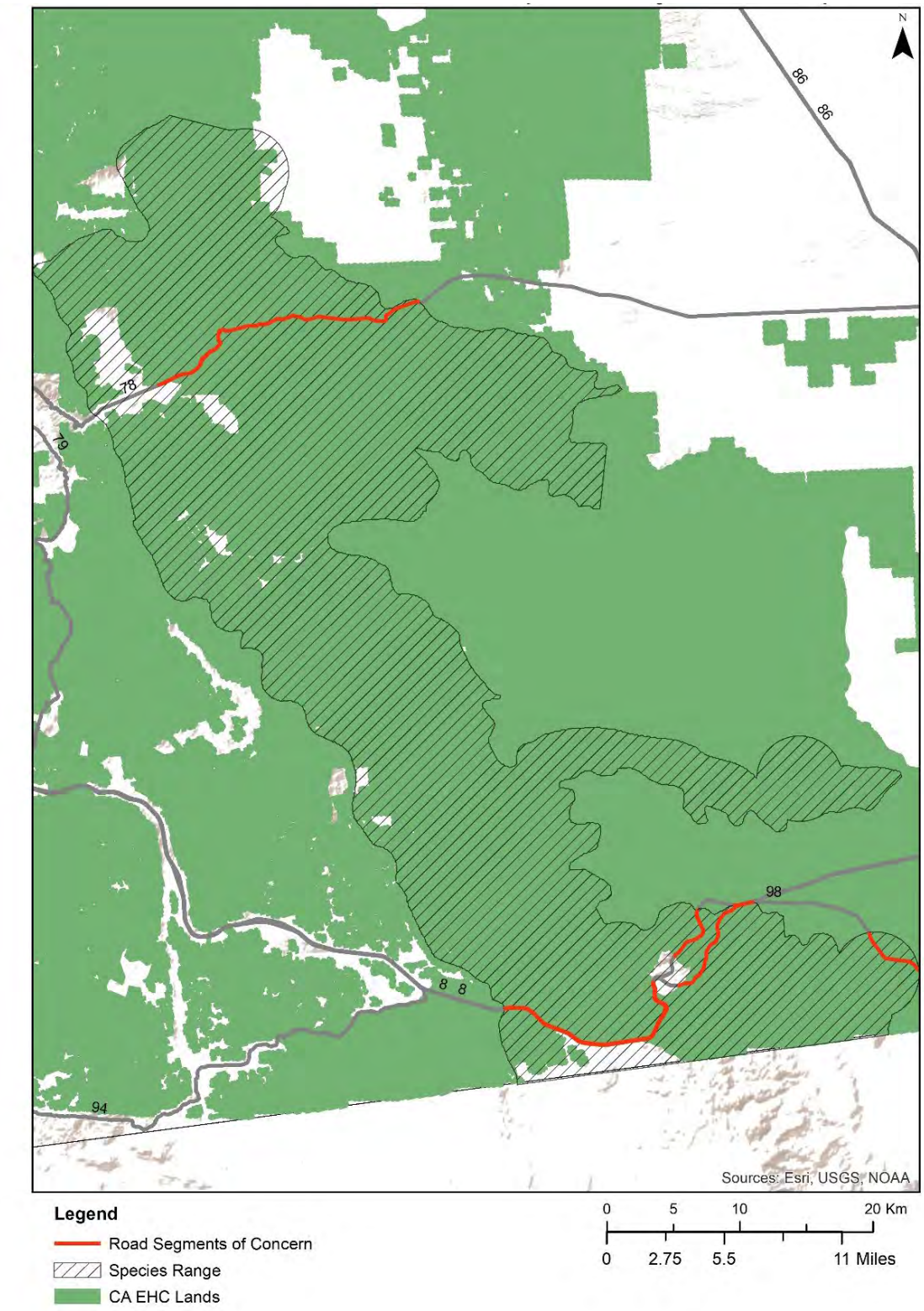


Figure 11. Highway Segments of Concern: Switak's Banded Gecko (*Coleonyx switaki*)

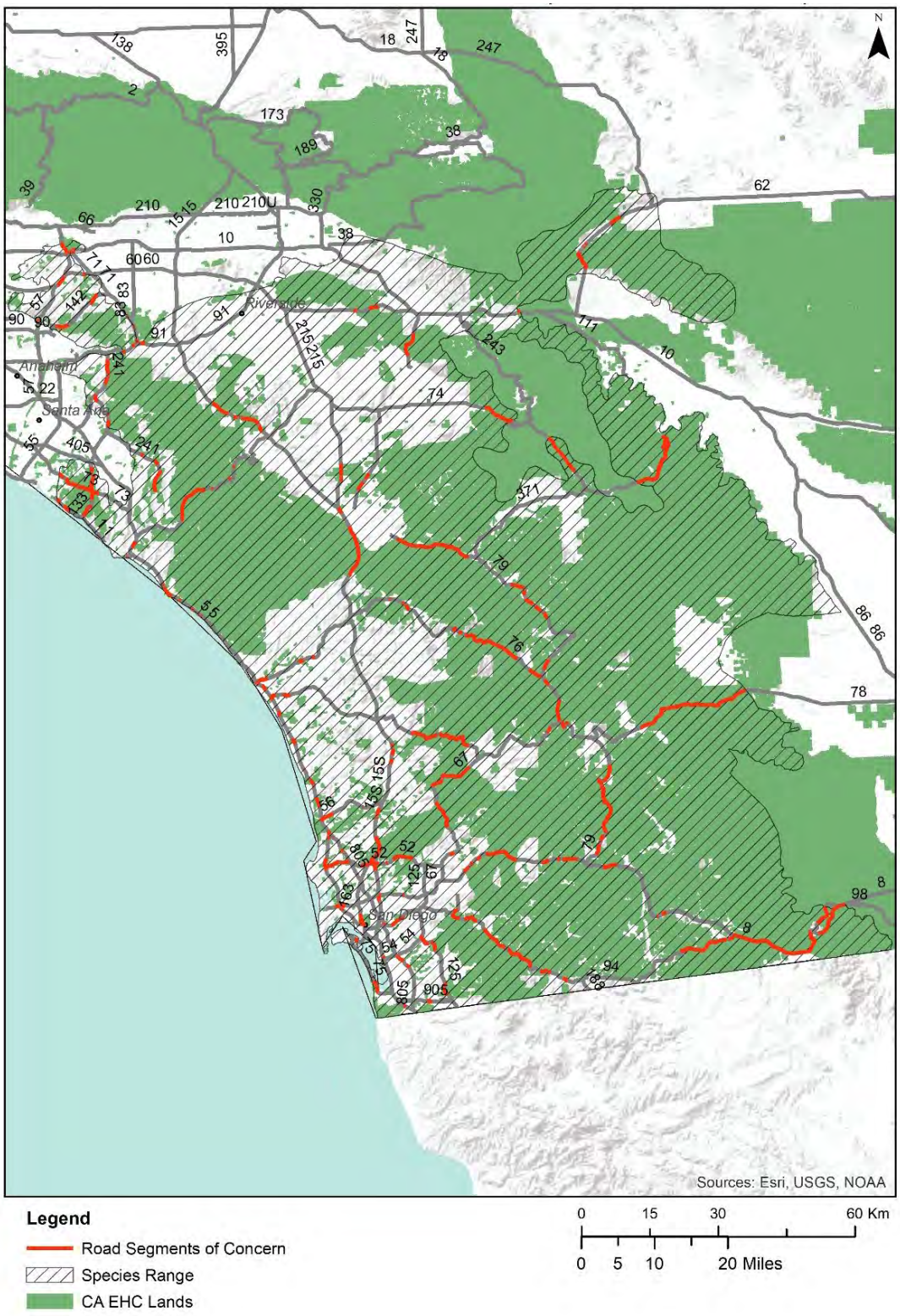


Figure 12. Highway Segments of Concern: Red Diamond Rattlesnake (*Crotalus ruber*)

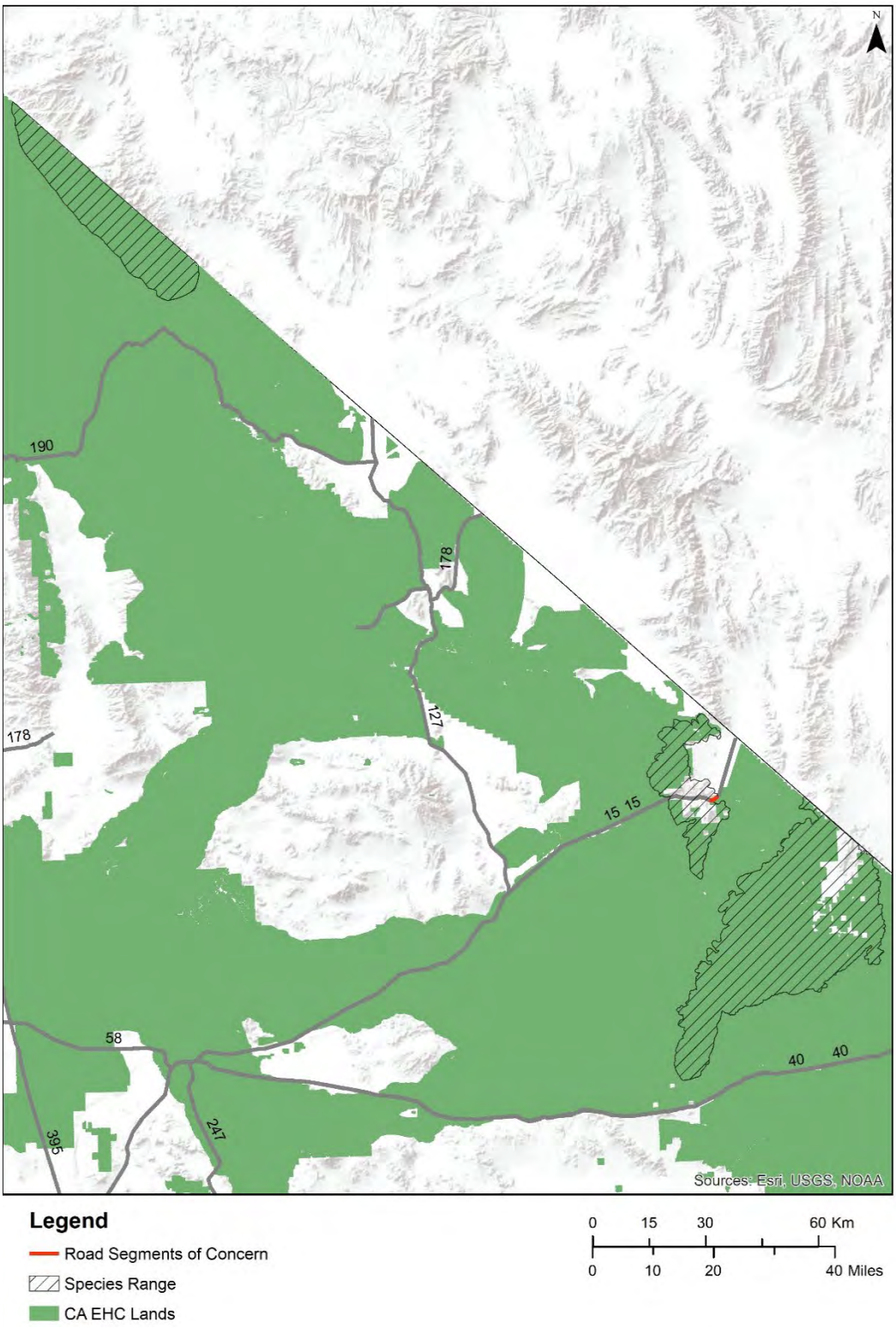


Figure 13. Highway Segments of Concern: Regal Ring-necked Snake (*Diadophis punctatus regalis*)

Figure 14. Highway Segments of Concern: California Giant Salamander (*Dicamptodon ensatus*)

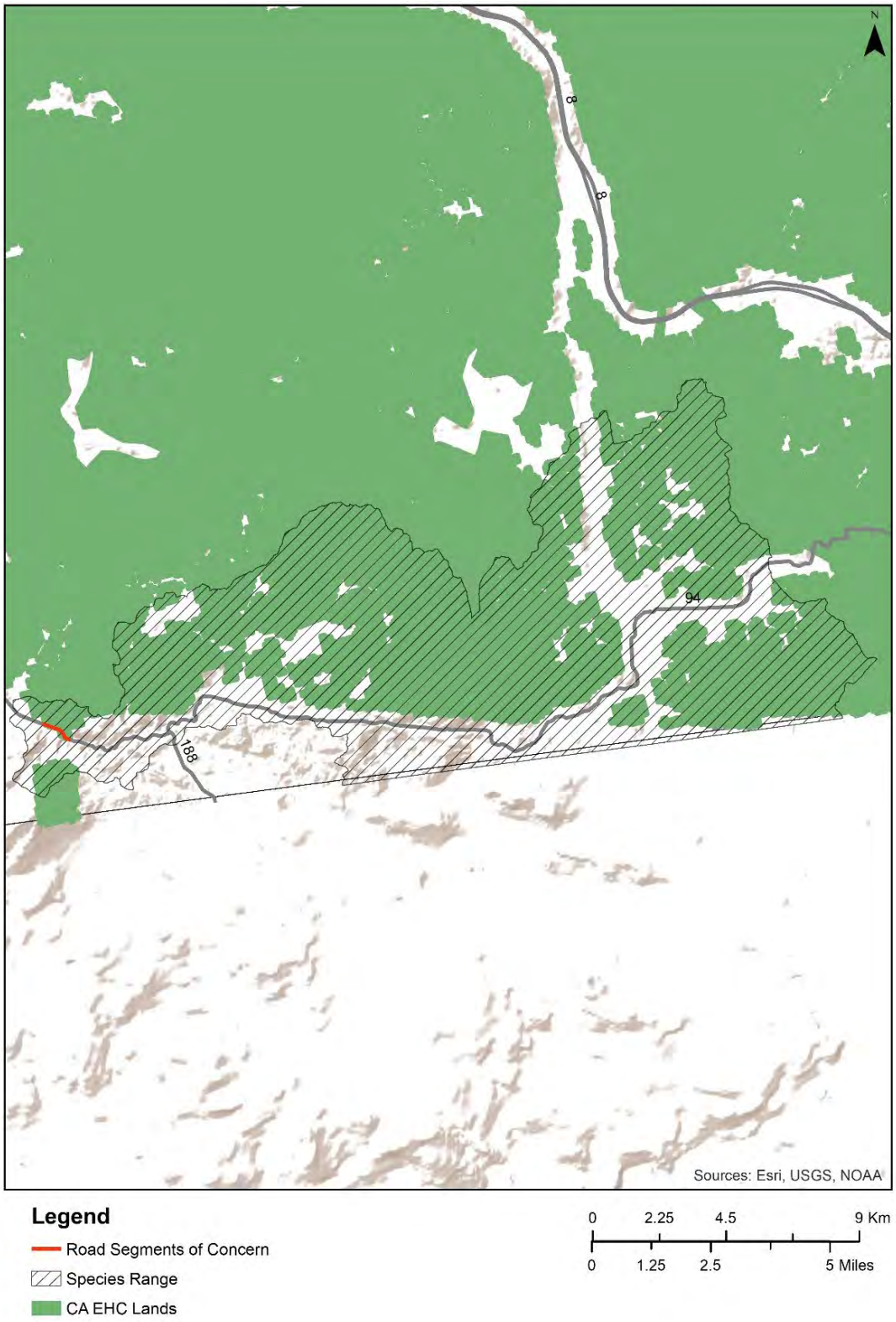


Figure 15. Highway Segments of Concern: Cope's Leopard Lizard (*Gambelia copeii*)

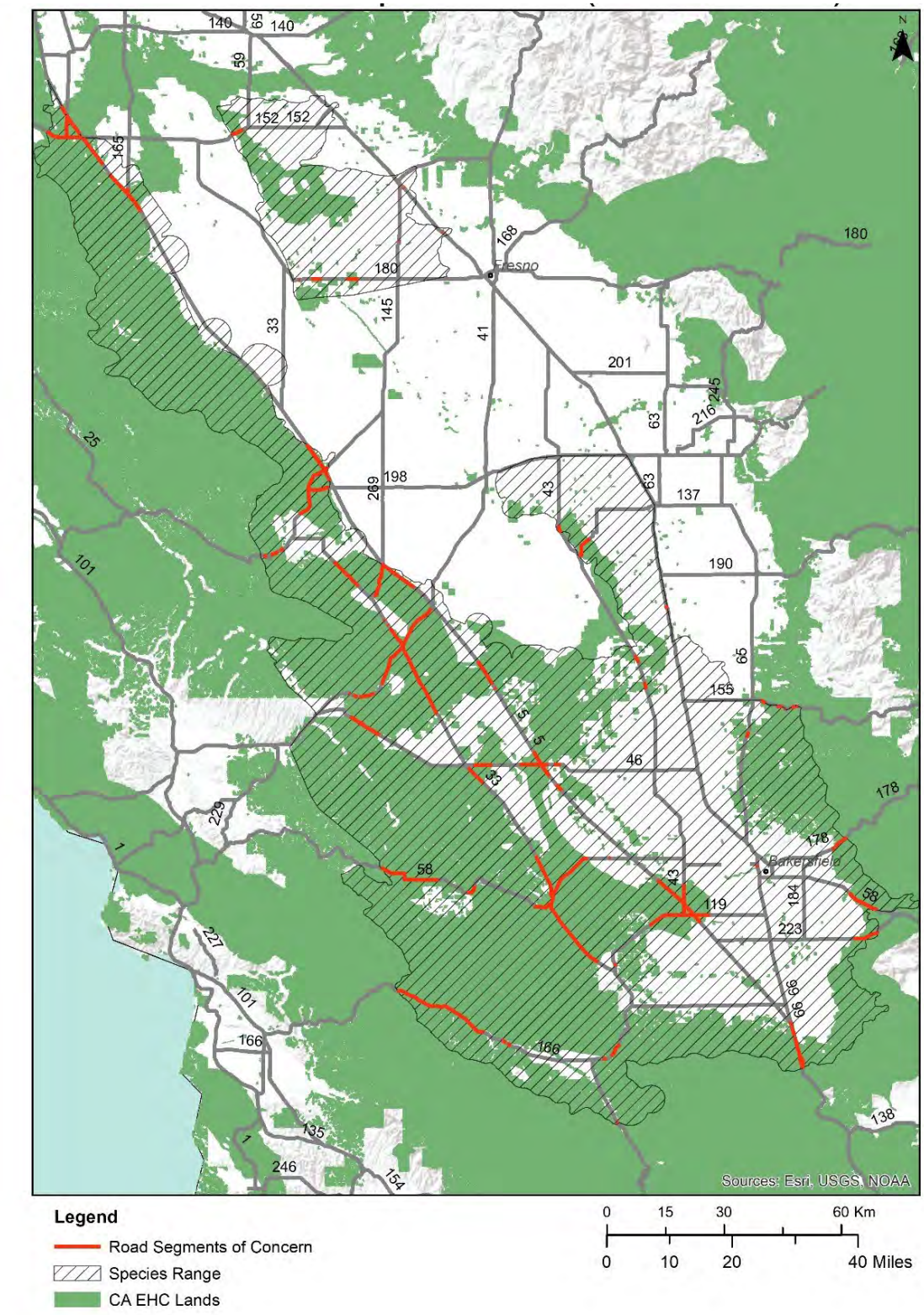


Figure 16. Highway Segments of Concern: Blunt-nosed Leopard Lizard (*Gambelia sila*)

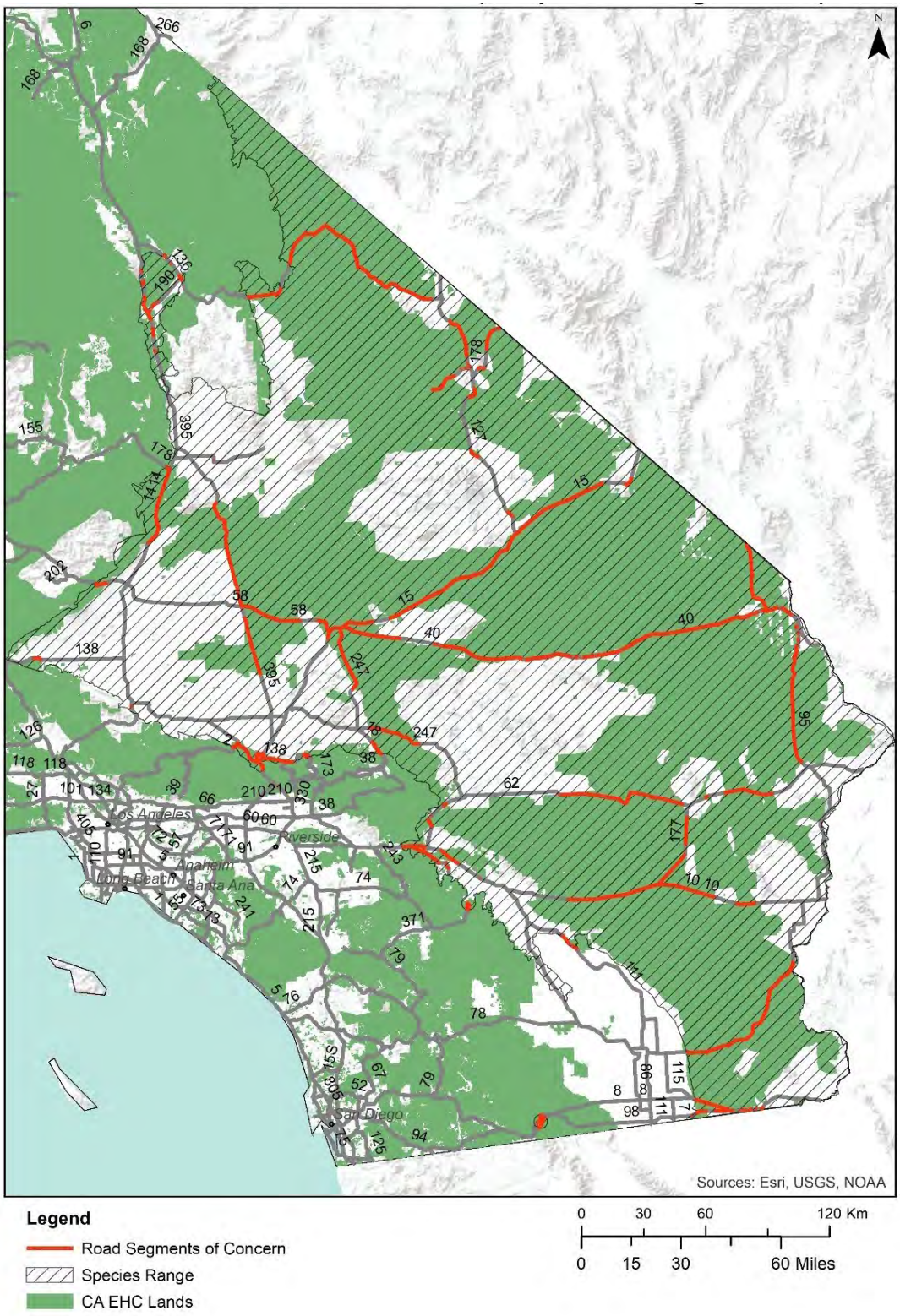


Figure 17. Highway Segments of Concern: Mohave Desert Tortoise (*Gopherus agassizii*)

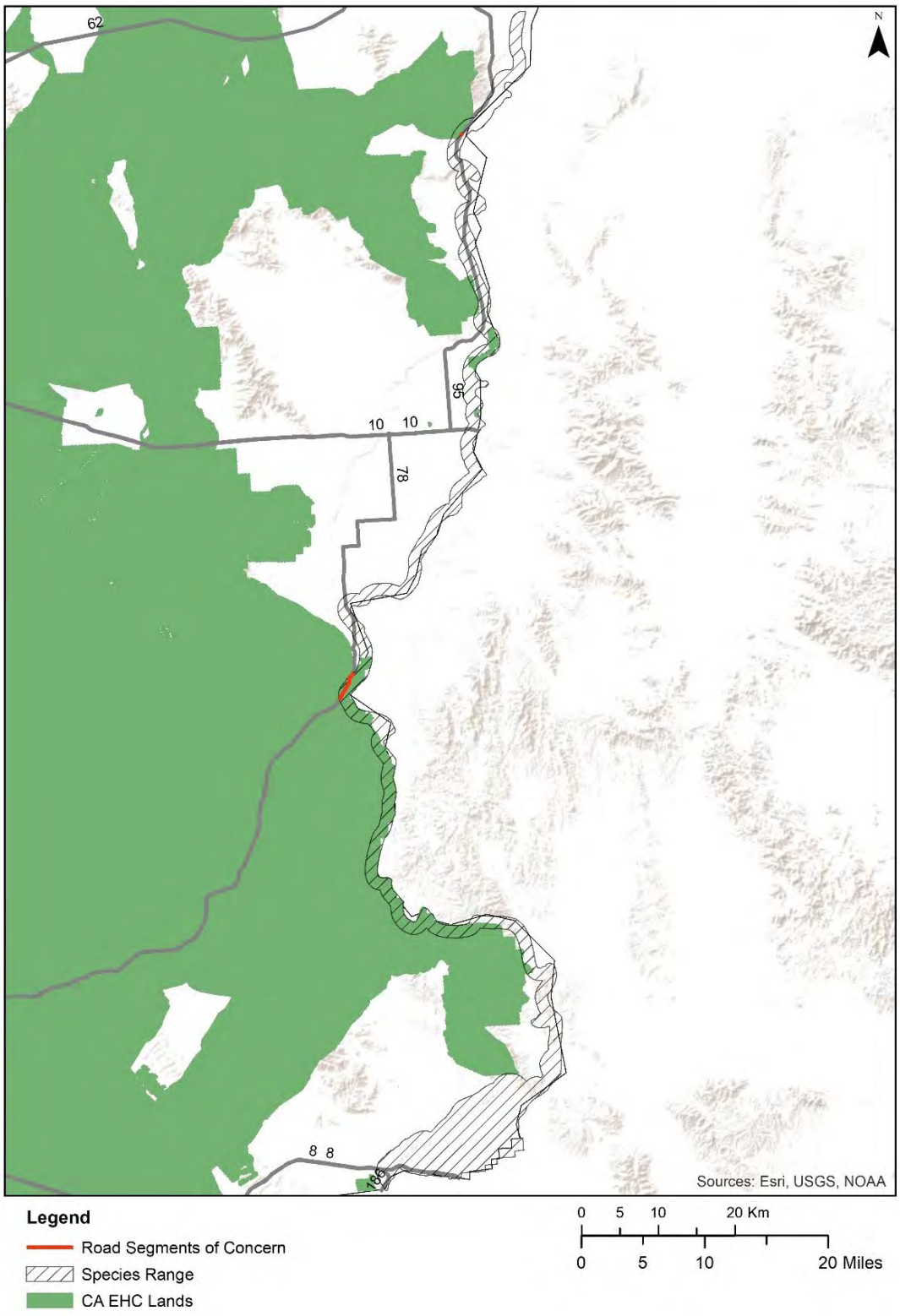


Figure 18. Highway Segments of Concern: Sonoran Desert Toad (*Incilius alvarius)*
Note: Possibly extinct in CA.

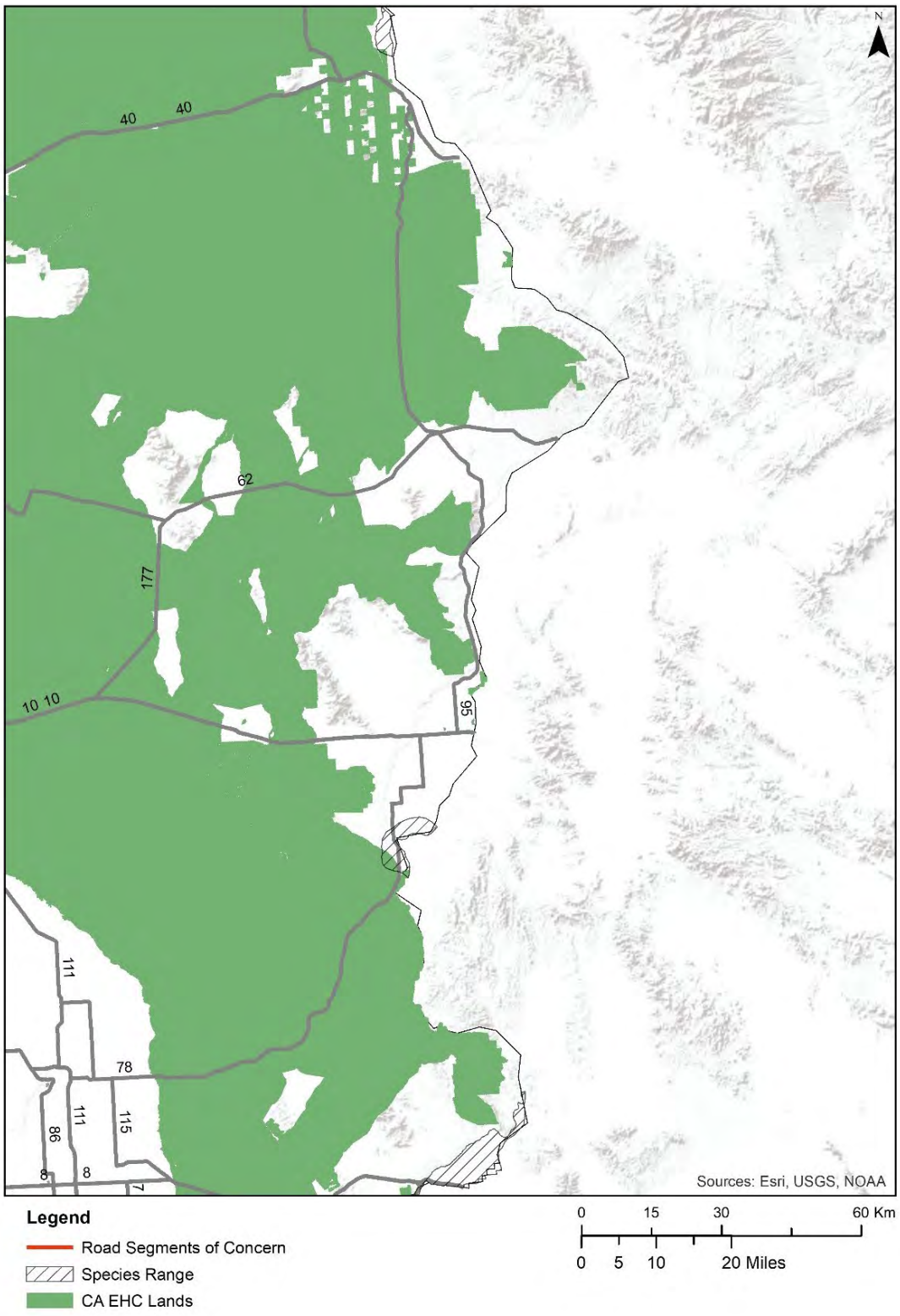


Figure 19. Highway Segments of Concern: Sonoran Mud Turtle (*Kinosternon sonoriense*)

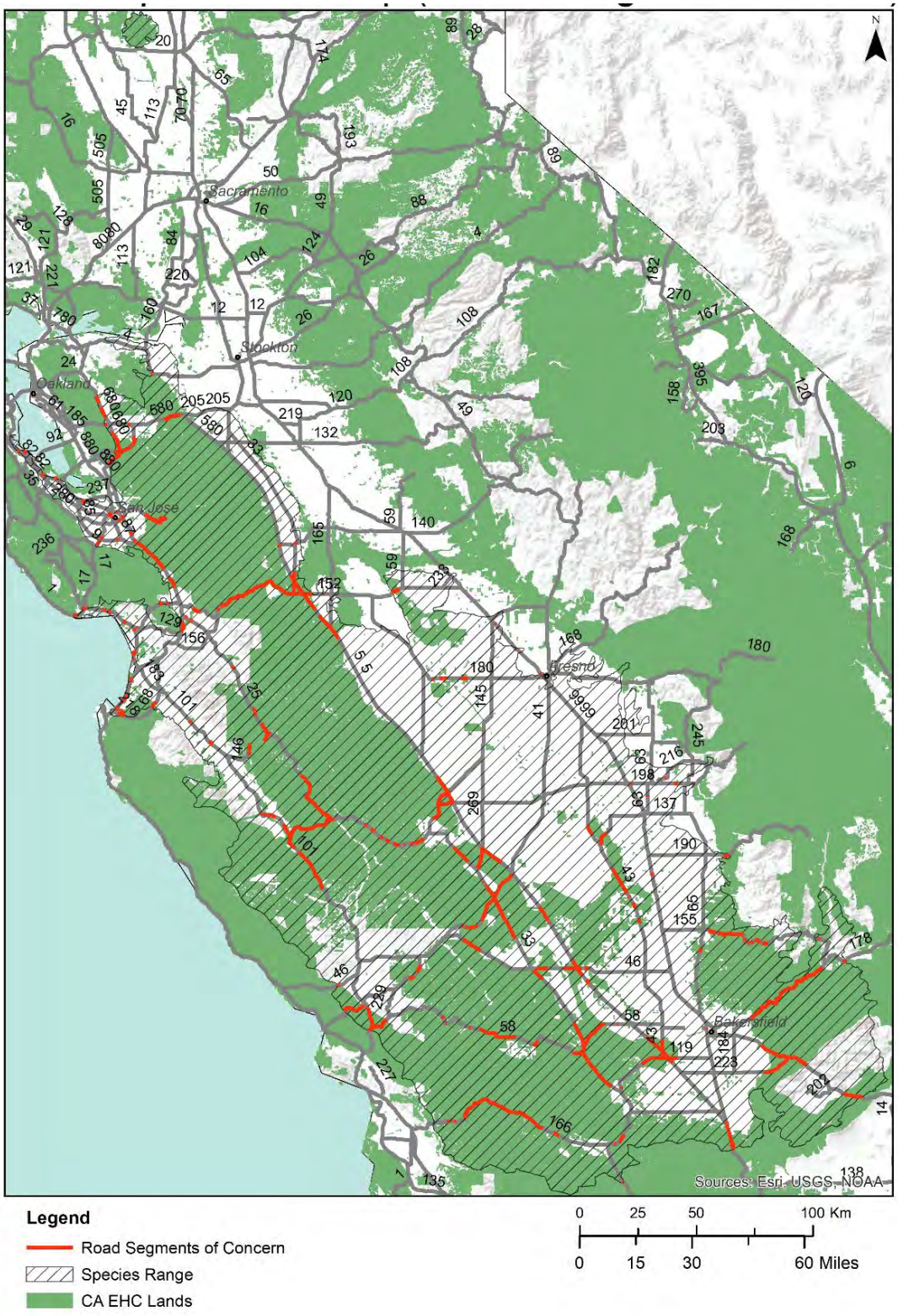


Figure 20. Highway Segments of Concern: San Joaquin Coachwhip (*Masticophis flagellum ruddocki*)

Figure 21. Highway Segments of Concern: Baja California Coachwhip (*Masticophis fuliginosus*)

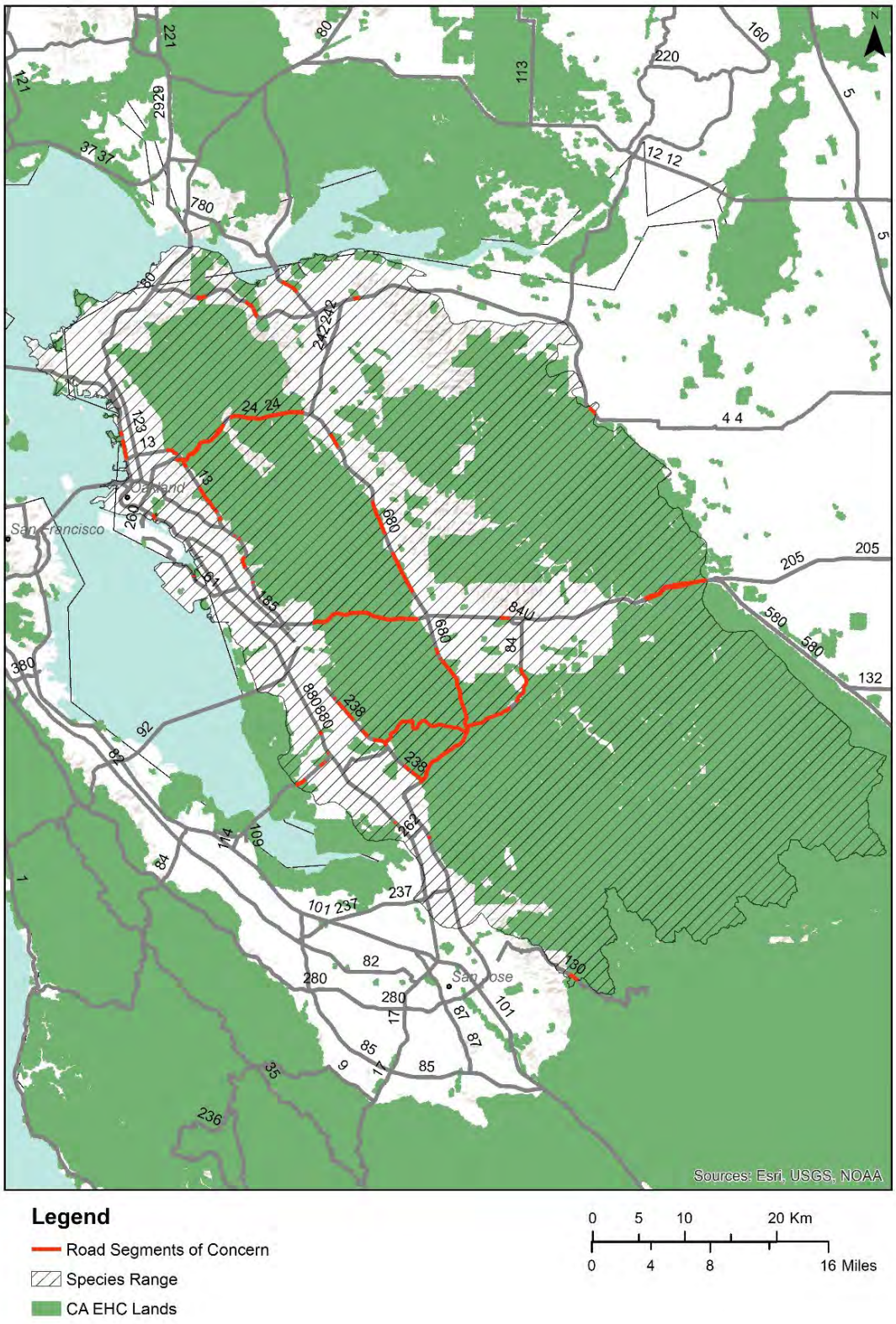


Figure 22. Highway Segments of Concern: Alameda Striped Racer (*Masticophis lateralis euryxanthus*)

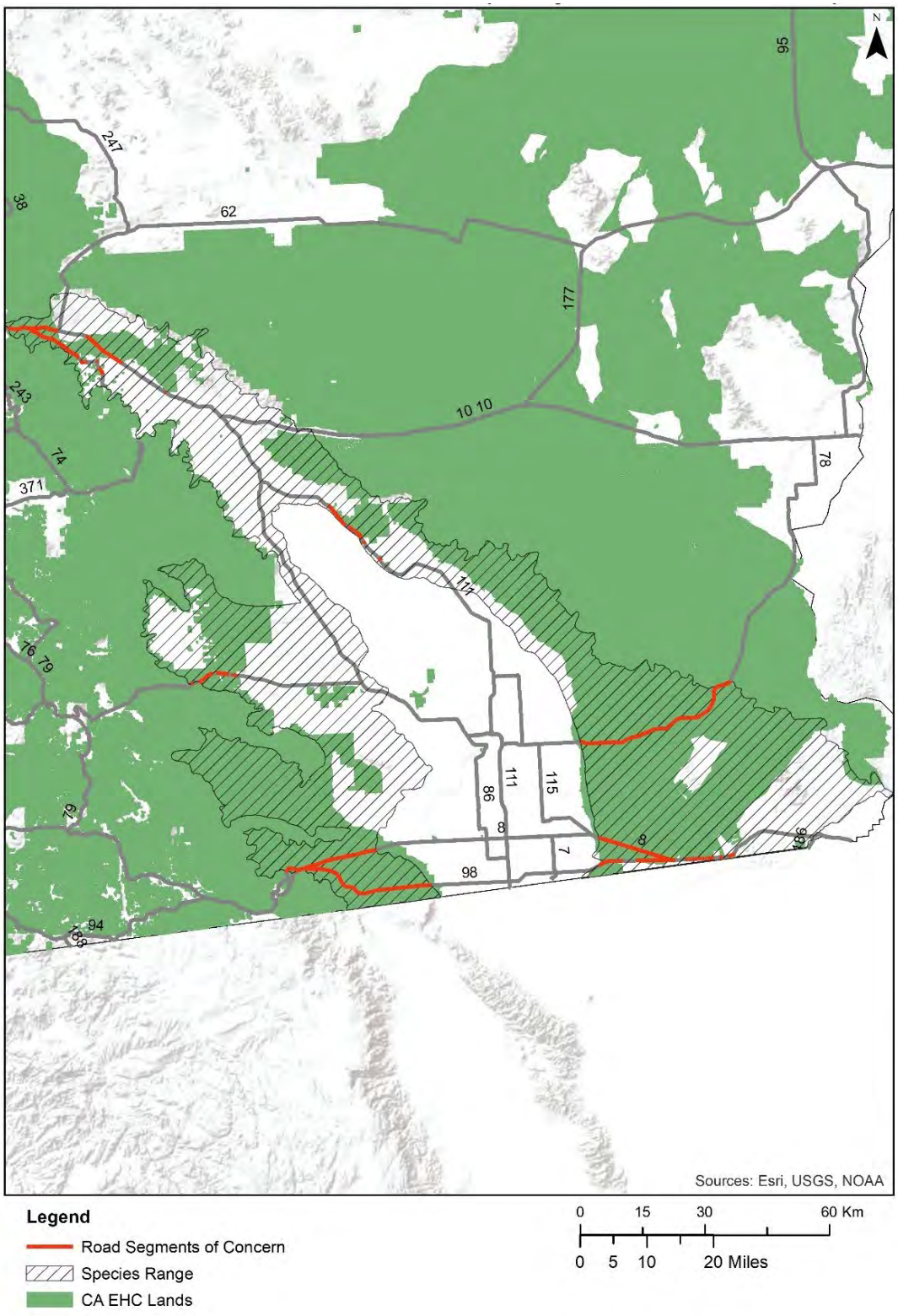


Figure 23. Highway Segments of Concern: Flat-tail Horned Lizard (*Phrynosoma mcallii*)

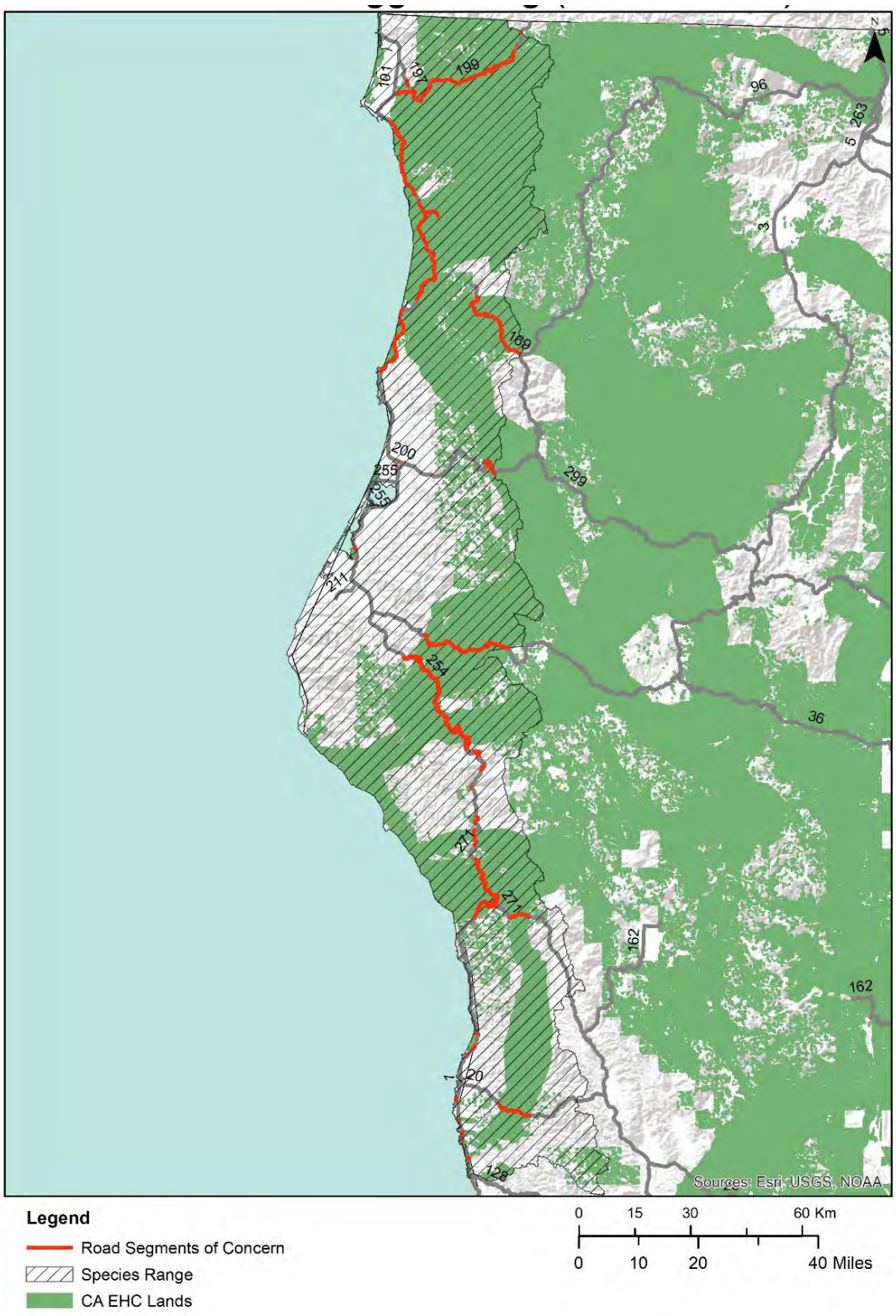


Figure 24. Highway Segments of Concern: Northern Red-legged Frog (*Rana aurora*)

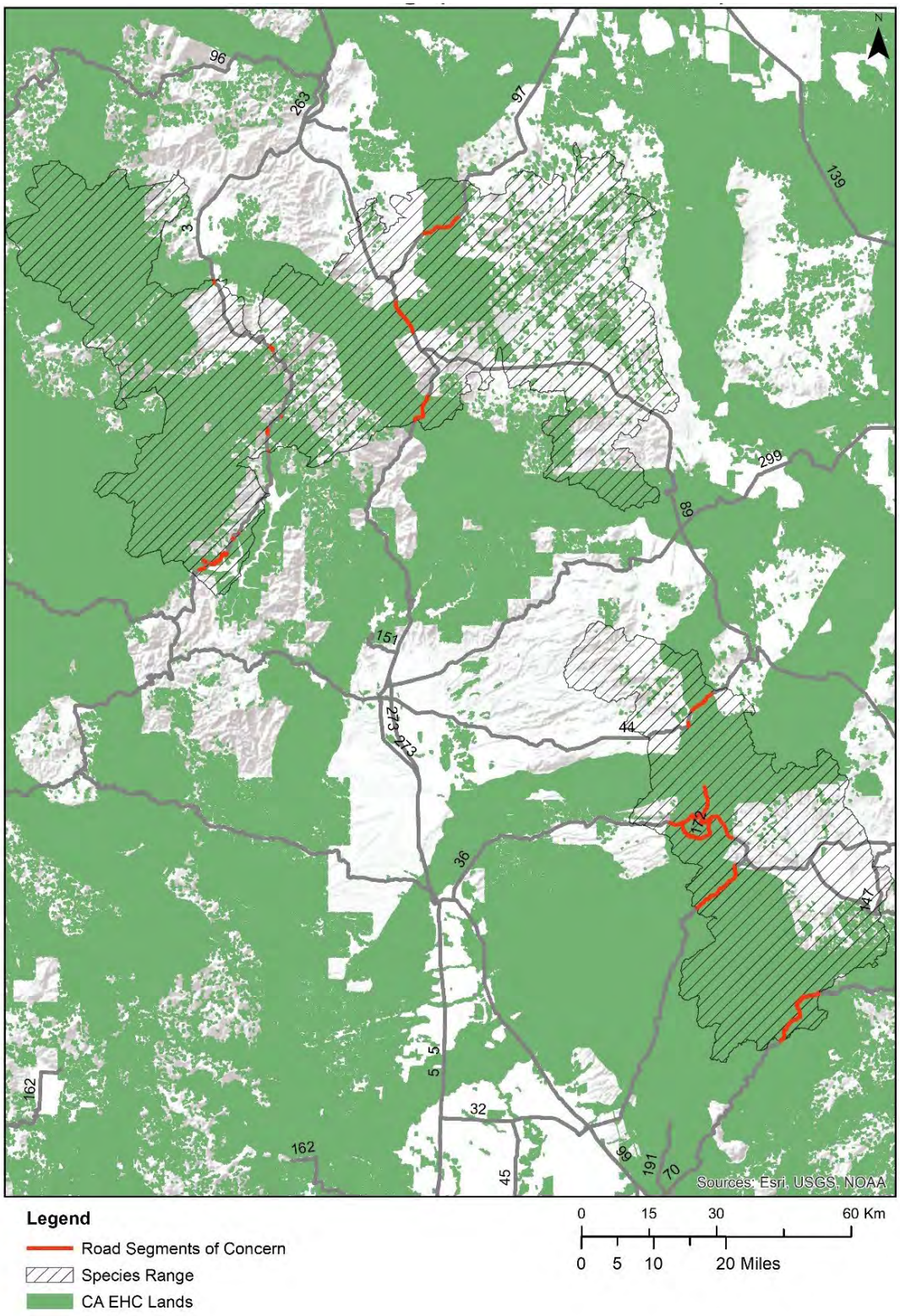


Figure 25. Highway Segments of Concern: Cascades Frog (*Rana cascadae*)

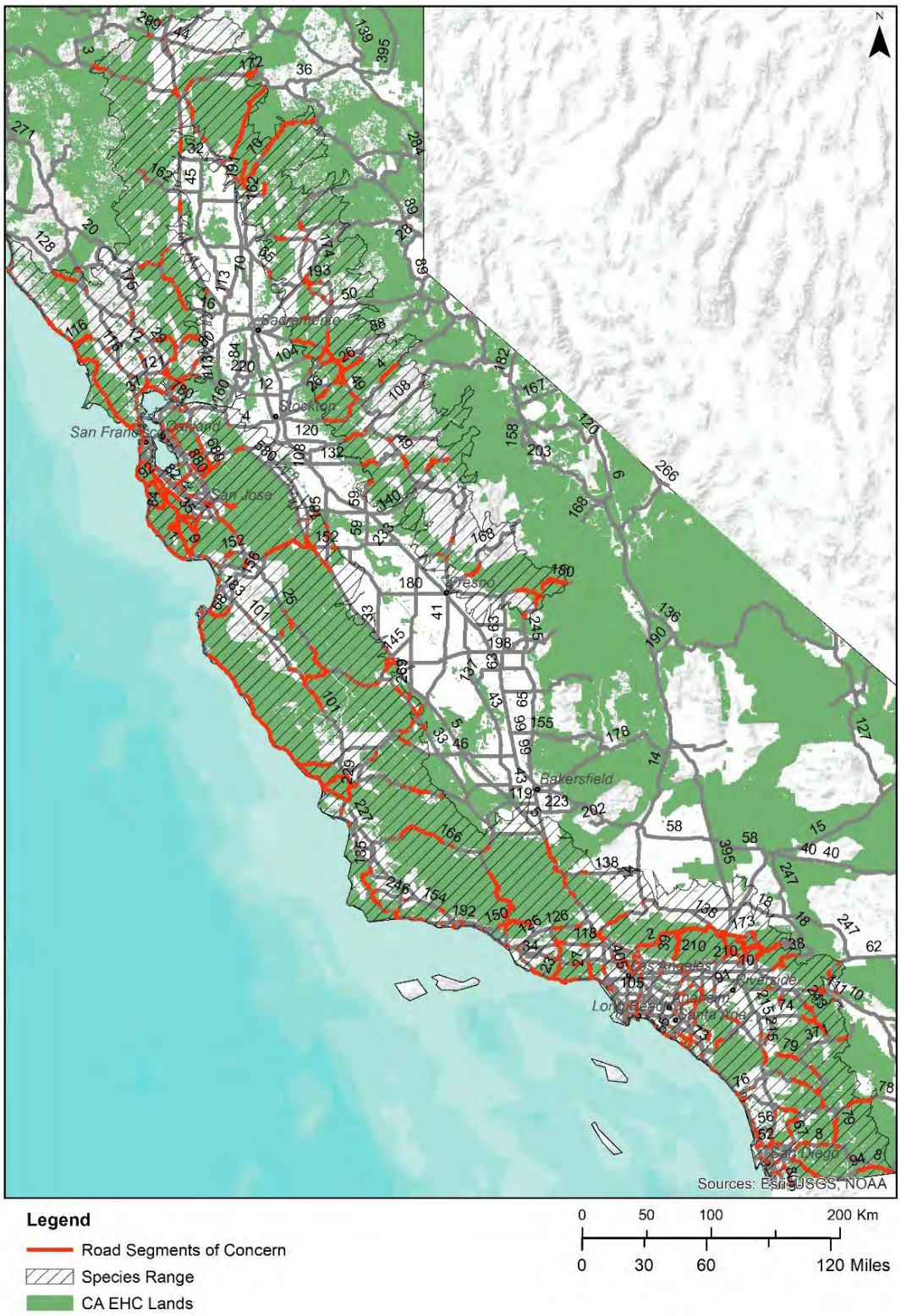


Figure 26. Highway Segments of Concern: California Red-legged Frog (*Rana draytonii*)

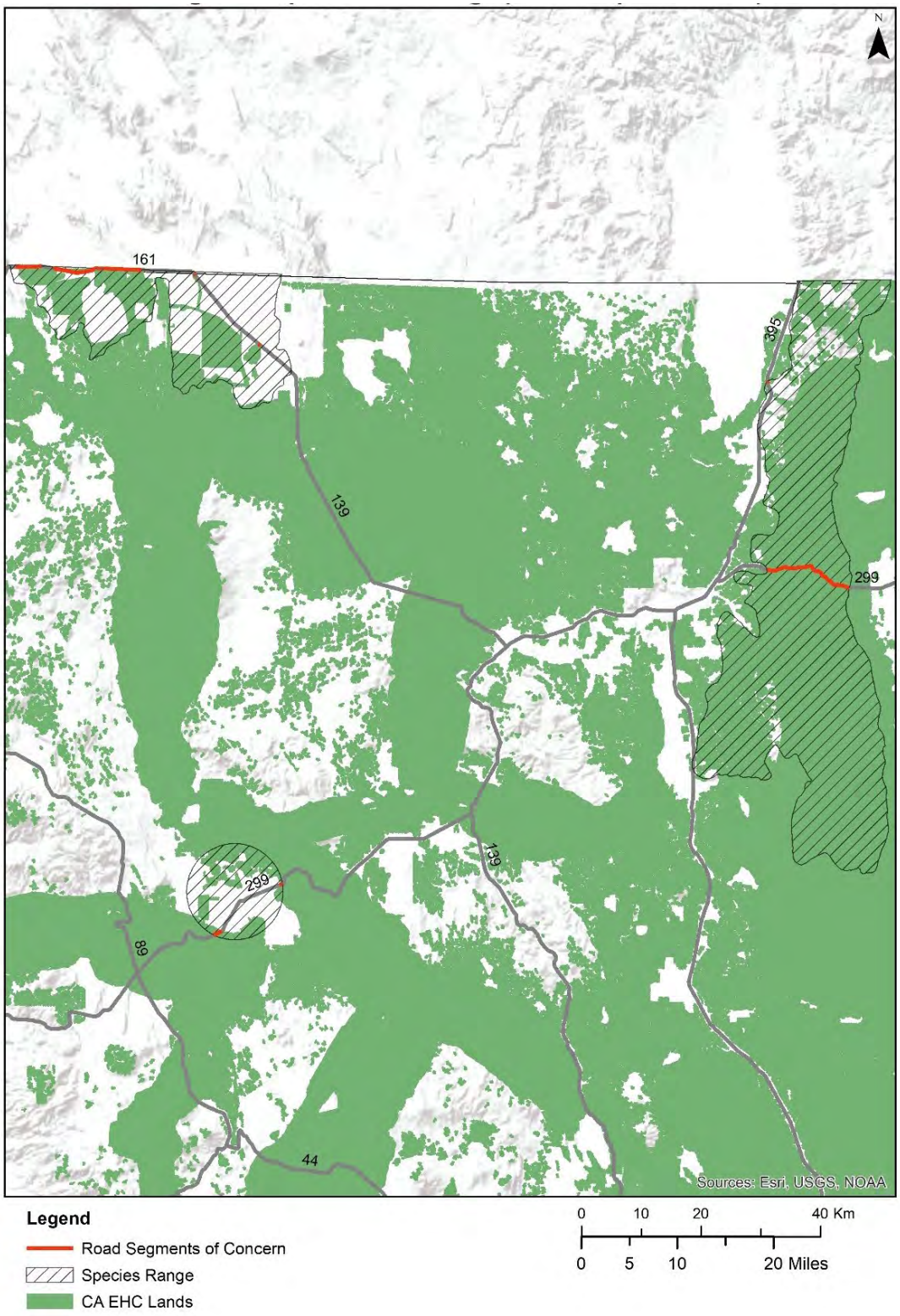


Figure 27. Highway Segments of Concern: Oregon Spotted Frog (*Rana pretiosa*)
Note: Possibly extinct in CA.

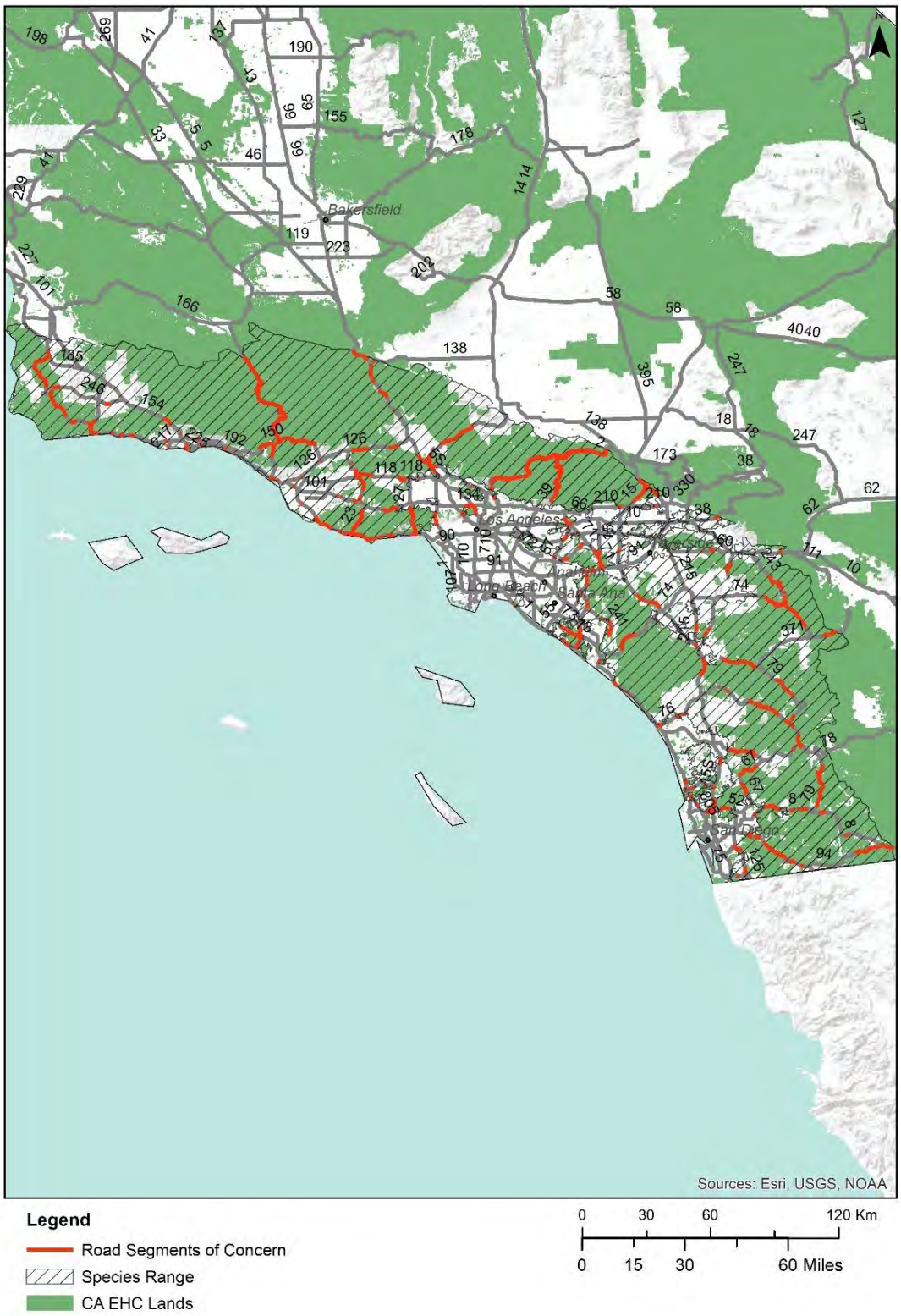


Figure 28. Highway Segments of Concern: Coast Patch-nosed Snake (*Salvadora hexalepis virgultea*)

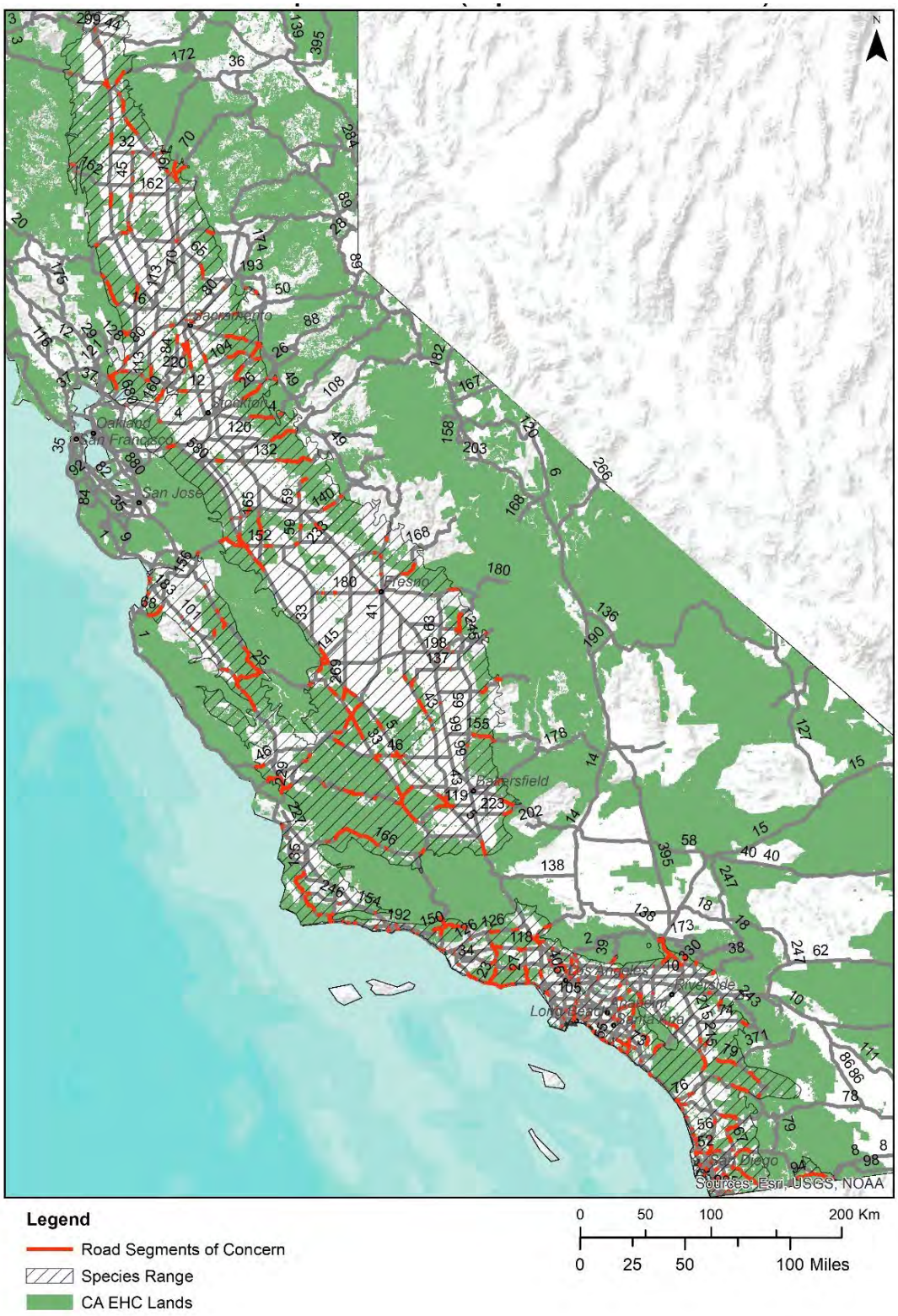


Figure 29. Highway Segments of Concern: Western Spadefoot (*Spea hammondii*)

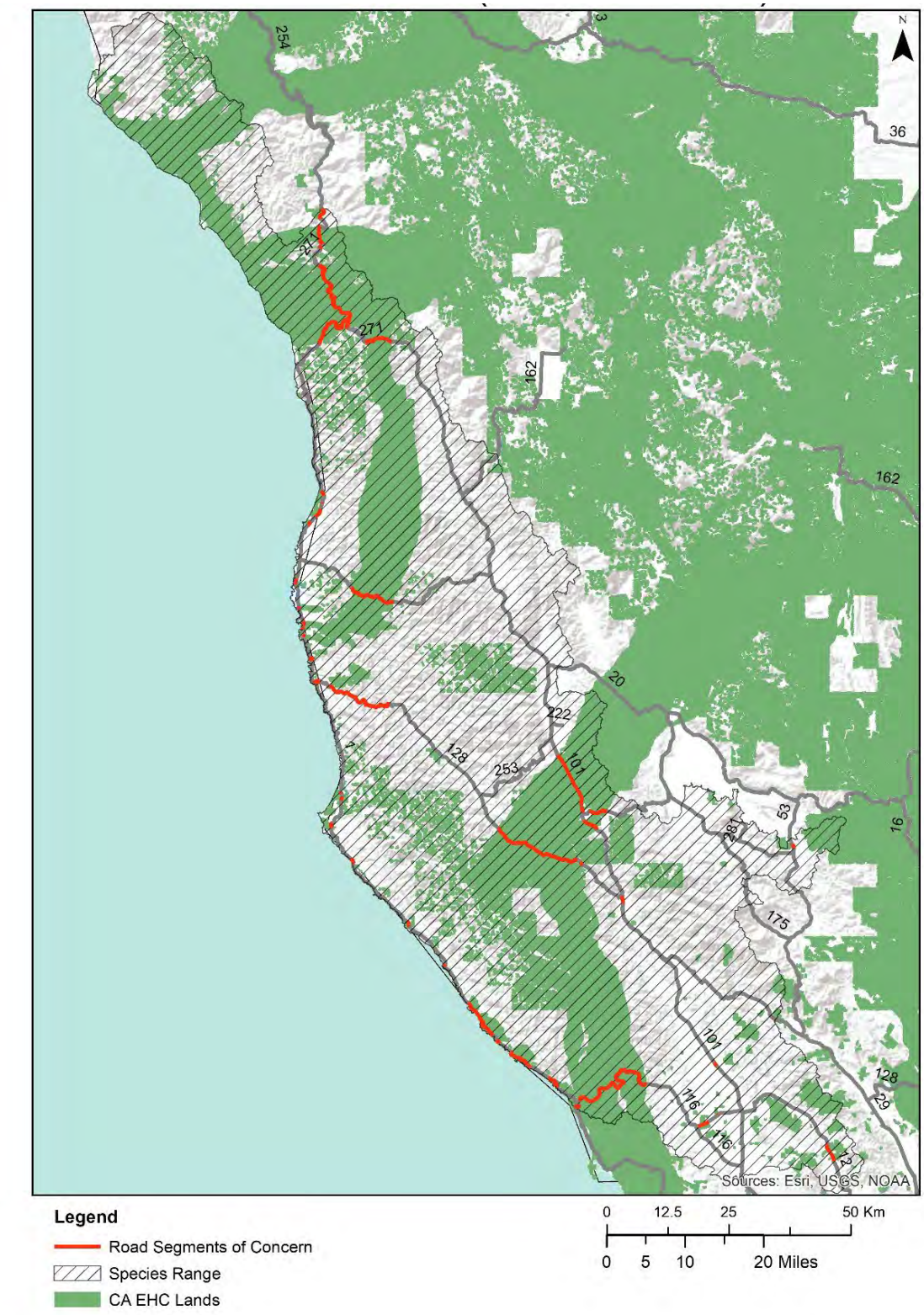


Figure 30. Highway Segments of Concern: Red-bellied Newt (*Taricha rivularis*)

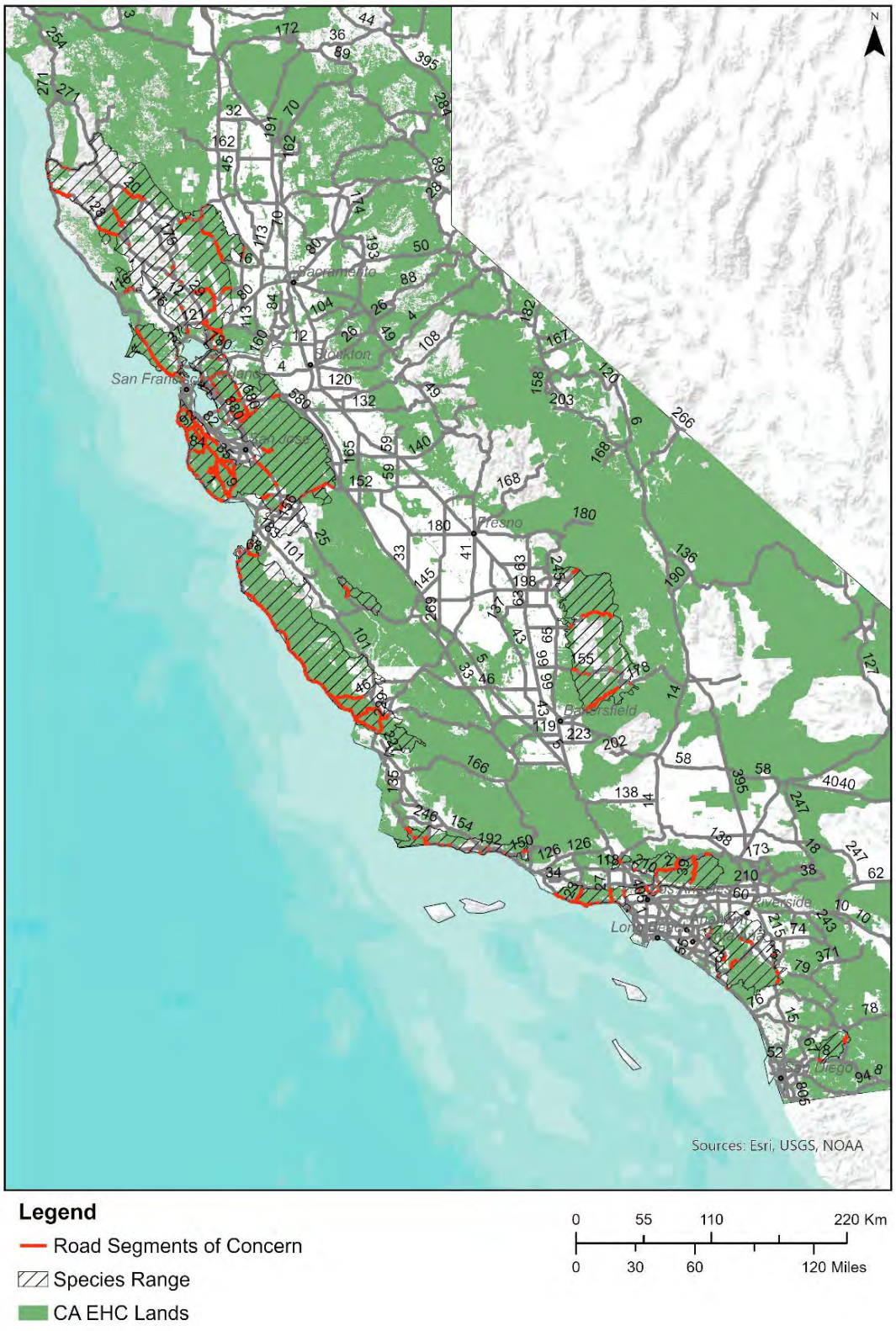


Figure 31. Highway Segments of Concern: Coast Range Newt (*Taricha torosa*)

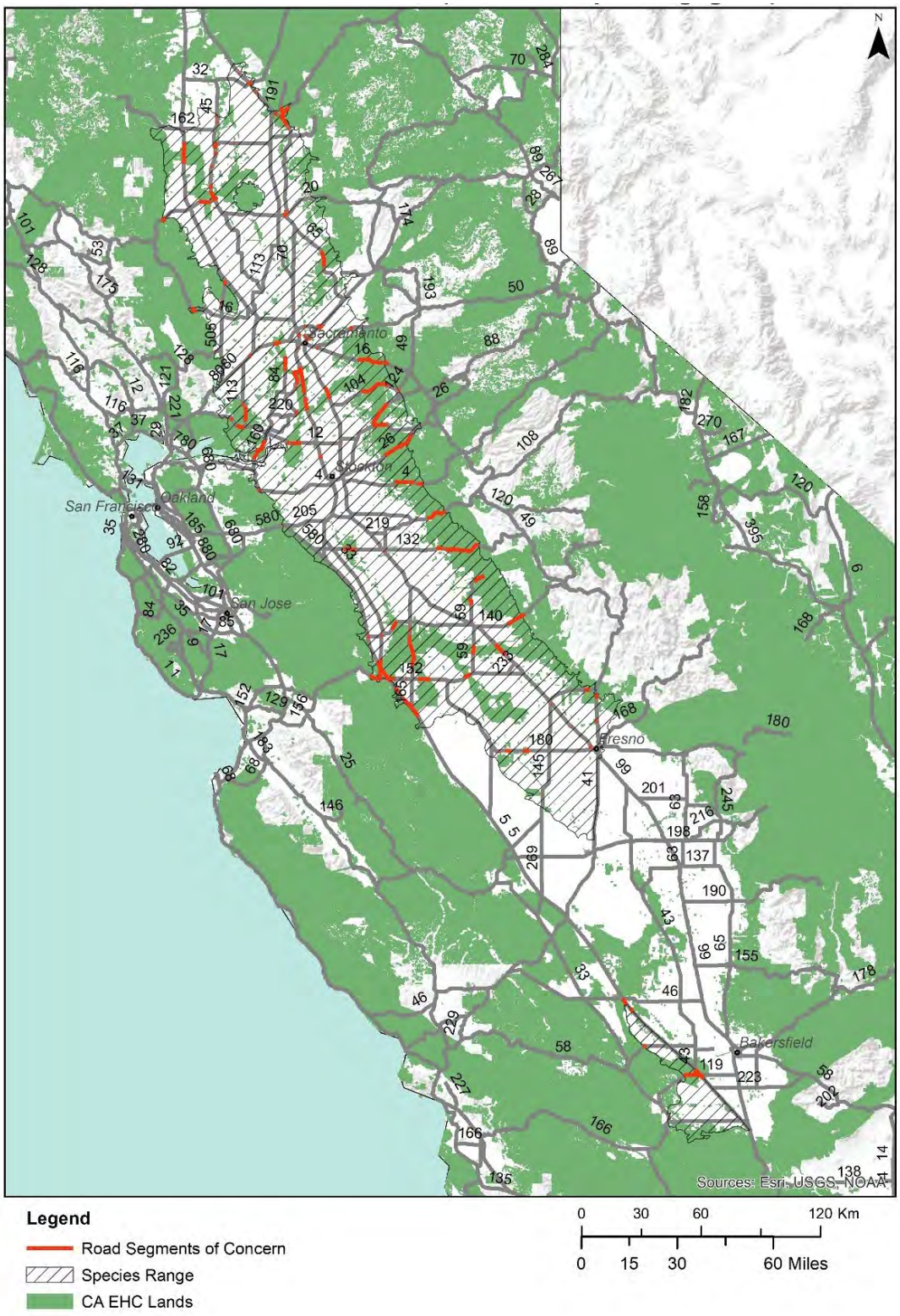


Figure 32. Highway Segments of Concern: Giant Gartersnake (*Thamnophis gigas*)

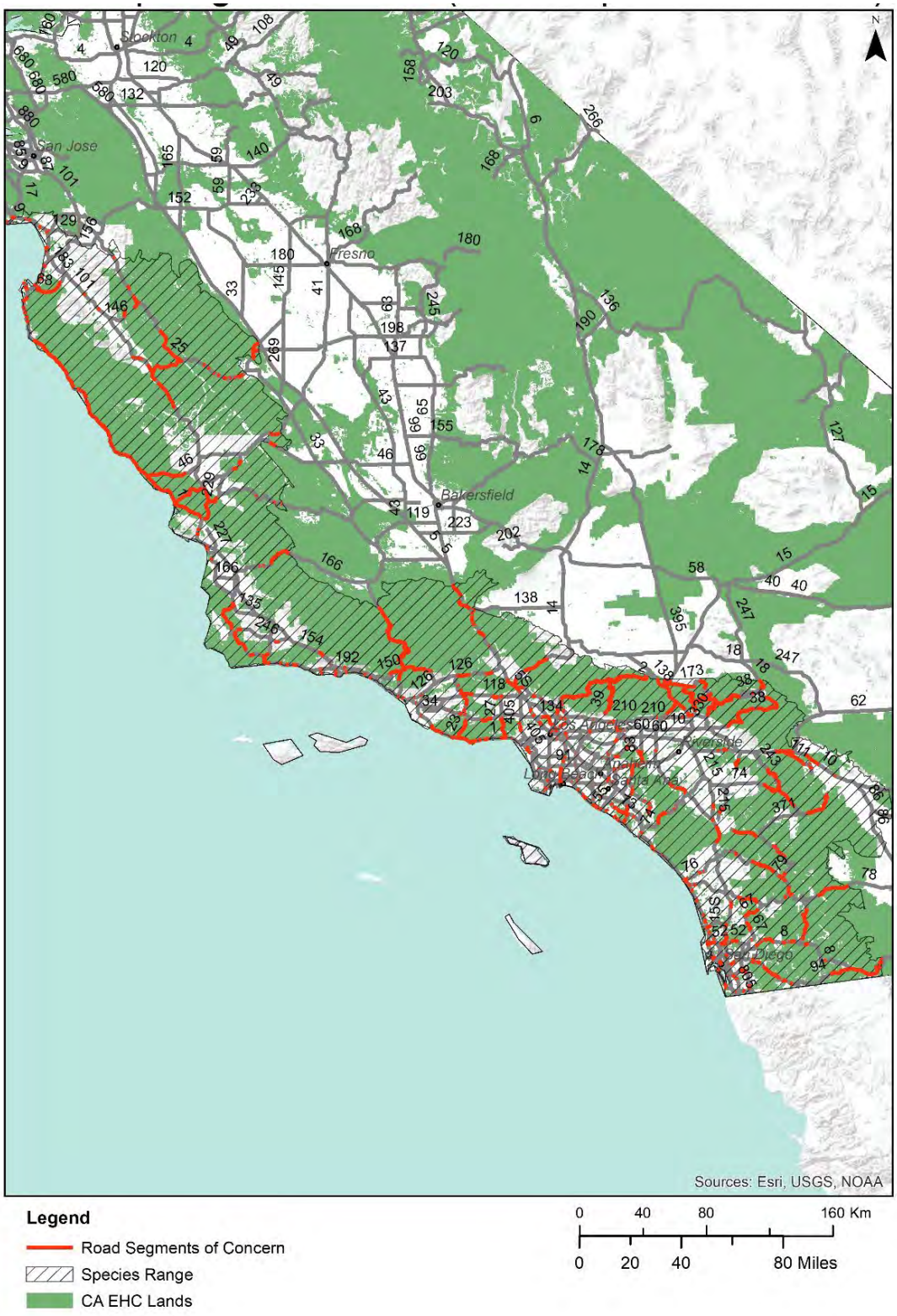


Figure 33. Highway Segments of Concern: Two-striped Gartersnake (*Thamnophis hammondii*)

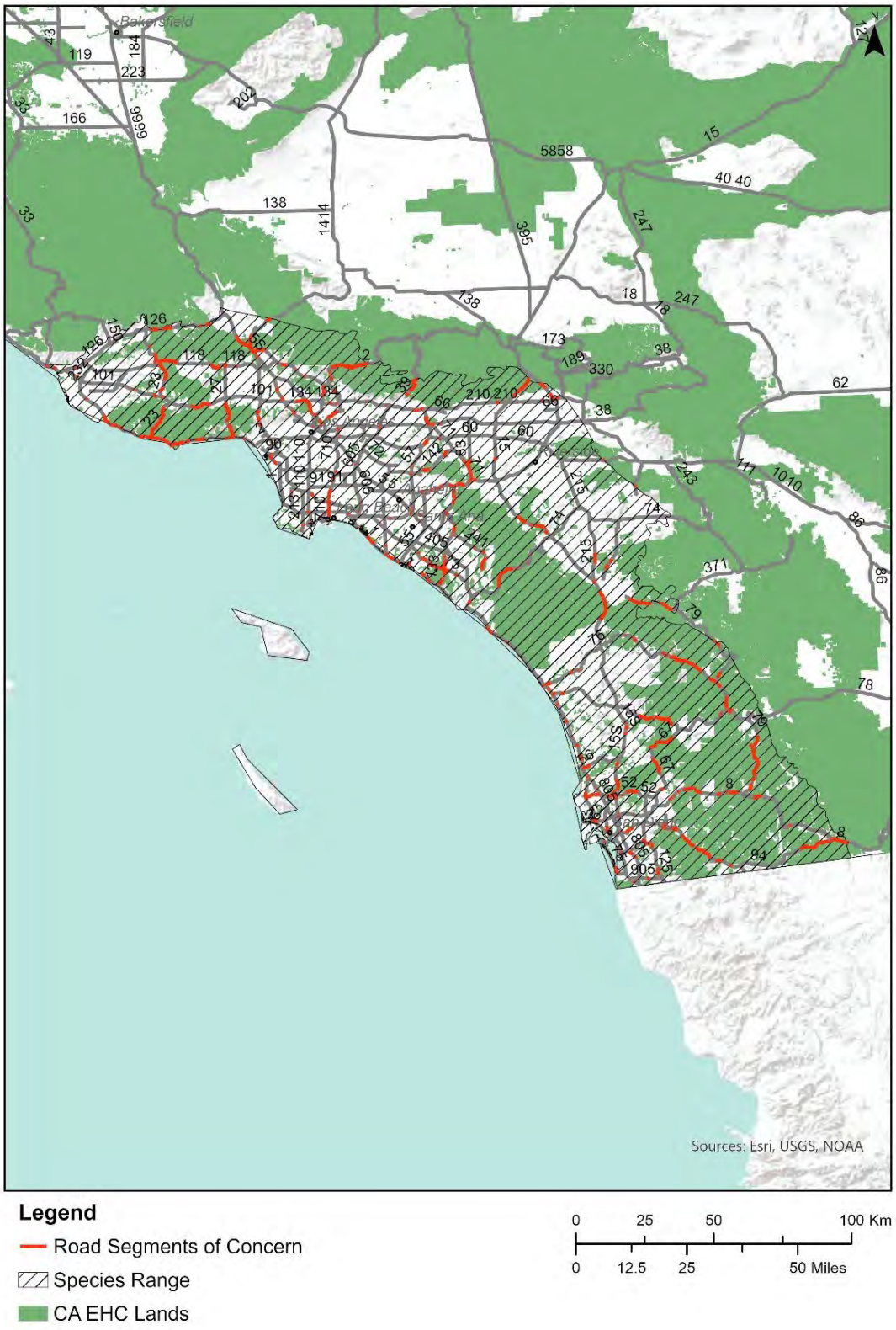


Figure 34. Highway Segments of Concern: California Red-sided Gartersnake (*Thamnophis sirtalis infernalis*)

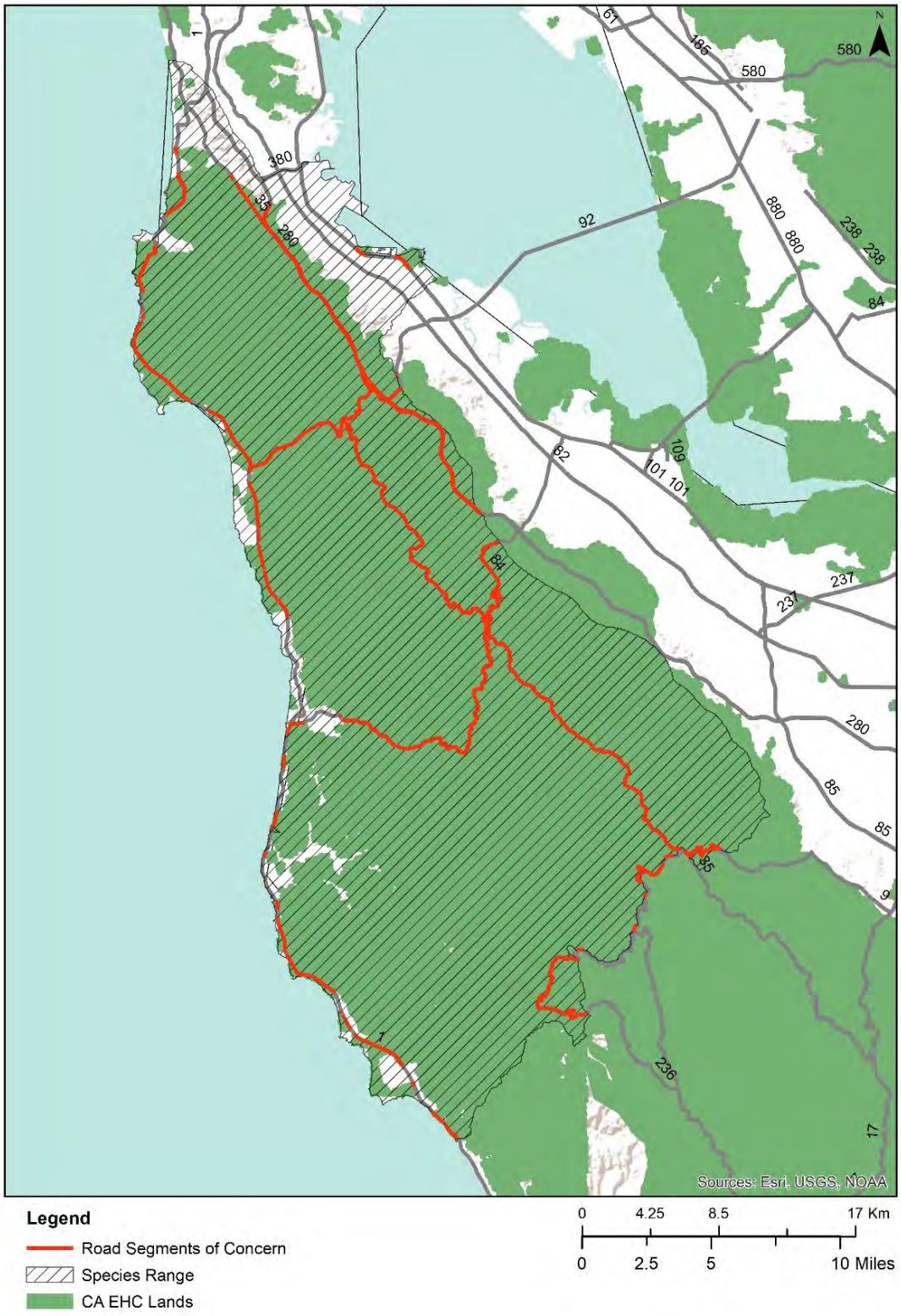


Figure 35. Highway Segments of Concern: San Francisco Gartersnake (*Thamnophis sirtalis tetrataenia*)

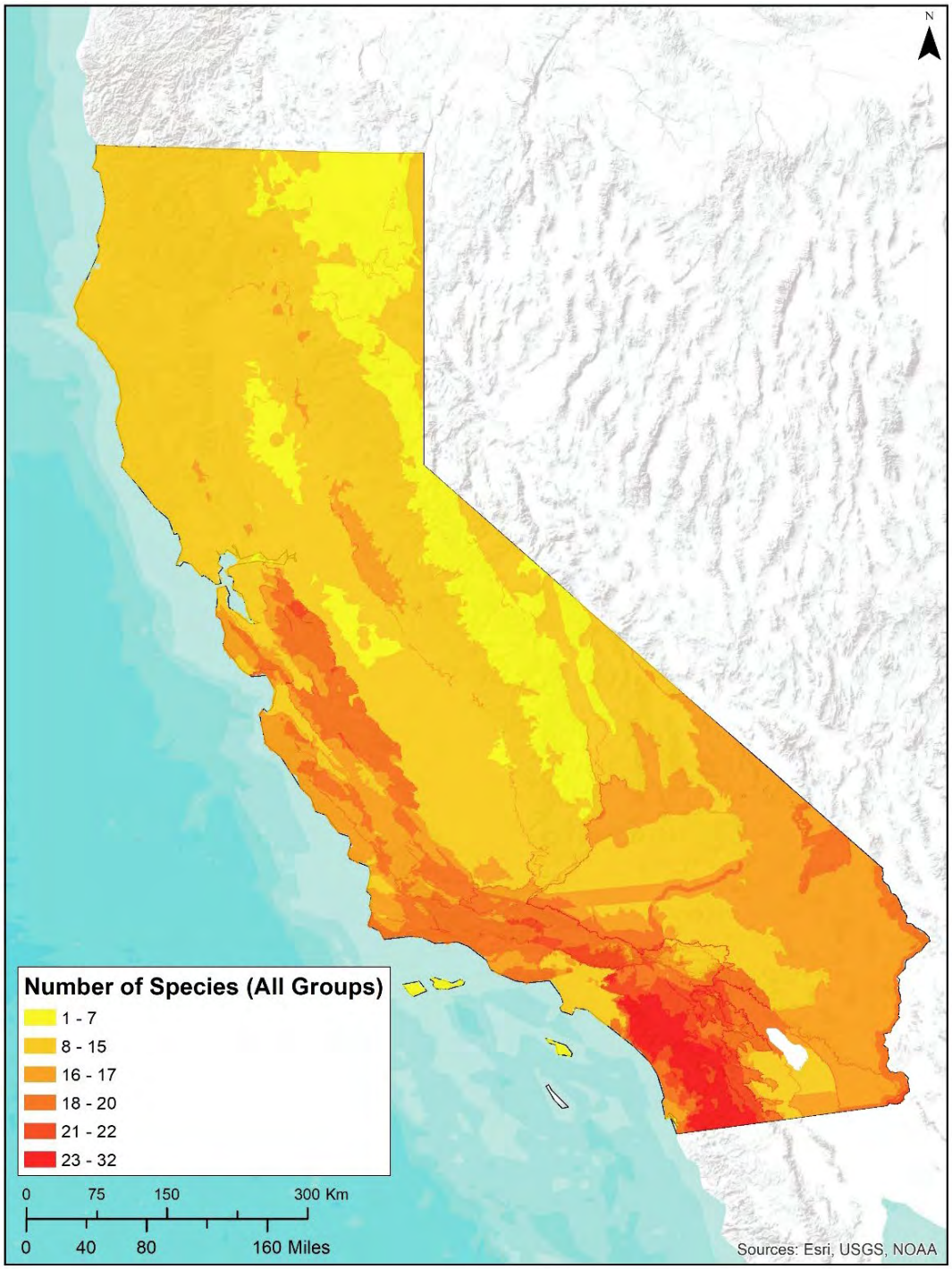


Figure 36. Range Density of Reptiles and Amphibians at High and Very-high Risk of Negative Road Impacts.

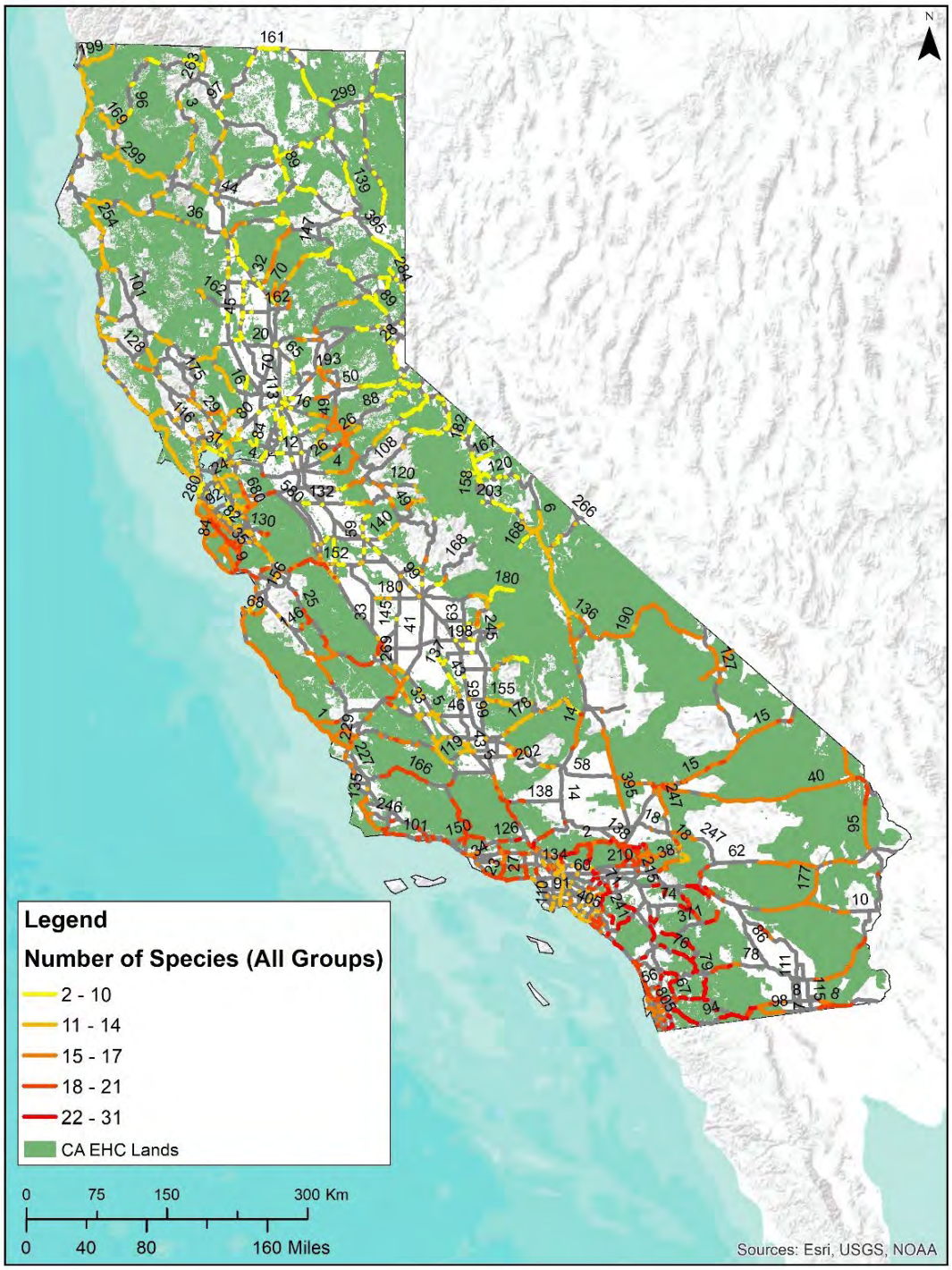


Figure 36. Range Density of Reptiles and Amphibians at High and Very-high Risk of Negative Road Impacts in Relation to California Highways

## References

Spencer, WD, P Beier, K Penrod, K Winters, C Paulman, H Rustigian-Romsos, J Strittholt, M Parisi, and A Pettler. 2010. California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.

Thomson, RC, AH Wright and NB Shaffer (2016) California amphibian and reptile species of special concern. Univ of California Press.

# Chapter 4. Movement of California Tiger Salamanders Along Barrier Fencing and Underpasses in Stanford, CA

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## Introduction

Many migratory amphibians make annual population level migrations among breeding wetlands and over-wintering and/or summer foraging upland terrestrial habitats. This requires high levels of connectivity among these habitats (Semlitch 2008, Hamer and McDonnell 2008, Hamer et al. 2015). Because roads often intersect these migratory pathways, all California migratory salamanders, toads and some frogs ranked in the highest risk categories for potential negative road effects, as analyzed by Brehme et al. (2018).

There is substantial evidence that habitat fragmentation and mortality due to roads negatively affect many of these amphibians. For instance, newts regularly migrate long distances over land between breeding ponds and terrestrial foraging habitats (2 km; Trenham 1998). Large numbers are found dead on roads during dispersal periods and newt species are often the first to disappear in fragmented landscapes (Gibbs 1998, Trenham 1998, Shields pers. comm.). Similarly, road mortality and habitat fragmentation are primary threats to the California tiger salamander and other Ambystomid salamanders because terrestrial habitat is used for interpond migration and overwintering (Semlitsch 1998, Trenham et al. 2001, Bolster 2010). There is also evidence that migrating bufonid toads are particularly susceptible to negative impacts from roads (Trenham et al. 2003, Orłowski 2007, Eigenbrod et al. 2008).

To reduce the negative impacts from road mortality on these vulnerable populations, it has been standard practice to build safe crossings in the form of small passages (e.g. culverts, tunnels, etc.) connected by barrier fencing as mitigation. There are a wide variety of small passages and barrier materials that have been constructed with varying degrees of success, although post mitigation monitoring is relatively rare (see review by Langton and Clevenger 2017). The permeability of tunnel systems to amphibian movement may be influenced by openness ratio ((height*width)/length), moisture and temperature conditions within the passage, noise and vibrations, and the correct placement of passages in the landscape (Jochimsen et al. 2004, Hamer et al. 2015, Langton and Clevenger 2017, Helldin and Petrovan 2019).

However, in addition to crossing success within the passage(s), the permeability of crossing systems to amphibian population movements is also dependent upon the proportion of migrating animals that even reach the passage opening. There is evidence that road mitigation systems with inadequate underpass spacing may filter movements of pond breeding amphibians (e.g. Langton 1989, Allaback and Laabs 2002, Pagnucco et al. 2012, Ottburg and van der Grift 2017, Matos et al. 2019). Individuals from a population of the common toad, *Bufo bufo*, in the Netherlands turned around or “gave-up” after an average of 50 m if they did not reach an underpass (Ottburg and van

der Grift 2017). The authors considered this the main factor causing a steep population decline in the five years after the tunnel and barrier system was installed. The extent of this potential problem with other mitigation systems and species is largely unknown.

Currently, little science is available in California to inform decisions about the number of crossings and spacing between crossings. Therefore, we studied whether this "giving up" behavior is exhibited in pond breeding amphibians in California, and if so, at what distances different migratory species (and age classes of species) give-up when moving along barrier fencing? This information could inform best management practices for underpass spacing for these species.

There is also some evidence that animals may spend more time trying to climb or interact with transparent fencing compared to solid fencing (Ruby et al. 1994, Milburn-Rodriguez et al. 2016). Therefore, we were interested in whether fencing opacity affects the probability or speed at which CTS and other amphibians find wildlife crossings. Finally, we were also interested in whether 'turnarounds' at fence ends may be effective in altering the trajectory of CTS movement.

We studied a population of California tiger salamanders (CTS: *Ambystoma californiense*) in Stanford, CA to investigate these kinds of behaviors. In this location, a busy two-lane paved road (Juniper Serra Blvd: ave. 17,300 vehicles per day; (City of Menlo Park 2017)) transects upland habitat and Lagunita Lake, a historic CTS breeding site. Large rates of CTS road mortality spurred the construction of a three-tunnel system (5 m apart) in 2003 with approximately 5–10 m of barrier fencing on each side. For our study, we expanded the footprint of existing barrier fencing 150 m in each direction using solid fencing in one direction semi-transparent mesh fencing on the other side.

We addressed the following questions in this study:

1. What is the probability a salamander will reach an underpass based upon the distance from the underpass an animal first encounters the barrier wall?
2. How quickly do CTS travel along the barrier wall toward the underpass?
3. How does the opacity of fencing effect the questions above?
    a. Solid barrier (high-density polyethylene (HDPE-2); Animex®)
    b. Semi-transparent barrier (water- permeable rigid polymer matrix; ERTEC® E-Fence, referred to hereon as "mesh")
4. Are fence end 'turnarounds' effective in redirecting the trajectory of CTS movement?
5. Once CTS reach the tunnels, what is the permeability of the road crossing tunnel system to CTS passage?

## Methods

*Field Study*

We studied the movement of CTS adjacent to three existing underpasses along Junipero Serra Blvd. in Stanford, CA (Stanford University) in the winter breeding seasons of 2017/18 and 2018/19. The road bisects a historic CTS breeding pond (Lake Lagunita) and upland CTS habitat (Figure 1).

Figure 1. Map of Barrier and Tunnel Study System at Stanford University Between Upland and Breeding Habitat for CTS.

A total of 300 m of barrier fencing was installed along the south side of Juniper Serra Blvd. (150 m in each direction); the new fencing was connected to 5 m of existing barrier fencing adjacent to three salamander tunnels (ACO Wildlife ®). The tunnels, installed in 2003, are 14 m in length and spaced 5 m apart. One portion of the fencing installed was semi-transparent mesh (ERTEC ® rigid polymer matrix) and the other portion was solid (Animex ® high-density polyethylene (HDPE-2)). To minimize potential for vandalism, the fencing was placed within existing security fencing present on site. Jump-outs (ERTEC® cones and high berms) were installed a minimum of every 25 m along the fence to provide CTS and other small vertebrates a way to get back into the habitat if they ended up on the roadside of the barrier fencing. At outer fence ends, turnarounds were installed to redirect animals away from the road and back toward the upland habitat in a U-shaped fashion. The turnarounds were approximately 2 m long and 1 m in width. Fencing was installed with the bottom buried in the ground according to manufacturers' guidelines.

HALT ® camera systems (Hobbs and Brehme 2017) were placed every 25 m along the new fence lines from 0 to 125 m from the existing tunnel system (Figure 2). Each 0 m camera was approximately 5–8 m from the closest tunnel opening where our newly installed fencing intersected with the existing barrier fencing.

At fence end turnarounds, HALT camera systems were placed above the fence end at the turn-around to record video of animals' movement trajectory after coming out of the turn-around. Due to evidence of CTS turning around but not being recorded on video, in 2019, we narrowed the terminal end of the turnaround from 1 m to approximately 0.35 m from the main fence creating a tear drop shape. This allowed us to install the HALT trigger at the turnaround opening so that we could record animals entering and exiting the turnaround. In 2019, we also placed these camera systems within each tunnel opening and exit to record tunnel permeability. Cameras were set whenever rain was predicted and checked on a weekly basis during the winter adult migration season from the uplands toward the pond (Nov.–Feb.). Each time we set and checked the cameras, we took a photo of a battery powered atomic clock in order to calibrate exact minutes and seconds upon processing. All work was performed under Stanford University Habitat Conservation Plan (Federal incidental take permit # TE182827-0) and California State Consistency Determination (2080-2016-001-03)

A) B) C)

Figure2. Solid (A) and Mesh (B) Fence Lines with Cameras Within Wood Structures and Plastic Bins Facing Down Toward HALT Triggers. Fencing Leads to a Series of 3 Tunnels Under the Roadway (C).

*Analysis*

Photos of all CTS were analyzed using pattern recognition software to identify individuals by their unique spot patterns ($I^3S$ Spot; Van Tienhoven et al. 2007; Figure 3). Camera location, time, and direction of movement were recorded for each individual. Snout to vent length was measured with Program ImageJ (Rasband 1997–2018) using the 1 cm grids from the HALT trigger for calibration.

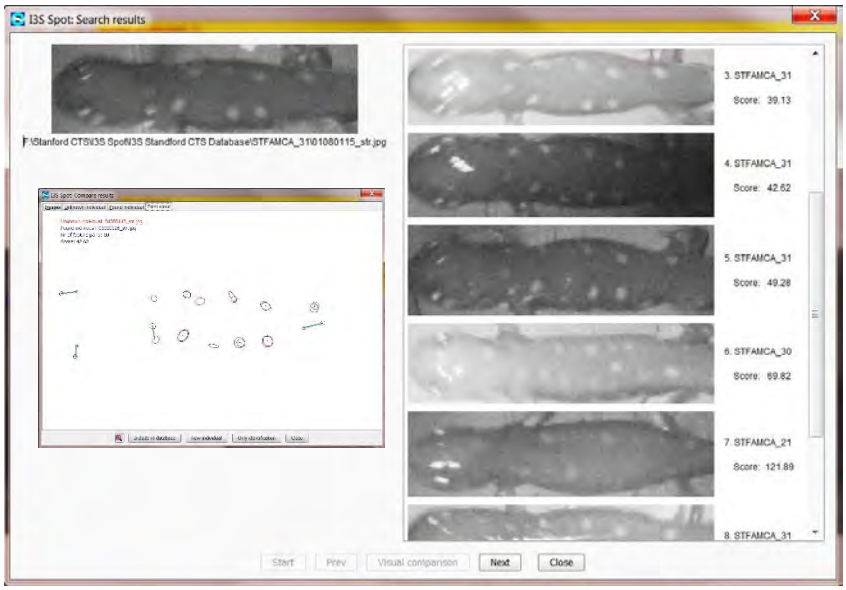


Figure 3. Example of CTS Identified to Individual Using $I^3S$ Software to Distinguish Spot Patterns (top 3 on right are same individual)

For individual CTS, we then calculated movement distances along the fence lines, numbers of turn arounds, speed, and "success" at reaching 0 m cameras next to underpass system. Because cameras were placed 25 m apart, our margin of error for estimating fence movement distance ranged between 0 and 25 m. For instance, if an animal was only detected at a single camera between 25 m and 125m, then our average estimated distance was 25 m (12.5 m before reaching the camera and 12.5 m after exiting the camera). Similarly, if an individual was detected at multiple consecutive cameras moving in the same direction, our margin of error was typically 25 m. In the instances where individuals were detected at consecutive cameras, we also calculated the movement speed between segments. If such an individual then turned around and was re-detected at a camera while moving in the other direction, we were able to estimate the distance travelled along the fence before turning around by multiplying the time between detections by its average speed. Because of this, if individuals travelled back and forth several times, we were able to more accurately estimate the total distance of fence line traversed (fence movement distance). If an individual reached the 0 m camera (where the experimental fence lines attached to the short length of existing fence), this was considered a "success" at reaching the passage system with no added error for distance moved afterward.

We used Markov Chain Monte Carlo (MCMC) implemented in the R programming language and the runjags package (Denwood 2016) to interface with JAGS (Just Another Gibbs Sampler) to sample values of all unknown parameters from the joint posterior distribution. In each case, four chains were sampled to perform standard diagnostics for convergence. In all cases, non-informative prior distributions were used for all parameters.

### *Logistic Regression for Success in Reaching Underpass Opening*

We modeled the probability of success of CTS in reaching the 0 m camera near the crossing opening. For this, we used a Bayesian approach to logistic regression modeling (Congdon 2006; Figure 4). The response was a Bernoulli random variable, where 0 indicates failure and 1 indicates success in being detected by the camera at the opening of the crossing (ReachedTunnel). The probability of success for the Bernoulli distribution is a logistic (i.e. p = exp(y)/(1 + exp(y)) function of the linear component of the model that consists of four predictors (FenceType, InitLoc, InitAway, InitLocAway) and five parameters that include an intercept and a regression coefficient corresponding to each of the predictors. FenceType is a binary variable where 0 indicates a mesh fence and 1 indicates a solid fence. InitLoc is the position along the fence where the animal was first detected in meters from the crossing opening (with error described in the previous paragraph), InitAway is a binary variable where 0 indicates that the animal was initially moving toward the crossing and 1 indicates it was initially moving away from the crossing, and InitLocAway is an interaction (product of) InitLoc and InitAway. All predictors were standardized (the mean subtracted from each value and then divided by the standard deviation) prior to modeling. The priors for the parameters were non-informative normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the probability of success.

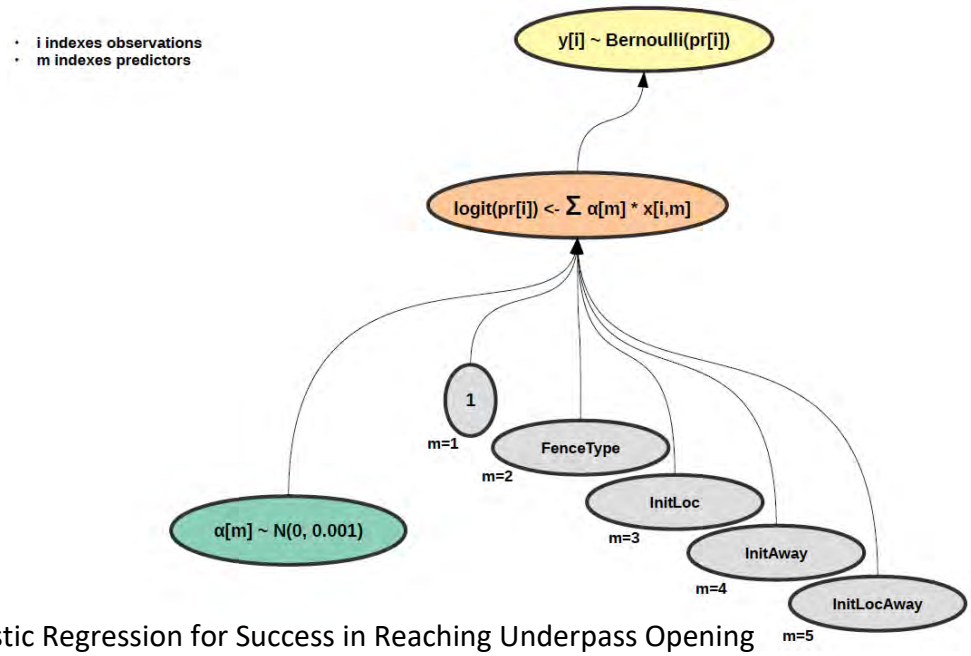


Figure 4. Logistic Regression for Success in Reaching Underpass Opening

*Gamma Regression for Distance Moved Along Fence*

We also modeled the distance that CTS moved along the fence. We used a Bayesian approach to regression modeling of the probability of successfully reaching the underpass opening (Figure 5). The response was assumed to be a gamma distributed random variable, which is a continuous positive variable representing the distance the animal moved along the fence as described. The gamma distribution has a shape parameter, which we assumed to be independent of any predictors, and a rate parameter that we model as an exponential (i.e. rate = exp(y)) function of the linear component of the model that consists of four predictors FenceType, InitLoc, InitAway, ReachedTunnel, InitLocAway and six parameters that include an intercept and a regression coefficient corresponding to each of the predictors. All predictors, except for ReachedTunnel, were standardized prior to modeling. The prior for the shape parameter was a non-informative exponential distribution with a rate of 0.00001. The priors for the regression parameters for the rate were normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the distance moved along the fence.

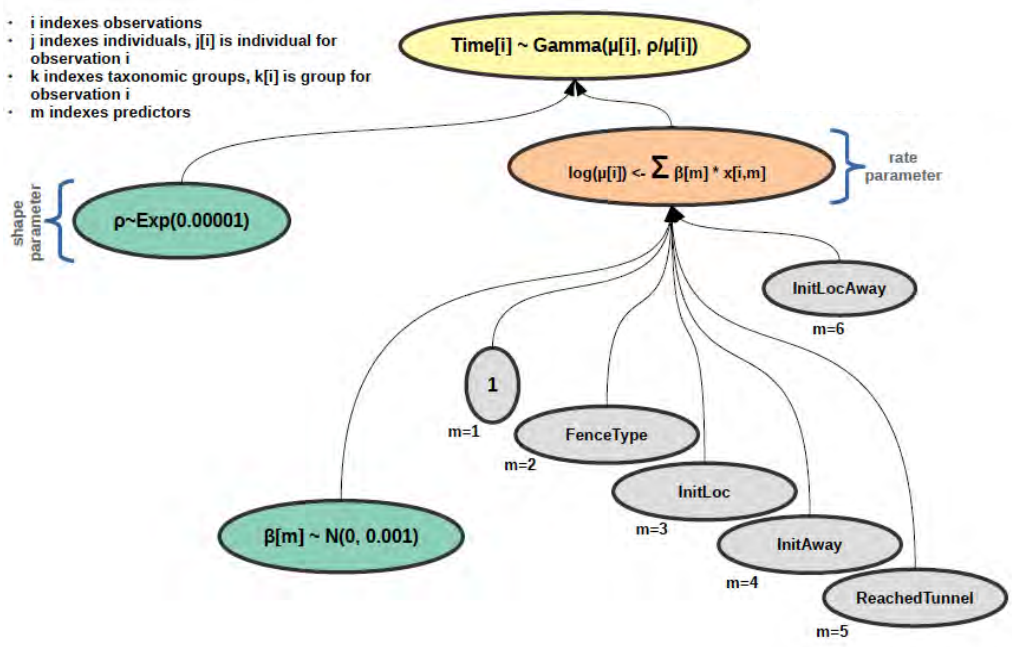


Figure 5. Gamma Regression for Distance Moved Along Fence

Tunnel System Permeability was calculated as the number of complete passes (individual detected at entrance and exit) divided by number of attempts. Other data, such as speed and turnaround rates, were also calculated.

## Results

We documented 41 adult CTS over 4 nights in 2018 and 50 adults over 18 nights in 2019 moving along the fence-line. We did not compare individuals between years, and therefore, considered individual movements from 2018 and 2019 as independent in the analysis. Total precipitation during the winter months from November to March was 3.7 in. and 27.0 in. for 2018 and 2019, respectively (World Weather Online; Palo Alto). The average winter rainfall is 13 in. (Western Regional Climate Center Stn 046646-4). The Stanford University Conservation Program observed no recruitment in 2018 but confirmed high recruitment of CTS in 2019 (A. Launer and E. Adelsheim, pers. comm.).

Of the 91 CTS movements, 37 were along the solid fence line and 54 were along the mesh fence line. Fifty-six percent of CTS moved an estimated 25 m or less. Mean fence movement distances averaged approximately 40 m and did not differ by fence type. However, CTS movement speed was 43% slower and CTS changed direction an average of three times more frequently along the mesh fence than the solid fence (Table 1, Figure 6). Upon reaching the fence, 64% of CTS initially turned and moved in the direction of the passage system while 36% initially moved away from the passages. Two out of the three CTS that reached the fence ends 150 m from the passage system turned around and were subsequently documented on another camera 25-125 m away continuing to move back along the fence line.

Table 1. CTS Movement Metrics by Fence Type

| | | Fence Distance (m) | | Movement Speed (m/min)* | | Direction Changes (turnarounds/25m) | |
|---|---|---|---|---|---|---|---|
| Fence Type | Sample Size | Mean | 90% CI | Mean | 90% CI | Mean | 90% CI |
| Solid | 37 (14*) | 41.8 | 32.0- 47.8 | 2.1 | 1.7-2.5 | 0.13 | 0.04- 0.23 |
| Mesh | 54 (26*) | 39.3 | 34.5- 42.2 | 1.2 | 1.0-1.4 | 0.41 | 0.15- 0.67 |

*individuals that passed more than one camera where movement speed was calculated

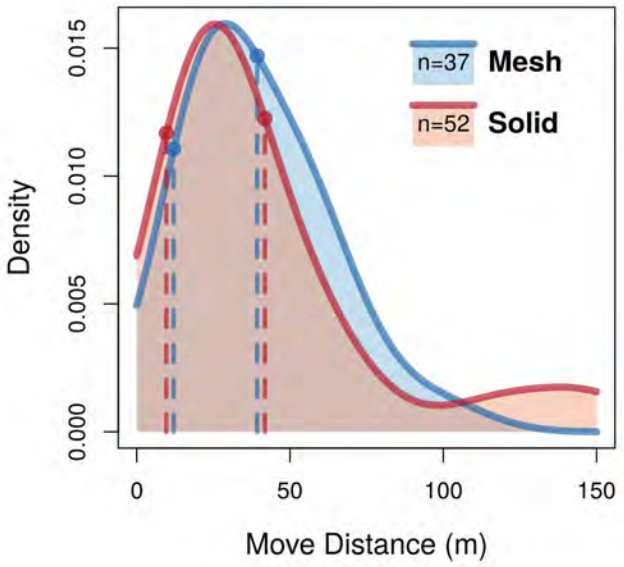


Figure 6. Distributions of Movement Distances by Fence Type. Lines Represent the Mean and Lower 90% Confidence Level Based on Cumulative Density of Observed Data.

The linear regression modeling indicates CTS moved longer distances if they encountered the fence farther away from the tunnel system. However, this was only if their initial direction choice was toward the tunnel system (Figure 7). There was no difference in predicted move distances for those CTS that encountered the fence and initially turned in the "wrong" direction

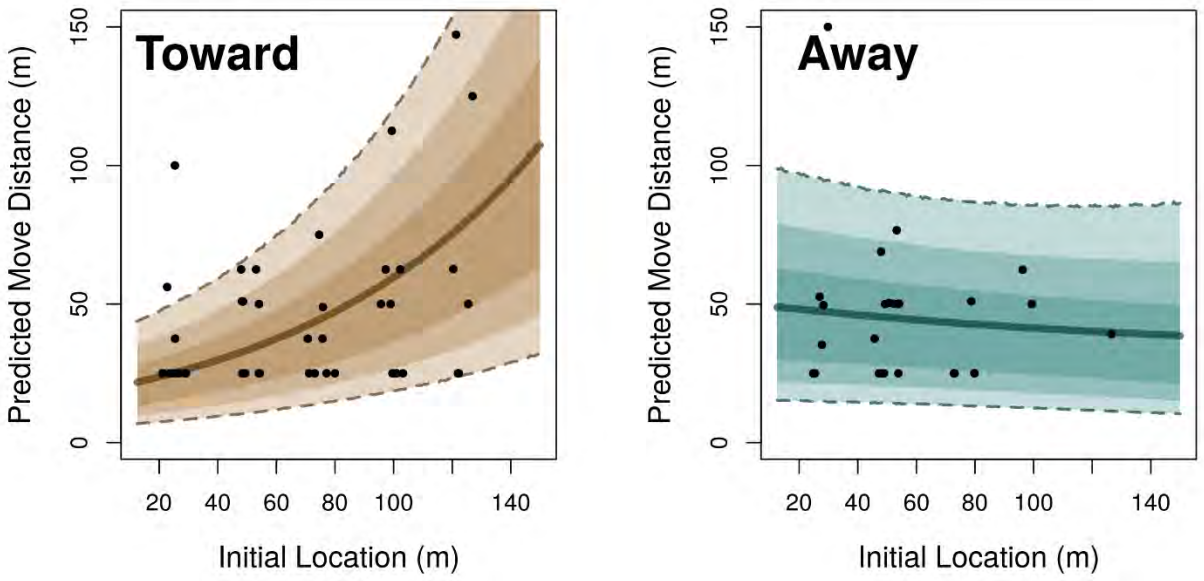


Figure 7. Movement Distance by Initial Location and Direction of Travel (Toward or Away from Underpass) with 90% Confidence Intervals.

The probability that CTS reached the tunnel system (0 m camera) decreased rapidly with increasing distance from the tunnels and was also highly dependent upon their initial direction choice. The average predicted probability of an individual reaching the tunnel system if the CTS encountered the fence at a distance of 25 m and was moving toward the tunnels was 0.48. This was reduced to only 0.15 if the CTS was initially moving away from the tunnels. Model estimated probabilities of success were lower along the mesh fencing than solid fencing, but fence type was not a significant predictor of success at reaching the underpass system (Table 2, Figure 8).

Table 2. Predicted Probabilities of Reaching Underpass by Initial Location and Direction of Travel (Toward or Away from Underpass)

| | Solid Fencing | | | | Mesh Fencing | | | |
|---|---|---|---|---|---|---|---|---|
| | TOWARD Underpass | | AWAY from Underpass | | TOWARD Underpass | | AWAY from Underpass | |
| Initial Distance | Probability of Success | 90% CI | Probability of Success | 90% CI | Probability of Success | 90% CI | Probability of Success | 90% CI |
| 12.5 | .76 | .57- .91 | .35 | .11- .64 | .60 | .37- .81 | .20 | .05- .42 |
| 25 | .59 | .38- .79 | .21 | .04- .46 | .40 | .21- .61 | .11 | .02- .24 |
| 50 | .24 | .08- .44 | .07 | .00- .25 | .13 | .04- .26 | .03 | .00- .10 |
| 75 | .07 | .01- .19 | .03 | .00-.15 | .03 | .00- .09 | .01 | .00- .06 |
| 100 | .02 | .00- .07 | .02 | .00-.10 | .01 | .00- .03 | .01 | .00- .04 |
| 125 | .01 | .00- .03 | .01 | .00- .06 | .00 | .00- .01 | .00 | .00- .02 |

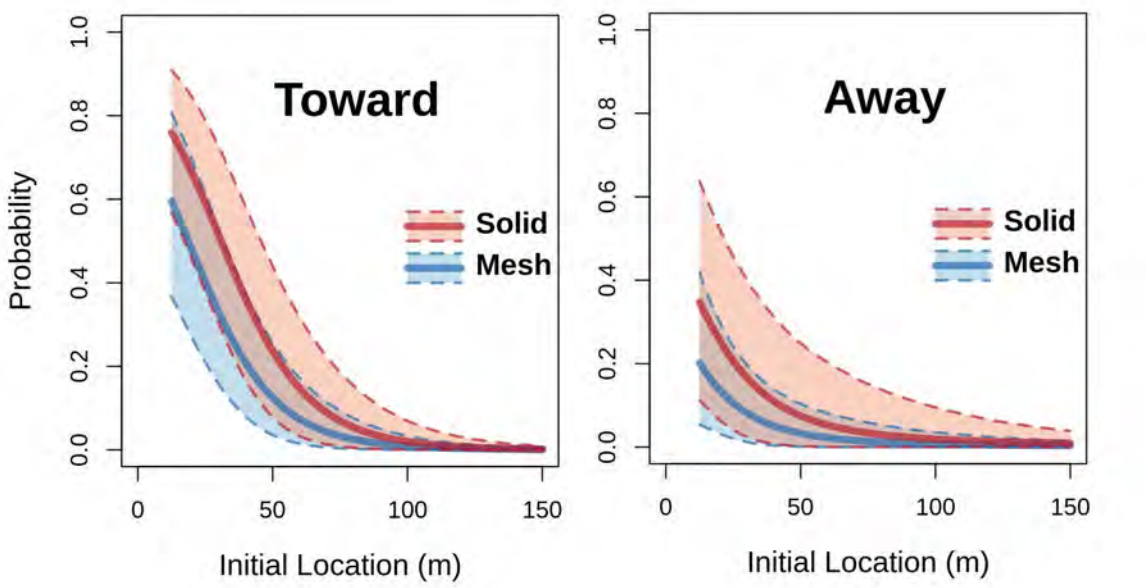


Figure 8. Probability of Reaching Underpass by Initial Location and Direction of Travel (Toward or Away from Underpass) with 90% Confidence Intervals.

Based upon timing, speed, and diagonal views of CTS entering and exiting the tunnels, we estimate that 5 to 11 out of the 51 CTS we documented traveling along the upland fence lines passed through the tunnel system from upland habitat toward the lake and 11 to 16 CTS entered the tunnels in the 20 m wide passage system without ever interacting with the fence. Once CTS entered a tunnel, there was a very high probability of them making it to the other side (0.89). Speed of passage through the tunnels was consistent with the speed at which CTS moved along the solid fencing (Table 3).

Table 3. Underpass System Permeability Metrics (2019)

| No. CTS entered | No. CTS turned around | No. CTS successful passage | Tunnel System Permeability | Average Individual Passage Time (min:sec) | | Average Passage speed (m/min) | |
|---|---|---|---|---|---|---|---|
| | | | | Mean | 90% CI | Mean | 90% CI |
| 41[a] | 4 | 33[b] | 0.89 | 6:33[c] | 4:48- 8:18[c] | 2.1[c] | 1.5- 2.8[c] |

[a] 4 CTS unknown if complete passage due to camera battery failure

[b] 22 CTS passed from upland to lake, 10 CTS passed from lake to upland, 1 CTS passed 3x from lake to upland to lake to upland

[c] a single passage time of 11 hours 18 min was excluded. Only CTS individual that spent day in passage.

## Discussion

Our results showed that a relatively small proportion of the CTS that were documented migrating from upland habitat reached the passage system leading to breeding habitat at Lagunita Lake. CTS moved an average distance of 40 m along barrier fencing before "giving up" and their probability of making it to the passage system decreased rapidly with increasing distance from the tunnels.

The average distance moved by an individual CTS was 40 m. Approximately half of the individuals moved longer distances and half moved shorter distances before "giving up." This did not mean that all individuals moved along the barrier fencing in one direction and then either made it to the tunnel or gave up. Many individuals moved back and forth along the fencing and the 40 m represents the average span of total fence distance moved. Although this was an average, we estimated a fence span distance of less than 12.5 m would encompass 90% of population movements from the movement density distribution. Because our cameras were set 25 m apart, we were unable to estimate the specific distance with high confidence. Our logistic model predicted that 66% of individuals encountering the fence at the median distance of 12.5 m would successfully reach the tunnel system if headed toward the passage. For suggesting minimum distances between passages across a migratory pathway, we assume that either direction a CTS turns, it will encounter a passage. Therefore, these results suggest that underpasses spaced less than 12.5 m from one another along CTS migratory pathways could provide a high level of connectivity to the population. Future studies with cameras placed closer together will allow for more precise estimates for targeted levels of permeability.

In addition to distance moved, the direction the salamanders turned when reaching the barrier fencing was a large factor in whether they reached the passage system. CTS that reached the barrier fencing and then travelled in the wrong direction (away from the passages) were significantly less likely to reach the crossing than CTS that made the correct initial direction choice. In fact, CTS that made the correct initial direction choice were also more likely to travel longer distances to reach the passages.

Other studies have estimated average movement distances of migrating long-toed salamanders along fencing to be 27 m or less (Allaback and Laabs 2003, Pagnucco et al. 2012). These results are consistent with our findings and it would be expected that CTS move farther based upon their larger body size and longer migration distances. It is possible that not all CTS were making migratory movements during our study, as they may have been foraging. However, in that case we would expect to document the same individuals on multiple dates along the fence line which was rare in our study (2 out of 91 individuals). This was the first study to passively monitor individual movements of amphibians along fencelines and tunnels using new active trigger camera traps (HALT; Hobbs and Brehme 2017).

Previous studies have employed capture-recapture by hand and with pitfall traps to actively track individuals (Allaback and Laabs 2003, Pagnucco et al. 2012, Ottburg and van der Ree 2019, Matos et al. 2019). These active methods can potentially alter animal behavior, direction, speed, movement distances and require subsampling over the active period of the target species. Matos

(2019) successfully used hand capture-recapture and fluorescent dye to track short distance foraging movements of newts (<26 m), however this method is not effective for monitoring movements over longer distances or time periods (e.g. Eggert 2002, Brehme et al. 2013). The use of these cameras coupled with individual identification by spot patterns allowed us to passively monitor species movements across the entire season along the fencing and underpasses unaffected by human presence. By calibrating cameras to atomic clocks, we were able to monitor not only distance but the precise speed of all individuals that passed by more than one camera.

It is also relevant to note that the barrier fencing was placed along a slightly curved road that created an approximate 10 to 20 degree angle leading to the passages and was perpendicular to the assumed main migratory path. Caltrans best management practices and others recommend installing barrier fencing at an angle into the habitat ("V" shaped toward the tunnel) in order to better lead migrating amphibians toward the tunnels (Federal Ministry of Transport 2000, Iuell et al. 2003, Schmidt and Zumbach 2008, Clevenger and Huijser 2011, Gunson et al. 2016, Langton and Clevenger 2020). There have not been any published studies we are aware of that directly compare the success of these configurations. However, the use of more directional fencing at a greater angle is expected reduce the proportion of individuals moving in the wrong direction away from the passage entrance. This configuration would also be expected increase movement distances along fencing because it is closer to the trajectory of the migrating amphibians. For these reasons, it is estimated that distances between passages can be farther apart with more directional fencing than with perpendicular fencing to accomplish the same level of permeability (e.g. Langton and Clevenger 2020). However, these "V" shaped configurations typically require planning of multiple passages that are spaced apart across an entire migratory pathway. In this case, there is a single crossing structure of 3 passages and placing fencing at greater angles would have excluded a substantial amount of upland CTS habitat.

If fencing must be set parallel to the roadway along an easement, it is possible that small turnarounds placed at frequent intervals along the fencing would be effective in turning individuals moving away from the tunnels in the right direction closer to the tunnel system (rather than only at fence ends). Turnarounds were shown to be effective for two out of three individuals that reached the fence ends in our study and have been shown to be effective at changing the initial trajectory of movement for lizards, snakes and toads in San Diego (Chapter 7). Future studies on the effects of multiple turnarounds are planned for this and other study sites.

The transparency of fencing (mesh vs. solid) did not significantly affect the movement distances or probability of CTS making it to the underpass system. However, the speed and time of travel were significant by fence type. CTS moving along solid fencing moved at almost twice the average speed and were 3 times less likely to turn around and repeatedly move back and forth. This indicates that CTS moving along fencing that they can see through results in them expending a higher amount of energy to make it to the crossing. We and others have shown in other studies (Ruby et al. 1994, Milburn-Rodríguez et al. 2016, Chapter 6) that animals interact with transparent fencing with behaviors such as poking, attempting to climb, and moving back and forth. Higher energy and time expenditures of these behaviors may have negative impacts on breeding success (Carr 2011, Navas et al. 2016). However, mesh fencing has benefits in ease of installation,

increased permeability to wind and water, and reduced temperature and wind differentials from the surrounding environment (Boyle et al. 2019, Langton and Clevenger 2020). In concurrent studies on lizards, snakes and toads (Chapter 6), we have found that addition of a visual barrier along the bottom edge of the fence is effective in both reducing these fence interaction behaviors and increasing the speed of movement to that comparable to a full solid barrier. The potential use of visual barriers should allow flexibility in choosing fence materials for amphibian crossing systems. We intend to test this as part of a Before-After Control-Impact study at the Stanford CTS site.

Therefore, the likelihood by distance that animals reach a passage can inform the planning and spacing of crossing systems for migratory amphibians and other migratory species. Without considering this, it is possible that barrier effects of the mitigation could be worse to survivorship and connectivity than the original road mortality problem (Jaeger and Fahrig 2004, Ottburg and van der Grift 2017). This applies when high connectivity is important for the persistence of the population, such as with migratory amphibian species that must make population level movements between upland and breeding habitats (Semlitsch 2008, Hamer and McDonnell 2008, Hamer et al. 2015).

Finally, CTS that did reach the opening of the underpass system at Stanford University had a very high probability (89%) of making a complete crossing to the other side. The tunnels in our study were specially built for amphibians in that they are made of inert materials and incorporate a grid ceiling to allow natural light, moisture and rainfall to permeate the length of the passage. These have been shown to be highly permeable to amphibian movement in other locations, particularly throughout Europe (see review by Langton and Clevenger 2017). Maintenance of barrier fencing and tunnel systems is important for long term success. This includes regular inspection and repair of fencing, maintenance of vegetation by the fencing to prevent climbing, and clearing of excess debris from the tunnels (e.g. Schmidt and Zumbach 2008, van der Ree et al. 2015, Langton and Clevenger 2020).

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# Chapter 5. Movement of Yosemite Toads Along Barrier Fencing and a Novel Elevated Road Segment in Sierra National Forest, CA

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## Introduction

Amphibians have been identified as being particularly susceptible to the negative effects of roads within their habitat (e.g. Forman et al. 2003, Rytwinski and Fahrig 2012, Andrews et al. 2015a, 2015b). Many are slow moving, do not avoid roads, and are simply too small for drivers to avoid. During rains many amphibians make long linear terrestrial movements regardless of the presence of intersecting roadways (Glista et al. 2008). In particular, pond breeding amphibians use both aquatic and terrestrial habitat for breeding, development, foraging, and overwintering, and therefore, require connectivity within and between aquatic and terrestrial habitats to support basic life history requirements. Increased mortality of amphibian populations from vehicles using roads that intersect breeding and upland habitat, if significant, can result in reduced population sizes and increased probability of extirpation (e.g. Hamer et al. 2008, Semlitsch 2008, Brehme et al. 2018, Ottburg and van der Grift 2019).

Bufonid toads can move large distances (>1 km) in both aquatic and terrestrial habitats to satisfy their annual resource requirements, and there is evidence that bufonid toads are particularly susceptible to negative impacts from roads (Trenham et al. 2003, Orłowski 2007, Eigenbrod et al. 2008). Endangered and threatened species are considered at risk of extirpation, often due to multiple stressors, and are thus thought to be less likely to be resilient to additional road impacts. Because of these attributes, the Yosemite toad ranked in the highest risk category for susceptibility to negative road impacts in a recent road risk assessment of 166 species of reptiles and amphibians in California (Brehme et al. 2018).

The Yosemite toad is a relatively long-lived toad (12–15 years) that inhabits high elevation, open, montane meadows, willow thickets, and adjoining forests in the Sierra Nevada, California. This species breeds in shallow edges of snowmelt pools and ponds or along edges of lakes and slow-moving streams. Some breeding sites dry up before larvae metamorphose. Females may breed every other year or once every three years. Although still distributed over most of its original range with many populations actively breeding and recruiting (Shaffer et al. 2000), the species has declined or disappeared from more than 50% of the sites from which it has been recorded (Jennings and Hayes 1994, Drost and Fellers 1996, USFWS 2014). Hypotheses for declines include habitat loss and degradation, disease (chytridiomycosis), airborne contaminants, livestock grazing, drought, fish predation, raven predation, road mortality and vehicle vibration effects (e.g. Hammerson et al. 2004, Davidson and Fellers 2005, USFWS 2014).

In 2017, the U.S. Forest Service, Sierra National Forest reported 126 Yosemite toads that had been run over and killed by vehicles on Forest Service roads. Of these, 92 subadults were

found on the 9S09 road between June 24 and October 24. The Forest Service and U.S. Fish and Wildlife Service are particularly concerned about the potential for increased Yosemite toad road mortality due to increased vehicular traffic projected for these roads in the future.

### *Elevated Road Segment*

A common road mitigation strategy for amphibians is to install small passages under the roadway in combination with attached barriers or fencing (1 to 2 feet or more high). The barriers are used to prevent animals from going out onto the roadway and to funnel them toward the passage(s). However, there is evidence that inadequate underpass spacing between uplands and breeding ponds may result in population declines in pond breeding amphibians (Ottburg and van der Grift 2019).

The life history of the Yosemite toad presented a unique challenge to this common mitigation strategy. Yosemite toad adults move from upland habitats to wetlands to breed during early snow melt in the spring, and then migrate back into the upland habitats shortly after breeding. Therefore, a passage-barrier system would likely only be effective for reducing road mortality during post breeding toad migrations to uplands after most of the snow has melted or during the summer migrations (including juveniles). Secondly, Yosemite toads have been shown to travel in straight line trajectories over wide areas, resulting in long lengths of roadways where they are susceptible to road mortality without any clearly defined “hot spots”.

Finally, the road is on a flat landscape, with an upland slope on one side and downward slope on the other. Burrowing passage(s) under the road would require a significant amount of grading and re-contouring on the upland slope side to make passage entrances accessible.

To meet these challenges, in June of 2018, we designed and installed a new road crossing structure in a high road mortality section of 9S09 (Figure 1). The crossing structure is an elevated roadway segment placed on top of the existing road surface and composed of hardwood laminated billet road mats that are designed for use by heavy equipment at construction sites (Emtek®). The road mats are approximately 6 in. thick and were installed on top of 8-in. high support bars installed on and perpendicular to the road, allowing for passage of small animals. They were built to meet codes and specifications for U.S. Forest Service, County, and City roads.

Diagram: Side view depiction of elevated road segment (rectangle with vertical lines) with barrier fencing (lines) and openings for toad passage underneath (solid rectangles); not to scale.

Figure 1. Diagram and Photos of Elevated Road Segment.

This proposed study is part of a larger USGS research program in collaboration with the Western Transportation Institute (WTI; Montana State University) for the California Department of Transportation (Caltrans). The larger study provides research to inform best management practices for barrier and crossing systems for sensitive amphibians and reptiles in California.

### *Movement along Barrier Fencing*

The common toad, *Bufo bufo*, in the Netherlands turned around after an average of 50 m if they did not reach an underpass (Ottburg and van der Grift 2019). As with the California tiger salamander (Chapter 4), the distance Yosemite toads may travel along a barrier fence to find a passable crossing is unknown. Therefore, a study was warranted to determine toad movement distances along barriers to inform proper passage spacing for the Yosemite toad. There is also evidence that animals may spend more time trying to climb or get through opaque fencing

compared to solid fencing (Milburn-Rodríguez et al. 2016). Therefore, we were also interested in whether fencing opacity affects the probability or speed at which the toads and other amphibians find wildlife crossings.

The results of this study will help to gauge effectiveness of this new road crossing structure, identify underpass spacing needs, evaluate barrier materials, and assess the effectiveness of fence end turnarounds for pond breeding amphibians.

Research questions:

1) What is the probability a Yosemite toad will reach an underpass based upon the distance from the underpass an animal first encounters the barrier wall?
2) How quickly do toads travel along the barrier wall toward the crossing structure?
3) How does the opacity of fencing effect the questions above?
    a. Solid barrier (high-density polyethylene (HDPE-2); Animex®)
    b. Semi-transparent barrier (water- permeable rigid polymer matrix; ERTEC® E-Fence, referred to hereon as "mesh")
5) Is the elevated roadway segment effective in reducing road mortality while maintaining connectivity between breeding wetlands and uplands for the Yosemite toad?

Study Location:

U.S. Forest Service Road 9S09 in Sierra National Forest, CA between Yosemite toad breeding and upland habitat.

## Methods

### *Field Study*

We studied the movement of Yosemite toads adjacent to and under the ERS structure along 9S09 in Sierra National Forest, CA in the breeding seasons of 2018 and 2019. The road bisects a Yosemite toad breeding meadow and upland habitat (Figure 2).

B) B)

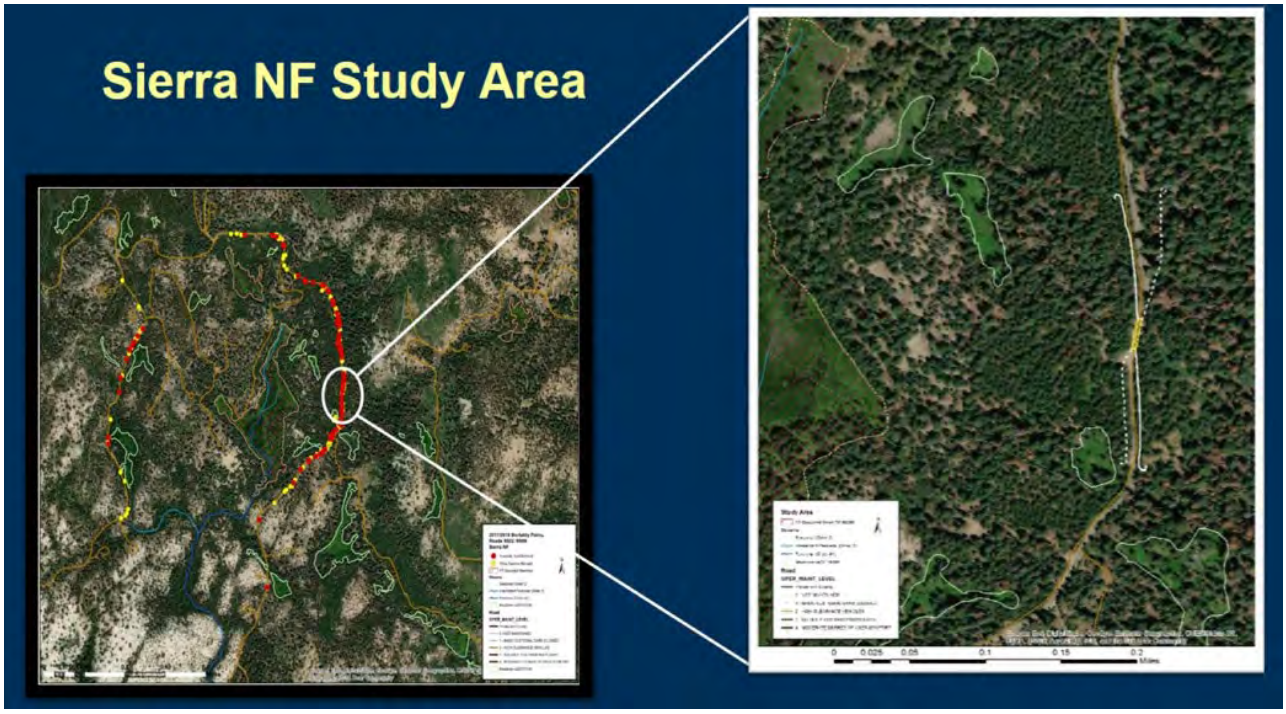


Figure 2. Maps of A) Yosemite Toad Road Mortality and B) Location of Barrier and Elevated Road Crossing in Sierra National Forest Between Upland and Breeding Habitat.

A total of approximately 480 m of barrier fencing was installed along the east and west sides of 9S09 (~120 m in each direction) connected to the ERS crossing. One portion of the fencing installed was semi-transparent (ERTEC ® rigid polymer matrix E-Fence$^{TM}$) and the other portion was solid (Animex® high-density polyethylene (HDPE-2)). Jump-outs (ERTEC® cones and high berms) were installed a minimum of every 10 m along the fence to provide toads and other small vertebrates a way to get back into the habitat if they ended up on the road side of the barrier fencing. At outer fence ends, turnarounds were installed to redirect animals away from the road and back toward the upland habitat in a U-shaped fashion. The turnarounds were approximately 2 m long and 1 m in width. Fencing was installed with the bottom buried in the ground according to manufacturers' guidelines.

HALT ® camera systems (Hobbs and Brehme 2017) were placed against the fencing every 20 m along the new fence lines from 0 to 100 m from the ERS (Figures 3 and 4). Each 0 m camera was approximately 8 m from the closest ERS opening to allow them to be shielded from the view of forest visitors. Cameras were set up on the wetland side as soon as possible after the road opened (spring) and were checked weekly to collect data on toads during their upland migration.

Figure 3. Schematic of Elevated Road Segment, Mesh Fencing (Dotted Lines), Solid Fencing (Lines), HALT Cameras (Circles), and Time Lapse Cameras (Black Circles); Not to Scale.

At fence end turnarounds, HALT camera systems were placed above the end terminal to record video of animals' movement trajectory after reaching the fence-ends (2018). Due to evidence of CTS turning around but not being recorded on video, in 2019, we narrowed the end of the turnaround so that the edge of the "U" was 0.4 m from the beginning of the turnaround creating a tear drop shape. This allowed us to install the trigger at the turnaround opening so that we could record animals entering and exiting the turnaround.

The extreme width of the ERS underpass made it impossible to sample completely; therefore, we had to subsample underpass activity in both space and time. For this, we placed HALT camera systems under both ERS intersections with the fence line on the west side to record tunnel entrances. We then set eight Reconyx cameras set to a time lapse of every 5 minutes on the upland side under the ERS to gather more data on animal movements.

All cameras were set as soon as the snow melted and road opened, and then checked on a weekly basis during the late spring and summer (May–Oct. 2018 and July–Oct 2019). Each time we set and checked the cameras, we took a photo of a battery powered atomic clock in order to calibrate exact minutes and seconds upon processing.

Road mortality surveys were conducted along 9S09 by the U.S. Forest Service.

Figure 4. Solid (A) and Mesh (B) Fence Lines. Along the Fences are Jump Outs and Cameras within Plastic Bins Facing Down Toward HALT Triggers.

*Analysis*

*Movement along fence line*

Photos of all Yosemite Toads were analyzed using pattern recognition software to identify individuals by their unique spot patterns ($I^3S$ Spot; Van Tienhoven et al. 2007; Figure 5). Camera location, time, and direction of movement were recorded for each individual. Snout to vent length was measured with Program ImageJ (Rasband 1997-2018) using the 1 cm grids from the HALT trigger for calibration.

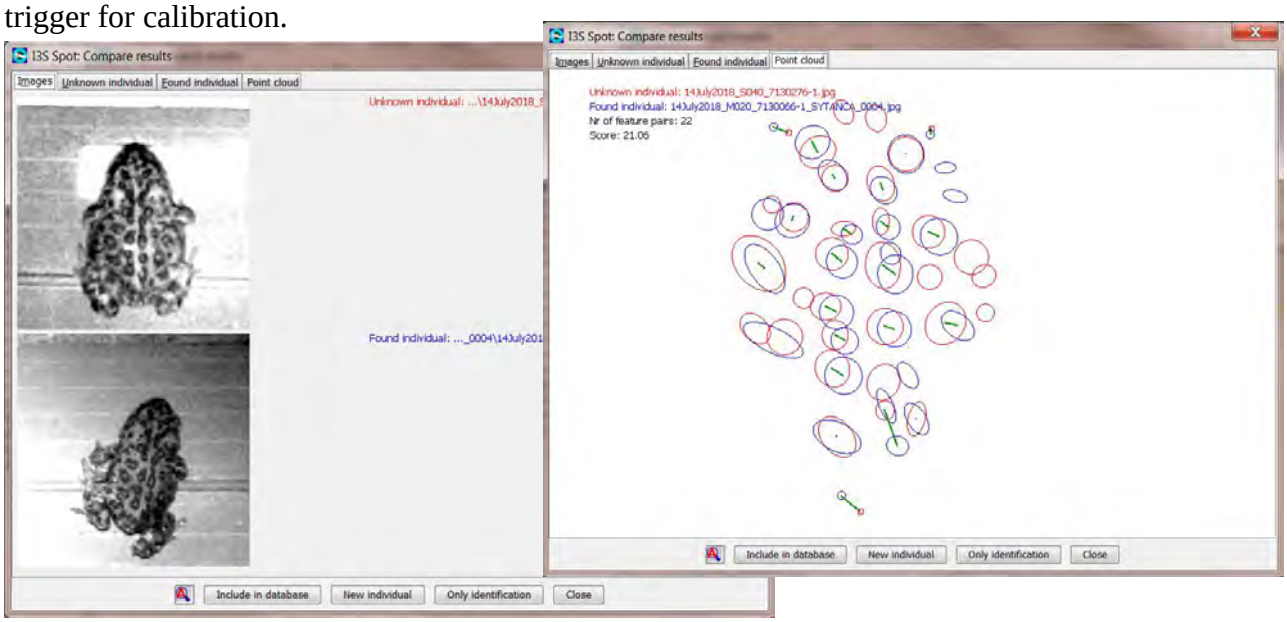


Figure 5. Example of Yosemite Toad Identified to Individual Using i3s Software to Distinguish Spot Patterns.

For individual Yosemite Toads, we then calculated movement distances along the fence lines, numbers of turn arounds, speed, and "success" at reaching 0 m cameras next to underpass system. Because cameras were placed 20 m apart, our margin of error for estimating fence movement distance ranged between 0 and 20 m. For instance, if an animal was only detected at a single camera, then our average estimated distance was 20 m (10 m before reaching the camera and 10 m after exiting the camera). Similarly, if an individual was detected at multiple consecutive cameras moving in the same direction, our margin of error was typically 20 m. In the instances where individuals were detected at consecutive cameras, we also calculated the movement speed between segments. If such an individual then turned around and was re-detected at a camera while moving in the other direction, we estimated the distance travelled along the fence before turning around by multiplying the time between detections by its average speed. Because of this, if individuals travelled back and forth several times, we were able to more accurately estimate the total distance of fence line traversed (fence movement distance). If an individual reached the 0 m camera (where the experimental fence lines attached to the short length of existing fence), this was considered a "success" at reaching the passage system with no added error for distance moved afterward.

For models of movement along fence line, we used Markov Chain Monte Carlo (MCMC) implemented in the R programming language and the runjags package to interface with JAGS (Just Another Gibbs Sampler) to sample values of all unknown parameters from the joint posterior distribution. In each case, four chains were sampled to perform standard diagnostics for convergence. In all cases, non-informative prior distributions were used for all parameters.

### *Logistic Regression for Success in Reaching Underpass Opening*

We modeled the probability of success of Yosemite toads in reaching the 0 m camera near the crossing opening. For this, we used a Bayesian approach to logistic regression modeling (Figure 6). The response was a Bernoulli random variable, where 0 indicates failure and 1 indicates success in being detected by the camera at the opening of the crossing (ReachedTunnel). The probability of success for the Bernoulli distribution is a logistic (i.e. $p = \exp(y)/(1 + \exp(y))$ function of the linear component of the model that consists of four predictors (FenceType, InitLoc, InitAway, InitLocAway) and five parameters that include an intercept and a regression coefficient corresponding to each of the predictors. FenceType is a binary variable where 0 indicates a mesh fence and 1 indicates a solid fence. InitLoc is the position along the fence where the animal was first detected in meters from the crossing opening (with error described in the previous paragraph), InitAway is a binary variable where 0 indicates that the animal was initially moving toward the crossing and 1 indicates it was initially moving away from the crossing, and InitLocAway is an interaction (product of) InitLoc and InitAway. All predictors were standardized (the mean subtracted from each value and then divided by the standard deviation) prior to modeling. The priors for the parameters were non-informative normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the probability of success.

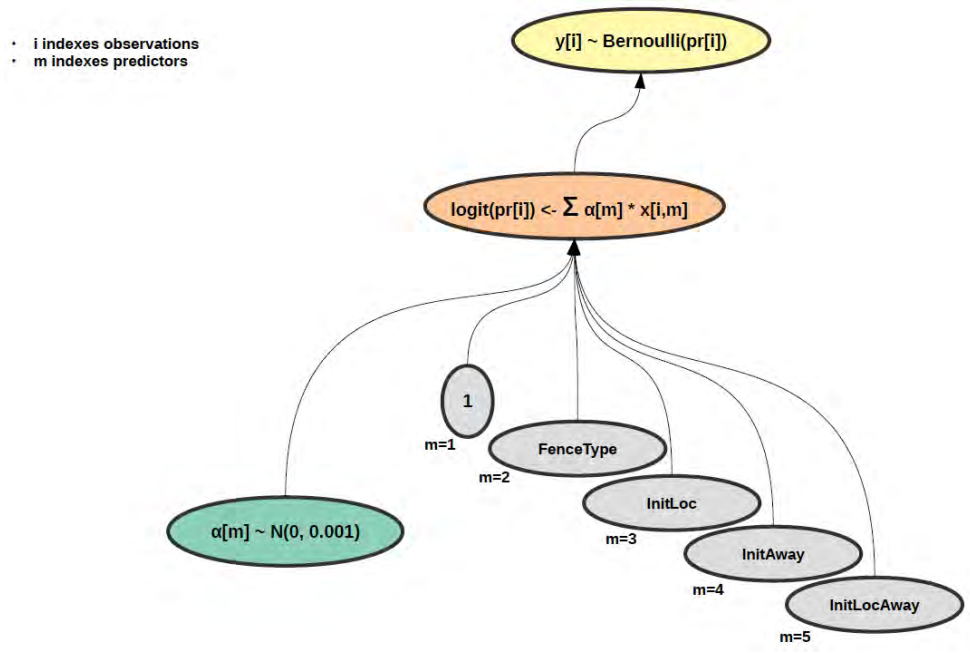


Figure 6. Logistic Regression for Success in Reaching Underpass Opening

*Gamma Regression for Distance Moved Along Fence*

We also modeled the distance that Yosemite toads moved along the fence. We used a Bayesian approach to regression modeling of the probability of successfully reaching the underpass opening (Figure 7). The response was assumed to be a gamma distributed random variable, which is a continuous positive variable representing the distance the animal moved along the fence as described. The gamma distribution has a shape parameter, which we assumed to be independent of any predictors, and a rate parameter that we model as an exponential (i.e. rate = exp(y)) function of the linear component of the model that consists of four predictors FenceType, InitLoc, InitAway, ReachedTunnel, InitLocAway and six parameters that include an intercept and a regression coefficient corresponding to each of the predictors. All predictors, except for ReachedTunnel, were standardized prior to modeling. The prior for the shape parameter was a non-informative exponential distribution with a rate of 0.00001. The priors for the regression parameters for the rate were normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the distance moved along the fence.

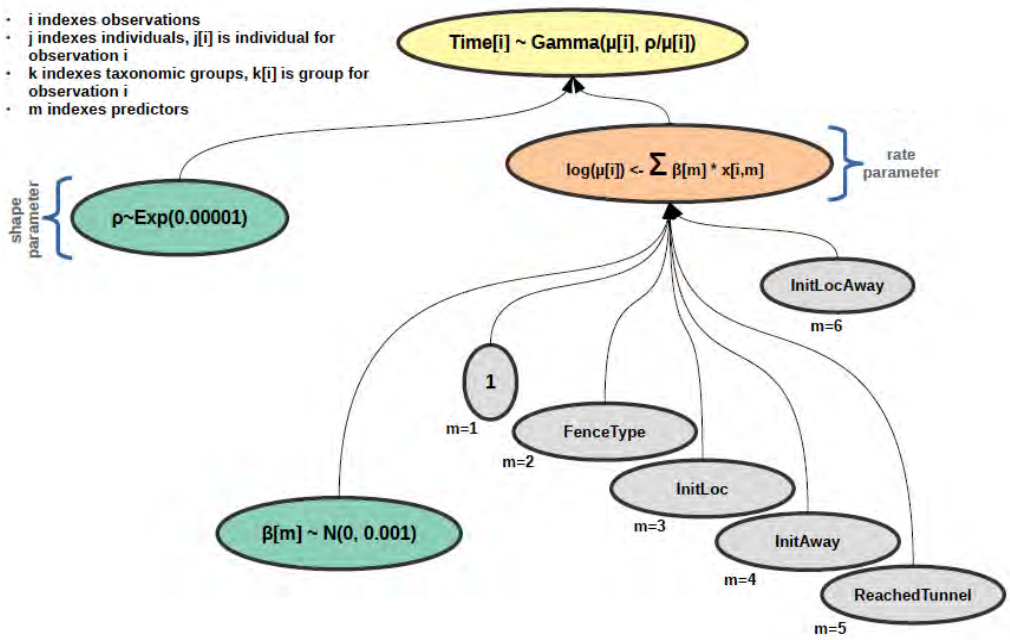


Figure 7. Gamma Regression for Distance Moved Along Fence

*Elevated Road Segment Crossing*

Because the ERS crossing system is so wide (>100 ft), it was not possible to monitor the entire underpass. Therefore, we subsampled by placing two HALT cameras along the fence lines underneath the ERS (wetland side) and eight Reconyx time lapse cameras underneath middle portions of the ERS on the upland side (Figure 1: not to scale). All active trigger camera images were considered a single species event if within one minute of each other. Because of the large number of time lapse images generated, they were only scanned for the presence of Yosemite toads during time periods they were detected with the HALT cameras along the fence lines.

To assess ERS crossing permeability, we analyzed the number of individual Yosemite toads monitored along the fence that reached the passage. For all species, we also compared the relative number of species detections immediately outside the ERS (red circles; 0 m cameras) vs. under the ERS on each side (yellow circles; Figure 8).

Red circles: HALT cameras immediately outside of ERS system
Yellow circles: HALT cameras underneath ERS adjacent to the fence line
Black open circles: Time lapse cameras placed underneath the ERS on the upland (terrestrial) side facing toward the wetland habitat side. Note: length of ERS not to scale and numbers of time lapse cameras greater than depicted (8).

Figure 8. Schematic of General Locations of Cameras Used to Monitor ERS Permeability (Red and Yellow Circles).

## Results

Due to road closures during winter and spring months, we began monitoring upland toad movements immediately after snow melt and during the summer months when toads are typically active and moving during rainfall events. Total summer precipitation in nearby Huntington Lake during the monitoring periods was 1.12 in. for 2018 (June-Oct) and 0.59 in. for 2019 (July- Oct) after the snow melt (Huntington Lake Historical Weather; worldweatheronline). Both summer seasons were approximately 3.0 in. below average rainfall during these periods (Western Regional Climate Center 044176-5). Breeding and recruitment were documented by USFS in 2019; however, we likely missed most of the upland dispersal at the site due to the extended period of snowpack through June and lack of access to the site during this time.

### *Fence Movement*

We documented a total of 37 individually identified Yosemite toads in 2018 (24 over 12 nights) and 2019 (13 over 6 nights) moving along the fence-line. Five or fewer individuals (5 photos) were not included in the initial analysis due to low confidence in these identifications. Of the 37 individuals in the analysis, 19 were subadults (<44 mm snout-to-vent length (SVL)) and 18 were adults (>44 mm SVL). Among fence types, eight subadults and 13 adults were recorded along the mesh and 11 subadults and five adults were recorded along the solid. We considered individual movements from 2018 to 2019 as independent in the analysis.

Because our sample size was low, confidence intervals are extremely wide for most parameters. We present averages and confidence intervals of fence distance, movement speed, and direction changes (i.e. back and forth movements) among fence types and age classes in Table 1.

Fence movement distances averaged approximately 52 m (Table 1, Figure 9) and did not significantly differ by fence type or age class, although mean distance moved was farther along the solid (63 m) than mesh (43 m) fencing. With these preliminary data, there were no significant differences in the response variables by fence type. Yosemite toads moved an average of 1 m/min and changed directions an average of 0.5 times per 20 m (i.e. per camera location). Adults were 71% faster than subadults and changed directions 75% more often, although not significantly.

Seven out of 10 Yosemite toads changed course at a turnaround back toward the fence line or out into habitat, and of these, four toads were subsequently documented on other cameras 40-80 m away continuing to move back along the fence line.

Table 1. Yosemite Toad Movement Metrics by Fence Type and Age Class

| | | | **Fence Distance Moved (m)** | | **Movement Speed (m/s)*** | | **Direction Changes per 20m** | |
|---|---|---|---|---|---|---|---|---|
| | | Sample Size | Mean | 90% CI | Mean | 90% CI | Mean | 90% CI |
| By Fence Type | Solid | 16 (13*) | 63.3 | 10- 109 | 1.0 | 0.7- 1.3 | 0.6 | 0.3- 0.9 |
| | Mesh | 21 (9*) | 43.2 | 10- 105 | 0.9 | 0.6- 1.2 | 0.5 | 0.2- 0.8 |
| By Age Class | Subadult | 19 (13*) | 48.9 | 38.3- 59.6 | 0.7 | 0.6- 0.9 | 0.4 | 0.2- 0.6 |
| | Adult | 18 (9*) | 43.1 | 30.0- 56.3 | 1.2 | 1.0- 1.5 | 0.7 | 0.4- 1.0 |
| **All Toads** | | **37** | **52.3** | **10- 110** | **1.0** | **0.6- 1.3** | **0.5** | **0.3- 0.7** |

*individuals that passed more than one camera w here movement speed w as calculated

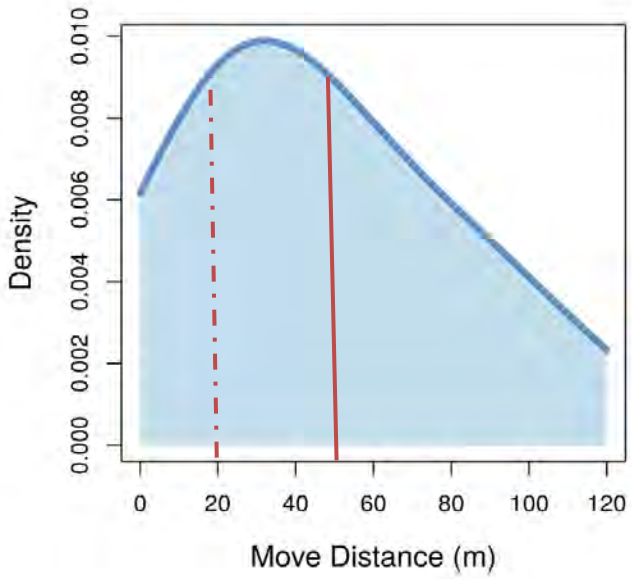


Figure 9. Distributions of Movement Distances. Lines Represent Mean (Solid) and Lower 90% Confidence Interval (Dashed).

The linear regression modeling showed a general pattern similar to that of CTS but with low slopes and low confidence. Yosemite toads moved shorter distances if they encountered the fence closer to the tunnel system and their initial direction was toward the tunnel system. There was no difference in predicted move distances for the toads that encountered the fence and turned in the "wrong" (away) direction (Figure 10).

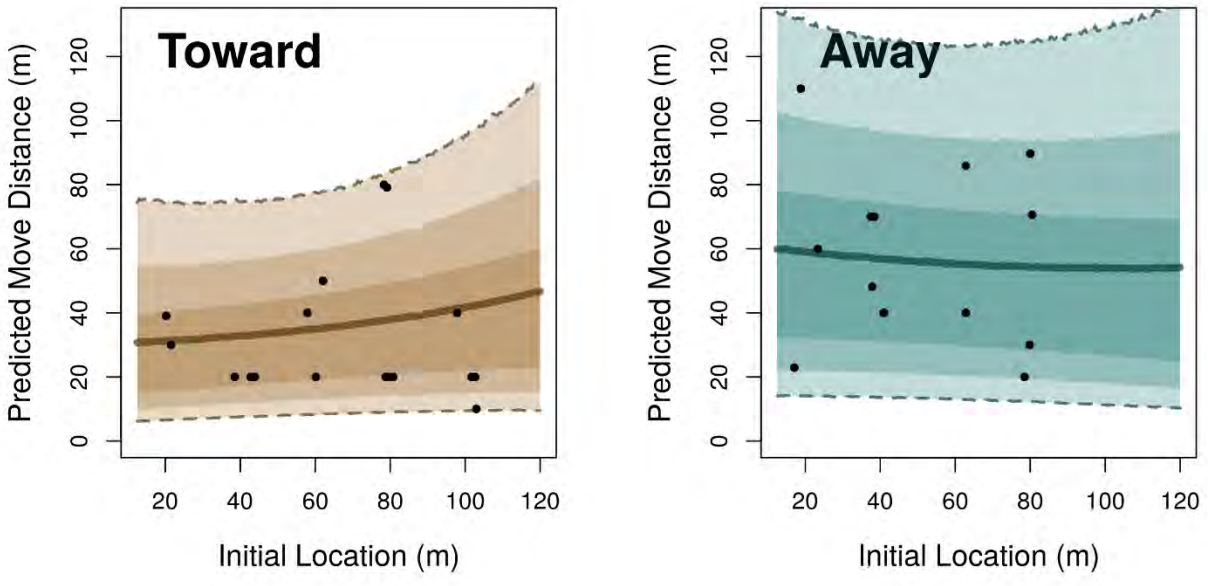


Figure 10. Movement Distance by Initial Location and Direction of Travel (Toward or Away from Underpass) with 90% Confidence Intervals.

The probability that Yosemite toads reached the tunnel system (0 m camera) decreased rapidly with increasing distance from the ERS system and was also highly dependent upon their initial direction choice. Yosemite toads had a high probability of reaching the ERS underpass if they encountered the fence at a distance of 20 m (mesh fencing) to 40 m (solid fencing) and were moving toward the ERS. Probabilities rapidly declined beyond those distances and were low if the toads were moving away from the ERS (Table 2, Figure 11). The estimates close to 1.0 and 0.0 indicated more data is needed to more accurately predict the probabilities of success in this system.

Table 2. Probability of Reaching Underpass by Initial Location, Direction of Travel (Toward or Away from Underpass), and Fence Type.

| | Solid Fencing | | | | Mesh Fencing | | | |
|---|---|---|---|---|---|---|---|---|
| | TOWARD Underpass | | AWAY from Underpass | | TOWARD Underpass | | AWAY from Underpass | |
| Initial Location (m) | Probability of Success | 90% CI | Probability of Success | 90% CI | Probability of Success | 90% CI | Probability of Success | 90% CI |
| 10 | 1.00 | 1.00- 1.00 | .48 | .21- .75 | 1.00 | .99- 1.00 | .01 | .00- .06 |
| 20 | 1.00 | 1.00- 1.00 | .44 | .20- .70 | .91 | .41- 1.00 | .01 | .00- .05 |
| 40 | .65 | .00- 1.00 | .37 | .14- .63 | .02 | .00- .11 | .01 | .00- .04 |
| 60 | .04 | .00- .27 | .32 | .07-.63 | .00 | .00- .00 | .01 | .00- .03 |
| 80 | .00 | .00- .00 | .28 | .04-.68 | .00 | .00- .00 | .00 | .00- .02 |
| 100 | .00 | .00- .00 | .25 | .01-.72 | .00 | .00- .00 | .00 | .00- .02 |

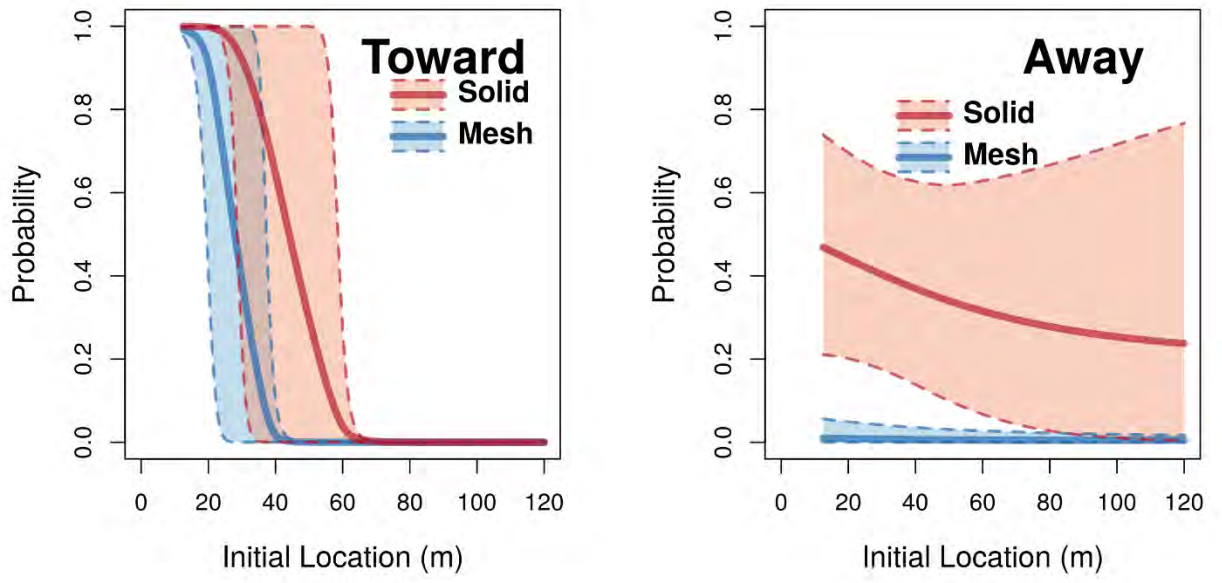


Figure 11. Probability of Reaching Underpass by Initial Location, Direction of Travel (Toward or Away from ERS), and Fence Type with 90% Confidence Intervals. Note that more samples are needed to better inform the models.

*Underpass Permeability*

Of the eight Yosemite toads that were tracked moving toward the ERS system at one of the "0 m" cameras (~5 m from the ERS entrance), three moved underneath at the first immediate right/left turn from the barrier fencing into the ERS and two moved along the length of the ERS (not underneath) to the barrier fencing on the other side. It is possible the other three toads moved under the bridge but not across a HALT trigger. Toads were detected on the time lapse cameras during the periods of their activity but could not be identified to individual.

Twenty-four other Yosemite toads that moved under the ERS were detected by one of the two HALT triggers (16 toads) or by a time lapse camera (8 toads). These data represent only a subsample of available linear width of the ERS system, so we suspect many more Yosemite toads passed under the crossing. At an average movement speed of 1 m/min and a field of depth of about 1 m, we estimate the eight time-lapse cameras subsampled toads across approximately 40% of the linear length of the ERS for 20% of the time. Because of this, we expect the total number of toads that moved under the ERS was likely closer to 100 during the time periods monitored.

The relative activity of Yosemite toads immediately inside vs. outside (~5 m from opening) of the ERS crossing system was almost equal (20 vs. 19 events; Table 3). The relative activity of other animals varied by species and groups. In general, mammals were detected at greater rates underneath vs. outside the ERS system (ratio 3.1), while reptiles and amphibians were detected at slightly lower rates underneath vs. outside the ERS system (ratios 0.70 and 0.83).

| | | | RELATIVE ACTIVITY | | |
|---|---|---|---|---|---|
| | | | Outside | Inside | Ratio |
| AMPH | Pacific Treefrog | *Hyla regilla* | 209 | 174 | 0.83 |
| | **Yosemite Toad** | ***Anaxyrus californica*** | **20** | **19** | 0.95 |
| | Sierra Nevada Ensatina | *Ensatina eschscholtzii platensis* | 12 | 4 | 0.33 |
| | Unknown salamander | | 0 | 3 | na |
| | | Subtotal Amphibians | 241 | 200 | 0.83 |
| REPT | Mountain Gartersnake | *Thamnophis elegans elegans* | 25 | 14 | 0.56 |
| | Rubber Boa | *Charina bottae* | 6 | 4 | 0.67 |
| | Sierra Alligator Lizard | *Elgaria multicarinata* | 6 | 7 | 1.17 |
| | Western Fence Lizard | *Sceloporus occidentalis* | 6 | 2 | 0.33 |
| | Unknown lizard | | 1 | 4 | 4.00 |
| | | Subtotal Reptiles | 44 | 31 | 0.70 |
| MAMMALS | Mice/Rats | *Family Rodentia* | 165 | 534 | 3.24 |
| | CA ground squirrel | *Otospermophilus beecheyi* | 19 | 38 | 2.00 |
| | Long-tailed Weasel | *Mustela frenata* | 0 | 1 | >1.0 |
| | Spotted skunk | *Spilogale putorius* | 0 | 4 | >1.0 |
| | American marten | *Martes americana* | 0 | 2 | >1.0 |
| | Chipmunk | *Neotamias spp.* | 3 | 1 | 0.33 |
| | CA Vole | *Microtus californicus* | 2 | 1 | 0.50 |
| | Shrew | *Sorex spp.* | 1 | 16 | 16.00 |
| | Yellow-bellied Marmot | *Marmota flaviventris* | 1 | 1 | 1.00 |
| | | Subtotal Mammals | 191 | 598 | 3.13 |

Table 3. Relative Activity by Species Immediately Inside vs. Outside Elevated Road Segment.

## Discussion

Although the sample size was low due to seasonal weather and sampling constraints, we found similarities between the fence movement behavior of Yosemite toads and CTS (Chapter 4). On average, Yosemite toads moved a distance of 52 m along barrier fencing before "giving up" and their probability of making it to the crossing decreased rapidly with increasing distance from the ERS. This is very close to the 50 m average that Ottberg and van der Grift (2019) reported for *Bufo bufo* in the Netherlands. Many individuals moved back and forth along the fencing and the average of 52 m represents the average span of total fence distance moved. Therefore, approximately half moved greater distances and half moved smaller distances with approximately 90% of toads estimated to move 20 m or more. Because our cameras were set 20 m apart, we were unable to estimate the specific distances with high confidence. However, these preliminary results suggest that passages spaced within 20 m of one another along Yosemite toad migratory pathways should provide connectivity to 90% of the population.

As with CTS, the likelihood that only some animals will reach a passage informs planning and monitoring of crossing systems for migratory amphibians and other migratory species. Without considering this in planning for distances between crossings, there is a potential for crossing systems constructed to reduce road mortality to become a barrier to population level movements.

In addition to distance moved, the direction Yosemite toads turned when reaching the barrier fencing was a large factor in whether they reached the crossing. Toads that reached the barrier fencing and then travelled in the wrong direction (away from the tunnels) were significantly less likely to reach the crossing than toads that made the correct initial direction choice. In fact, it appeared that, as with CTS, toads that made the correct initial direction choice were also more likely to travel longer distances to reach the tunnels.

It is possible that not all Yosemite toads were making migratory movements during our study, as they may have been foraging. However, in that case we would expect to document the same individuals on multiple dates along the fence line which was rare in our study.

The transparency of fencing (mesh vs. solid) did not significantly affect the movement distances or probability of making it to the underpass system, although the estimated probabilities were slightly less for the semi-transparent fencing. Unlike CTS, there was no apparent difference in speed or turnaround rates (moving back and forth) by fence type in the preliminary data for Yosemite toads.

We caution that a greater sample size is needed to accurately predict the probability of success by initial distance from passage, direction choice, and effects of fence type and age class on Yosemite toad movements along the fence lines. Continued data collection in future years and placement of additional cameras at 10 m along the fence lines will allow for higher confidence in these estimates.

Finally, initial results showed that the ERS crossing has a high potential to provide increased connectivity for Yosemite toads and a wide range of other amphibian, reptile, and small mammal species while greatly reducing road mortality (no road mortality of Yosemite toads has

been documented in the project footprint since installation of the ERS; S. Barnes, USFS, pers. comm.). This new prototype crossing can be made to any length, creating a wide passage without constricting migratory movements to small tunnels. The prototype ERS also allows natural light, moisture and rainfall to permeate the length of the passage so that climate and moisture underneath is similar to that outside. The large width of the passage does present challenges in monitoring successful crossings due to the wide monitoring area. We are exploring the use of different camera systems, additional cameras, and wildlife tracking techniques to better monitor movements near and underneath the passage in the future.

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# Chapter 6. Effect of Fence Opacity on the Movement of Reptiles and Amphibians and the Effectiveness of Two Jump-out Designs.

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## Introduction

Options for road barrier materials vary greatly from solid concrete, composites, and plastics to transparent and semi-transparent wire and plastic meshes. Meshes are typically easy to work with and are permeable to water and air movement; however, there is some evidence that animals may spend more time trying to climb or get through transparent fencing than solid fencing (Milburn-Rodriguez et al. 2016). Thus, opacity could influence both barrier effectiveness and the probability and speed with which an animal finds a wildlife crossing.

"Jump-outs" are commonly built along road barrier fencing to ensure that large animals can escape if they get caught within the road barrier sections (Clevenger and Huijser 2011, van der Ree et al. 2015, Hopkins et al. 2018). However, few jump-outs have been designed, tested, or used for allowing the escape of herpetofauna back into the habitat if they become trapped along a road with barrier fencing on both sides.

We conducted studies at the Rancho Jamul Ecological Reserve (RJER) in Jamul, California, to compare the behavior and movement speed of herpetofauna in relation to transparent, semi-transparent, and solid fencing. In addition, we tested the effectiveness of two jump-out designs. The results of these studies will help to inform transportation agencies on these important components of road barrier and crossing systems.

Herpetofauna Groups Targeted: Snakes, lizards, toads

Research questions:

1. Are transparent, semi-transparent mesh, and solid barriers equally effective as barriers to movement?
2. How quickly do individuals travel along barriers of differing opacity?
3. Are jump-outs of differing designs effective in allowing herpetofauna to escape if trapped within the roadway?

## Methods

### *Field Study*

At Rancho Jamul Ecological Reserve, we set up a multi-faceted fenced enclosure to study the behavior and speed of animals along different fence materials and the effectiveness of jump-outs (Figure 1). The fenced behavioral enclosure was installed along a habitat edge between riparian scrub and coastal scrub habitat in the reserve. The behavioral enclosure consisted of a 12 m long, 45 cm wide linear "runway" with 2 m long alternating segments of hardware cloth, black

plastic mesh (ERTEC® rigid polymer matrix fence with climbing barrier at top), and solid black (Animex® high-density polyethylene (HDPE-2)) barrier fencing 60 inches in original height buried to a depth of 10–15 cm. The alternating segments contained the same barrier fencing on both sides of the runway and each fence type was randomly repeated two times along the runway. To prevent bias based upon the location of the fencing, the order of the fencing types was changed during the middle of the study. The bare soil floor of the enclosure was tamped down with a steel dirt tamper to prevent digging and hiding behaviors. We also buried 1 in. PVC pipes ¾ in. deep along the floor in between each fence segment perpendicular to the runway to provide a white strip between segments. This allowed us to easily discern when an animal moved from one segment to another.

We built a 4 m introduction section made of white solid fencing for introduction and habituation of test animals before they made the decision to start moving along the test runway. At the end of the runway, we built an exit section with four jump outs. Two "high" jump outs were built as earthen ramps leading up to the top of the fence, with an approximate 50 cm drop to jump out into the habitat. Two "low" jump-outs were modified rectangular cones (ERTEC®) with a diameter of 22 cm installed halfway up the barrier fencing with a small earthen ramp and an approximate 20 cm drop into the habitat (Figure 2). The cones were modified by increasing the size of the opening on the exit side to a diameter of approximately 10 cm. An outer fence around the exit section allowed us to capture animals once they exited the jump-out and return them to the original place of capture. The entire behavioral enclosure was covered on top at a height of approximately 1.5 m with shade sail cloth to prevent spots of sunlight and shade from influencing animal behaviors.

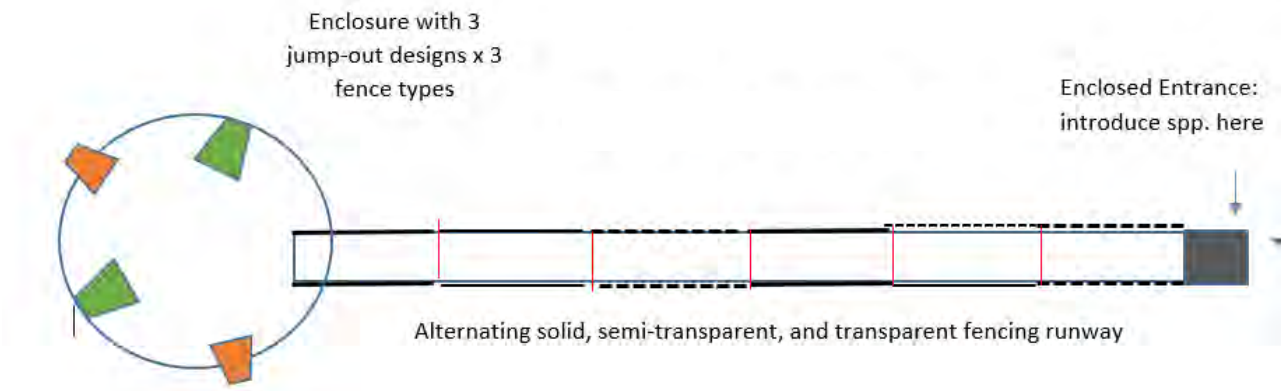


Figure 1. Graphic of Behavioral Enclosure

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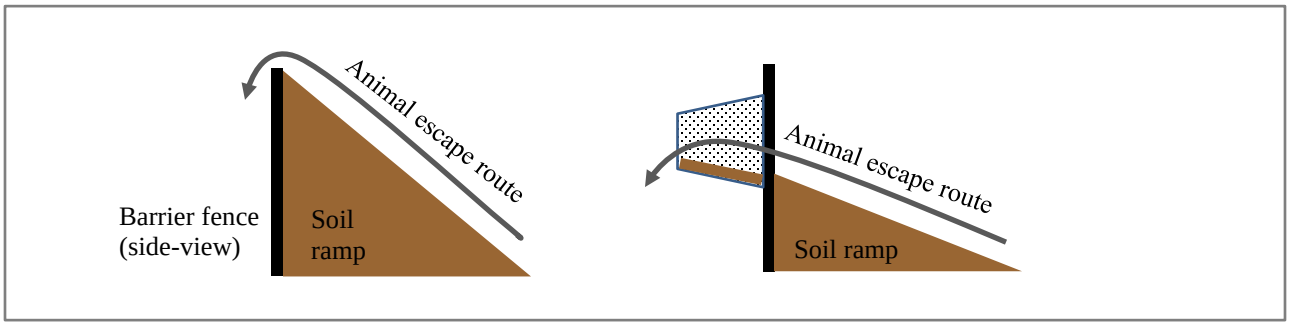

Figure 2. Diagram of Jump-Out Configurations a) Over Fence and b) Through Fence.

Trials were run in spring and summer months from June through September in 2018 and March through June in 2019. To determine if animals would respond differently to the transparent and semi-transparent fencing in the presence of a visual barrier, from late August through September of 2018 and June of 2019, we placed black duct tape along the bottom of the first segments of hardware cloth and mesh fencing approximately 15 cm (6 in.) in height.

We captured animals using visual searching and linear trap arrays with pitfall traps and snake traps within 150 m of the behavioral enclosure as described in Fisher et al. (2008). The traps were set in the early morning, checked throughout the day, and closed at mid-day. Some snakes were also opportunistically collected if observed while checking the pitfall arrays. Each animal included in the trials was weighed, measured, temporarily marked with ink (Sharpie®), placed into a holding bag (snake bag/pillowcase) and brought to the enclosure.

Captured animals were placed one at a time within the introduction section approximately 2 m from the first fence segment. Observers were stationed behind camouflage netting at the entrance and exit sides of the behavioral enclosure. The first observer on the exit side operated a stationary video camera on a tripod to record all animal movements within the enclosure and was behind camouflage netting throughout the entire trial. The second observer gently released each animal from its holding bag or snake trap into the enclosure approximately 2 m from the first fence trial segment while behind the camouflage netting. Each animal was then observed until it left the behavioral enclosure or for 30 minutes (if it did not complete the trial). Examples of reptiles moving through the enclosure are provided in Figure 3. After the trial, each animal was immediately released to its original place of capture. Once back at the field office, the observers uploaded videos and recorded the following:

- Direction and pathway of all movements
- Time spent along each fence segment
- Whether a solid visual barrier was present (on mesh or HC fencing)
- Behaviors observed at each fence segment: Poking, climbing, moving back and forth, sitting
- Number of fence segments completed
- Whether animals escaped by climbing over fencing
- What exits were approached and used

Figure 3. Photos of A) California Striped Racer (*Masticophis lateralis*) Poking at Hardware Cloth, B) Orange-Throated Whiptail (*Aspedoscelis hyperythrus*) Poking at Hardware Cloth, C) Rosy Boa (*Lichanura trivirgata)* Moving Through Runway Toward Exit Structures, D) Orange-Throated Whiptail Exiting High Ramp and E) Red-Diamond Rattlesnake (*Crotalus ruber*) Exiting Escape Funnel.

*Analysis*

Only data from individual animals that completed at least three fence segments (one of each type) were used in the analysis. Many animals turned around one or more times during their trial and travelled by the same fence lines on repeated occasions. We used all data where a complete pass was made and accounted for this with a covariate "FirstSegment" indicating whether it was the individuals first encounter with that fence type.

*Movement Time along Fence Types: Logistic Regression:*

We first modelled the probabilities of fence interaction behaviors using logistic regression. For this we only used the individuals first encounter with each fence type (Hardware Cloth, Mesh, Solid +/- Visual Barrier). To determine whether the probability of fence interaction behaviors differed across fence types and by taxonomic group (lizards, snakes, toads) and the effect of a visual barrier, we fitted a general linear model with a binomial distribution and logit-link function (Program R):

Fence Interaction Behavior (0/1) ~ FenceType*VisualBarrier + TaxonomicGroup

*Movement Time along Fence Types: Linear Regression:*

Individuals of different species and taxonomic groups had widely varying times along the fence lines within the behavioral enclosure. To minimize this variation and to determine whether speed of movement was affected by fence type, we did two things. First, we removed records of segment passes where the behavior "sitting" was recorded. This behavior was not considered an interaction with the fence but represented varying, and sometimes long, periods of time where an animal would "freeze." Second, we standardized all time data to z-distributions by individual (mean= 0, data as number of standard deviations from the mean). As an example, an individual with times of 5, 10, and 15 min across fences A, B, and C would be transformed to -1, 0, 1. Likewise, another individual with times of 1, 2, and 3 min across fences A, B, and C would be transformed to -1, 0, 1. This allowed us to account for the wide variability of speed among individuals and focus on their relative responses to the different fence types.

We then modelled the data using linear regression fitted by least squares to determine whether time differed across fence types and if the installation of a visual barrier affected time spent along the fence types by taxonomic group (lizards, snakes, toads)(Program R):

Standardized Time ~ FenceType*VisualBarrier + TaxonomicGroup + FirstSegment

For both types of models described, we also ran mixed model versions based on maximum likelihood with the individual as a random variable; the mixed models had convergence issues due to the large number of parameters (i.e. overparameterization). However, the model coefficients and standard error estimates were very similar between the general linear and mixed model types. Further analyses of this study will be conducted using Bayesian methods for a manuscript.

## Results

We captured a total of 174 individuals to use in our trials. Of these, 66% (114) completed at least one full set of fence types and thus were used in the behavioral modelling. Eighty individuals completed moving through all fence lines to the exit arena and of these, 87.5% (70) exited using one of the jump-outs (Table 1).

Table 1. Numbers of Species Used in Trials with Outcomes

| Taxon | Species | Number Escaped | Fence lines passed (out of 6) <3 | 3-5* | 6* | Number exited |
|---|---|---|---|---|---|---|
| Frog | *SubTotal* | | | 1 | | |
| | *Pseudacris regilla* | | | 1 | | |
| Lizard | *SubTotal* | | 46 | 24 | 57 | 49 |
| | *Aspidoscelis hyperythrus* | | 23 | 7 | 42 | 38 |
| | *Aspidoscelis tigris* | | 1 | 2 | 2 | 2 |
| | *Elgaria multicarinata* | | 2 | 1 | 2 | 1 |
| | *Sceloporus occidentalis* | | 11 | 13 | 6 | 5 |
| | *Sceloporus orcutti* | | | | 1 | |
| | *Uta stansburiana* | | 9 | 1 | 3 | 2 |
| | *Plestiodon skiltonianus* | 1 | 1 | | 0 | |
| Snake | *SubTotal* | | 6 | 6 | 21 | 20 |
| | *Crotalus ruber* | | | | 3 | 3 |
| | *Crotalus oreganus* | | | | 2 | 2 |
| | *Lampropeltis getula* | | | | 2 | 2 |
| | *Lichanura trivirgata* | | | | 1 | 1 |
| | *Coluber fuliginosus* | | | | 2 | 1 |
| | *Coluber lateralis* | | 3 | 2 | 5 | 5 |
| | *Pituophis catenifer* | | 2 | 3 | 5 | 5 |
| | *Tantilla planiceps* | | 1 | | 0 | |
| | *Thamnophis hammondii* | | | 1 | 2 | 2 |
| Toad | *SubTotal* | | 6 | 3 | 2 | 1 |
| | *Anaxyrus boreas* | | 2 | 2 | 2 | 1 |
| | *Spea hammondii* | | 4 | 1 | 0 | |
| | Grand Total | 1 | 59 | 34 | 80 | 70 |

*used in modelling

All behavioral models showed that fence type was significant in predicting the probability that herpetofauna would exhibit fence interaction behaviors (Tables 2–4, Figures 4–6). Poking, moving back and forth, and climbing behaviors were more common as the transparency of the fence increased (solid > mesh> hardware cloth). Across taxonomic groups, toads showed higher probabilities of fence interaction behaviors than lizards and snakes, although the variability in the data was greater for toads. Along with the greater probability of these behaviors, the time it took for herpetofauna to pass each fence type increased as the transparency of the fence increased (Table 5, Figure 7).

The addition of a 15 cm (6 in) visual barrier along the bottom of the mesh and hardware cloth fencing reduced the probability of poking and back and forth movements among all taxa and was particularly significant in reducing poking behaviors of lizards and snakes. When a visual barrier was present, there was little difference in the probability of fence interaction behaviors among the fence types. Similarly, a visual barrier significantly reduced the time it took for individuals to move along the mesh and hardware cloth fencing so that there was little difference in individual speed among all fence types.

Table 2. Effect of Fence Type on Animal Behavior: Poking and Looking

| Coefficients: | Estimate | Std. Error | t-value | Pr(>\|t\|) | |
|---|---|---|---|---|---|
| (Intercept= Solid) | *-3.215* | *0.412* | *-7.811* | *5.65E-15* | *** |
| FenceTypeMesh | *2.482* | *0.425* | *5.847* | *5.01E-09* | *** |
| FenceTypeHC | *3.582* | *0.430* | *8.325* | *< 2e-16* | *** |
| VB011 | *-1.228* | *1.150* | *-1.067* | *0.286* | |
| TypeSnake | *0.281* | *0.262* | *1.074* | *0.283* | |
| TypeToad | *3.044* | *0.734* | *4.150* | *3.32E-05* | *** |
| FirstSegType1 | *0.232* | *0.252* | *0.918* | *0.359* | |
| FenceTypeMesh:VB011 | *-0.885* | *1.313* | *-0.674* | *0.500* | |
| FenceTypeHC:VB011 | *-0.640* | *1.236* | *-0.518* | *0.604* | |

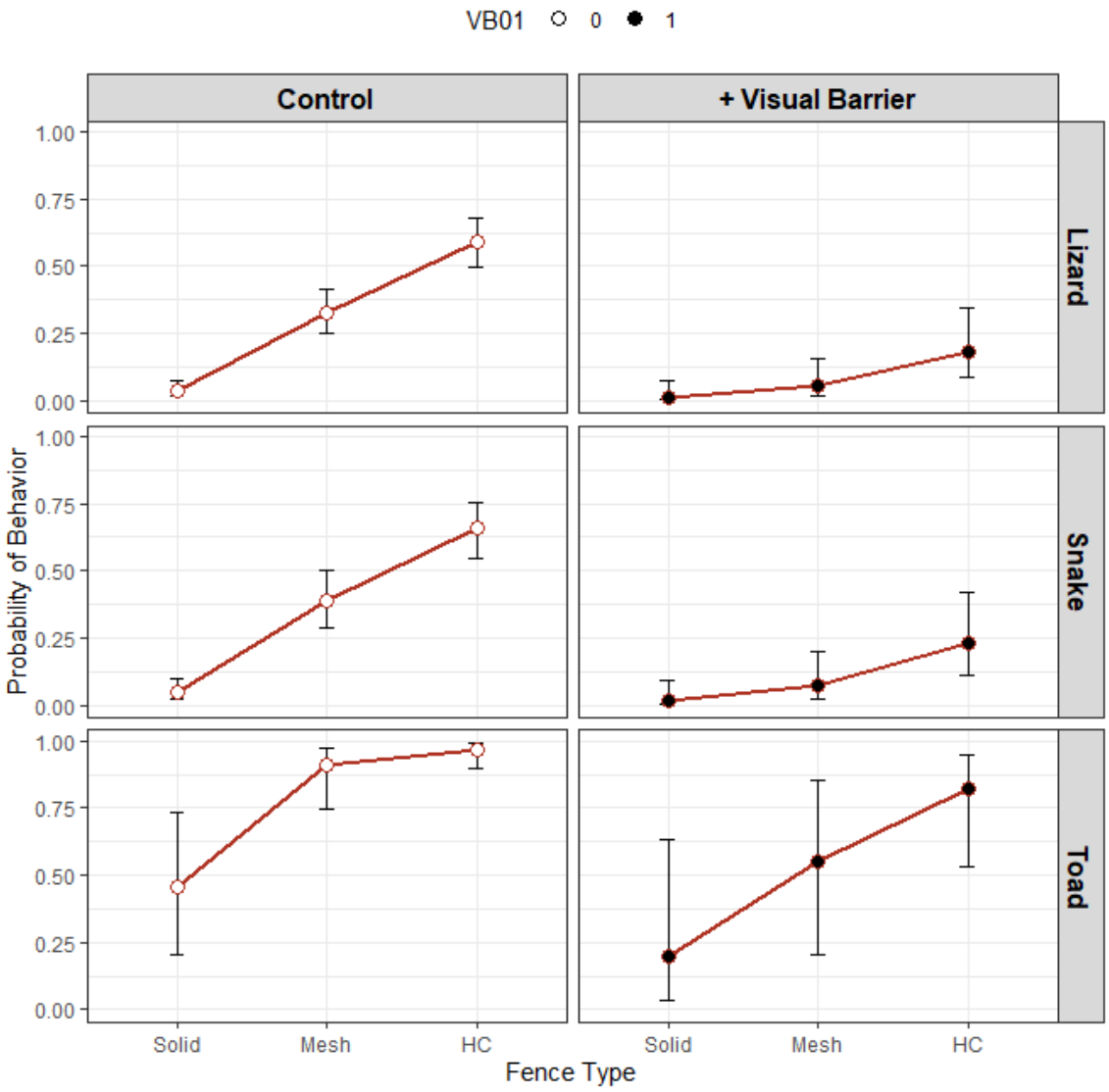


Figure 4. Effect of Fence Type on Animal Behavior: Poking and Looking

VB= visual barrier, HC= hardware cloth

Table 3. Effect of Fence Type on Animal Behavior: Back and Forth Movements

| Coefficients: | Estimate | Std. Error | t-value | Pr(>\|t\|) | |
|---|---|---|---|---|---|
| (Intercept= Solid) | *-2.928* | *0.418* | *-7.001* | *2.53E-12* | *** |
| FenceTypeMesh | *1.606* | *0.452* | *3.552* | *3.83E-04* | *** |
| FenceTypeHC | *2.245* | *0.444* | *5.053* | *4.36E-07* | *** |
| VB011 | *-0.715* | *1.102* | *-0.649* | *0.516* | |
| TypeSnake | *-0.752* | *0.338* | *-2.225* | *0.026* | * |
| TypeToad | *1.076* | *0.742* | *1.451* | *0.147* | |
| FirstSegType1 | *0.075* | *0.284* | *0.265* | *0.791* | |
| FenceTypeMesh:VB011 | *0.020* | *1.235* | *0.016* | *0.987* | |
| FenceTypeHC:VB011 | *-1.265* | *1.334* | *-0.948* | *0.343* | |

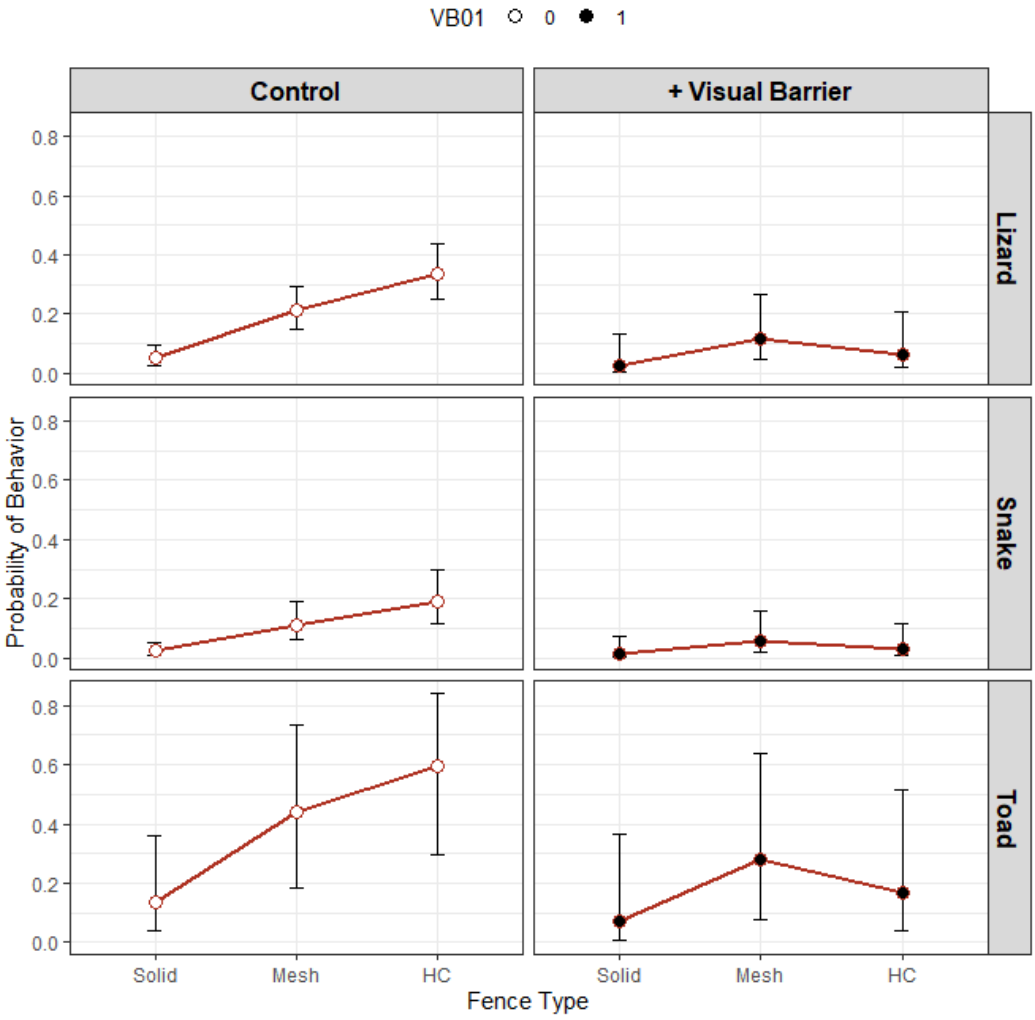


Figure 5. Effect of Fence Type on Animal Behavior: Back and Forth Movements

VB= visual barrier, HC= hardware cloth

Table 4. Effect of Fence Type on Animal Behavior: Climbing

| Coefficients: | Estimate | Std. Error | t-value | Pr(>\|t\|) | |
|---|---|---|---|---|---|
| (Intercept= Solid) | *-3.319* | *0.521* | *-6.373* | *0.000* | *** |
| FenceTypeMesh | *1.105* | *0.576* | *1.917* | *0.055* | . |
| FenceTypeHC | *1.662* | *0.561* | *2.963* | *0.003* | ** |
| VB011 | *-16.458* | *1711.284* | *-0.010* | *0.992* | |
| TypeSnake | *-1.850* | *0.745* | *-2.484* | *0.013* | * |
| TypeToad | *2.020* | *0.790* | *2.558* | *0.011* | * |
| FirstSegType1 | *0.102* | *0.390* | *0.261* | *0.794* | |
| FenceTypeMesh:VB011 | *-0.938* | *2465.362* | *0.000* | *1.000* | |
| FenceTypeHC:VB011 | *14.523* | *1711.284* | *0.008* | *0.993* | |

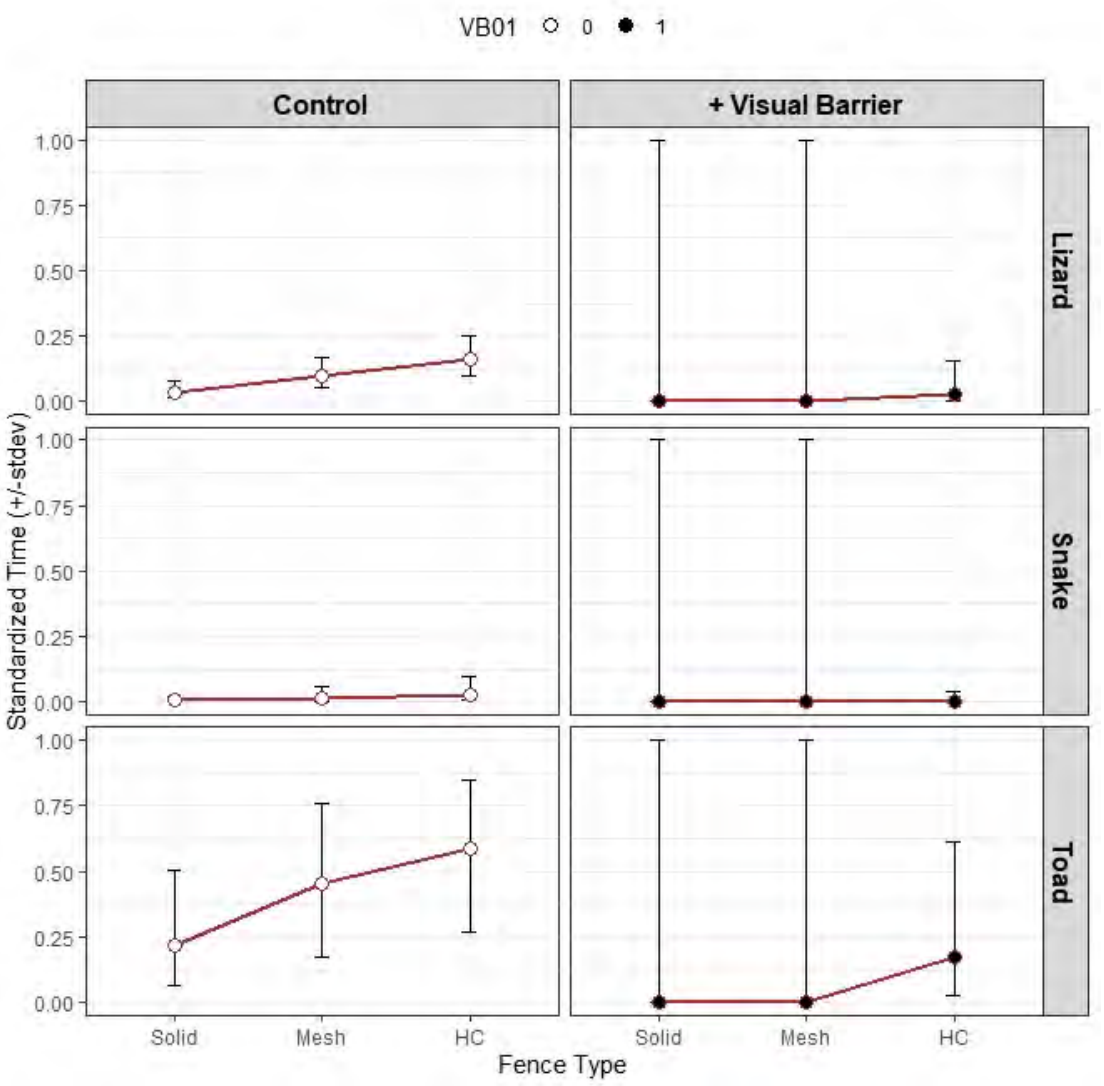


Figure 6. Effect of Fence Type on Animal Behavior: Climbing

VB= visual barrier, HC= hardware cloth

Table 5. Effect of Fence Type on Relative Movement Time

| Coefficients: | Estimate | Std. Error | t-value | Pr(>\|t\|) | |
|---|---|---|---|---|---|
| (Intercept= Solid) | *-0.31719* | *0.06641* | *-4.776* | *2.11E-06* | *** |
| FenceTypeMesh | *0.24439* | *0.09012* | *2.712* | *0.00683* | ** |
| FenceTypeHC | *0.72434* | *0.09106* | *7.955* | *5.71E-15* | *** |
| VB011 | *0.56038* | *0.1081* | *5.184* | *2.72E-07* | *** |
| TypeSnake | *0.04315* | *0.08091* | *0.533* | *0.59394* | |
| TypeToad | *-0.02768* | *0.17773* | *-0.156* | *0.87626* | |
| FirstSegType1 | *-0.13039* | *0.07296* | *-1.787* | *0.07427* | . |
| FenceTypeMesh:VB011 | *-0.4652* | *0.16574* | *-2.807* | *0.00512* | ** |
| FenceTypeHC:VB011 | *-1.01179* | *0.15753* | *-6.423* | *2.22E-10* | *** |

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

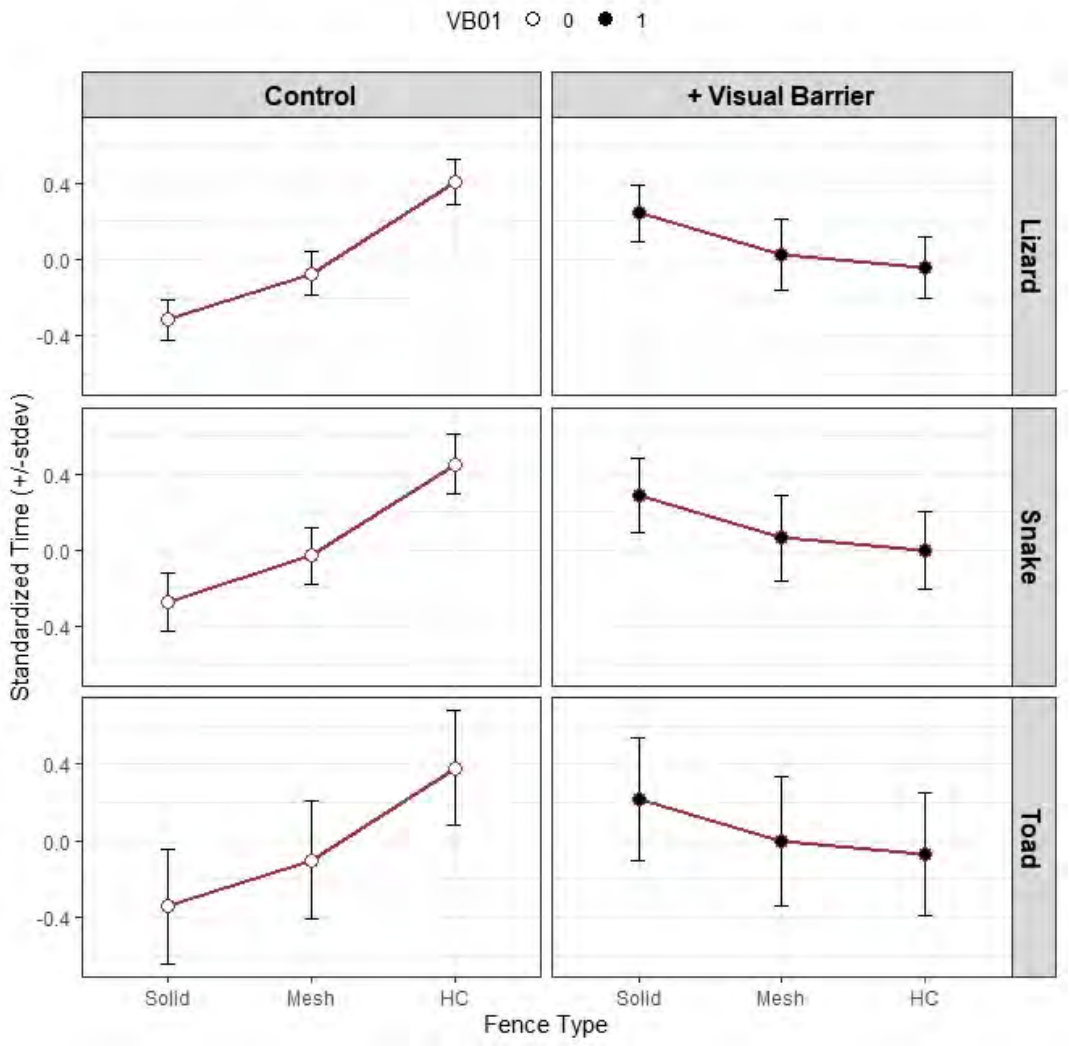


Figure 7. Effect of Fence Type on Relative Movement Time

*Effectiveness of jump-outs*

A total of 75% of lizards (43/57), 95% of snakes (20/21), and 50% of toads (1/2) used a jump-out to escape the enclosure. There was little difference between the use of the high ramp and low funnel jump-outs by lizards and snakes (Figure 8). We observed that lizards often sat on top of the high ramp for long periods of time before jumping to the ground, whereas there was little hesitation with the low jump-outs. A higher proportion of lizards (16–23%) did not exit via the jump-outs. Many of these sat in the exit arena until they timed out or moved back in the direction of the entrance.

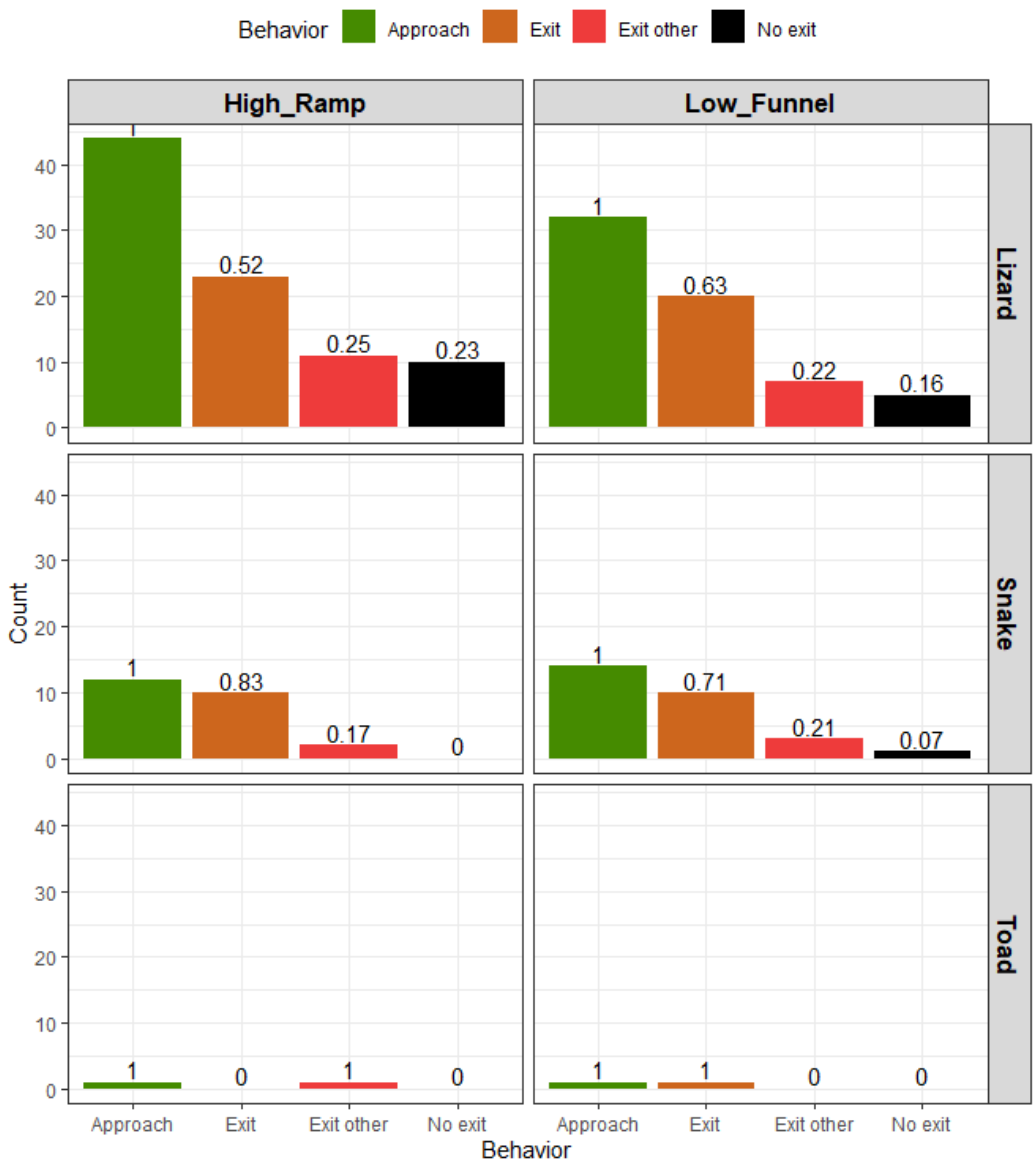


Figure 8. Proportion of Herpetofauna Groups that Approached and Used 2 Jump-Out Designs.

## Discussion

Our results provide evidence that herpetofauna are more likely to interact with the transparent and semi-transparent fences by poking it with their noses, pacing back and forth, and attempting to climb. The transparent and semi-transparent fencing types used in this study are not only see-through but are permeable to the movement of air. Because sight and chemoreception senses are typically well developed in reptiles, it is not clear to what extent these different senses are driving fence interaction behaviors. However, animals exhibiting these behaviors appear to be trying to find a way through the fence to the other side.

Although fence interaction behaviors have been documented elsewhere in comparing hardware cloth and solid fencing (Ruby et al. 1994, Milburn-Rodríguez et al. 2016), our study shows a gradation of response from solid to semi-transparent to transparent fencing in all taxa studied. In addition, our study shows that these behaviors result in animals moving slower, or spending more time, along transparent/permeable fencing in comparison to solid fencing. This may not be a concern when the purpose of the fence is primarily to exclude animals. However, effect of fence opacity on movement rates should be considered when a dual objective is to lead species toward a road crossing structure, particularly when high permeability and population connectivity across the structure is desired (Simlitsch 2008, Hamer et al. 2015, Brehme et al. 2018).

There are reasons why hardware cloth, mesh, or solid barriers may be desirable in particular landscapes, habitats, and climates with considerations that include rain and wind permeability, durability, and aesthetics (Langton and Clevenger 2020). Our study is the first to show that addition of a simple visual barrier at ground level (6 inches our study) can result in substantial decreases in fence interaction behaviors and in increased rates of movement. For most response measures, herpetofauna responses to mesh and hardware cloth fencing with a visual barrier were not significantly different than to the solid barrier. This may allow for more flexibility in the decision-making and planning processes for barrier systems for herpetofauna. With any barrier or fencing system, proper maintenance is extremely important for its continued success (Hamer et al. 2015, Baxter-Gilbert et al. 2015, Langton and Clevenger 2020).

Finally, we showed that two jump-out configurations were largely effective in allowing animals trapped on the wrong side of the barriers to escape back into the habitat. Animals can easily get trapped on the wrong (road) side of barrier fencing by entering through a tear or opening in the fencing or by entering the roadway at the end of the exclusion fencing. Although jump-outs are commonly built structures along wildlife fencing for large mammals, they have not commonly been incorporated into transportation planning for small animal barriers. Jump-outs for herpetofauna can be provided at regular intervals along barriers with interval distances determined by target species movement distances. It is also important that any jump-out design for herpetofauna consider the safety of other wildlife. For short barrier fencing, most other wildlife can simply jump over the barrier. For larger barrier systems, escape routes may include multiple size jump-outs for a wider variety of species.

## Acknowledgements

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# Chapter 7. Effectiveness of Turnarounds in Changing the Trajectory of Reptiles and Amphibians in San Diego, CA.

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## Introduction

It is common practice to install 'turnarounds' at fence ends and where barriers are unable to span across private road entries and easements (e.g. Clevenger and Huijser 2011, Ontario Ministry of Natural Resources and Forestry 2016, Langton and Clevenger 2020). For this, road barriers end in a "U" shape and are designed to redirect animals back in the opposite direction at fence ends and keep them off the roadway. Although they are recommended in many countries and in guidance documents (e.g. Iuell et al. 2003, Clevenger and Huijser 2011, Gunson et al. 2016), there are no systematic studies to our knowledge that have addressed the relative effectiveness of turnarounds (Langton and Clevenger 2017).

We conducted studies at the Rancho Jamul Ecological Reserve in Jamul, California to test the effectiveness of turnarounds in changing the trajectory of movement for herpetofauna and small mammals. We also compared effectiveness and time spent within the turnarounds based upon fence type: transparent, semi-transparent, and solid fencing. The results of these studies will help to inform transportation agencies on these important components of road barrier and crossing systems.

Research questions:

1. Are fence end turnarounds effective in redirecting the trajectory of animal movement?
2. Is the effectiveness of turnarounds influenced by the opacity of barrier fencing?

## Methods

We installed three 20 m segments of solid barrier fencing within coastal sage scrub habitat in RJER adjacent to a dirt road. At the ends of each segment, we installed another 4 m of fencing and a turn-around approximately 1.5 m long and 1 m wide. The turnarounds ended approximately 0.4 m from the fence lines and extended another 0.4 m parallel to the fence (Figure 1). We used three materials with increasing opacity; hardware cloth (0.25 inch), mesh (ERTEC® rigid polymer matrix E-Fence), or solid fencing (Animex® high-density polyethylene (HDPE-2)). The placement of the turnarounds was mixed so that each segment ended with two of the different fence type materials. At the opening of each turnaround, we installed a HALT® active infrared trigger and camera system that allowed us to document animals going into and out of the turnarounds, as well as determine their trajectory upon leaving the turnaround. The cameras were placed 4.25 m from the end of the turnaround (2.25 m from trigger) with a frame of view that allowed us to follow the

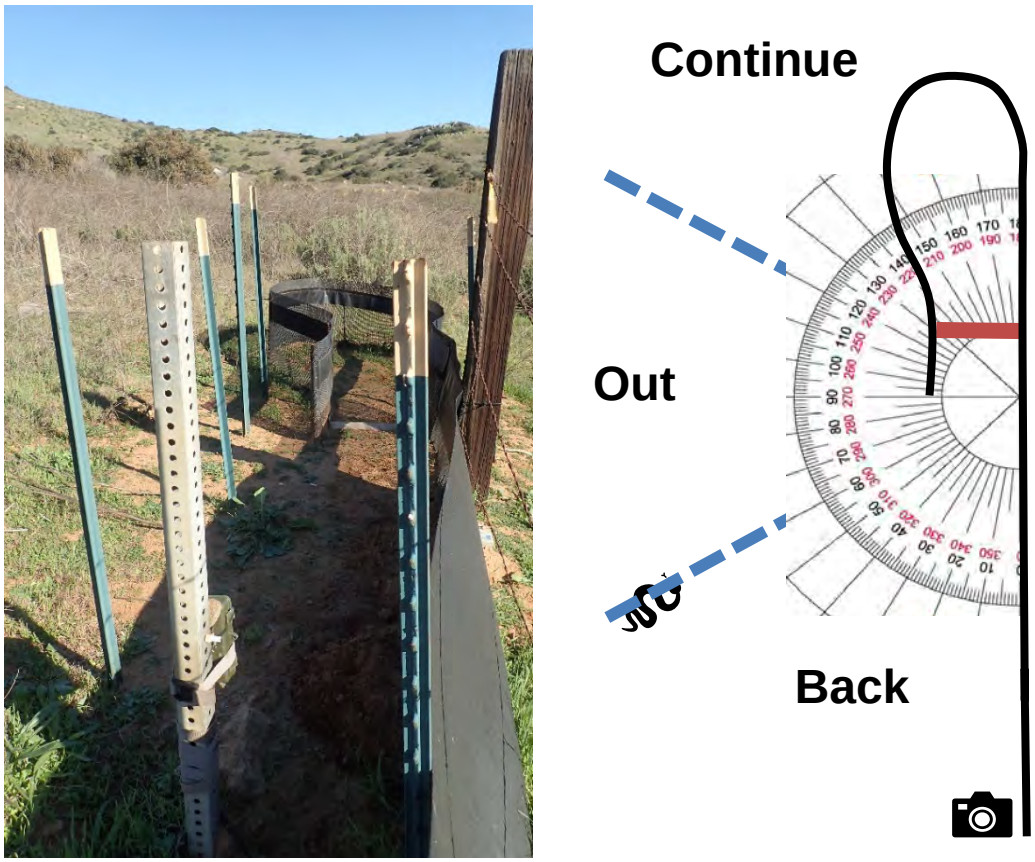
movement of animals for approximately 1 m in any direction and were set to record video for 25 seconds upon an animal activating the trigger. Cameras were set with 32-64GB SD cards and left on and checked on a weekly or biweekly basis from March 1 to Sept. 8, 2019.

## Analysis

We watched all videos and recorded the following:

- Turnaround Fence Type and Segment number
- Species
- Time of entry and exit
- Distance and direction of travel

Individuals were only included in the analysis if the animals moved at least 0.7 m away from the end of the turnaround. If the same individual moved in and out of the turnaround more than once, only their final trajectory was recorded. Final direction of travel was recorded as three categories: Continue, Out, and Back (Figures 1 and 2). We also did not include data where an individual encountered another individual that may have affected the direction of travel.




Note: Extra stakes in ground to keep cows away from turnaround

Figure 1. Example of A) Turnaround with Camera and Trigger Set Up and B) Direction of Movement Categories.

Figure 2. Example of A) Cottontail Rabbit (*Sylvilagus audubonii*) Continuing in the Same Direction, B) Red-Diamond Rattlesnake (*Crotalus ruber*) Moving Away into the Habitat, and C) Western Toad (*Anaxyrus boreas*) Moving Back along the Fenceline after Leaving the Turnaround. Screenshots taken from Videos Showing Animals Continuing in the Same Direction Out of View.

To determine if the turnarounds were successful in changing the trajectory of movement among taxonomic groups and fence types, we analyzed the choice made by each subject after they reached the turnaround using a multinomial logit choice model (Figure 3). Each individual had a choice of turning back (1, "back"), exiting out of the structure (2, "out"), or continuing in the same direction of travel (3, "continue"). This model is a multinomial generalization of the logistic model which models a binomial response (with one trial, hence a Bernoulli random variable). For each choice, we first calculate a "probability potential." The first choice (back) is a "reference" and is assigned a probability potential of "1" in all cases. The remaining two responses have probability potentials that are an exponential (i.e. rate = exp(y)) function of the linear component of the model that depend on two predictor variables that encode fence type and three variables for taxonomic group, a response-specific intercept and two regression coefficients. The final probabilities for each choice were calculated as the probability potential for that choice divided by the sum of all the probability potentials. This ensured that sum of the probabilities for the choice made for each observation added to one. The taxon-specific parameters were drawn from normal distributions with means and precisions based on parameters drawn from "all taxa" hyper-prior distributions. The hyperprior means were drawn from a normal distribution with mean 0 and 0.001 precision. The precisions were calculated as one over a squared standard deviation, with the standard deviation drawn from a uniform distribution on an interval from 0 to 1000. The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of turn around fence type on the choice made by each subject.

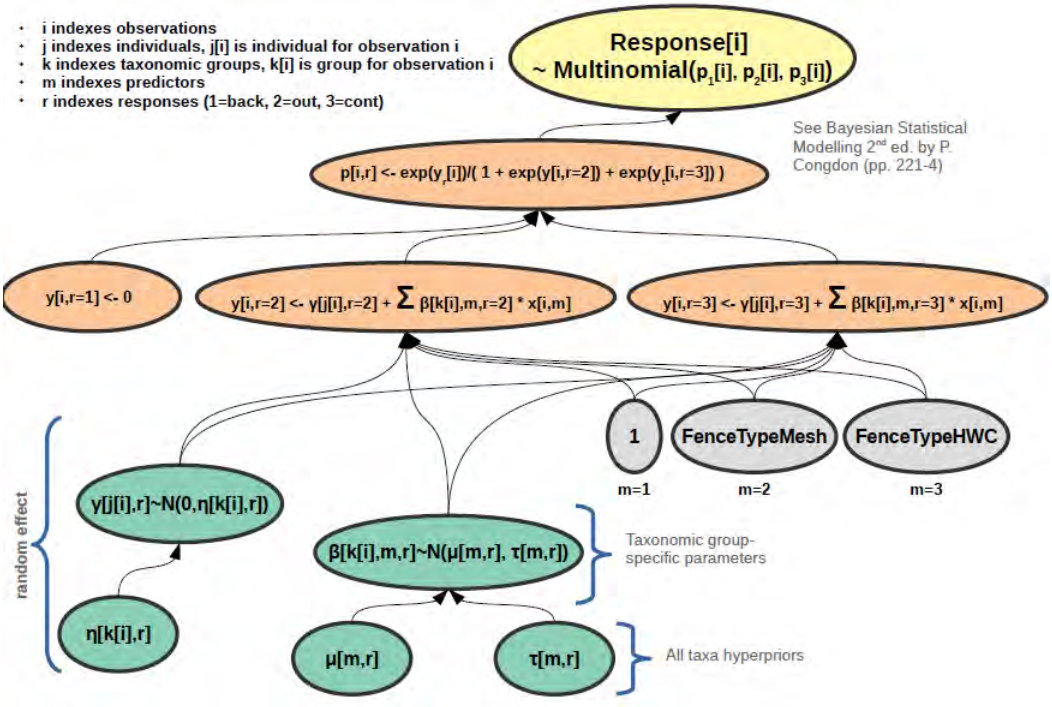



Figure 3. Turn Around Study: Multinomial Logit Choice Model for Response to Turn Around Structure

*Time Spent in Turnarounds: Linear Regression:*

We modelled time spent in the turnarounds using linear regression fitted by least squares to determine if time differed across fence types and taxonomic group (lizards, snakes, toads, and small mammals)(Program R):

Time ~ FenceType* TaxonomicGroup

## Results

We captured useable video of 790 individual turnaround encounters that met our distance criteria. This represented 264 lizard, 96 snake, 59 toad, one frog, and 370 small mammal movements (Table 1). Among all herpetofauna, 92% changed course back toward the fence line or back out into the habitat. A total of 64% of lizard, 68% of snake, 80% of toads and 43% of small mammal movements were made back along the original fence line after encountering a turnaround.

Table 1. Species Documented Using Turnarounds and Movement Trajectory Results

| | | Fence lines passed (out of 6) | | | Proportion |
|---|---|---|---|---|---|
| Taxon | Species | Continued | Out | Back | Back+ Out |
| Lizard | *SubTotal* | 26 | 69 | 169 | 0.90 |
| | *Aspidoscelis hyperythrus* | 12 | 53 | 69 | 0.91 |
| | *Aspidoscelis tigris* | | | 2 | 1.00 |
| | *Elgaria multicarinata* | | | 1 | 1.00 |
| | *Plestiodon gilberti* | | | 1 | 1.00 |
| | *Plestiodon skiltonianus* | | 1 | | 1.00 |
| | *Sceloporus occidentalis* | 3 | 1 | 15 | 0.84 |
| | *Uta stansburiana* | 11 | 14 | 79 | 0.89 |
| | *Unknown lizard* | | | 2 | 1.00 |
| Snake | *SubTotal* | 1 | 30 | 65 | 0.99 |
| | *Coluber fuliginosus* | | 2 | 12 | 1.00 |
| | *Coluber lateralis* | 1 | 9 | 23 | 0.97 |
| | *Coluber flagellum* | | 6 | 9 | 1.00 |
| | *Crotalus oreganus* | | 6 | 5 | 1.00 |
| | *Crotalus ruber* | | 2 | 1 | 1.00 |
| | *Lampropeltis getula* | | 2 | 3 | 1.00 |
| | *Pituophis catenifer* | | 2 | 11 | 1.00 |
| | *Salvadora hexalepis* | | 1 | | 1.00 |
| | *Unknown snake* | | | 1 | 1.00 |
| Toad/Frog | *SubTotal* | 5 | 8 | 47 | 0.92 |
| | *Anaxyrus boreas* | 4 | 5 | 31 | 0.90 |
| | *Pseudacris regilla* | | | 1 | 1.00 |
| | *Unknown anuran* | 1 | 3 | 15 | 0.95 |
| Small Mammal | *SubTotal* | 120 | 91 | 159 | 0.68 |
| | *Chaetodipus spp.* | 3 | 15 | 33 | 0.94 |
| | *Dipodomys simulans* | 29 | 22 | 36 | 0.67 |
| | *Microtus californicus* | 3 | 2 | 2 | 0.57 |
| | *Neotoma spp.* | 5 | 2 | | 0.29 |
| | *Notiosorex crawfordii* | 1 | 1 | 2 | 0.75 |
| | *Otospermophilus beecheyi* | 41 | 16 | 35 | 0.55 |
| | *Peromyscus spp.* | 37 | 30 | 47 | 0.68 |
| | *Reithrodontomys megalotis* | | 1 | 1 | 1.00 |
| | *Thomomys bottae* | | 2 | 1 | 1.00 |
| | *Unknown rodent* | 1 | | 2 | 0.67 |
| | Grand Total | 152 | 198 | 440 | 0.81 |

Across fence types, results of the multinomial logit choice model showed high probabilities (ρ) that lizards, snakes, and toads changed their trajectory of movement (back, out) after encountering and exiting a turnaround (Lizard ρ= 0.88, 90% CI 0.70–1.00, Snakes ρ= 0.98, 90% CI 0.77–1.00, Toad ρ= 0.90, 90% CI 0.62–1.00). Responses by lizards and toads, but not snakes, varied by fence type (Figure 4). Lizards and toads were generally more likely to change their trajectory (back, out) after encountering mesh and hardware cloth turnarounds in comparison to solid turnarounds.

Mammals had an overall lower probability than herpetofauna of changing their trajectory after exiting turnarounds (back and out ρ= 0.59, 90% CI 0.41–0.84). By fence type, mammals were more likely to change their trajectory (back, out) after encountering hardware cloth turnarounds in comparison to solid and mesh turnarounds.

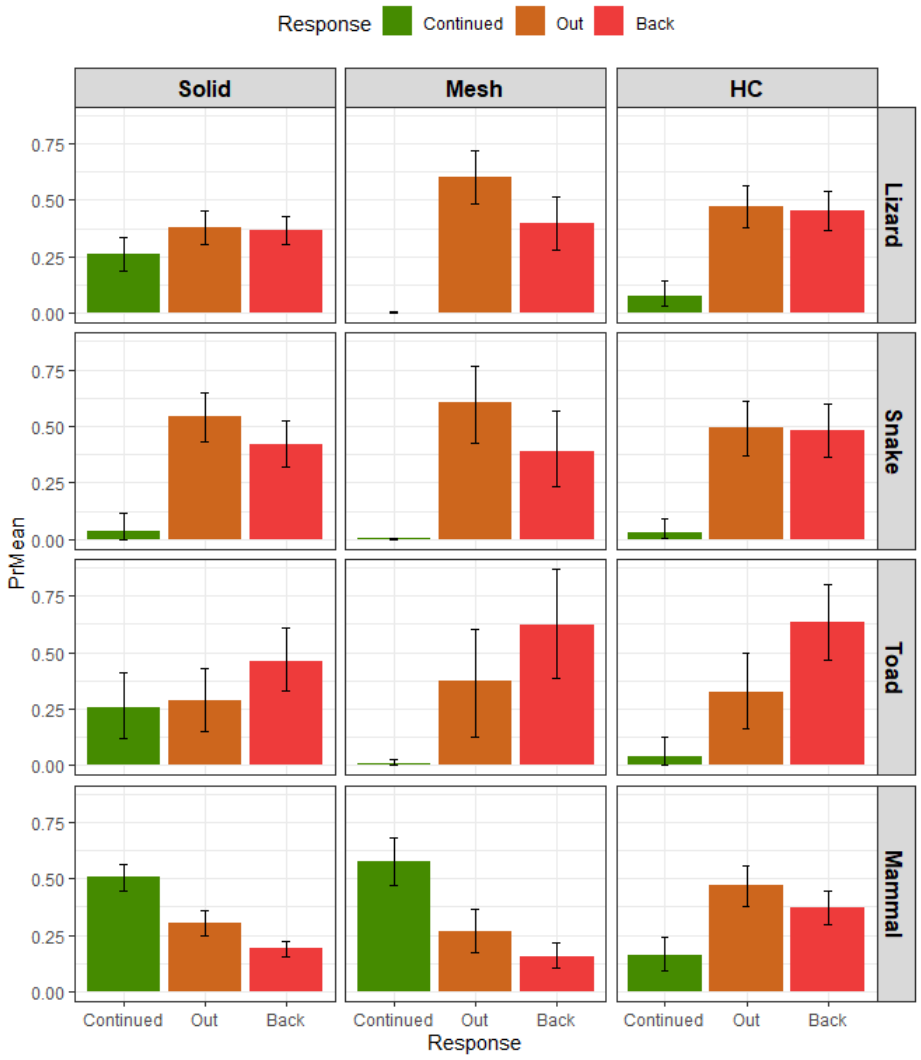



Figure 4. Directional Probabilities After Exiting Turnaround by Taxonomic Group and Fence Type (+/- 90% CI)

By Fence Type, all groups except toads spent significantly less time in the solid turnarounds than in the hardware cloth turnarounds ($p<0.001$; Table 2, Figure 5). Overall by taxon, mammals spent the least time in turnarounds (ave. model estim.=0.4 min), followed by snakes (ave. model estim=1.9 min), lizards (ave. model estim= 2.7 min), and toads (ave. model estim=3.0 min).

Table 2. Effects and Interactions of Fence Type and Taxon on Time spent in Turnaround

| Coefficients: | Estimate | Std. Error | t-value | Pr(>\|t\|) | |
|---|---|---|---|---|---|
| (Intercept= Solid/Lizard) | *0.105* | *0.136* | *0.777* | *0.437* | |
| FenceTypeMesh | *1.083* | *0.286* | *3.788* | *1.65E-04* | *** |
| FenceTypeHC | *1.240* | *0.218* | *5.683* | *1.96E-08* | *** |
| TaxGroup1Mammal | *-1.424* | *0.177* | *-8.063* | *3.31E-15* | *** |
| TaxGroup1Snake | *-0.009* | *0.275* | *-0.032* | *0.974* | |
| TaxGroup1Toad | *0.698* | *0.307* | *2.271* | *0.023* | * |
| FenceTypeMesh:TaxGroup1Mammal | *-0.926* | *0.371* | *-2.498* | *0.013* | * |
| FenceTypeHC:TaxGroup1Mammal | *-0.587* | *0.298* | *-1.971* | *0.049* | * |
| FenceTypeMesh:TaxGroup1Snake | *-0.699* | *0.560* | *-1.248* | *0.212* | |
| FenceTypeHC:TaxGroup1Snake | *-0.263* | *0.400* | *-0.658* | *0.511* | |
| FenceTypeMesh:TaxGroup1Toad | *-0.498* | *0.665* | *-0.748* | *0.454* | |
| FenceTypeHC:TaxGroup1Toad | *-1.030* | *0.500* | *-2.059* | *0.040* | * |
| (Intercept= Solid/Lizard) | *0.105* | *0.136* | *0.777* | *0.437* | |

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

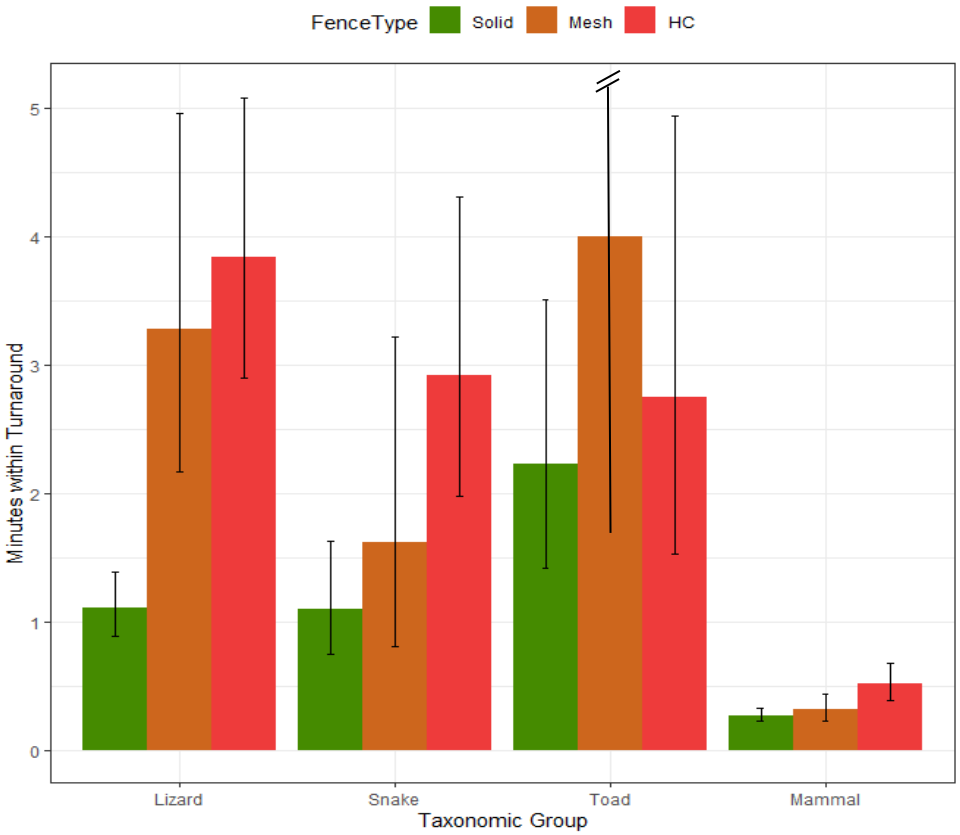



Figure 5. Estimated Time Spent in Turnaround by Taxonomic Group and Fence Type (+/- 90% CI)

## Discussion

Our study is the first to show that small turnarounds at fence ends can be effective in changing the trajectory of movement for a majority of herpetofauna and small mammals. We documented that over 90% of herpetofauna (lizards, snakes and toads), as well as 69% of small mammals, changed course after leaving the turnaround. Of these 67% of herpetofauna and 43% of small mammals moved back along the original fence line. We (Chapter 5), and others (Ruby et al. 1994, Milburn-Rodríguez et al. 2016) have shown that animals spend more time interacting with fencing that they can see and smell through (e.g. poking, back and forth movements, climbing). We observed this in the turnaround study as well, as lizards, snakes and small mammals spent increased amounts of time in transparent/permeable and semi-transparent/permeable turnarounds than solid turnarounds.

Turnarounds made of solid fencing appeared to be less effective in changing the movement trajectory of lizards and toads in comparison to mesh and hardware cloth fencing. In addition, both solid and semi-transparent mesh fencing appeared to be less effective in changing the trajectory of small mammals in comparison to more transparent hardware cloth. These results could be related to animals interacting with the fencing and spending more time in the more transparent turnarounds, so that they were less likely to remember and continue on their original trajectory. The results may also be related to the different types of spatial learning and memory used for navigation when animals are subjected to solid barriers (egocentric) in comparison to transparent barriers (allocentric) as has been shown in maze-food trials with rodents (Violle et al. 2009, Vorhees and Williams 2014). Validation of these findings in other locations and possibly more specific research studies addressing spatial learning and movement responses in reptiles, amphibians, and small mammals in their natural environments would be needed to further our understanding of these results.

We did not compare different sizes or shapes of turnarounds in our study; however, we hypothesize that having the end of the turnaround close to the original fence line (or turning back in toward the fence line) may help to steer animals back to the original barrier in the other direction. We chose not to install large turnarounds as we wanted to reduce the probability of animals becoming stressed or 'trapped' in the turnarounds for long periods of time. However, longer turnarounds or larger turnarounds encompassing smaller turnarounds may increase the probability that animals do not make it onto the roadways (Langton and Clevenger 2020). Our study also suggests the use of transparent or semi-transparent fencing for turnarounds may potentially increase their effectiveness.

In this study, we only documented animal movement for up to 1 m (3.4 feet) after leaving the turnaround. It is entirely possible that animals changed course again after they left the field of view of the video camera. In our Stanford and Sierra movement studies (Chapters 3 and 4), two out of three CTS that presumably reached a turnaround at the fence end were subsequently documented on another camera 25-125 m away moving back along the fence line. Preliminary results suggest seven out of 10 Yosemite toads changed course at a turnaround, while three continued in the direction past the fence ends. Of the seven toads that changed course, four were

subsequently documented on another camera 40-80 m away moving back along the fence line toward the passage. Further studies using more cameras and/or tracking methods are needed to better understand how turnarounds affect movement of animals over a longer distances and time frames. Higher mortality of herpetofauna has been well documented at fence ends even with turnarounds (Gunson et al. 2014, Langton and Clevenger 2017, Helldin and Petrovan 2019). However, the high proportion of herpetofauna that changed directions in our study supports the use of turnarounds in attempts to reduce the chances that small animals go out onto the roadway at fence ends and potentially to help 'steer' them back toward to a crossing structure.

In our migrating California tiger salamander (Chapter 4) and Yosemite toad studies (Chapter 5), we also found that these amphibian species were much less likely to encounter a crossing structure if they started out in the 'wrong' direction (i.e. moving away from the crossing after encountering a barrier). Many animals "gave up" before reaching the fence ends. These results suggest that more regularly placed turnarounds along the fence lines may allow them to correct their trajectory sooner and possibly increase their chances of making it to crossing structures. If effective, this strategy may help to increase the permeability of crossing structures to individual and population movements of reptiles and amphibians (and small mammals). These studies are currently in the planning stages.

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# How does climate change cause extinction?

Abigail E. Cahill†, Matthew E. Aiello-Lammens†, M. Caitlin Fisher-Reid, Xia Hua, Caitlin J. Karanewsky, Hae Yeong Ryu, Gena C. Sbeglia, Fabrizio Spagnolo, John B. Waldron, Omar Warsi and John J. Wiens

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Anthropogenic climate change is predicted to be a major cause of species extinctions in the next 100 years. But what will actually cause these extinctions? For example, will it be limited physiological tolerance to high temperatures, changing biotic interactions or other factors? Here, we systematically review the proximate causes of climate-change related extinctions and their empirical support. We find 136 case studies of climatic impacts that are potentially relevant to this topic. However, only seven identified proximate causes of demonstrated local extinctions due to anthropogenic climate change. Among these seven studies, the proximate causes vary widely. Surprisingly, none show a straightforward relationship between local extinction and limited tolerances to high temperature. Instead, many studies implicate species interactions as an important proximate cause, especially decreases in food availability. We find very similar patterns in studies showing decreases in abundance associated with climate change, and in those studies showing impacts of climatic oscillations. Collectively, these results highlight our disturbingly limited knowledge of this crucial issue but also support the idea that changing species interactions are an important cause of documented population declines and extinctions related to climate change. Finally, we briefly outline general research strategies for identifying these proximate causes in future studies.

## 1. Introduction

Anthropogenic climate change is recognized as a major threat to global biodiversity, one that may lead to the extinction of thousands of species over the next 100 years [1–7]. Climate change is an especially pernicious threat, as it may be difficult to protect species from its effects, even within reserves [8,9]. Furthermore, climate change may have important interactions with other anthropogenic impacts (e.g. habitat loss [2,6]). Given this, understanding the responses of species to modern climate change is one of the most pressing issues facing biologists today.

But what do we actually know about how climate change causes extinction? It might seem that limited physiological tolerances to high temperatures should be the major factor that causes climate change to threaten the persistence of populations and species, and many studies have justifiably focused on these tolerances [10–13]. However, there may be many other proximate causes of extinction, even when anthropogenic climate change is the ultimate cause. These proximate factors include negative impacts of heat-avoidance behaviour [14], the climate-related loss of host and pollinator species [15,16] and positive impacts of climate change on pathogens and competitors [17,18], among others. The relative importance of these factors is unclear and has not, to our knowledge, previously been reviewed, despite increasing interest in mechanisms underlying the impacts of climate change [19].

Identifying these proximate causes may be critical for many reasons. For example, different proximate factors may call for different conservation strategies to ameliorate their effects [20]. These different proximate factors may

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also influence the accuracy with which the impacts of climate change are predicted and may drive populations to extinction at different rates.

In this paper, we address three topics related to how anthropogenic climate change causes extinction. First, we briefly review and categorize the many proposed factors that potentially lead to extinction from climate change. Second, we argue that there is already abundant evidence for current local extinctions as a result of climate change, based on the widespread pattern of range contractions at the warm edges of species' ranges (low latitude and low elevation). Third, and most importantly, we perform to the best of our knowledge, the first large-scale review of empirical studies that have addressed the proximate causes of local extinctions related to climate change. This review reveals some unexpected results. We find that despite intensive research on the impacts of climate change, only a handful of studies have demonstrated a proximate cause of local extinctions. Further, among those studies that have identified a proximate cause, very few implicate limited physiological tolerance to high temperatures as the main, direct cause. Instead, a diverse set of factors are supported, with species interactions being particularly important. Finally, we outline some of the research approaches that can be used to examine the proximate factors causing extinction from climate change.

## 2. Proximate factors causing extinction from climate change

We briefly review and categorize the diverse proximate factors that may cause extinctions due to climate change. We organize these factors by distinguishing between abiotic and biotic factors (following the literature on species range limits [21]). However, all factors are ultimately related to abiotic climate change.

We make several caveats about this classification. First, we emphasize broad categories of factors, so some specific factors may not be included. Second, some factors are presently hypothetical and have not yet been demonstrated as causes of extinction. Third, we recognize that these factors are not mutually exclusive and may act synergistically to drive extinction. They may also interact with other, non-climatic factors (e.g. habitat modification [2,6]) and many different ecological and demographic factors may come into play as populations approach extinction [22]. Finally, we do not address factors that impede climate-induced dispersal.

### (a) Abiotic factors

#### (i) Temperature (physiological tolerances)

Many effects of anthropogenic climate change follow from an increase in temperature. The most obvious proximate factor causing extinction is temperatures that exceed the physiological tolerance of the species [10,12]. This factor may be most important in sessile organisms and those with limited thermoregulatory ability, and in regions and time scales in which temperature increase is greatest.

The impacts of temperature may also be more indirect, but still related to physiological tolerances. For example, in spiny lizards (*Sceloporus*), local extinctions seem to occur because higher temperatures restrict surface activity during the spring breeding season to a daily time window that is overly short [23]. Similarly, increased air temperatures may both decrease activity time and increase energy maintenance costs, leading organisms to die from starvation rather than from overheating [14]. In aquatic organisms, increased water temperatures may lead to increased metabolic demand for oxygen while reducing the oxygen content of the water [24]. Variability in temperature may also be an important proximate cause of extinction [25], including both extreme events and large differences over the course of a year. In temperate and polar latitudes, a mismatch between photoperiod cues and temperature may be important, with fixed photoperiod responses leading to activity patterns that are inappropriate for the changed climate [26]. Here, both low and high temperatures could increase mortality rates and lead to population extinction.

#### (ii) Precipitation (physiological tolerances)

Anthropogenic changes are also modifying precipitation patterns [27], and these changes may drive extinction in a variety of ways. For example, decreasing precipitation may lead directly to water stress, death and local extinction for terrestrial species [28], and loss of habitat for freshwater species or life stages [29,30]. There may also be synergistic effects between heat and drought stress (e.g. in trees [31]). Changing precipitation may be more important to some species than changing temperature, sometimes leading to range shifts in the direction opposite to those predicted by rising temperatures [32].

#### (iii) Other abiotic factors

Other abiotic, non-climatic factors may drive extinctions that are ultimately caused by climate change. For example, climate change can increase fire frequency, and these fires may be proximate causes of extinction (e.g. in South African plants [33]). Similarly, increases in temperature lead to melting ice-caps and rising sea levels [27], which may eliminate coastal habitats and modify the salinity of freshwater habitats [34].

### (b) Biotic factors

The biotic factors that are the proximate causes of extinction from climate change can be placed in three general categories.

#### (i) Negative impacts on beneficial species

Climate change may cause local extinction of a given species by causing declines in a species upon which it depends. These may include prey for predators [35], hosts for parasites and specialized herbivores [16], species that create necessary microhabitats [36] and species that are essential for reproduction (e.g. pollinators [15]).

#### (ii) Positive impacts on harmful species

Alternately, climate change may cause extinction through positive effects on species that have negative interactions with a focal species, including competitors [37,38], predators [39,40] and pathogens [41–43]. Warming temperatures can also benefit introduced species, exacerbating their negative effects on native flora and fauna [44].

#### (iii) Temporal mismatch between interacting species

Climate change may also create incongruence between the activity times of interacting species [45]. These phenological

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mismatches may occur when interacting species respond to different environmental cues (e.g. temperature versus photoperiod for winter emergence) that are not congruently influenced by climate change [46]. We consider this category to be distinct from the other two because the differences in activity times are not necessarily negative or positive impacts on the species that are interacting with the focal species.

## 3. Are there current extinctions due to climate change?

Our goal is to understand which proximate factors cause extinctions due to climate change. However, we first need to establish that such extinctions are presently occurring. Few global species extinctions are thought to have been caused by climate change. For example, only 20 of 864 species extinctions are considered by the International Union for Conservation of Nature (IUCN) [47] to potentially be the result of climate change, either wholly or in part (using the same search criteria as a recent review [9]), and the evidence linking them to climate change is typically very tenuous (see the electronic supplementary material, table S1). However, there is abundant evidence for local extinctions from contractions at the warm edges of species' ranges. A pattern of range shifts (generally polewards and upwards) has been documented in hundreds of species of plants and animals [48,49], and is one of the strongest signals of biotic change from global warming. These shifts result from two processes: cold-edge expansion and warm-edge contraction (see the electronic supplementary material, figure S1). Much has been written about cold-edge expansions [21,50], and these may be more common than warm-edge contractions [51]. Nevertheless, many warm-edge contractions have been documented [52–58], including large-scale review studies spanning hundreds of species [48,59]. These warm-edge populations are a logical place to look for the causes of climate-related extinctions, especially because they may already be at the limits of their climatic tolerances [60]. Importantly, this pattern of warm-edge contraction provides evidence that many local extinctions have already occurred as a result of climate change.

We generally assume that the proximate factors causing local extinction from climate change are associated with the death of individuals. However, others factors may be involved as well. These include emigration of individuals into adjacent localities, declines in recruitment, or a combination of these and other factors. The question of whether climate-related local extinctions occur through death, dispersal or other processes has received little attention (but see [61,62]), and represents another important but poorly explored area in climate-change research.

## 4. What causes extinction due to climate change? current evidence

Given that there are many different potential causes of extinction as a result of climate change, and given that many populations have already gone extinct (as evidenced by warm-edge range contractions), what proximate causes of climate-related extinction have actually been documented? We conducted a systematic review of the literature to address this question.

### (a) Causes of extinction: methods

We conducted three searches in the ISI Web of Science database, using the following keywords: (i) (('locally extinct' OR 'local extinction' OR 'extinc*') AND (caus*) AND ('climate change' OR 'global warming')); (ii) (('locally extinct' OR 'local extinction') AND ('climate change' OR 'global warming')); and (iii) (('extinc*' OR 'extirpat*') AND ('climate change' OR 'global warming' OR 'changing climate' OR 'global change')). The first two were conducted on 7 December 2011 and the third on 4 February 2012. Each search identified a partially overlapping set of studies (687 unique studies overall). We then reduced this to 136 studies which suggested that climate change is associated with local extinctions or declines (see the electronic supplementary material, appendix S1).

Among these 136 studies, we then identified those that reported an association between local extinction and climatic variables and that also identified a specific proximate cause for these extinctions (see the electronic supplementary material, appendix S1). The evidence linking these proximate causes to anthropogenic climate change varied considerably, but included studies integrating experimental and correlative results [23,63], and those that also accounted for factors unrelated to climate change [64]. Although we did not perform a separate, comprehensive search for all studies of climate-related declines, we also include studies of population declines that were connected to potential local extinctions as a second category of studies. Studies of declines should also be informative, given that the factors causing population declines may ultimately lead to extinctions [65]. All studies reported declines in abundance but some also considered declines in other parameters (e.g. fecundity). We also included studies of impacts from natural oscillations (such as the El Niño-Southern Oscillation, ENSO) as a third category of results.

### (b) Causes of extinction: results

#### (i) Proximate causes of local extinctions

Of 136 studies focusing on local extinctions associated with climate change (see the electronic supplementary material, appendix S1), only seven identified the proximate causes of these extinctions (table 1 and figure 1*a*). Surprisingly, none of the seven studies shows a straightforward relationship between local extinction and limited tolerances to high temperature. For example, for the two studies that relate extinctions most directly to changing temperatures, the proximate factor is related either to how temperature limits surface activity time during the breeding season [23] or to a complex relationship between extreme temperatures (both cold and hot), precipitation and physiology [25,63]. Most studies (four of seven) implicate species interactions as the proximate cause, especially decreases in food availability [35,64,66]. Many authors have predicted that altered species interactions may be an important cause of extinction resulting from climate change (e.g. [67,68]), and our results empirically support the importance of these interactions (relative to other factors) among documented cases of local extinction.

#### (ii) Proximate causes of population declines

Seven studies identified proximate causes of population declines (table 2). The frequency of different proximate causes is intriguingly similar to those for population extinctions (figure 1*a*,*b*). Specifically, species interactions are the

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**Table 1.** Studies documenting the proximate causes of local extinction due to anthropogenic climatic change.

| species | location | hypothesized proximate cause of local extinction | reference |
|---|---|---|---|
| American pika (*Ochotona princeps*) | Great Basin region, USA | limited tolerance to temperature extremes (both high and low) | [25,63] |
| planarian (*Crenobia alpina*) | Wales, UK | loss of prey as result of increasing stream temperatures | [35] |
| desert bighorn sheep (*Ovis canadensis*) | California, USA | decrease in precipitation leading to altered plant community (food) | [64] |
| checkerspot butterfly (*Euphydryas editha bayensis*) | San Francisco Bay area, CA, USA | increase in variability of precipitation corresponding with reduction of temporal overlap between larvae and host plants | [66] |
| fish (*Gobiodon* sp. A) | New Britain, Papua New Guinea | destruction of obligate coral habitat due to coral bleaching caused by increasing water temperatures | [36] |
| 48 lizard species (genus *Sceloporus*) | Mexico | increased maximum air temperature approaches physiological limit, seemingly causing decreased surface activity during the reproductive season | [23] |
| Adrar Mountain fish species | Mauritania | loss of water bodies due to drought | [30] |

proximate cause of declines in the majority of studies, with declines in food availability being the most common cause [69,71,72], along with disease [70]. Drying of aquatic habitats is the cause in one study [29]. Two studies show physiological tolerances to abiotic factors as responsible for declines, with the declines being due to desiccation stress in desert trees [28], and due to oxygen limitation at high temperatures in a fish [24]. However, we find again that no studies show a straightforward relationship between population declines and temperatures exceeding the critical thermal limits of physiological tolerance.

### (iii) Proximate causes of extinction due to 'natural' climatic oscillations

Among the 136 studies, four documented proximate causes of climate-change related extinctions that were associated with climatic oscillations (table 3). These oscillations may increase in frequency and severity due to anthropogenic impacts ([77], but see [78]). All four studies reinforce the importance of species interactions as the proximate cause of many extinctions attributable to climate change (figure 1*c*), including climate-related losses of food resources [73,75], loss of an algal symbiont ('coral bleaching'; [74]) and pathogen infection [76].

Two of the most widely discussed examples of climate-change related extinctions involve chytrid fungus in amphibians and coral bleaching (including many examples given above [36,70,74,75]). In both cases, local extinctions are strongly connected to natural climatic oscillations (e.g. [74]), but the links to anthropogenic climate change are still uncertain. For example, Pounds *et al*. [42] concluded that chytrid-related declines and extinctions in the frog genus *Atelopus* are related to anthropogenic warming, but Rohr & Raffel [70] subsequently suggested that chytrid spread in *Atelopus* was largely due to El Niño events. The link between anthropogenic climate change and local extinction of coral populations through bleaching also remains speculative [79]. For example, severe climate anomalies can cause bleaching and coral mortality [80], but bleaching itself does not always lead to mass mortality [81].

## (c) Proximate causes of extinction: synthesis

Our review of the proximate causes of population extinctions and declines due to climate change reveals three main results, which are concordant across the three categories of studies (extinctions, declines and climatic oscillations). First, very few studies have documented proximate factors (18 of 136). Second, a diversity of proximate causes are empirically supported. Third, changing interspecific interactions are the most commonly demonstrated causes of extinctions and declines (figure 1). Specifically, changes in biotic interactions leading to reduced food availability are the single most common proximate factor (figure 1). In contrast, limited physiological tolerances to high temperatures are supported only infrequently and indirectly (figure 1). Interestingly, the impacts of species interactions may be particularly difficult to document, inviting underestimation. However, we caution that these generalizations are based on few studies. For example, all three datasets (tables 1–3) are dominated by vertebrates, with only one plant study represented. Thus, the frequencies of documented proximate causes may change as the pool of studies becomes more taxonomically representative.

Finally, we note that we did not specifically address global species extinctions associated with climate change in our review. However, IUCN lists 20 species as extinct or extinct in the wild that potentially declined because of climate change (see the electronic supplementary material, table S1). Of these 20 species, seven are frogs that were possibly infected by chytrid fungus, which may be facilitated by climate change (see above). Four are snails, which may have become extinct as a result of drought. Two are freshwater fishes that lost their habitats because of drought. Among the six birds, two were also potentially affected by drought. The other four birds are island species possibly impacted by storms (the severity of which may be related to climate change), but these all had clear non-climatic threats. A similar pattern occurs in one island rodent species. In almost all cases, the links between extinction and anthropogenic climate change are speculative (but see [82]), which is why these cases were not included previously in our review. Intriguingly, none of the 20 is clearly related to

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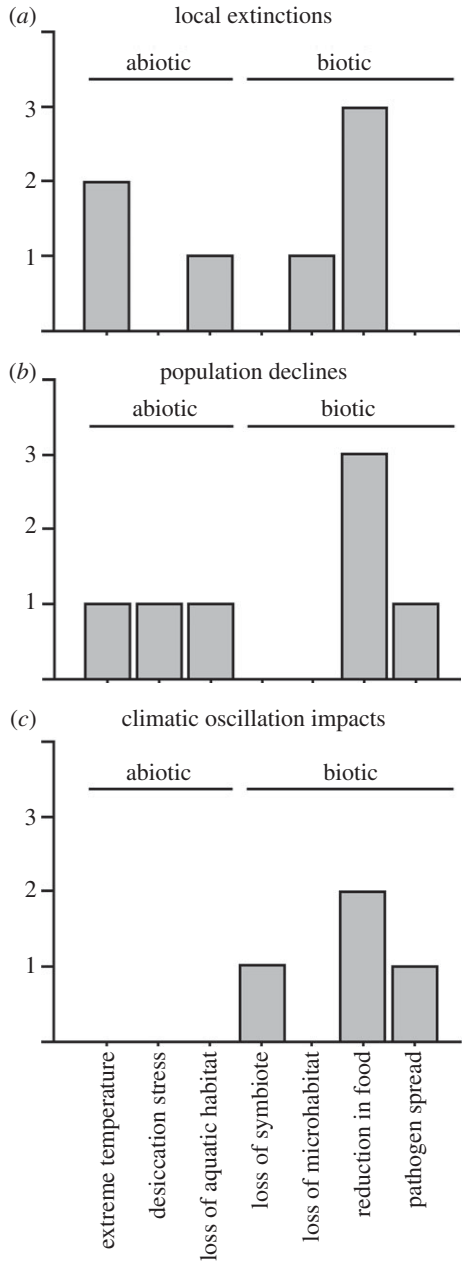


**Figure 1.** Summary of the frequency of different proximate causes of extinction due to climate change, among published studies. (*a*) 'local extinctions' refers to studies of local extinctions related to anthropogenic climate change (table 1), (*b*) 'population declines' refers to studies of declines in population abundance related to anthropogenic climate change (table 2), whereas (*c*) 'climatic oscillation impacts' refers to studies showing declines related to natural climatic oscillations (table 3) (but these oscillations may also be influenced by human factors, see relevant text). We note that there is some ambiguity in assigning some studies to a single, simple category.

limited tolerances to high temperatures (see the electronic supplementary material, table S1).

## 5. Approaches for finding the proximate causes of climate-related extinction

Our review demonstrates that disturbingly little is known about the proximate causes of extinctions due to recent climate change. How can this important gap be filled? Many approaches are possible, and we very briefly summarize two general frameworks that are beginning to be used. One focuses on individual species at multiple localities [23,25,63], the other on species assemblages at a particular locality [83–85]. These approaches are summarized graphically in the electronic supplementary material, figure S2.

Focusing on individual species (see the electronic supplementary material, figure S2), one must first document local extinctions or declines. To test whether populations have gone extinct, the present and past geographical ranges of the species can be compared. These analyses need not require surveying the entire species range, but could focus on a more limited series of transects (e.g. near the lowest latitudes and elevations, where ranges may already be limited by climatic factors [69,86]). The historical range can be determined from literature records and/or museum specimen localities [87]. These latter data are becoming increasingly available through online databases (e.g. GBIF; http://www.gbif.org/). Next, the species range (or select transects) should be resurveyed to document which populations are extant [23,56]. Evaluating whether populations persist is not trivial, and recent studies [56,88] have applied specialized approaches (e.g. occupancy modelling [89]). Furthermore, resurveys should account for false absences that may be misinterpreted as extinctions and for biases created by unequal sampling effort in space and time [87,90,91].

Documenting climate-related declines presents different challenges than documenting extinctions, given that most species lack data on population parameters over time. Some populations have been the focus of long-term monitoring, facilitating detailed studies of climate change impacts [86,92]. Large-scale databases on population dynamics through time are now becoming available. For example, the Global Population Dynamics Database [93] contains nearly 5000 time-series datasets. However, for many species, resurveying ranges to document local extinctions may be a necessary first step instead.

Given demonstrable local extinctions or declines, the next step is to determine whether these are related to large-scale trends in global climate change. Peery *et al.* [94] summarize six approaches that can be used to relate environmental factors to population declines [95]. These same approaches can be applied to connect global climate change and local extinctions. Relationships between changes in climate over time and population extinction versus persistence can be tested using GIS-based climatic data for relatively fine time scales (e.g. each month and year; PRISM; [96]). These analyses should preferably include data on other potential causes of local extinction not directly related to climate change, such as human habitat modification [64]. These analyses should help establish whether the observed local extinctions or declines are indeed due to climate change. If so, the next step is to understand their proximate causes.

Correlative analyses can be carried out to generate and test hypotheses about which proximate causes may be involved. Biophysical modelling [97] may be especially useful for these analyses, as it can incorporate many important factors, such as microclimate [98] and related variables (e.g. shade, wind speed, cloudiness, humidity) and relevant behavioural, ecological, demographic and physiological parameters [14,23]. Dissecting the specific aspects of climate that are most strongly associated with local extinctions may be important (e.g. is it warmer temperatures in the hottest part of the year, or the coldest?). Correlative studies can also test potential biotic factors, including the association between population extinctions or declines and the abundance of other species with negative impacts on the species in question (e.g. competitors, pathogens) or reductions in

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**Table 2.** Studies documenting the proximate causes of declines in abundance due to anthropogenic climatic change.

| species | location | hypothesized proximate cause of decline | reference |
|---|---|---|---|
| aloe tree (*Aloe dichotoma*) | Namib desert | desiccation stress owing to decreasing precipitation | [28] |
| four species of amphibians | Yellowstone National Park, USA | increasing temperature and decreasing precipitation cause a decline in habitat availability (pond drying) | [29] |
| plover (*Pluvialis apricaria*) | United Kingdom | high summer temperatures reduce abundance of craneflies (prey) | [69] |
| eelpout (*Zoarces viviparus*) | Baltic Sea | oxygen limitation at high temperatures | [24] |
| frogs (genus *Atelopus*) | Central and South America | climate change facilitates spread of pathogen (chytrid fungus) | [70] |
| grey jay (*Perisoreus canadensis*) | Ontario, Canada | warm autumns cause rotting in hoarded food, compromising overwinter survival and breeding success in the following year | [71] |
| Cassin's auklet (*Ptychoramphus aleuticus*) | California, USA | changes in upwelling timing and strength lower both adult survival and breeding success by changing food availability | [72] |

**Table 3.** Studies that report proximate causes of declines in abundance or fitness associated with El Niño-Southern Oscilliation (ENSO) events.

| species | location | hypothesized proximate cause of decline | reference |
|---|---|---|---|
| fig wasps (Hymenoptera: Agonidae) | Borneo | ENSO event causes obligate host trees (*Ficus* sp.) to fail to produce inflorescences, resulting in local extinction of pollinating wasps | [73] |
| corals | Panama and Ecuador | high sea surface temperatures cause bleaching and mortality | [74] |
| butterflyfish | Indian Ocean | climate-related loss of coral food source | [75] |
| toad (*Bufo boreas*) | Western USA | warming reduces water depth in ponds, which increases ultraviolet-B exposure of embryos, which in turn increases risk of fungal infection | [76] |

species necessary for persistence (e.g. prey, hosts). Two-species occupancy models [99] could be applied to test for the impacts of these and other types of interspecific interactions. Identifying the particular interactions that are responsible for climate-related extinctions may be challenging, given the diversity of interactions and species that may be involved. However, our results suggest that changing biotic interactions may be the most common proximate causes of climate-related extinction (figure 1).

Once potential factors are identified with correlative studies, these can be tested with mechanistic analyses. These could include experimental tests of physiological tolerances to relevant temperature and precipitation regimes [10,24,86,100], and laboratory and field tests of species interactions [39]. Transplant experiments that move individuals from extant populations into nearby localities where the species has recently gone extinct [100] may be particularly useful (for species in which this is practical). In many ways, experimental analyses can provide the strongest tests of the hypothesized causes of local extinctions. However, these should be informed by broader correlative studies. For example, simply testing the physiological tolerances of a species to extremely high temperatures may say little about the causes of climate-associated local extinction in that species if those extinctions are actually caused by warmer temperatures in winter or the spread of a competitor.

The second major approach (see the electronic supplementary material, figure S2) is to focus on species assemblages at single localities over time [83–85], rather than analysing multiple localities across the range of one or more species. Given data on species composition at different points in time, the local extinctions or declines of certain species can be tested for association with temporal changes in climate. These losses can then be related to specific biological traits (e.g. greater loss of species with temperature-cued flowering times versus those using photoperiod, or species for which the site is near their southern versus northern range limits [84]). These relationships can then point the way to more mechanistic and experimental studies.

## 6. Questions for future research

Understanding the proximate factors that cause climate-related extinctions should be an urgent priority for future research and should open the door to many additional applied and basic questions. Are there specific conservation and management strategies that can be matched to specific

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extinction causes? Are there phylogenetic trends or life-history correlates [20] of these factors that may allow researchers to predict which factors will be important in a species without having to conduct lengthy studies within that species? Do different factors influence the ability of niche models to accurately predict range shifts and extinctions due to climate change (e.g. physiological tolerances versus species interactions)? Can species adapt to some potential causes of extinction and not others?

## 7. Conclusions

Climate change is now recognized as a major threat to global biodiversity, and one that is already causing widespread local extinctions. However, the specific causes of these present and future extinctions are much less clear. Here, we have reviewed the presently available evidence for the proximate causes of extinction from climate change. Our review shows that only a handful of studies have focused specifically on these factors, and very few suggest a straightforward relationship between limited tolerance to high temperatures and local extinction. Instead, a diverse set of factors is implicated, including effects of precipitation, food abundance and mismatched timing with host species. Overall, we argue that understanding the proximate causes of extinction from climate change should be an urgent priority for future research. For example, it is hard to imagine truly effective strategies for species conservation that ignore these proximate causes. We also outline some general approaches that may be used to identify these causes. However, we make the important caveat that the relative importance of different proximate causes may change radically over the next 100 years as climate continues to change, and limited physiological tolerances to high temperatures may become the dominant cause of extinction. Nevertheless, our review suggests the disturbing possibility that there may be many extinctions due to other proximate causes long before physiological tolerances to high temperatures become predominant.

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California Department of Forestry and Fire Protection

# Emergency Fund
# Fire Suppression Expenditures

| Fiscal Year | Expenditures |
|---|---|
| 1979—1980 | $11,978,000 |
| 1980—1981 | $21,178,000 |
| 1981—1982 | $12,582,000 |
| 1982—1983 | $8,619,000 |
| 1983—1984 | $12,358,000 |
| 1984—1985 | $16,847,000 |
| 1985—1986 | $35,510,000 |
| 1986—1987 | $14,799,000 |
| 1987—1988 | $56,769,000 |
| 1988—1989 | $57,983,000 |
| 1989—1990 | $39,345,000 |
| 1990—1991 | $70,825,000 |
| 1991—1992 | $22,524,000 |
| 1992—1993 | $85,591,000 |
| 1993—1994 | $65,679,000 |
| 1994—1995 | $69,858,000 |
| 1995—1996 | $60.4 million |
| 1996—1997 | $107 million |
| 1997—1998 | $47.7 million |
| 1998—1999 | $43.8 million |
| 1999—2000 | $178.5 million |
| 2000—2001 | $114 million |
| 2001—2002 | $166 million |
| 2002—2003 | $135 million |
| 2003—2004 | $252 million |
| 2004—2005 | $170 million |
| 2005—2006 | $117 million |
| 2006—2007 | $206 million |
| 2007—2008 | $524 million |
| 2008—2009 | $499 million |
| 2009—2010 | $274+ million |
| 2010—2011 | $90.1 million |
| 2011—2012 | $140 million |
| 2012—2013 | $310 million |
| 2013—2014 | $242 million |
| 2014—2015 | $402 million |
| 2015—2016 | $608 million |
| 2016—2017 | $534 million |
| 2017—2018 | $773 million |
| 2018—2019* | $635 million (EST) |
| 2019—2020** | $ 91 million (EST) |

October 2019
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*E-fund expenditures for FY 2018-19 are estimates. Final numbers are pending.
**E-fund expenditures for FY 2019-20 are YTD estimates. Numbers are updated at the beginning of each month.

# INDEPENDENT EXTERNAL SPRINKLERS
# to protect your home during a wildfire

## From the California Chaparral Institute

We've been investigating external sprinklers for quite some time. The idea requires a paradigm shift for people because sprinklers have traditionally been for the protection of lives inside a structure. Now that we increasingly facing a different threat, wind-driven fire from the outside, we need to look at structure protection from a new perspective. Other countries outside of the United States, notably Australia and Canada, have employed external sprinklers in the wildland-urban-interface (WUI) with success.

**The basic idea is that <u>a wet house is nearly impossible to ignite</u>.**

**EXAMPLES**

The first time we encountered the idea was right after the 2003 Cedar Fire in San Diego County, California. The owners of a home in Wildcat Canyon were convinced the under-eave misters they installed allowed the structure to survive the wildfire. The rural canyon in which they lived was one of the hardest hit. The owners had turned on the gravity fed system supplied by a 5,000-gallon water tank just before they evacuated. When they returned, their home was one

of the few structures left standing in the canyon. The misters had soaked an area of about six feet wide all around the home. They wrote a full description of their experience. It is available here:
http://www.californiachaparral.org/images/Conniry_Story.pdf

The idea has been slowly catching on.

Another family in San Diego County built a more elaborate under-eave misting system that actually uses wind to help distribute the water. The builder, Dr. Joseph Mitchell, has a complete description of his system on his website here:
http://www.mbartek.com/weeds-info

Dr. Mitchell has also published a paper in the Fire Safety Journal than provides design and performance details on his mister system. It is available here:
http://www.californiachaparral.org/images/Mitchell_JW_Ex_Sprinklers_WEEDS_2006.pdf

A couple in Santa Barbara claimed their external sprinklers saved their home during the 2009 Jesusita Fire while they sheltered in place. Most of the homes around them burned. They were interviewed by a local news station:
https://youtu.be/g0PGC0YEjZY

During interviews after the 2017 Thomas Fire, we have encountered several people who were convinced that the external sprinklers they had installed played an important role in saving their homes. In fact, the National Fire Protection Association and Firewise USA are both beginning to produce educational materials about external sprinklers for people in the WUI. There is a sample of one of their handouts at the end of this summary paper.

**INSTALLERS**

There are a few start-up companies in the US that are promoting the idea. For example:

Roof Saver Sprinklers
www.roofsaversprinklers.com
waveGuard
https://www.waveguardco.com/

The larger, more established companies we are familiar with are either Canadian or Australian. However, in conversations with these companies, they indicated they had investigated marketing their systems in the states, but decided against it because of the tendency for Americans to file liability claims. Here is one of the bigger firms in Canada:
SPIEDR: https://www.spiedr.com/spiedr-structure-protection-sprinklers/

There are a multitude of videos available on YouTube describing external sprinkler systems. One of the best is a detailed explanation of an innovative, computer-controlled system from Australia:
https://youtu.be/y2z-sQfMHko

**RECOMMENDATIONS**

There's a lot of potential for these systems.

Unfortunately, when the idea of external sprinklers is brought up, many seem to misunderstand the concept and immediately cite power failures and water pressure as limiting factors. To function properly, external sprinklers must be independent. This means the water source needs to be a backyard pool, or as in the case of the family in Wildcat Canyon, a 5,000-gallon water tank. The water has to be either gravity fed or on an independent gas or diesel-powered pump. These systems can be turned on when the owner evacuates, or remotely by cell phone or other electronic device. Based on our own observations, we believe many of the homes that burned in eastern Ventura during the 2017 Thomas Fire could have been likely saved if they had properly designed external sprinkler systems protecting them.

Policy makers should consider requiring new homes built in the WUI have independent external sprinkler systems. Clusters of homes could be served by a single system. Where realistic, communities already built in very high fire hazard zones could be given 10 years to retrofit homes (singly or in group). Pre-disaster FEMA grants could be made available for the most vulnerable communities as they have been for the mountain towns of Big Bear and Idyllwild, California, to retrofit flammable building features.

For more on how to protect your home from wildfire, please visit our webpage at:
http://www.californiachaparral.org/bprotectingyourhome.html

WILDFIRE RESEARCH FACT SHEET

# EXTERIOR SPRINKLER SYSTEMS

Are exterior sprinkler systems an option for protecting a home during a wildfire, after residents have evacuated the property?

## Functionality and Installation

The function of an exterior sprinkler system is to minimize the opportunity for ignition by wetting the home and surrounding property. Sprinkler systems should be able to protect a home against the three basic wildfire exposures: wind-blown embers, radiant heat and direct flame contact.
Sprinklers systems can be mounted in one or more locations, including:

- The roof (Photo 1).
- Under the eave at the edge of the roof.
- On the property, in which case the sprinklers are directed at the home from multiple locations surrounding it.

Ember ignition of combustibles located on or near the home can result in a radiant and/or flame contact exposure (Photo 2). Water should reach all vulnerable areas for the system to have maximum effect both on and near the home (Photo 3).

**Photo 1.** Roof mounted sprinkler.

**Photo 2.** In order to be effective, external sprinklers must be able to wet all areas where ignition can occur, or be sufficiently effective in quenching embers that approach the home so they won't have enough energy to ignite combustible items.

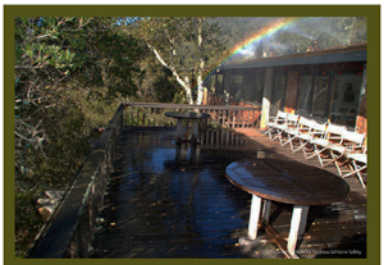

**Photo 3.** Roof-edge mounted sprinkler. Note these sprinklers did not deliver water in the near-home area. With this scenario, a sufficient number of wind-blown embers would have to be quenched in order to avoid ignition of the siding and decking in this zone, particularly at the deck-to-wall intersection.

## Potential Issues

Post-fire assessments have shown exterior sprinkler systems can be effective in helping a home survive a wildfire, but potential issues exist with their use. These issues include:

- The water supply should be adequate to deliver water, when needed, for the time embers could threaten a home. This period could be up to 8 hours.
    - Check with your local fire department if your sprinkler system uses water from a municipal supply; they may have suggestions to help minimize water consumption.
- The effectiveness of a sprinkler system is questionable when a neighboring home is burning, since this would result in an extended radiant heat and/or contact exposure to the home.
- These systems can be activated manually or by an automated device, such as a sensor that detects heat or flame, or by an SMS-enabled cell phone. The ability of these systems to activate based strictly on an ember exposure has not been determined. Since wind-blown embers can be transported for up to a mile from the flame front of a wildfire, this may be a limitation.
- The most threatening wildfires occur during high-wind events and the homeowner should consider how the distribution/transport of water droplets may be influenced by elevated wind speeds.

## Recommendations

Given the potential issues regarding performance, it's recommended that use be a supplement to, and not a replacement for, already proven mitigation strategies, such as the reduction of potential fuels throughout the home ignition zones, along with removal of roof and gutter debris, and use of noncombustible and fire/ember-ignition resistant building materials and installation design details.

Insurance Institute for Business & Home Safety

NFPA FIREWISE USA® RESIDENTS REDUCING WILDFIRE RISKS

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PG&E OUTAGES: Bay Area Power Outage Survival Guide

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# Power Outage Results In Multiple Crashes, Injuries At Santa Rosa Intersections

October 9, 2019 at 2:47 pm **Filed Under:** Car crashes, PG&E, Power Outage, public safety power shutoff

SANTA ROSA (CBS SF) — Widespread power outages in the North Bay have resulted in a number of auto accidents at intersections where traffic signals were not working, according to authorities.

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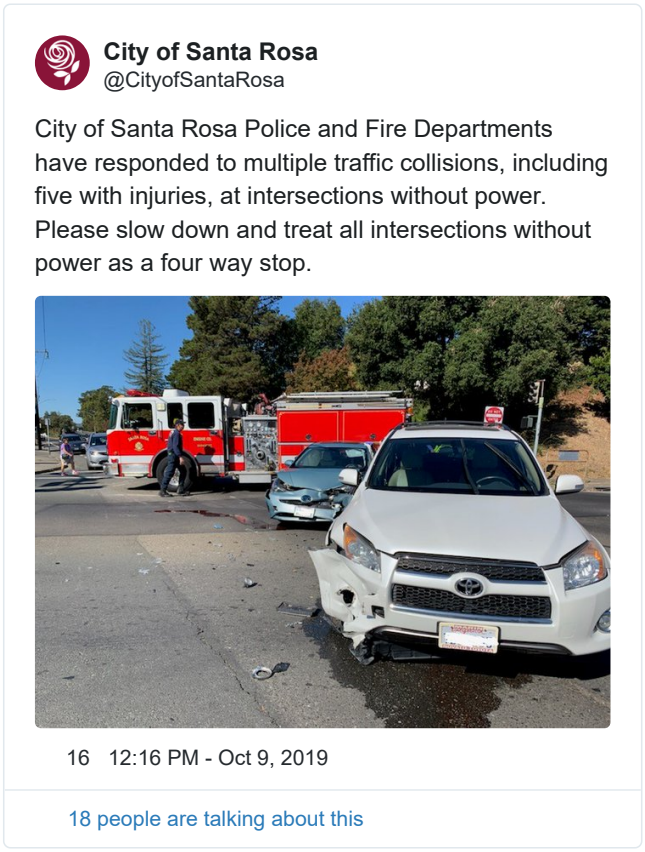
Delayed PG&E Power Shutdown Begins In East Bay, South Bay, Santa Cruz County

PG&E Confirms It Will Shut Off Power To Quarter Million Bay Area Customers

Bay Area Power Outage Survival Guide

The City of Santa Rosa said in a tweet on Wednesday that there have been "multiple" traffic collisions at intersections without power, including five crashes that resulted in injuries.

Drivers were urged to slow down and reminded to treat intersections without power as four-way stops.




PG&E has shut off power in parts of Sonoma, Solano, Marin and Napa counties as part of a Public Safety Power Shutoff, designed to prevent deadly wildfires during dangerous wind conditions Wednesday and Thursday.

Power shutdowns have been postponed until at least 8 p.m. for the East Bay, the South Bay and the Peninsula, according to officials.

The utility is currently under Chapter 11 bankruptcy protection after its power lines ignited several massive wildfires in Northern California since 2017. Victims of those fires have filed millions of dollars in damage lawsuits against the utility.

San Jose Residents Brace For Evening Power Outages, Nightmare Commute

Fire Crews Gain Upper Hand On San Bruno Mountain Brush Fire

UC Berkeley, Several Other Bay Area Schools Cancel Wednesday Classes

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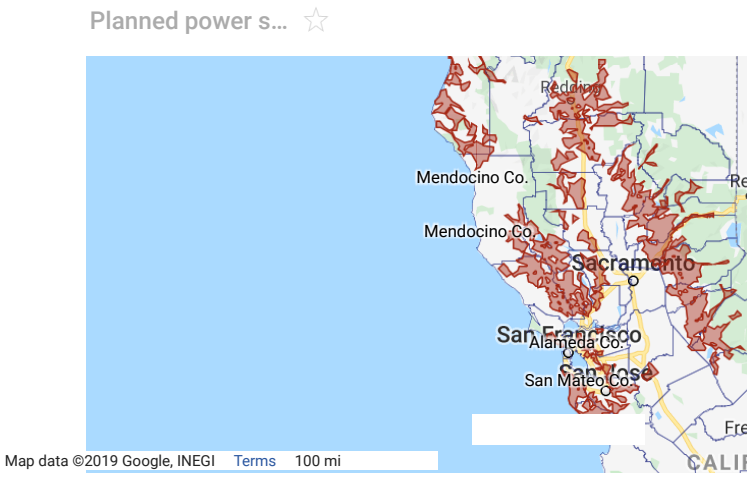
Power Outage Results In Multiple Crashes, Injuries At Santa Rosa Intersections

Newsom: Californians Should Be 'Outraged' Over PG&E Power Shutoffs




**ALSO READ:**

- **Bay Area Power Outage Survival Guide**
- Emergency Centers Activated Ahead Of Power Shutoffs
- PG&E Web Page On Power Outages Crashes From High User Volume
- Bay Area Schools Cancel Classes Amid Mass Power Outages

Comments

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# Population persistence in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of dispersal

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ABSTRACT

Linear infrastructures, one of several forms of land-use, are a major driver of biodiversity loss. Roads impact populations at many levels, with direct road mortality and barrier effect contributing to decreased population abundance, higher isolation and subdivision, and therefore to increased extinction risk. In this paper, we compared the effect of road mortality and of the barrier effect on population isolation, persistence and size, and assessed the interaction of these effects with dispersal. We used a spatially explicit, process-based model of population dynamics in landscapes fragmented by varying levels of road density. We modelled a barrier effect independently from road mortality by varying the probability with which individuals avoid crossing roads. Both road mortality and the barrier effect caused population isolation. While road mortality alone had stronger negative effects than the barrier effect without extra mortality, the latter also resulted in decreased population size. Yet, road avoidance could, in some cases, rescue populations from extinction. Populations with a large dispersal distance were more negatively affected as road mortality increased. However, when there was no road mortality they maintained larger sizes than populations with a short dispersal distance. Our results highlight the much higher relative importance of road mortality than the barrier effect for population size and persistence, and the importance of assessing relevant species traits for effective long-term transportation planning and conservation management. Our model can be used in species-specific situations and with real landscape configurations in applications such as conservation planning.

## 1. Introduction

The current biodiversity crisis is mainly driven by land-use change (Pereira et al., 2012; Maxwell et al., 2016). Roads, one of many forms of land-use, cause major impacts on populations. As the road network is predicted to strongly increase in the coming years (van der Ree et al., 2015), it is crucial to assess its impact on populations, in order to apply suitable mitigation measures, and improve conservation and road planning.

Roads cause habitat loss and fragmentation, and decrease habitat quality. Roads also cause direct mortality through wildlife collisions with vehicles, and act as a barrier to movement (van der Ree et al., 2015). These direct and indirect impacts of roads can contribute to population isolation and subdivision, to decreases in population abundance, and therefore can increase population extinction risk (van der Ree et al., 2015; Ascensão et al., 2016), although there are also positive effects for some species (e.g., see Rytwinski and Fahrig, 2012, 2013).

Species traits can also influence population-level responses to land-use change (Pereira and Daily, 2006), and should be considered when assessing the effects of roads. Specifically, dispersal has been identified as an important factor but its influence on population persistence is still not fully understood. For example, while the role of dispersal is beneficial in metapopulation models (e.g., Hanski, 1998), because more patches can be colonized if dispersal is large, in source-sink models or reaction-diffusion models (e.g., Skellam, 1951; Pulliam, 1988) dispersal affects populations negatively, because it can lead to colonization of habitats where population growth rates are negative (sink habitats) (Pereira and Borda-de-Água, 2013). Moreover, dispersal can be associated with increased mortality risk (e.g., Nathan et al., 2012), with some studies suggesting there is an optimal intermediate dispersal rate

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for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

The detrimental effect of dispersal in disturbed habitats is supported by several empirical studies (e.g., fragmented forests: Gibbs, 1998; Van Houtan et al., 2007). In the specific case of roads, a higher mobility has been related to negative effects of roads in mammal and bird species (Rytwinski and Fahrig, 2012). Furthermore, using a theoretical approach, Borda-de-Água et al. (2011) predicted that the larger the mean dispersal distance in a population, the larger would be the minimum area necessary for this population to persist in a landscape fragmented by roads.

In this paper we focus on dispersal movement as the process whereby individuals leave their initial location, move across a more or less suitable environment, and settle in a new location (Clobert et al., 2012; Matthysen, 2012). Our model does not currently include other types of movement (such as daily movements).

Direct road mortality introduces an additional source of mortality besides natural mortality. In addition, roads can also act as a barrier that does not introduce additional mortality, when the animals do not cross the roads. This barrier effect can be due to physical structures (such as fences) or to road avoidance behavior (e.g., Jaeger and Fahrig, 2004; Grilo et al., 2012), and for simplicity in this paper we refer to it simply as barrier effect. Although this can rescue individuals from road mortality to some extent, the negative consequences of habitat loss and fragmentation may be higher when such barrier effect is present, since road avoidance can lead to population isolation and to higher exposure to demographic and environmental stochasticity (Rytwinski and Fahrig, 2012; Ascensão et al., 2016). Moreover, the effects of road mortality and of road avoidance can be confounded and are still to be properly disentangled. For example, reduced population abundance near roads may be due to direct road mortality, or due to road avoidance behavior (e.g., Fahrig et al., 1995).

Although there is evidence that the effects of roads on population abundance are in general negative (Rytwinski and Fahrig, 2015), the impact of roads on population persistence has not been so commonly addressed (but see, for example Borda-de-Água et al., 2014 and Ceia-Hasse et al., 2017).

The key issue addressed in this paper was to disentangle the influence of an additional source of mortality (direct road mortality) versus the influence of a barrier effect to movement that does not introduce such additional mortality on population isolation, persistence and size, as well as the influence of dispersal, in fragmented landscapes. We addressed this using roads. We use a spatially explicit, process-based model of population dynamics. Our questions were: (1) What is the importance of road mortality versus isolation, for population persistence and size in landscapes fragmented by roads?; (2) How does dispersal influence the size and the persistence of populations under varying levels of road mortality and of a barrier effect?

## 2. Materials and methods

We used an individual-based toy model of population dynamics to perform a theoretical study on the effects of road mortality, barrier effect and dispersal on population isolation, size and persistence of a virtual species. Our study is not based on any empirical data and thus is more appropriately considered under the virtual ecology rationale (e.g., Grimm, 1999; Zurell et al., 2010).

### 2.1. Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Grimm et al., 2006, 2010). The model was implemented as an ANSI C++ program, which can be downloaded from https://github.com/anaceiahasse/landsim.

#### 2.1.1. Purpose

The purpose of the model is to simulate population dynamics in fragmented landscapes. Specifically, in this study, the model simulated population dynamics in landscapes fragmented by roads, with special emphasis on the effects of road mortality, of a barrier effect without mortality, and on the influence of dispersal distance.

#### 2.1.2. Entities, state variables, and scales

The entities of the model are the landscape and the individuals, i.e., the model keeps track of the features of the landscape and of the female population (the model only considers female individuals for simplicity).

The landscape is a two-dimensional grid of $N$ x $N$ square cells with reflecting boundaries. An alternative approach to deal with edge effects would have been to consider periodic boundary conditions (i.e., torus geometry) instead of reflecting boundaries. However, given a dispersal step size of only one cell and the large size of the grid, both approaches can lead to similar outcomes. Each cell of the landscape is assigned to one of $n$ possible types with values varying between 0 and 1. In the present case, each cell belongs to one of two possible types, "high-quality" habitat (non-road) or "road", with values of "1″ and "0″, respectively. We generated several landscapes with different proportions of road cells, where roads were placed perpendicularly to one another (Fig. 1, Table 1). We used simple hypothetical regular road networks because our main objective was to disentangle the effects of sink mortality versus those of a barrier effect that does not introduce additional mortality. Sink mortality here corresponds to road mortality, and it is the probability that an individual dies when crossing a road (see Section 2.1.7.3 below). Our goal was to derive general principles that can be the basis to understanding and model more specific or complex cases.

Individuals are characterized by the following state variables: age, developmental stage (juvenile or adult), position in the landscape; and by the following attributes: fecundity, age at first breeding, natural survival probability, home range size, dispersal distance, road mortality probability, road avoidance probability (Table 1).

#### 2.1.3. Process overview and scheduling

Each simulation time step consists of the following sequential events (Fig. 2, Table 1): reproduction; natural mortality; dispersal of juveniles; juvenile density-dependent mortality. Section 2.1.7 describes the submodels implementing these processes. Juveniles that establish a home range are inserted into the adult population at the end of each simulation time step, thereby updating population size and landscape cell availability for the following time step. At the beginning of each simulation time step, the age of each individual is updated (increased by 1), and the sequential steps listed above ensue.

#### 2.1.4. Design concepts

*2.1.4.1. Basic principles.* Roads can contribute to population isolation, decreased size and increased extinction risk through direct mortality and barrier effects (e.g., van der Ree et al., 2015; Ascensão et al., 2016). Dispersal can also influence how roads impact populations (e.g., Borda-de-Água et al., 2011; Rytwinski and Fahrig, 2012). The model allows assessing the relative importance of these factors for population isolation, persistence and size, which is not yet fully understood.

*2.1.4.2. Emergence.* Population dynamics emerges from the model (i.e. from the set of rules defined, parameter values used and landscape configuration).

*2.1.4.3. Adaptation.* Juveniles choose the direction in which they disperse according to cell type (road versus high-quality habitat cell) and occupancy (they may avoid dispersing into road cells with a given probability and they do not disperse to occupied cells, respectively).

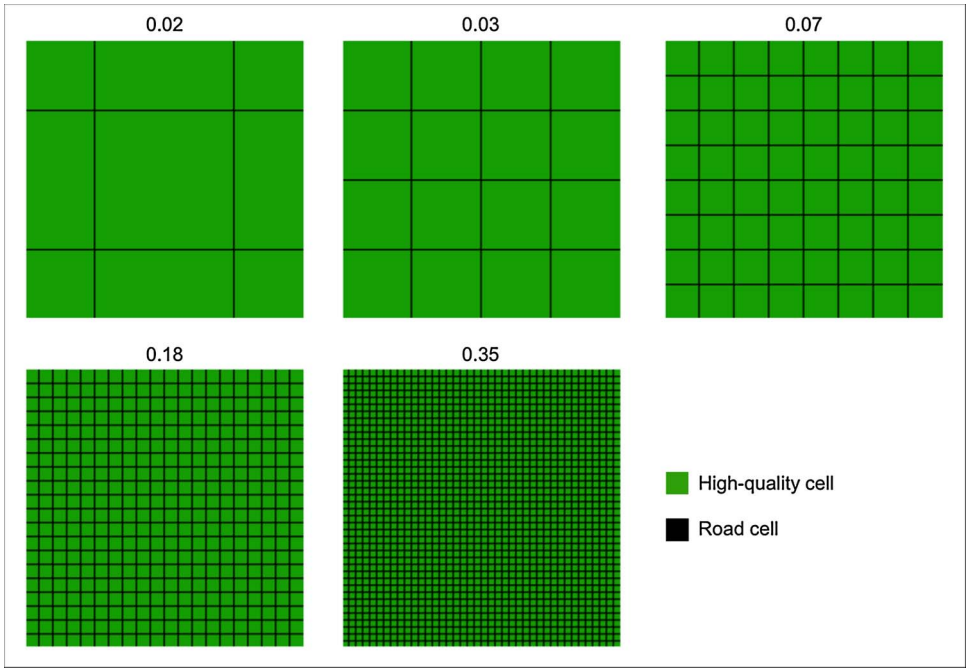


**Fig. 1.** Landscape configurations used in simulations. Each landscape is a grid of 200 × 200 cells composed of high-quality habitat cells, and road cells. Numbers on top of each panel indicate the proportion of road cells in each landscape.

**Table 1**
Model parameters and values used in the simulations.

| Parameter | Value | |
|---|---|---|
| | 1st set of simulations | 2nd set of simulations |
| Landscape size ($N$ x $N$) | 200 × 200 cells | |
| Initial population size | 10 individuals | |
| Number of replicates | 100 | |
| Number of time steps | 1000 | |
| Fecundity ($b_i$) | 2 | |
| Survival probability ($s$) | 0.4 | |
| Dispersal distance ($d$) | 5 or 50 cells | |
| Road mortality, Road avoidance ($m_{RM}$, $p_{RA}$) | (0.0, 0.0); (0.0, 1.0); (1.0, 0.0) | varied from 0 to 1 in steps of 0.1 |
| Proportion of road cells in the landscape | 0.02, 0.03, 0.07, 0.18, 0.35 | 0.07, 0.35 |

*2.1.4.4. Sensing.* During dispersal, juveniles evaluate cell type (road versus non-road cell) and occupancy.

*2.1.4.5. Interaction.* Juveniles do not disperse through cells that are already occupied.

*2.1.4.6. Stochasticity.* Stochasticity was incorporated in several processes (reproduction, natural mortality, dispersal of juveniles); see Section 2.1.7 for details.

*2.1.4.7. Observation.* For each model run, we recorded population size at the end of each simulation and averaged population size across replicates. We calculated the probability of extinction as the proportion of replicates in which populations went extinct before the end of the simulation.

*2.1.5. Initialization*

The model starts by settling an initial population of females at breeding age in the landscape. After the initial population is created, each simulation time step consists of the events described in Section 2.1.7 (Submodels). In all simulations, the initial population size was 10 individuals, set at random in the landscape. See Table 1 for the remaining parameter values used in the simulations and Fig. 3 for a representation of the settlement of the initial population in the landscape and of the colonization of the landscape.

*2.1.6. Input data*

The model does not import data of driving environmental variables.

*2.1.7. Submodels*

*2.1.7.1. Reproduction.* Females reproduce after one year and once they have established their home range. The number of female juveniles that a breeding female produces follows a Poisson distribution with mean equal to its fecundity $b_i$.

*2.1.7.2. Natural mortality.* Adults and juveniles die with probability (1 - $s$). When an individual dies it is removed from the population and its home range cell is made available for dispersing individuals.

*2.1.7.3. Dispersal of juveniles.* In our model adults do not move, and do not get killed by direct road mortality. Only juveniles disperse. Each juvenile disperses a fixed number of cells from its mother cell. A dispersal step is always to one of the four neighboring cells (von Neumann neighborhood), and is composed of the following events (Fig. 2b): (1) the individual evaluates whether its four neighboring cells are occupied or free, and does not disperse to occupied cells; (2) the individual evaluates whether the free neighboring cells correspond to roads or not, and can avoid dispersing through road cells with probability $p_{RA}$; (3) if the individual disperses through a road cell, sink dispersal mortality (road mortality) is applied with probability $m_{RM}$. The dispersal process is not stopped when the individual finds a first suitable empty cell; instead it continues until the individual either dies (due to road mortality), or disperses over his dispersal distance, $d$. An individual is allowed to move back to a cell it has previously visited. Therefore, two neighboring unoccupied cells are sufficient for an individual to survive over any number of dispersal steps. Moreover, each juvenile disperses from its mother cell, but given natural mortality that cell may be freed, and in that case it can be occupied by a juvenile. The default probability of dispersing to any neighboring cell is 1. However, if all four neighboring cells are occupied, and since

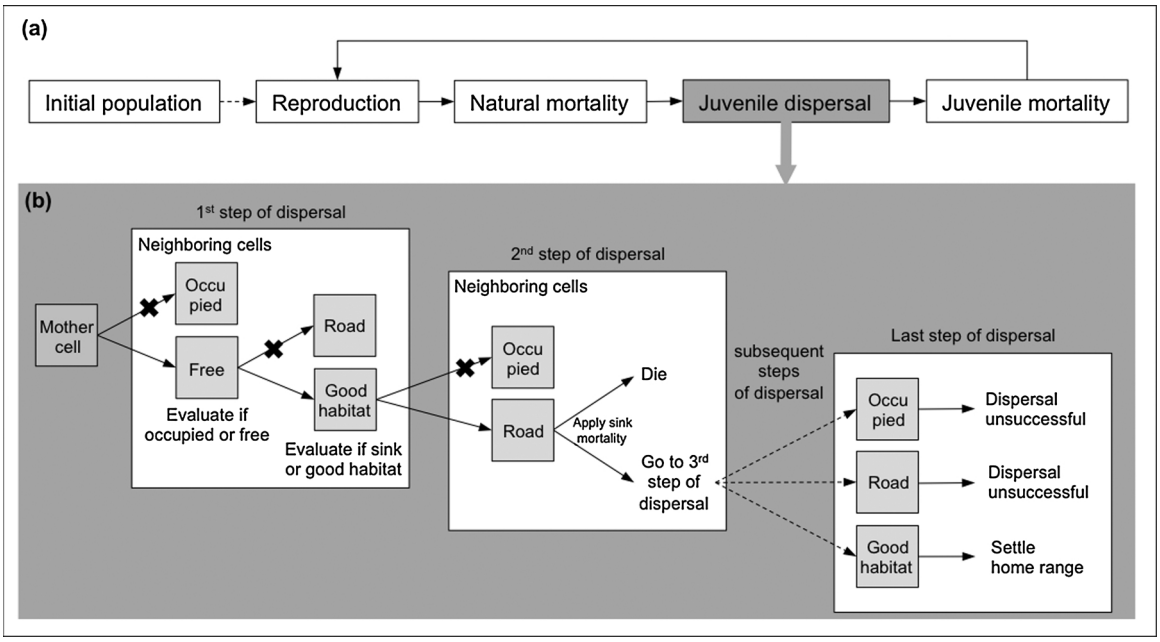


**Fig. 2.** Scheme of the model. (a) Schematic representation of the complete model simulation steps. (b) Schematic representation of juvenile dispersal. The x in (b) indicate that the individual does not disperse to occupied cells, and that it will disperse to a good habitat cell over a road cell.

individuals do not disperse to occupied cells, then the individual cannot move and dispersal is unsuccessful. If the cell in which the individual is at the end of dispersal is a road, dispersal is also unsuccessful. If dispersal is successful, the individual can settle a home range. In this study, we set the home range size to one cell and only one individual can establish its home range in each cell.

*2.1.7.4. Juvenile density-dependent mortality*. Following unsuccessful

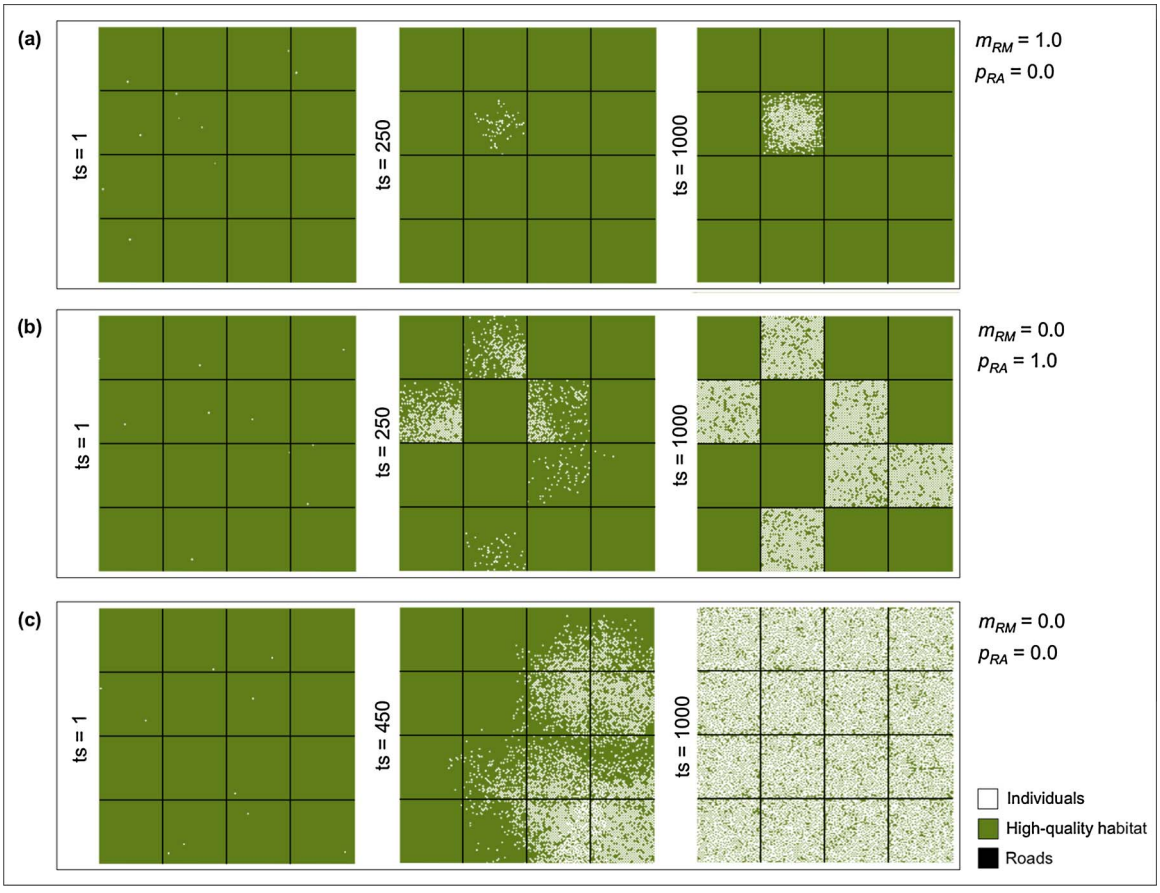


**Fig. 3.** Representation of the colonization of the landscape by a population under different combinations of values of road mortality probability ($m_{RM}$) and of road avoidance probability ($p_{RA}$), in different time steps (ts) of a model run. In the example shown, the dispersal distance is set to 50 cells (i.e. large dispersal) and the proportion of road cells in the landscape is 0.03.

dispersal, juveniles that did not establish their home range are removed from the population.

### 2.2. Simulations

We created five landscapes of 200 × 200 cells with perpendicular roads, each with a different proportion of road cells (Fig. 1, Table 1). We used two dispersal distances: short (5 cells), and large (50 cells), the latter of which we deemed reasonable considering the total size of the grid (40,000 cells). We modelled a barrier effect independently from sink mortality by varying the probability with which individuals do not cross roads while dispersing.

We performed two sets of simulations. In the first set of simulations, we assessed the effect of different extreme scenarios of road mortality and of road avoidance in landscapes with different proportions of road cells: (i) road mortality probability was one and there was no road avoidance; (ii) road avoidance probability was one and there was no road mortality; (iii) road mortality and road avoidance probabilities were both zero, for each dispersal distance and each road density. To assess the combined effects of road mortality and of road avoidance, in the second set of simulations we varied road mortality and road avoidance probabilities both at the same time independently from 0 to 1 in steps of 0.1 (i.e., using all combinations possible), for each dispersal distance (Table 1).

In all simulations, we used fixed values of the remaining parameters (Table 1), simulating the dynamics of hypothetical animal populations in hypothetical landscapes, because our main objective was to obtain general predictions on the differential effects of road mortality versus a barrier effect that did not introduce additional mortality (due to road avoidance behavior or physical structures such as fences), under different levels of dispersal.

We ran each simulation for 1000 time steps, to ensure that population size did not vary by more than 10% between consecutive simulation time steps, for at least the last 10 simulation time steps, and ran 100 replicates for each combination of values of parameters (Table 1).

Our computer program was extensively debugged, thus we are confident that the program is reproducing accurately the intended model. Being an individual-based model computer simulation, we performed our simulations under a set of assumptions that we deemed reasonable, and we tested them for a wide range of parameter values, obtaining the expected results.

Our model takes as input the model parameters and a two-dimensional matrix with the landscape. It produces a file containing the location of the home range of each adult in the landscape at each time step, and the population age structure at each time step. To apply the model to other species and landscape configurations, users can choose the values of the parameters specific to the species or population of interest, and a matrix with the desired landscape configuration.

## 3. Results

In our simulations, isolation occurred due to road mortality or to road avoidance (Fig. 3). With complete road mortality and no avoidance (Fig. 3a), or with complete avoidance and no road mortality (Fig. 3b), the landscape was only partially occupied. In contrast, when there was no mortality and no avoidance (Fig. 3c), the whole landscape was occupied.

When there was no road mortality and no road avoidance, the probability of extinction was higher and the population size was smaller at higher road densities, suggesting an effect due to habitat loss (Fig. 4). Nevertheless, with no road mortality and no road avoidance, the probability of extinction was zero or close to zero, even with high road density (Fig. 4a); and the population size was considerably larger than with either complete road avoidance, or complete road mortality (Fig. 4b). These results suggest that in such cases there was an effect of road avoidance or of road mortality, respectively.

The probability of extinction was higher and the population size was smaller when there was road mortality alone, than when there was road avoidance alone, except at the highest road density (Fig. 4). However, population size was much smaller at all road densities when there was road avoidance than in the case with no road avoidance and no road mortality (Fig. 4b).

When assessing the combined effects of road mortality and of road avoidance for different dispersal distances at the highest road density, the probability of extinction increased and the population size decreased with increasing road mortality (horizontal lines in Fig. 5). For a constant value of road mortality (vertical lines in Fig. 5), probability of extinction decreased and population size increased with increasing road avoidance. However, at this road density, the good habitat patches delimited by roads were small (16 cells), and populations went extinct when road avoidance was complete, even without road mortality.

The role of dispersal varied with road mortality. The probability of extinction increased and the population size decreased much faster with increasing road mortality for the large than for the short dispersal distance. However, when there was no road mortality, the probability of extinction was higher (Fig. 5a) and the population size was smaller (Fig. 5b) for the short dispersal distance.

Similar patterns were observed when assessing these effects at a lower road density (proportion of road cells in the landscape = 0.07; Fig. S1 in Appendix). However, they were less obvious than in the case of high road density, especially for the short dispersal distance: the probability of extinction was low, and the population sizes varied less. Nevertheless, population size strongly decreased with complete road avoidance, or with complete road mortality, for both dispersal distances, as in the case of high road density (Fig. 5).

Note that for the short dispersal distance and also for most of the large dispersal distance simulations in Fig. S1, while the probability of population extinction is close to zero, the population size is low, both when road mortality is one, and when road avoidance is one. This is because many individuals die on roads (when road mortality is one), or the population can only occupy part of the landscape (when road avoidance is one).

## 4. Discussion

Our results allow to make inferences about the differential effects of sink mortality versus those of a barrier effect without additional mortality, and the role of dispersal, on population persistence, isolation and size, which were the goals of this study. While habitat amount was kept constant when road mortality probability and road avoidance probability were varied with a same road density, it should nevertheless be taken into account that by generating landscapes with habitats and roads as grid cells, and by using a regular road network pattern, landscapes with higher road densities have lower total habitat amount and smaller habitat patches. In this sense, there were three effects present (i.e., road mortality, road avoidance, and habitat amount change).

### 4.1. Importance of road mortality versus a barrier effect without mortality for population persistence and size

Road mortality alone had a stronger negative effect on the probability of persistence and on population size than road avoidance alone. Road avoidance could also in some cases rescue populations under low to moderate road mortality from extinction, as suggested by other authors, since road avoidance decreases the probability that individuals cross roads, therefore reducing mortality caused by collision with vehicles (Jaeger and Fahrig, 2004; Rytwinski and Fahrig, 2013). Previous studies also suggest that the genetic effects of road mortality are stronger than those of the barrier effect without road mortality (e.g., Jackson and Fahrig, 2011; Ascensão et al., 2013).

In our simulations, population isolation occurred both when there was road mortality, or when there was a barrier effect without

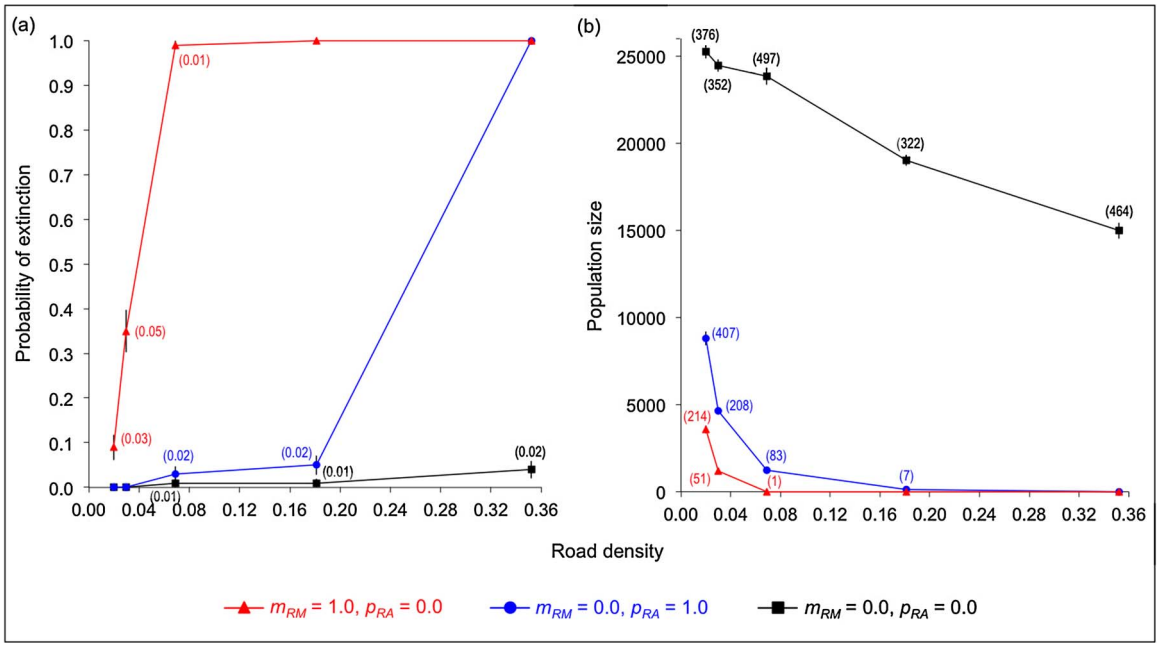


**Fig. 4.** Probability of population extinction (a) and population size (b) for the different proportions of road cells in the landscape, for different combinations of values of road mortality probability ($m_{RM}$) and of road avoidance probability ($p_{RA}$). Results shown are for the large dispersal distance (50 cells). Error bars correspond to the standard error of the mean, whose values are indicated in brackets (when different from zero).

additional mortality. Populations persisted even when road avoidance was very high, provided that the road mortality was low to moderate. Only complete road avoidance led populations to extinction, when road density was the highest. In those cases, individuals were isolated within the small patches of good habitat that were bounded by roads, and the resulting small populations exhibited an increased extinction risk due to demographic stochasticity (Lande, 1993).

Habitat fragmentation impairs species persistence and ecosystem functions. Moreover, the several effects of fragmentation are interlinked and can operate over long time scales (Haddad et al., 2015). In our analysis, population sizes were negatively affected when road avoidance was complete regardless of the road density, even if there was no road mortality. Population sizes were much smaller when compared to the cases with no road avoidance (and no road mortality). This may influence population persistence in the long-term, especially if other factors of disturbance come into play. For example, we did not vary habitat quality (all non-road cells had maximum habitat quality), because our aim was to obtain general predictions on the differential effects of road mortality versus those of a barrier effect without mortality. However, habitat quality can influence how roads affect populations (e.g., Grilo et al., 2014) and therefore the habitat quality of the non-road cells could be varied in more detailed studies, for example by including species-specific information on habitat preferences.

Moreover, although not included explicitly in our analysis, traffic volume is also important to consider when assessing the effects of roads on populations and in landscape connectivity studies, since traffic intensity may influence both road mortality and road avoidance, and thus population persistence (Jaeger et al., 2006; Jaeger, 2007; Charry and Jones, 2009; van Langevelde and Jaarsma, 2009; van Strien and Grêt-Regamey, 2016). Several studies suggest that road mortality may be higher at intermediate traffic volumes than high traffic volumes, because at higher traffic volumes road avoidance will be higher for many species (e.g., Seiler 2005; Grilo et al., 2015).

However, the focus of our analysis was on comparing the effects of road mortality vs. those of a barrier that does not introduce additional mortality, which can be due to road avoidance behavior but also due to physical structures such as fences (e.g., Jaeger and Fahrig, 2004; Grilo et al., 2012). Hence we modeled these directly as the probability of an individual dying on a road while crossing it, and the probability of an individual not crossing a road, regardless of the cause (e.g., road surface avoidance behavior, road avoidance due to traffic, fences), and therefore we did not consider traffic volume explicitly.

Additionally, while in our simulations individuals only evaluated their immediate neighboring cells in each step of dispersal, some species avoid roads from a distance (e.g., Jaeger et al., 2005), which may exacerbate the effects of habitat loss and fragmentation. Including microevolution in our individual-based model, which is fundamental to capture the response of organisms to changing conditions (Grimm and Berger, 2016), would also allow analysing eco-evolutionary responses to fragmentation (Haddad et al., 2015).

### 4.2. *Influence of dispersal distance on population persistence and size*

The role of dispersal distance varied depending on the values of road mortality. In fragmented landscapes, as was the case in all our simulations since roads were always present, populations with a larger dispersal distance showed a lower probability of extinction and maintained larger sizes, provided an additional source of mortality due to roads was not present. However, a large dispersal distance was detrimental for population size and persistence as road mortality increased.

We used fixed dispersal distances in our simulations. However, dispersal distance is usually stochastic (e.g., Nathan et al., 2012), and therefore it would not only be interesting but also add realism to the model by implementing dispersal kernels to determine dispersal distances (e.g., Austerlitz et al., 2004; Chipperfield et al., 2011), instead of using fixed dispersal distances.

Furthermore, in our simulations, dispersing individuals only evaluated their immediate four neighboring cells in each dispersal step, which can be considered as a biased random walk (e.g., Turchin 1998). While this has been a common choice to model movement with an orientation component (e.g., Börger et al., 2008), expanding the perceptive range of dispersing individuals would increase the realism and facilitate the transferability of the model to concrete situations.

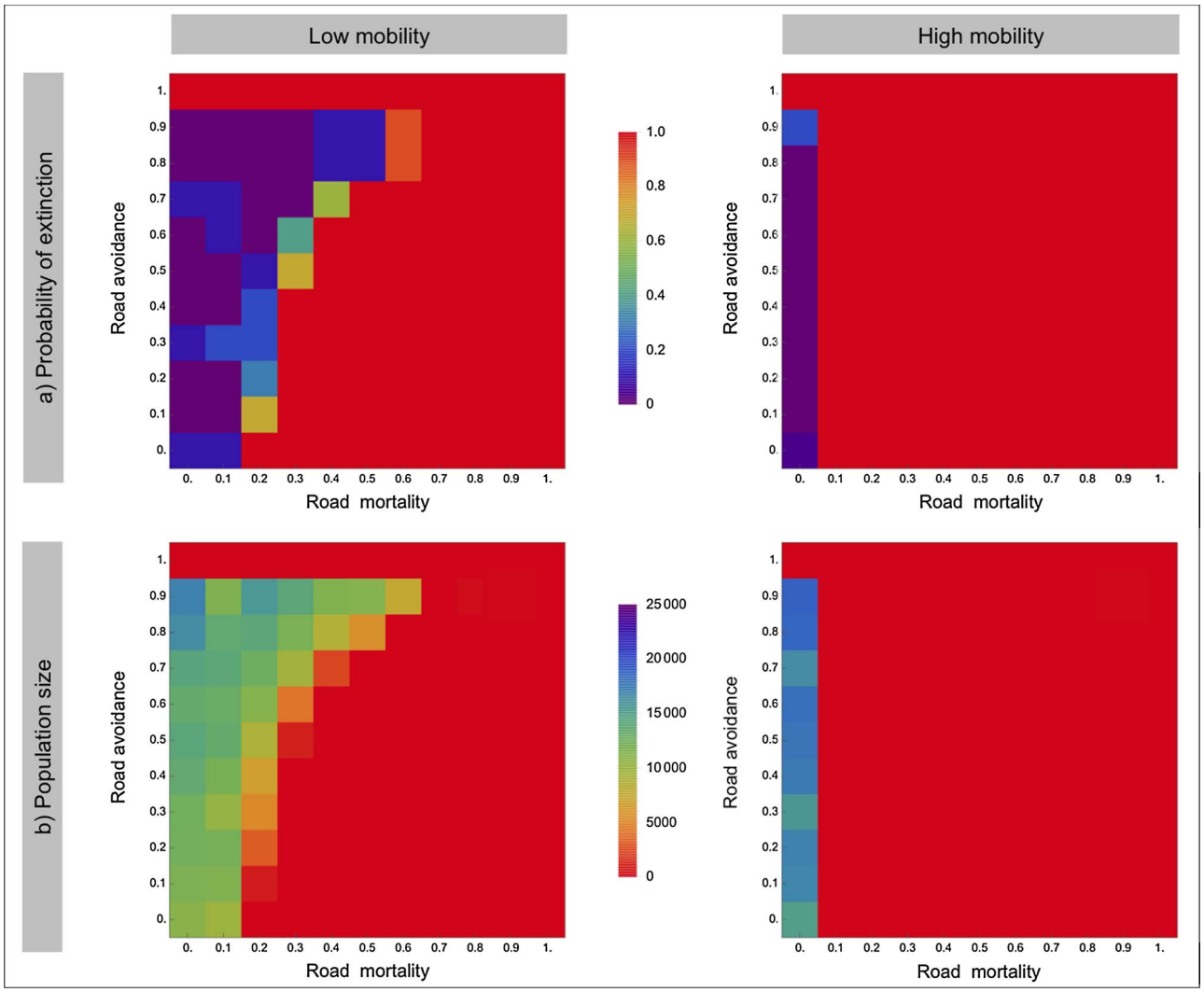


**Fig. 5.** Probability of population extinction (a) and population size (b) as a function of road mortality and road avoidance, for different dispersal distances (Low mobility = 5 cells; High mobility = 50 cells) in the landscape with the highest proportion of road cells in the landscape (0.35).

### 4.3. Limitations

The type of movement (juvenile dispersal) considered in our paper can have a large influence on individual fitness and population structure (Matthysen, 2012). However, our model does not currently include other types of movement (such as daily movements), and thus adults do not get killed due to road mortality. This is a simplification, because in real contexts animals will encounter roads during other types of movement as well. Therefore, it would be important to include such types of movement in the analysis.

Furthermore, in our model each juvenile disperses over a fixed number of cells, which implies that individuals may end their dispersal movement on a road (or right of way). This could correspond to situations where there are no other options for dispersal, e.g., all neighboring areas already occupied or corresponding to unsuitable habitat, but it should be considered as a simplification of real cases.

We used two dispersal distances in our simulations because we wanted to ensure that we were comparing the roles of contrasting dispersal distances, i.e., a short vs. a large dispersal distance. Including a wider range of dispersal distances could help further understand the role of dispersal in these fragmented landscapes, as some studies suggest there is an optimal intermediate dispersal rate for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

We used a virtual species and simple hypothetical regular road networks because our main goal was to disentangle the effects of road mortality versus those of a barrier effect without such mortality. However, this implies that our results hold for the virtual species in the regular road network used.

### 4.4. Conclusions and future research directions

Our results highlight the much higher relative importance of road mortality than the barrier effect (without road mortality), and of assessing relevant species traits such as dispersal distance. We emphasize three results of our study: first, that even though population persistence was not impaired when road avoidance was complete (except when suitable habitat patches became too small to sustain viable populations), population size was considerably decreased, which is important to consider in long-term conservation management; secondly, that a large dispersal distance is not necessarily always detrimental for population size and persistence in fragmented landscapes if mortality in unsuitable habitats is low, which calls for further investigation; and thirdly, that population isolation occurred in extreme cases (i.e., complete road mortality or a complete barrier effect without road mortality). These may be especially important for species expected (Rytwinski and Fahrig, 2013) or observed (e.g., some snakes and turtles; Shepard et al., 2008) to avoid roads, and for species for which road avoidance increases with increasing traffic volume (e.g., carnivores and

ungulates; Dyer et al., 2002; Alexander et al., 2005; Leblond et al., 2013).

Finally, our model can stimulate other studies, either theoretical or empirical. Our results hold for the virtual species in the regular road network used, but our model can be applied to species-specific situations, by using the specific trait values of the species or population of interest. Information on model parameter values (initial population size, fecundity, age at first breeding, survival probability, home range size, dispersal distance, road mortality, or road avoidance) can be obtained from published databases, individual studies, or derived from related or ecologically similar species, and using allometric relationships (e.g., Jones et al., 2009; Borda-de-Água et al., 2014; Salguero-Gómez et al., 2016; Ceia-Hasse et al., 2017). For example, data on population density can be used to determine the initial population size. Data availability is usually higher for vertebrates and within these for mammals, followed by birds. This is also true for data on road mortality, and especially on road avoidance behavior, for which species-specific information is lacking for many species (Rytwinski and Fahrig, 2012).

Furthermore, although we used only simple hypothetical regular road networks in our simulations, the modelled landscape can represent real landscapes with real road configurations, and can hence also be used to evaluate the impact of different mitigation options for increasing population persistence, in environmental impact assessments, and for conservation planning.

## Acknowledgments

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.01.021.

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Los Angeles Times

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# PG&E power outages bring darkness, stress and debt to California's poor and elderly

Michele Newton, left, and her daughter, Brenna Delwisch, have evacuated to a hotel at their own expense because Newton requires electricity to run a breathing machine at night. (Anita Chabria / Los Angeles Times)

By ANITA CHABRIA, TARYN LUNA

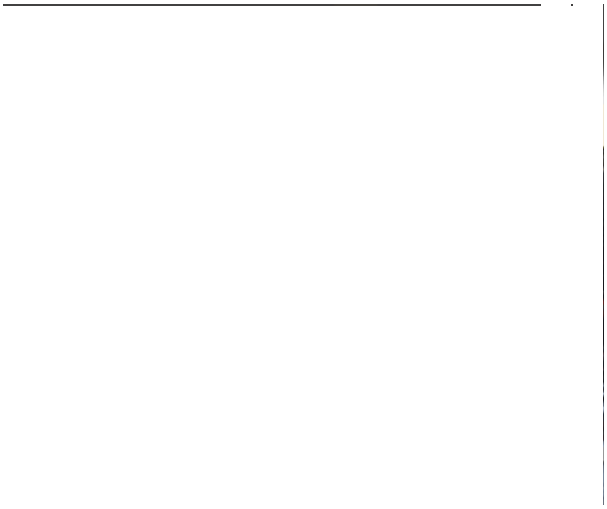
OCT. 11, 2019
11:21 AM

CLEARLAKE, Calif. — When PG&E cut power to her family's remote Northern California ranch just after midnight Tuesday, Brenna Delwisch fought to stay awake.

She was afraid if she slept, her mom would die.

A few years ago, her mother, Michele Newton, suffered a stroke and an aortic dissection, an explosion of heart arteries that can be fatal. Ever since, Newton has been afflicted with severe sleep apnea. At night, she wears a continuous positive airway pressure machine that keeps her breathing normally.

Without it, said Delwisch, "it's like [her] chest is arguing with whether to breathe or not. It looks like a struggle."



Delwisch, 33, watched that struggle, until she simply couldn't stay awake any longer. Around 5 a.m., exhausted from anxiety, she gave up.

"I am not vigilant enough anymore," she told Newton, a single mom who worked at gas stations and restaurants to raise her two kids. "You have to wake up."

Delwisch and Newton are among the 65,000 people in Lake County, one of the most impoverished in the state, who are learning by trial what happens when utilities cut power to people living on the edge.

This week, as Pacific Gas & Electric Co. shut off electricity to hundreds of thousands to reduce wildfire risks, many Lake County residents discovered they weren't ready, despite warnings that the cuts were coming. There were too many loose ends in their often complicated and precarious lives that hadn't been accounted for by themselves or government agencies.

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**PG&E's blackouts were 'not surgical by any stretch.' Its systems may be to blame**

Oct. 11, 2019

Few understood what the challenges would be until they were in the dark: A mom who couldn't refill her son's medication for bipolar disorder; a schizophrenic man who couldn't quiet the voices in his head without the television on; the people on dialysis who had to travel to another town.

Even little things became hard. Ice and charcoal were scarce, making it difficult to keep food cold or cook a meal. Freezing showers were too intimidating for elderly nursing home residents as fall arrives with 45-degree nights here.

"You don't know until it happens how it's really going to affect you," said Tara Drolma, 72, who was watching the power fade on her emergency battery, and wondering if she would have to choose between charging her electric wheelchair or her heart monitor.

The planned outages are meant to save lives and property. Many in Lake County, which has endured multiple fires in recent years, including the Mendicino Complex fire last year, are too familiar with the risk of an errant spark.

The landlocked county butts up against Sonoma and Napa on its south end, and is swallowed by the Mendocino National Forest to the north. In between, Clear Lake, the largest freshwater lake in the state, is the heart of the county. Most people live in scattered towns along its banks.

Around its bucolic waters, charred remains of trees fill the rolling hills like desolate gray cenotaphs. Almost everyone here has been evacuated or lost a home from fire. Some have lost loved ones.

Even so, after two days of darkness, many now see the outages as bitter medicine. While a blackout might mean just spoiled food and inconvenience in places with more resources and money, Lake County is poor — its poverty rate is close to double the state average — and many residents say the last few days have compounded their challenges.

The county has 2,200 people who receive in-home services because of age or disabilities, higher than the per-capita state average. Some are now accumulating new credit card debt as they purchase generators and backup batteries, check into hotels and upgrade wireless data plans to stay informed.

All the time, they are working to keep medical devices such as oxygen tanks functioning, and find basic necessities. There seemed to be little in the way of a safety net beyond inexpensive meals at the senior centers and charging stations around the lake set up by PG&E. Many complained reliable information was hard to find.

“Clearly [the power cuts] are really impacting a certain segment of the population and have the potential to be disastrous,” said Crystal Markytan, director of social services for Lake County. “It’s not a little thing. You don’t realize how dependent you are on power.”

Gov. Gavin Newsom on Thursday night broadly criticized PG&E for its handling of the cuts, saying: “What has occurred in the last 48 hours is unacceptable. ... You’ve got people that can’t even access water, or medical supplies. We’re seeing a scale and scope of something that no state in the 21st century should experience.”

CALIFORNIA

**Full coverage: California power outages**

Oct. 9, 2019

Little help has been given to address the individual hardships of people such as Delwisch, Newton and Drolma, who all said they felt more aid should be provided if power is cut. The state included $75 million in its most recent budget to address emergency response to outages, and PG&E contacted customers in its database of medically fragile customers, as well as providing charging stations and other aid in some places before the recent cutoff.

But Democratic Sen. Mike McGuire, who represents a swath of Northern California, including Lake County, said both PG&E and the state must do more.

“We need to rethink everything about this shutdown and how to take care of the most vulnerable in our communities,” McGuire said. “These shutdowns can be life and death.”

McGuire said he believes the state should require PG&E to open its own office of emergency services; dedicate a budget to providing emergency services; and create a reliable list of vulnerable Californians who may need aid in a blackout. McGuire said the current reliance on lists of customers who have reduced rates for medical reasons is not accurate. Renters without their own PG&E accounts or residents of some mobile home parks, for example, would not be on it.

“PG&E has made a large assumption by utilizing their care database, but it is wildy inaccurate and doesn’t do the job to keep the most vulnerable in their service territory safe,” said McGuire.

Outages are not considered the same as natural disasters such as fires, said Markytan, and despite the state funding, there are not the same resources to fund shelters or disaster aid on the level of a fire evacuation. That means individuals and counties are largely on their own to bear the expense and disruption of a shut-off.

Markytan said “the crux of my concern” is explaining that difference to people who don’t differentiate between being displaced by fire or power outages.

The county worked hard to inform residents that outages were coming, and provided what aid it could, she said. Her agency worked with the fire department to provide four extra people to help

answer non-urgent 911 calls, but she said she “can’t even imagine” what would happen during an extended outage.

She said there is no county funding dedicated to power cuts, and no shelter sites. If the county found money to open a shelter, it wouldn’t be equipped with a generator. Markytan said she hopes lessons learned from this shut-off can help improve responses if there is a next one.

“This is the first big one,” she said. “It’s really piecemeal at this point.”

In the meantime, the power shut-offs have further exposed the divide between the haves and the have-nots here. Delwisch’s brother, a Navy contractor in Hawaii, gave his sister money to book her, Newton and two of their Chihuahuas into an Econolodge a few hours away, where there was still power. That cost about $350.

They spent another $300 on Amazon buying a backup battery for the breathing machine. Delwisch called the sums “astronomical” and said she’s lucky to have a sibling who can help.

She wondered if others are as fortunate. Is PG&E “forcing people to leave their houses and wind up someplace they are more vulnerable?” Delwisch asked.

Tara Drolma, 72, said her backup battery is running low and she may have to choose between charging her electric wheelchair or her heart monitor if power is not restored soon. (Anita Chabria / Los Angeles Times)

In a house that requires traversing four gravel roads off the main highway to reach, Drolma said the outage had left her with few options other than waiting it out. Her backup battery was down to 59% on Thursday afternoon. In spring, after a threatened outage that never happened, she purchased a pair of solar panels, putting the $2,500 on a credit card and hoping to pay it off slowly. But they are still in boxes, waiting for someone to help her set them up.

With her computer dead, she paid to increase her cellular data plan, which she considers her only lifeline to information. For meals, she has been eating bread and canned tuna, and a cold potato left over from before the power went out.

“If I had money this would be a non-issue,” said Drolma.

A few miles away in Clearlake, about 250 people came through an electrical charging station set up by PG&E in a back room of the senior center on Thursday. The day before, about 150 used it, said PG&E representative Conrad Asper.

Liz Taft walked a half-mile pushing her brother-in-law's oxygen machine to recharge it for him at a senior center after PG&E cut power in Lake County. (Anita Chabria/Los Angeles Times)

One of those sitting at the long tables was Liz Taft. She had put her brother-in-law's oxygen machine in a red cart and pulled it a half-mile here to recharge it. About 3 feet tall, the machine provides him with about 16 hours of oxygen, and it isn't light. It ran empty about 9 a.m. Thursday, but he needs it for his chronic obstructive pulmonary disease. Around noon, Taft was worried what the hours without it would do to him.

"It may mean he may wind up at the hospital," said Taft, wondering why the shut-offs had hit so many so hard. "It's ridiculous."

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# Living near major roads and the incidence of dementia, Parkinson's disease, and multiple sclerosis: a population-based cohort study

*Hong Chen, Jeffrey C Kwong, Ray Copes, Karen Tu, Paul J Villeneuve, Aaron van Donkelaar, Perry Hystad, Randall V Martin, Brian J Murray, Barry Jessiman, Andrew S Wilton, Alexander Kopp, Richard T Burnett*

## Summary

**Background** **Emerging evidence suggests that living near major roads might adversely affect cognition. However, little is known about its relationship with the incidence of dementia, Parkinson's disease, and multiple sclerosis. We aimed to investigate the association between residential proximity to major roadways and the incidence of these three neurological diseases in Ontario, Canada.**

**Methods** **In this population-based cohort study, we assembled two population-based cohorts including all adults aged 20–50 years (about 4·4 million; multiple sclerosis cohort) and all adults aged 55–85 years (about 2·2 million; dementia or Parkinson's disease cohort) who resided in Ontario, Canada on April 1, 2001. Eligible patients were free of these neurological diseases, Ontario residents for 5 years or longer, and Canadian-born. We ascertained the individual's proximity to major roadways based on their residential postal-code address in 1996, 5 years before cohort inception. Incident diagnoses of dementia, Parkinson's disease, and multiple sclerosis were ascertained from provincial health administrative databases with validated algorithms. We assessed the associations between traffic proximity and incident dementia, Parkinson's disease, and multiple sclerosis using Cox proportional hazards models, adjusting for individual and contextual factors such as diabetes, brain injury, and neighbourhood income. We did various sensitivity analyses, such as adjusting for access to neurologists and exposure to selected air pollutants, and restricting to never movers and urban dwellers.**

**Findings** **Between 2001, and 2012, we identified 243 611 incident cases of dementia, 31 577 cases of Parkinson's disease, and 9247 cases of multiple sclerosis. The adjusted hazard ratio (HR) of incident dementia was 1·07 for people living less than 50 m from a major traffic road (95% CI 1·06–1·08), 1·04 (1·02–1·05) for 50–100 m, 1·02 (1·01–1·03) for 101–200 m, and 1·00 (0·99–1·01) for 201–300 m versus further than 300 m ($p$ for trend=0·0349). The associations were robust to sensitivity analyses and seemed stronger among urban residents, especially those who lived in major cities (HR 1·12, 95% CI 1·10–1·14 for people living <50 m from a major traffic road), and who never moved (1·12, 1·10–1·14 for people living <50 m from a major traffic road). No association was found with Parkinson's disease or multiple sclerosis.**

**Interpretation** **In this large population-based cohort, living close to heavy traffic was associated with a higher incidence of dementia, but not with Parkinson's disease or multiple sclerosis.**

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## Introduction

Dementia, Parkinson's disease, and multiple sclerosis are among the most common neurodegenerative diseases, with devastating effects on individuals, families, and society. Globally, about 55 million people have these disorders, with rising numbers expected given increasing longevity.[1,2] Without cures, identification of modifiable risk factors is important.

Despite the mounting global effect of these neurodegenerative diseases, their cause remains largely unknown.[3–5] Concern is growing that exposures associated with traffic such as air pollution and noise might contribute to neurodegenerative pathology.[6,7] Results of studies showed that air pollutants and diesel exhaust induce oxidative stress and neuroinflammation,[8] activate microglia,[9] and stimulate neural antibodies.[10] Exposure to more noise also impairs cognitive abilities in rats.[11] Similarly, a few epidemiologic studies[12–14] linked traffic-related noise and air pollution to cognitive decline and increased incidence of Parkinson's disease[15] and Alzheimer's disease.[16] Traffic exposure might affect various neurodegenerative processes.

Studies also showed that living near roads was associated with reduced white matter hyperintensity volume[17] and cognition,[18,19] but its effect on the incidence of dementia, Parkinson's disease, and multiple sclerosis is unknown. Living near traffic is a multifaceted exposure representing heightened exposure to nitrogen oxides, ultrafine particles, fine particulate matter (≤2·5 μm in diameter or $PM_{2.5}$), heavy metals, polycyclic aromatic hydrocarbons, volatile organic compounds, noise, and other factors. Because hundreds of millions of people

## Research in context

### Evidence before this study

We searched the MEDLINE and Embase databases for epidemiological studies of the associations between exposure to roadway traffic and the risk in adults (older than 18 years of age) of developing dementia, Parkinson's disease, or multiple sclerosis. Studies published in the peer-review literature up to Feb 1, 2016, were included, regardless of the language of publication. We perused the bibliographies of these articles and of previously published reviews. We searched the bibliographic databases using the keywords traffic exposure, mobile source, roadway, proximity or near, air pollution, and with the following health outcomes: dementia; Alzheimer's disease; cognition; Parkinson's disease; multiple sclerosis. A few studies found an association between living close to major roadways and cognitive decline and changes in the brain structure. There is also some evidence linking traffic-related noise and air pollution to cognitive decline and the incidence of dementia, and to a lesser degree, Parkinson's disease. No study has so far investigated the onset of all three major neurodegenerative diseases (dementia, Parkinson's disease, and multiple sclerosis) in association with near-road exposure. Moreover, the few existing studies involved relatively small study populations and nearly half were cross-sectional.

### Added value of this study

We report that living close to heavy traffic is associated with increased incidence of dementia. Using the same populations and methods, however, we did not find an association between residential proximity to traffic and Parkinson's disease or multiple sclerosis. The cause of these major neurodegenerative diseases remains largely unclear. This study sheds important insights into a possible role of near-road exposure on the development of dementia. Our study overcomes several limitations of previous studies, since it has large cohorts comprising almost the entire adult population in Ontario, the most populous province in Canada, and lagged exposure up to 10 years to reduce concerns about reverse causality. With demographic characteristics similar to the USA and many European countries, findings from this study will be highly generalisable to populations in many other regions.

### Implications of all the available evidence

Increasing population growth and continuing urbanisation globally has placed many people close to heavy traffic. With the widespread exposure to traffic and growing population with dementia, even a modest effect from near-road exposure can pose an enormous public health burden. This study suggests that improvements in environmental health policies and land use planning aimed at reducing traffic exposure can have considerable potential for prevention of dementia, which would lead to a broad public health implication. This study adds weight to previous observations suggesting that roadway traffic is an important source of environmental stressors that could give rise to neurological disorders and that future investigation targeting the effects of different aspects of traffic such as traffic-related air pollutants and noise on neurological health is merited.

worldwide live close to major roads, we sought to investigate the association between exposure to traffic, measured by residential proximity to major roadways, and the incidence of dementia, Parkinson's disease, and multiple sclerosis in a large population-based cohort in Ontario, Canada.

## Methods

See Online for appendix

### Study design

We did a population-based cohort study of all Ontario adults to determine the incidence of dementia, Parkinson's disease, and multiple sclerosis. Eligible participants were, as of April 1, 2001, Ontario residents for 5 years or longer, aged 20–85 years, and Canadian-born. We created the study population using Ontario's Registered Persons Database, a registry of all residents who have ever had health insurance. This database covers virtually all Ontario residents.[20]

Because dementia and Parkinson's disease onset occurs predominantly in people aged 55 years or older, whereas multiple sclerosis onset is most common in adults younger than 50 years, we separated the study population into two analytical cohorts: individuals aged 20–50 years (multiple sclerosis cohort); and individuals aged 55–85 years (dementia or Parkinson's disease cohort). We further excluded individuals with any of these three disorders at baseline, yielding a total of 4 372 720 and 2 165 268 participants in each cohort.

The Research Ethics Board of Sunnybrook Health Sciences Centre, Toronto, approved the study.

We ascertained incident diagnoses of dementia, Parkinson's disease, and multiple sclerosis using validated databases (see appendix). Details of these databases are available elsewhere.[20] These databases have been validated previously using chart review, with sensitivity of 78–84% and specificity of 99–100%.[21–23] They were created using hospital discharge abstracts from the Canadian Institute for Health Information, physician service claims from the Ontario Health Insurance Plan database, and prescription medication claims from the Ontario Drug Benefits programme database. Hospital, laboratory, and physician services in Ontario are funded by the provincial government through a single-payer universal medicare system that covers virtually all residents.[20] Drug coverage is provided to those aged 65 years or older, and social assistance recipients. We linked the cohorts to these databases using encrypted unique identifiers to ascertain incident cases.

### Residential proximity to roads

We calculated residential proximity to major roadways or highways based on 6-character postal-code addresses in 1996, 5 years before cohort inception. Postal codes in urban areas represent the centroid of the blocks or single large buildings in which cohort members lived. Distance (m) was measured using ArcGIS. Major traffic roads include primary urban roads and arterial roads (ie, a major thoroughfare with medium to large traffic capacity with a combination of controlled access and intersections at grade level) whereas highways include expressways and primary and secondary highways, according to Ontario Government Road Network Data Standards. Consistent with previous studies,[17,24] we created five distance categories: less than 50 m from major traffic road, 50–100 m, 101–200 m, 201–300 m, and more than 300 m. We also considered a continuous measure of distance.

### Covariates

We selected accepted or suspected risk factors for neurodegenerative pathology, including age, sex, pre-existing comorbidities, and socioeconomic status.[3–5] The comorbidities included traumatic brain injury, diabetes, hypertension, stroke, coronary heart disease, congestive heart failure, and arrhythmia. We ascertained the presence of comorbidities at baseline using hospital discharge abstracts, physician service claims, and validated chronic disease databases (appendix).

Several individual-level socioeconomic status and behavioural factors, such as education, smoking, and physical activity are also implicated in neurological health,[3–5] but were unavailable. Since neighbourhood-level socioeconomic status is strongly associated with these factors,[25,26] we derived four neighbourhood-level variables: income quintile, a measure of relative household income accounting for household size and community; percentage of population aged 15 years or older with less than high school education; unemployment rate; and percentage of recent immigrants, using 2001 Canadian Census dissemination area data. A dissemination area (with 400–700 people) is the smallest census geographic area for which census data are disseminated. We further derived neighbourhood-level deprivation based on the Ontario Marginalization Index that quantifies the degree of marginalisation in health and social wellbeing (appendix).

To control for regional differences in the incidence of dementia, Parkinson's disease, and multiple sclerosis, we created a variable for urban residence (yes/no), density of neurologists using the ICES Physician Database to represent accessibility to neurological care, and the latitude of residence given the reported latitude gradient with multiple sclerosis.[3] Additionally, we created a dichotomous variable classifying Ontario into the Greater Toronto Area, a densely-populated urban mega-region, and all other areas. Toronto tends to differ from other areas with respect to sociodemographic characteristics, health care access, and population health status.

To explore whether exposure to air pollutants, especially nitrogen dioxide ($NO_2$) and $PM_{2.5}$ might explain the roadway proximity-outcome association, we obtained long-term measures of $PM_{2.5}$ and $NO_2$ for all participants (appendix). Briefly, estimates of ground-level concentrations of $PM_{2.5}$ were derived from satellite observations of aerosol optical depth in combination with outputs from a global atmospheric chemistry transport model (GEOS-Chem CTM).[27] The $PM_{2.5}$ estimates were further adjusted using information on urban land cover, elevation, and aerosol composition using a geographically weighted regression. We used estimates between 1998 (the earliest year with available data) and 2001 (the year of cohort inception), thus producing four-year mean concentration of $PM_{2.5}$ at a spatial resolution of 1×1 km and covering all North America below 70°N, which includes all of Ontario. These

| | Multiple sclerosis cohort* (n=4 372 720) | | Dementia/Parkinson's disease cohort* (n=2 165 268) | |
|---|---|---|---|---|
| | Subject count | % | Subject count | % |
| Age at entry (years); mean (SD) | 35·9 (8·7) | .. | 66·8 (8·2) | .. |
| 20–29 | 1 198 499 | 27·4 | .. | .. |
| 30–39 | 1 475 303 | 33·7 | .. | .. |
| 40–50 | 1 698 918 | 38·9 | .. | .. |
| 55–64 | .. | .. | 978 235 | 45·2 |
| 65–74 | .. | .. | 731 685 | 33·8 |
| 75–85 | .. | .. | 455 348 | 21·0 |
| Sex | | | | |
| Male | 2 178 448 | 49·8 | 1 013 010 | 46·8 |
| Female | 2 194 272 | 50·2 | 1 152 258 | 53·2 |
| Pre-existing comorbidity† | | | | |
| Coronary heart disease | 21 957 | 0·5 | 213 071 | 9·8 |
| Stroke | 6005 | 0·2 | 66 241 | 3·1 |
| Congestive heart failure | 4687 | 0·1 | 120 550 | 5·6 |
| Diabetes | 105 088 | 2·4 | 323 544 | 15·0 |
| Hypertension | 295 996 | 6·8 | 1 038 119 | 48·0 |
| Arrhythmia | 11 717 | 0·3 | 93 495 | 4·3 |
| Traumatic brain injury | 302 869 | 6·9 | 90 694 | 4·2 |
| Area-level risk factors‡ | | | | |
| Low-income cutoff quintile | | | | |
| Lowest | 784 958 | 18·0 | 400 839 | 18·5 |
| Lower middle | 867 694 | 19·8 | 447 184 | 20·7 |
| Middle | 903 386 | 20·7 | 437 336 | 20·2 |
| Upper middle | 915 524 | 20·9 | 420 427 | 19·4 |
| Upper | 901 158 | 20·6 | 459 482 | 21·2 |
| Percentage of rural residents | 724 024 | 16·6 | 410 575 | 19·0 |
| Percentage of recent immigrants | .. | 3·6 | .. | 3·3 |
| Percentage ≥15 years of age with less than high school education | .. | 25·5 | .. | 26·9 |
| Percentage ≥15 years of age without employment | .. | 6·2 | .. | 6·2 |

Data are n or %, unless otherwise specified. *Multiple sclerosis cohort comprised all adults aged 20–50 years and dementia/Parkinson's disease cohort comprised all adults aged 55–85 years in Ontario, Canada, in 2001. †In the 10 years before cohort onset. ‡From Canadian Census 2001, at the census dissemination area level.

***Table 1*: Baseline characteristics of the study population**

| | Incidence of dementia (n=243 611)‡ | | | Incidence of Parkinson's disease (n=31577)‡ | | | Incidence of multiple sclerosis (n=9247)‡ | | |
|---|---|---|---|---|---|---|---|---|---|
| | HR | 95% CI | $p_{trend}$ | HR | 95% CI | $p_{trend}$ | HR | 95% CI | $p_{trend}$ |
| Distance† by category | | | | | | | | | |
| <50 m | 1·07 | 1·06–1·08 | 0·0349 | 1·01 | 0·98–1·04 | 0·12 | 1·02 | 0·95–1·09 | 0·72 |
| 50–100 m | 1·04 | 1·02–1·05 | .. | 1·01 | 0·97–1·05 | .. | 0·93 | 0·86–1·01 | .. |
| 101–200 m | 1·02 | 1·01–1·03 | .. | 0·99 | 0·96–1·03 | .. | 1·01 | 0·95–1·08 | .. |
| 201–300 m | 1·00 | 0·99–1·01 | .. | 0·99 | 0·96–1·02 | .. | 1·01 | 0·94–1·08 | .. |
| >300 m | Reference | .. | .. | Reference | .. | .. | Reference | .. | .. |
| Log(distance)§ | 0·91 | 0·89–0·92 | .. | 0·99 | 0·97–1·01 | .. | 1·00 | 0·98–1·02 | .. |

Cox proportional hazards model with age as the time-scale, stratified by an indicator for living in the Greater Toronto Area or not, adjusted for sex, history of diabetes, hypertension, coronary heart disease, stroke, congestive heart failure, arrhythmia, and traumatic brain injury, income quintile, urban/rural indicator, census division-level unemployment rate, education, recent immigrants, as well as the subtraction of these variables at the census dissemination level from their census division. For multiple sclerosis, the model was also adjusted for latitude. †Major traffic roads include primary urban roads and arterial roads whereas highways include expressways and primary and secondary highways, as defined by Ontario Government Road Network Data Standards. ‡Incidence of dementia and Parkinson's disease was analysed among all adults aged 55–85 years (dementia/Parkinson's disease cohort) whereas incidence of multiple sclerosis was analysed among all adults aged 20–50 years (multiple sclerosis cohort). §Distance was fitted as a continuous variable, using natural logarithm of distance. Hazard ratios (HRs) expressed per IQR increase in distance (dementia/Parkinson's disease cohort: 310 m and multiple sclerosis cohort: 320 m).

***Table 2*: Hazard ratios and 95% CIs for the associations between residential proximity to major roadways in 1996 and the risks of incident dementia, Parkinson's disease, and multiple sclerosis in Ontario, during the follow-up period 2001–12**

satellite-based estimates of $PM_{2.5}$ closely agree with ground measurements at fixed-site monitoring stations across North America ($R^2$ 0·82, n=1440).[27] Similarly, we derived long-term exposure to $NO_2$ from a national land-use regression (LUR) model developed from Environment Canada's National Air Pollution Surveillance Network monitoring data, 2005–11 satellite $NO_2$ estimates, area of industrial land use, road length, and mean summer rain fall.[28] The estimates were further calibrated by incorporating local-scale variations of $NO_2$ from vehicle emissions by applying spatially-varying multipliers that represented distance-decay gradient in $NO_2$. The final LUR model explained 73% of the variation in annual 2006 measurements of $NO_2$, with a root mean square error of 2·9 parts per billion (ppb).[28] The resulting LUR $NO_2$ estimates were available for each year between 1998 and 2001, after applying temporal adjustment.

## Statistical analysis

We used Cox proportional hazards models with age as the time-scale to assess the relationship between residential proximity to major roadways and the incidence of dementia, Parkinson's disease, and multiple sclerosis. For each outcome, follow up time (in days) was measured from April 1, 2001 until diagnosis date, ineligibility for provincial health insurance, death, or March 31, 2012.

Separate models were developed for each disease. All models were stratified by region (living in Toronto or not), and adjusted for sex, comorbidities, urban residency, and neighbourhood-level income, education, unemployment, and immigration status. To adjust for regional variations in the neighbourhood-level variables across Ontario, we included them as the average for each census division (equivalent to county), and as the difference between the values for each census dissemination area and the census division mean. We further adjusted for latitude for multiple sclerosis cohort. The analyses were repeated using distance as categorical and continuous variables.

We routinely tested for deviation from the proportional hazards assumption by adding the cross-product of each variable with the natural logarithm of the time variable, but we did not find any violation of this assumption ($p>0·05$). We calculated adjusted hazard ratios (HRs) and 95% CIs for each category of roadway proximity compared with the furthest category (>300 m). Linear trend was assessed by assigning the median distance (in natural log) to each category and fitting the term as a continuous variable in a regression model. In analyses with distance as a continuous variable, we considered the natural log of distance because this exposure has been linearly related to mortality and morbidity outcomes in Ontario and elsewhere.[17,24]

## Sensitivity analyses

We controlled for access to neurologists, deprivation index, and a North/South indicator (appendix). We also adjusted for a linear term for time to account for potential changes in the risk of the three disorders over time.

We assessed whether HR might be influenced by any spatial dependence among participants. We fitted models with a frailty term for census division (ie, county) to account for the possibility that participants in the same community could share similar risk factors than those living in different locations. We assumed a gamma distribution for the frailties, with an exchangeable correlation structure within county.

We assessed the potential influence of unmeasured individual-level socioeconomic status and behavioural variables, especially education, smoking, obesity, and

| | Main model ‡ | | Indirectly adjusted for smoking | | Further indirectly adjusted for BMI, physical activity | | Further indirectly adjusted for education | |
|---|---|---|---|---|---|---|---|---|
| | Hazard ratio | 95% CI | Hazard ratio | 95% CI | Hazard ratio | 95% CI | Hazard ratio | 95% CI |
| Distance† by category | | | | | | | | |
| <50 m | 1·07 | 1·06–1·08 | 1·06 | 1·05–1·08 | 1·06 | 1·05–1·08 | 1·06 | 1·05–1·08 |
| 50–100 m | 1·04 | 1·02–1·05 | 1·03 | 1·02–1·05 | 1·03 | 1·02–1·05 | 1·04 | 1·02–1·06 |
| 101–200 m | 1·02 | 1·01–1·03 | 1·01 | 1·00–1·02 | 1·01 | 1·00–1·03 | 1·02 | 1·01–1·04 |
| 201–300 m | 1·00 | 0·99–1·01 | 1·00 | 0·98–1·01 | 1·00 | 0·99–1·02 | 1·01 | 0·99–1·03 |
| >300 m | Reference | .. | Reference | .. | Reference | .. | Reference | .. |
| Log (distance)§ | 0·91 | 0·89–0·92 | 0·92 | 0·90–0·93 | 0·92 | 0·90–0·93 | 0·92 | 0·90–0·93 |

Indirect adjustment for smoking, body-mass index (BMI), physical activity, and attained education. Data of smoking, BMI, physical activity, and educational attainment were obtained from Ontario respondents to the 1996 cycle of National Population Health Survey and the 2000–01, 2003 cycles of Canadian Community Health Survey, and who were 50 to 85 years old at the time of the surveys (n=16 441). †Major traffic roads include primary urban roads and arterial roads whereas highways include expressways and primary and secondary highways, as defined by Ontario Government Road Network Data Standards. ‡Cox proportional hazards model with age as time axis, stratified by an indicator for living in the Greater Toronto Area or not, adjusted for sex, history of diabetes, hypertension, coronary heart disease, stroke, congestive heart failure, arrhythmia, and traumatic brain injury, income quintile, urban/rural indicator, census division-level unemployment, education, and recent immigrants, as well as the subtraction of these variables at the census dissemination level from their census division. §Distance was fitted as a continuous variable, using natural logarithm of distance. The hazard ratios were expressed per interquartile-range increase in distance (310 m).

***Table 3:*** **Hazard ratios and 95% CI for associations between residential proximity to major roadways in 1996 and the risk of incident dementia in Ontario during the follow-up period 2001–12**

| | Parkinson's disease | | | | Multiple sclerosis | | | |
|---|---|---|---|---|---|---|---|---|
| | Main model‡ | | Indirectly adjusted for smoking and physical activity‖ | | Main model‡ | | Indirectly adjusted for smoking‖ | |
| | Hazard ratio | 95% CI | Hazard ratio | 95% CI | Hazard ratio | 95% CI | Hazard ratio | 95% CI |
| Distance† by category | | | | | | | | |
| <50 m | 1·01 | 0·98–1·04 | 1·01 | 0·98–1·05 | 1·02 | 0·95–1·09 | 1·00 | 0·93–1·07 |
| 50–100 m | 1·01 | 0·97–1·05 | 1·02 | 0·98–1·06 | 0·93 | 0·86–1·01 | 0·93 | 0·86–1·01 |
| 101–200 m | 0·99 | 0·96–1·03 | 0·99 | 0·96–1·03 | 1·01 | 0·95–1·08 | 1·00 | 0·93–1·06 |
| 201–300 m | 0·99 | 0·96–1·02 | 1·00 | 0·97–1·03 | 1·01 | 0·94–1·08 | 1·00 | 0·93–1·07 |
| >300 m | Reference | .. | Reference | .. | Reference | .. | Reference | .. |
| Log (distance)§ | 0·99 | 0·97–1·01 | 1·00 | 0·98–1·02 | 1·00 | 0·98–1·02 | 0·99 | 0·97–1·02 |

Indirect adjustment for smoking and physical activity for Parkinson's disease, and for smoking for multiple sclerosis. Data of smoking and physical activity were obtained from Ontario respondents to the 1996 cycle of National Population Health Survey and the 2000–01 and 2003 cycles of Canadian Community Health Survey. For Parkinson's disease, respondents aged 50–85 years at the time of the surveys were included (n=16 441) and for multiple sclerosis, those who were 20–55 years old were included (n=31 635). †Major traffic roads include primary urban roads and arterial roads whereas highways include expressways and primary and secondary highways, as defined by Ontario Government Road Network Data Standards. ‡Cox proportional hazards model with age as time axis, stratified by an indicator for living in the Greater Toronto Area or not, adjusted for sex, history of diabetes, hypertension, coronary heart disease, stroke, congestive heart failure, arrhythmia, and traumatic brain injury, income quintile, urban/rural indicator, census division-level unemployment, education, and recent immigrants, as well as the subtraction of these variables at the census dissemination level from their census division. For multiple sclerosis, the model was also adjusted for latitude. §Distance was fitted as a continuous variable, using natural logarithm of distance. HRs expressed per interquartile-range increase in distance (dementia/Parkinson's disease cohort: 310 m and multiple sclerosis cohort: 320 m). ||For Parkinson's disease, $p_{trend}$=0·38 and for multiple sclerosis, $p_{trend}$=0·53.

***Table 4:*** **Hazard ratios and 95% CI for associations between residential proximity to major roadways in 1996 and risk of incident Parkinson's disease and multiple sclerosis in Ontario, during the follow-up period 2001–12**

physical activity on our results. To do this, we used a method to mathematically adjust HR for these variables while simultaneously controlling for all variables available in the model (ie, age, sex, comorbidities, and socioeconomic status; appendix). Details of this method are presented elsewhere.[29] Briefly, this method requires spatial associations between the unmeasured and observed variables from an auxiliary dataset. Following previous Canadian studies,[30] we obtained the relationships using data from the 1996–97 cycle of the National Population Health Survey and the 2000–01 and 2003 cycles of the Canadian Community Health Survey, which constituted a representative sample of the study cohorts (appendix). This information along with estimated associations between these unmeasured variables and incident dementia, Parkinson's disease, and multiple sclerosis from the literature, were used to estimate their effect on HR. Based on systematic reviews of dementia, Parkinson's disease, and multiple sclerosis, we considered all four variables in our analysis with dementia, smoking and physical activity with Parkinson's disease, and smoking with multiple sclerosis (appendix).

Furthermore, we additionally adjusted for $PM_{2·5}$ and $NO_2$, excluded events occurring in the first 2 and 5 years

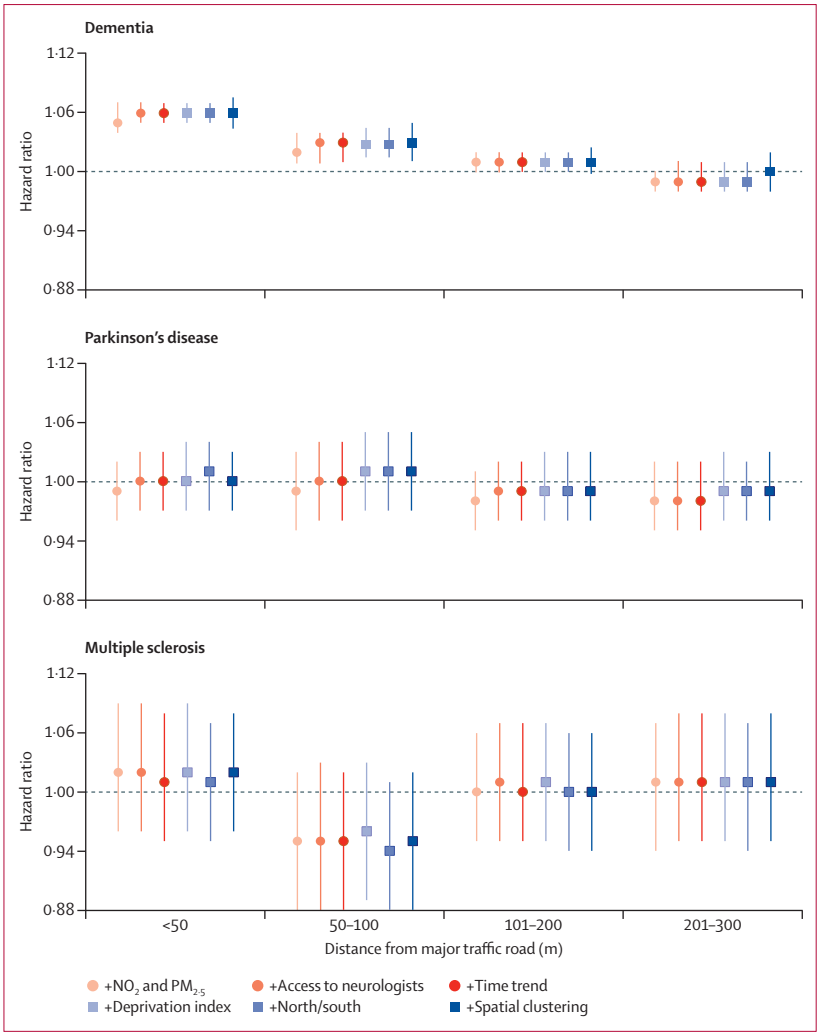


***Figure 1*: Estimated associations between residential proximity to major roadways in 1996 and the risk of incident dementia, Parkinson's disease, multiple sclerosis in Ontario, 2001–12**
Measured by six sensitivity analyses to further control for potential confounding factors. Model further adjusted for exposure to $NO_2$ and $PM_{2·5}$ access to neurologists, time trend, deprivation, an indicator for North/South Ontario, and a frailty term to account for potential spatial clustering.

during follow-up to lag exposure up to 10 years, excluded people residing in long-term care facilities (often located near major roadways) at baseline, and restricted the dementia/Parkinson's disease cohort to those aged 65 years or older because drug information was unavailable for younger adults. Lastly, we further adjusted for rurality index and neighbourhood-level percentage of visible minority, and restricted the analysis to people who never moved since 1996, to urban residents, and to residents of six major urban centres in Ontario (Toronto, Hamilton, Ottawa, London, Windsor, and Sarnia) (appendix).

### Role of the funding source

The funder had no role in study design, data collection, data analysis, data interpretation, or writing of the report. The corresponding author had full access to all the data in the study and had final responsibility for the decision to submit for publication.

## Results

The multiple sclerosis cohort comprised 46·7 million person-years of observations and the dementia/Parkinson's disease cohort contributed 20·1 million person-years. At baseline, the mean age was 35·9 years (SD 8·7 years) for the multiple sclerosis cohort and 66·8 years (8·2 years) for the dementia/Parkinson's disease cohort (table 1). Of the multiple sclerosis cohort, 50% were male, 17% were rural residents, 2% had diabetes, and 7% had hypertension, whereas 47% of the dementia/Parkinson's disease cohort were male, 19% were rural residents, 15% had diabetes, and 48% had hypertension. Average unemployment among census dissemination areas was 6% and the mean percentage of population with less than high school education was about 26% in both cohorts.

Nearly half of the cohorts lived within 200 m from a major road and 95% were within 1000 m (appendix). Of the cohorts, the average concentration of $PM_{2·5}$ according to participants' residences in 1996, 5 years before cohort inception, was 9·7 μg/m³ (range 1·3–19·8 μg/m³), while the average concentration of $NO_2$ was 15·4 ppb (2·2–62·0 ppb). Between 2001–12, we identified 243611 incident cases of dementia, 31577 incident cases of Parkinson's disease, and 9247 incident cases of multiple sclerosis.

In both categorical and continuous analyses, living closer to a major road was associated with increased incidence of dementia, with fully adjusted HR of 1·07 (95% CI 1·06–1·08) for people living less than 50 m, 1·04 (1·02–1·05) for people living 50–100 m, 1·02 (1·01–1·03) for people living 101–200 m, and 1·00 (0·99–1·01) for people living 201–300 m away from a major roadway versus more than 300 m from a major roadway ($P_{trend}$=0·0349; table 2). An interquartile-range increase in residential proximity to a major road was associated with a 9% (95% CI 8–11%) lower incidence of dementia. In contrast, there was no evidence linking traffic proximity to Parkinson's disease or multiple sclerosis (HR 1·00 for both; table 2).

The association between traffic exposure and dementia was insensitive to additional controls for smoking, obesity, physical activity, and education (HR 1·06 for living <50 m away from a major road, 1·04 for 51–100 m, and 1·02 for 101–200 m; table 3). Similarly, the associations between traffic exposure and Parkinson's disease and multiple sclerosis remained unchanged after adjusting for smoking and physical activity (table 4).

Further adjustment for access to neurologists, deprivation, time trend, and a North/South indicator did not alter the associations, nor did adding a frailty term in the survival model to account for potential spatial clustering (figure 1). Adjustment for $NO_2$ and $PM_{2·5}$ modestly attenuated the association between traffic

proximity and dementia (HR 1·05 for living <50 m away from a major road and HR 1·02 for 51–100 m away from a major road *vs* 1·07 and 1·04 without adjustment). Importantly, $NO_2$ was significantly associated with dementia, whereas $PM_{2·5}$ was associated with both dementia and Parkinson's disease (appendix).

In sensitivity analyses, the magnitude of associations were similar after further excluding the first 2 and 5 years of follow-up, restricting to people aged 65 years or older, excluding those living in long-term care facilities, or considering other sensitivity analyses (figure 2 and appendix). However, the association between living less than 50 m from a major roadway and dementia appeared stronger among participants who lived in urban areas, who lived in one of the six major cities, or who never moved (HR 1·09–1·12, depending on the analysis).

## Discussion

In this large population-based cohort, living near major roadways was associated with increased dementia incidence. The associations seemed stronger among urban residents, especially those living in major urban centres and those who never moved. Although the increase in risk might appear moderate (eg, HRs varied from 1·07–1·12 for living <50 m away from a major road, depending on the region), this translates to 7–11% of dementia cases in patients who live near major roads attributable to traffic exposure (appendix). The associations were robust to various sensitivity analyses, except for additional adjustment for $PM_{2·5}$ and $NO_2$ which led to a modest attenuation. It is noteworthy that both $NO_2$ and $PM_{2·5}$ were positively associated with dementia. Lastly, we found no association between roadway proximity and incidence of Parkinson's disease or multiple sclerosis.

To our knowledge, this is the first study to investigate the onset of three major neurodegenerative diseases in association with near-roadway exposure. Previous studies have linked living near roadways to cognitive decline in cohorts of older adults in Boston MA, USA[18] and in the Ruhr area, Germany,[19] and to smaller white matter hyperintensity volume in the Framingham Offspring cohort.[17] Living near major roads substantially increases an individual's exposure to traffic-related air pollution (eg, ultrafine particles, nitrogen oxides, and particles from wear of tyres and friction materials), and noise.[17] Although the mechanisms through which traffic exposure might affect brain health are unknown, systemic inflammation arising from traffic-related air pollution is probably important. In studies of both experimental animals and in autopsy samples of sudden accidental deaths in human beings, particulates and diesel exhaust provoke oxidative stress and systemic inflammatory responses, disrupt the blood-brain barrier, precipitate Aβ peptides, and activate microglia.[8,9] Ultrafine particles have also been found in the olfactory bulb and the frontal cortical areas in the brain of highly exposed dogs and human beings.[8] Furthermore,

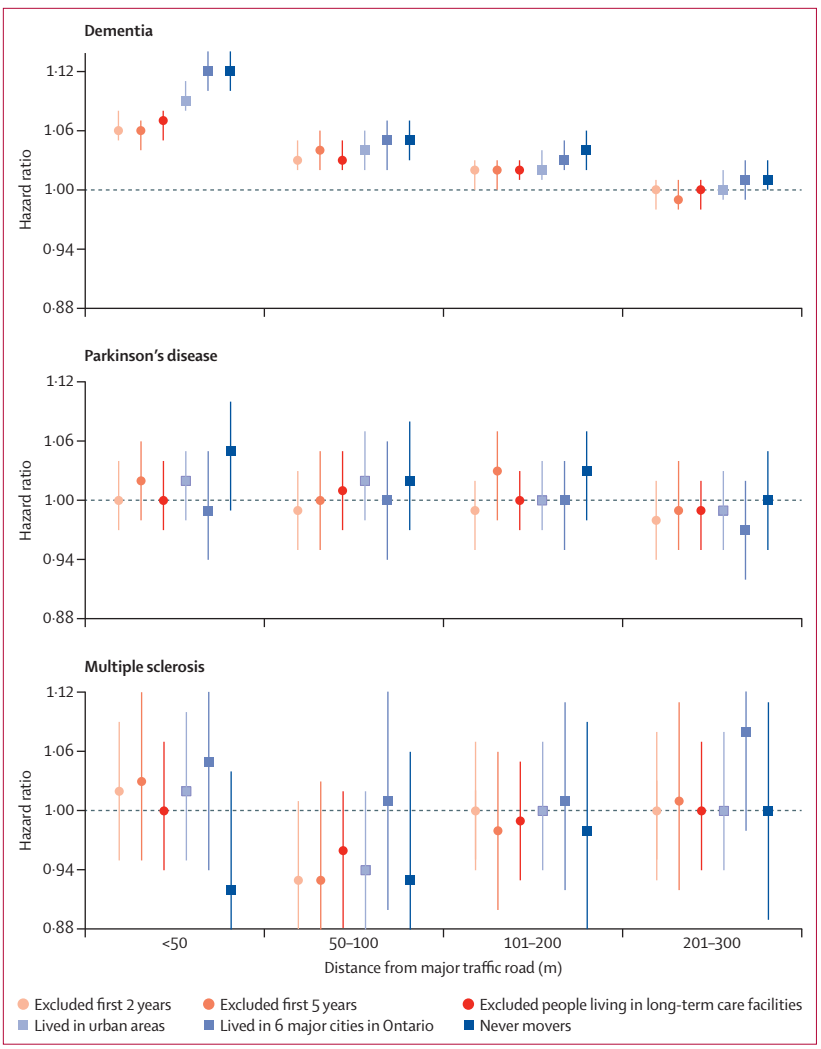


***Figure 2*: Association between residential proximity to major roadways in 1996 and the risk of incident dementia, Parkinson's disease, multiple sclerosis in Ontario, 2001–12**
Hazard ratios and 95% CIs from six additional sensitivity analyses (excluding first 2 years of follow-up, excluding first 5 years of follow-up, excluding people living in long-term care facilities, restricting to urban residents, restricting to six major cities in Ontario, and restricting to those who did not move after 1996).

emerging epidemiologic evidence relates nitrogen oxides and black carbon, markers for traffic-related pollution, to dementia incidence[12] and cognitive impairment.[14] We observed that exposures to $NO_2$ and $PM_{2·5}$ were related to dementia and that adjusting for these two pollutants attenuated its association with roadway proximity, suggesting that the effect of traffic exposure might, at least in part, operate through this mechanism. Given the potentially significant implications of exposure to traffic-related pollutants on dementia risk, understanding their effects merit further investigation.

The fact that $PM_{2·5}$ and $NO_2$ did not fully explain the near-road effect on dementia suggests that additional pollutants or other factors such as noise might play a role. Although we were unable to directly examine these factors, traffic-related noise has been linked to cognitive

impairment in a cohort in Germany.[13] In rat models, noise exposure directly impaired cognition.[11] Additionally, sleep loss from noise contributes to sleep fragmentation, which is associated with reduced cognition.[5] Living near busy roads might also reduce physical activity, which could subsequently affect neurological health. However, we found little change in our results after indirect adjustment for this variable.

Compared with dementia, less is known about the effect of traffic exposure on Parkinson's disease and multiple sclerosis. Only three studies have examined the relationship between traffic exposure and Parkinson's disease: a positive association between $NO_2$ and incident Parkinson's disease was reported in a case-control study in Denmark,[15] whereas in another case-control study in the USA, no association with $NO_2$ was found.[31] Additionally, in a cross-sectional study in Ontario, Parkinson's disease prevalence was not associated with roadway proximity nor $NO_2$.[32] For multiple sclerosis, one time-series study found a relationship between daily hospital admissions and particulate pollution,[33] but no studies have assessed the effect of living close to traffic. In this study, we observed an association only between traffic proximity and dementia, which might be attributable to relatively few cases of Parkinson's disease and multiple sclerosis. Another possibility is that traffic exposure could augment neurodegeneration through pathways that are related to dementia but not Parkinson's disease or multiple sclerosis.[3–5]

Our study has some limitations. First, we could not identify undiagnosed cases of dementia, Parkinson's disease, and multiple sclerosis. However, the estimates were unchanged when we adjusted for access to neurologists, a North/South indicator, deprivation, and time trends. With universal health care in Ontario, incomplete diagnosis might lead to underestimation of the true effect because this measurement error was probably independent of the exposure.

Second, we did not have information on medications that might potentially influence dementia risk (eg, anti-inflammatory medication and NSAIDs), although it is unclear whether these factors would be associated with traffic exposure. Furthermore, we lacked information on individual socioeconomic status and behavioural variables. To control for these unmeasured variables, we adjusted for neighbourhood socioeconomic status and comorbidities. Since neighbourhood socioeconomic status is strongly associated with individual socioeconomic status and behavioural variables,[25,26] and comorbidities and neurodegenerative diseases share some common behavioural factors, adjusting for these variables should reduce the influence of these unmeasured variables on HR (appendix). We further controlled indirectly for these variables, and found similar results. Although we cannot rule out residual confounding, the null findings for Parkinson's disease and multiple sclerosis do not support this possibility.

Third, our exposure assessment was based on postal-code addresses, which do not completely reflect personal exposure. $PM_{2.5}$ is a complex mixture with a secondary aerosol component that might not originate from vehicle emissions. Finally, roadway proximity does not account for traffic density and meteorological conditions that might influence exposure to air pollution and noise. Given the inherent imprecision of this exposure, our assessment of near-road exposure was probably subject to non-differential misclassification that probably attenuated our results.

The strengths of this study include the large cohorts made up of almost the entire adult population in Ontario. The many cases ascertained from validated registries enabled us to investigate fine-scale changes in traffic exposure and to examine the effect from exposures lagged up to 10 years. Our study also benefited from quantifying and comparing the effects on three major neurodegenerative diseases from traffic exposures using the same methods. Furthermore, the availability of detailed information on medical and residential history allowed us to control for important risk factors (eg, head trauma) and assess the influence of residential mobility.

## Conclusions

In this large cohort, living near major roadways was associated with higher incidence of dementia, but not Parkinson's disease or multiple sclerosis. Given the potentially significant implications of traffic exposure on dementia risk, understanding the effect of different aspects of traffic merits further investigation.

**Contributors**

HC, RTB, JCK, PJV, KT, BJM, RC, and BJ contributed to the study design. HC, ASW, and AK prepared and cleaned the data. HC, AvD, PH, and RVM contributed to the exposure assessment. RTB provided substantial scientific input in statistical methods and interpretation of the results. HC, RTB, JCK, PJV, KT, BJM, ASW, and AK contributed to the data analyses. HC took the lead in drafting the manuscript. All authors contributed to interpretation of data, provided critical revisions to the manuscript, and approved the final draft.

**Declaration of interests**

We declare no competing interests.

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# Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation

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**Abstract:** *I examined the effects of habitat fragmentation on the distribution and abundance of mammalian carnivores in coastal southern California and tested the prediction that responses to fragmentation varied with the body size of carnivore species. I conducted track surveys for nine native and two exotic carnivore species in 29 urban habitat fragments and 10 control sites. Fragment area and isolation were the two strongest landscape descriptors of predator distribution and abundance. Six species were sensitive to fragmentation, generally disappearing as habitat patches became smaller and more isolated; three species were enhanced by fragmentation, with increased abundance in highly fragmented sites; and two species were tolerant of fragmentation, with little to no effect of landscape variables on their distribution and abundance. Within urban habitat fragments, the carnivore visitation rate increased at sites with more exotic cover and closer to the urban edge, a pattern driven largely by the increased abundance of fragmentation-enhanced carnivores at edge sites. Finally, body size, in conjunction with other ecological characteristics, partially accounted for the heterogeneity in responses to fragmentation among carnivore species. These differential sensitivities are useful criteria for choosing appropriate focal species for ecological research and conservation planning, a choice that depends on the scale of fragmentation in a region and the commensurate responses of carnivore populations at that scale.*

Sensibilidad Relativa a la Fragmentación del Hábitat de Mamíferos Carnívoros

**Resumen:** *Examiné los efectos de la fragmentación del hábitat sobre la distribución y abundancia de mamíferos carnívoros en la costa del sur de California y evalué la predicción de que las respuestas a la fragmentación variaban con el tamaño corporal de carnívoros. Se realizaron muestreos de huellas para nueve especies nativas y dos exóticas en 29 fragmentos de hábitat urbano y 10 sitios control. El área fragmentada y su aislamiento fueron los dos principales descriptores de la distribución y abundancia de depredadores. Seis especies fueron sensibles a la fragmentación, generalmente las especies desaparecían conforme los fragmentos eran más pequeños y aislados, tres especies fueron favorecidas por la fragmentación, con incremento en su abundancia en sitios altamente fragmentados, y dos especies fueron tolerantes a la fragmentación con poco o ningún efecto de las variables del paisaje sobre su distribución y abundancia. Dentro de los fragmentos de hábitat urbano, las tasas de presencia de carnívoros incrementaron en sitios con mayor cobertura exótica y cercanos al borde urbano, un patrón dirigido principalmente por el incremento en la abundancia de carnívoros favorecidos por la fragmentación en el borde de los sitios. Finalmente, el tamaño corporal, conjuntamente con otras características ecológicas, fueron parcialmente responsables de la heterogeneidad en respuestas a la fragmentación entre especies de carnívoros. Estas sensibilidades diferenciales son un criterio útil para seleccionar especies focales apropiadas para investigaciones ecológicas y la planeación de la conservación, una selección que depende de la escala de fragmentación en una región y de las respuestas apropiadas de las poblaciones de carnívoros a esa escala.*

## Introduction

The destruction of habitat has been targeted as one of the most serious threats to biological diversity world-

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wide (Wilcove et al. 1998), and in areas with increasing urbanization, the loss and fragmentation of habitat is virtually inevitable. Mediterranean scrub habitats in coastal southern California are particularly threatened. Intensive development in the region over the past century has destroyed all but 10% of the native coastal sage scrub habitat (McCaull 1994). This habitat loss has created a "hotspot" of endangerment and extinction for the highly endemic biota in the region (Dobson et al. 1997). Mammalian carnivores are thought to be particularly vulnerable to local extinction in fragmented landscapes because of their relatively large ranges, low numbers, and direct persecution by humans (Noss et al. 1996; Woodroffe & Ginsberg 1998). The decline and extirpation of top predators from fragmented systems may generate trophic cascades that alter the structure of ecological communities (Crooks & Soulé 1999). Indeed, the persistence of these environmentally sensitive and ecologically pivotal species may be indicative of the integrity of entire ecosystems (Noss et al 1996). As such, mammalian carnivores can serve as useful tools for the study of ecological disturbances or for conservation planning and reserve design (Soulé & Terborgh 1999).

Mammalian predators are difficult to study, however, because of their low densities, nocturnal and secretive habits, and wariness of humans (Sargeant et al. 1998). As a result, the ecology of many carnivore species and their responses to ecological disturbances such as fragmentation are often poorly understood. Although considered members of the same ecological guild, carnivores may vary in their responses to fragmentation. In particular, differences in body size among carnivore species have been proposed as an important determinant of extinction probability (Brown 1986; Belovsky 1987). The relationship between body size and extinction risk in animals is complex, however, and has been the subject of considerable debate, with studies predicting and reporting positive, negative, or no relation of body size to extinction probability (reviewed by Johst & Brandl 1997). Few studies have evaluated if, how, or why carnivore species differ in their relative sensitivities to fragmentation effects.

My goal was to analyze the effects of the loss and fragmentation of habitat on mammalian carnivores in the urbanizing landscape of coastal southern California. Habitat fragmentation must be viewed as a multiscale problem, with fragmentation effects depending on the scale of fragmentation and the movement patterns of target species (Andren 1994). I therefore surveyed a suite of carnivore species that occur across a range of fragmentation levels and evaluated their responses to fragmentation at two spatial scales: (1) landscape-level heterogeneity among fragments and (2) local heterogeneity at sites within fragments. To allow for a more comprehensive assessment of relative sensitivities to fragmentation, I not only documented the presence or absence of each carnivore species, but also measured their relative abundance at each site. Finally, I tested the prediction that responses to fragmentation vary with body size in carnivore species, explored other ecological traits of these predators that may contribute to extinction risk, and used these differential sensitivities to evaluate the utility of mammalian carnivores as focal species with which to assess the degree of functional landscape connectivity.

## Methods

### Study Areas

I conducted carnivore surveys in 29 urban habitat fragments in coastal San Diego County from Fall 1995 through Summer 1997. Twenty-eight of these fragments were originally studied by Soulé et al. (1988). The fragments, completely surrounded by human-modified landscapes, are typically dendritic canyons dissecting coastal mesas, although a few also contain mesa-top habitat. The fragments support a mosaic of shrub habitat, including mixed chaparral, chamise chaparral, maritime succulent shrub, and coastal sage scrub, the dominant assemblage in most sites. Disturbed areas within fragments were typically dominated by ruderal weed species, ornamental plants invading from surrounding residences, fire-retardant ground cover such as South African iceplant (*Carpobrotus edulis*), and non-native trees (e.g., palms and species of *Eucalyptus* and *Acacia*) (Alberts et al. 1993).

From Fall 1995 through Summer 2000, I conducted carnivore surveys in less disturbed areas in coastal southern California to act as controls to the small, urban habitat remnants. These control areas varied in size and degree of isolation (Table 1), ranging from relatively small reserves isolated within urban developments (e.g., Point Loma Ecological Reserve) to large blocks of habitat relatively continuous with larger natural areas (e.g., Miramar Marine Corps Air Station).

### Carnivore Surveys

I assessed the distribution and relative abundance of nine native and two non-native predator species through track surveys. Native species were the mountain lion (*Felis concolor*), bobcat (*Felis rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), badger (*Taxidea taxus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), western spotted skunk (*Spilogale gracilis*), and long-tailed weasel (*Mustela frenata*). Non-native target species were the domestic cat (*Felis catus*) and Virginia opossum (*Didelphis virginiana*), a marsupial introduced to California around 1910 (Jameson & Peeters 1988).

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**Table 1. Landscape variables and distributions of 11 mammalian carnivore species for 10 control sites and 29 urban habitat fragments in coastal southern California (1, present; 0, absent).**

| | *Area (ha)* | *Age (yrs)* | *Distance Y (m)* | *Distance Z (m)* | *Long-tailed weasel* | *Spotted skunk* | *Badger* | *Mountain lion* | *Bobcat* | *Coyote* | *Gray fox* | *Striped skunk* | *Raccoon* | *Opossum* | *Domestic cat* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Control sites | | | | | | | | | | | | | | | |
| Miramar Marine Corps Air Station | 5806 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| Chino Hills State Park | 4452 | 0 | 200 | 200 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Limestone Canyon/Whiting Ranch | 4450 | 0 | 15 | 15 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| San Joaquin Hills | 4219 | 22 | 5353 | 2930 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Weir Canyon | 1923 | 0 | 69 | 69 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| Santa Margarita Ecological Reserve | 1763 | 0 | 30 | 30 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 |
| Starr Ranch | 1548 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Tenaja | 1191 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Torrey Pines State Reserve | 428 | 0 | 68 | 68 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Point Loma Ecological Reserve | 264 | 45 | 5700 | 5700 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| Urban fragments | | | | | | | | | | | | | | | |
| Florida | 102 | 59 | 2100 | 233 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| Torrey Pines Extenstion | 74 | 20 | 91 | 91 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Balboa Terrace | 56 | 43 | 121 | 117 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Alta La Jolla | 34 | 23 | 121 | 93 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Kate Sessions | 31 | 25 | 121 | 93 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Zena | 15 | 45 | 2865 | 467 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| Canon | 12 | 67 | 1219 | 1167 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| Laurel | 10 | 88 | 1554 | 350 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 32nd Street South | 10 | 65 | 304 | 233 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Pottery | 10 | 23 | 45 | 70 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| Washington | 9 | 83 | 365 | 187 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Syracuse | 9 | 27 | 40 | 70 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| Baja | 8 | 40 | 670 | 70 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Raffee | 8 | 28 | 61 | 163 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Solana | 8 | 20 | 550 | 187 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| Acuna | 7 | 31 | 110 | 47 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| Juan | 7 | 32 | 228 | 70 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Chollas | 6 | 45 | 1005 | 467 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Mil Cumbres | 6 | 20 | 550 | 23 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| Chateau | 6 | 29 | 110 | 47 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| Oak Crest | 6 | 15 | 400 | 140 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| 54th | 4 | 29 | 609 | 187 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 60th | 4 | 46 | 335 | 350 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Spruce | 4 | 95 | 1767 | 93 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Titus | 3 | 86 | 280 | 163 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Montanosa | 3 | 11 | 91 | 93 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| El Mac | 2 | 41 | 883 | 163 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| Poinsettia | 2 | 59 | 350 | 350 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |
| Talbot | 2 | 64 | 1219 | 933 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| Urban fragment occupancy | | | | | 0 | 0 | 0 | 0 | 2 | 26 | 25 | 21 | 19 | 26 | 25 |
| Total occupancy | | | | | 2 | 2 | 3 | 7 | 11 | 36 | 34 | 30 | 28 | 34 | 26 |

I established a series of track-detection stations at approximately 250-m intervals along dirt roads or trails (human and/or wildlife) along the main axis of each study area (Linhart & Knowlton 1975; Conner et al. 1983; Sargeant et al. 1998). Each track station consisted of a 1-m-diameter, 1-cm-deep, circle of freshly sifted gypsum baited with a liquid carnivore scent lure (Russ Carman's Pro-Choice and Canine Call, Sterling Fur & Tool, Sterling, Ohio) every other day. Track transects were checked and reset daily for 5 consecutive days. Tracks on each station were measured and identified to species; tracks with ambiguous identifications were omitted from analyses. Track surveys were conducted once each sampling quarter: fall (September–November), winter (December–February), spring (March–May), and summer (June–August). Each site was sampled for 1–2 years.

The track index of each carnivore species in each quarterly sampling session was expressed as the total number of visits recorded for a species, divided by the total sampling effort. I defined a visit as at least one track of a species on a track station (Conner et al. 1983). Mathematically, the track index ($I$) was calculated as

$$I = \ln[\{v_j/(s_j n_j)\} + 1],$$

where $v_j$ is the number of stations visited by a species in transect $j$, $s_j$ is the number of stations in transect $j$, and $n_j$ is the number of nights that stations were operative in transect $j$. Thus, $I$ for each species represents the visitation rate per track station per night in each study area. Although this index cannot be directly translated into numbers of individuals and hence does not measure absolute densities, it does provide an index of the relative abundance of a species at each sampling point (Conner et al. 1983; Sargeant et al. 1998). For each species, I averaged track indices across quarterly sampling sessions to derive a mean index at each study area for the duration of the study. Indices were log-transformed to meet normality assumptions in the statistical analyses. Overall, track surveys totaled 6540 station-nights ($s_j\, n_j$) among all study sites.

### Landscape Variables

I used area, age, and isolation to assess the effects of landscape-level fragmentation on carnivore populations (Table 1). I measured the total area of each fragment based on digitized images of scaled aerial photographs taken in 1995. Total area of each control site was defined as the reserve boundaries within which the surveys were conducted. Because control sites were often adjacent to unfragmented habitat, area approximations represent minimum estimates.

Fragment age, defined as the number of years since isolation of the habitat fragment by urban development, was based on dated aerial photographs and building permit records (Soulé et al. 1988). Because fragment age is highly negatively correlated to the proportion of native shrub cover within fragments (Suarez et al. 1998; Crooks et al. 2001), I used age to measure a time effect per se in the fragments and to represent the cumulative loss of native habitat in the entire fragment since isolation. Age was scored as zero for control sites that were directly adjacent to larger natural areas (Miramar Marine Corps Air Station, Starr Ranch Audubon Sanctuary, Tenaja Corridor) or that were separated from such areas by only a roadway and not by urban development (Chino Hills State Parks, Limestone Canyon/Whiting Ranch, Santa Margarita Ecological Reserve, Torrey Pines State Reserve, Weir Canyon).

Two variables were calculated to characterize the degree of isolation of each site: distance $Y$, the distance to the closest habitat patch (measured from patch edge to patch edge) of equal or larger size (Soulé et al. 1988), and distance $Z$, the shortest distance to any other habitat fragment, reserve, or possible movement linkage to such sites (e.g., riparian channels, power line easements, golf courses). Isolation was scored as zero for control sites directly adjacent to a larger natural area and as the width of the roadway for control sites isolated from larger habitat blocks by a roadway.

All landscape variables were log-transformed to meet normality assumptions in the statistical analyses. When only the urban habitat fragments were considered, fragment age was positively related to distance $Y$ ($r = 0.564$, $p = 0.001$) and distance $Z$ ($r = 0.526$, $p = 0.003$), and distance $Y$ was positively related to distance $Z$ ($r = 0.362$, $p = 0.053$). When both habitat fragments and control areas were included, area was negatively related to age ($r = -0.813$, $p < 0.001$), distance $Y$ ($r = -0.467$, $p = 0.003$), and distance $Z$ ($r = -0.299$, $p = 0.065$); age was positively related to distance $Y$ ($r = 0.741$, $p < 0.001$) and distance $Z$ ($r = 0.597$, $p < 0.001$); and distance $Y$ was positively related to distance $Z$ ($r = 0.761$, $p < 0.001$).

#### SPECIES RICHNESS AND DISTRIBUTION

Island biogeography theory predicts that landscape variables such as size and isolation should help determine the number of species on islands (MacArthur & Wilson 1967). To test this prediction, I calculated two measures of carnivore species richness for each study area: (1) the number of carnivore species detected at the site during the course of the study and (2) the number of native carnivore species detected, excluding the non-native opossum and domestic cat. A species was present in a study area if it was detected on track stations within the site at least once during the course of the study. Presence was verified with a combination of remotely triggered cameras, scat surveys, and opportunistic visual sightings. Presence of a species does not necessarily imply that the site can support resident animals or populations. Like-

wise, failure to detect a species at a site does not indicate that the species has never visited the area, but rather that it was not recorded during sampling sessions.

I used backward-elimination multiple regression to identify which landscape variables (size, age, and isolation) were the best predictors of carnivore species richness in a study site. Independent variables with $p < 0.15$ were included in all regression models to minimize exclusion of important predictors from the model, and tolerance values were set at 0.10 throughout to control for multicollinearity (Tabachnick & Fidell 1996). Comparison-wide error rates were examined in all statistical analyses (Mead 1988; Stuart-Oaten 1995) ( $p < 0.05$, statistically significant; $0.05 < p < 0.10$, marginally significant). I first conducted the multiple-regression analyses including only the 29 urban habitat fragments and then including all 39 study sites.

I used logistic-regression analyses to evaluate the effect of landscape variables on the distribution of individual carnivore species. First, I constructed bivariate logistic-regression models to evaluate the separate effects of area and isolation (distance $Z$) on the probability of occurrence for each species across all 39 study sites. Area and distance $Z$ were chosen because preliminary analyses indicated that they were the two strongest predictors of carnivore distribution. For species with significant area and isolation effects, I plotted logistic-regression curves of the probability of occurrence of each species as a function of area, holding isolation constant by substituting its median value into a two-way (area $\times$ isolation) logistic model. Likewise, I constructed isolation curves after holding area constant by substituting its median value into the two-way logistic model. From these curves, I calculated the area and isolation at which the probability of occurrence of the species equaled 50% and used these estimates to represent the relative area and isolation requirements for each species (following Crooks et al. 2001). Finally, I used multiple-logistic-regression models to graphically evaluate the combined effect of area and isolation on probability of occurrence for each species.

Logistic-regression estimates of probability of occurrences and relative area and isolation requirements are not intended, however, to represent the actual fragment size or isolation necessary to ensure the long-term persistence of a population (Hinsley et al. 1996). Rather, probability of occurrence measures the probability of an individual visiting the study area at least once during the course of the study, and the area and isolation estimates generated are intended to function only as relative indices of sensitivity to fragmentation. Area and isolation estimates are likely to be more accurate for those species with the most detections.

#### RELATIVE ABUNDANCE

I used backward-elimination regression models to identify which landscape variables were the best predictors of the track indices of each species in each study area. The analyses were first conducted including only the 29 urban habitat fragments. Mountain lions, spotted skunks, badgers, and long-tailed weasels were omitted from these analyses because they were not detected in any urban habitat fragments. Bobcats, detected in only two fragments, were also omitted.

I repeated the multiple-regression analyses across all 39 fragments and control sites, including mountain lions and bobcats in the analyses. Spotted skunks, badgers, and long-tailed weasels were again omitted due to low detection rates. Because the track indices for mountain lions and bobcats were zero for many sites, the results of these regressions must be interpreted with caution. The final regression models were determined largely by the patterns of species' presence or absence across sites and not by variation in relative abundance among sites where they occurred. Nevertheless, I report regression models for mountain lions and bobcats to allow for further evaluation of the effects of landscape variables on these species and for further comparisons of their fragmentation sensitivities to those of other carnivore species.

### Local Variables

Habitat heterogeneity within these urban habitat fragments is an important determinant of the persistence of native scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000), all potential prey for carnivore species. I measured three variables to investigate the effect of habitat heterogeneity on carnivore populations: distance to the urban edge, percent cover of native shrubs, and percent cover of exotic vegetation. I estimated the distance of each track station to the nearest urban edge (the backyards of the houses bordering the fragment) and log-transformed these values to meet normality assumptions in the statistical analyses. I used a Braun-Blanquet categorical scale (Kent & Coker 1992) to estimate the percent cover of native shrubs and of total exotic cover within a 20-m radius around each track station. The cover scale was 0 (<1%), 1 (1–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), and 5 (76–100%). Distance to edge was positively related to shrub cover ($r = 0.281$, $p = 0.007$) and negatively related to exotic cover ($r = -0.341$, $p = 0.001$), and shrub cover was negatively related to exotic cover ($r = -0.694$, $p < 0.001$).

#### SPECIES RICHNESS AND RELATIVE ABUNDANCE

I calculated the total number of carnivore species and the number of native carnivore species detected at each track station in the 29 urban habitat fragments during the course of the study; two exotic species (opossum and domestic cat) and five native species (bobcat, coyote, gray fox, striped skunk, and raccoon) were detected

in the urban fragments and were hence included in the analyses. I then used backward-elimination multiple regression to identify which local variables were the best predictors of carnivore species richness at each station.

I calculated the mean track index for each species at each track station in the 29 urban habitat fragments to generate relative abundance indices. Again, mountain lions, spotted skunks, long-tailed weasels, badgers, and bobcats were omitted from these analyses due to low detection rates within fragments. I then used backward-elimination multiple regression to identify which local variables were the best predictors of the relative abundance of each species at a station. Some species were absent from some fragments, however, an absence driven in part by landscape variables such as area, age, and isolation. I therefore conducted the regressions for each species after excluding from the analyses all fragments where that species was never detected. By excluding these fragments I could account for the effects of landscape-level fragmentation on the presence or absence of a species and therefore more fully analyze the effects of local variables within fragments where that species occurred.

To further evaluate the effect of the urban edge on carnivores within fragments, for each species I graphed the mean track index at each station as a function of the distance of that station from the urban edge. Edge distances were classified into five categories: 0–24 m ($n$ = 14 stations), 25–49 m ($n$ = 35), 50–99 m ($n$ = 16), 100–199 ($n$ = 19), and >200 m ($n$ = 7). Direct comparisons of track indices between species can be misleading, because the response of species to track stations may differ (Conner et al. 1983; Sargeant et al. 1998). To allow for more meaningful comparisons of track indices, I standardized the index for each species by dividing each value by the maximum track index recorded for that species. Therefore, these standardized track indices for each species ranged on a scale of 0 to 1.

### Body Size and Fragmentation Sensitivity

I evaluated the relationship between body mass and sensitivity to fragmentation among carnivore species through linear-regression analysis. As an index of sensitivity to fragmentation, I calculated the average area of study sites occupied by each species, multiplying the area of each study site by the standardized track index (scale 0 to 1) of that species at that site. With area weighted by relative abundance per sampling point, the indices accounted not just for occupancy but also for differences in the relative abundance of a species among study sites. For example, for a given species, some study sites supported resident populations, whereas other study sites were only visited temporarily during the course of the study. Average area weighted by relative abundance accounted for such differences. In addition, I also compared body mass to typical home-range sizes and population densities reported in the literature for these species.

## Results

### Landscape Heterogeneity: Comparisons among Fragments

#### SPECIES RICHNESS AND DISTRIBUTION

The distribution of carnivore species varied across study sites (Table 1). Coyotes, opossums, gray foxes, domestic cats, striped skunks, and raccoons were detected in most urban fragments. Bobcats were detected in 9 of the 10 control sites but in only 2 urban habitat fragments, and mountain lions were detected in only 7 control sites and no urban fragments. I recorded few to no visits of mountain lions and bobcats in the habitat fragments, despite higher sampling intensity per unit area (station-nights/total area of site) in the 29 fragments (mean = 8.30 station-nights/ha, SE = 0.910) than in the 10 control sites (mean = 0.43 station-nights/ha, SE = 0.158) ($t$ = 4.58, $p < 0.001$). Detections of spotted skunks, long-tailed weasels, and badgers were rare and occurred only in the larger habitat blocks.

Among the 29 urban habitat fragments, no landscape variables were retained as predictors of the total number of carnivore species in backward-elimination regression models (Table 2). When the opossum and domestic cat were excluded, however, the species richness of native carnivores exhibited a weak negative trend with fragment isolation (distance $Z$) and a weak positive trend with fragment age. When control sites were included in the analyses, both total carnivore species richness and native carnivore species richness increased with the area of the study site.

Logistic-regression models for each species indicated that the probability of occurrence across all sites was positively related to fragment area for coyotes ($\chi^2$ = 5.57, $p$ = 0.018), bobcats ($\chi^2$ = 29.85, $p < 0.001$), mountain lions ($\chi^2$ = 27.35, $p < 0.001$), spotted skunks ($\chi^2$ = 5.85, $p$ = 0.016), long-tailed weasels ($\chi^2$ = 5.37, $p$ = 0.021), and badgers ($\chi^2$ = 9.73, $p$ = 0.002). In contrast to these native carnivores, the probability of occurrence of domestic cats was higher in smaller fragments ($\chi^2$ = 22.63, $p < 0.001$). Area was not a significant predictor of probability of occurrence for gray foxes ($\chi^2$ = 0.24, $p$ = 0.627), striped skunks ($\chi^2$ = 1.81, $p$ = 0.178), raccoons ($\chi^2$ = 2.02, $p$ = 0.155), or opossums ($\chi^2$ = 0.357, $p$ = 0.550).

Logistic-regression models indicated that probability of occurrence across all sites decreased with fragment isolation (distance $Z$) for coyotes ($\chi^2$ = 6.92, $p$ = 0.008), bobcats ($\chi^2$ = 11.57, $p < 0.001$), and mountain lions ($\chi^2$ = 11.88, $p < 0.001$). In contrast, probability of oc-

**Table 2. Backward-elimination regression models of the effects of landscape variables on carnivore species richness and relative abundance among 29 urban habitat fragments and 10 control sites in coastal southern California.[a]**

| *Variables* | $R^2$ | *Whole-model* p | *Coefficient* | p |
|---|---|---|---|---|
| Urban habitat fragments | | | | |
| total species richness | | | | |
| n.s.[b] | | | | |
| native species richness | 0.146 | 0.129 | | |
| distance *Z* | | | −0.408 | 0.067 |
| age | | | +0.374 | 0.091 |
| coyote | 0.133 | 0.052 | | |
| area | | | +0.365 | 0.052 |
| gray fox | 0.114 | 0.074 | | |
| area | | | −0.336 | 0.074 |
| domestic cat | 0.393 | 0.002 | | |
| area | | | −0.550 | 0.001 |
| distance *Z* | | | +0.246 | 0.122 |
| opossum | 0.164 | 0.029 | | |
| area | | | −0.405 | 0.029 |
| striped skunk | | | | |
| n.s. | | | | |
| raccoon | | | | |
| n.s. | | | | |
| All sites | | | | |
| total species richness | 0.194 | <0.001 | | |
| area | | | +0.440 | <0.001 |
| native species richness | 0.372 | <0.001 | | |
| area | | | +0.610 | <0.001 |
| coyote | 0.15 | 0.015 | | |
| area | | | +0.388 | 0.015 |
| bobcat | 0.595 | <0.001 | | |
| age | | | −0.921 | <0.001 |
| distance *Y* | | | +0.607 | 0.004 |
| distance *Z* | | | −0.376 | 0.030 |
| mountain lion | 0.277 | <0.001 | | |
| age | | | −0.526 | <0.001 |
| gray fox | 0.197 | 0.005 | | |
| area | | | −0.444 | 0.005 |
| raccoon | 0.081 | 0.081 | | |
| area | | | −0.284 | 0.081 |
| domestic cat | 0.335 | <0.001 | | |
| area | | | −0.579 | 0.001 |
| opossum | 0.241 | 0.002 | | |
| area | | | −0.491 | 0.002 |
| striped skunk | | | | |
| n.s. | | | | |

[a]*Independent variables are fragment area, age, and isolation (distance* Y *and distance* Z*). Independent variables with* $p < 0.15$ *were included in the final regression models.*
[b]*No independent variables were retained in the regression model (*$p > 0.15$*); n.s., not significant.*

currence was higher in more isolated fragments for domestic cats ($\chi^2 = 4.25$, $p = 0.039$). Isolation was not a significant predictor of probability of occurrence for gray foxes ($\chi^2 = 0.35$, $p = 0.553$), opossums ($\chi^2 = 1.88$, $p = 0.171$), spotted skunks ($\chi^2 = 0.18$, $p = 0.671$), striped skunks ($\chi^2 = 0.69$, $p = 0.407$), raccoons ($\chi^2 = 0.06$, $p = 0.811$), long-tailed weasels ($\chi^2 = 1.74$, $p = 0.187$), or badgers ($\chi^2 = 2.62$, $p = 0.106$).

After I controlled for isolation effects, the estimated area at which probability of occurrence was 50% was 1 ha for coyotes, 1.8 $km^2$ for bobcats, and 23 $km^2$ for mountain lions (Fig. 1a). The probability of occurrence for domestic cats dropped below 50% in fragments larger than 1.4 $km^2$; cats were never detected in the interior of control sites, and few if any feral cats occurred in these sites.

After I controlled for area effects, the estimated fragment isolation (distance *Z*) at which probability of occurrence was 50% was 883 m for coyotes and 6 m for bobcats (Fig. 1b). The probability of occurrence for mountain lions was <50% across the entire isolation range of fragments. In contrast, the probability of occurrence for domestic cats was >50% across the entire range of fragment isolation.

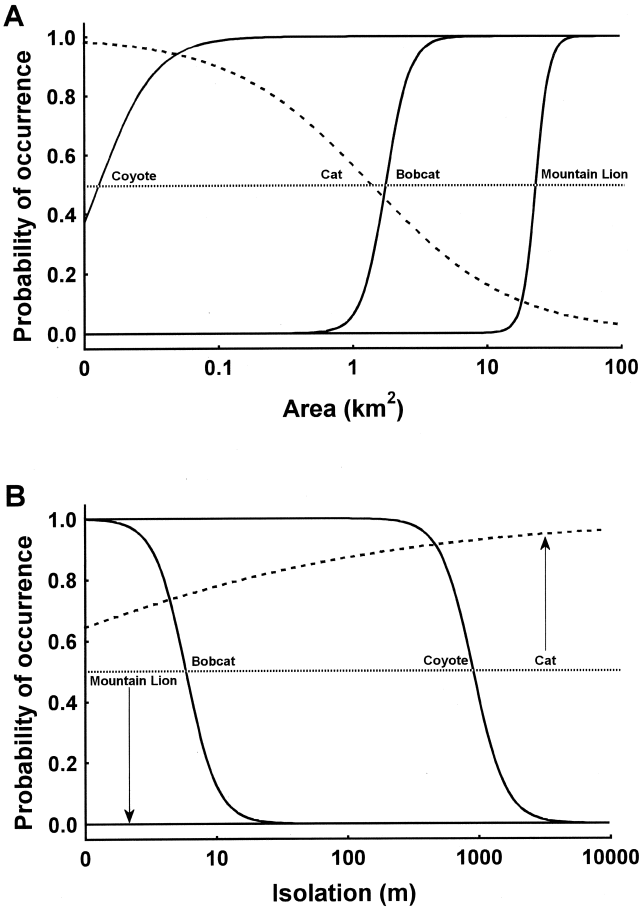


*Figure 1. Logistic-regression models of the probability of occurrence of native (solid lines) and exotic (dashed line) carnivores as a function of (a) fragment area and (b) isolation. Area and isolation curves were constructed after the other independent variable was held constant by substituting its median values into a two-way (area × isolation) logistic-regression model. Only species with significant area and isolation effects are presented. Dotted line represents 50% probability of occurrence.*

Multiple logistic-regression models of the combined effect of area and isolation on mountain lions, bobcats, and coyotes generated "extinction surfaces" that consisted of plateaus of occupancy at larger and less isolated sites that declined to basins of local extinctions at small and isolated fragments (Fig. 2). The effect of the area-isolation interaction, and hence the contour of the extinction surfaces, varied among species. The plateau for mountain lions was small and occurred only in the largest unfragmented sites, with large basins across all other study areas. The plateau for bobcats spanned a wider range of sites, but probability of occurrence dropped to zero in sites that were both small and isolated. Bobcats occurred in relatively small sites, but only those with little to no isolation. The plateau of coyotes was large, with a low probability of occurrence in only the smallest, most isolated urban fragments. Domestic cats exhibited a surface that was the inverse of these native predators. Their probability of occurrence was high in small and isolated fragments but lower in larger, less fragmented sites.

It should be emphasized, however, that the probability of residency or long-term viability of populations is undoubtedly lower than these probabilities of occurrence, particularly in smaller and isolated sites. For example, coyotes visited some fragments only temporarily during the course of the study. In some quarterly sampling sessions they were detected and in others they were not. Although the plateau of occupancy for coyotes encompassed most combinations of area and isolation, residency declined with fragment area. The average area of the 13 fragments in which coyotes came and went (mean = 0.75 [5.6 ha back-transformed], SD = 0.20) was smaller ($t = 3.01$, $p = 0.006$) than the average area of the 13 fragments in which coyotes were detected in every quarterly sampling session (mean = 1.19 [15.6 ha back-transformed], SD = 0.95).

#### RELATIVE ABUNDANCE

When only the 29 urban habitat fragments were included in the analyses, the relative abundance of coyotes at each sampling point was higher in larger fragments, whereas track indices of gray foxes, domestic cats, and opossums were higher in smaller fragments (Table 2). No variables were retained in the final model for raccoons and striped skunks ($p > 0.15$).

When control sites were also included in the regressions, coyote track indices at each sampling point again tended to be higher in larger sites. In contrast, the track indices of gray foxes, domestic cats, opossums, and raccoons were higher in smaller sites (Table 2). No landscape variables were retained in the models for the relative abundance of striped skunks.

When control sites were included in the regression models, fragment age was retained as the most significant predictor of the relative abundance of mountain lions and bobcats (Table 2); both species were less abundant in older sites. Mountain lions and bobcats were detected in relatively few sites, most of which were control areas not isolated by urban development (age = 0) and, for bobcats, a couple of recently isolated fragments (Table 1). This pattern generated the significant, negative slope between relative abundance and age for the two species.

The relative abundance of bobcats decreased with distance to the nearest movement linkage or natural area (distance $Z$) but, paradoxically, increased with distance to the nearest habitat patch of equal or larger size (distance $Y$). Bobcats were detected at sites that were relatively distant from larger natural areas (high values of

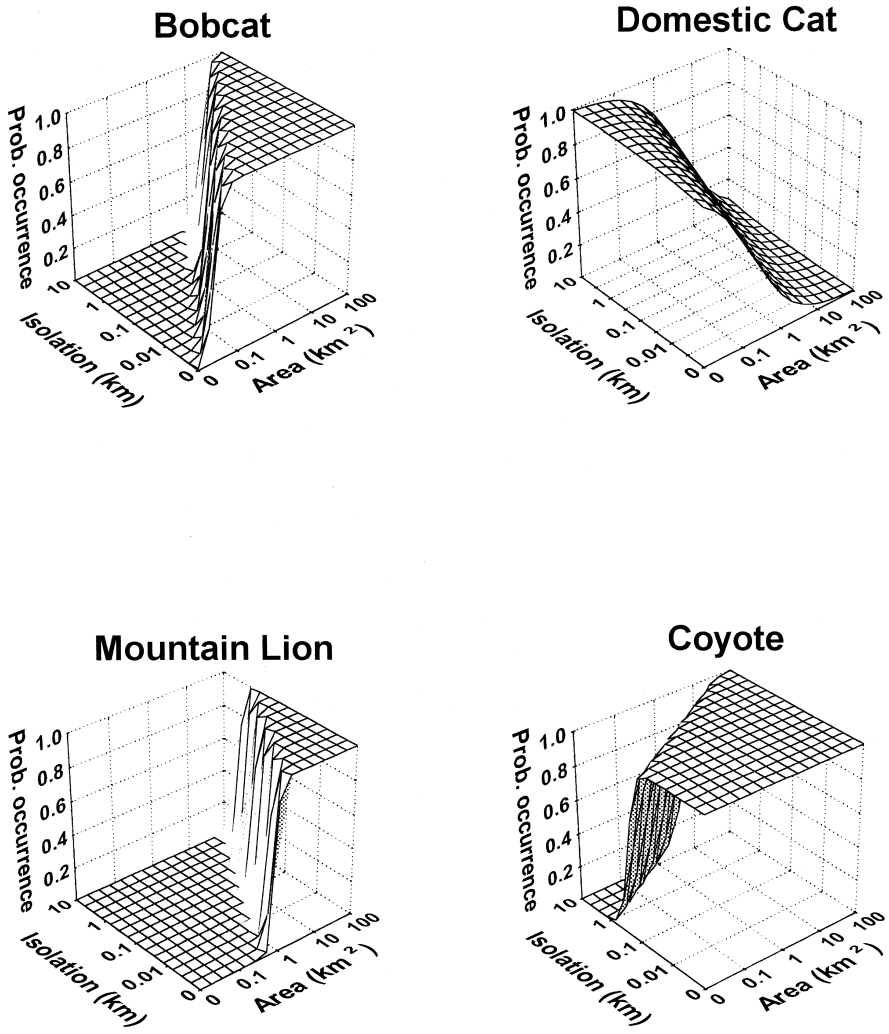


*Figure 2. Multiple logistic-regression models of the probability of occurrence of mountain lions, bobcats, coyotes, and domestic cats as a function of fragment area and isolation. Only species with significant area and isolation effects are presented.*

distance $Y$), but only if they were large or were near movement linkages to larger habitat blocks (low value of distance $Z$). For example, bobcats have persisted in the San Joaquin Hills, an isolated (distance $Y = 5353$ m) but large (4219 ha) habitat block. Bobcats were also detected in Mil Cumbres, a small (6 ha) urban fragment that was isolated from larger natural areas (distance $Y = 550$ m) but that was near a golf course (distance $Z = 23$ m), which likely served as a movement linkage to natural areas to the east.

### Local Heterogeneity: Comparisons within Fragments

#### SPECIES RICHNESS AND RELATIVE ABUNDANCE

The number of carnivore species detected was greater at track stations closer to the urban edge (Table 3). This pattern was largely determined by non-native species. When exotic predators (domestic cats, opossums) were excluded from the analyses, the number of native species detected at each station did not vary significantly with any local variables.

The relative abundance of gray foxes and opossums was higher at track stations near the urban edge within fragments where each species occurred (Table 3). The abundance of domestic cat exhibited a weak negative trend with distance to urban edge. The relative abundance of striped skunks tended to be higher at greater distances from the urban edge. Domestic cats and raccoons tended to be more abundant at stations with more exotic cover. No local variables entered the model for the relative abundance of coyotes.

A graphical analysis revealed that the coyote rate of visitation to track stations was high both near the urban edge and into the interior of the urban habitat fragments (Fig. 3). The abundance of striped skunks also was relatively high in the interior of fragments. In contrast, the abundance of opossums, gray foxes, domestic cats, and raccoons was relatively high within 50 m from urban development, but then tended to decline into the interior of the habitat fragment.

### Body Size and Fragmentation Sensitivity

When all species were included in the regression, the relationship between body mass (Table 4) and the average

**Table 3. Backward-elimination regression models of the effects of local habitat variables on carnivore species richness and relative abundance at 92 track stations within 29 urban habitat fragments in southern California.[a]**

| *Variables* | $R^2$ | *Whole-model* p | *Coefficient* | p |
|---|---|---|---|---|
| Total species richness | 0.049 | 0.036 | | |
| edge | | | −0.222 | 0.036 |
| Native species richness | | | | |
| n.s.[b] | | | | |
| Coyote (87 stations) | | | | |
| n.s. | | | | |
| Gray fox (85) | 0.146 | <0.001 | | |
| edge | | | −0.382 | <0.001 |
| Striped skunk (69) | 0.042 | 0.095 | | |
| edge | | | 0.205 | 0.095 |
| Raccoon (62) | 0.056 | 0.066 | | |
| exotic | | | 0.237 | 0.066 |
| Domestic cat (73) | 0.143 | 0.005 | | |
| exotic | | | 0.242 | 0.057 |
| edge | | | −0.205 | 0.105 |
| Opossum (79) | 0.079 | 0.013 | | |
| edge | | | −0.281 | 0.013 |

[a]*Independent variables are distance to urban edge, native shrub cover, and total exotic cover. Independent variables with* $p < 0.15$ *were included in the final regression models. For each species, stations were included only in analyses for those fragments where the species was detected.*
[b]*No independent variables were retained in the regression model (*$p > 0.15$*); n.s., not significant.*

area of study sites occupied by each carnivore species, weighted by the standardized track index of each species at each site, was not significant ($r = -0.392$, $p = 0.233$) (Fig. 4a). Spotted skunks, long-tailed weasels, and badgers, however, appeared to be outliers to an otherwise positive relationship between body size and average area of sites occupied. When these three species were excluded from the regression, the positive relationship was significant ($r = 0.725$, $p = 0.042$). Body mass was also positively related to typical home-range sizes (Fig. 4b: $r = 0.720$, $p = 0.012$) and negatively related to typical population densities (Fig. 4c: $r = -0.705$, $p = 0.015$) recorded for these species (Table 4).

## Discussion

### Landscape Heterogeneity and Carnivore Populations

Fragment area and isolation were the two strongest landscape predictors of predator distribution and abundance. Badgers, long-tailed weasels, spotted skunks, mountain lions, bobcats, and coyotes appear to be the species most sensitive to fragmentation, with a lower probability of occurrence and relative abundance per unit area in smaller and more isolated habitat patches. In contrast, the probability of occurrence and relative abundance of domestic cats, gray foxes, and opossums tended to decrease with fragment area and increase with fragment isolation. Landscape descriptors had relatively little effect on the distribution and abundance of raccoons and striped skunks. Because some carnivores were fragmentation-sensitive, some fragmentation-enhanced, and some fragmentation-tolerant, landscape variables appear to affect species composition more than species richness.

The probability of occurrence of mountain lions, bobcats, and coyotes declined in sequence as habitat patches became smaller and more isolated (Fig. 1). Because mountain lions, bobcats, and coyotes generally occurred in fragments above some threshold of size and isolation, local extinctions of their populations in a fragmenting landscape appear deterministic and predictable (Brown 1986). Such thresholds also suggest that, depending on the species and the degree of fragmentation, a single large reserve would have a higher probability of supporting populations of these predators than archipelagos of similar but smaller isolates (Soulé & Simberloff 1986). For example, our models predict that the probability of occurrence of bobcats will be low in 10 1-km$^2$ isolates but higher in a 10-km$^2$ reserve, and that the probability of occurrence of mountain lions will be low in 10 10-km$^2$ isolates but higher in a 100-km$^2$ reserve (Fig. 1).

Unlike true islands, habitat patches are part of a landscape mosaic, and the presence of a given species in a patch may be a function not only of patch size and isolation, but also of how the species perceives the intervening matrix (Andren 1994; Rosenblatt et al. 1999). In previous studies in this system, fragment age and area were the most important landscape predictors of the distribution and abundance of native plants (Alberts et al. 1993), scrub-breeding birds (Soulé et al. 1988; Crooks et al. 2001), rodents (Bolger et al. 1997), and invertebrates

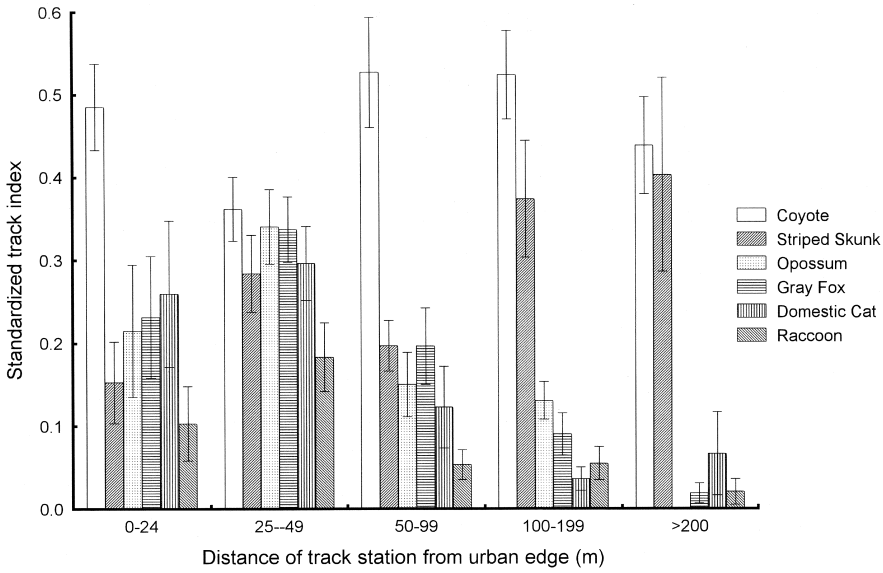


*Figure 3. Track indices of carnivore species within urban habitat fragments as a function of the distance of the station from the urban edge. Track indices are standardized for each species.*

(Suarez et al. 1998; Bolger et al. 2000). With limited exceptions, isolation effects were absent for these species, likely due to their strict habitat requirements and low dispersal capabilities (Soulé et al. 1992). For these taxa, little to no dispersal across developed areas resulted in complete isolation once fragmentation had occurred, with the fragments operating as true islands immersed within a relatively inhospitable matrix. My results also indicate that fragment isolation was not a strong predictor of the distribution and abundance of human-tolerant mesopredators, although the causal mechanisms differed. Unlike many native scrub-breeding birds, rodents, and invertebrates, mesopredator species such as raccoons, striped skunks, opossums, and domestic cats move through and reside within developed areas and thus perceive the urban matrix as somewhat permeable. High rates of movement through the matrix within which fragments are embedded should also minimize the effects of fragment isolation.

### Local Heterogeneity and Carnivore Populations

Within the urban fragments, exotic cover and distance to the urban edge were the strongest local predictors of carnivore distribution and abundance. These two variables were correlated, with more exotic cover and less native shrub cover closer to the urban edge. Previous studies have found that scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000) require native vegetation to persist in these fragments. Unlike many of these species, however, the mammalian carnivores detected in the habitat fragments are resource generalists that likely benefit from the supplemental food resources

**Table 4. Ecological characteristics of mammalian carnivores detected in coastal southern California.[a]**

| *Species* | *Weight (kg)* | *Home range ($km^2$)* | *Density ($km^2$)* | *Reference* |
|---|---|---|---|---|
| Mountain lion | 69.5 (36.0–103.0) | 492 (112–829) | 0.027 (0.005–0.048) | Beier & Barrett 1993; Nowak 1999 |
| Coyote | 13.5 (7.0–20.0) | 5.69 (0.66–11.96) | 0.3 (0.2–0.4) | Nowak 1999; Sauvajot et al. 2000 |
| Bobcat | 9.7 (4.1–15.3) | 2.94 (0.24–5.63) | 1.34 (1.15–1.53) | Lembeck 1986; Nowak 1999 |
| Badger | 8.0 (4–12) | 2.0 (1.6–2.4) | 2.70 (0.39–5.0) | Messick 1987; Nowak 1999 |
| Raccoon | 7.0 (2.0–12.0) | 0.52 (0.39–0.65) | 11.2 (2.3–20.0) | Nowak 1999 |
| Gray fox | 4.4 (1.8–7.0) | 0.69 (0.22–1.87) | 5.2 (0.4–10.0) | Nowak 1999; Riley 1999 |
| Domestic cat[b] | 3.9 (3.3–4.5) | 0.40 (0.001–3.80) | 150 (2–500) | Barratt 1997; Nowak 1999 |
| Opossum | 3.8 (2.0–5.5) | 0.20 (0.05–2.54) | 26 (2–116) | Nowak 1999 |
| Striped skunk | 1.6 (0.7–2.5) | 0.21 (0.11–0.37) | 3.3 (1.8–4.8) | Nowak 1999 |
| Spotted skunk | 0.6 (0.2–1.0) | 0.49 (0.34–0.65) | 24.4 (8.8–40) | Crooks & Van Vuren 1995; Kinlaw 1995; Nowak 1999 |
| Long-tailed weasel | 0.2 (0.09–0.34) | 0.62 (0.04–1.20) | 19.4 (0.38–38) | Nowak 1999 |

[a]*Estimates of body size, home range, and population density vary considerably (Nowak 1999). Values are typical averages and ranges (in parentheses). If no average estimate was provided, median values, calculated from the ranges, are presented. Body-mass estimates were taken from Nowak (1999). Where available, home ranges and population densities were taken from studies conducted in California.*
[b]*Estimates include studies from suburban, urban, rural, and island cat populations.*

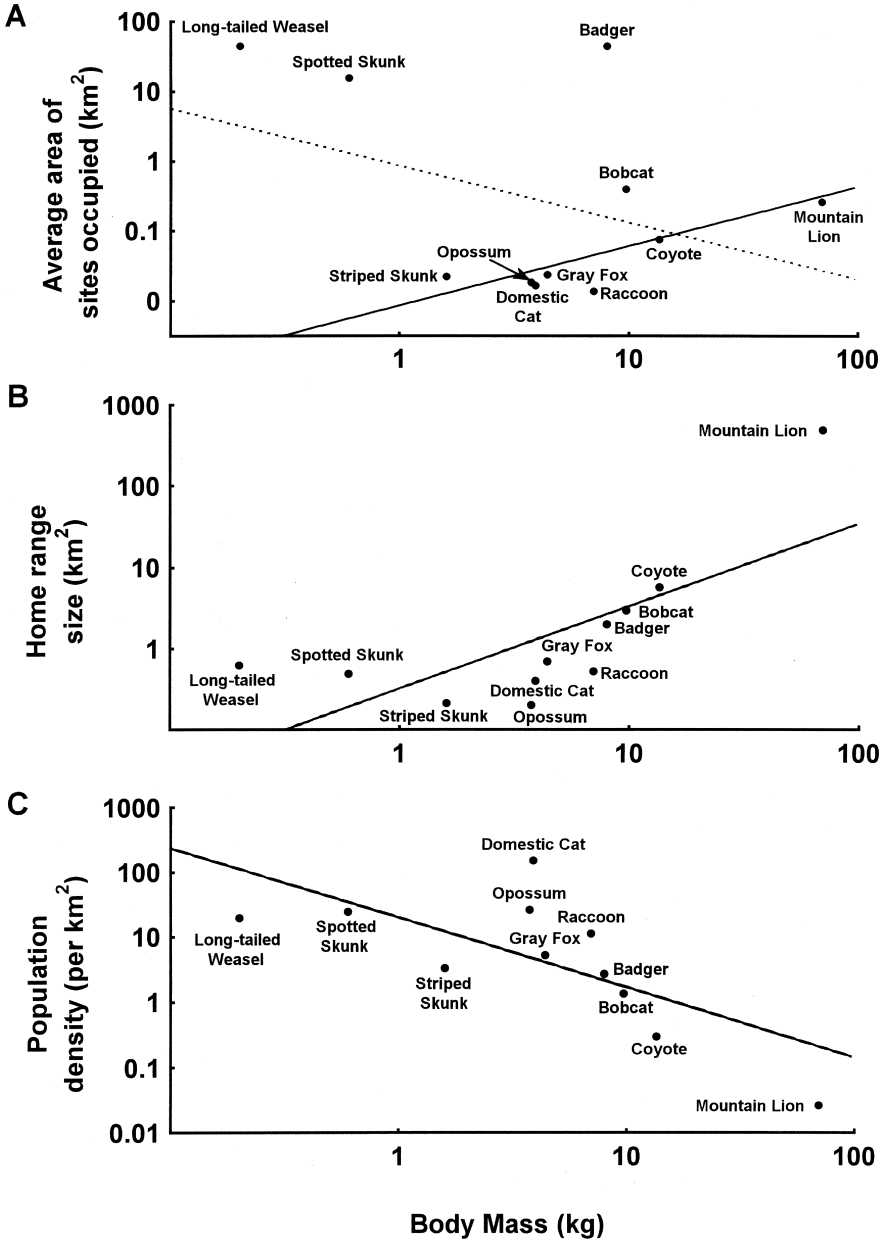


*Figure 4. Relationship between log body mass and (a) log average area of sites occupied by mammalian carnivores, weighted by the relative abundance of each species at each site, (b) log home-range size (*r = *0.720,* p = *0.012; see Table 4 for values), and (c) log population density (*r = *−0.705,* p = *0.015; see Table 4 for values). Dotted line in (a) is the least-squares regression fit including all species in the analysis (*r = *−0.392,* p = *0.233), and the solid line in (a) is the regression excluding spotted skunks, long-tailed weasels, and badgers (*r = *0.725,* p = *0.042).*

(e.g., garden fruits and vegetables, garbage, direct feeding by humans) associated with residential developments. As a result, the carnivore visitation rate actually increased at sites with more exotic cover and closer to the urban edge, a pattern determined largely by the increased abundance of fragmentation-enhanced mesopredators (gray foxes, opossums, and domestic cats) at edge sites within habitat fragments. Although some carnivores within the habitat fragments seem tolerant of disturbance, these fragments have already lost an entire suite of predator species, including mountain lions, bobcats, spotted skunks, long-tailed weasels, and badgers. Furthermore, the habitat fragments are relatively small (<100 ha), so the most "interior" sites within the fragments are still relatively near (<250 m) urban edges.

Unlike true islands, "edge effects" that emanate from the human-dominated matrix can increase the extinction probability of isolated populations (Murcia 1995; Woodroffe & Ginsberg 1998). Human-tolerant mesopredators in southern California represent such an edge effect. They occur within the developed matrix, are more abundant along the edges of habitat fragments, and are effective predators on birds, bird nests, and other vertebrates in this system and elsewhere (Crooks & Soulé 1999). Several factors likely account for increased numbers and activity of mesopredators in disturbed landscapes. Residential developments represent suitable habitat for some mesopredator species whose distributions are closely associated with human-dominated landscapes (Donovan et al. 1997). In addition to

habitat suitability, however, dominance interactions between carnivores affect mesopredator populations. When large, dominant predators disappear in fragmented systems, smaller, subordinant predators can subsequently undergo an ecological release, a pattern termed mesopredator release (Soulé et al. 1988; Crooks & Soulé 1999). In the San Diego habitat fragments, Crooks and Soulé (1999) found that lower visitation rates of coyotes in small, isolated remnants resulted in elevated numbers and activity of urban mesopredators, even after statistically controlling for potential confounding variables such as fragment area, age, and isolation. Mesopredator species therefore appear to be ecologically released by fragmentation not only because they can adapt well to urban environments, but also because such sites may provide refugia from dominant predators.

### All Carnivores Are Not Created Equal

Although they are generally considered part of the same ecological guild, I found that carnivores were heterogeneous in their sensitivities to landscape and local fragmentation variables. As predicted, body-size differences partially accounted for this heterogeneity in response. Body mass was positively related to typical home-range sizes (Fig. 4b) and negatively related to typical population densities (Fig. 4c) recorded for these species, patterns consistent with those observed among mammals (Lindstedt et al. 1986). Due to their wide ranges and low densities, larger-bodied carnivores generally required larger areas (Fig. 4a), eventually disappearing in habitat fragments that were not connected by movement corridors. Obvious exceptions to the allometry of body size and fragmentation sensitivity, however, were spotted skunks, long-tailed weasels, and badgers, small- to medium-bodied species that exhibit relatively small home ranges and high population densities but that were detected only in the largest habitat blocks. Unlike the generalist urban mesopredators, these relatively specialized mustelids tend to be primarily carnivorous and somewhat restricted in their habitat preferences (Nowak 1999). Such specializations likely contribute to their patchy distribution in coastal southern California and increase their vulnerability to environmental disturbances. Clearly, in addition to body size, other ecological traits such as diet, resource specialization, social structure, and behavior contribute to species-specific responses to fragmentation effects.

Differential sensitivities to fragmentation can be useful criteria when focal species are chosen for ecological research and conservation planning. Mammalian carnivores can be excellent focal organisms with which to evaluate the degree of functional landscape-level connectivity, because they are area-dependent species that require movement corridors for persistence (Beier 1993; Noss et al. 1996; Soulé & Terborgh 1999). The choice of appropriate carnivore focal species, however, depends on the scale or intensity of fragmentation in an area and the corresponding responses of carnivore populations to fragmentation effects at that scale. As Figs. 1 and 2 make evident, the scale of landscape-level connectivity in southern California varies widely, ranging from small, isolated urban remnants to large, intact habitat blocks.

At one extreme of the connectivity scale are the highly fragmented landscapes of urban coastal southern California (e.g., patch size $<1$ km$^2$; Fig. 1a). Coyotes and urban mesopredators can be useful focal species with which to understand the effects of fragmentation at this scale. Fragmentation-enhanced predators such as opossums and domestic cats can function as direct, positive indicators of environmental disturbances associated with urban development, edge effects, and the invasion of exotic predators and competitors into natural systems. Coyotes have also persisted in developed areas in southern California. The remarkable behavioral plasticity of coyotes and their ability to succeed in disturbed areas limits their utility as an indicator of connectivity across much of coastal southern California. Nevertheless, coyote occupancy, residency, and relative abundance declined with fragment area and isolation, to the point of local extinctions of coyote populations in the smallest, most isolated urban remnants. Coyotes can therefore serve as useful indicators of functional connectivity in highly fragmented areas, particularly those sites that have already lost more vulnerable predators such as bobcats and mountain lions (Figs. 1 & 2). Furthermore, the ecologically pivotal role of coyotes (Crooks & Soulé 1999) warrants their inclusion in research and conservation plans, particularly in regions with active predator-control programs.

Mountain lions are situated at the opposite end of the connectivity scale (e.g., patch size $>100$ km$^2$; Fig. 1a) and appear extremely sensitive to the loss and fragmentation of habitat. The large body size and solitary behavior of mountain lions translate to large home ranges and low population densities (Table 4). Therefore, many of the isolated habitat remnants in urban southern California are likely too small and too isolated to permanently support any resident lion populations (Figs. 1 & 2) (see also Beier 1993). Consequently, mountain lions or other large, apex predators may not be the most effective indicator species with which to evaluate the degree of functional landscape-level connectivity in moderately to highly fragmented landscapes. The mountain lion's requirement for a large home range and its sensitivity to environmental perturbations, however, can make it a valuable focal species in larger, more intact habitat blocks (Beier 1993).

Finally, bobcats were intermediate in their sensitivity to fragmentation, a degree of sensitivity commensurate to the scale of fragmentation across much of coastal

southern California (e.g., 1 $km^2$ <patch size < 100 $km^2$; Fig. 1a). Bobcats were less sensitive to disturbance than mountain lions, which seldom occurred in fragmented areas, yet were more sensitive than coyotes and mesopredators, which were detected in even small urban habitat fragments. Bobcats are generally solitary and are strictly carnivorous (Nowak 1999), resulting in low densities and in resource specializations that likely increase their probability of local extinction. Landscape connectivity appears to be the key to the persistence of bobcat populations in developing landscapes. They can persist in fragmented habitats, but, as my results suggest, only in those landscapes with adequate movement linkages to larger natural areas. The status of bobcat populations is therefore a valuable indicator of the degree of functional, landscape-level connectivity across much of the fragmented landscapes of coastal southern California. In other systems, the choice of indicator species will require information on the level of fragmentation and connectivity in that region and how species respond to fragmentation effects at that scale.

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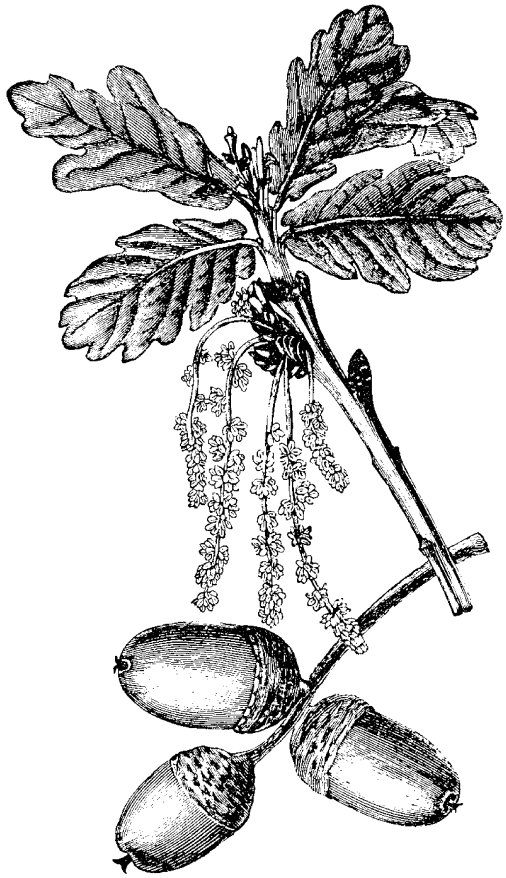

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# Effects of habitat loss and fragmentation on amphibians: A review and prospectus

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ABSTRACT

Habitat loss and fragmentation are among the largest threats to amphibian populations. However, most studies have not provided clear insights into their population-level implications. There is a critical need to investigate the mechanisms that underlie patterns of distribution and abundance. In order to understand the population- and species-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how the influences of multiple factors interact across extensive landscapes to influence population size and population connectivity. The goal of this paper is to summarize the state of knowledge, identify information gaps and suggest research approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. Reliable inferences require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Habitat connectivity appears to play a key role in regional viability of amphibian populations. In amphibians, population connectivity is predominantly effected through juvenile dispersal. The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Rigorous understanding of the effects of habitat loss and fragmentation on amphibians will require species-specific, multi-scale, mechanistic investigations, and will be benefit from integrating large empirical field studies with molecular genetics and simulation modeling. Molecular genetic methods are particularly suited to quantifying the influences of habitat structure across large spatial extents on gene flow and population connectivity. Conservation strategies would benefit by moving from generalizations to species and process specific recommendations and by moving from site-specific actions to implementing conservation plans at multiple scales across broad landscapes.

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## 1. Introduction

### 1.1. *The extinction crisis and amphibians*

Earth is facing the largest mass extinction in 65 million years (Lawton and May, 1995; Vitousek et al., 1997; Wilson, 1999; Myers and Knoll, 2001; Balmford et al., 2003). Current global extinction rates for animals and plants are estimated to be up to 1000 times higher than the background rate in the fossil record (Wilson, 1999; Baillie et al., 2004). Vertebrate animal taxa are disappearing at disproportionately high rates, and amphibians are the group with the highest proportion of

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species threatened with extinction (Stuart et al., 2004; Beebee and Griffiths, 2005). The 2004 IUCN red list of threatened and endangered species identifies one in three of the world's amphibian species as threatened with extinction (Baillie et al., 2004).

### 1.2. *Vulnerability of amphibians*

The apparent vulnerability of amphibians (Pechmann et al., 1991; Houlahan et al., 2000; Kiesecker et al., 2001; Baillie et al., 2004) may be due to a complex of factors, including: (1) relatively low vagilities, which amplifies the effects of habitat fragmentation (Sinsch, 1990; Gibbs, 1998; deMaynadier and Hunter, 2000; Bowne and Bowers, 2004), (2) high vulnerability to death when moving across roads and through inhospitable terrain, which depresses population growth rates (Fahrig et al., 1995; Carr and Fahrig, 2001; Carr et al., 2002), (3) often narrow habitat tolerances, which exacerbates the effects of habitat loss, degradation, and edge effects (Findlay and Houlahan, 1997; Semlitsch, 2000; Houlahan and Findlay, 2003), and (4) high vulnerability to pathogens, invasive species, climate change, increased ultraviolate-B exposure and environmental pollution (Pounds et al., 1999; Broomhall et al., 2000; Kiesecker et al., 2001; Blaustein et al., 2000; Hecnar, 1995; Bridges and Semlitsch, 2000; Davidson et al., 2001; Stuart et al., 2004).

### 1.3. *Importance of habitat loss and fragmentation*

Habitat loss and fragmentation contribute directly to most of these threats (Carr and Fahrig, 2001; Bowne and Bowers, 2004; Houlahan and Findlay, 2003). Recent research has provided information on the relationships between certain amphibians and certain attributes of habitat loss and fragmentation, and has clearly implicated the effects of habitat fragmentation on juvenile dispersal as one of the key issues in the conservation of pond breeding amphibians (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1994; Vos and Chardon, 1998). However, most studies of the influences of habitat loss, fragmentation, or related mortality risks have not provided clear insights into the population-level implications of these impacts (Carr et al., 2002). There is a clear need for studies that focus on the mechanisms that drive patterns of distribution and abundance (Marsh and Trenham, 2001; Bowne and Bowers, 2004).

### 1.4. *Moving from sites to landscapes; ponds to populations*

In order to understand the population-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how multiple factors interact across large spatial extents to influence population size and population connectivity (Ruggiero et al., 1994; McGarigal and Cushman, 2002; Bowne and Bowers, 2004). Non-spatial studies conducted at local scales do not provide a basis for inferences at the landscape or regional level (McGarigal and Cushman, 2002). There is often a gross mismatch between the scale of ecological research and population-level responses (Kareiva and Anderson, 1988; Ruggiero et al., 1994). For example, correlations between organism abundance and the area of various landcover types within a certain distance of a breeding pond does not provide information necessary to infer how habitat patterns interact with the spatial distribution of breeding ponds to influence distribution and abundance. Landscape-level studies that represent the spatial patterns of the environment in a manner relevant to the organisms of question, and that address species-specific movement and abundance characteristics are essential to extend fine-scale species environment relationships to the population-level (McGarigal and Cushman, 2002).

### 1.5. *Purpose and goals*

The overall goal of this paper is to summarize the state of knowledge, identify information gaps and suggest approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. The paper is divided into four major components. The first is a review of current knowledge about relationships between habitat loss and fragmentation and pond-breeding amphibian populations at landscape and regional scales. Using this review as context, the second section identifies some important information gaps and research needs. Next, I propose several research approaches that may be effective at filling these information gaps. Then, I suggest several ideas to link research more effectively to conservation, and suggest interim conservation strategies.

## 2. The state of knowledge

### 2.1. *Habitat area in uplands*

Relatively few landscape-level studies of amphibian density and movement have been conducted (Houlahan et al., 2000; McGarigal and Cushman, 2002). Most existing studies have focused on relationships between forest cover and species occurrence. These have shown positive relationships between amphibian populations and area of forest in the surrounding landscape (Dupuis and Steventon, 1999; Knutson et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005), and negative relationships with urban development (Delis et al., 1996) and roads (Fahrig et al., 1995; Carr et al., 2002). Studies of landscape composition effects have found relationships between forest cover and amphibian presence at spatial scales ranging from 100 m to over 3000 m radii (Hecnar and M'Closkey, 1997; Knutson et al., 1999; Lehtinen et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005). Several studies also note a general pattern of increased species richness with increasing forest cover (Gibbs, 1998; Kolozsvary and Swihart, 1999; Houlahan et al., 2000).

Despite these generalizations, reliable inferences about habitat area effects require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Species-specific characterization of habitat is essential if scientists are to evaluate the effects of habitat loss on populations. For example, the suggestion that forest cover in the landscape benefits amphibians may not apply to species that are fully aquatic or that depend on nonforested upland habitat. Also, some

populations of amphibians have been enhanced by human construction of ponds and wetlands in areas where breeding sites were previously limited, such as arid environments. In addition, the location and slope of critical thresholds in habitat amount are species specific, and related to reproductive potential, dispersal ability, home range size, habitat specificity, and other characteristics (Monkkonen and Reunanen, 1999; Fahrig, 2001). Thus, it is essential to explicitly link the habitat tolerances of a species to the extent and pattern of those habitats in the landscape if one is to produce reliable inferences about relationships between habitat area and species distributions.

### 2.2. *Habitat isolation*

Several studies have suggested that habitat area is often more important than habitat configuration (Fahrig, 1998, 2003; Cushman and McGarigal, 2004). The evidence for amphibians is equivocal on this question. Guerry and Hunter (2002) found positive associations between nine amphibian species, area of forested habitat and proximity of ponds to forest habitat. Seven of the nine species were associated with forest area. Three of the nine were associated with pond-forest adjacency. This indicates that habitat area and isolation are both important, and that the degree of importance is a species-specific property which likely reflects a combination of life-history and behavioral characteristics.

A growing body of work suggests that roads can have substantial negative effects on amphibian persistence (Vos and Chardon, 1998; Carr and Fahrig, 2001). Habitat fragmentation by roads and other barriers decreases dispersal (Gibbs, 1998; deMaynadier and Hunter, 2000), increases mortality (Fahrig et al., 1995; Carr and Fahrig, 2001) and reduces genetic diversity (Reh and Seitz, 1990). Habitat fragmentation leads to reduced patch size patches, increased patch isolation, and increased risk of demographic, stochastic and genetic events. This increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande, 1988; Sjögren-Gulve, 1994).

### 2.3. *Connectivity: a key to persistence*

A number of researchers have proposed that habitat connectivity is a key to regional viability of amphibian populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Semlitsch and Bodie, 1998; Skelly et al., 1999; Marsh and Trenham, 2001; Rothermel and Semlitsch, 2002). Amphibians generally have lower rates of movement per generation than invertebrates, mammals or reptiles (Bowne and Bowers, 2004). Low recruitment of dispersing individuals probably plays a major role in decline and extinction of amphibian populations in fragmented landscapes (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1998; Vos and Chardon, 1998; Bulger et al., 2003). Breeding sites lacking connectivity to suitable terrestrial habitat may be population sinks due to high mortality of juveniles during emigration (Rothermel, 2004). A number of studies have indicated that populations may decline if immigration is prevented (Brown and Kodric-Brown, 1977; Harrison, 1991) and may not be recolonized following a local extinction (Semlitsch and Bodie, 1998). Connectivity seems to be of particular importance as even in unfragmented landscapes, amphibian populations experience relatively frequent local extinction and turnover (Edenhamn, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003). Thus, dispersal is critical for recolonization of local populations and maintenance of regional populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999).

### 2.4. *Role of juvenile dispersal in population connectivity*

In amphibians, population connectivity is predominantly effected through juvenile dispersal (Madison, 1997; Preisser et al., 2001; Guerry and Hunter, 2002; Rothermel, 2004). Many studies have indicated that post-metamorphic dispersal contributes more to regional persistence than does adult dispersal (Sinsch, 1992, 1997; Sinsch and Seidel, 1995). For example, Preisser et al. (2001) found that adults of a variety of amphibian species move up to 125 m from breeding ponds, while juvenile *Ambystoma* sp. salamanders dispersed up to 670 m, and Wood frog (*Rana sylvatica*) over 1000 m. From this they concluded that juvenile dispersal is essential for landscape connectivity for these species. Other studies have reached similar conclusions based on the relatively small movement distances and philopatry of adults and relatively large dispersal distances of juveniles (Breden, 1987; Berven and Grudzien, 1990).

### 2.5. *Effects of fragmentation on population connectivity*

There are several important implications of habitat fragmentation on species persistence. First, a number of studies have shown that high levels of post-metamorphic survival are often required to maintain local populations. For example, one study found that survival to first reproduction had to exceed 18% in order to maintain local populations of the California tiger salamander (*Ambysotma californiense*) (Trenham et al., 2000). However, as they report survival to maturity of less than 5%, they conclude their study population is a sink that would be doomed to extinction in the absence of substantial immigration. In addition, a population model developed for marbled salamander (*Ambystoma opacum*) suggested that post-metamorphic survival had to exceed 70% to maintain local populations (Taylor and Scott, 1997). Second, a number of studies have shown substantial reductions in dispersal success and juvenile survival in fragmented landscapes. For example, Rothermel (2004) found an average of only 9% of juvenile spotted salamander (*Ambystoma maculatum*) released 50 m from a forest edge survived their initial migration to forest. Habitat loss and fragmentation can substantially reduce the abilities of juvenile amphibians to disperse across landscapes and the resulting reductions in post-metamorphic survival and population connectivity can threaten viability.

Recently, a number of studies have investigated the relationships between landscape structure and amphibian dispersal with experimental methods. Both spotted salamanders and wood frogs avoid crossing fields, pastures, clearcuts, lawns, and roads (Windmiller, 1996; Gibbs, 1998; deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Regosin et al., 2003; Marsh et al., 2004). Wood frogs have also been

shown to orient toward forest (deMaynadier and Hunter, 1999). Rothermel and Semlitsch (2002) studied the orientation and movement of several amphibian species in open field and forest environments. They found that orientation of spotted salamander and wood frog is biased toward forest. Spotted salamanders moved three times as far into forest as into fields (Rothermel and Semlitsch, 2002). Lower recapture rates in fields reflected high mortality rates due to desiccation and predation. Also, avoidance of open-canopy habitats by juvenile American toads (*Bufo americanus*) indicates that predictions of dispersal behavior based on adult habitat use may be misleading (Rothermel and Semlitsch, 2002). Rothermel (2004) conducted an experimental study of movement of spotted salamanders and American toads in grass fields at distances of 5 or 50 m from a forest edge. Less than 15% of salamanders and toads released 50 m from the forest edge reached forest, suggesting that few juvenile amphibians would be able to migrate greater distances across pastures (Rothermel, 2004). The authors conclude that fields are substantially resistant, and thus forest fragmentation reduces dispersal rates for these species (Rothermel and Semlitsch, 2002; Marsh et al., 2004; Rothermel, 2004).

Recent research has also suggested that the short-term impacts of habitat fragmentation often increase both with population size and dispersal ability, but particularly strongly with increasing dispersal ability (Gibbs, 1998; Newcomb Homan et al., 2004). This pattern is opposite to what many researchers expect on theoretical grounds, namely that species with larger populations and larger dispersal abilities will be less impacted by fragmentation due to their relatively greater abilities to disperse between breeding sites in fragmented landscapes. For example, in a study of five amphibian species across a gradient of habitat loss, Gibbs (1998) found that organisms with low dispersal rates had better persistence in landscapes with low habitat area. This effect has also been seen in comparison of wood frog and spotted salamander habitat occupancy (Newcomb Homan et al., 2004). A possible explanation is that greater dispersal ability results in greater mortality risk in fragmented landscapes. Carr and Fahrig (2001) suggest that highly vagile organisms may be at a disadvantage in landscapes with roads because of increased likelihood of mortality. An example of this may be the response of red-spotted newt (*Notophthalmus viridescens*) in fragmented landscapes (Guerry and Hunter, 2002). Red-spotted newts appear to have high sensitivity to habitat loss and forest fragmentation. In one study, they were the first species to disappear from a fragmented landscape (Gibbs, 1998). The terrestrial stage of red-spotted newts may last seven years (Forester and Lykens, 1991) in which they may travel long distances from the natal pond (Gill, 1978). Declines in fragmented landscapes are probably often related to elevated losses of juveniles in the terrestrial period (Gibbs, 1998). The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. In a fragmented landscape individuals of species with large dispersal abilities will generally encounter roads and other anthropogenic barriers at higher rates than less vagile species. This will tend to increase mortality rates for these species. The combined effects of roads and landcover may result in high rates of death among dispersing juveniles, which can imperil local and regional populations by decreasing recruitment (Sinsch, 1992, 1997; Sinsch and Seidel, 1995).

It appears that species with large dispersal abilities and those with relatively small dispersal abilities are both threatened by habitat loss and fragmentation, but in different ways. Those with large dispersal abilities are vulnerable to elevated dispersing mortality, which appears sufficient to lead to local extinctions (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999). However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Once these local populations are isolated by fragmentation they may be ultimately doomed to extinction. Amphibian populations experience relatively frequent extinction and turnover (Edenhamn, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003), thus population connectivity is ultimately important even for populations of species that are not directly impacted by habitat loss or elevated mortality risks in dispersing.

## 3. Challenges to general knowledge

### 3.1. *Lack of species-level information*

Despite these generalizations, there are several obstacles that must be overcome before scientists will be able to reliably predict population-level responses of specific species to changes in habitat area or isolation. In most parts of world, there is very limited knowledge of the species–environment relationships of amphibians, their responses to habitat loss and fragmentation and the factors controlling population connectivity (Hazell, 2003). Knowledge is still quite rudimentary about the population-level implications of habitat area, edge, isolation, and road mortality relationships. The precision of knowledge about the habitat relationships, life-history, vagility and behavior of most amphibian species is insufficient. Few studies report population level effects of inter-patch movement and few document movement rates (Bowne and Bowers, 2004). In addition, those studies that do measure movements rarely produce results that can be generally applied, as dispersal data are highly sensitive to sampling scheme and landscape characterization (Carr and Fahrig, 2001). Amphibians exhibit a great range of habitat requirements and dispersal abilities (Stebbins and Cohen, 1995). Little is known about the factors influencing dispersal (Rothermel and Semlitsch, 2002; Rothermel, 2004). Information about the dispersal abilities and relative cost or risk of crossing various landcover types is insufficient for most species to reliably model responses to real landscape mosaics. Additional research is needed to determine appropriate threshold distances and cover-class resistance values for migrating amphibians (Rothermel, 2004). Furthermore, the high variability of population sizes through time confounds efforts to isolate mechanisms through correlative means (Alford and Richards, 1999). The combination of variable population sizes and imprecise knowledge of dispersal parameters and habitat tolerances presents a daunting challenge for researchers attempting to infer population-level impacts of habitat loss and fragmentation on amphibians.

Another obstacle to population-level predictions is that few landscape level studies of habitat fragmentation effects have been conducted. McGarigal and Cushman (2002) reviewed 134 papers on habitat fragmentation published between 1995 and 2000. They identified a paucity of experimental studies at the landscape-level. Most studies were patch-based, and poorly replicated or unreplicated, which greatly limits the inferences that can be reliably drawn. Importantly, they identified amphibians and reptiles as the animal taxa most poorly studied, accounting for only 4% of papers on the effects of habitat fragmentation.

## 4. Research needs

### 4.1. *Importance of species-specific, multi-scale, mechanistic investigations*

Survival of amphibian populations in fragmented landscapes depends on the interaction between the pattern of roads, landcover types, the distribution of breeding ponds, the population sizes in those ponds and the dispersal characteristics of the species (Fahrig, 1998; Carr and Fahrig, 2001). For example, Porej et al. (2004) emphasize the importance of considering scaling differences among species and the structure of the landscape mosaic when investigating thresholds and minimum patch sizes. Furthermore Marsh and Trenham (2001) suggest that pond isolation is often better explained by details of the structure of terrestrial habitats than the distribution of breeding habitats in that landscape, and urge researchers to focus on mechanisms underlying patterns of dispersal and abundance. Petranka et al. (2004) found that there is often a lack of demographic independence within clusters of local breeding ponds, and that the degree of spatial synchrony in local populations varied between species and in response to localized disturbances. Predicting such effects would require information about species specific responses to disturbance, population sizes, movement rates and abilities. Both Monkkonen and Reunanen (1999) and Fahrig (2001) predicted that the location and slope of critical thresholds in habitat amount should be species-specific, and based on a variety of traits including reproductive potential, emigration success, home range size, habitat specificity, dispersal ability and other behaviors.

Each species experiences and responds to ecological conditions in its environment uniquely. Thus, reliable understanding of interactions between species and their environments requires careful attention to both scale and the characterization of the environment. First, species-environment relationships may differ greatly among species across scales (Cushman and McGarigal, 2004). The environmental patterns that are important at one scale for a species may not be those that influence it at coarser or finer scales (Grand and Cushman, 2003). Thus, researchers must adopt multi-scale approaches that allow for assessment of the interaction of environmental patterns across scales (Wiens, 1989; Cushman and McGarigal, 2003). Second, the environment is experienced differently among species. Thus, researchers should select and characterize the environmental attributes on a species-specific basis. For amphibians, this often means assessing interrelationships between multiple environmental attributes, across a range of scales, for entire landscapes containing dozens or hundreds of local breeding populations. Only by analyzing species-relevant habitat patterns at scales relevant to the populations of those species will it be possible to obtain reliable inferences about the impacts of habitat loss and fragmentation on amphibian populations (McGarigal and Cushman, 2002).

## 5. Research approaches

### 5.1. *Empirical approaches*

There are at least four major ways that one could empirically test relationships between the presence or movement of a particular species and environmental structure at the landscape-level. First, one could conduct large-scale, correlative studies of distribution in relation to habitat composition and configuration at a range of scales (Hecnar and M'Closkey, 1996; Knutson et al., 1999; Kolozsvary and Swihart, 1999; Vallan, 2000; Guerry and Hunter, 2002; Weyrauch and Grubb, 2004). Such studies, if replicated sufficiently at the landscape level, can provide reliable information about relationships between landscape structure and the distribution of specific amphibians. The major challenges to such studies are obtaining sufficient replication at the landscape-level to achieve reasonable statistical power, sampling sufficiently large landscapes to allow adequate consideration of environmental patterns at a range of spatial scales, and representing environmental conditions and landscape structures in manners that are relevant to each species in question (McGarigal and Cushman, 2002). These types of studies are also limited in inference because they do not directly measure biological responses such as mortality, movement and productivity. Presence does not always equate to quality. Patterns of distribution do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns.

Two alternative approaches are mark-recapture and telemetry studies (deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Rothermel, 2004). By quantifying movement rates, distances and routes of dispersing juveniles through complex environments researchers can describe species-specific responses to environmental conditions. Importantly, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal and Cushman, 2002). The challenge in these studies is one of cost and sample sizes. Large-scale manipulative field experiments and mark-recapture metapopulation studies are exceptionally expensive to implement, take a number of years to produce reliable results, and generally do not provide large landscape-level sample sizes due to financial and logistical constraints. Likewise, telemetry studies are often limited by spatial scope, sample size and pseudoreplication (Litvaitis et al., 1994).

A fourth alternative involves using molecular genetic methods to empirically derive rates of gene flow among ponds and effective population sizes (Schwartz et al., 1998;

Manel et al., 2003; Curtis and Taylor, 2004; Funk et al., 2005). Molecular genetic methods offer a particularly attractive approach to quantifying gene flow across heterogeneous landscapes, as the logistical and financial costs of extensive mark-recapture study grids are obviated. The genetic characteristics of subpopulations at each sampled pond can provide both information on its effective population size and the degree to which it differs genetically from other ponds. Such methods allow one to quantify rates of gene flow between ponds, assuming time lags between landscape change and genetic response have been accounted for. This in turn allows researchers to test specific hypotheses about the role of specific landscape features and environmental conditions in affecting population connectivity (Manel et al., 2003).

### 5.2. *Simulation models*

Simulation models offer a flexible way to investigate the behavior of idealized ecological processes in idealized landscapes. It is important to understand that this idealization in simulation modeling is both a limitation and an asset. It is a limitation in that a simulation is never equivalent to the phenomena being simulated. Decisions are made on which processes to include, at which scales, their relative weights, the functional structure of each and how they interact. Similarly, decisions are made on how to represent the structure and composition of landscapes and how to represent the behavior and ecology of organisms. These decisions fundamentally determine the results, and error in them results inevitably in error in the predictions.

However, the fact that such decisions determine results can also be an advantage. By varying functional parameters, environmental characterization, and organism attributes, scientists can investigate hypotheses about the relative influence of different factors, their interactions, and ranges of organism characteristics, such as gradients of population size or dispersal ability. This provides a means for thorough evaluation of complexes of factors that would be impossible to investigate directly in the field.

### 5.3. *Integrating simulation models and empirical field studies*

Simulation results are not compelling unless verified by empirical data. Reliable model predictions depend on accurate algorithmic implementation of the process–pattern relationships that dominate the behavior of the phenomena being simulated. Models require extensive empirical understandings for their formulation, and require extensive empirical data for their verification. It can be said that models without data are not compelling, and data without models are not informative.

A powerful research paradigm is based on confronting models with rigorous empirical data to test the applicability and generality of relationships, and account for the influences of spatial patterns, temporal fluctuations and time lags (Kareiva and Anderson, 1988). It is an iterative process, with models proposing relationships, data refuting or supporting models, models being refined as a result and producing new predictions to be empirically tested. Field studies should be designed specifically to provide information needed to parameterize and test simulation models. In this effort, manipulative experiments may provide the best information, given their ability to isolate particular factors. However, the most promising area for integrating models with field data is in the area of landscape genetics (Manel et al., 2003). Simulation models can produce explicit predictions of the level of connectivity among populations across landscapes. Molecular genetics can quantify actual rates and patterns of gene flow. The intersection of these two provides a means to optimize the fit of simulation models to actual patterns of gene flow in complex landscapes. This optimization of the fit of spatial models to patterns of gene flow in real populations provides an unprecedented means to explore and understand the interactions between environmental patterns across a range of spatial scales and the connectivity of populations, which is among the most important questions in conservation biology.

## 6. Conservation strategies

### 6.1. *From general to specific*

A number of researchers have proposed generalized conclusions and conservation recommendations based on the observation that forest habitat area, habitat connectivity and road density are related to population persistence and population connectivity. These generalizations include that the effects of adjacent land use on amphibians can extend over large distances (Houlahan and Findlay, 2003), and that the proximity and area of upland/breeding habitat play a key role in determining occupancy (Laan and Verboom, 1990; Pope et al., 2000). It is clearly important to account for impact of uplands surrounding wetlands (Dodd and Cade, 1998; Semlitsch, 1998) as amphibian conservation often requires maintaining relatively large forest areas and relatively low road densities in the regional landscape (Houlahan et al., 2000). However, it is not clear how to translate these general understandings to specific management recommendations for individual species in any given landscape. There are large differences among amphibian species in terms of their habitat requirements and sensitivity to landscape change. Effective conservation requires specific predictions that can be applied to unique situations to produce conservation recommendations tailored to the system, species and situation.

### 6.2. *Core area conservation*

Several researchers have proposed conservation strategies based on protecting core areas based on limited adult migration and adult philopatry. For example, Bulger et al. (2003) suggested that specific protections for migrating California red-legged frogs *(Rana aurora draytoni)* were usually unwarranted and that protecting breeding sites is critical. Other researchers propose core zone widths based on adult migrations. For example, Semlitsch (1998) and Semlitsch and Bodie (2003) suggest core zones up to 218 meters for pond breeding amphibians and up to 290 meters for amphibians in general. Other researchers stress the importance of forest in core zones for persistence of spotted salamander, marbled

salamander, Jefferson's salamander (*Ambystoma jeffersonianum*), and wood frog, based on the fact that they are unlikely to persist and travel long distances in non-forest habitat (Whitford and Vinegar, 1966; Thompson et al., 1980; Douglas and Monroe, 1981; Kleeberger and Werner, 1983; deMaynadier and Hunter, 1998; Rothermel and Semlitsch, 2002). While these core zones have been advocated by some as a guide for setting biologically meaningful buffers for wetlands and riparian zones (Semlitsch and Bodie, 2003), they are insufficient as a basis for a conservation strategy for pond breeding amphibians. Any effective conservation strategy must consider more than critical core habitat for adults (Porej et al., 2004). Juvenile dispersal and habitat connectivity are at least as important (Carr and Fahrig, 2001).

### 6.3. *Landscape-level, population-based conservation strategies*

Just as it is necessary to move from site-specific to landscape-level analyses to understand the ecological relationships between amphibian populations and their environments, it is also necessary to base conservation planning on landscape-level and population-based approaches. Non-spatial conservation plans implemented at specific sites are unlikely to provide adequate conservation of populations that depend on dispersal across complex landscapes for persistence. Just as there is often a gross mismatch between the scale of ecological research and population-level responses, there is usually the same mismatch between the scale of conservation planning and the scale of population responses.

Effective conservation planning will require vast improvements in our understanding of the factors that influence vital rates, mortality and dispersal in complex landscapes. Given the urgency of the crisis facing amphibian populations (Baillie et al., 2004), it is imperative that conservation planners make the most effective use of the information currently available. This will entail extending information from empirical research on the relationships between population size, reproduction, dispersal, mortality and habitat factors across a range of scales to spatially explicit conservation proposals. These extensions can be made in a variety of ways, including through landscape genetic analysis and spatially explicit simulation models.

## 7. Summary

- Habitat loss and fragmentation are among the largest threats to amphibian populations.
- The extent, pattern and quality of terrestrial habitat in landscape mosaics are as important for many species as the quality of breeding sites.
- Many species of amphibians appear vulnerable to both the loss and fragmentation of nonbreeding upland habitat.
- Population connectivity appears to be a key to regional viability, and is primarily effected through juvenile dispersal.
- In fragmented landscapes, dispersal survival is often lower than required for population viability.
- The preponderance of evidence suggests that the short term impacts of habitat loss and fragmentation increase with dispersal ability.
- Species with limited dispersal abilities are equally imperiled by habitat loss and fragmentation over longer time periods.
- Combining molecular genetics and spatial modeling of organism movement provides a means to improve understanding of how habitat amounts and configurations influence dispersal, survival and population dynamics.
- Effective conservation of amphibian populations is limited by the lack of species-specific ecological knowledge, and lack of landscape-level studies of the effects of habitat loss and fragmentation on movement, survival rates, and population dynamics.
- Conservation strategies could benefit from taking multiscale, landscape-level approaches that integrate knowledge of species biology with broad-scale evaluations of the area and accessibility of both breeding and nonbreeding habitat.

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21

# Biological corridors and connectivity

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*hring utan ymbbearh, þæt heo þone fyrdhom ðurhfon ne mihte, locene leoðosyrcan laþan fingrum.*

*On his shoulder lay braided breast-mail, barring death, withstanding entrance of edge or blade.*

**Beowulf (Old English epic poem, c. 10th Century)**

## Introduction

The ability of individual animals to move across complex landscapes is critical for maintaining regional populations in the short term (Fahrig 2003; Cushman 2006), and for species to shift their geographic range in response to climate change (Heller & Zavaleta 2009). As organisms move through spatially complex landscapes, they respond to multiple biotic and abiotic factors to maximize access to resources and mates while minimizing fitness costs such as mortality risks. Habitat fragmentation decreases dispersal success (Gibbs 1998), increases mortality (Fahrig et al. 1995) and reduces genetic diversity (Reh & Seitz 1990; Wilson & Provan 2003). Local populations may decline if immigration is prevented (Brown & Kodric-Brown 1977; Harrison 1991) and may prevent recolonization following local extinction (Semlitsch & Bodie 1998).

The goal of this chapter is to describe the state of the art in quantitative corridor and connectivity modelling. We will review several critical issues in modelling, and provide expert guidance and examples to help practitioners implement effective programmes to preserve, enhance or create connectivity among wildlife populations. We first

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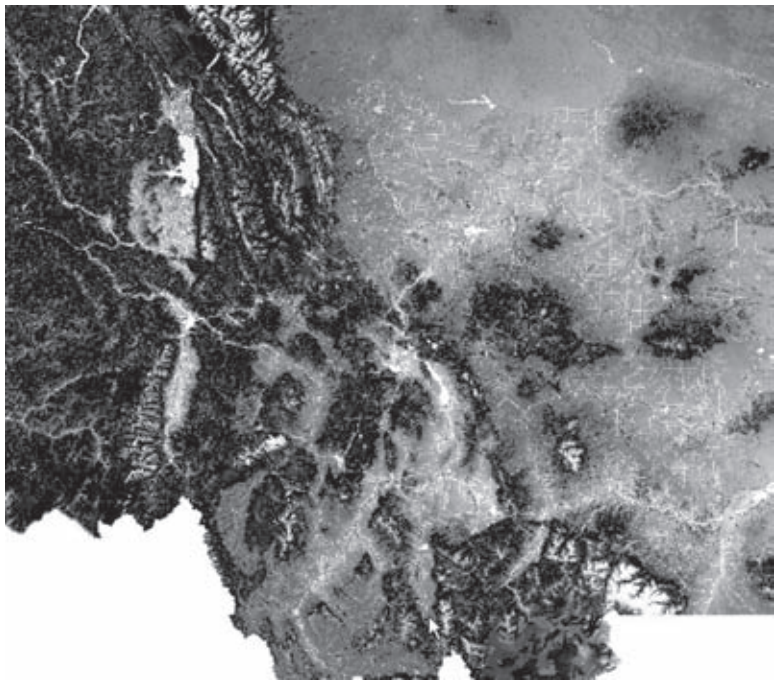


**Figure 21.1** Example landscape resistance map for American black bear in an area of the US northern Rocky Mountains encompassing Montana and northern Idaho. Dark areas are low resistance for movement, while light areas are high resistance for movement. The resistance map was developed by Cushman et al. (2006) and validated with independent data by Cushman & Lewis (2010) and in multiple independent study areas by Short Bull et al. (2011).

review the fundamental task of estimating landscape resistance, comparing expert opinion and empirical methods. Next, we describe current methods of predicting connectivity from resistance surfaces. Then we discuss how to develop linkage designs that can maintain connectivity for multiple species, and under changing climate. We conclude with discussion of how effectively to validate connectivity model predictions.

## Estimating landscape resistance

Most current methods of predicting population connectivity and mapping areas significant in facilitating animal movements begin with landscape resistance maps (Figure 21.1). Landscape resistance maps depict the cost of movement through any location in the landscape (pixel cell in a raster map) as a function of landscape features of that cell (e.g. high resistance might be assigned to a road or a body of water). In its most basic sense, landscape resistance reflects the local movement cost incurred by an animal. More formally, the resistance reflects the step-wise cost of moving through each cell for least-cost analyses (Singleton et al. 2002) or the relative probability of moving into the cell for circuit theory-based analyses (McRae et al. 2008).

### Expert versus empirical estimation

Most published studies using landscape resistance maps have estimated resistance of landscape features to movement based on expert opinion alone (e.g. Compton et al. 2007). However, non-human species perceive landscapes in ways that may not correspond to human assumptions concerning connectivity and habitat quality (With et al. 1997). Using

unvalidated expert opinion to develop resistance maps has been a major weakness of most past landscape resistance modelling efforts (Seoane et al. 2005).

## Methods for empirically estimating resistance

### *Habitat quality as surrogate for landscape resistance*

Habitat quality can be predicted based on patterns of occupancy in relation to ecological conditions, such as through resource selection functions (e.g. Guerry & Hunter 2002; Weyrauch & Grubb 2004). The simplest way to estimate relationships empirically between population connectivity and environmental conditions is to assume that habitat quality directly equates to population connectivity. Predictions of habitat quality based on patterns of occurrence studies are limited because they do not directly measure biological responses such as mortality, movement and productivity (Cushman 2006). Patterns of species occurrence do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns (Van Horne 1983). More importantly, in the context of connectivity modelling, suitability for occupancy and suitability for dispersal may not be driven by the same factors at the same scales (e.g. Shirk et al. 2010; Wasserman et al. 2010). Habitat selection reflects the behaviour of individual organisms to maximize fitness within home ranges, while population connectivity is driven by dispersal, migration and mating events. These are functionally and biologically different processes. Few studies have formally evaluated the performance of habitat suitability models as surrogates for landscape resistance, but those that have generally have found them to perform poorly (e.g. Shirk et al. 2010; Wasserman et al. 2010). This highlights the importance of not assuming that habitat relationships optimally reflect the landscape features governing population connectivity.

### *Mark-recapture and experimental movement studies*

By quantifying movement rates, distances travelled and routes of animals through complex environments, researchers can quantitatively describe species-specific responses to environmental conditions and landscape structure. For example, a study by Gamble et al. (2007) quantified dispersal in relation to topography and vegetation for several pond-breeding amphibians, demonstrating the value of mark-recapture approaches to evaluating population connectivity. In addition, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. For example, Haddad & Baum (1999) used a large-scale experiment to find that three habitat-restricted butterfly species reached higher densities in patches connected by corridors than in similar, isolated patches.

These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal & Cushman 2002). Unfortunately, large-scale manipulative field experiments and mark-recapture meta-population studies are expensive, take several years, and generally suffer from small sample sizes. Another potential limitation is that these studies focus on short-term, fine-scale movement path selection of individual animals, which may not scale up to population-level effects on migration and gene flow.

### *Telemetry*

Advances in wildlife telemetry technology have enabled collection of very accurate and frequent location data for individual animals. Landscape resistance modelling based on telemetry is a powerful technique to address the factors that affect organism movement directly on scales of space and time greater than are possible with mark-recapture and experimental movement studies (e.g. Osborn & Parker 2003; Cushman et al. 2005,

2010a). GPS telemetry data enable direct assessment of the influences of landscape features on movement path selection. For example, Cushman et al. (2010a) modelled the influence of landscape features on elephant movement path selection using telemetry data, showing that elephants (*Loxodonta africana*) select movement paths near water, avoid human settlements and do not cross wildlife cordon fences. Similarly, Cushman & Lewis (2010) used satellite telemetry data to show that American black bears (*Ursus americanus*) choose movement paths that avoid roads and human residences and concentrate activity in forested areas at middle elevations. Directly associating movement paths with landscape features enables the development of species-specific landscape resistance models that are more reliable than those produced by expert opinion.

### *Landscape genetics*

Gene flow among populations is necessary to support the long-term viability of populations, as it maintains local genetic variation and spreads potentially advantageous genes. Thus it is important to infer the functional connectivity among populations and across landscapes (van Dyck & Baguette 2005). The ultimate validation of any method of estimating functional connectivity lies in how well it explains gene flow (Cushman et al. 2006; Shirk et al. 2010; Wasserman et al. 2010; Short Bull et al. 2011). Genetic methods can directly measure dispersal and immigration (Waples 1998; Landguth et al. 2010). Logistical and financial costs associated with tracking individual animals are obviated and because genetic data integrate time and space, slow rates of dispersal through complex landscapes are measurable. Landscape genetic analyses enable direct association of movement cost across resistance surfaces with genetic differentiation, which enables empirical derivation and validation of connectivity maps. For example, Wasserman et al. (2010) used non-invasive monitoring to collect genetic data from several hundred individual American marten (*Martes americana*) across a 4000 square kilometer study area, and were able to use multivariate landscape genetic modelling to identify the landscape features that affect gene flow.

## Combining multiple methods to produce robust estimates of resistance

Every method of estimation has its own limitations, so it is valuable to use multiple methods and independent data sets to estimate resistance. The strongest inferences are derived from multiple analyses of different kinds of data that produce a consistent result (Cushman & Lewis 2010). For example, landscape genetics and GPS telemetry are two complementary analyses that can be combined to produce robust estimates of landscape resistance. Using movement data to predict landscape resistance, and comparing that to landscape resistance predicted from landscape genetic analyses of the same species in the same study area, is a useful way to verify the robustness of landscape connectivity hypotheses (e.g. Cushman & Lewis 2010). In addition, such analyses would illuminate the multi-scale drivers of population connectivity, since mating and dispersal movement behaviours are the mechanisms through which gene flow operates in animal populations. At the present time, only a few research programmes have estimated resistance from a combination of approaches (Coulon et al. 2008; Cushman & Lewis 2010; Shanahan et al. 2011; see Box 21.1).

## From landscape resistance to population connectivity

While resistance is point specific, connectivity is route specific (Cushman et al. 2008). Therefore, while resistance models can provide the foundation for applied analyses of population connectivity, they do not, in themselves, provide sufficient information to evaluate the existence, strength and location of barriers and movement corridors. Connectivity must be evaluated with respect to the paths, costs and success of moving across a landscape. The resistance model is the

**Box 21.1** Combining landscape genetics and telemetry to estimate landscape resistance for American black bear

Cushman et al. (2006) used causal modelling with landscape genetics data to evaluate support for 110 alternative hypotheses describing the effects of landscape variables on population connectivity in an American black bear (*Ursus americanus*) population in northern Idaho, USA. Their analysis rejected hypotheses of isolation by distance and isolation by a geographical barrier, and affirmed a landscape resistance model which predicts that rates of gene flow are related to elevation, forest cover, roads and human development. Cushman & Lewis (2010) used conditional logistic regression to predict landscape resistance based on black bear GPS telemetry data in the same landscape. They used a path-level spatial randomization method to assess the effects of multiple landscape features on movement path selection (e.g. Cushman et al 2010a). The path-level randomization approach provides a robust means to compare the landscape features an animal encounters in its actual path with those that would be encountered in a large sample of available paths of identical length and topology. They found that consistent landscape factors influence genetic differentiation and movement path selection, with strong similarities between the predicted landscape resistance surfaces. Genetic differentiation among individual American black bears is driven by spring movement (mating and dispersal) in relation to residential development, roads, elevation and forest cover. The real value of this study is that it used two independent data sets and different kinds of analyses to validate the results, and it quantified the scale and strength of bear behavioural response to several landscape features. For example, it showed that gene flow is maximum at middle elevations due to impassable snow pack at high elevations in the dispersal season, and concentrated human populations in low-elevation valleys, and that bears strongly avoid roads and human resistances (e.g. near-total avoidance within a 200 m radius buffer around human structures).

foundation for these analyses, but it is explicit consideration of movement paths across the resistance surface that provides the key information for conservation and management.

## Identifying corridors using least-cost modelling

In recent years least-cost (LC) modelling (part of graph theory, see below) has become the dominant modelling tool to evaluate functional landscape connectivity, especially in applied studies. This is mainly because:

- it produces an unambiguous corridor or path as an output, whereas most other approaches do not
- it is available in most commercial GIS packages as well as open source software
- LC models generate visually attractive and easy to communicate representations of connectivity (maps) and quantitative metrics of effective distance (cost values) in the same units (meters) as Euclidean distance (Adriaensen et al. 2003; Fagan & Calabrese 2006).

These attributes make LC modelling very well suited for quantitative landscape analyses and for evaluating effects of future scenarios on connectivity.

In LC models the only inputs are the map of sources and targets and the map of resistance values (R; Figure 21.2a). The cost layer is the first and central level of output of a LC analysis (see Figure 21.2a), and provides the functional cost distance values from the designated source to all locations in the geographical extent of the analysis. The least-cost path (Figure 21.2b) is the series of cells in the landscape which results in the minimum cumulative cost value (LC path value) to move from a source cell/cells to the target cell/cells under investigation. The LC path indicates the location of the cheapest route, but gives no information on how cost values are distributed over the landscape. For example, it does not indicate other zones in the landscape resulting in comparable costs (Figure 21.2c) or how wide the LC path zone is (Adriaensen et al. 2003; Pinto & Keitt 2009).

There are several methods available to produce biologically informative measures of landscape connectivity from such cost surfaces. One of these is the combination of several cost

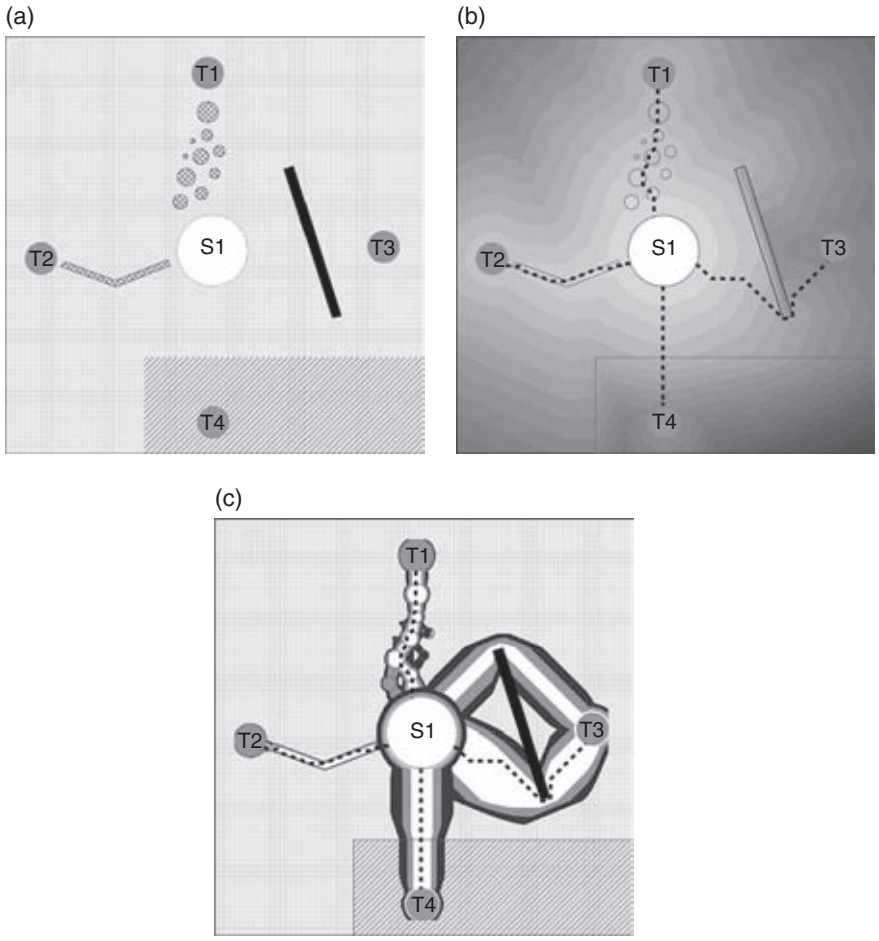



**Figure 21.2** Input (a) to output (b-c) in LC modelling using a simple virtual landscape to show the basics of this modelling approach. (a) Landcover map showing a hypothetical landscape (source area S1: forest; target areas T1–4: woodlots; grassland (dotted); intensive cropland (hatched); hedgerow and bushes (cross-hatched); open water (solid black). (b) Cost layer from source area S1 and LC path to 4 target areas (dashed lines). (c) Corridor map showing 1–10% corridor buffers derived from bidirectional cost layers from source area S1. Result of 4 corridor analyses superimposed (targets=T1–4): white, increase in minimum cumulative cost less than 1% of LCP; light grey 1–5%; dark grey 5–10%.

layers into one 'corridor' layer (other names: bidirectional cost layer, conditional minimum transit cost [CMTC, Pinto & Keitt 2009]; see Figure 21.2c), in which the value of each cell is the overall cost to reach the target cell T from source cell S, but with the constraint to go through the cell under investigation. The LC path is a special case of this (with all cells having a value equal to the LC path value and thus the minimum present in the corridor layer). The LC path will always be the path of minimal corridor values but elsewhere in the landscape, there could be other zones with nearly equal cost values (see Figure 21.2c). Corridor maps give a more realistic view of the functionally cheapest routes in the landscape from the designated source to the destination (Adriaensen et al. 2003) (Box 21.2). For example, the width of corridors can be determined by taking percent slices of the landscape representing the lowest cumulative resistance (e.g. Singleton et al. 2002; Spencer et al. 2010) or by limiting

**Box 21.2** Landscape connectivity in the Taita Hills

The Restoration and Increase of Connectivity among Fragmented Forest Patches in the Taita Hills, South-east Kenya project (CEPF project 1095347968; Adriaensen et al. 2007) included a detailed analysis of functional landscape connectivity in the area. In this project, evidence of the distribution and population status of bird species in the remaining small cloud forest patches on the hill tops (black patches) was successfully combined with output of LC models to support and prioritize habitat restoration actions in plantations with exotic trees (white patches). Forest restoration is now being implemented in a set of five pilot projects.

Least-cost models were used to model the location of exotic tree plantations in relation to modelled connectivity corridors for forest interior birds (dark grey zones), in order to evaluate their potential roles as stepping stones to promote recolonization after rehabilitation of the plantations. In the map shown, corridors between all pairs of remaining forest plots were superimposed (resistance set R1S5 for eco-type 'sensitive interior forest bird', including the critically endangered Taita thrush *Turdus helleri*).

corridors to a maximum cost-weighted cut-off distance above that of the LC path (WHCWG 2010). Regional connectivity assessments can require mapping corridors between hundreds to thousands of core area pairs (e.g. Spencer et al. 2010; WHCWG 2010). The development of GIS tools to automate corridor mapping, including decisions of which pairs

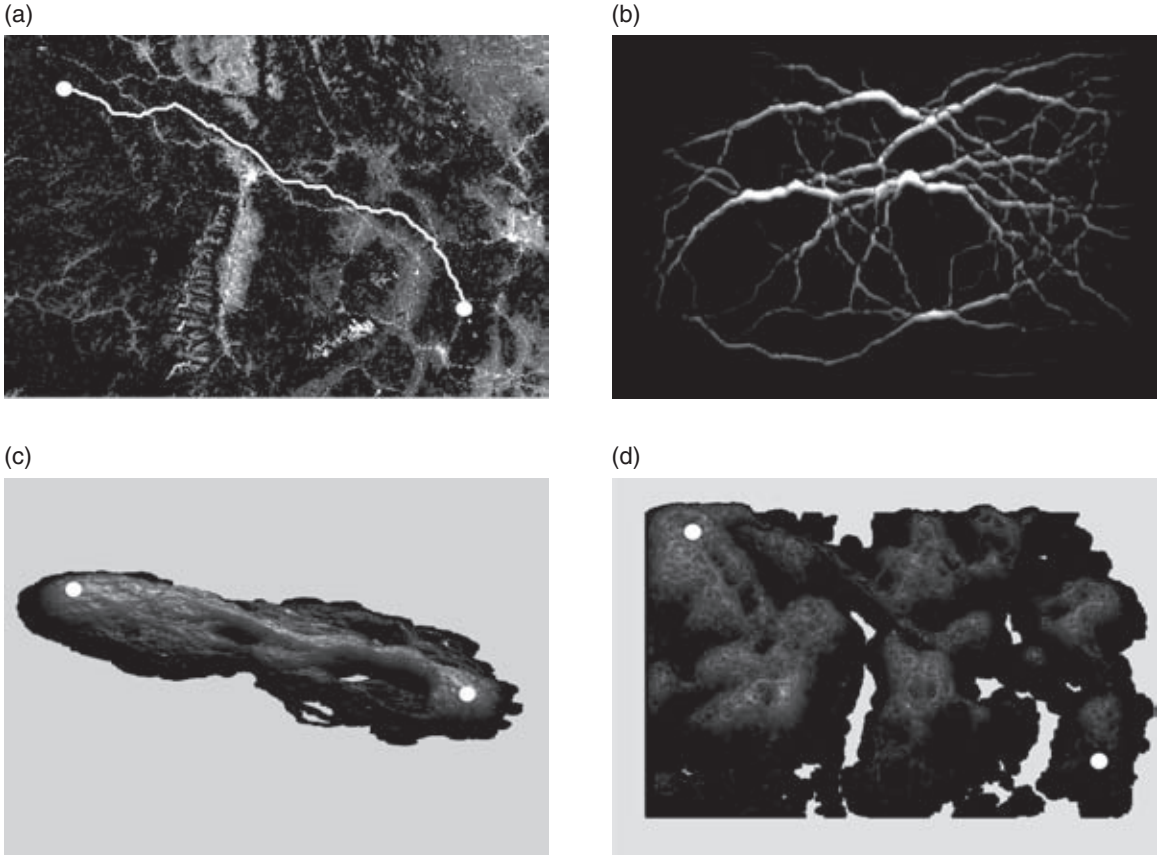



**Figure 21.3** Comparison of four connectivity modelling methods applied to a single study area and resistance map. The study area is northern Idaho, USA. The resistance map is shown in panel (a) as a colour scale from blue (low resistance) to red (high resistance), and reflects landscape resistance to black bear gene flow (Cushman et al. 2006). Panel (a) shows a single least-cost path (white line) between two point locations (white dots). Panel (b) shows a factorial least-cost path analysis between several hundred source points. Panel (c) shows the least-cost corridor between the same two source points as in (a). Panel (d) shows the cumulative resistant kernel model of synoptic landscape connectivity.

of core areas to connect (e.g. McRae & Kavanagh 2011), makes this easy.

## Factorial least-cost paths

One limitation of traditional LC path and LC corridor analyses is that they are limited to prediction of connectivity between single sources and single destinations (Figure 21.3a). While this may be ideal in the case where one is interested in the lowest cost routes between two focal conservation areas, there are many situations where a more synoptic analysis of connectivity is valuable. For example, it may be that there is a need to calculate corridor connectivity between thousands of sources and a single destination (e.g. Cushman et al. 2010a) or between hundreds of sources and hundreds of destinations distributed across a complex landscape (e.g. Cushman et al. 2008, Cushman et al. 2011; Figure 21.3b). For example, Cushman et al. (2008) used factorial least cost path analysis to predict the most important movement

routes for bears between Yellowstone National Park and the Canadian border in the United States Northern Rocky Mountains, showing that there are few major connections and locating several dozen potential barriers. This, in turn, focuses attention on where restoration and mitigation efforts would be most effective. A factorial implementation of least cost paths (e.g. UNICOR; Landguth et al. 2011) permits integration of a vast number of least cost paths to show synoptic connectivity across large and complex landscapes (Figure 21.3b). For example (Cushman et al. 2011) mapped regional corridor networks for several species of conservation concern across a vast area of the United States great plains using UNICOR (Landguth et al. 2011). The analysis identified which species have the most fragmented populations and mapped the most important corridor linkages among population core areas, focusing conservation efforts on the most important locations.

## Other ways to analyse connectivity

Ecologists often use the term *graph theory* to refer to a family of analyses in which patches are reduced to nodes at patch centroids, with centroids connected by lines or 'edges' (e.g. Bunn et al. 2000; Urban & Keitt 2001; Minor & Urban 2007). Such graphs underlie many methods in connectivity analysis, including LC corridor modelling. Advances in computing and algorithms borrowed from other disciplines have allowed applications of graph algorithms to continuous landscapes instead of simple networks. Rayfield et al. (2011) review graph-based connectivity measures and provide a framework for classifying them as applications to connectivity conservation.

### Circuit theory

Connectivity analyses based on electrical circuit theory use networks of electrical nodes connected by resistors as models for networks of populations, habitat patches or locations on a landscape connected by movement. Because connectivity increases with multiple pathways in electrical networks, distance metrics based on electrical connectivity are applicable to processes (e.g. gene flow; McRae 2006) that respond positively to increasing numbers of pathways. Additionally, previous work has shown that current, voltage and resistance in electrical circuits all have mathematical relationships with random walks (Doyle & Snell 1984; Chandra et al. 1997). Random walks can predict the expected routes that an animal with a preference for low-resistance habitat will take as it moves through a landscape. The precise relationships between circuit theory and random walks mean that circuits can be related to movement ecology and population genetics via random walk and coalescent theories, providing concrete interpretations of connectivity measures (McRae 2006; McRae et al. 2008).

Circuit and LC models represent two extremes in assumptions about movement and connectivity. Least-cost corridors calculate the routes expected to be taken by animals with perfect or near-perfect knowledge of the landscape, whereas current maps generated from circuit models predict movement routes taken by random walkers, with all possible paths contributing to connectivity. Neither will entirely correctly predict movement behaviour of real animals (Spear et al. 2010, and see below) but there are benefits to both models, as we show in the example in Figure 21.4. Least-cost analyses can show what routes/zones would permit the most efficient movement, which can be important for conservation planning; if a large portion of a landscape is likely to be developed, identifying those areas which, if conserved, provide the easiest movement routes will be important. Circuit theory has the advantage of identifying and quantifying 'pinch points' (see Figure 21.4), i.e. constrictions in corridors that, if lost, could sever connectivity entirely. Such areas can be prioritized for early conservation action because options are limited. Circuit algorithms also integrate across all movement pathways to

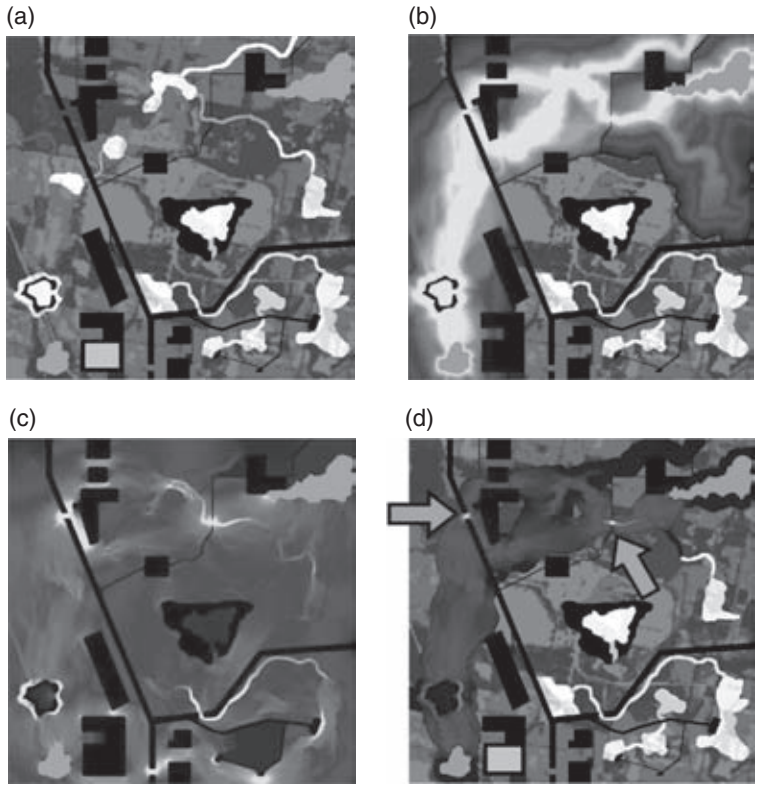



**Figure 21.4** Example of how circuit theory can be used to identify and prioritize important areas for connectivity conservation. (a) Simple landscape, with two patches to be connected (green) separated by a matrix with varying resistance to dispersal (low resistance in white, higher resistance in darker shades, and complete barriers in black). (b) Least-cost corridor between the patches (lowest resistance routes in yellow, highest in blue). (c) Current flow between the same two habitat patches derived using Circuitscape (McRae & Shah 2009), with highest current densities shown in yellow (from McRae et al. 2008). Circuit analyses complement least-cost path results by identifying important alternative pathways and 'pinch points', where loss of a small area could disproportionately compromise connectivity. (d) A promising application is restricting circuit analyses to least-cost corridor slices to take advantage of the strengths of both approaches (from McRae & Kavanagh 2011). This hybrid approach shows both the most efficient movement pathways and critical 'pinch points' within them, which glow yellow. These could be prioritized over areas that contribute little to connectivity, such as the corridor at the top right of the map that has been coloured dark blue because it does not provide connectivity between the patches.

provide measures of redundancy, i.e. availability of alternative pathways for movement (see Figure 21.4). New applications allow identification of barriers that have a strong effect on connectivity, which can be useful for highlighting opportunities to restore connectivity, e.g. through re-establishment of natural vegetation or installation of highway crossing structures (McRae, unpublished data).

## Centrality analyses

A promising graph-theoretic approach to connectivity modelling is centrality analysis, which ranks the importance of habitat patches or corridors in providing movement across an entire network, i.e. as 'gatekeepers' of flow across a landscape (Carroll et al. 2011). Centrality analyses can be based in LC path,

circuit theory or other connectivity analysis methods. The difference is that, instead of mapping corridors or current flow between single pairs of core areas, they add up results from connectivity analyses between all pairs of nodes (sites or cells) on a landscape. Centrality analyses can be applied to raster GIS data or networks to identify core areas, linkages or grid cells that are particularly important for overall connectivity. Because centrality metrics can incorporate connectivity between all pairs of nodes on a landscape, they can eliminate the need to identify specific pairs of habitat patches to connect. For example, betweenness centrality (Freeman et al. 1991) identifies the shortest paths connecting all pairs of nodes in a network, and sums the number of such shortest paths involving each intervening node. This procedure identifies areas lying on a large proportion of the shortest paths in a network, the loss of which can disproportionately disrupt connectivity across the network as a whole. The Connectivity Analysis Toolkit (Carroll 2010) specializes in centrality analysis, and supports metrics based on betweenness, current flow (Newman 2005), maximum flow (Freeman et al. 1991) and minimum-cost flow (Ahuja et al. 1993). It also allows time-series analyses of connectivity across landscapes where habitats shift through time (Phillips et al. 2008).

## Resistant kernels

The resistant kernel approach to connectivity modelling is based on least-cost dispersal from some defined set of sources. The model calculates the expected density of dispersing individuals in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010b). Once the expected density around each source cell is calculated, the kernels surrounding all sources are summed to give the total expected density at each pixel (see Figure 21.3d). The results of the model are surfaces of expected density of dispersing organisms at any location in the landscape. For example, Cushman et al. (2010b) used resistant kernel modelling to evaluate the interactive effects of roads and human land use change on population connectivity for a large number of pond-breeding species in Massachusetts (USA). The resistant kernel approach quantified expected density of dispersers in the upland environment as functions of breeding population size, dispersal ability and quantified the relative impacts of roads and land use on population connectivity (Figure 21.5).

The resistant kernel approach to modelling landscape connectivity has a number of advantages as a robust approach to assessing current population connectivity (Compton et al. 2007; Cushman et al. 2010b, 2011). First, unlike most approaches to mapping corridors , it is spatially synoptic and provides prediction and mapping of expected migration rates for every pixel in the whole study area, rather than only for a few selected 'linkage zones' (e.g. Compton et al. 2007). Second, scale dependency of dispersal ability can be directly included to assess how species of different vagilities will be affected by landscape change and fragmentation under a range of scenarios (e.g. Cushman et al. 2010b). Third, it is computationally efficient, enabling simulation and mapping at a fine spatial scale across large geographical extents (e.g. Cushman et al. 2010b, 2011).

## Individual-based movement models

Individual-based (IB) models explicitly simulate the processes acting on the individual to predict movement. IB models predict movement paths of simulated dispersers based on parameters such as energetic cost of movement in different patch types, turning angles within patches and at patch transitions, movement speeds, duration of movement events, mortality risks in different patch types, and likelihoods of movements between patch types. Thus, IB models usually incorporate much more detail and thus greater realism than other

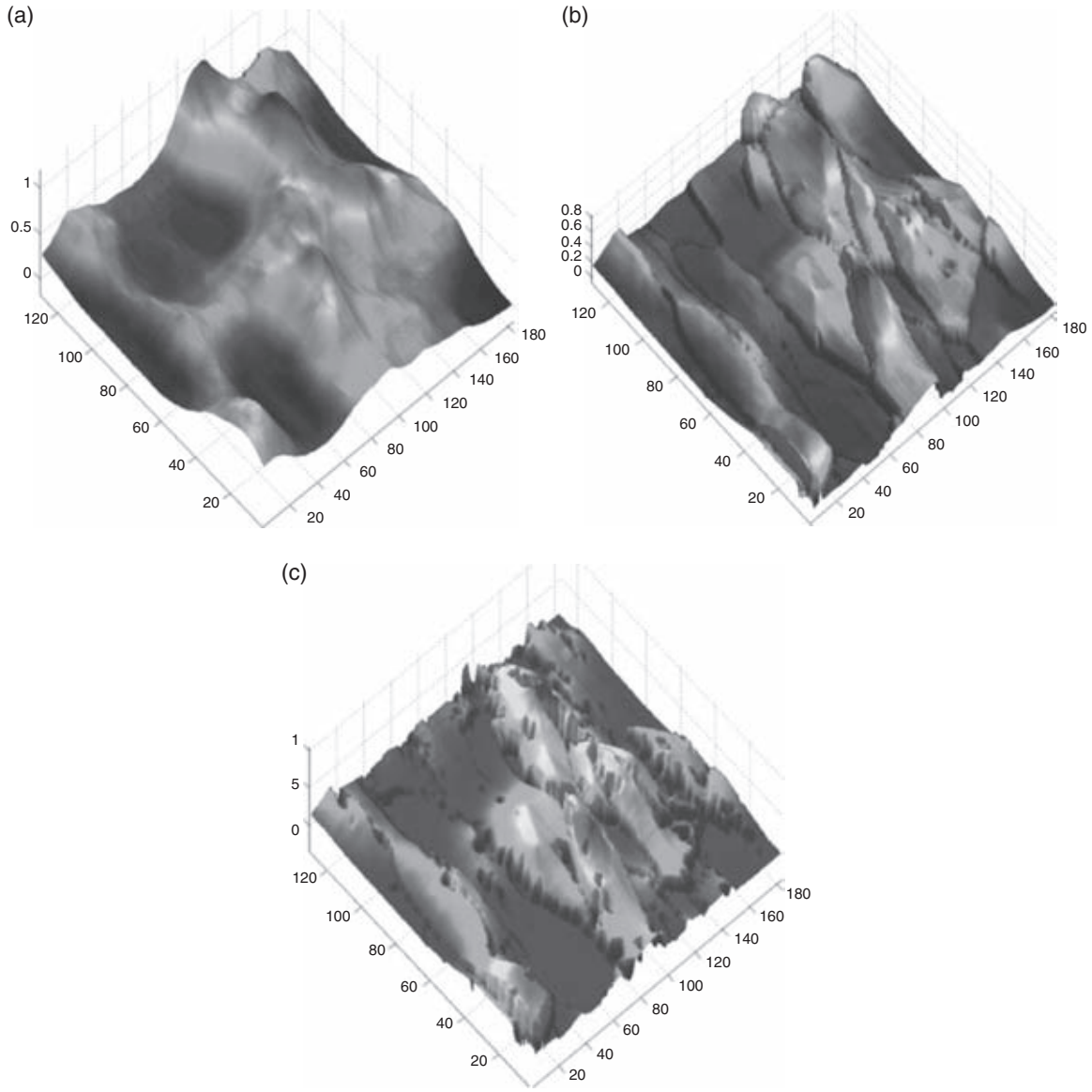



**Figure 21.5** Example of resistant kernel results from Cushman et al. (2010b) showing predicted density of dispersing individuals in upland habitat under three hypotheses: (a) connectivity is unaffected by land use and roads and only a function of distance, (b) connectivity is reduced by roads but not by differences in land cover and land use, (c) connectivity is affected by roads and land use/land cover.

connectivity models, such as demographic and dispersal data, in addition to landscape characteristics.

There are three broad categories of models that simulate individual movement (raster based, vector based and network based), which differ according to whether the landscape is represented as fields, features or graphs. Conceived as fields, a landscape is a continuous surface defined by one or more variables (layers) that can be measured at any point within the field. Fields usually model continuous data such

as elevation, or temperature gradients, but can also represent categorical data such as habitat classification. If movement through the landscape is dependent on the variables of the field, then raster-based movement rules are most appropriate. Features are discrete entities that occupy positions in space, such as lines (rivers, roads, hedgerows) and polygons (lakes, woodland). The interiors of polygons are considered to be homogeneous. Movement between features is usually simulated using vector-based models. Finally, graphs represent the positional relationship between discrete elements in a landscape; a graph consists of a set of nodes that may represent continuous or categorical data, and a set of edges, which are dimensionless but describe how the nodes are connected to one another. Edges may be temporally referenced, indicating changes in graph connectivity over time. Network-based models are used to simulate IB movement in graphs. Examples of all three of these categories are discussed below.

### *Movement rules and models*

Regardless of whether movement models are raster, vector or network based, they encode a series of rules that predict how the dispersal behaviour of individual animals is expected to interact with the spatial pattern of landscape structure (King & With 2002). Variations in patch quality, boundaries between patches, the nature of the mosaic, and overall landscape connectivity all affect the permeability of the landscape to dispersing individuals (Wiens 1997). The limited empirical information on the behavioural responses of animals to landscape structure (Turner et al. 1995; Lima & Zollner 1996) means that model parameters are usually based on observed habitat preference, dispersal rates in different patches, and how the energetic costs of crossing a landscape affect distance moved as well as direction taken. For example, the rules employed by Boone & Hunter (1996) simulated IB searching behaviour in grizzly bears by encoding permeability into the cells of habitat patches. Highly permeable habitat patches produced straight paths and long distance movements whereas patches of low permeability caused convoluted paths and short displacement.

### *Raster-based models*

Raster- or grid-based representations of the landscape permit the greatest flexibility with which movement interacts with the landscape, and are appropriate where the dispersal matrix is heterogeneous (Wiegand et al. 1999). The landscape is represented as a series of tessellated shapes, usually square grid cells, and the model animal moves through each cell based on movement rules.

An advantage of this approach to modelling is the inclusion of a clear relationship between a cell and its neighbours, facilitating the description of local interactions by state transition rules. Each cell stores its own state variables that influence the decisions made by individuals through the landscape it represents. However, there are three principal disadvantages to raster-based models.

- The resolution of the grid is limited by memory capacity and simulation speed, and raster-based models have a tendency to be computationally demanding.
- The fixed spatial structure implies a fixed relationship between the spatial scale in the simulation and the scale of individual movements of the organism investigated.
- The geometry chosen to represent landscape in raster-based models (i.e. square grid, hexagonal grid, Dirichlet tessellation, etc.) can substantially affect the simulated behaviour of the individual dispersers even if the rules for movement and settlement are the same between different geometries (Holland et al. 2007).

### *Vector-based models*

Vector-based models simulate organisms dispersing through continuous or homogeneous landscapes. If the motivations for these movements

are random or quasi-random search patterns, they can be simulated using correlated random walk algorithms (Kareiva & Shigesada 1983). Alternatively, if individual movements are targeted searches for resources with a particular spatial or temporal distribution, movement decisions will be informed by the underlying landscape structure. Finally, if motivation for movement is prompted by the desire to avoid or join conspecifics, it will result in density-dependent movement rules. Where motivations for movement are known and appropriate, IB models benefit from vector-based dispersal simulations, which are less computationally demanding than the raster-based alternative.

#### *Network-based models*

Network-based models differ from the other types in that they do not include a continuous representation of the landscape. Rather, connectivity between locations is represented by an edge between nodes. Network-based models usually specify an *a priori* representation of patch size, patch adjacency and other criteria (e.g. Lookingbill et al. 2010). Edges are formed when movement is possible between nodes. Dispersal corridors can be represented as nodes as well as edges in network visualizations of a landscape used as analytic connectivity models (McRae et al. 2008). They calculate walks through the network that minimize total weight, suggesting optimal pathways for dispersal. In IB models, network-based landscapes are utilized probabilistically (Lookingbill et al. 2010; Morzillo et al. 2011), and may result in biologically plausible but analytically suboptimal solutions. Graph-theoretic approaches to network analysis can be applied to the utilized networks of IB models to identify the nodes and edges that maintain cohesion of the network. For example, Gurnell et al. (2006) identified routes of entry for invasive grey squirrels into potential conservation areas for the endangered red squirrel in northern England through network analysis.

### Corridors based on shifting climate envelopes

This approach produces 'temporal corridors' that track how a species' climatic envelope (suitable temperature and moisture regimes) might move across a landscape under climate change scenarios. Like some types of individual-based models, this approach avoids the concept of resistance that is central to most previous approaches. The heart of this approach is either a dispersal chain model (Williams et al. 2005) or a network flow model (Phillips et al. 2008), either of which identifies cells with suitable climate envelopes that are spatially contiguous for long enough to allow the species to establish new populations in cells as they become suitable. Although dispersal chain and network flow models are conceptually sound, they depend completely on the outputs of three other models, namely models of future emissions of greenhouse gasses, models of future climate resulting from how the atmosphere and oceans respond to these emissions, and climate envelope models for the focal species. Unfortunately, each of these latter three models is plagued with massive uncertainty (summarized in Beier & Brost 2010). In the future, ensemble modelling (building many alternative corridors based on various combinations of emission scenarios, circulation models and climate envelope models) might identify corridors robust across the range of assumptions in the ensemble.

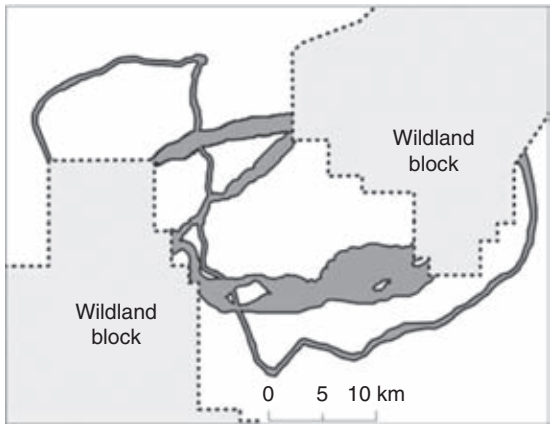
## Beyond single species

### From optimal corridors for single species to linkage designs for multiple species

Up to this point, we have described methods of mapping an optimal corridor, or areas important for connectivity, for a single species. Beier et al. (2008) proposed the term *linkages* to denote lands intended to support movement of

**Box 21.3** Example of optimizing multispecies linkage

A hypothetical linkage design including optimal corridors for eight focal species, expanded to include patches of modelled breeding habitat for an additional five focal species for which corridor models were not appropriate, and a narrow riparian strand for fishes. Each strand needs to be >1 km wide in order to create large interior spaces free of edge effects, support meta-populations of species needing multiple generations to achieve gene flow through the corridor, and support ecological processes more complex than animal movement.




multiple focal species and ecosystem processes. To design linkages, conservation planners can select a suite of representative focal species suitable to serve as a collective umbrella for the entire biota. For instance, each of 27 linkage plans in California and Arizona (Beier et al. 2006, 2007) was designed to meet the needs of 10–30 focal mammals, reptiles, fishes, amphibians, plants and invertebrates. Focal species included species requiring dispersal for meta-population persistence, species with short or habitat-restricted dispersal movements, species tied to an important ecological process (e.g. predation, pollination, fire regime), and species reluctant to traverse barriers in the planning area. Although large carnivores are appropriate focal species and flagships (Servheen et al. 2001; Singleton et al. 2002), most of them are highly mobile habitat generalists and thus inadequate umbrellas for other species (Beier et al. 2009; Minor & Lookingbill 2010).

A simple unweighted union of single-species corridors is an obvious way to produce a linkage design to promote the goal of 'no species left behind' (Beier et al. 2006, 2007; Adriaensen et al. 2007; Cushman et al. 2011) (Box 21.3). But corridor models are not appropriate for some focal species, such as many flying animals, that do not move across the landscape in pixel-to-pixel fashion. To support movement of these species, Beier et al. (2008) recommend draping maps of known or modelled breeding habitat over the union of corridors, and enlarging the union to include patches that would decrease the inter-patch distances that dispersers would need to cross. The linkage design should be further expanded to include major riverine connections, which provide natural corridors for aquatic and some upland organisms, and promote other ecological processes and flows such as movement of sediment, water and nutrients.

## Coarse-filter linkage designs for climate change

Climate change poses a challenge to all types of conservation planning, including linkage

design. As climate changes, existing land covers in some planning areas will not merely shift but will disappear as plant associations reassemble (Hunter et al. 1988; Lovejoy & Hannah 2005). Linkage designs should be robust to such changes, and should allow species to shift their ranges into and out of the planning area. To address this, one could attempt to model corridors for the shifting climate envelopes of all species (above). A simpler alternative is to design linkages with a coarse-filter approach based on the abiotic drivers of land cover and species distributions (Hunter et al. 1988; Anderson & Ferree 2010). This idea is grounded in the foundational ecological concept (Jenny 1941; Amundson & Jenny 1997) that biodiversity at any point in time is determined by the interaction of the recent species pool with climate, soils and topography.

Beier & Brost (2010) and Brost & Beier (2012) developed multivariate procedures to identify *land facets*, defined as recurring landscape units with uniform topographic and soil attributes, from readily available digital maps of elevation and soils. They used multivariate dissimilarity as a measure of pixel resistance for each land facet type. Finally, they used least-cost modelling to design land facet corridors, and joined these corridors into a linkage design. Other coarse-filter approaches are feasible. For instance, Rouget et al. (2006) suggest that species will shift their ranges by sequentially colonizing areas that lie along the most gentle and monotonic temperature gradients. Assuming these gradients in temperature are conserved in a changing climate, it may be possible to identify corridors along today's most gentle and monotonic temperature gradients, without the need for uncertain models of future climate.

Linkage designs should be produced by a combination of coarse-filter and focal species approaches. In each of three landscapes, Beier & Brost (in preparation) developed two linkages designs – one based on land facets and the other on focal species. The land facet linkage designs included optimal corridors for 25 of 28 focal species, whereas the focal species designs encompassed optimal corridors for 21 of 32 land facets. Neither approach on its own was likely to meet all conservation goals.

## Validation of predicted corridors

Corridors resulting from models have sometimes been criticized because they lack supporting movement data (Simberloff et al. 1992; Rosenberg et al. 1997) and because they may contain errors in model parameters or incorrect assumptions (Spear et al. 2010). Therefore, additional vetting of modelled corridors in the field is strongly recommended.

Many field studies have evaluated the efficacy of existing corridors, such as corridors that follow linear features like fencerows or rivers (Hill 1995; Castellón & Sieving 2006), or that were constructed as part of experimental landscapes (Berggren et al. 2002; Haddad et al. 2003). There have also been tests of species' response to conservation action in established corridors (Duke at al. 2001; Shepherd & Whittington 2006). But field testing of modelled corridors, like the ones described in this chapter, have been scarce.

Modelled corridors may cover large spatial extents and span multiple land ownerships and management types, or even national borders, making the collection of field data logistically complex and resource intensive. If corridors are modelled for dispersal movement, capturing infrequent dispersal events is akin to finding a needle in a haystack, so collecting sufficient data to reliably test predicted corridors can be difficult. Finally, modelled corridors can only be truly validated if movement through the corridor is documented along with the outcome for which the corridor was intended, whether that be by successful migration to summer or winter ranges, successful recolonization of habitat patches, safe passage across a road, demographic rescue, or successful breeding and gene flow.

Even if all aspects of linkage cannot be validated, a partial field study will add confidence and transparency to a corridor project. For

example, Clevenger et al. (2002) developed two habitat models for black bears, one based on expert opinion and the other based on data from the literature. They identified road crossing zones from these models, and using data on crossings by real bears, they tested if the predicted linkages were used more than would be expected by chance. They found that the linkage models based on data from the literature outperformed the expert opinion models. The authors indicated that the expert opinion models may not have performed as well due to an overestimation of the importance of riparian habitat.

As an additional example of empirical field validation of corridors, Quinby (2006) used existing data from the annual breeding bird survey to test the utility of a proposed corridor. More bird species were found inside the corridor than outside it, confirming its validity. Chardon et al. (2003) used presence/absence data on the speckled wood butterfly from two different landscapes to compare the explanatory power of Euclidean distance and effective-distance connectivity models. They found that cost-distance was better able to predict connectivity than Euclidean distance. Zeller et al. (2011) used interviews with local residents to collect detection/non-detection data on jaguars and seven prey species in a grid-based design. The data were analysed by a site-occupancy model to determine probability of habitat use inside and outside the modelled corridor. It was found that probabilities of habitat use were mostly higher outside the modelled corridor, a conclusion which prompted a redesign of the final corridor.

The fact that there have been few studies to validate corridor models calls for more attention to this topic. Corridor validation techniques not only need to be improved upon, they need to be accessible to researchers and land managers working at different scales and on various species. Bridging the gap between corridor identification and corridor implementation will increasingly depend upon these validation studies, since land managers do not want to be left to implement a corridor of questionable efficacy, or be blamed for creating a sub-par corridor while more appropriate lands are unprotected from development and fragmentation (Hess & Fischer 2001; Morrison & Boyce 2008).

## Conclusions

Population connectivity is critical for maintaining viable regional populations in the short term and to enable species to shift their geographic range in response to future climate change and other pressures such as land use change. In this chapter, we described the state of the art in quantitative corridor and connectivity modelling approaches. The first step in most quantitative connectivity analyses is to estimate and map landscape resistance. Traditional expert opinion is less useful for developing landscape resistance maps now that new and effective approaches using empirical data provide a much more reliable and robust means to map landscape resistance. There are a number of ways to predict or describe connectivity from resistance surfaces. Least-cost paths, least-cost corridors, circuit theory, centrality analyses, and resistant kernels are all powerful approaches suitable for different objectives. The efficient application of corridor analyses to future applied conservation problems must develop corridor designs to maintain connectivity for multiple species, and under changing climate. Finally, empirical validation of predicted corridors and linkages is essential to demonstrate their functionality and guide improvement of future corridor designs.

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PLANT ECOLOGY

# Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

Ellen I. Damschen[1]*, Lars A. Brudvig[2], Melissa A. Burt[3]†, Robert J. Fletcher Jr.[4], Nick M. Haddad[3], Douglas J. Levey[5], John L. Orrock[1], Julian Resasco[6], Joshua J. Tewksbury[7,8,9]

**Deleterious effects of habitat fragmentation and benefits of connecting fragments could be significantly underestimated because changes in colonization and extinction rates that drive changes in biodiversity can take decades to accrue. In a large and well-replicated habitat fragmentation experiment, we find that annual colonization rates for 239 plant species in connected fragments are 5% higher and annual extinction rates 2% lower than in unconnected fragments. This has resulted in a steady, nonasymptotic increase in diversity, with nearly 14% more species in connected fragments after almost two decades. Our results show that the full biodiversity value of connectivity is much greater than previously estimated, cannot be effectively evaluated at short time scales, and can be maximized by connecting habitat sooner rather than later.**

Habitat loss and fragmentation are leading threats to biodiversity in ecosystems across the globe (*1*–*4*). In a world replete with small, isolated fragments, where 70% of the world's forest area is within just 1 km of an edge, biodiversity loss is mounting (*1*). Increasing habitat connectivity is a key conservation strategy to minimize biodiversity losses by facilitating dispersal and rescuing declining populations from extinction (*5*). However, it is not known if restoring connectivity among habitat fragments will increase biodiversity by promoting the colonization of new species.

A well-established body of ecological theory predicts the importance of connectivity for biodiversity. Metapopulation theory (*6*, *7*) illustrates how increasing connectivity is predicted to lead to greater regional population persistence by promoting colonization of new habitats, increasing recolonization of habitats where extinction has occurred (recolonization rescue), and buffering existing populations against extinction via increased immigration (demographic rescue). Metacommunity theory (*8*, *9*) and island biogeography theory (*10*) integrate these population-level effects of connectivity to yield predictions regarding biodiversity. These developments provide strong theoretical reasons to expect that modifying connectivity can increase biodiversity by increasing colonization and decreasing extinction, but they also caution that nonintuitive effects (e.g., synchronization of population dynamics or modification of interactions) are possible (*8*, *11*).

Despite the presumed importance of connectivity for community diversity in both basic and applied ecology (*12*, *13*), empirical evidence for predictions from theory has been mixed (*14*–*16*). A primary challenge in evaluating these predictions in empirical systems is that ecological processes vary greatly in space and time: The dynamic nature of colonization and extinction processes necessitates well-replicated, large-scale, and long-term studies to draw meaningful inference about the ultimate role of connectivity in affecting diversity. For example, changes in biodiversity due to either lost or restored connectivity do not occur instantaneously. In fragmented habitats, species can continue to persist for years before eventually going extinct (*17*), resulting in an "extinction debt" paid over decades or even centuries (*18*, *19*). Similarly, "colonization credits" can accrue when habitat connectivity is restored among species-impoverished habitats, catalyzing the potential for biodiversity gains (*20*–*23*). Species may not colonize immediately because of low dispersal rates, which are difficult to measure, making the extent of colonization credits unknown (*20*, *23*). This lack of information is important because colonization credits could forestall or even reverse extinction debt.

We tested the long-term effects of habitat connectivity on plant colonization and extinction dynamics and their resulting impacts on species richness over nearly two decades in a habitat fragmentation experiment at the Savannah River Site in South Carolina, USA. This experiment manipulates connectivity through the creation of habitat corridors—thin strips of habitat that connect otherwise isolated habitat fragments (*24*). Ten experimental landscapes each contain four 1.375-ha fragments of equal area that are either unconnected or connected to a central 1-ha fragment by a 150 m–by–25 m corridor (Fig. 1). Fragments and corridors are being restored to longleaf pine savanna, a threatened ecosystem within a global biodiversity hotspot (*25*), and are surrounded by dense pine plantations that limit herbaceous plant growth. For 18 years, we censused occupancy of all plant species as communities assembled after each restored fragment's creation. Connected and unconnected fragments were randomly assigned and did not differ in species richness at the start of the experiment [fig. S1; see also supplementary materials and methods (*26*)].

Habitat connectivity has increased rates of colonization and decreased rates of extinction. As communities assembled, connectivity increased the average annual species colonization rate by 5% and decreased the average annual extinction rate by 2% beyond expected successional dynamics (Fig. 2A and fig. S2). These apparently small differences in annual rates are persistent and have compounded over time, generating large increases in species richness in fragments connected by corridors, magnifying colonization credits (Fig. 2B and fig. S3). These impacts occur across 239 plant species with diverse life histories, including species of conservation and restoration concern from the longleaf pine ecosystem (fig. S6) and species that vary in their dispersal ability (fig. S7).

Higher colonization rates and lower extinction rates have shortened the average time for a species to colonize a fragment (Fig. 3) and have driven a large increase in plant species richness (Fig. 2B and figs. S3 and S5). Corridor-connected fragments now support, on average, 24 additional plant species compared with unconnected fragments (200 versus 176 in connected versus unconnected fragments, respectively; fig. S3), an increase of 14%. Notably, connectivity's effects on species richness continue to accumulate; our best-fit models of species richness differences over time show no asymptote. Moreover, connectivity's impacts on colonization and extinction rates remain consistent across the 18 years of this study (Fig. 2 and figs. S4 and S5) (*26*).

Our results underscore that typical experiments of 1 to 5 years in duration (*1*, *27*) likely underestimate the impact of long-term connectivity restoration on community diversity. Connectivity's impacts are not fully realized until the ongoing, lagged assembly processes and responses equilibrate. Theory from spatial ecology and community assembly predicts that connectivity's effect on diversity will eventually reach an asymptote because of local ecological processes constraining species richness (e.g., competition) and because local communities draw from a finite number of species in the region (*10*, *28*). Long-term empirical investigations of how landscape configuration alters colonization

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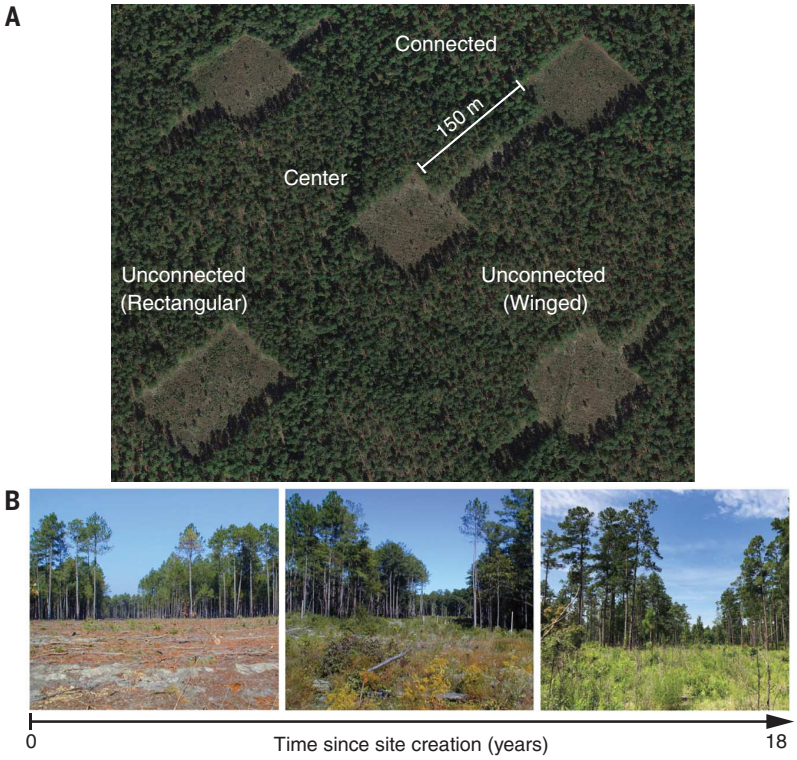


**Fig. 1. A long-term habitat connectivity experiment.** (**A**) One of 10 experimental landscapes ($N$ = 10), each containing a center fragment that is connected or unconnected (winged and rectangular) to peripheral fragments of open longleaf pine savanna surrounded by dense pine plantations [additional details in (*26*)]. [Credit: Google Earth 2019] (**B**) Plant communities within fragments have assembled over nearly two decades and are being restored to native longleaf pine savanna using frequent, low-intensity fires that mimic the historic fire regime. See (*26*) for further information on the study design. [Credits (left to right): M. A. Burt, N. M. Haddad, and E. I. Damschen]

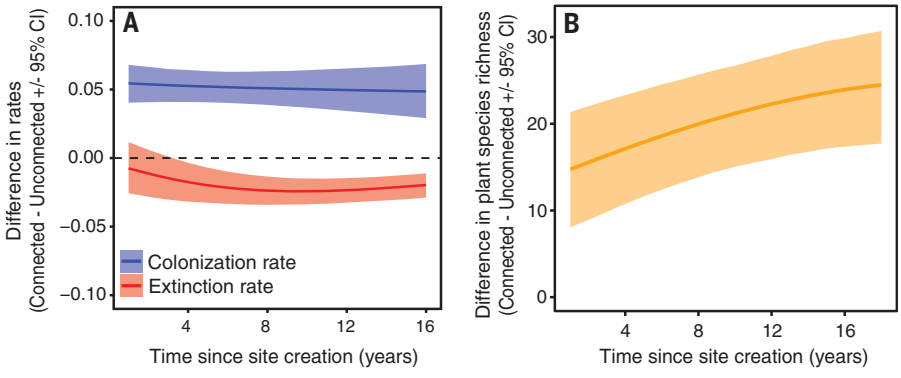


**Fig. 2. Connectivity reduces extinction and increases colonization rates over two decades, resulting in accruals of species in connected fragments.** (**A**) Average colonization rates are 5% greater and extinction rates are 2% lower for species in connected fragments than rates for those in unconnected fragments. These rates are constant over time. The net accrual of colonization credits increases biodiversity in connected fragments. (**B**) Plant species richness in connected fragments has increased at a greater rate than in unconnected fragments. Shown is the difference in estimated species richness over time, illustrating greater increases in richness in connected versus unconnected fragments. This rate increase has been consistent for nearly two decades and has resulted in connected fragments having 24 more plant species than unconnected fragments (fig. S3). A linear model (on the logit scale) is the best fit for the difference in species richness between connected and unconnected fragments over time (*26*). Shaded regions represent 95% confidence intervals.

and extinction rates are critical for determining and predicting human-induced changes to the environment; communities will almost never exhibit instantaneous responses or equilibrial dynamics (*29*).

We show that connectivity directly alters colonization and extinction dynamics among fragments, providing mechanisms for observed landscape-level biodiversity patterns (*30*). Our

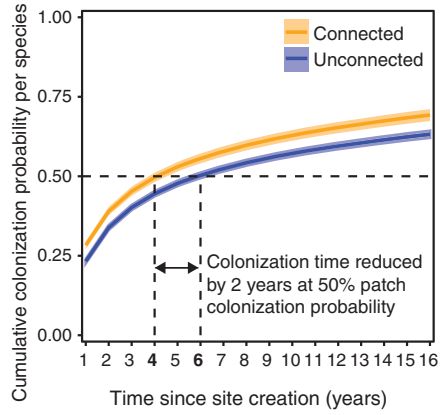


**Fig. 3. Connectivity reduces colonization timing, resulting in colonization credits.** The average cumulative probability of each individual species colonizing connected fragments is 1 to 6 years earlier than in unconnected fragments, resulting in reduced colonization lags and increased colonization credits. For example, the point at which a single species has a 50% likelihood of colonizing a habitat fragment (dotted lines) occurs a full 2 years earlier in connected versus unconnected fragments. Shaded regions represent 95% confidence intervals.

results contrast with hypotheses that attribute biodiversity change to habitat area alone and those that do not attempt to isolate underlying mechanisms (*14*). In our study system, connectivity leads to wholesale temporal shifts in community assembly, driven by lags in colonization that generate colonization credits, regardless of whether an equilibrium is achieved. Connecting fragments with corridors results in a 1- to 6-year reduction in the time it takes an individual species to colonize new habitat fragments, relative to the time needed for colonization of unconnected fragments (Fig. 3). For example, the 50% likelihood of a single species colonizing a fragment (dotted lines in Fig. 3) occurs a full 2 years earlier in connected fragments than for that same species in unconnected fragments (Fig. 3). These temporal shifts in the speed of colonization (Fig. 3 and fig. S8) have unexplored and potentially important ramifications for time-dependent ecological processes (e.g., priority effects). Although less explored, our results also suggest that corridor-mediated changes in the movement of individuals and alleles may affect evolutionary processes by altering effective population size and gene flow (*31*). Our results raise the need for theory to better integrate temporal duration in conservation and management.

Conservation strategies to mitigate biodiversity losses due to habitat fragmentation and loss are urgently needed, and habitat corridors feature prominently in global conservation plans (*4*). Our study shows that efforts to increase connectivity will pay off over the long term. Conservation plans that ignore connectivity, such as plans that focus solely on habitat area, will

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leave unrealized the substantial, complementary, and persistent gains in biodiversity attributable specifically to landscape connectivity (*30*, *32*).

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## SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Results
Figs. S1 to S8
Table S1
References (*34*–*61*)
Supplementary Code

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# Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

Ellen I. Damschen, Lars A. Brudvig, Melissa A. Burt, Robert J. Fletcher Jr., Nick M. Haddad, Douglas J. Levey, John L. Orrock, Julian Resasco and Joshua J. Tewksbury

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**Habitat connectivity enhances diversity**

Fragmentation of ecosystems leads to loss of biodiversity in the remaining habitat patches, but retaining connecting corridors can reduce these losses. Using long-term data from a large, replicated experiment, Damschen *et al.* show quantitatively how these losses are reduced. In their pine savanna system, corridors reduced the likelihood of plant extinction in patches by about 2% per year and increased the likelihood of patch colonization by about 5% per year. These benefits continued to accrue over the course of the 18-year experiment. By the end of monitoring, connected patches had 14% more species than unconnected patches. Restoring habitat connectivity may thus be a powerful technique for conserving biodiversity, and investment in connections can be expected to magnify conservation benefit.

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# Supplementary Materials for

## Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

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**Other Supplementary Material for this manuscript includes the following:**
(available at science.sciencemag.org/content/365/6460/1478/suppl/DC1)

Supplementary Code (.pdf)

## Materials and Methods

Landscape experiment

In 2000, we initiated a landscape experiment to test whether habitat corridors promote connectivity and impact community diversity. The experiment is at the Savannah River Site, a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA. Established by the U.S. Department of Energy, the site is managed by the US Forest Service under agreement with the Department of Energy.

The experiment consists of 10 replicate landscapes (experimental blocks), each comprised of five open-habitat fragments created by clearing mature pine plantation forest and restoring fragments to native longleaf pine savanna. There is a strong contrast between the open fragments and the surrounding closed-canopy pine plantation matrix. Eight landscapes were created prior to the 2000 growing season (i.e., before April) and two additional landscapes were created prior to the 2007 growing season. Two of the original eight landscapes were discontinued following the 2007 growing season due to management constraints and one was destroyed by a wind event following the 2015 growing season. The remaining five landscapes initiated in 2000 and the two landscapes initiated in 2007 continue through the end of this study. When examining patterns over time, landscapes are evaluated based on the number of years since that landscape was created. All available replicate landscapes (blocks) are used for each time point in this study. This staggered initiation of replicate landscapes also provides a benefit by separating connectivity effects due to time since replicate initiation from annual effects attributable to specific years.

Each landscape contains a center fragment (100 × 100 m, 1 ha) surrounded by four peripheral fragments that are each 150 m from the center fragment (Fig. 1). The center fragment is connected to one peripheral fragment by a 150 × 25 m corridor and the other three peripheral fragments are isolated from the center fragment by dense, mature loblolly (*Pinus taeda*) or longleaf pine (*Pinus palustris*) plantation forest. Unconnected fragments are equal in area to the connected peripheral fragment plus its corridor (1.375 ha) and are either rectangular (100 × 137.5 m) or winged. Winged fragments have two 75 × 25 m projections, each with the dimensions of half of a corridor, extending from each side of a 100 × 100 m fragment (Fig. 1). The identity of peripheral fragments (connected, rectangle, winged) was randomly assigned within each landscape, with one duplicate winged or rectangle fragment in each landscape. This study design allows us to separate influences of corridors mediated through connectivity from those mediated through differences in edge-to-area ratio. Specifically, impacts of connectivity are assessed by comparing response variables in winged and connected fragments (comparable edge-to-area ratio, different connectivity). Impacts of edge-to-area ratio are assessed by comparing the same variables in winged and rectangle fragments (comparable connectivity, different edge-to-area ratio). Because analyses used in this study showed no differences among unconnected fragment types (Table S1), response variables were averaged for those fragment types. The center fragment is not included in analyses comparing fragment types, therefore comparisons are always made for fragments of equal area. This approach is directly comparable to an earlier analysis of species richness in these fragments (*27*).

Through periodic prescribed fire and removal of establishing hardwood trees, we have restored fragments to their historical ecosystem type: open-canopy longleaf pine savanna. We used standard management practices in this ecosystem (*34*) and applied them consistently across experimental treatments (i.e., we managed all fragment types in the same way). Prescribed fires

are implemented and controlled by our partners at the USDA Forest Service-Savannah River consistent with the historic fire regime and with fire management in longleaf pine savanna conservation today (*35*). Low-intensity surface fires are ignited every two to three years during the dormant season (November - April) and are allowed to burn across large burn areas that include all experimental fragments for a given experimental landscape (block). Longleaf pine savanna species are fire-adapted and many species readily re-sprout after fire. Thus, ecological communities in our experimental landscapes recover quickly following fire, yet fire results in both mortality of resident species and recruitment opportunities for new species (*36*). Consistent with restoration practices in this ecosystem (*34*), we have also reduced woody encroachment in our fragments by cutting hardwood tree species with brush saws every three-to-four years and applying targeted herbicide to cut stumps and/or the base of individual stems. These management practices allow the fragments to undergo succession toward mature longleaf pine savanna, characterized by low density overstory longleaf pine trees and an understory dominated by highly diverse perennial herbs and grasses (*36*), while maintaining the contrast between our experimental fragments and surrounding matrix over the duration of the study.

Data collection

To quantify plant species richness and rates of extinction and colonization within our fragments, we annually survey each fragment for all plant species occurrences. We conduct surveys between May 15 and July 15, when most species in our system are visually identifiable. Here, we include data from 2001 through 2018 (except 2004 when active management prevented sampling). The goal of each survey is to census all species in each fragment by systematically walking the area of each fragment in a set pattern around permanent 3m-tall poles placed in a 12.5m grid. This grid consists of 88 small (12.5 × 12.5 m) sampling units in each fragment. For each census, we record all species in the first sampling unit and then record only new species in subsequent sampling units. This method allows us to consistently cover the entire area of each fragment and compile a list of all vascular plant species observed in each fragment as well as the order in which they were detected across the 88 sampling units. Over the entire 18-year time series, we have kept the number of observers to a minimum – three (Damschen, Brudvig, and Burt). These observers standardize sampling effort and taxonomic identification rules prior to each annual survey. Resulting estimates of species richness for each fragment are from equal areas (1.375 ha). Taxonomy follows (*38*) and (*39*). In rare cases where identification is not possible at the species level (2% of taxa), we combine species to the genus level.

We assigned each plant species one of three primary dispersal modes: wind, animal, or gravity. We chose these modes because they capture distinctive classes of seed movement. We determined dispersal modes by first searching the Kew Garden Seed Information Database (*40*). If species were not in that database, we searched the primary literature with ISI Web of Science for papers that described dispersal for the species and/or genus. In some cases, we also searched reliable plant natural history websites to cross-reference obtained information. All designations were independently reviewed by two plant ecologists within our plant ecology research team (E. Damschen, L. Brudvig, M. Burt, C. Warneke, Q. Sorenson). Any conflicting or missing designations were discussed and decided by this entire team and decided on based on morphological and field observations (11% of species). Wind dispersal included both wind and tumbling dispersal mechanisms. Animal dispersal included endozoochory and epizoochory by birds and mammals and myrmecochory by ants. Gravity dispersal included ballistic dispersal mechanisms and species lacking apparent morphology to assist dispersal.

We also determined whether each species was associated with longleaf pine savannas (i.e., "longleaf pine species"). We were interested in assessing the responses of these species because they are of particular conservation and restoration concern and could respond more strongly to the contrasting habitat differences between the fragments and matrix in our experimental landscapes. We classified species as longleaf pine indicator species if they met one or both of the following criteria: 1) designation as longleaf pine upland species in published species lists for the Savannah River Site (*41, 42*), or 2) designation as "indicator species" in previous analyses of longleaf pine savanna plant communities at the Savannah River Site (*43*).

Because soil moisture is an important determinant of plant diversity in longleaf pine savannas (*44, 45*), we quantified soil water holding capacity. We used the same methods as Damschen et al. (*27*) by collecting 96-136, 10-cm deep × 2.5-cm diameter soil cores, evenly distributed across each fragment. We then determined soil water holding capacity as (wet mass - dry mass)/dry mass for each sample (*46*) and used the average of all samples from a fragment in our analyses.

All data are available from the Environmental Data Initiative and Data One (*33*).

Analyses

We modeled changes in plant communities using multi-species occupancy models and their extensions to capture both changes in species richness and colonization-extinction dynamics (*47, 48*). Occupancy modeling provides two major benefits. First, it can account for species-specific imperfect detection (observation errors). Second, it estimates species directly rather than modeling summary statistics of communities (e.g., species richness), such that species identity is honored and tracked in the modeling process. The latter benefit also allows for understanding how species-specific characteristics (e.g., dispersal mode) may impact communities while also providing a means to derive community-level parameters (e.g., species richness). This general approach uses a hierarchical framework. To ensure that results were robust to the modeling framework we used, we used a negative binomial regression to contrast results to those from modeling species richness without accounting for imperfect detection.

As part of our occupancy modeling, we estimated imperfect detection using detection histories for each species in each fragment for each year. We used spatial replicates based on the long-term sampling design to create those detection histories. For each fragment, we pooled 88 samples that covered the entire fragment into $J = 8$ replicates. This sampling strategy is best viewed as a 'removal' design (*49*), where once a species is detected, it is no longer tracked in fragment *i*. For example, a detection history for species *k* at fragment *i* in year *t* could be [0 0 0 0 1 NA NA NA], where NA refers to no data, given the 'removal' design. For most analyses, we focus on comparing communities in connected (corridor) versus unconnected (rectangular and winged) fragments and did not include the center fragment in modeling (but see below for interpreting if colonization of corridor fragments arose from center fragments).

We first modeled the entire plant community ($K = 309$ species) to estimate potential effects of corridors over time on species richness. To model species richness over time, we used an 'implicit dynamics' formulation of the multi-species occupancy model (*50*). In this context, we modeled the probability of occurrence $\psi$ for species *k* in time *t* at fragment *i* as:

$$z_{k,i,t} \sim \text{Bernoulli}\left(\psi_{k,i,t}\right) \quad (1)$$

where *z* is the latent occupancy state (0,1). We modeled $\psi$ as:

$$logit\left(\psi_{k,i,t}\right) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (2)$$

such that each species *k* had a different, treatment-specific intercept and slope over time (i.e., an interaction of treatment*species*time). Note that in this model, we initially considered site as a random effect to account for within-site repeated measures over time, which provided similar results. We removed this effect in the final model to simplify model structure given the large number of latent parameters (e.g,. species-specific effects).

Our observation model was described as:

$$y_{k,i,t,j} \sim \text{Bernoulli}\left(z_{k,i,t} p_k\right) \quad (3)$$

Where $y_{k,i,t,j}$ is the detection of species *k* in fragment *i* at year *t* for replicate observation *j* and $p_k$ is the probability of detection of species *k*, conditional on presence. We allowed detection to vary by species.

This model formulation assumes a linear effect of time since corridor creation (on the logit scale) on species-specific occurrence; however, this effect can appear non-linear on the probability (and species richness) scale, as in logistic regression. We also considered two types of non-linear functions (considering the log of time or adding a quadratic term of time), neither of which were supported by the data based on the Deviance Information Criterion, DIC (lower values indicate better fit; linear time: 93634; log time: 93840; quadratic time: 94352). We also initially considered the potential effects of soil moisture in this model, but found no support for its effect based on DIC (soils ignored: 93634; soils included: 99562). Thus, we did not include soil moisture in final models. We contrasted these results to modeling raw species richness with non-linear effects over time using a negative binomial regression, finding similar support for a linear effect of time and qualitatively similar patterns of changes in species richness as found in the multi-species occupancy model (Figs. S4, S5).

For a subset of the community (i.e., those species with > 10 detections over time; $K = 239$ species of the possible 309 species), we explicitly modeled colonization-extinction dynamics. While the entire community could be modeled to interpret colonization-extinction dynamics, little information is available for rare species to interpret treatment effects and how they change over time. Thus, such an approach would make the implicit assumption that rare species, which contribute a comparatively small amount of data on extinction and colonization, respond similarly to treatments as more common species, such that rare species dynamics do not have a large impact on conclusions (*48*). Because of this effect, we use the 239 species subset of more common species to make conclusions on colonization-extinction dynamics. We note, however, that modeling colonization-extinction dynamics of all species showed similar patterns.

We followed methods of Dorazio et al. (*48*), who extended the multi-species occupancy framework for capturing colonization-extinction dynamics. The dynamics of species occurrence can be described and estimated with time-series data by assuming a first-order Markov process, where $z_{k,i}$ at time *t* is contingent on $z_{k,i}$ at time *t* - 1, as well as local colonization, $\gamma$, and local extinction, $\varepsilon$, processes. If we define $\phi = 1 - \varepsilon$, then:

$$z_{k,i,t} = \text{Bernoulli}\left(z_{k,i,t-1}\phi_{k,i,t-1} + \left(1 - z_{k,i,t-1}\right)\gamma_{k,i,t-1}\right). \quad (4)$$

This framework requires estimating occupancy at time 1, and then colonization-extinction dynamics in subsequent time steps. We also considered an alternative parameterization that accounts for potential rescue effects ("pseudo-rescue effects" sensu Hanski 1999) replacing $\phi_{k,i,t-1}$ in equation 4 as (*51*):

$$\phi^*_{k,i,t-1} = \left(1 - \left(1 - \phi_{k,i,t-1}\right)\right)\left(1 - \gamma_{k,i,t-1}\right). \quad (5)$$

To further interpret support of rescue effects, we contrasted similar models as described in equations 4-5 but fit to single species (i.e., 'dynamic occupancy models'; *52*). We also note that

rescue effects are also often interpreted as occurring when connectivity (e.g., corridors) decrease local extinction rates, although it can be unclear if such patterns are driven by rescue effect mechanisms (*53*).

We allowed for $\psi$ to vary by species (we also initially considered that $\psi$ could vary by treatment; however, there was no support for this added complexity so we do not consider it further, See Fig. S1). We also allowed for $\gamma$ and $\varepsilon$ to vary by treatment over time for each species as:

$$logit(\gamma_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (6)$$

$$logit(\phi_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (7)$$

From this model, we then summarized the average $\varepsilon$ and $\gamma$ across species and associated 95% credible intervals for each treatment over time based on the species-specific posterior distributions of model parameters. We averaged unconnected treatments (winged, rectangular) because the rates of change for these treatments were similar (Table S1).

To determine if the results are consistent for species of conservation and restoration concern and to determine whether movement ability of species influences our results, we also summarize colonization-extinction dynamics on two types of species traits: 1) longleaf indicator status; and 2) dispersal mode (see Data Collection for descriptions of these characteristics).

To better interpret if colonization was driven by corridors, we re-ran the colonization-extinction model (using equation 4) and included the center fragment (Fig. 1) into the model. Based on this model, we determined if connected fragments tended to be colonized sooner than unconnected fragments for species that occurred (i.e., $z_{k,i,t}$ =1) in center fragments prior to other fragments within each landscape.

We assumed vague priors for all parameters ($N \sim (0, 100)$), and used uniform hyperpriors for standard deviation parameters ($U \sim (0, 10)$). We ran all models in jags using the jagsUI package to call jags from R. We ran four chains for 37,500 Markov chain Monte Carlo (MCMC) iterations and thinned chains by 50 after a burn-in of 15000 and an adaptation phase of 15000, ultimately saving 3000 samples from the posteriors. We assessed model convergence using the Gelman-Rubin statistic R-hat, assuming that an R-hat > 1.05 indicated convergence problems (*50, 54*).

## Supplementary Text

Supplementary Results

Plant species in may have arrived in fragments through three different pathways. First, seeds could have arrived in the area where we created our experimental fragments before our experiment was created and remained in the soil seed bank. In our study system, the soil seed bank is dominated by annual herbs and graminoids, a small subset of the total species in our study system, and whose composition did not differ by fragment type at the start of our study (*27*). Second, plants were present in the pine plantation understory before our experiment was created, and some regrew after forest harvest. Our assignment of treatments to fragments was randomized and we have previously confirmed that species richness and composition did not differ by fragment type at the start of our study (*27*) (Figure S1). Third, species may arrive from the regional species pool into one of the fragments within an experimental landscape. The increased colonization rates and decreased extinction rates in connected fragments suggests that

species are more likely to move to a connected fragment than unconnected fragments. Based on temporal changes in $z_{k,i,t}$ from the colonization-extinction model that include all five fragments in each experimental landscape, we found species that first arrived in the center fragment of an experimental landscape (block) were more likely to next colonize a connected fragment than an unconnected fragment (Fig. S8). Our analysis of the order of colonization events showed that connected fragments were colonized sooner than unconnected fragments in 60% of the species (out of 120 species for which this situation occurred), but the distribution was highly skewed (Fig. S8), providing evidence of corridors facilitating colonization of species from center fragments. This evidence is bolstered by studies of individual species' movement in our experiment that overwhelmingly show increased rates of movement between connected fragments when compared to unconnected fragments (*55*).

It is also possible that rescue effects – instances where immigration prevents extinction (*5*) – are responsible for the lower extinction rates in connected fragments. When we evaluated the potential for rescue effects for the entire community, the model parameterization that included rescue effects (Eq. 5) did not fit the data as well as when no rescue effects were assumed (based on DIC: assuming rescue effect, DIC = 194,151.7, assuming no rescue effect, DIC = 192,533.7). Thus, there was no strong support for rescue effects at the community level. When evaluating whether models that included rescue effects were important for individual species, there was support for rescue effects for 54% of the 239 species based on DIC (i.e., lower DIC for the rescue effects parameterization than assuming no rescue effects). This support did not explain variation in species responses to corridors (i.e., variation in DIC did not correlate with corridor effect sizes based on treatment parameters in Eq. 6-7; $r < |0.07|$). Thus, we focused on the non-rescue effect model parameterization above for all general results in the main text. However, it is important to note that while rescue effects do not generally explain the community-level patterns we report, they can and do occur for some species.

Finally, once species arrive within fragments, connectivity may alter species interactions in ways that minimize species extinctions or promote colonization. For example, we have documented higher pollination rates in connected than unconnected fragments (*56*, *57*), which may increase seed set and population size, thereby lowering the likelihood of extinction. Additionally, changes in seed predation caused by connectivity may create competition-free microsites that facilitate colonization (*58*). Corridors also increase the temperature at which prescribed fires burn, opening microsites for plant colonization and reducing dominance by woody species, which can increase persistence of subordinate herbs (*59*). Populations may also benefit from corridors by increasing gene flow and reducing impacts of inbreeding depression (*60*). Gene flow takes place through seed dispersal and pollination, both of which are facilitated by corridors in our study system (*56*, *57*, *61*).

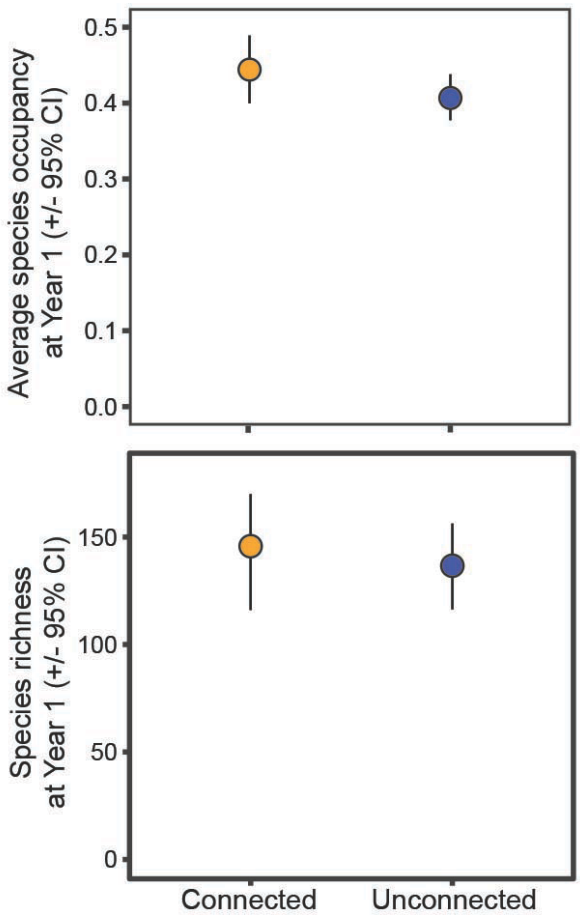


**Fig. S1. Starting conditions did not vary by treatment.** Initial probability of **(A)** species occurrence and **(B)** species richness did not differ by fragment type.

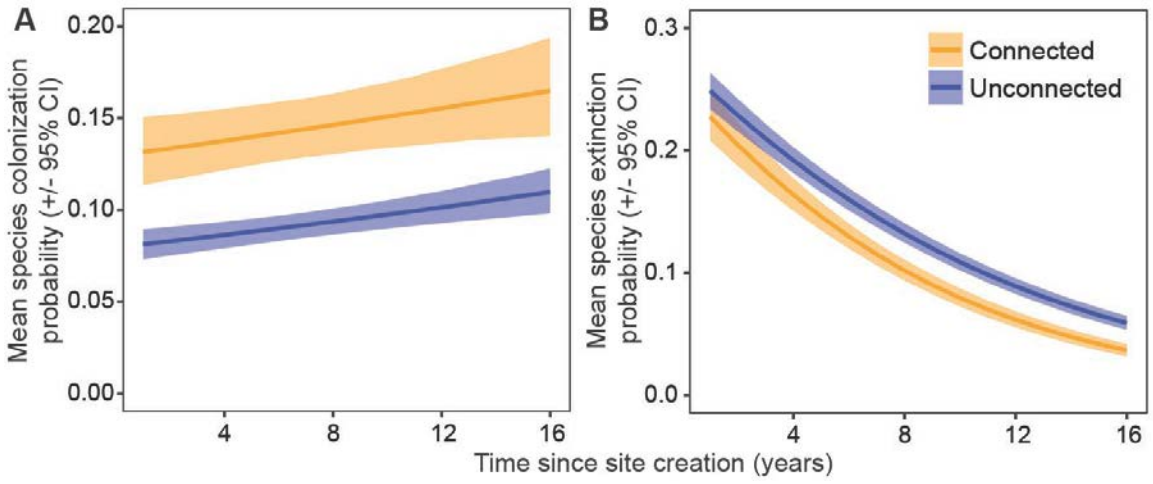


**Fig. S2. (A) Colonization and (B) extinction rates over time for connected and unconnected fragments.** The difference in these rates were used to produce Fig. 2A.

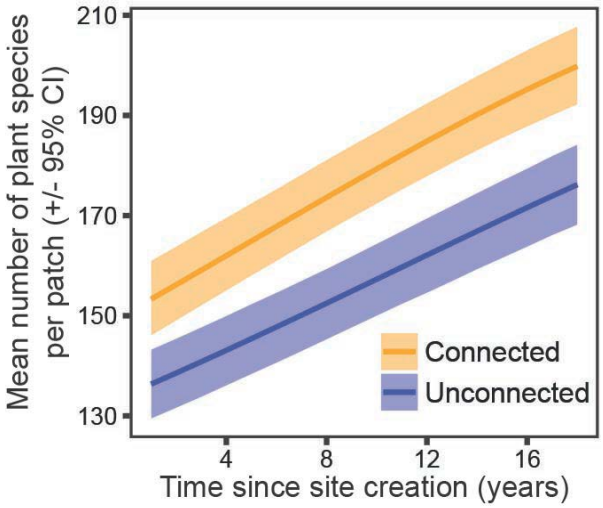


**Fig. S3. Estimated species richness over time in connected and unconnected fragments.** In the last time point (Year 18), on average there are 24 more species in connected than unconnected fragments (200 vs 176 species, respectively). The difference in these rates were used to produce Fig. 2B.

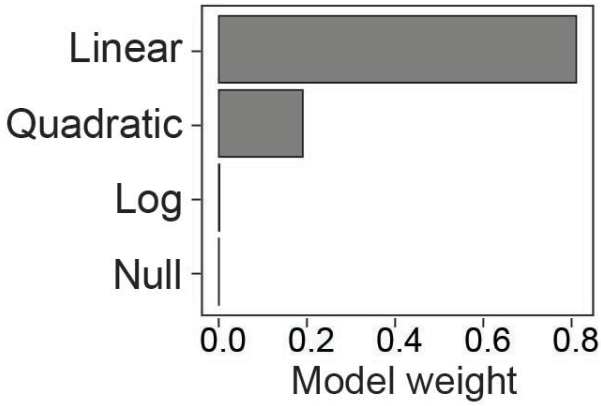


**Fig. S4. A linear model is the best fit for the difference in species richness between connected and unconnected fragments over time.** Model weights represent AIC model weights taken from negative binomial regressions that included the main and interactive effects of treatment and time since site creation (treated as either a linear, log-linear, or quadratic effect of time, in contrast to no effect of time represented as 'Null'. Higher model weight signifies greater support for a model relative to the other models considered, with a value of 1 indicating full support. Consequently, these weights suggest overwhelming support of a linear effect of treatments over time relative to potential non-linear (log time, quadratic time) effects of time.

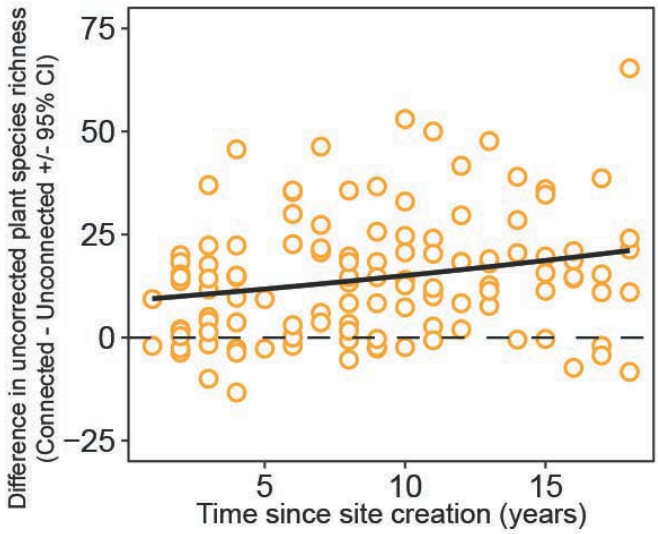


**Fig. S5. The linear increase over time is evident in the difference in uncorrected, raw plant species richness over time between connected and unconnected fragments.** Predicted line comes from the linear model (Fig. S4).

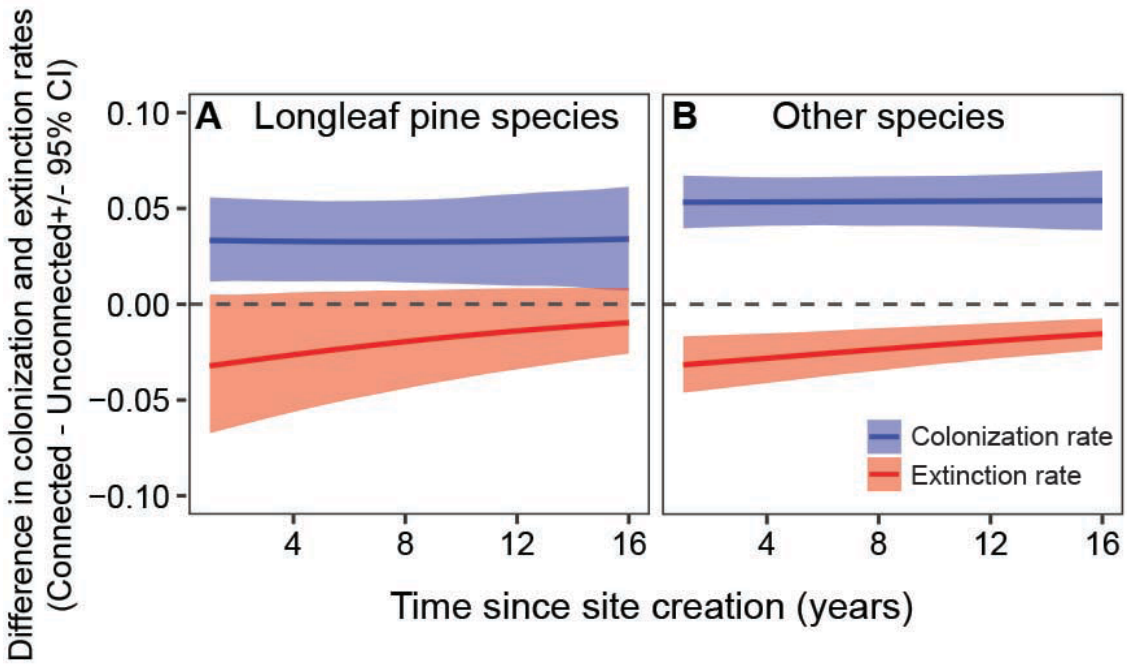


**Fig. S6. Plant species (A) associated with longleaf pine habitat and (B) other species respond similarly to connectivity over time**, although uncertainty is greater for species associated with longleaf pine habitat due to a smaller number of species**.** The difference between connected and unconnected fragments for colonization and extinction probabilities is shown for both groups.

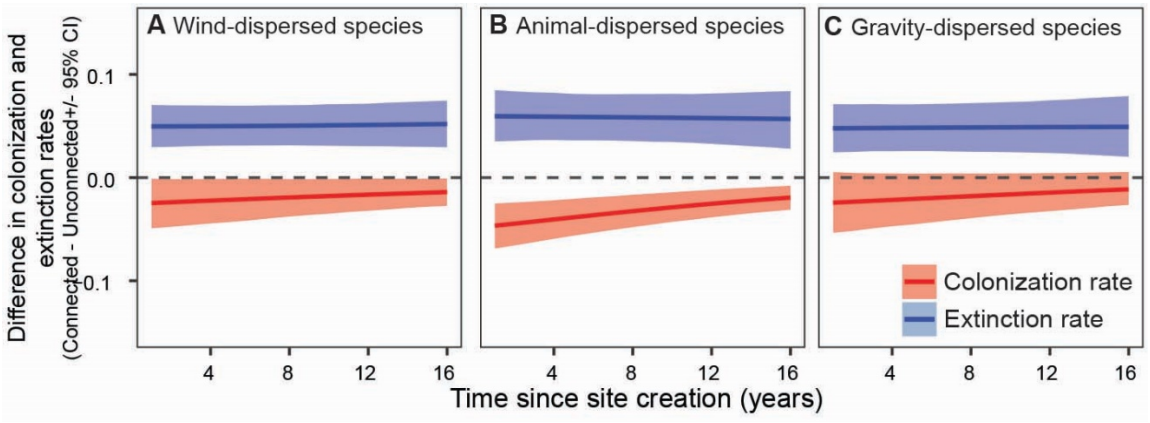


**Fig. S7. Plant species respond similarly to connectivity over time across seed dispersal modes.** The difference between connected and unconnected fragments for colonization and extinction probabilities of **(A)** wind-dispersed, **(B)** animal-dispersed, and **(C)** gravity-dispersed plant species over time.

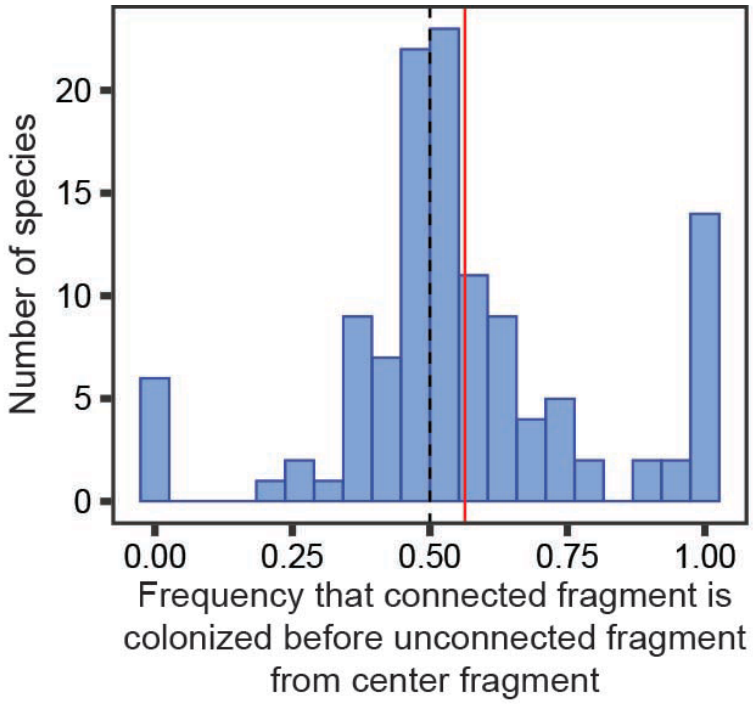


**Fig. S8. Colonization events from the center fragment reach connected fragments sooner than unconnected fragments.** When species arrived for the first time in an experimental block in the center fragment, connected fragments were colonized sooner than unconnected fragments for 60% of the species (out of 120 species for which this situation occurred; mean frequency = 0.56). The distribution was highly skewed providing some evidence of corridors facilitating colonization of species from center fragments.

**Table S1. Summary of parameter estimates (on the logit scale) from multi-species occupancy model used to derive species richness over time.** We show average estimates across species because this model estimates a parameter for each species (K = 309) regarding species detectability, treatment intercepts and rates of change over time. Estimates are provided for connected, unconnected rectangular, and unconnected winged fragments. LCL and UCL are lower and upper confidence limits, respectively.

| Parameter | Estimate | 95% LCL | 95% UCL |
|---|---|---|---|
| Species mean detectability | -2.123 | -2.466 | -1.773 |
| Species mean occupancy | | | |
| Connected intercept | 0.447 | 0.294 | 0.607 |
| Rectangular intercept | -0.220 | -0.379 | -0.065 |
| Winged intercept | 0.251 | 0.098 | 0.407 |
| Connected time effect | 0.672 | 0.574 | 0.768 |
| Rectangular time effect | 0.491 | 0.404 | 0.578 |
| Winged time effect | 0.553 | 0.467 | 0.672 |

**Supplementary Code.** The code used to estimate occupancy, species richness, and colonization-extinction dynamics over time is provided as a separate supplementary file.

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The New York Times

CALIFORNIA TODAY

# *California Today: The Increasing Strain on State Firefighters*

**By Jose A. Del Real and Inyoung Kang**

July 30, 2018

*Good morning.*

*(Want to get California Today by email?* Here's the sign-up.*)*

Firefighters are working 24- to 36-hour shifts to put out several large fires across the state, often with little rest between assignments. For many, the strain of this recent spate of blazes has been compounded with a wildfire season that has become year-round and more intense.

"There used to be a rhythm to this, and you could at least count on that rhythm," said Brian Rice, who retired from fighting fires in 2011 and is now president of California Professional Firefighters, a statewide union.

Since 2012, there has not been a month without a wildfire, according to state emergency management officials. The intensity of the fires has appeared to increase as well; the fires in 2017 were among the most destructive in California's history, leaving 46 people dead and causing nearly $12 billion in damage.

Mike Daw, the executive director of the Firefighters Burn Institute, which works with injured firefighters through the U.C. Davis Burn Unit in Sacramento, said that firefighters often do not report injuries that might sideline them. Those injuries are often exacerbated over time, especially because mutual assistance programs in California mean that firefighters can end up battling fires all over the state.

"Firefighters are a unique culture," he said. "They're putting themselves in danger, and a lot of times they feel like they can endure more than a normal human being can."

Michael Feyh, a captain with the Sacramento Fire Department, said that fatigue and sleep deprivation are significant problems for firefighters and can leave them particularly vulnerable in already dangerous situations.

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And the emotional trauma after injuries or high-stakes events, he said, is often not discussed enough.

“It’s not just burns, its all the things that come with the trauma — what people see throughout their careers,” he said. “It’s hard to get guys to come forward and accept that they could be getting some help and get counseling.”

Mr. Feyh knows the risks firsthand. In 2010, he sustained second- and third-degree burns on 10 percent to 15 percent of his body, largely around his face, while responding to a report of a gas leak. The house exploded, sending him flying 20 feet and leading to the burns as well as orthopedic injuries that took about a year to heal.

“And it’s not just the individual, either; we go to work and our families always have in the back of their minds that something can happen,” Mr. Feyh said. “My wife had her worst nightmare come true.”

Ashley Iverson lost her husband, Cory, in December while he was fighting the Thomas Fire in Ventura County. Mr. Iverson, a fire apparatus engineer with CalFire, had already worked a 24-hour shift but was helping put out spot fires when he became trapped in a gulch. The fire reached him before he could escape.

Thousands honored his sacrifice at a funeral in San Diego, his hometown, just days before Christmas. Ms. Iverson was four months pregnant at the time, and today is caring for their two daughters. Sometimes she is overcome by pain, she said. “How can I raise my kids without my best friend? Why don’t they get to have him in their lives?”

Ms. Iverson hopes to turn her husband’s tragic death into something positive. She is laying the groundwork for a foundation in his name that will advocate expanding mental health awareness among fire responders and firefighters. She said she finds comfort in knowing that he had dedicated himself to helping people.

“After it happened, I took a breath. O.K., the worst has happened. Now what? Where do we go from here?” Ms. Iverson said. “A lot of widows, their life is over. I feel like Cory has given me legs. I’m just so damn proud of him and everything he did.”

## California Online

*(Please note: We regularly highlight articles on news sites that have limited access for nonsubscribers.)*

A fire truck on Highway 299 as the Carr Fire continued to burn near Whiskeytown on Sunday. Josh Edelson/Agence France-Presse — Getty Images

• The death toll in the **Carr Fire** rose to six as firefighters continued to battle the blaze over the weekend. A woman and her two young great-grandchildren were among the dead in Redding. [The New York Times]

• Urban sprawl and climate change are making areas **increasingly vulnerable to wildfires**, experts say. [The Associated Press]

• In the face of sharp opposition and questions about how to pay for it, construction of California's **high-speed rail line** is roaring ahead. [The New York Times]

• A ballot initiative aimed to address **prohibitive housing costs** could divide California Democrats. [Politico]

• California students are flocking to **universities in Arizona**. [Sacramento Bee]

• L.A. paid tribute to the restaurant critic Jonathan Gold over the weekend with a **"City of Gold."** [Los Angeles Times]

• President Trump has joined anxious Republicans in pouring millions into **close House races** in California. [San Francisco Chronicle]

• "If we want to understand a world where Russia and China are ramping up their **spy games** against the United States, then we need to pay attention to what's happening in San Francisco." [Politico]

• **A Silicon Valley life cycle:** The chief executive of Social Finance was ousted last year after questions about sexual misconduct. Months later, two venture capitalists who were on his board have invested $17 million in his new start-up. [The New York Times]

• **Maternal death rates** are rising in the U.S., but California is bucking the trend. [NPR]

Beautycon is at the forefront of a trend known as experiential retail that combines marketing, entertainment and shopping. Anna Beeke for The New York Times

• Sephora meets Coachella: Our Styles reporter went to the L.A. Convention Center for **Beautycon**, an event that is equal parts competitive shopping scene, feel-good festival and marketing bonanza. (Here's what she learned.) [The New York Times]

• With so many players who can play multiple positions, the **Dodgers** are making it work, our baseball columnist writes. [The New York Times]

• **In memoriam:** Bill Loud, the patriarch in "An American Family" on PBS, which shocked viewers with its depiction of domestic dramas in Santa Barbara. He was 97. [The New York Times]

This undeveloped property in Los Angeles, promoted as the Mountain of Beverly Hills, has 360-degree views. You can spot many of the city's major landmarks in the distance, from Century City to downtown. Beth Coller for The New York Times

• Would you pay **$1 billion** for this view? A Beverly Hills property is being pitched as L.A.'s most expensive residence ever. [The New York Times]

## Coming Up This Week

• The 2018 International Surf Festival kicks off **Wednesday**, with events in Torrance Beach, Manhattan Beach, Hermosa Beach and Redondo Beach.

• The Del Norte County Fair runs from **Thursday to Sunday**.

## And Finally …

Indian Rock Park offers easy bouldering and rewarding vistas at the top.
Jason Henry for The New York Times

A lot has changed in Berkeley since the heyday of the Free Speech Movement in the 1960s.

But the college town has made "an extraordinary effort to stay true to its freethinking, iconoclastic roots," our Frugal Traveler columnist writes.

He wandered the area sampling cheap eats, nearby parks and the music shops off Telegraph Avenue. And he confirmed what a generation before him knew: This funky trifecta of great food, live music and outdoor activities makes Berkeley ideal for a quick — and frugal — Bay Area getaway.

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*California Today is edited by Julie Bloom, who grew up in Los Angeles and graduated from U.C. Berkeley.*

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PLoS one

# A Rapid, Strong, and Convergent Genetic Response to Urban Habitat Fragmentation in Four Divergent and Widespread Vertebrates

**Kathleen Semple Delaney[1]*¤, Seth P. D. Riley[2], Robert N. Fisher[3]**

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## Abstract

***Background:*** Urbanization is a major cause of habitat fragmentation worldwide. Ecological and conservation theory predicts many potential impacts of habitat fragmentation on natural populations, including genetic impacts. Habitat fragmentation by urbanization causes populations of animals and plants to be isolated in patches of suitable habitat that are surrounded by non-native vegetation or severely altered vegetation, asphalt, concrete, and human structures. This can lead to genetic divergence between patches and in turn to decreased genetic diversity within patches through genetic drift and inbreeding.

***Methodology/Principal Findings:*** We examined population genetic patterns using microsatellites in four common vertebrate species, three lizards and one bird, in highly fragmented urban southern California. Despite significant phylogenetic, ecological, and mobility differences between these species, all four showed similar and significant reductions in gene flow over relatively short geographic and temporal scales. For all four species, the greatest genetic divergence was found where development was oldest and most intensive. All four animals also showed significant reduction in gene flow associated with intervening roads and freeways, the degree of patch isolation, and the time since isolation.

***Conclusions/Significance:*** Despite wide acceptance of the idea in principle, evidence of significant population genetic changes associated with fragmentation at small spatial and temporal scales has been rare, even in smaller terrestrial vertebrates, and especially for birds. Given the striking pattern of similar and rapid effects across four common and widespread species, including a volant bird, intense urbanization may represent the most severe form of fragmentation, with minimal effective movement through the urban matrix.

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## Introduction

Habitat loss and the resulting fragmentation can have many impacts on wildlife populations. However, the effects of fragmentation may vary based on many factors including the size, configuration, and age of habitat patches, the vagility of the species in question, and the characteristics of the matrix between patches. Urban development may represent a particularly intense form of fragmentation for many animals. Species that are particularly sensitive to urban development may be quickly lost from urban areas [1,2,3]. For species that remain widely distributed across fragmented landscapes, connectivity and gene flow between populations may be reduced, leading to longer-term problems such as inbreeding, loss of genetic diversity, and even local extinction [4,5,6,7]. If local extinction occurs, then more isolated patches will be harder to re-colonize [4]. In addition, the loss of genetic diversity within isolated patches can lead to a decrease in a species' ability to adapt to environmental change [8,9].

An increasing number of studies of the genetic effects of fragmentation have occurred in the past decade or so, although 30–40% of these have not shown significant effects and many are in non-urban landscapes such as fragmented forests [10]. Urbanization is a common cause of fragmentation, and conservation efforts point to the extreme land use changes associated with urbanization as one of the largest threats to biodiversity [11]. However, to date, fine-scale (within 5–10 km) genetic effects of urban fragmentation have been documented for few species [12,13,14,15,16,17], and many studies find little effect [18,19,20]. Moreover, studies of the genetic effects of fragmentation are overwhelmingly on a single species, and we know of no studies

where genetic patterns were compared in the same urban landscape for species from different broad taxa, such as reptiles (Class *Reptilia*) and birds (Class *Aves*), and with radically different means of locomotion, such as flying and crawling.

We investigated the genetic effects of urban fragmentation on three lizards, the side-blotched lizard (*Uta stansburiana*), western skink (*Plestiodon skiltonianus*) and western fence lizard (*Sceloporus occidentalis*), and one bird, the wrentit (*Chamaea fasciata*) in Santa Monica Mountains National Recreation Area (SMMNRA), a national park near Los Angeles. The three lizard species have widespread distributions in California [21], are small in size, are still relatively common and widespread in natural habitat throughout the area [22], and have low dispersal capabilities [23,24,25,26,27]. Side-blotched lizards and fence lizards are both in the family *Iguanidae*, but side-blotched lizards are considerably smaller and prefer more open habitat. Western skinks are in a distantly-related different family (*Scincidae*) and locally prefer grassland habitat, although all three species are broadly sympatric in the region.

Wrentits are small birds (approximately 15 g) with a distribution that is limited to the west coast of North America and follows the scrub and chaparral habitat that they prefer[28]. Wrentits are monogamous, hold small (1–2.5 acres), year-round multi-purpose territories [28], and have short dispersal distances [29]. Wrentits are obviously very different phylogenetically and ecologically from the lizards and also have the ability to fly, which could potentially increase their movement across the landscape. A bird isolated in a habitat fragment could presumably simply fly over urban areas to disperse to other suitable habitats, thereby preventing genetic divergence between patches. However, because wrentits have short dispersal distances, small territories, and relatively specific habitat requirements, it is possible that wrentits could be affected by habitat fragmentation.

The landscape of southern California continues to be rapidly altered by urbanization and the resulting habitat loss and fragmentation, even though it is part of the California Floristic Province and is one of Conservation International's world biodiversity hotspots ([30,31], www.biodiversityhotspots.org). Because it is in the Los Angeles area, SMMNRA is under intense development pressure and urbanization might increase to as much as 47% of the area by 2050, whereas only 11% was urbanized in 2000 [32]. Given the low vagility of these four focal species, it is possible that movement out of suitable habitat across a highly urbanized landscape is rare. This isolation could increase the genetic divergence between populations living in fragments and also decrease genetic variability within fragments. If urbanization is not an impenetrable barrier to movement, migration between patches by individuals could mitigate negative genetic effects [4,33,34]. Understanding plant and animal responses to habitat destruction and fragmentation will be important for maintenance of this important biodiversity hotspot, especially in the face of unknown consequences of global climate change.

## Results

We attempted to genotype approximately 20 individuals from each species for each sample site (Fig. 1a, Table 1), although for some locations fewer than 20 were captured. Microsatellite loci in lizards did not significantly deviate from HWE, however three loci in wrentits did (Ase48, Ase64, Ase50). We didn't find an excess of homozygotes, which could indicate the presence of null alleles, at any of the three loci; so analyses were done using all loci. All microsatellite loci were in linkage equilibrium for all 4 species, except that in western skinks 2 pairs of loci were significantly linked ($p = 0.05$; Eufa1×Elo34, Elo34×Eufa27).

### Genetic Divergence

Pairwise $F_{ST}$ values indicated many significant genetic differences between patches for all four species (84% of comparisons were significant for side-blotched lizards, 89% for fence lizards, 87% for skinks, and 71% for wrentits; Table S1). Average pairwise $F_{ST}$ between patches was highest in the wrentit at 0.095 (range 0.012–0.299). Among lizards, the level of differentiation was highest for side-blotched lizards, with an average pairwise $F_{ST}$ of 0.073 (range −0.006–0.200), and very similar for western skinks (mean $F_{ST} = 0.040$, range 0.003–0.104) and western fence lizards (mean $F_{ST} = 0.040$, range 0.003–0.095). As a baseline comparison from continuous habitat, when we computed genetic distances between the sampling arrays within large and core patches and between several other sites outside of our urban study area (but within the park, see Methods), we found lower average $F_{ST}$ for all three lizard species (side-blotched lizards, 0.02; western fence lizard, 0.016; western skinks, 0.013), and fewer significant pairwise $F_{ST}$ (side-blotched lizards, 12.5%; western fence lizards, 16.7%; western skinks, 30%; Table S2). For wrentits, genetic samples were also collected from two coastal canyons outside of our study area, and the $F_{ST}$ between these two sites was non-significant ($F_{ST} = 0.026$). Significant genetic distances between patches could also be caused by isolation by geographic distance. We found no significant correlations between genetic distance ($F_{ST}$) and geographic distance in any of the four species, suggesting no pattern of isolation by distance (Table 2). However, partial Mantel tests showed that genetic distances for all four species were significantly correlated with highway presence, roads presence, and time since isolation (patch age) when geographic distance was held constant (Table 2).

Alleles in Space allows for visualization of genetic divergence over geographic space. We found that the largest area of genetic divergence for all four species was located in the area surrounding and including Highway 23 (Fig. 1b). There was also an area of higher divergence in the eastern part of the study area for two of the four species (wrentits, Fig. 1c; and western skinks, Fig. 1e).

Genetic clustering analysis revealed that the most likely number of genetic groups for all four species was between three and five (Table S3, Fig. 2). For wrentits (Fig. 2a) there were three most likely clusters, with the main genetic break again located across the developed areas surrounding and including Highway 23. For side-blotched lizards (Fig. 2b) and skinks (Fig. 2d) the most likely number of clusters was five, and for western fence lizards (Fig. 2c) it was four.

### Genetic Diversity

Mean heterozygosity ($H_e$) and the mean number of effective alleles ($N_A$) were not significantly lower in smaller patches for any of the four species (Table S4). However, relatedness was higher in small patches for all three lizard species (side-blotched lizard difference = 0.03, $t = 4.1$, $p = 0.003$, d.f. = 6.2; fence lizard difference = 0.02, $t = 4.5$, $p = 0.001$, d.f. = 7; skink difference = 0.02, $t = 2.25$, $p = 0.03$, d.f. = 6). Rarefaction analysis indicated that the number of loci used produced consistent average relatedness results for all species and that the addition of the last locus added a 0.5% (fence lizards), 0.8% (side-blotched lizards), 1.4% (western skinks), and 0.1% (wrentits) change in relatedness estimates.

We tested the relationship between genetic diversity and the degree of isolation of each habitat patch and found that for wrentits, $H_e$ was lower in more isolated patches ($R^2 = 0.498$, $p = 0.051$,

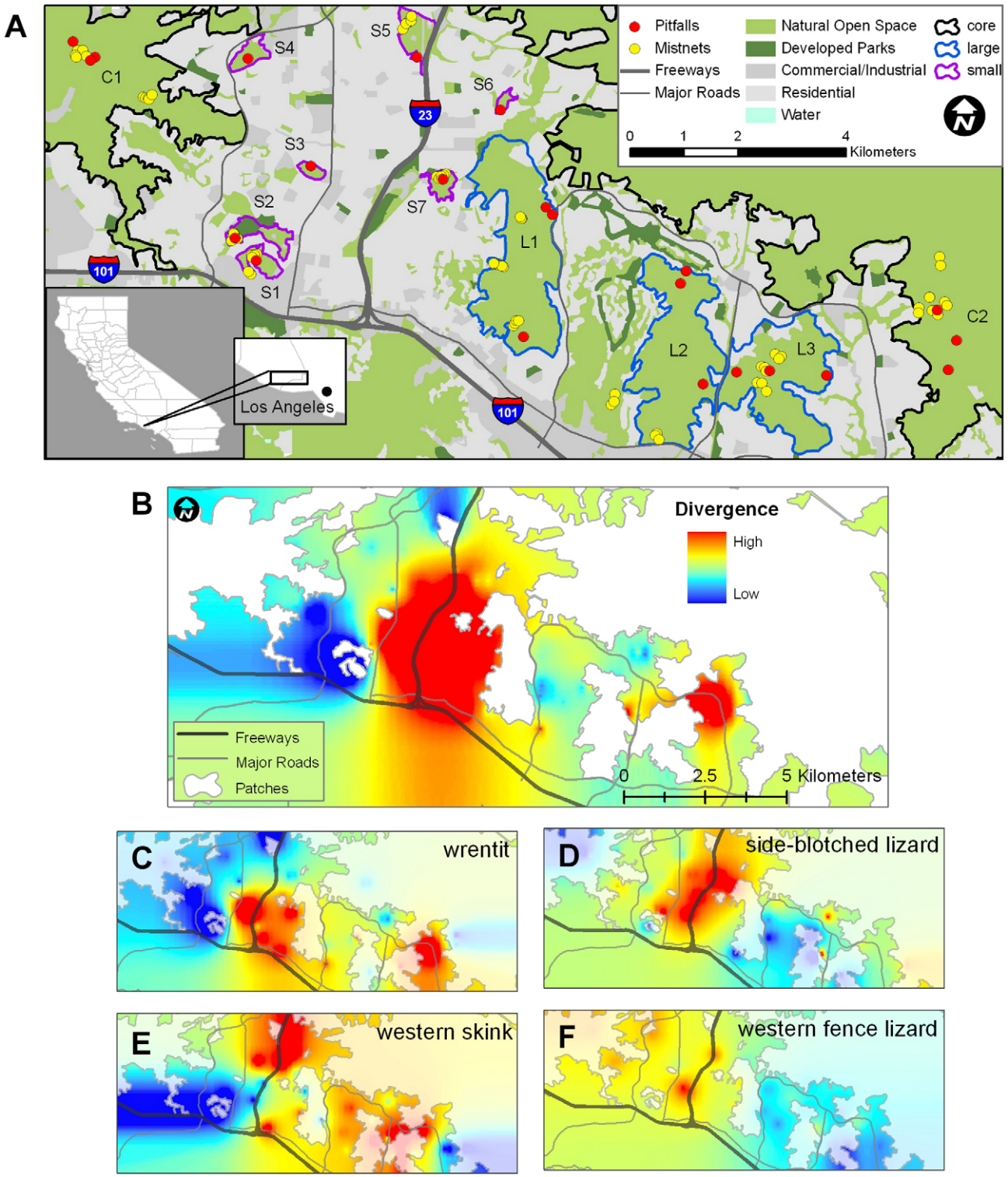


**Figure 1. Study area and genetic divergence.** A. Sampling sites (mist-net and pitfall locations), roads, and habitat patches (S = small, L = large, C = core) within the study area (Sample sizes are shown in Table 1). B. Mean genetic divergence mapped on the Simi Hills landscape for all four species, and separately for C. wrentits, D. side-blotched lizards, E. western skinks, and F. western fence lizards.
doi:10.1371/journal.pone.0012767.g001

d.f. = 7), as was $N_A$ ($R^2 = 0.55$, $p = 0.035$, d.f. = 7; Fig. 3a). Relatedness was higher in more isolated patches for all three lizard species (side-blotched lizard $R^2 = 0.4$, $p = 0.03$, d.f. = 10; fence lizards $R^2 = 0.52$, $p = 0.002$, d.f. = 8; western skink $R^2 = 0.33$, $p = 0.05$, d.f. = 9; Fig. 3b). There were no correlations between genetic diversity and patch age for any of the four species (Table S5).

**Table 1.** Patch metrics (area, isolation, and age) and the number of samples genotyped by species.

| Patch metrics | | | | | Number of samples genotyped | | | |
|---|---|---|---|---|---|---|---|---|
| Patch type | Sample site/patch | Area (ha) | Isolation (PROX)[a] | Age (years)[b] | Wrentit | Side-blotched lizard | Western fence lizard | Western skink |
| Small | S1 | 267.2 | 119.3 | 13 | 0 | 14 | 14 | 16 |
| | S2 | 376.6 | 115.4 | 13 | 3 | 15 | 18 | 17 |
| | S3 | 104.8 | 52.8 | 33 | 0 | 18 | 0 | 18 |
| | S4 | 254.8 | 6404.8 | 23 | 0 | 17 | 0 | 0 |
| | S5 | 450.2 | 195.9 | 33 | 5 | 14 | 18 | 5 |
| | S6 | 78.2 | 747.4 | 13 | 0 | 17 | 0 | 20 |
| | S7 | 206.5 | 133.1 | 43 | 8 | 15 | 16 | 10 |
| Large | L1 | 4445.4 | 18428.1 | 28 | 7 | 0 | 18 | 28 |
| | L2 | 3905.7 | 1598.1 | 23 | 8 | 22 | 17 | 29 |
| | L3 | 3276.1 | 30121.0 | 18 | 12 | 18 | 17 | 18 |
| Core | C1 | 25453.6 | 6368.9 | 23 | 11 | 7 | 15 | 0 |
| | C2 | 121014.2 | 10718.8 | 13 | 15 | 24 | 14 | 18 |

[a]Patch isolation values (PROX) decrease with increasing isolation of patches.
[b]Patch age was calculated as the number of years since the patch was 100% isolated from other open natural space.
doi:10.1371/journal.pone.0012767.t001

## Discussion

### Loss of genetic connectivity

Using three different methods, traditional pair-wise genetic distance analysis ($F_{ST}$; Table S1), landscape genetic analysis (Fig. 1b), and Bayesian genetic clustering (Fig. 2), we found significant genetic differences between sample locations in all four species. Moreover, the three methods showed strikingly similar and strong genetic effects of fragmentation. All four species exhibited the largest genetic divergence over the oldest (based on building dates, see Methods) and widest expanse of urban areas surrounding and including Highway 23 (Fig. 1b).

Pairwise $F_{ST}$ between habitat patches showed that the genetic divergence was significant, especially given the short amount of time that the habitat fragments have been isolated from each other and from core areas. For all four species, average $F_{ST}$ values within continuous habitat were 2.5 to 3.6 times lower than in fragmented habitat, and the majority of comparisons were non-significant (Table S2). This suggests that microsatellite allele frequencies within and between habitat patches are changing on a very short time scale. Several other reptile and amphibian studies have found similar genetic divergences on similar time scales. For example, genetic divergence between fragmented populations of two gecko species in Australia was higher than divergence between samples in un-fragmented landscapes [35]. In that study, forested habitat patches were fragmented beginning around 1900 by wheat fields, which can be dry and barren during the non-growing season. In our study, however, the intervening landscape is concrete, asphalt, buildings, or urban yard landscaping, and although fragmentation began in the 1940s, many patches were only 50–75% isolated until 1980, making the isolation more recent. The long-lived tuatara (*Sphenodon punctatus*) was shown to have small yet significant genetic structuring (overall $R_{ST} = 0.012$) over less than 500 meters on a recently fragmented island [18]. Overall divergence was driven by one remnant forest fragment which was most isolated by island topography. Therefore, it was unclear that human activity, in this case pasture cleared for livestock grazing, was the cause of the genetic divergence. The eastern red-backed salamander (*Plethodon cinereus*), an even smaller and less mobile animal then the lizards we investigated, had pairwise $F_{ST}$ between patches similar in value to the lizards in our study [14]. In that study, habitat fragmentation was also caused by 20$^{th}$ Century urbanization.

For birds, few studies have shown large pairwise $F_{ST}$ between patches on such a small scale. For example, a study of the

**Table 2.** Mantel and partial Mantel tests with genetic distance and landscape features.

| Mantel Tests | Wrentit | | Side-blotched lizard | | Western skink | | Western fence lizard | |
|---|---|---|---|---|---|---|---|---|
| | r | *p* | r | *p* | r | *p* | r | *p* |
| $F_{ST}$ and GD[a] | −0.015 | 0.500 | −0.011 | 0.509 | 0.178 | 0.162 | 0.042 | 0.408 |
| Partial test, HWY[b] | 0.430 | 0.001 | 0.259 | 0.027 | 0.442 | 0.007 | 0.255 | 0.049 |
| Partial test, RDS[b] | 0.425 | 0.031 | 0.314 | 0.015 | 0.495 | 0.012 | 0.399 | 0.016 |
| Partial test, AGE[b] | 0.458 | 0.009 | 0.393 | 0.033 | 0.466 | 0.045 | 0.760 | 0.002 |

[a]Mantel test correlations between genetic distance ($F_{ST}$) and geographic distance (GD).
[b]Partial Mantel tests for partial correlations between the presence of Highway 23 only (HWY), the presence of major roads including Highway 23 (RDS), and the age of isolation between patches (patch age; AGE) while controlling for geographic distance.
doi:10.1371/journal.pone.0012767.t002

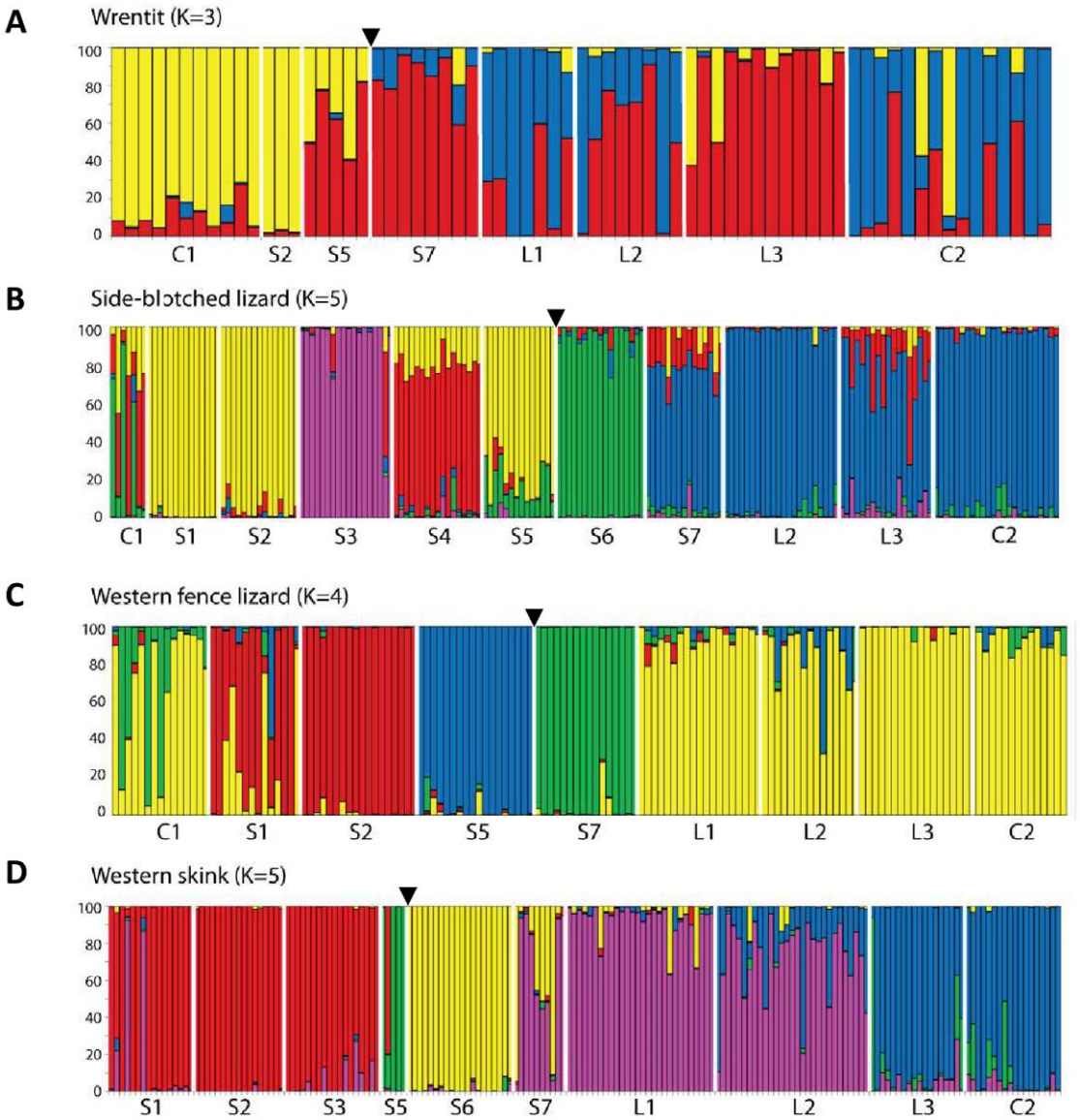


**Figure 2. Genetic clustering analysis reveals the most likely K.** Each column represents one individual and colors correspond to the percentage of assignment to each cluster. Patch names (Fig. 1a) are on the X-axis organized from west (left) to east (right). A black triangle indicates the location of the 23 freeway.
doi:10.1371/journal.pone.0012767.g002

capercaillie (*Tetrao urogallus*) in the Black Forest in Germany showed significant pairwise $F_{ST}$ between sites, ranging from 0.007 to 0.036 [36]. In their study area, which was approximately 10 times the size of ours, suitable forest habitat was fragmented by other forest types and grassland, as opposed to by residential and commercial development. A study [37] of white-ruffed manikins (*Corapipo altera*) showed similar results to the capercaillie. There was some genetic structuring shown between remnant forest fragments, however all significant pairwise $F_{ST}$ could be attributed to one forest fragment. In addition, pairwise $F_{ST}$ between forest fragments ranged from 0.001 to 0.029 for manikins, whereas in our study the pairwise $F_{ST}$ were approximately 10 times higher. Finally, a study of great tits (*Parus major*) in forest parks within the city of Barcelona found many significant pairwise $F_{ST}$ between parks (average 0.067), but the parks actually had higher genetic diversity than the surrounding forest, and there was significant gene flow both between parks and from the parks to the forest [38]. Overall, there are few comparable studies of avian fine-scale genetic structure, particularly in urban landscapes, but wrentits in southern California appear to have the highest amount of genetic structure documented to date.

The Bayesian clustering analysis confirmed the loss of genetic connectivity for each species in our study area. Similar analyses in other bird studies have consistently shown that one genetic cluster is most likely [36,37,39,40], with only the great tit study finding two clusters [38]. For the lizards, in many of the small patches most or all individuals were given close to 100% assignment to that patch (e.g. S3 for side-blotched lizards, S5 and S7 for fence lizards, and S6 for skinks; Figure 2), which suggests a remarkable amount of genetic isolation within patches over relatively short geographic and temporal scales (Table S6). The short dispersal distances for all four species suggest that gene flow even within the natural landscape may be limited (for lizards, we did find a few significant $F_{ST}$ values between sampling sites within continuous habitat), and therefore may be extremely restricted in a fragmented landscape.

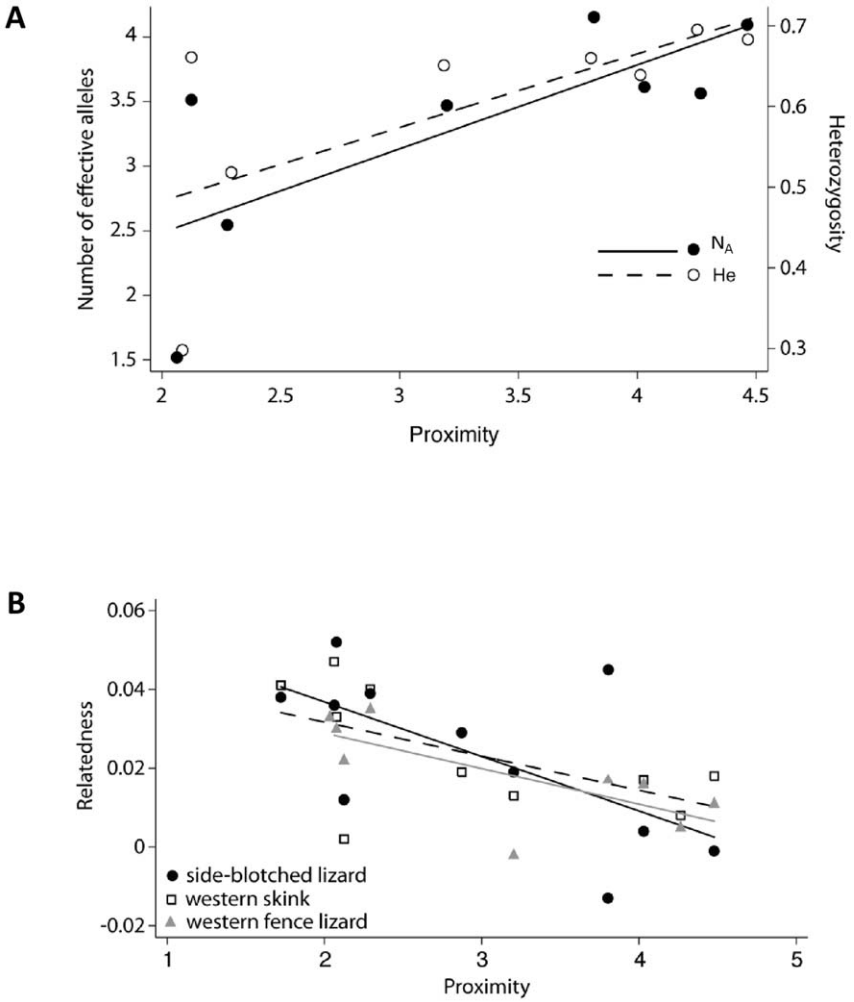


**Figure 3. Relationship between genetic diversity (heterozygosity, number of effective alleles, and relatedness) and patch proximity[a] (log transformed).** A. wrentits ($H_e$: $R^2 = 0.698$, $p = 0.051$, d.f. = 7; $N_A$: $R^2 = 0.55$, $p = 0.035$, d.f. = 7) and B. three lizard species ($R_{LR}$: side-blotched lizard $R^2 = 0.4$, $p = 0.03$, d.f. = 10; western skink $R^2 = 0.33$, $p = 0.05$, d.f. = 9; western fence lizard $R^2 = 0.52$, $p = 0.002$, d.f. = 8). [a] Patch proximity is the inverse of patch isolation.
doi:10.1371/journal.pone.0012767.g003

In one of the few other studies using Bayesian genetic clustering analysis, red-backed salamanders (*Plethodon cinereus*) were found to have two genetic clusters on either side of a large highway running through the urbanized study area [41]. Our genetic clustering results suggest that the intense fragmentation from urbanization may be a particularly strong barrier to animal movement and gene flow for all four species.

Along with significant divergence between patches, we also found significant correlations between specific causes (roads) and measures (patch age) of fragmentation and genetic divergence in all four species (Table 2). Further, our landscape genetic results revealed that the areas surrounding and including Highway 23 in the city of Thousand Oaks, which are the oldest and most densely urbanized, consistently had the highest peaks of differentiation, again for all four species (Fig. 1b). The concordance of these results for all four species is remarkable given their differences in mobility, ecology, and taxonomy. A second area of high genetic divergence in the eastern portion of our study area, also characterized by a major road surrounded by a wide swath of residential development, was shared by two species, wrentits and skinks. Other species have also shown fine-scale genetic changes related to roads and fragmentation in this region. Coyotes and bobcats exhibited significant genetic differentiation across Highway 101, the largest highway in the study area [42]. It is unknown if the species in our study would cross such a large barrier, but with short dispersal distances and small home range sizes, those events would likely be rare. Similarly, in smaller and less mobile species, a loss of genetic connectivity and diversity was found in two Jerusalem crickets (*Stenopelmatus 'santa monica'* and *Stenopelmatus 'mahogani'*) across the same region [16,43]. Genetic divergence in Jerusalem crickets was significantly associated with urban development and the presence of highways within the Simi Hills.

The significant genetic divergence and loss of genetic diversity over short geographic and temporal scales in these four vertebrates suggest that the urban matrix is relatively impenetrable for these animals. Anecdotal observations suggest that *S. occidentalis*, but not *P. skiltonianus* or *U. stansburiana*, will move through or persist in the residential areas of the urban matrix (RNF personal observation). However, reliable data on the urban movement and habitat use of these species does not exist. In fact, knowledge about use of the urban matrix by native animal species is extremely limited in general, but would be very valuable for understanding the

conservation and management implications of urbanization. Urbanized areas may be dangerous places for these small vertebrates. Residential neighborhoods often introduce predators such as domestic cats, which may regularly prey on native vertebrates [44]. Of course residential areas also include roads, which lizards and birds may actively avoid, or which may be a significant source of mortality [45,46,47].

### Loss of genetic diversity

When the landscape is fragmented and gene flow is restricted, as we have shown for these four species, genetic diversity may be reduced in populations within smaller or more isolated habitat patches. Although we found no relationships between patch age and genetic diversity, we found significant relationships between genetic diversity measures and patch size or isolation for all four species. All three lizards had increased relatedness in smaller patches and with increasing patch isolation (Fig. 3b). Other reptile species have shown increased relatedness within habitat patches that were fragmented by agriculture [48,49,50]. In wrentits, although we did not find increased within-patch relatedness, we found lowered heterozygosity ($H_e$) and fewer alleles ($N_A$) in smaller patches (Fig. 3a). Decreased gene flow can result in decreased $H_e$ and $N_A$ in small patches as alleles are lost over the generations. This effect tends to be gradual and may not threaten populations in the short term, however, inbreeding within habitat patches tends to happen quickly and can lead to inbreeding depression [51]. Lizard relatedness values suggest that inbreeding is occurring within smaller and more isolated patches. The difference between taxa may be attributed to the increased effective isolation of lizards on suitable habitat patches as a result of more restricted dispersal ability compared to wrentits. Our results suggest that populations within smaller and more isolated patches may have an increased risk of harmful genetic effects and, over the long-term, even extirpation. In fact, the absence of individuals from certain study patches (e.g. skinks and fence lizards absent from S4; Table 1) suggests that populations that were presumably present at the time of patch isolation may have been extirpated.

In a relatively short time, we have documented significant genetic divergence between isolated patches and decreased genetic diversity in all four species. However, although time since isolation (patch age) was strongly correlated with genetic divergence between patches, the effects on genetic diversity in these animals were significantly related to patch size and degree of patch isolation, but not to patch age. This would suggest that the habitat is still relatively suitable in habitat fragments, resulting in relatively stable populations that are not going through bottlenecks, such that more time since isolation is not as important a factor. But patches that are smaller from the outset simply cannot support as large a population, and therefore are more subject to the deleterious effects of genetic drift, specifically the loss of genetic diversity. Patches that are more isolated may in turn be less likely to receive new dispersers, i.e. they would benefit less from the ''rescue effect'' that could offset reductions in genetic diversity [52]. Presumably patches that were both small and isolated would suffer the most ill effects.

### Conservation implications

The extreme urbanization within the Simi Hills area has had a significant effect on lizard and bird population genetics. Unlike some other studies of landscape level genetic changes where a species' habitat is naturally patchy, this study examined genetic responses to species living in habitat that was likely once relatively continuous [42]. While these species are still widely distributed and relatively abundant throughout the study area, genetic effects of fragmentation have been manifested in a relatively short period of 40 years or less. This may be the most profound and potentially disturbing result of our study: the vulnerability even of species that are perceived to be common and thereby likely less affected by habitat fragmentation. This may be particularly true for low-vagility organisms, and for those with more specific habitat requirements. As a chaparral and coastal sage scrub requiring species, wrentits are likely rare in developed areas and have been shown to go extinct in habitat patches as urbanization progresses [2,53,54].

For rarer species in the region, such as horned lizards (*Phrynosoma coronatum*) and whiptail lizards (*Aspidoscelis tigris*), whose distributions have already been reduced by urban development [55], the genetic effects of fragmentation may be even more profound. Many endangered species in southern California are declining because of habitat loss, and many of these species also have low dispersal abilities along with more specific habitat requirements (e.g. light-footed clapper rail, *Rallus longirostris obsoletus*; Belding's savannah sparrow, *Passerculus sandwichensis beldingi*; red-legged frog, *Rana draytonii*; least bell's vireo, *Vireo bellii pusillus*). It is also unknown how stressors, such as increasing local or global temperature and urbanization, might affect species in southern California. A recent study of *Sceloporus* lizards in Mexico found that 12% of local populations have gone extinct since 1975 [56]. Sites where these common lizards were extirpated were too hot for too many hours of the day, presumably due to increasing global temperatures, which caused lizards to seek refuge from the heat instead of spending time foraging. In addition, our results have implications for endangered species such as the California gnatcatcher, where lack of differentiation at certain loci (e.g. mtDNA; [57]) may not reflect important genetic differentiation detectable with other markers such as microsatellites.

## Materials and Methods

### Study Area

Southern California is characterized by a Mediterranean climate with cool, wet winters and hot, dry summers. Vegetation consisted of coastal sage scrub, chaparral, riparian habitat, and oak woodlands. Our study site is within SMMNRA, the USA's largest urban national park (154,095 acres or 623.6 $km^2$; www.nps.gov/samo/parkmgmt/statistics.htm), which is located in Los Angeles and Ventura counties, California, USA (Fig. 1a). Approximately half of the land within the park boundary is privately owned, although some public acquisitions continue. Habitat patches within our study area were within 12.5 kilometers (km) of each other but were separated by roads of all sizes, housing, and commercial development (Fig. 1a). Most building started in the middle of the 20$^{th}$ Century, and none of the habitat patches have been completely isolated for longer than 43 years (Table 1; [58]). Two major freeways (101 and 23) and many busy four-lane roads run through the study area (Fig. 1a). The peak average daily traffic in this area is approximately 180,000 cars per day for the 101 Freeway and 90,000 cars per day for Highway 23 (Caltrans, www.ca.dot.gov). Both freeways are mostly surrounded by commercial and residential development. Within the study area there are large core areas of relatively undisturbed habitat, although some low-impact human recreation does occur. Within the urban mosaic, habitat patches were surrounded by high- or low-density housing, highways and other roads, golf courses and other landscaped areas.

We collected samples from habitat fragments which we characterized as ''small'' (75–450 ha) or ''large'' (3200–4400 ha) and from larger areas of continuous habitat which we called

"core" areas (Fig. 1a). There were 7 small patches (S1-S7), 3 large patches (L1-L3) and 2 core areas (C1 and C2). Patch area ($m^2$) and degree of isolation (PROX) were calculated using FRAGSTATS [59]. PROX is the sum of patch area divided by the nearest edge-to-edge distance squared between all of the patches within a defined search radius and the focal patch. PROX approaches 0 if the patch has no neighbors within the search radius (a 20 km radius encompassed our entire study site) specified in FRAGSTATS, therefore patches with smaller PROX numbers are more isolated. Building dates for roads, housing developments, and commercial areas were used to calculate the ages (in years) at which patches were 100% isolated up to the time of trapping for this study (patch age; Table 1). Patches were considered 100% isolated when they were completely surrounded on all edges by either commercial buildings, housing, or roads or a combination of these. We also made a matrix of patch ages (for pair wise comparisons) by calculating the number of years that each patch was separated from each other patch.

## Field sampling

To capture lizards we used arrays of pitfall traps and drift fencing. All samples for this study were collected between October 2000 and September 2005. Each array had seven 19-liter buckets buried in the ground with the lip of the bucket flush with the ground to act as a pitfall trap [55,60]. Buckets were arranged in a "Y" configuration and buried approximately 7.5 m apart. Between the buckets, short drift fencing (0.5 m tall) consisting of erosion cloth acted to intercept reptiles moving through the habitat and directed them towards the buckets. Shade and moisture were provided for each bucket to maximize the chance of survival for reptiles, amphibians, or small mammals that were trapped. Pitfall traps were checked daily for a week at one-month intervals [22]. Each reptile was identified to species and snout to vent length was measured in mm. Each individual was assigned a unique number, was permanently marked by toe clipping [61,62] and a small sample from the tip of the tail was taken. Toes and tail tips were stored in 70% ethanol at 4°C or −80°C depending on storage space.

To capture birds, we used mist-nets. Trapping occurred from August 2004 to May 2006. Generally, we would open mist-nets (9–12 m long, 30 cm mesh) at sunrise and close them as the temperature increased to a potentially unsafe level in mid-morning. We targeted wrentits by playing male territorial songs with portable speakers placed at the base of the net. Once a bird was caught in the net, it was immediately removed and a U.S. Fish and Wildlife Service band was placed on its leg. We also took measurements of culmen length (mm), culmen width (mm), unflattened wing chord length (cm), tail length (cm), tarsus length (cm) and mass (g). Culmen length was taken from the anterior end of the nares to the tip of the beak using calipers. For genetic samples, we punctured the brachial vein on the wing of each bird with a small gauge needle and collected the blood that pooled there with a small capillary tube. Bleeding usually stopped after 10 seconds which yielded approximately 100 µl of blood. Blood was then placed in avian blood buffer [63].

All samples used in this study came from animals that were captured, handled, and released according to relevant national and international scientific guidelines. We used common field and handling methods that minimize stress and long-term effects of capture. We also researched methods alternative to toe-clipping of reptiles and determined that there were no less harmful yet permanent ways of marking individuals [62]. We obtained approval for our animal capture protocol from the UCLA Office of the Protection of Animals (OPRS).

We extracted genomic DNA with the Qiagen DNA mini kit (Qiagen Inc.). DNA samples were stored in TE buffer (10 mM Tris-Cl pH 8.0, 1 mM EDTA pH 8.0) at −20°C. We used six to eight microsatellite markers for each species (Table S6, J. Archie, Pers. Comm.; [64,65,66,67]). We used flourescently-labeled forward microsatellite primers when available. Alternatively, we used a three-primer genotyping protocol, where the forward microsatellite primer had an M13 sequence attached to the 5′ end (5′-GTAAAACGACGGCCAG-3′) and a third primer with the complementary M13 sequence was dye-labeled [68,69]. The forward, reverse and M13-dye primers were then used in a three-primer PCR protocol using Multiplex Mix (Qiagen Inc.) and 0.01% Bovine Serum Albumin (BSA) to generate microsatellite alleles which are flourescently labeled. Genotypes were run on an ABI 3700 sequencer and alleles were visualized using GENEMAPPER (Applied Biosystems, Inc.).

## Genetic Analysis

We used the computer program CONVERT to translate our microsatellite genotype files into the correct input format for various analysis programs [70]. We used FSTAT 2.9.3 [71] to test for deviations from Hardy-Weinberg equilibrium (HWE) within samples using 1000 permutations. We also used FSTAT to test for linkage disequilibrium (LD) between loci. P-values were adjusted for multiple tests using a sequential Bonferonni correction [72]. For HWE and LD, all samples for each species were assumed to be a single population.

**Genetic divergence.** We used the program ARLEQUIN to estimate pair-wise $F_{ST}$ values between patches using the infinite-allele model and 1000 permutations for significance [73,74]. We also calculated pair-wise $F_{ST}$ between arrays within large and core patches with ARLEQUIN to show genetic divergence between sampling sites that were located within a patch of continuous habitat. For this calculation we also included some sampling sites from core areas of continuous habitat that were outside of the Simi Hills (our study area), but within SMMNRA, with an average of 4.28 km (range 1.8–6.6 km) separating these sites.

To examine patterns of sample clustering based on genetic similarity, we used the program STRUCTURE v. 2.3.1 [75]. We chose the LOCPRIOR model [76], assumed populations were not admixed and that allele frequencies were correlated between populations, and ran 100,000 MCMC chains with a 10,000 burn-in. We ran seven runs each of K = 1 to K = number of sample sites (Fig. 1a) for each species. We compiled results from our STRUCTURE runs with the program STRUCTURE HARVESTER (Dent Earl, http://taylor0.biology.ucla.edu/struct_harvest/). To determine the most likely K, we calculated the posterior probabilities of the mean of seven runs at each K (Table S3; [75]).

Isolation by distance, as revealed by a correlation between pairwise genetic and geographic (Euclidean) distances using a Mantel test, was performed using IBDWS 3.14 [77]. IBDWS uses a Reduced Major Axis (RMA) regression to estimate the slope and intercept of the isolation by distance relationship.

To test for the effect of major roads, highways, and patch age on genetic divergence, we performed partial Mantel tests [78] in IBDWS 3.14. Partial Mantel tests determined correlations of roads presence (RDS), highway presence (HWY), and patch age of isolation (AGE) on a genetic divergence matrix, while holding geographic distance constant. Tests were performed separately, one for each of these three variables, and all animals that were captured within a patch were used to calculate a patch average genetic divergence ($F_{ST}$; as calculated in ARLEQUIN, see above). The presence of major roads and the presence of Highway 23 were used separately in the analysis because the highway in our

study area is larger and has more traffic than other roads. Also, several habitat fragments are only separated by major roads. Age of isolation was chosen because this measure incorporates not only when roads and freeways were built, but also when residential and commercial developments were erected.

We mapped genetic distance on the landscape using Alleles in Space (AIS) and the landscape shape interpolation [79]. We used a Delaunay triangulation-based connectivity network to identify midpoints between our sample sites, then the raw genetic distance ($D_{ij}$) at each midpoint was calculated [79]. This genetic distance measure is similar to Nei's standard genetic distance ($D_s$; [80]), where $D_{ij}$ is 0 if individuals are completely genetically identical, and $D_{ij}$ is 1 if individuals are completely genetically dissimilar. We did not calculate the residual genetic distance, because we did not find a significant isolation by distance effect in the Simi Hills samples for any species (see Results). By this method, a landscape of genetic distances between sampling sites are expressed as "surface heights" and are displayed as a 3-dimensional graph. To better visualize the AIS height output, we imported the output file into ArcGIS 9.3 (ESRI Corporation, Redlands, CA) and created a 2-dimensional color hot-spot map overlaid on the geographic study area. Colors correspond to "heights" of genetic distance between points (e. g. Fig. 1b).

**Genetic diversity.** We used the program GENALEX [81] to calculate the genetic diversity indices of within-patch expected heterozygosity ($H_e$), observed heterozygosity ($H_o$), number of effective alleles ($N_A$), and relatedness ($R_{LR}$) [82]. We used the Lynch & Ritland (1999) estimator of relatedness because it has been shown to perform well in simulations for a wide range of marker data and population structure [83]. We performed a rarefaction analysis using the web-based program RERAT [84] which uses multiple simulations to determine the change in relatedness values as additional microsatellite loci are added. In RERAT, we performed 100 simulations and used the Lynch and Ritland (1999) relatedness analysis for each of the four species. For lizards, cores and large patches had three pitfall trap arrays while small patches had one (Fig. 1a). To reduce bias because of array clustering, we calculated pair wise relatedness of all individuals caught in the same array, and then used the mean of those within-array measures to calculate within patch relatedness.

We used the program STATA 9 (StataCorp, College Station, TX) to transform variables until they approached normal distributions and then to examine the relationship between the indices of genetic diversity and the size, degree of isolation, and age of the habitat patches. We used unpaired t-tests (with unequal variance when necessary) and Bonferroni corrections to compare genetic diversity measures between small and large/core habitat patches. Degrees of freedom for t-tests were calculated using the Satterthwaite (1946) method [85]. We lumped large patches and core areas for this analysis because, for these small species, population size is likely equivalently large in the large patches and the core areas, and because the numbers of sites were relatively small for core areas ($n = 2$) and large patches ($n = 3$). To test for a relationship between patch isolation and genetic diversity, we used linear regression to examine the relationship of the genetic diversity indices with the size, pair wise age of isolation, and proximity (PROX) of the habitat patches, where the degree of isolation of a patch is the inverse of proximity. Spearman's rank correlations were used to test for significant associations between patch age and genetic diversity.

## Supporting Information

**Table S1** $F_{ST}$ between sample sites for 4 species. Significant pairwise $F_{ST}$ values are in bold (see Fig. 1a for sample site locations).
Found at: doi:10.1371/journal.pone.0012767.s001 (0.22 MB DOC)

**Table S2** Pairwise $F_{ST}$ and the number of significant comparisons between patches in and continuous habitat.
Found at: doi:10.1371/journal.pone.0012767.s002 (0.05 MB DOC)

**Table S3** Estimated posterior probabilities for K. Most likely number of genetic clusters (K) identified with the program Structure is shown in bold.
Found at: doi:10.1371/journal.pone.0012767.s003 (0.07 MB DOC)

**Table S4** Mean genetic diversity measurements within patches (number of effective alleles, $N_A$; relatedness, $R_{LR}$; heterozygosity, $H_e$).
Found at: doi:10.1371/journal.pone.0012767.s004 (0.12 MB DOC)

**Table S5** Spearman's Rho correlation coefficients. The number of individuals genotyped (N), the number of alleles (A), expected ($H_e$) and observed ($H_o$) heterozygosity.
Found at: doi:10.1371/journal.pone.0012767.s005 (0.04 MB DOC)

**Table S6** Microsatellite primers used for each species. The number of individuals genotyped (N), the number of alleles (A), expected ($H_e$) and observed ($H_o$) heterozygosity.
Found at: doi:10.1371/journal.pone.0012767.s006 (0.14 MB DOC)

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## Author Contributions

Conceived and designed the experiments: KSD SPDR RNF. Performed the experiments: KSD. Analyzed the data: KSD. Contributed reagents/materials/analysis tools: KSD SPDR. Wrote the paper: KSD SPDR.

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# The relationship of respiratory and cardiovascular hospital admissions to the southern California wildfires of 2003

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## Abstract

**Objective—**There is limited information on the public health impact of wildfires. The relationship of cardiorespiratory hospital admissions (n = 40 856) to wildfire-related particulate matter ($PM_{2.5}$) during catastrophic wildfires in southern California in October 2003 was evaluated.

**Methods—**Zip code level $PM_{2.5}$ concentrations were estimated using spatial interpolations from measured $PM_{2.5}$, light extinction, meteorological conditions, and smoke information from MODIS satellite images at 250 m resolution. Generalised estimating equations for Poisson data were used to assess the relationship between daily admissions and $PM_{2.5}$, adjusted for weather, fungal spores (associated with asthma), weekend, zip code-level population and sociodemographics.

**Results—**Associations of 2-day average $PM_{2.5}$ with respiratory admissions were stronger during than before or after the fires. Average increases of 70 μg/m$^3$ $PM_{2.5}$ during heavy smoke conditions compared with $PM_{2.5}$ in the pre-wildfire period were associated with 34% increases in asthma admissions. The strongest wildfire-related $PM_{2.5}$ associations were for people ages 65– 99 years (10.1% increase per 10 μg/m$^3$ $PM_{2.5}$, 95% CI 3.0% to 17.8%) and ages 0–4 years (8.3%, 95% CI 2.2% to 14.9%) followed by ages 20–64 years (4.1%, 95% CI 20.5% to 9.0%). There were no

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$PM_{2.5}$–asthma associations in children ages 5–18 years, although their admission rates significantly increased after the fires. Per 10 μg/$m^3$ wildfire-related $PM_{2.5}$, acute bronchitis admissions across all ages increased by 9.6% (95% CI 1.8% to 17.9%), chronic obstructive pulmonary disease admissions for ages 20–64 years by 6.9% (95% CI 0.9% to 13.1%), and pneumonia admissions for ages 5–18 years by 6.4% (95% CI 21.0% to 14.2%). Acute bronchitis and pneumonia admissions also increased after the fires. There was limited evidence of a small impact of wildfire-related $PM_{2.5}$ on cardiovascular admissions.

**Conclusions—**Wildfire-related $PM_{2.5}$ led to increased respiratory hospital admissions, especially asthma, suggesting that better preventive measures are required to reduce morbidity among vulnerable populations.

The numbers of wildfires and their duration in the USA have increased over the past two decades due to warmer temperatures, earlier snowmelts and less rainfall, all of which are expected to worsen because of global warming.[1] These phenomena will likely impact public health. However, although the adverse effects of urban fine particulate air pollution ($PM_{2.5}$ or particles with an aerodynamic diameter of <2.5 μm) on cardiovascular and respiratory health have been well documented,[2] far fewer studies have evaluated the impacts of wildfire-generated $PM_{2.5}$. $PM_{2.5}$ is the air pollutant with the greatest increase in concentrations during fire events,[3] followed by particulate matter with an aerodynamic diameter of <10 μm ($PM_{10}$).[4] Studies that have evaluated the impacts of wildfire PM on hospital admissions, emergency department visits or clinic visits found associations with respiratory outcomes.[5–11] There is little research on the impact of wildfire smoke on cardiovascular outcomes; two studies have found no significant associations.[89] There have been conflicting reports on wildfire smoke and total mortality.[1213] Several other studies have found adverse impacts of wildfire smoke on respiratory symptoms, medication use and lung function.[1014–16]

We present here the largest study to date evaluating the relationships of hospital admissions for cardiorespiratory outcomes to wildfire-associated $PM_{2.5}$ using data from the catastrophic wildfires that struck southern California in the autumn of 2003. We linked $PM_{2.5}$ concentrations estimated at the zip code level[17] to a population-based dataset of hospital admissions using spatial time series analyses of data before, during and after the fires. Strong, dry winds from inland deserts fanned flames from nine distinct fires, which burned nearly three quarters of a million acres and destroyed approximately 5000 residences and outbuildings. The wildfires generated large amounts of dense smoke that covered much of urban southern California (2003 population of 20.5 million).[18] $PM_{2.5}$ and $PM_{10}$ concentrations far exceeded US federal regulatory standards.[317] The goal of the present study is to assess the impact of this large wildfire event on serious morbidity.

## METHODS

### Hospital admission data

Hospital admission data for children and adults were obtained from the California State Office of Statewide Health Planning and Development (OSHPD). Specifically, we analysed 40 856 hospital admissions from the period before the wildfire episode (1–20 October), the

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episode period across southern California (21–30 October) and the period following the episode (31 October–15 November), for individuals who lived in affected counties and were diagnosed with the respiratory and cardiovascular illnesses listed in table 1. Other variables from OSHPD included in analyses were age, sex, race, ethnicity, five-digit zip code and admission date. Patient zip code data from OSHPD were geocoded to zip code centroids and linked to air monitoring data and U.S. Census 2000 sociodemographic data. Institutional Review Board approvals were obtained from the California State Health and Human Services Agency, Committee for the Protection of Human Subjects, and from the University of California, Irvine Office of Research Administration.

Analyses were stratified by age groups: paediatric (0–4 and 5– 19 years), adult (20–64 years) and elderly (65–99 years), except for chronic obstructive pulmonary disease (COPD, 20–64 and 65–99 years) and cardiovascular outcomes (45–99 years). Census demographic characteristics were missing for 474 admissions due to unmatched zip codes. We also analysed associations for asthma by gender because of differences in the age-dependent prevalence of asthma.

## Exposures

We estimated daily $PM_{10}$ and $PM_{2.5}$ concentrations at a zip code level from 1 October through 15 November 2003. These data are presented in more detail in our previous publication.[17] To our knowledge, this was the first study that systematically examined and estimated daily particle concentrations at such a fine spatial resolution over a relatively large study domain for this type of application. Spatially-resolved particle mass data are superior to using only the nearest available monitoring station data because they are expected to better represent personal exposures. We used available air pollution data from governmental network sites to build prediction models. Missing gravimetric PM concentrations from every 3rd or 6th day measurements or due to the incapacitation of monitors by the fires were estimated based on (1) temporal profiles of continuous hourly PM data at co-located or closely located sites and (2) light extinction from visibility data, meteorological conditions and smoke information extracted from moderate resolution imaging spectroradiometer (MODIS) satellite images at a 250 m resolution. Moderately strong prediction equations were developed for gravimetric PM mass at monitoring stations. Light extinction coefficient and MODIS satellite smoke data were the most important predictors of those measurements. Measured $PM_{2.5}$ was more accurately predicted in regression models compared with $PM_{10}$ ($R^2$ 0.78 vs 0.65, respectively). Therefore, the present analysis focuses only on $PM_{2.5}$.

Spatial interpolations of $PM_{2.5}$ concentrations were performed using inverse distance weighting, kriging or cokriging methods for the non-fire periods. Since the fire and smoke created highly heterogeneous pollution surfaces, typical inverse distance weighting and kriging were not suitable during the wildfire period. Therefore, polygons were created based on satellite images to represent each smoke-covered area under different smoke densities. $PM_{2.5}$ concentrations in each smoke-polygon were assigned separately, using measured or estimated concentrations from the predictive models (as described above). For each non-fire and fire day, the spatial $PM_{2.5}$ surfaces and zip code boundary map were overlaid and corresponding $PM_{2.5}$ concentrations were assigned to each zip code centroid (fig 1).

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Measurements of daily airborne fungal spores (see online supplement) were carried out in another ongoing study in Riverside County.[19] Pollen concentrations were low and therefore were not included in the analysis. We assumed that Riverside ambient fungal data reflected region-wide trends.

## Analysis

Outcomes were the total number of admissions for a diagnostic group within each zip code on each day of the study period. We hypothesised that associations between the wildfires and hospital admission rates would primarily be attributable to an increase in daily zip code-specific levels of $PM_{2.5}$ resulting from the fires. However, it is difficult to separate wildfire-generated PM from other PM sources in this heavily urbanised region. To this end, we constructed a wildfire indicator representing prewildfire, wildfire and post-wildfire periods, and tested the interaction between $PM_{2.5}$ and this indicator. We considered product terms to be significant at the $p<0.1$ level. Because dates of the wildfires varied throughout southern California, dates for the wildfire period indicator were defined to be county-specific based on MODIS satellite images of smoke covering any part of the county's urban areas (table 2).

The choice of adjustment covariates was motivated by biological plausibility that the covariate might confound the relationship between wildfire-related $PM_{2.5}$ and hospital admissions or an a priori belief that the variable could affect both $PM_{2.5}$ and admissions. Meteorological covariates from the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html) included relative humidity, temperature and surface pressure gradient. So-called Santa Ana winds coming off the inland desert regions to the east (a large negative pressure gradient) are a strong determinant of wildfire events. There are few data on the effects of Santa Ana winds on asthma or other outcomes, but it is anticipated that hot dry desert winds associated with this weather pattern bring with them high concentrations of bioaerosols. Therefore, for asthma admissions, we also included fungal spores as a covariate. Deuteromycetes (eg, *Alternaria*) tend to increase during hot, dry windy periods.[20]

In addition, we decided a priori that spatial heterogeneity in census demographic factors at the aggregate zip code level (age, gender, race and income distributions) could confound associations. The distributions of each of these potential confounders were obtained at the zip code level from the 2000 U.S. Census (percentage of non-Caucasians, percentage of females, median household income and age distributions). Income was recoded into discrete variables by quartile. To control for zip code population age distribution, we first calculated the percentage of individuals in a zip code younger than 20 years and older than 65 years. Each zip code was then classified into one of four age categories by cross-classification of young (proportion of individuals <20 years old higher than the median proportion across all zip codes) and old (proportion of individuals>65 years old higher than the median proportion across all zip codes).

We also tested various functions of time including weekend versus weekday, day of the week and a smooth of time. In order to investigate residual confounding by date, we allowed for a flexible functional form (via smoothing splines, with degrees of freedom ranging from 1 to 10) (see online supplement). Controlling for day-of-week trend or the flexible time-

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adjusted models showed the $PM_{2.5}$ associations were robust with respect to these adjustments. We also tested various forms of temperature and relative humidity, including raw continuous scales, smoothed and categorical forms. Those models exhibiting the best fit with the fewest assumptions for functional form included weekend versus weekday, and temperature and relative humidity categorised into quartiles. The full set of adjustment covariates included these variables plus local pressure gradient, fungal spores (for asthma), county, and zip code-level distributions of median household income, age, gender and race. Effects of covariates on point estimates of $PM_{2.5}$ were small.

Generalised estimating equations for Poisson data[21] were used to estimate the marginal association of daily hospital admission rates with daily $PM_{2.5}$ levels and presence of the wildfires. Log-transformed zip code-specific population estimates were used as the offset (denominator) term in all models. Age-specific population estimates were used as an offset term in the analysis of age group-specific outcomes. In order to obtain asymptotically valid inferences, covariate estimation was carried out using an independence working correlation structure in combination with empirical variance estimates clustering on zip code.[2223] We note that the use of an independence working correlation structure was motivated by the desire to obtain consistent parameter estimates in the presence of time-varying covariates.[24]

Multiple lag models were considered to investigate associations between $PM_{2.5}$ and hospital admission rates, including a 7-day polynomial distributed lag,[25] and stratified analyses considering different lag associations. We found the 2-day moving average of $PM_{2.5}$ (average of today and yesterday) provided the best fitting model that adequately captured the association between $PM_{2.5}$ and admissions.

## RESULTS

### PM exposures

During the wildfires, smoke events dramatically increased local PM concentrations and created highly heterogeneous pollution surfaces.[17] For reference, the US National Ambient Air Quality Standard for 24 h average $PM_{2.5}$ is 35 $\mu g/m^3$. The highest 24 h concentrations were ≥240 $\mu g/m^3$ at two sites in San Diego County. Table 2 contains county-level descriptive statistics for $PM_{2.5}$. As expected, average $PM_{2.5}$ concentrations during the wildfire period increased in all counties. Average PM levels during the period following the fires were observed to be lower in all counties relative to the period prior to the fires. This is because of the onshore flow that brought in the cool and moist clean air from the Pacific Ocean that helped end the wildfires.

### Spatial time series analysis of hospital admissions

**$PM_{2.5}$ associations: interactions with wildfire period—**We found that associations of 2-day lagged average of $PM_{2.5}$ with admissions for most respiratory outcomes were stronger during as compared with before or after the wildfires in models including a product term of wildfire period and $PM_{2.5}$, but the interaction was $p<0.1$ primarily for asthma.

Table 3 shows estimates for the relative change in rates for admissions in relation to a 10 $\mu g/m^3$ increase in $PM_{2.5}$. The table includes results for age and sex (asthma only) subgroups

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for the entire monitored period, and for wildfire periods. In product term models of $PM_{2.5}$ by wildfire period, $PM_{2.5}$ during the wildfire period was associated with combined respiratory admissions. Asthma admissions across all ages increased by 4.8% (95% CI 2.1% to 7.6%) in relation to $PM_{2.5}$ during the wildfire period, but there was no $PM_{2.5}$ association before or after the fires. The strongest wildfire-related $PM_{2.5}$ associations with asthma admissions were for the elderly, ages 65–99 years (10.1% increase), and children ages 0–4 years (8.3%), followed by adults ages 20–64 years (4.1%). There were no $PM_{2.5}$ associations in school aged children. Among women ages 20– 64 years, the strongest asthma and $PM_{2.5}$ association was during the wildfires, but for men those ages it was after the wildfires. Among women ages 65–99, the strongest $PM_{2.5}$ association was after the wildfires, but for men those ages it was during the wildfires. Fungal spores were also significantly associated with asthma admissions in the adjusted model that included $PM_{2.5}$ (see online supplement).

The wildfires led to notably higher particle concentrations, so that a 10 $\mu g/m^3$ increase in $PM_{2.5}$ used for effect estimates in table 3 represents only a small part of that increase. The overall population-weighted concentrations of predicted 24 h $PM_{2.5}$ at the zip code level were 90 $\mu g/m^3$ and 75 $\mu g/m^3$, under heavy and light smoke conditions, respectively, in contrast to concentrations of 20 $\mu g/m^3$ during the non-fire period.[17] Therefore, we rescaled effect estimates to represent the wildfire-related increases in $PM_{2.5}$. A 55 $\mu g/m^3$ increase in $PM_{2.5}$ during light smoke and a 70 $\mu g/m^3$ increase in $PM_{2.5}$ during heavy smoke conditions are predicted to lead to an adjusted 26% and 34% increase in asthma admissions for all ages, respectively.

For combined ages, acute bronchitis admissions increased more in relation to 10 $\mu g/m^3$ $PM_{2.5}$ during the wildfires (9.6%), but there was no association before or after the fires. In subgroup analyses, this association was still evident in children ages 0–4 years and the elderly.

COPD admissions for people ages 20–64 years significantly increased by 6.8% from 10 $\mu g/m^3$ $PM_{2.5}$ during the wildfires, but there was no association before or after the fires. The COPD increase with $PM_{2.5}$ during the fires was smaller for subjects ages 65–99 years (3.1%).

$PM_{2.5}$ was also associated with increased overall pneumonia admissions, both before (4.5%) and during the fires (2.8%). This was consistent across ages, except children ages 5–19 years showed an association only during the wildfires. There were no associations of $PM_{2.5}$ with admissions for upper respiratory infections (not shown).

There was a small relative increase in admission rates for total cardiovascular outcomes in people ages 45–99 years in relation to $PM_{2.5}$ during the fires. There were suggestions of a small increase in admissions for congestive heart failure in relation to $PM_{2.5}$ during the wildfires ($p<0.1$ compared with the pre-wildfire period), and an even smaller increase in admissions for ischaemic heart disease, but for both outcomes, the 95% confidence intervals crossed 1.0. $PM_{2.5}$ was inversely associated with cardiac dysrhythmia admissions across all periods. Admissions for cerebrovascular disease and stroke were positively associated with $PM_{2.5}$ (1.9%) across all periods.

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**Associations with wildfire period—**In this analysis of the wildfire indicator variable, the prewildfire period is the referent time. Models were adjusted for the same covariates as $PM_{2.5}$ models, and are shown unadjusted and adjusted for $PM_{2.5}$ (table 4). Generally, there was little change in point estimates adjusting for $PM_{2.5}$. There were significantly increased risks for all respiratory hospital admissions after the fires compared with the pre-fire period. Admissions increased for all ages by 17% ($p<0.001$), and in age groups 5–19 years by 37% ($p<0.008$) and 65–99 years by 15% ($p<0.004$). Unexpected decreased risks of respiratory admissions were found during the fires compared with the pre-fire period in 0–4 year olds and elderly adults.

The period following the fires was associated with a 26% increase in the rate of asthma admissions for all ages. Asthma admissions were also increased during the fires among those aged 5–19 years (25%) and 20–64 years (27%), but associations for both groups were stronger after the fires (56% and 36%, respectively).

Increased risk of asthma admissions for the period during the wildfires was stronger in females ages 5–19 years (49%, $p<0.02$) than males (11%, $p = 0.5$) and in females ages 20–64 years (41%, $p<0.001$) than males (27.6%, $p = 0.7$) (not shown). Increased risk of asthma admissions for the period after the wildfires was also stronger in females ages 5–19 years (81%, $p<0.01$) than males (39%, $p<0.11$) and in females ages 20–64 years (47%, $p<0.02$) than males (12%, $p = 0.7$).

Admissions for acute bronchitis and bronchiolitis for combined ages were increased by 48% after the fires. The association for the post-fire period was seen in both ages 0–4 years (51%) and ages 20–64 years (137%). Pneumonia admissions for ages 0– 4, 20–64 and 65–99 years were 46%, 30% and 27% higher during the period after the fires, respectively.

There was a 6.1% increased risk of combined cardiovascular admissions ($p<0.05$), and an 11.3% increased risk of congestive heart failure admissions after the fires ($p<0.06$). However, risk of cardiovascular admissions was lower during the fires by 4.4%. A relative increase in cerebrovascular disease and stroke admissions during the wildfires may have been attributable to a cross-period effect of $PM_{2.5}$ (table 3) because this period association was confounded in the model adjusting for $PM_{2.5}$.

## DISCUSSION

This is the first study to systematically examine and estimate the impacts on hospital admissions from wildfire-related $PM_{2.5}$ at such a fine spatial resolution (zip codes) over a large urban region. During the wildfire period, smoke events dramatically increased $PM_{2.5}$ compared to the preceding non-fire period. The wildfires and associated $PM_{2.5}$ were significantly associated with hospital admissions for respiratory illnesses, especially asthma, but also acute bronchitis and COPD. The impact on cardiovascular admissions was weaker.

Although product terms between $PM_{2.5}$ and the wildfire period indicator were not significant at the $p<0.1$ level in many models, we still observed a trend of stronger associations for $PM_{2.5}$ with respiratory admissions during the wildfire period. Some models showed increased admissions in relation to $PM_{2.5}$ before the wildfires, possibly due to the

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relatively high concentration of urban PM seen during this hot period (table 2). Some models also showed increased admissions in relation to $PM_{2.5}$ after the wildfires, despite much lower $PM_{2.5}$ concentrations. This may have been attributable to notable increases in respiratory admissions seen then, possibly due to a delayed impact of wildfire smoke.

Models with the wildfire period indicator support this possibility and suggest that some effects of wildfires are not entirely explained by $PM_{2.5}$ exposures. Results yielded inconsistencies for respiratory and cardiovascular admissions when comparing product term models for $PM_{2.5}$ by period to models using the period indicator alone. There were nominal associations of daily $PM_{2.5}$ during the wildfires with cardiovascular admissions, but the period indicator showed associations only after the wildfires. Non-asthma respiratory admission rates were also most strongly increased after the wildfires ended compared with the pre-fire period, while the $PM_{2.5}$ association was generally strongest during the wildfires. We also found the period following the wildfires was significantly associated with higher overall asthma admission rates. These associations were stronger among females. Asthma admissions were increased during the fires as well, but evident only among females ages 5–19 and ages 20–64. Possible reasons for stronger associations among females include the differential impact of hormones and the menstrual cycle, airway function and structure, atopy and perception of symptoms.[26]

Although there was no association of asthma admissions with $PM_{2.5}$ in young people ages 5–19 years, the periods during and after the wildfires were significantly associated with increased admissions in this group. We speculate this may be attributable to unmeasured volatile (non-particulate) toxic air pollutants, including those associated with the more than 5000 buildings that burned. Alternatively, factors associated with the fires, such as psychosocial stress, could have led to effects that were independent of $PM_{2.5}$.

Associations with the post-wildfire period and wildfire-related $PM_{2.5}$ were also found for acute bronchitis and bronchiolitis, and pneumonia. This is the first report of wildfire associations with admissions for acute bronchitis and bronchiolitis, and pneumonia.

We also found a significantly increased risk of admissions for total cardiovascular outcomes and congestive heart failure after the fires. It is possible that systemic inflammation increases more strongly in relation to sustained multiday exposures to air pollutants than with acute single day exposures, as recently shown in our panel study of subjects with coronary artery disease.[27] Analyses of the London ‘‘killer smog’’ of 1952,[28] and recent analyses of particulate air pollution in Dublin, Ireland,[29] suggest that there may be delayed effects for weeks to months. The post-fire increases in cardiorespiratory admissions may be attributed to the following:

1. People may delay deciding to go to hospital until symptoms become too severe[30];
2. Cumulative biological effects of wildfire PM may culminate in severe symptoms many days after the initial cardiorespiratory impact. For example, most subjects with asthma show a progressive clinical and functional deterioration that takes place over hours to weeks[31];

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3. Sustained effects of wildfire PM may lead to susceptibility to, or increased severity of, later respiratory infections, possibly through alterations in immune function or respiratory clearance mechanisms.

The strongest evidence for delayed effects in our study was the post-fire increase in asthma admissions combined with the association between asthma admission and $PM_{2.5}$ during the wildfires. However, given past annual trends (see online supplement), it is possible that asthma admissions following the wildfire period would have increased at this time of year anyway. This also applies to the post-fire increases in admissions for acute bronchitis and bronchiolitis, and pneumonia. Other limitations are that the period analysis does not have the temporal resolution of the daily time series analysis of $PM_{2.5}$. Therefore, differences in results of these analyses could result due to imprecision in the estimate for the non-quantitative indicator variable. Furthermore, power may be limited for specific outcomes subdivided by gender and age, which would apply to several nominally significant associations we found.

Our results for respiratory admissions are consistent with two other studies of the 2003 southern California wildfires using other less severe outcomes and focusing on particular regions, including emergency department visits in San Diego county[1132] and respiratory symptoms in 16 towns in southern California.[16] Kunzli et al[16] reported results for school children in an ongoing cohort study who were potentially affected by the wildfires. They found parental self-reports of the smell of fire smoke indoors were associated with reported asthma attacks, wheezing, cough, bronchitis, colds, upper respiratory symptoms, medication usage and physician visits. Authors also analysed the impacts of between-community differences in $PM_{10}$ using data from our study.[17] Changes in $PM_{10}$ were associated with upper respiratory symptoms, cough and unspecified medication use.

Several investigations of wildfires have identified people with asthma as an especially sensitive subpopulation, using analyses of emergency department visits in California mountain counties during wildfires in 1987,[6] emergency department visits in eight Florida hospitals during wildfires in 1998,[5] and hospital admissions during the 1997 Indonesian wildfires.[9] A report from Australia examining smoke from bushfires and asthma emergency department visits found no association.[33]

Other time series studies have shown associations of asthma hospital admissions with urban air pollution.[34] However, the period of observation in our investigation is far shorter than most time series investigations, and thus statistical power is lower. Despite this, we found strong associations between $PM_{2.5}$ and hospital admissions. We attribute this to the large increase in wildfire-related PM, and the spatial time series approach, which likely reduced exposure error compared with the typical use of widely-dispersed regional PM data. Nevertheless, we are still limited by aggregate (not personal) exposure data.

This is the first report of associations of wildfire-related $PM_{2.5}$ with admissions for acute bronchitis and bronchiolitis, and for pneumonia. Our results showing increased COPD admissions in relation to $PM_{2.5}$ during the wildfires are consistent with a study of increased COPD hospital admissions during the 1997 Indonesian wildfires,[9] increased COPD emergency department visits during the 1987 wildfires in California mountain counties,[6] and

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respiratory symptoms in a panel of 21 patients with COPD associated with a forest fire near Denver, Colorado in June 2002.[35]

Total cardiovascular and congestive heart failure admissions increased only in the period following the wildfires. However, there was a small relative increase in admission rates for total cardiovascular outcomes in relation to $PM_{2.5}$ during the fires.

Cerebrovascular disease and stroke were significantly increased in relation to $PM_{2.5}$ across the entire study period. Unexpected findings were the inverse associations for cardiac dysrhythmias and $PM_{2.5}$ across the whole period. While urban particles generally have been associated with a variety of adverse cardiovascular outcomes,[2] including stroke,[36] there is little research investigating the effects of smoke from wildfires or wood combustion on circulatory disease.[4] Our results can only be compared to null associations for cardiovascular hospital admissions during the 1997 Indonesian wildfires.[9] Moore et al[8] found that, although there was an excess of respiratory complaints, physician visits for cardiovascular illnesses in regions of British Columbia, Canada were not associated with wildfires.

The mechanisms explaining our findings for wildfire smoke are likely somewhat similar to those found for pollutant components from fossil fuel combustion. Evidence is mounting that urban air pollution triggers oxidative stress and inflammation.[2] A study of people exposed to forest fire smoke in Indonesia in 1997 showed increased circulating levels of interleukin-1b and interleukin-6 during the smoke period.[37] An experimental study of subjects exposed to clean air versus wood smoke in a chamber showed increased airway inflammatory responses (exhaled alveolar NO) and evidence of increased oxidative stress (malonadehyde in breath condensates).[38] An in vitro study using mouse alveolar macrophages tested the effects of size-segregated PM from transported wildfire smoke collected in Helsinki, Finland.[39] Investigators showed that although the transported particles induced less cytokine production per unit mass compared with urban particles, they found enhanced inflammatory and cytotoxic activities per cubic meter of air due to the increased particulate mass concentration in the accumulation mode size range (0.1–2.5 mm in diameter). This might explain our finding of a larger asthma association per 10 $\mu g/m^3$ $PM_{2.5}$ during the wildfires as compared with the pre-wildfire period as simply due to the considerably higher concentrations rather than higher toxicity of wildfire smoke.

It is also possible that unmeasured volatile and semivolatile organic compound components are important in the effects of wildfire smoke, but such data are rarely available. In the present study, these include toxic gases emitted from synthetic materials in the approximately 5000 residences and outbuildings that burned.

## Conclusions

We conclude the catastrophic wildfires that struck southern California in October of 2003 led to significantly increased hospital admissions for respiratory illnesses, especially asthma. Southern California experienced a second similar wildfire disaster in October 2007, yielding the two largest wildfire disasters in California's history within this recent 4-year period. A

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concern is that growing impacts of global warming on wildfire risk will continue to impact public health in similar regions across the globe.[1]

Given there were significant morbidity impacts associated with wildfire-related $PM_{2.5}$, we recommend that in addition to advisories to avoid outdoor activities that increase exposure during wildfires, preventive measures need to be taken where possible to reduce exacerbations of asthma. This may include the early use of anti-inflammatory medications at the first sign of increasing asthma symptoms. All of the health impacts identified in this study occurred in the face of numerous advisories by public health agencies and the media to avoid outdoor activities and to use air conditioning. Additional preventive measures in susceptible people including those with persistent asthma, such as the use of indoor air filters,[1040] should be considered and then systematically evaluated in future wildfires.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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**Main messages**

▶ Wildfire-related $PM_{2.5}$ led to significantly increased asthma, bronchitis and COPD hospital admissions.

▶ Sensitive subgroups included young children and the elderly.

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### Policy implications

▶ In addition to advisories to avoid outdoor activities that increase exposure during wildfires, preventive measures need to be taken where possible to reduce exacerbations of asthma

▶ Preventive measures may include advisories for the early use of anti-inflammatory medications at the first sign of increasing asthma symptoms.

▶ The health impacts of wildfires reported here are anticipated to increase worldwide due to global warming, which has broad policy implications.

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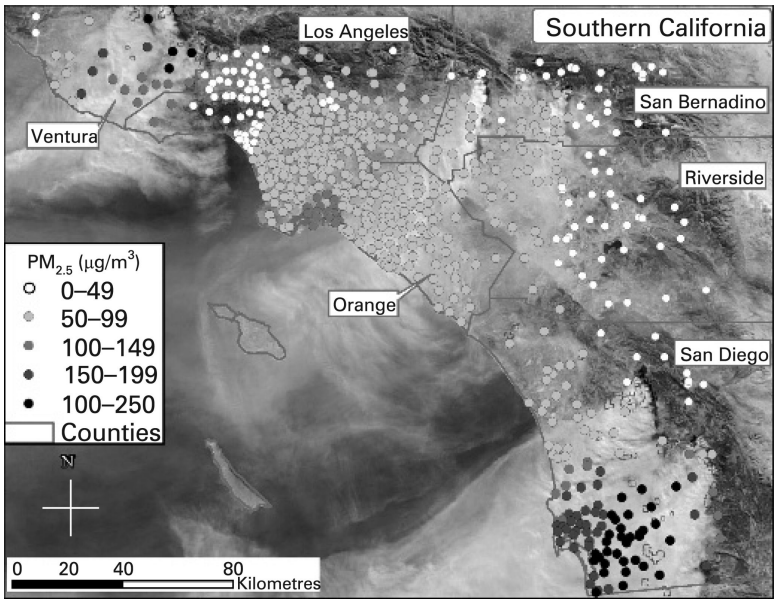


**Figure 1.**
Interpolated $PM_{2.5}$ concentrations ($\mu g/m^3$) at zip code centroids on 27 October 2003.

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## Table 1

Number of hospital admission by diagnostic* and age groups

| Diagnosis | Total events | Events with U.S. Census 2000 defined population† |
|---|---|---|
| All respiratory‡ | | |
| Ages 0–4 | 2158 | 2143 |
| Ages 5–19 | 1216 | 1205 |
| Ages 20–64 | 8480 | 8314 |
| Ages 65–99 | 9456 | 9357 |
| Total | 21 310 | 21 019 |
| Asthma (ICD-9 493), primary | | |
| Ages 0–4 | 606 | 600 |
| Ages 5–19 | 739 | 733 |
| Ages 20–64 | 1165 | 1151 |
| Ages 65–99 | 543 | 538 |
| Total | 3053 | 3022 |
| Acute bronchitis and bronchiolitis (ICD-9 466) | | |
| Ages 0–4 | 354 | 353 |
| Ages 5–19 | 23 | 23 |
| Ages 20–64 | 108 | 106 |
| Ages 65–99 | 137 | 136 |
| Total | 622 | 618 |
| Chronic obstructive pulmonary disease (ICD-9 491, 492 and 496) | | |
| Ages 20–64 | 927 | 910 |
| Ages 65–99 | 1973 | 1950 |
| Total | 2900 | 2860 |
| Pneumonia (ICD-9 480-87) | | |
| Ages 0–4 | 542 | 537 |
| Ages 5–19 | 298 | 293 |
| Ages 20–64 | 1721 | 1686 |
| Ages 65–99 | 3957 | 3924 |
| Total | 6518 | 6440 |
| Upper respiratory infections (ICD-9 460–65) | | |
| Ages 0–4 | 522 | 518 |
| Ages 5–19 | 77 | 77 |
| Ages 20–64 | 108 | 104 |
| Ages 65–99 | 47 | 47 |
| Total | 754 | 746 |
| All cardiovascular§ | | |
| Ages 45–99 | 27 486 | 27 170 |
| Ages 65–99 | 19 380 | 19 197 |
| Ischaemic heart disease (ICD-9 410–414) | | |

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| Diagnosis | Total events | Events with U.S. Census 2000 defined population† |
|---|---|---|
| Ages 45–99 | 10 448 | 10 319 |
| Ages 65–99 | 6491 | 6430 |
| Cardiac dysrhythmias (ICD-9 426, 427) | | |
| Ages 45–99 | 4051 | 4004 |
| Ages 65–99 | 3048 | 3018 |
| Congestive heart failure (ICD-9 402, 428) | | |
| Ages 45–99 | 6202 | 6144 |
| Ages 65–99 | 4750 | 4712 |
| Cerebrovascular disease and stroke (ICD-9 430–438) | | |
| Ages 45–99 | 5973 | 5908 |
| Ages 65–99 | 4465 | 4422 |

*Principal cause of admission was coded by version 9 of the International Classification of Diseases (ICD-9)

†population with available covariates for census population and census distribution of demographic characteristics used in the multivariate analysis. This excludes subjects aged ≥100 years (48 (0.23%) respiratory and 51 (0.18%) cardiovascular admissions) because 2000 census age categories needed in the analysis stopped at 99 years

‡includes all listed specific respiratory ICD-9 plus 7463 additional admissions for the following ICD-9 codes: 277 (cystic fibrosis), 490 (bronchitis NOS), 494 (bronchiectasis), 495 (extrinsic allergic alveolitis), 506 and 508 (other acute/subacute respiratory conditions due to fumes/vapours, or external agents, not separately analysed because n = 44), 786 (symptoms involving the respiratory system/other chest symptoms).

§includes all listed specific cardiovascular ICD-9 codes plus 812 additional admissions for ICD-9 codes 440–459 (diseases of the peripheral circulation).

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## Table 2

County-level mean particulate matter (PM2.5) levels,* Southern California, 1 October–15 November 2003

| Daily $PM_{25}$ levels ($mg/m^3$) | County | | | | | |
|---|---|---|---|---|---|---|
| | Los Angeles | Orange | Riverside | San Bernardino | San Diego | Ventura |
| Before fires | | | | | | |
| Dates | 01/10–23/10 | 01/10–23/10 | 01/10–20/10 | 01/10–20/10 | 01/10–24/10 | 01/10–22/10 |
| Concentration (SD) | 27.2 (12.4) | 23.3 (9.6) | 32.7 (14.7) | 35.7 (16.6) | 18.5 (6.7) | 18.4 (8.3) |
| During fires | | | | | | |
| Dates | 24/10–29/10 | 24/10–28/10 | 21/10–29/10 | 21/10–30/10 | 25/10–30/10 | 23/10–30/10 |
| Concentration (SD) | 54.1 (21) | 64.3 (26.5) | 42.1 (25.5) | 45.3 (28.7) | 76.1 (66.6) | 50.1 (50.5) |
| After fires | | | | | | |
| Dates | 30/10–15/11 | 29/10–15/11 | 30/10–15/11 | 31/10–15/11 | 31/10–15/11 | 31/10–15/11 |
| Concentration (SD) | 15.9 (5.5) | 15.5 (10.2) | 16.9 (8.6) | 18.4 (8.3) | 14.2 (7.2) | 12.9 (4.3) |

* $PM_{25}$ concentrations are calculated with equal weighting per zip code.

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## Table 3

Relative rate of asthma admissions in relation to a 10 μmg/$m^3$ increase in 2-day moving average particulate matter ($PM_{2.5}$)

| Hospital admissions outcome | All periods RR (95% CI)* | Pre-wildfire period RR (95% CI) | Wildfire period RR (95% CI) | p Value† | Post-wildfire period RR (95% CI) | p Value |
|---|---|---|---|---|---|---|
| All respiratory | | | | | | |
| All ages | 1.009 (0.999 to 1.018) | 1.022 (1.004 to 1.040) | 1.028 (1.014 to 1.041) | 0.639 | 0.999 (0.968 to 1.031) | 0.198 |
| Ages 0–4 | 0.994 (0.967 to 1.021) | 0.982 (0.921 to 1.046) | 1.045 (1.010 to 1.082) | 0.103 | 0.894 (0.807 to 0.991) | 0.126 |
| Ages 5–19 | 1.014 (0.983 to 1.046) | 1.026 (0.946 to 1.113) | 1.027 (0.984 to 1.076) | 0.990 | 0.958 (0.852 to 1.077) | 0.354 |
| Ages 20–64 | 1.015 (1.002 to 1.029) | 1.036 (1.007 to 1.066) | 1.024 (1.005 to 1.044) | 0.534 | 1.007 (0.960 to 1.056) | 0.315 |
| Ages 65–99 | 1.009 (0.996 to 1.022) | 1.022 (0.994 to 1.050) | 1.030 (1.011 to 1.049) | 0.649 | 1.024 (0.976 to 1.074) | 0.932 |
| Asthma | | | | | | |
| All ages | | | | | | |
| Males and females | 1.022 (1.001 to 1.042) | 0.998 (0.949 to 1.050) | 1.048 (1.021 to 1.076) | 0.097 | 0.986 (0.910 to 1.068) | 0.792 |
| Males | 1.010 (0.980 to 1.040) | 1.021 (0.944 to 1.106) | 1.031 (0.990 to 1.073) | 0.848 | 1.063 (0.948 to 1.192) | 0.553 |
| Females | 1.029 (1.001 to 1.058) | 0.979 (0.913 to 1.050) | 1.059 (1.022 to 1.097) | 0.056 | 0.928 (0.829 to 1.037) | 0.412 |
| Ages 0–4 | | | | | | |
| Males and females | 0.996 (0.947 to 1.048) | 0.924 (0.824 to 1.035) | 1.083 (1.021 to 1.149) | 0.017 | 0.924 (0.767 to 1.113) | 0.999 |
| Males | 1.018 (0.963 to 1.076) | 0.942 (0.815 to 1.089) | 1.086 (1.016 to 1.162) | 0.101 | 1.057 (0.839 to 1.332) | 0.380 |
| Females | 0.937 (0.845 to 1.040) | 0.880 (0.706 to 1.099) | 1.073 (0.965 to 1.194) | 0.116 | 0.699 (0.515 to 0.949) | 0.214 |
| Ages 5–19 | | | | | | |
| Males and females | 1.006 (0.966 to 1.048) | 1.045 (0.936 to 1.167) | 0.999 (0.935 to 1.068) | 0.492 | 0.918 (0.788 to 1.069) | 0.198 |
| Males | 0.991 (0.935 to 1.051) | 1.034 (0.892 to 1.198) | 0.969 (0.883 to 1.064) | 0.462 | 0.979 (0.806 to 1.189) | 0.671 |
| Females | 1.026 (0.964 to 1.092) | 1.065 (0.901 to 1.260) | 1.033 (0.943 to 1.132) | 0.768 | 0.831 (0.640 to 1.079) | 0.136 |
| Ages 20–64 | | | | | | |
| Males and females | 1.043 (1.012 to 1.076) | 1.037 (0.957 to 1.123) | 1.041 (0.995 to 1.090) | 0.931 | 1.000 (0.882 to 1.132) | 0.624 |
| Males | 1.013 (0.954 to 1.077) | 1.159 (0.996 to 1.349) | 0.939 (0.837 to 1.053) | 0.026 | 1.275 (1.020 to 1.595) | 0.486 |
| Females | 1.052 (1.015 to 1.090) | 0.995 (0.904 to 1.096) | 1.064 (1.014 to 1.116) | 0.247 | 0.908 (0.780 to 1.056) | 0.310 |
| Ages 65–99 | | | | | | |
| Males and females | 1.027 (0.974 to 1.082) | 0.951 (0.849 to 1.064) | 1.101 (1.030 to 1.178) | 0.032 | 1.168 (0.967 to 1.412) | 0.072 |
| Males | 1.046 (0.957 to 1.142) | 0.948 (0.804 to 1.116) | 1.185 (1.077 to 1.305) | 0.029 | 0.902 (0.629 to 1.294) | 0.804 |

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| Hospital admissions outcome | All periods RR (95% CI)* | Pre-wildfire period RR (95% CI) | Wildfire period RR (95% CI) | p Value† | Post-wildfire period RR (95% CI) | p Value |
|---|---|---|---|---|---|---|
| Females | 1.018 (0.958 to 1.081) | 0.947 (0.813 to 1.102) | 1.065 (0.977 to 1.162) | 0.195 | 1.263 (1.024 to 1.557) | 0.032 |
| Acute bronchitis and bronchiolitis | | | | | | |
| All ages | 1.044 (0.990 to 1.102) | 1.001 (0.890 to 1.126) | 1.096 (1.018 to 1.179) | 0.223 | 1.031 (0.870 to 1.222) | 0.779 |
| Ages 0–4 | 1.017 (0.949 to 1.089) | 0.987 (0.847 to 1.149) | 1.092 (0.997 to 1.195) | 0.276 | 0.910 (0.700 to 1.183) | 0.588 |
| Ages 5–19 | No convergence | | | | | |
| Ages 20–64 | 1.039 (0.912 to 1.183) | 1.001 (0.792 to 1.266) | 1.044 (0.872 to 1.252) | 0.778 | 1.259 (0.921 to 1.722) | 0.275 |
| Ages 65–99 | 1.134 (1.039 to 1.238) | 1.073 (0.764 to 1.505) | 1.143 (1.032 to 1.265) | 0.730 | 1.190 (0.865 to 1.638) | 0.652 |
| Chronic obstructive pulmonary disease | | | | | | |
| Ages 20–99 | 1.018 (0.994 to 1.042) | 1.007 (0.958 to 1.058) | 1.038 (1.004 to 1.075) | 0.320 | 1.024 (0.943 to 1.112) | 0.728 |
| Ages 20–64 | 1.022 (0.980 to 1.066) | 0.995 (0.916 to 1.081) | 1.068 (1.009 to 1.131) | 0.161 | 1.015 (0.893 to 1.153) | 0.781 |
| Ages 65–99 | 1.019 (0.992 to 1.048) | 1.014 (0.955 to 1.077) | 1.031 (0.990 to 1.074) | 0.660 | 1.023 (0.928 to 1.128) | 0.878 |
| Pneumonia | | | | | | |
| All ages | 1.009 (0.994 to 1.024) | 1.045 (1.012 to 1.078) | 1.028 (1.007 to 1.050) | 0.420 | 0.980 (0.927 to 1.035) | 0.045 |
| Ages 0–4 | 0.995 (0.944 to 1.049) | 1.048 (0.931 to 1.180) | 1.018 (0.948 to 1.092) | 0.691 | 0.823 (0.649 to 1.044) | 0.089 |
| Ages 5–19 | 1.030 (0.966 to 1.098) | 1.017 (0.882 to 1.172) | 1.064 (0.990 to 1.142) | 0.586 | 1.017 (0.767 to 1.349) | 0.998 |
| Ages 20–64 | 1.008 (0.982 to 1.035) | 1.041 (0.982 to 1.104) | 1.032 (0.994 to 1.072) | 0.823 | 1.013 (0.913 to 1.124) | 0.633 |
| Ages 65–99 | 1.011 (0.993 to 1.030) | 1.050 (1.006 to 1.097) | 1.029 (1.002 to 1.057) | 0.445 | 0.985 (0.920 to 1.055) | 0.127 |
| All cardiovascular | 0.996 (0.989 to 1.003) | 0.992 (0.976 to 1.009) | 1.008 (0.999 to 1.018) | 0.104 | 0.991 (0.964 to 1.019) | 0.955 |
| Ischaemic heart disease | 0.991 (0.980 to 1.003) | 0.990 (0.963 to 1.017) | 1.007 (0.990 to 1.024) | 0.313 | 0.989 (0.950 to 1.030) | 0.976 |
| Congestive heart failure | 0.989 (0.974 to 1.004) | 0.978 (0.942 to 1.015) | 1.016 (0.993 to 1.039) | 0.096 | 0.969 (0.914 to 1.027) | 0.791 |
| Cardiac dysrhythmia | 0.980 (0.962 to 0.998) | 0.979 (0.935 to 1.025) | 0.989 (0.961 to 1.017) | 0.721 | 0.976 (0.912 to 1.044) | 0.934 |
| Cerebrovascular disease and stroke | 1.019 (1.004 to 1.035) | 1.015 (0.980 to 1.052) | 1.016 (0.997 to 1.036) | 0.971 | 1.044 (0.987 to 1.104) | 0.379 |

*Rate ratio and 95% confidence interval per 10 μg/$m^3$ increase in 2-day moving average $PM_{2.5}$, adjusted for fungal spore counts (asthma only), race, gender, county, median income, weekend, relative humidity, temperature, age and pressure gradient. RR×100 is the percentage increase in hospital admissions. Estimates for the three strata are derived from the product term models, while estimates for the full period are from a model without interaction terms

†the product term p value for the difference with the pre-fire period.

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## Table 4

Relative rate of respiratory admissions in relation to wildfire period

| Hospital admissions outcome | n* | Pre-wildfire period (referent) | Wildfire period RR (95% CI)† | | Post-wildfire period RR (95% CI) | |
|---|---|---|---|---|---|---|
| | | | Unadjusted for $PM_{2.5}$ | Adjusted for $PM_{2.5}$ | Unadjusted for $PM_{2.5}$ | Adjusted for $PM_{2.5}$ |
| All respiratory | | | | | | |
| All ages | 21 019 | 1.00 | 0.961 (0.916 to 1.008) | 0.903 (0.850 to 0.960) | 1.143 (1.072 to 1.219) | 1.173 (1.097 to 1.253) |
| Ages 0–4 | 2143 | 1.00 | 0.865 (0.757 to 0.989) | 0.842 (0.717 to 0.988) | 1.152 (0.957 to 1.388) | 1.162 (0.954 to 1.415) |
| Ages 5–19 | 1205 | 1.00 | 1.098 (0.910 to 1.324) | 1.087 (0.863 to 1.370) | 1.373 (1.089 to 1.732) | 1.467 (1.142 to 1.883) |
| Ages 20–64 | 8314 | 1.00 | 0.991 (0.922 to 1.066) | 0.923 (0.843 to 1.012) | 1.074 (0.971 to 1.188) | 1.104 (0.992 to 1.228) |
| Ages 65–99 | 9357 | 1.00 | 0.932 (0.867 to 1.003) | 0.874 (0.795 to 0.959) | 1.147 (1.045 to 1.259) | 1.193 (1.084 to 1.313) |
| Asthma | | | | | | |
| All ages | 3022 | 1.00 | 1.088 (0.965 to 1.227) | 0.992 (0.856 to 1.149) | 1.264 (1.085 to 1.473) | 1.336 (1.134 to 1.573) |
| Ages 0–4 | 600 | 1.00 | 0.806 (0.632 to 1.029) | 0.714 (0.515 to 0.990) | 1.092 (0.759 to 1.572) | 1.133 (0.777 to 1.654) |
| Ages 5–19 | 733 | 1.00 | 1.254 (0.999 to 1.575) | 1.282 (0.958 to 1.716) | 1.564 (1.160 to 2.109) | 1.629 (1.184 to 2.243) |
| Ages 20–64 | 1151 | 1.00 | 1.273 (1.067 to 1.518) | 1.221 (0.979 to 1.524) | 1.362 (1.043 to 1.779) | 1.486 (1.111 to 1.987) |
| Ages 65–99 | 538 | 1.00 | 0.869 (0.657 to 1.151) | 0.645 (0.450 to 0.925) | 0.924 (0.606 to 1.408) | 1.005 (0.650 to 1.552) |
| Acute bronchitis/bronchiolitis | | | | | | |
| All ages | 618 | 1.00 | 1.143 (0.878 to 1.490) | 0.959 (0.696 to 1.321) | 1.482 (1.042 to 2.109) | 1.580 (1.089 to 2.291) |
| Ages 0–4 | 353 | 1.00 | 1.128 (0.819 to 1.555) | 0.899 (0.607 to 1.333) | 1.520 (0.947 to 2.440) | 1.547 (0.954 to 2.507) |
| Ages 5–19 | 23 | 1.00 | | | | |
| Ages 20–64 | 106 | 1.00 | 1.350 (0.688 to 2.648) | 1.320 (0.608 to 2.863) | 2.454 (1.068 to 5.640) | 2.515 (1.055 to 5.998) |
| Ages 65–99 | 136 | 1.00 | 1.166 (0.643 to 2.115) | 0.934 (0.422 to 2.066) | 0.911 (0.428 to 1.942) | 0.997 (0.439 to 2.262) |
| Chronic obstructive pulmonary disease | | | | | | |
| Ages 20–99 | 2860 | 1.00 | 0.988 (0.875 to 1.115) | 0.913 (0.779 to 1.069) | 1.043 (0.885 to 1.228) | 1.064 (0.897 to 1.262) |
| Ages 20–64 | 910 | 1.00 | 0.967 (0.779 to 1.201) | 0.873 (0.660 to 1.156) | 1.175 (0.862 to 1.601) | 1.311 (0.954 to 1.802) |
| Ages 65–99 | 1950 | 1.00 | 1.002 (0.869 to 1.156) | 0.926 (0.767 to 1.117) | 0.985 (0.811 to 1.196) | 0.981 (0.798 to 1.206) |
| Pneumonia | | | | | | |
| All ages | 6440 | 1.00 | 0.943 (0.868 to 1.025) | 0.888 (0.799 to 0.986) | 1.294 (1.158 to 1.446) | 1.318 (1.174 to 1.479) |
| Ages 0–4 | 537 | 1.00 | 0.938 (0.705 to 1.247) | 0.951 (0.678 to 1.333) | 1.458 (0.974 to 2.182) | 1.374 (0.885 to 2.133) |
| Ages 5–19 | 293 | 1.00 | 0.891 (0.604 to 1.312) | 0.830 (0.541 to 1.272) | 0.960 (0.588 to 1.569) | 0.969 (0.578 to 1.624) |

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| Hospital admissions outcome | n* | Pre-wildfire period (referent) | Wildfire period RR (95% CI)† | | Post-wildfire period RR (95% CI) | |
|---|---|---|---|---|---|---|
| | | | Unadjusted for $PM_{2.5}$ | Adjusted for $PM_{2.5}$ | Unadjusted for $PM_{2.5}$ | Adjusted for $PM_{2.5}$ |
| Ages 20–64 | 1686 | 1.00 | 0.927 (0.795 to 1.081) | 0.837 (0.690 to 1.016) | 1.314 (1.064 to 1.622) | 1.300 (1.047 to 1.615) |
| Ages 65–99 | 3924 | 1.00 | 0.959 (0.861 to 1.068) | 0.899 (0.782 to 1.033) | 1.277 (1.102 to 1.481) | 1.331 (1.142 to 1.552) |
| | | | Unadjusted for $PM_{2.5}$ | Adjusted for $PM_{2.5}$ | Unadjusted for $PM_{2.5}$ | Adjusted for $PM_{2.5}$ |
| All cardiovascular‡ | 27 170 | 1.00 | 0.958 (0.920 to 0.997) | 0.947 (0.902 to 0.994) | 1.061 (1.006 to 1.119) | 1.053 (0.994 to 1.114) |
| Ischaemic heart disease | 10319 | 1.00 | 0.913 (0.852 to 0.978) | 0.905 (0.832 to 0.985) | 1.029 (0.943 to 1.123) | 1.029 (0.936 to 1.131) |
| Congestive heart failure | 6144 | 1.00 | 0.891 (0.817 to 0.972) | 0.911 (0.819 to 1.014) | 1.113 (0.997 to 1.242) | 1.105 (0.982 to 1.244) |
| Cardiac dysrhythmia | 4004 | 1.00 | 0.968 (0.874 to 1.072) | 0.964 (0.851 to 1.093) | 1.089 (0.949 to 1.251) | 1.057 (0.914 to 1.223) |
| Cerebrovascular disease and stroke | 5908 | 1.00 | 1.066 (0.981 to 1.159) | 1.017 (0.922 to 1.123) | 1.013 (0.907 to 1.132) | 1.013 (0.902 to 1.138) |

*Number of hospital admissions for zip codes with defined populations

†adjusted for race, gender, county, median income, weekend, relative humidity, temperature, age and pressure gradient

‡cardiovascular admissions were for subjects ages 45-99 years. $PM_{2.5}$, particulate matter.

# Relationship between habitat and genetics in a wide-ranging large carnivore

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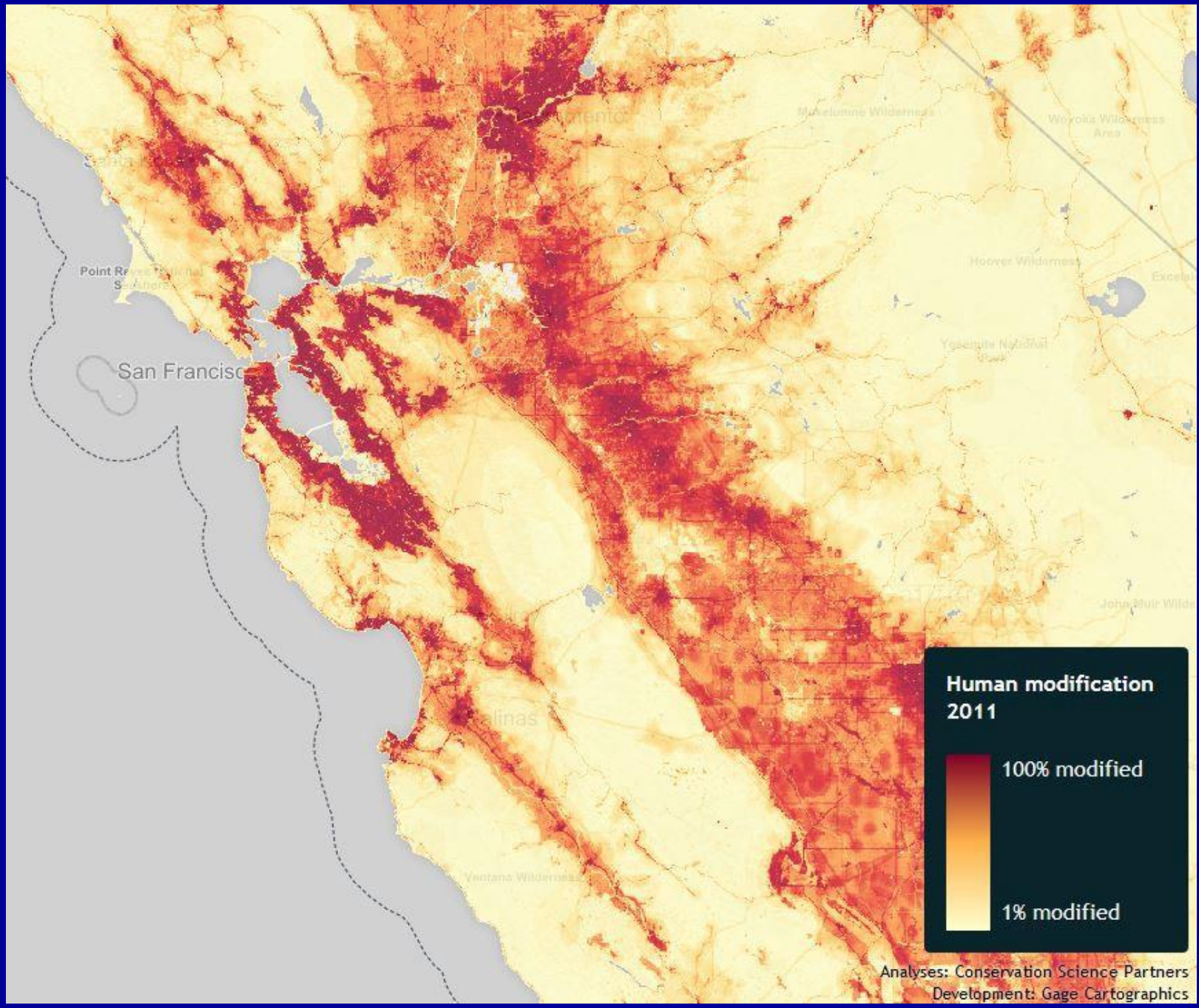
# Legal Status of California Mountain Lions

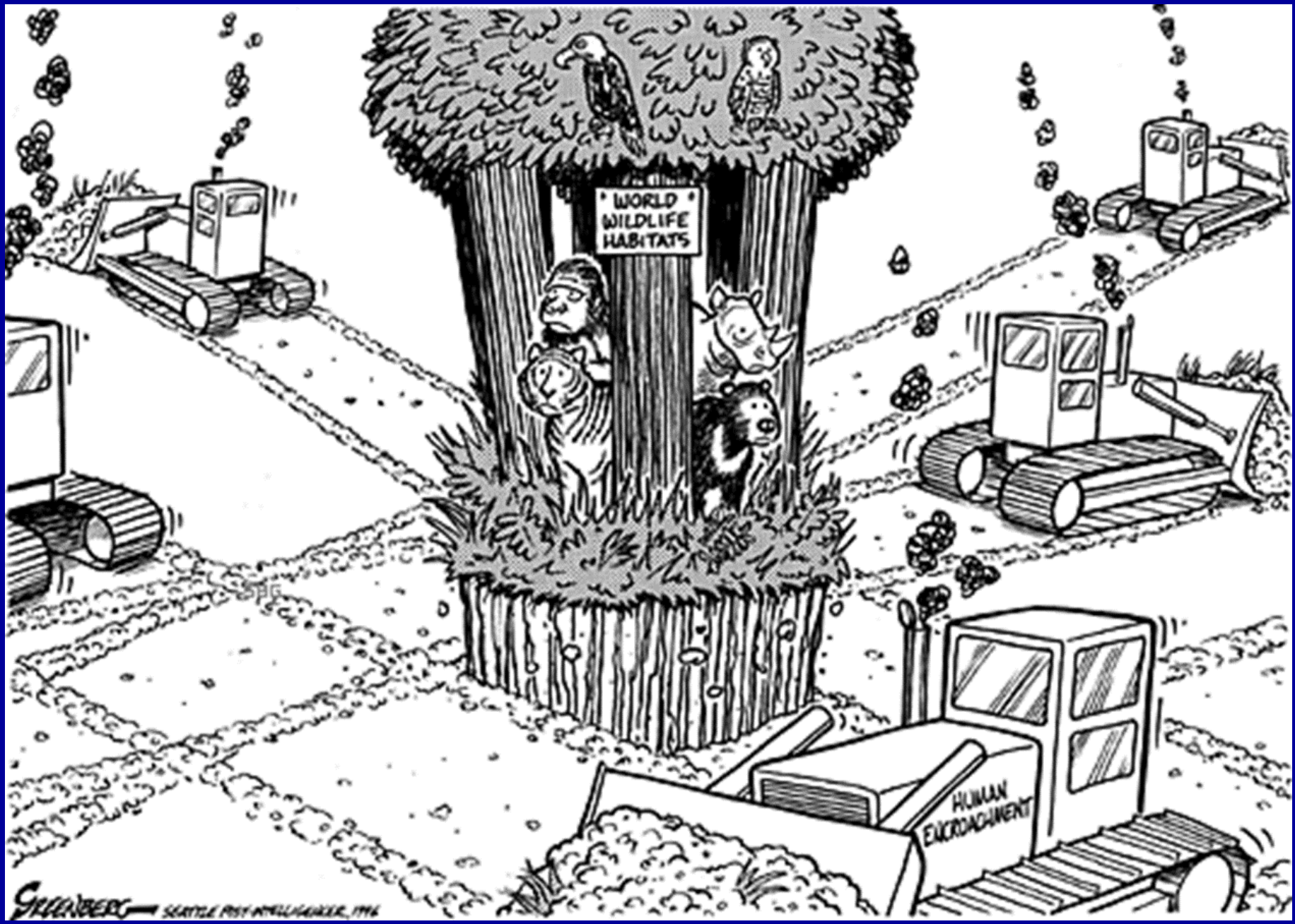
- 1907-1963 Bountied Predator
- 1963-1969 Nongame Mammal
- 1969-1972 Game Mammal
- 1972-1986 Protected Mammal
- 1986-1990 Game Mammal (no hunting)
- 1990-Now Specially Protected Mammal

# Human population growth

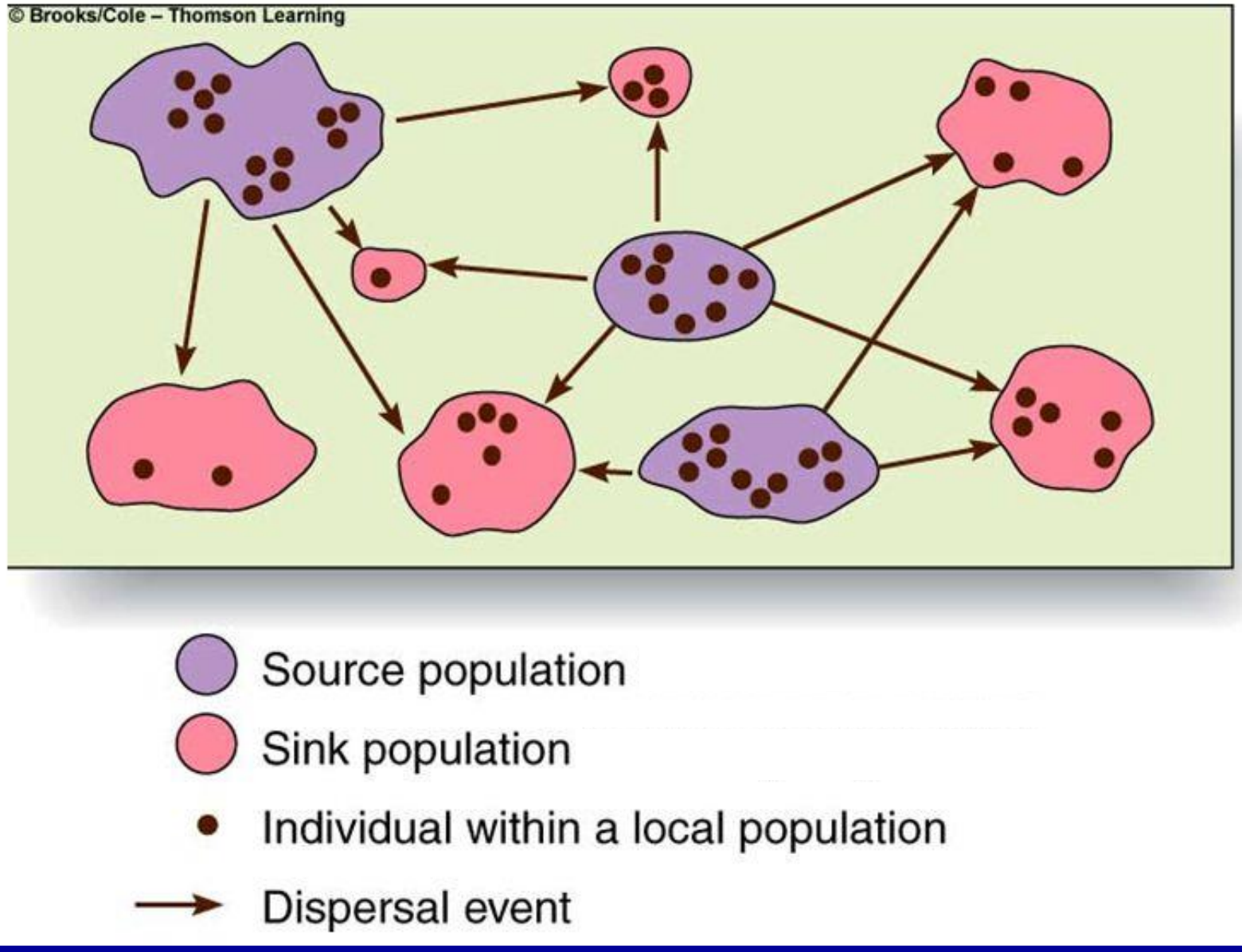
| Year | Population | % Growth |
|---|---|---|
| **1900** | 1,485,053 | 22.4% |
| **1910** | 2,377,549 | 60.1% |
| **1920** | 3,426,861 | 44.1% |
| **1930** | 5,677,251 | 65.7% |
| **1940** | 6,907,387 | 21.7% |
| **1950** | 10,586,223 | 53.3% |
| **1960** | 15,717,204 | 48.5% |
| **1970** | 19,953,134 | 27.0% |
| **1980** | 23,667,902 | 18.6% |
| **1990** | 29,760,021 | 25.7% |
| **2000** | 33,871,648 | 13.8% |
| **2010** | 37,253,956 | 10.0% |

*U.S. Census Bureau


San Francisco
Human modification
2011
100% modified
1% modified
Analyses: Conservation Science Partners
Development: Gage Cartographics


WORLD
WILDLIFE
HABITATS
HUMAN
ENCROACHMENT
GREENBERG — SEATTLE POST-INTELLIGENCER, 1996

Ernest et al. 2014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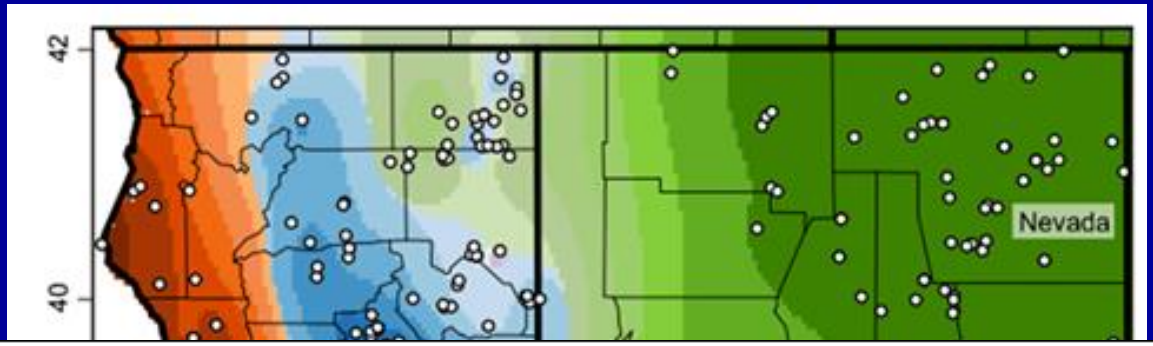
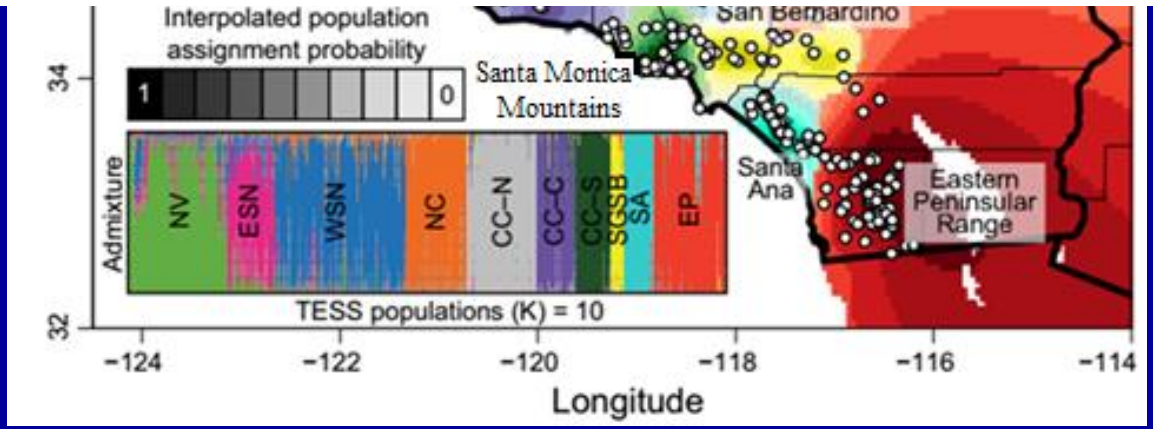
Source population
Sink population
Individual within a local population
Dispersal event

# Overarching goals

- Habitat vs genetics
- Protected habitat vs unprotected habitat




| Area | Expected Heterozygosity | Internal Relatedness | Effective Population Size |
|---|---|---|---|
| Western Sierra-Nevada Mtns | 0.52 | 0.09 | 156 |
| Eastern Sierra Nevada Mtns | 0.53 | 0.11 | 23 |
| North Coast | 0.41 | 0.28 | 83 |
| Santa Cruz Mtns | 0.42 | 0.27 | 17 |
| Central Coast | 0.46 | 0.19 | 57 |
| Santa Monica Mtns | 0.41 | 0.27 | 3 |
| Santa Ana Mtns | 0.33 | 0.39 | 16 |
| Eastern Peninsular Range | 0.44 | 0.21 | 32 |
| San Gabriel and San Bernardino Mtns | 0.42 | 0.29 | 5 |

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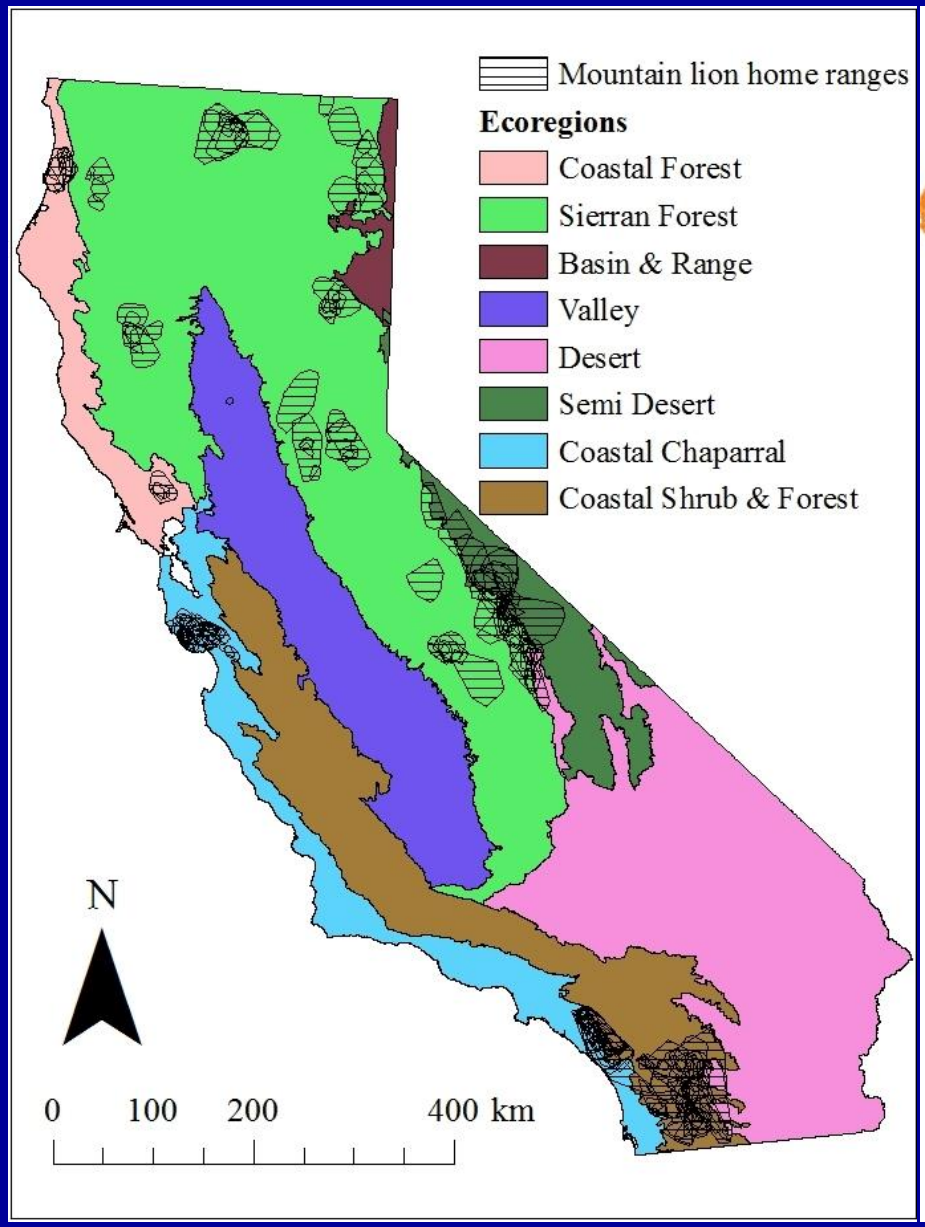
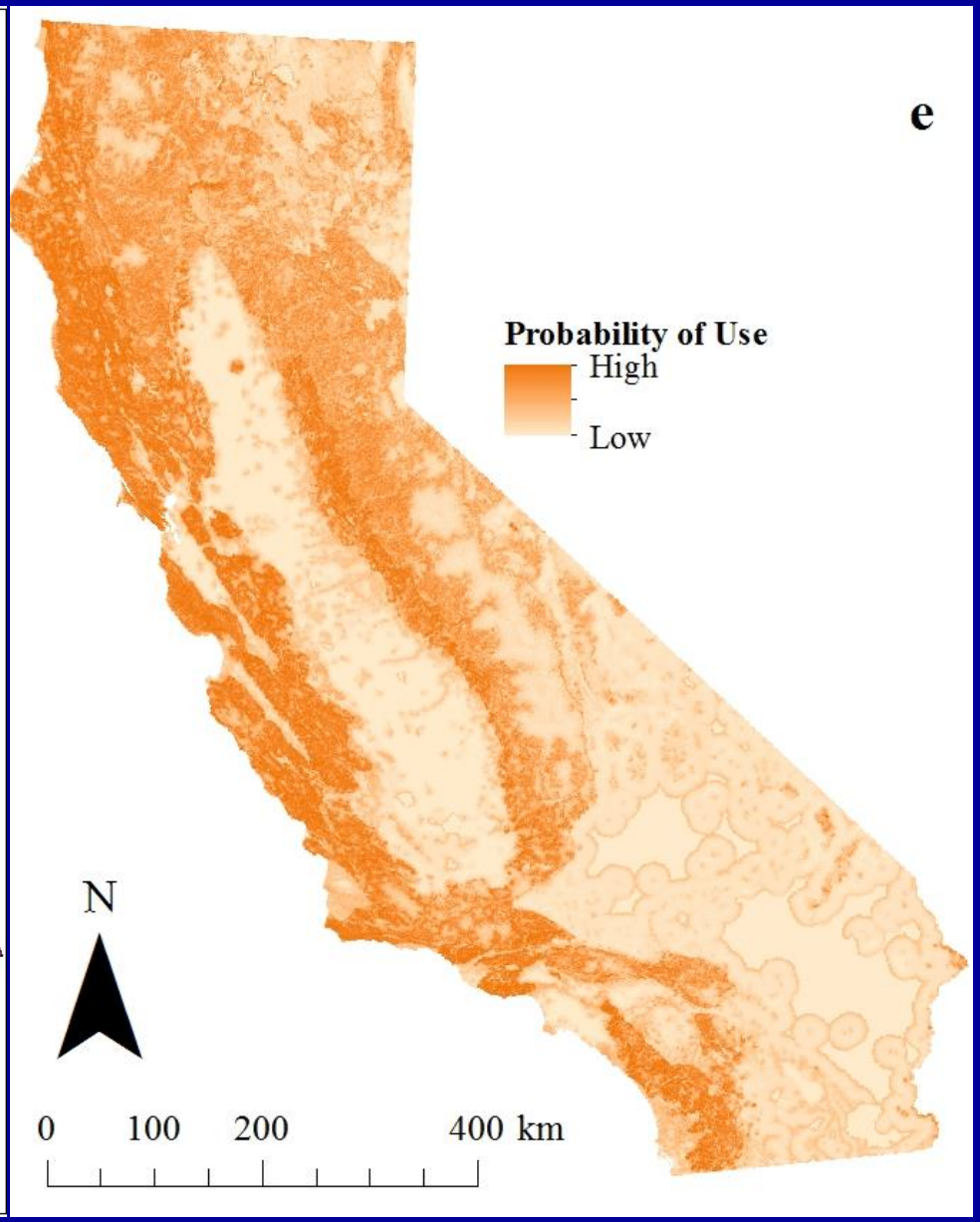

Mountain lion home ranges
Ecoregions
Coastal Forest
Sierran Forest
Basin & Range
Valley
Desert
Semi Desert
Coastal Chaparral
Coastal Shrub & Forest
N
0 100 200 400 km


e
Probability of Use
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N
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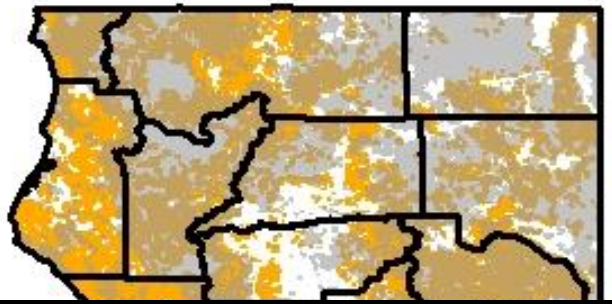
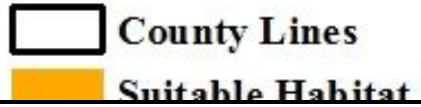





| Area | Suitable Habitat ($km^2$) | % Protected | Amount of Suitable Habitat ($km^2$) Protected |
|---|---|---|---|
| Western Sierra-Nevada Mtns | 45,531 | 0.54 | 24,701 |
| Eastern Sierra Nevada Mtns | 9,677 | 0.98 | 9,443 |
| North Coast | 28,802 | 0.46 | 13,147 |
| Santa Cruz Mtns | 5,848 | 0.39 | 2,294 |
| Central Coast | 17,695 | 0.42 | 7,398 |
| Santa Monica Mtns | 2,644 | 0.43 | 1,149 |
| Santa Ana Mtns | 1,919 | 0.61 | 1,162 |
| Eastern Peninsular Range | 6,671 | 0.66 | 4,377 |
| San Gabriel and San Bernardino Mtns | 3,881 | 0.83 | 3,212 |

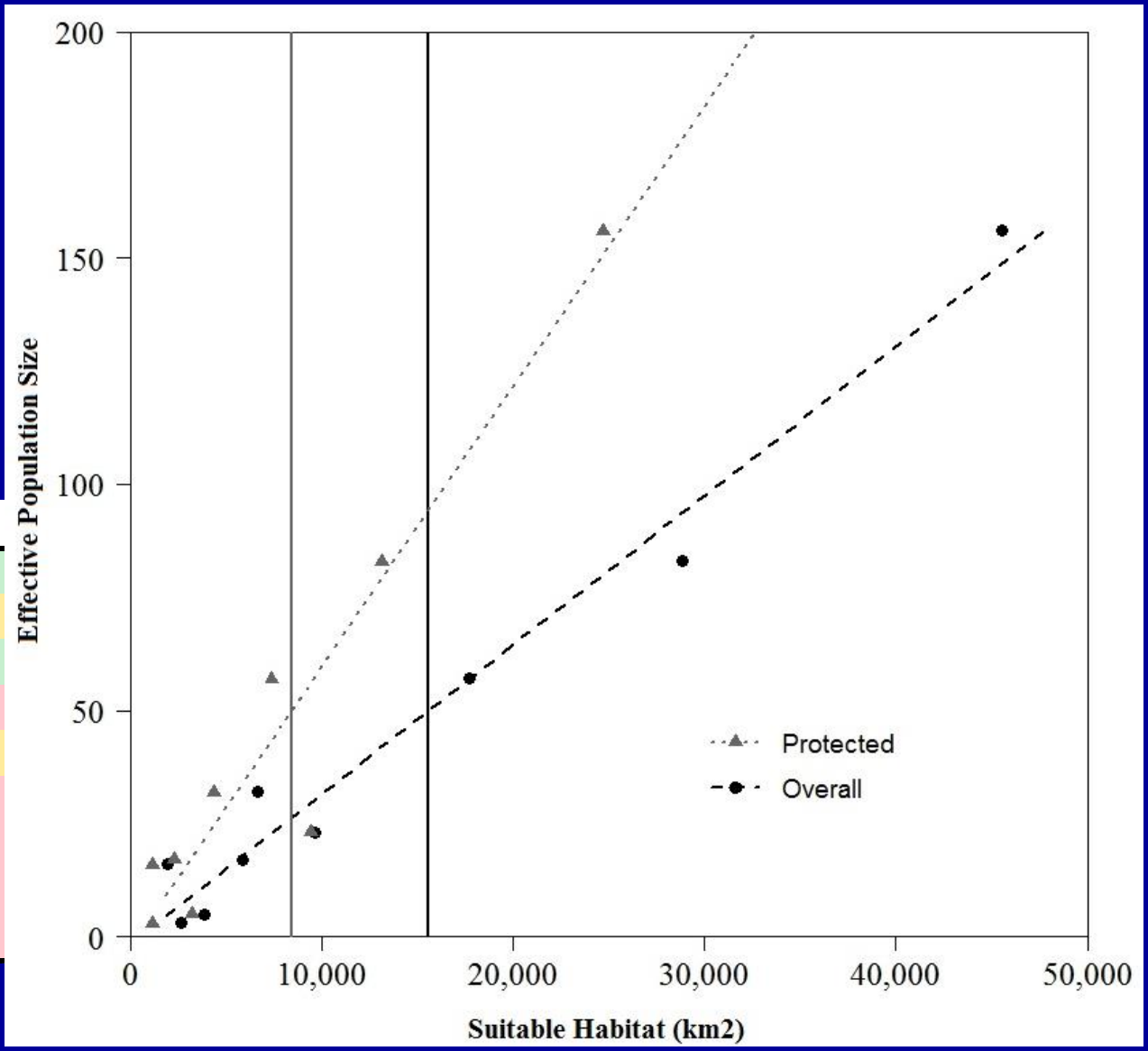
# Analyses

- Analyses
  - Effect. Pop. Size ~ Overall suitable habitat
  - Effect. Pop. Size ~ Protected suitable habitat
  - Minimum Threshold – Effect. Pop. Size n = 50

# Results

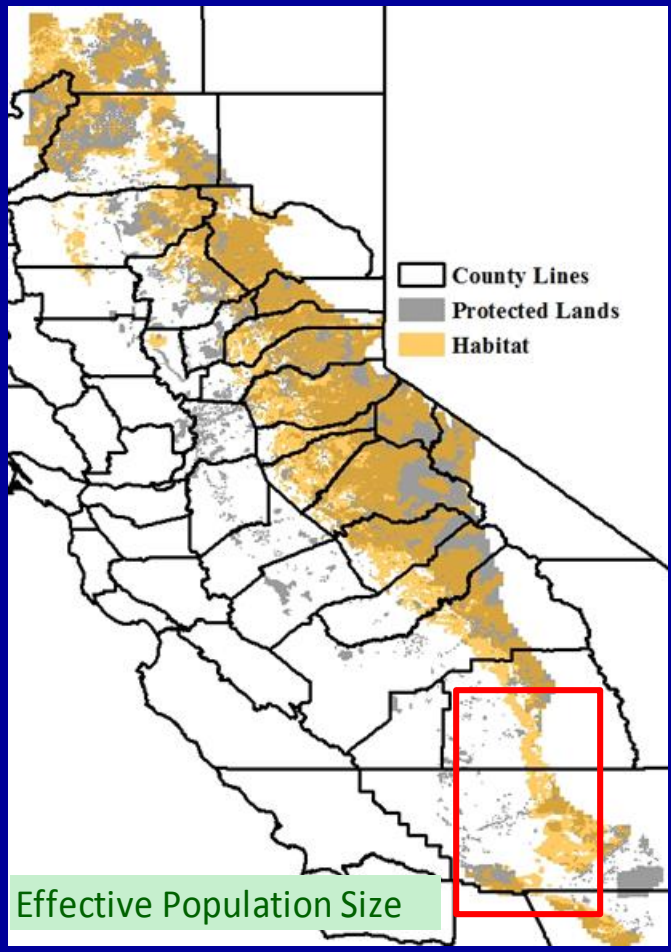
| | Effective Population Size | |
|---|---|---|
| | Overall | Protected |
| $R^2$ value | 0.97 | 0.91 |
| *p* value | <0.001 | <0.001 |
| Minimum Threshold (km2) | 15,600 | 8,450 |

| Area |
|---|
| Western Sierra-Nevada Mtns |
| Eastern Sierra Nevada Mtns |
| North Coast |
| Santa Cruz Mtns |
| Central Coast |
| Santa Monica Mtns |
| Santa Ana Mtns |
| Eastern Peninsular Range |
| San Gabriel and San Bernardino Mtns |



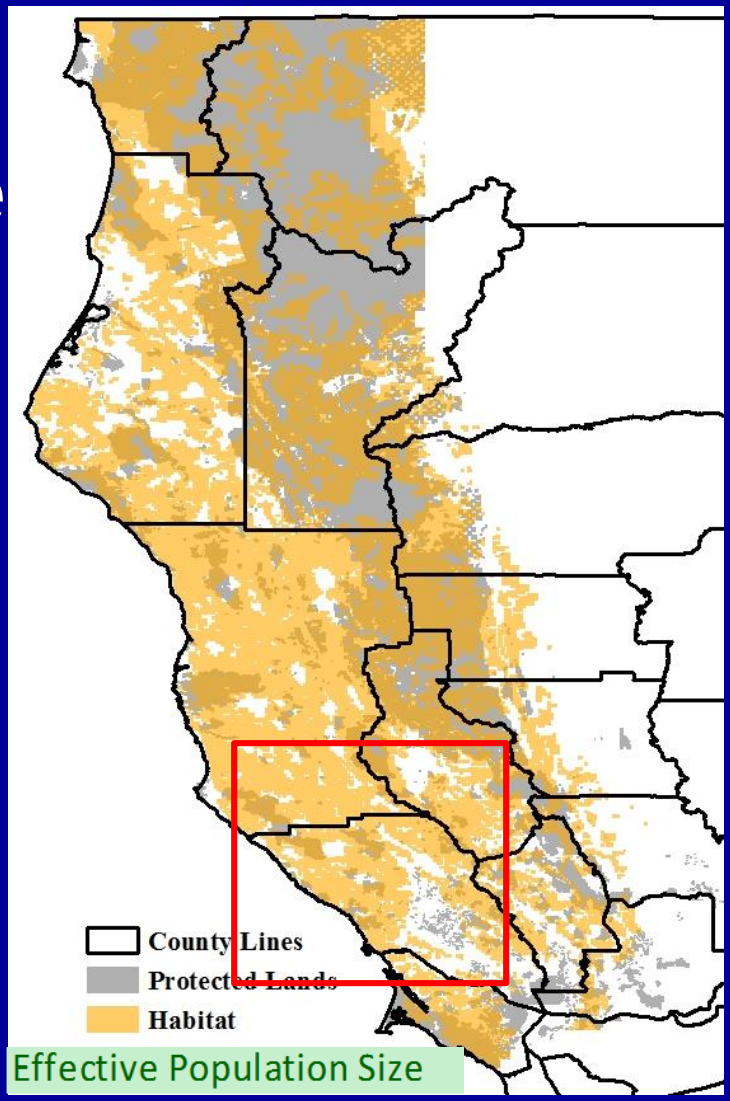
# Western Sierra

- No current concerns
- Important source for entire state & beyond
- Important to maintain habitat in southern extent



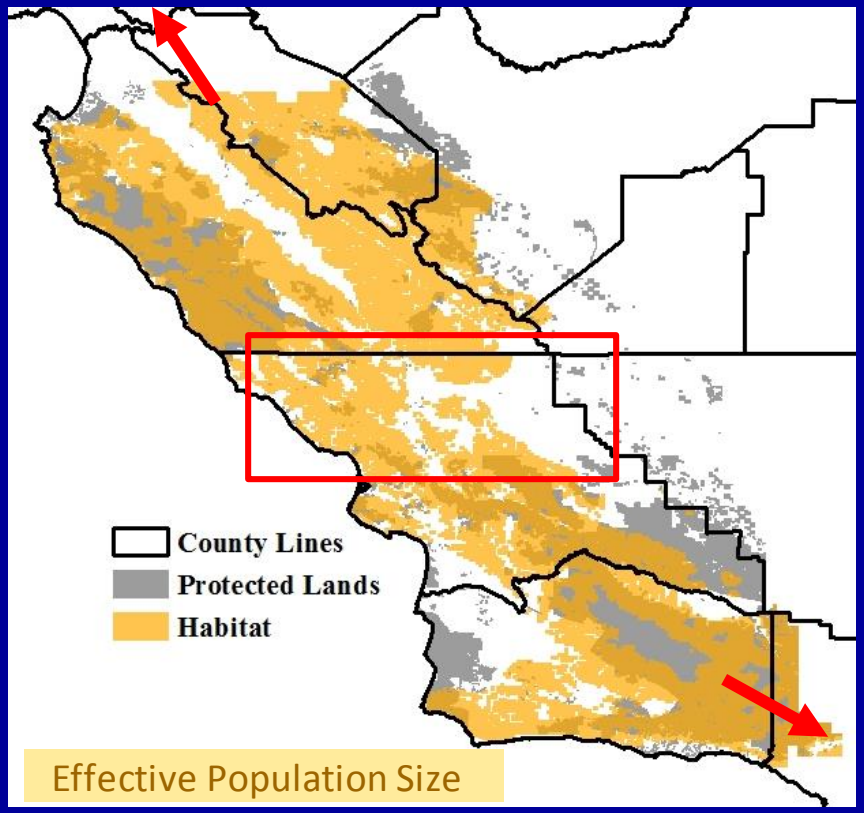
# North Coast

- No current concerns
- Southern extent a possible concern due to ‘habitat peninsula’ and little protected habitat



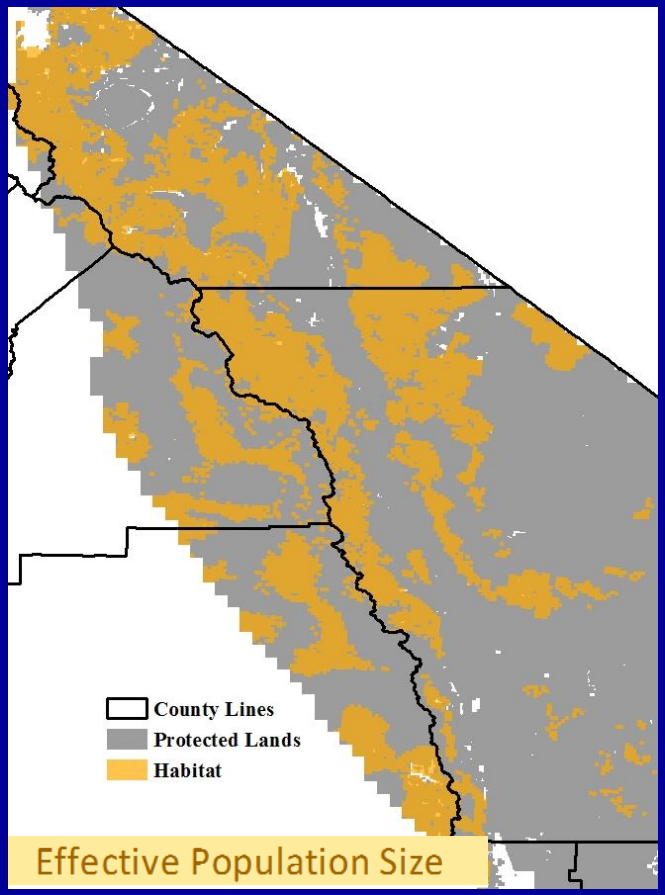
# Central Coast

- No current concerns
- Increase protected habitat
- Central section is vulnerable
- Improve connectivity to smaller adjacent areas



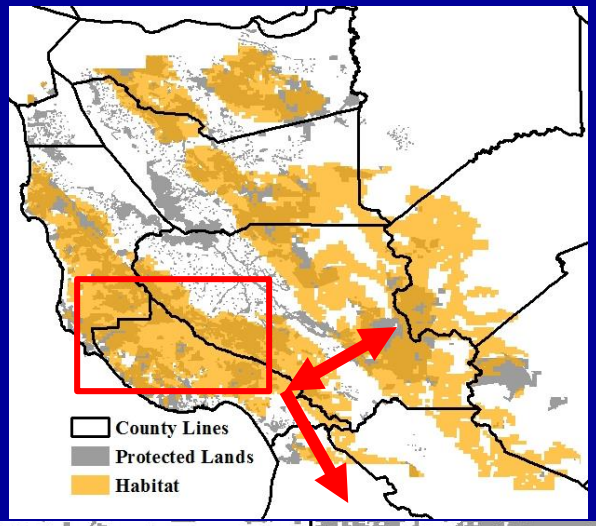
# Eastern Sierra

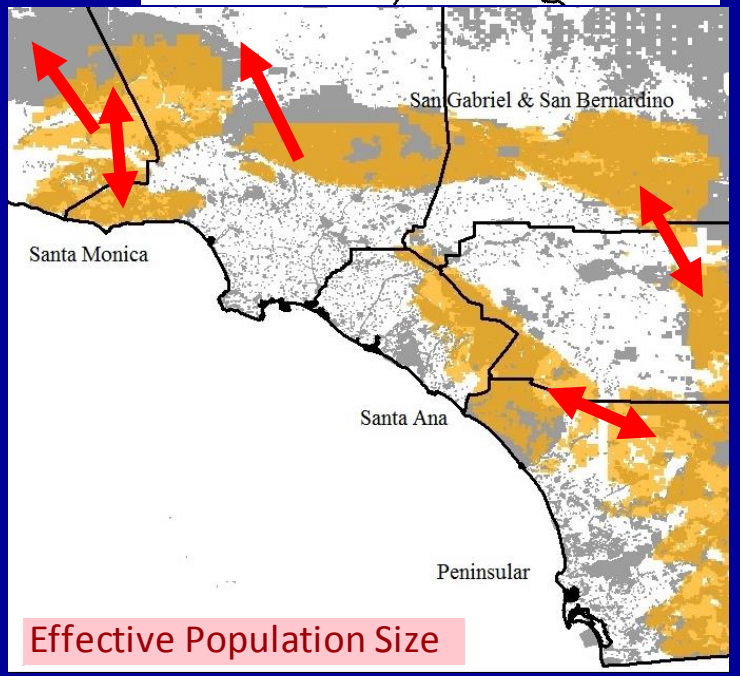
- Currently no concerns despite lower amount of habitat
- All habitat protected
- Maintenance of metapopulation dynamics likely promote persistence



# Santa Cruz & SoCal

- Current habitat/genetic concerns
- Internal habitat & connectivity at risk
- External connectivity limited
- Long-term viability of these areas a concern unless habitat protection & connectivity improved



# Summary

- Habitat predictor of genetic integrity
- Suitable habitat isn't as good as protected suitable habitat
- Regional habitat/genetic concerns in CA
- Improved habitat connectivity & protection = restored metapopulation dynamics = increased genetic integrity
- Ensuring habitat requirements for lions to persist ensures persistence of many other species (and ecological processes) too

# Path Forward?

- Conservation easements
- Open spaces
- Wildlife passage

# Thanks

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# INFLUENCE OF VEGETATION, TOPOGRAPHY, AND ROADS ON COUGAR MOVEMENT IN SOUTHERN CALIFORNIA

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***Abstract:*** Models of individual movement can help conserve wide-ranging carnivores on increasingly human-altered landscapes, and cannot be constructed solely by analyzing the daytime resting locations typically collected in carnivore studies. We examined the movements of 10 female and 7 male cougars (*Puma concolor*) at 15-min intervals during 44 nocturnal or diel periods of hunting or traveling in the Santa Ana Mountain Range of southern California, USA, between 1988 and 1992. Cougars tended to move in a meandering path (mean turning angle ~54°), and distance moved (mean and mode ~300 m) was not correlated with turning angle. Cougars used a broader range of habitats for nocturnal or diel movements than for previously described daybed locations for this same population. Riparian vegetation ranked highest in a compositional analysis of vegetation types selected during movement; grassland, woodland and urbanized sites were least selected. During periods of stasis (we presume many of these were stalking locations), patterns of selection were less marked. Cougars spent a disproportionate amount of time in highly ranked vegetation types, and traveled slowest through riparian habitats and fastest through human-dominated areas. Our results suggest that travel speed may provide an efficient index of habitat selection in concert with other types of analysis. Hunting or traveling individuals consistently used travel paths that were less rugged than their general surroundings. Traveling cougars avoided 2-lane paved roads, but dirt roads may have facilitated movement. Maintenance and restoration of corridors between large wildlands is essential to conserving cougars in southern California. Our results indicate that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in such corridors, that dirt roads should not impede cougar use of corridors, and that corridors should lie along routes with relatively gentle topography. Our results suggest that cougars do not key in on highway-crossing structures in a way that creates a prey trap. Our empirical frequency distributions of distances and turning angles, along with cougar responses to vegetation, topography, and roads can help parameterize an individually-based movement model for cougars in human-altered landscapes.

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***Key words:*** California, compositional analysis, cougar, habitat selection, movement, prey trap, *Puma concolor*, riparian, roads, scale, topography, travel speed, urbanized, vegetation.

Least-cost path analysis (Bunn et al. 2000, Paquet et al. 2001) and individual-based movement models (DeAngelis and Gross 1992, Bergman et al. 2000) for wide-ranging animals depend crucially on an understanding of how individuals move. These models, especially those built for terrestrial carnivores, can be used as tools for conservation planning and to assess, maintain, or improve habitat connectivity in human-dominated landscapes (Minta et al. 1999, Schadt et al. 2002). Animal movement probably depends on patterns of resource use relative to availability across multiple scales (Senft et al. 1987, Wiens 1989, Turchin 1998, Pace 2001), natural impediments in the landscape (With 1994), the animal's knowledge of its environment (including locations of conspecifics and primary prey), and human-induced habitat fragmentation and loss (Crooks 2002). A first step to modeling movement behavior is to study fine-scale movements and patterns of selection exhibited by individual animals (Wiens et al. 1993). If the broad-scale distribution patterns of individuals are the aggregate of fine-scaled movement behaviors (Turchin 1991, With 1994), then these behaviors may provide a mechanistic link to many ecological processes (Wiens et al. 1993).

Despite the increased use of wide-ranging nocturnal carnivores in conservation planning, little research has described their fine-scale movement patterns or factors influencing those movements. For instance, most studies of movement patterns of western cougars have described these patterns over weeks or months, based on ≤1 location per day, usually during daylight hours (Hemker et al. 1984, Anderson et al. 1992, Beier 1995, Ruth et al. 1998, Sweanor et al. 2000). Beier et al. (1995) described patterns in the distances cougars moved per 15-min interval as a function of time

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of day, sex, gross behavior state (e.g., hunting, feeding on previously-killed deer, raising cubs), but did not characterize cougar movements as a function of vegetation, topography, or other features in the animal's vicinity.

Cougar aversion to paved roads has been documented previously (Van Dyke et al. 1986, Belden and Hagedorn 1993, Sweanor et al. 2000, Dickson and Beier 2002), but all of these studies analyzed diurnal locations, presumably daybed locations in most cases, and no study has compared the observed number of paved road crossings with the number of crossings expected if cougars were indifferent to crossing. There has been increasing concern that highway crossing structures such as underpasses and culverts could funnel prey into areas where predators would exploit high prey density, creating a prey trap (Norman et al. 1998, Little et al. 2002), but there are no data supporting or refuting this possibility for cougars.

We attempted to address some of these information gaps by examining a subset of data collected and previously analyzed by Beier et al. (1995). Because cougar movement depends not only on habitat type and arrangement, but also on nonhabitat factors (e.g., location of a previously killed carcass, interactions with conspecifics), we attempted to isolate habitat factors by studying cougar movements during those periods when the focal animal was apparently not feeding on deer or interacting with other cougars. We studied animals during diel or nocturnal monitoring sessions to include periods of greatest daily movement. We also chose a time scale (movement during 15-min intervals) that minimized the risk that habitats traversed differed from those intersected by a line segment between consecutive locations, and we buffered these line segments to reflect the resolution of our measurements. Finally, we speculated that travel speed in a habitat might be a useful index of habitat selection. We reasoned that cougars would travel most quickly through habitats in which they are most uncomfortable (or that they perceive as less-profitable places to spend their time). If our data confirmed this pattern, travel speed could be used as a complement to more complex approaches such as compositional analysis.

Our objectives were to: (1) describe the travel path characteristics of individual cougars monitored during nocturnal or diel periods; (2) compare the vegetation, topography, and road density on paths used by and available to cougars during individual movement sessions; (3) investigate whether travel speed is correlated with habitat selection patterns; (4) identify landscape features that facilitated or inhibited cougar movements, with particular attention to cougar movements near 2-lane paved roads; and (5) describe the extent to which cougars might linger at road crossing structures to ambush prey.

## STUDY AREA

The Santa Ana Mountain Range (SAMR) encompassed approximately 2,060 $km^2$ of nonurban wildlands and included portions of Orange (38% of study area), Riverside (28%), and San Diego (34%) counties; over 1 million people lived in the cities and communities surrounding the SAMR (Beier 1993). Our study area boundaries were delineated where the core of the study area met a major freeway or where human dwellings exceeded 4 residences per ha. The Cleveland National Forest, Camp Pendleton Marine Corps Base, Fallbrook Naval Weapons Station, Caspers Regional Park and several smaller reserves (Padley 1990, Beier and Barrett 1993) comprised most of the protected cougar habitat in the area. Beier (1993, 1995) and Dickson (2001) provide maps of the study area.

Plant communities on the study area included chaparral, oak woodlands (*Quercus engelmannii* and *Q. agrifolia*), coastal scrub, annual grasses, and coniferous forests at higher elevations (Barbour and Major 1995). Citrus and avocado orchards and other nonnative vegetation types occurred in parts of the area. Although human influence on the SAMR was widespread and included cattle grazing, agriculture, military training facilities, and public recreation areas, much of the study area remained undeveloped. Maximum average daily temperature was 24°C and mean annual precipitation was 33 cm in lower elevations (Santa Ana Fire Station, Santa Ana, California, USA, 1948–2000), with somewhat cooler and more mesic conditions at higher elevations. Precipitation in the form of fog drip was common throughout the year and light snow accumulation was possible in winter at the higher elevations (Barbour and Major 1995). Elevations within the study area ranged from sea level at the coast to 1,717 m on Santiago Peak. The topography was rugged. Although perennial streamflow was intermittent, springs, seeps, and other water sources were widely available throughout the study area (Beier and Barrett 1993).

Other carnivores common to the SAMR included coyotes (*Canis latrans*), gray foxes (*Urocyon*

*cinereoargenteus*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*). Mule deer (*Odocoileus hemionus*) were common throughout the study area and were the most important prey species for this cougar population (Beier and Barrett 1993). Smaller prey included opossum (*Didelphis virginiana*), raccoon, and coyote (Beier and Barrett 1993).

## METHODS

### Radiotelemetry

Between May 1988 and December 1992, we captured, radiocollared, and monitored movements of cougars during distinct periods that ran from 1 hr before sunset until 1 hr after sunrise (nocturnal sessions) or for 24 hr (diel sessions, which always started and ended in the afternoon). During each session, we determined the location of a focal animal every 15 min using radiotelemetry. We obtained radiotelemetry locations from the ground using standard triangulation techniques (Mech 1983) conducted by a single observer using a vehicle. We attempted to track the focal animal at a distance >100 m to minimize influencing its movement and <500 m away to obtain accurate locations. To determine a single location, we took bearings within a span of 2–6 min. Because only a single observer was used and no network of precisely located receiving stations was available, we cannot compute meaningful error polygons (White and Garrott 1990). We minimized location errors by using only azimuths that differed by 60–120° and by getting close to the animal (White and Garrott 1990). We determined 85% and 96% of all locations from within 500 m and 1 km of the focal animal, respectively. We recorded these locations to the nearest 50 m of easting and northing; thus, movements ≤50 m in 15 min we typically recorded as stasis. We recorded each radiolocation as a Universal Transverse Mercator (UTM) point on a 1:24,000 U.S. Geological Survey (USGS) topographic map and then exported all points into a vector-based Geographic Information System (GIS; ArcView® 3.2a; Environmental Systems Research Institute, Redlands, California, USA).

By back-tracking movements with hounds on the day after a monitoring session to look for kills, tracks, and feces, and using other knowledge (such as vocalizations), Beier et al. (1995) classified the animal's behavior in each session into 1 of several categories. For this analysis, we used only sessions on adults (≥2 years old) and juveniles independent of their mother, excluding sessions involving copulation, raising cubs, feeding on a previously killed large mammal, or killing a large mammal. We assume that the focal animal was hunting or traveling during these sessions; cougars in these sessions traveled much farther, and for a much larger fraction of the night, than cougars in other behavior categories (Beier et al. 1995). We chose sessions with this pattern because it was the most common movement pattern and because this choice minimized the risk that cougar response to vegetation, topography, and roads would be obscured by other factors (presence of a kill, cub, or mate).

### Analysis of Movement and Selection

Within the GIS, we developed an ArcView® extension (CGRMVMNT) using an object-oriented programming language (AVENUE; Environmental Systems Research Institute). Using this extension, we calculated whether the animal was moving or static during each 15-min period (interval, hereafter), the straight-line distance and rate of movement between consecutive locations, proportion of a movement segment (the straight line connecting consecutive locations) intersecting each vegetation type, deviation angles for consecutive movement segments, and the maximum slope encountered during a movement segment. Additionally, we used the CGRMVMNT extension to calculate the proportion of vegetation types and the maximum slope available to an individual (see below). Our approach assumed a constant rate of movement during a movement interval, and attributed that rate to movement in each vegetation type traversed during the interval.

We use the term "habitat composition" to refer to a vector of proportions of vegetation types used by or available to an animal and where total habitat composition adds up to 100%. To account for error in assigning an individual radio-location to a single vegetation type, which can seriously bias analyses of selection (Rettie and McLoughlin 1999), we assumed that a cougar used all types within a 100-m radius of a linear movement segment or a static location in proportion to the area of that type within the buffered region (Fig. 1). We chose a 100-m radius buffer partly to encompass triangulation error in estimating animal locations (Beier et al. 1995) and to encompass errors inherent in the digital coverages used to analyze selection. Additionally, this buffer allows our analysis to detect the potential importance of habitat mosaics in the selection process (see Rettie and McLoughlin 1999).

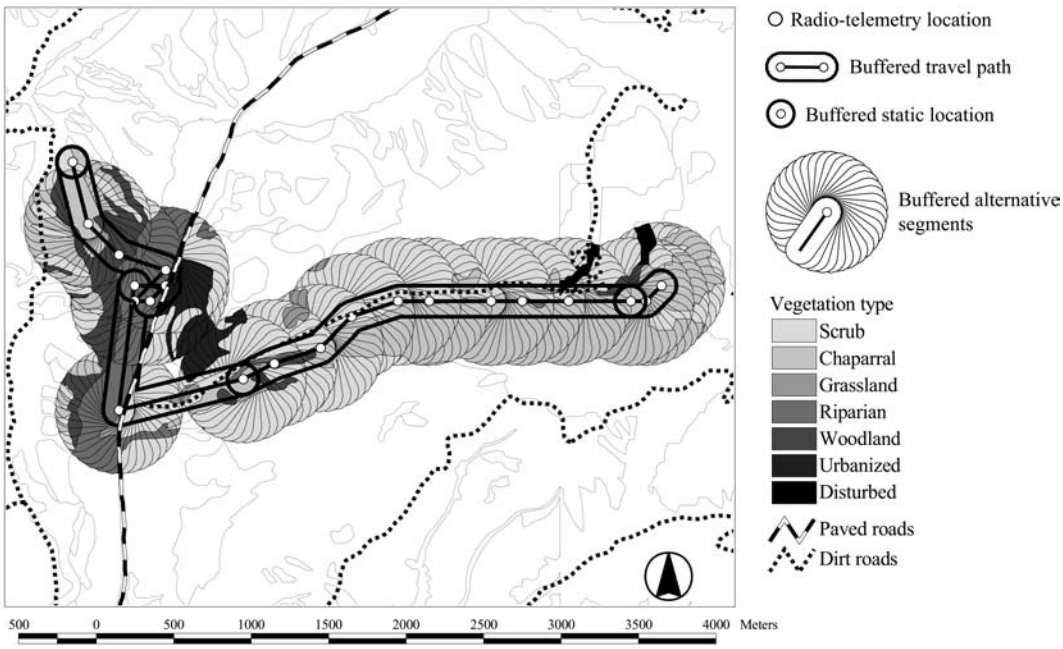


Fig. 1. Travel path through 7 vegetation types for female cougar F2 (session #100) monitored in the Santa Ana Mountain Range of southern California, USA, 1988–1992. This session began at 1800 hr, 6 Jul 1990 (eastern-most location) and ended at 0630 hr, 7 Jul 1990 (western-most location). Buffered static locations, travel path, and alternative segments generated by the CGRMVMNT extension are shown.

To evaluate selection for all movements during an individual session, we compared the average habitat composition of the buffered movement segments (used) to the average habitat composition of systematically assigned buffered movement segments (available). To estimate availability at each movement segment, we calculated the average proportion of each vegetation type captured within 35 alternative travel path segments (also buffered at 100 m) generated at 10° increments around the starting point of each movement segment and equal in length to the mean of all movement segments during that nocturnal or diel monitoring session (Fig. 1). To evaluate selection during static intervals within a session, we compared the average habitat composition of buffered radio-locations to the average habitat compositions of buffered movement segments during that session. For an individual monitored for >1 session, we first calculated used and available habitat compositions within a session, and then averaged across sessions so that each animal contributed only 1 composition to any inferential statistical analysis.

We used compositional analysis (Aitchison 1986, Aebischer and Robertson 1992, Aebischer et al. 1993) to rank cougar selection of habitats, with separate analyses for intervals of movement and stasis. Compositional analysis correctly uses the individual animal and not the radio-location as the sampling unit, thereby avoiding statistical problems arising from non-independence of proportions within a habitat composition (Aebischer et al. 1993). When cougar use of habitats was significantly nonrandom ($-N \ln\Lambda$ = test statistic, $\alpha < 0.05$), we used paired *t*-tests to compare mean utilization between all pairs of vegetation types ($\alpha < 0.05$). For each compositional analysis, we included only those habitat classes (e.g., vegetation types) available to all cougars, and included only those individual cougars using the same habitat classes. Because Aebischer et al. (1993) recommend a sample size ≥10 for compositional analyses, we pooled males and females together and did not test for sex effects on habitat selection.

For each movement session and individual cougar, we estimated the speed in each vegetation type,

$$S_v = \sum_{i=1}^{n} (s_i \times a_v) / \sum_{i=1}^{n} a_v,$$

where $n$ = number of movement segments during the session, $s_i$ = the average speed (km/h) during

each 15-min interval based on the straight-line distance between locations, and $a_v$ = area of vegetation type $v$ within each 100-m buffered segment, $i$. We used the unweighted average $S_v$ across sessions for each cougar as an estimate of that animal's speed in a particular vegetation type. To determine whether the rankings of speeds in vegetation types were correlated with the ranking of selection for each vegetation type, we used Spearman's rank order correlation coefficient ($r_s$ = test statistic, $\alpha < 0.05$). We also used a paired $t$-test to test for differences between male and female mean movement rates through each vegetation type ($t$ = test statistic, $\alpha < 0.05$).

We calculated the angular deviation from a straight line for all consecutive movement segments for all cougars. To test whether the circular distribution of deviation angles during movements ≥100 m was nonuniform, we performed a Rao's (1976) spacing test of uniformity ($U$ = test statistic, $\alpha < 0.05$). To determine whether mean movement distance was correlated with turning angle, we calculated an angular-linear correlation coefficient (Fisher 1993, Zar 1999; $nr^2_{al}$ = test statistic, $\alpha < 0.05$).

We had an insufficient number of observations to investigate seasonal differences in patterns of selection during movements. Similarly, we had too few observations of daytime movement to compare nocturnal and daytime movements: we monitored all 17 individuals overnight, but only 5 cougars during diel sessions that included daylight hours.

## Vegetation Types

Digital coverages of available vegetation types were acquired from Orange, Riverside, and San Diego counties. Vegetation polygons were identified by county personnel during 1990, 1992, 1993, and 1995 using LANDSAT Thematic Mapper and SPOT 2 satellite imagery, aerial photo interpretation, and field vegetation mapping surveys (ground-based and aerial). Although these data are nearly contemporaneous with our cougar locations, we checked all polygons classed as urban, disturbed, or agriculture in the vicinity of a session against field maps and notes, and made appropriate adjustments. We digitized and georeferenced all polygons using terrain-corrected satellite data and then digitally coded and projected these data as UTM coordinates (zone 11, North American Datum of 1927). These methods achieved a mean spatial accuracy of approximately 25 m and a minimum mapping unit between 0.2 and 2.0 ha. When possible, we more precisely delineated narrow riparian areas using the near infrared band of a SPOT image to detect greater leaf moisture content or by using hydrographic data layers. All vegetation types were categorized and classified by the 3 counties based on modifications to the Holland classification system (R. F. Holland. Preliminary Descriptions of the Terrestrial Natural Communities of California. California Department of Fish and Game, Nongame Heritage Program, Sacramento, California, USA, unpublished report). By consolidating infrequent vegetation types with similar types, our analyses used 9 general vegetation types: scrub, chaparral, grassland, riparian, forest, woodland, agriculture, urbanized (residential, industrial, or commercial developments), and disturbed (see Dickson 2001). We classified lakes, rivers, wetlands, vernal pools, beaches, and manmade watercourses (0.70% of the study area) within the riparian vegetation type. Cliff and rock habitats (0.04%) were most often adjacent to chaparral vegetation types, and so we reclassified these as such. Because coastal dunes (0.01%) were usually associated with scrub vegetation, we grouped these types together.

## Topography

We merged 26 USGS 1:24,000 digital elevation models (DEMs) to describe elevation and slope of the study area. We derived the slope (in degrees) of a cell location from the DEM using the ArcView® Spatial Analyst extension (Environmental Systems Research Institute, Redlands, California, USA). On the scale of individual movements, we considered maximum slope to be the most appropriate measure of topographic roughness encountered by an individual cougar. To calculate the maximum slope encountered (used) by an individual during a movement segment, we generated 100 alternative segments (of length equal to the original and terminating at a randomly located point within 50 m of the start and end point of the original) within a movement segment buffer and intersected these alternative segments with the DEM to derive an average value of maximum slope. We assumed that the maximum slope available to an individual was the average maximum slope value for the 35 alternative segments intersected with the DEM. We used a paired $t$-test to assess topographic selection for slope during all movement sessions for all individuals ($\alpha < 0.05$). For each individual monitored for >1 session, we calculated the mean

maximum slope encountered during each session and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

### Roads

We obtained 1995 U.S. Bureau of the Census Topologically Integrated Geographic Encoding and Referencing (TIGER) digital data coverages for all roads on the 3 counties. We modified these maps based on paper maps on which field crews had indicated accurate road location and condition (paved, dirt, absent) of mapped roads. To assess whether roads affected cougar movements, we calculated total paved and dirt road densities ($m/km^2$) for all buffered movement (used) and alternative (available) paths. For each session, we calculated road densities at each used and available segment. To determine available densities, we averaged across the 35 alternative segments. We used a paired *t*-test to determine whether mean road densities for each session differed ($\alpha < 0.05$) between movements and alternative paths.

We analyzed road crossings by comparing the minimum number of crossings of 2-lane paved roads during a diel session to the number of crossings that would have occurred if the focal animal were indifferent to paved roads. We excluded freeway crossings from our analyses because 5 years of study documented only a single non-fatal freeway crossing (except via underpasses). To avoid having simulated paths cross paved driveways and residential roads, we restricted all simulations to a study area that was clipped to exclude residential areas within or abutting potential cougar habitat.

We inferred a single crossing for any movement segment that crossed a paved road. To estimate the expected number of crossings, we constructed a simple individual-based movement model, and we generated 50 simulated paths for each session, each with the same number of movement segments as the actual travel path. Each simulation started using the initial bearing of the actual movement path, giving each simulation a tendency to move in the direction that the focal animal moved. Each subsequent movement segment in the simulations used a circular deviation angle and displacement selected at random, with replacement, from the observed distributions (Fig. 2). If a simulated travel path encountered a study area boundary or residential area, we forced the contacting segment to reflect back into the study area at a random deviation angle. We used a paired *t*-test to determine whether the mean number of actual road crossings was less ($\alpha < 0.05$) than expected. For individuals monitored for >1 session, we calculated a mean for each session and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

To examine whether cougars might exploit road crossing structures, such as underpasses or culverts, to trap prey, we examined the locations of all 5,562 daybed locations, 855 nocturnal static locations, and 145 cougar-killed prey carcasses in this study area during 1986–1992 (Beier and Barrett 1993, Beier 1995, Beier et al. 1995, Dickson and Beier 2002). We tallied the number of locations by type (daybed, static, carcass) that occurred within 300 m of a crossing structure under major roads (>2 lanes in each direction).

## RESULTS

We analyzed 44 tracking sessions (29 nocturnal, 15 diel), including 22 sessions on 10 female cougars and 22 sessions on 7 male cougars (Table 1). Although most cougars were monitored for 3 or more sessions, 5 individuals were monitored for only 1 nocturnal or diel session. The behavior of these 5 animals was thus measured with relatively low precision. Imprecision in measurements decreases the power of statistical tests but does not increase risk of type I error (because these errors are subsumed in the residual sum of squares). Such risk is even lower for compositional analysis, which forced us to drop some of these animals from analyses when, for example, the individual did not use all vegetation types.

### Movement Statistics

Total number of movement segments ≥50 m and static locations was 1,647 and 356, respectively. Following Beier et al. (1995) we assume that cougars were hunting during these sessions and that many static locations represented sites where cougars slowly stalked and attempted to ambush prey. Other static locations probably represented rest sites.

The mean number of movement segments per session was 36.4 (SD = 6.3) for females and 37.7 (SD = 7.7) for males. On average, tracking sessions lasted 19.9 hrs (SD = 5.1) for females and 17.3 hrs (SD = 1.9) for males. Total duration of movements during a session averaged 9.1 hrs (SD = 1.6) for females and 9.4 hrs (SD = 1.9) for males. During a session, female cougars traveled an average of 10.7 km (SD = 4.5) and males traveled 10.0

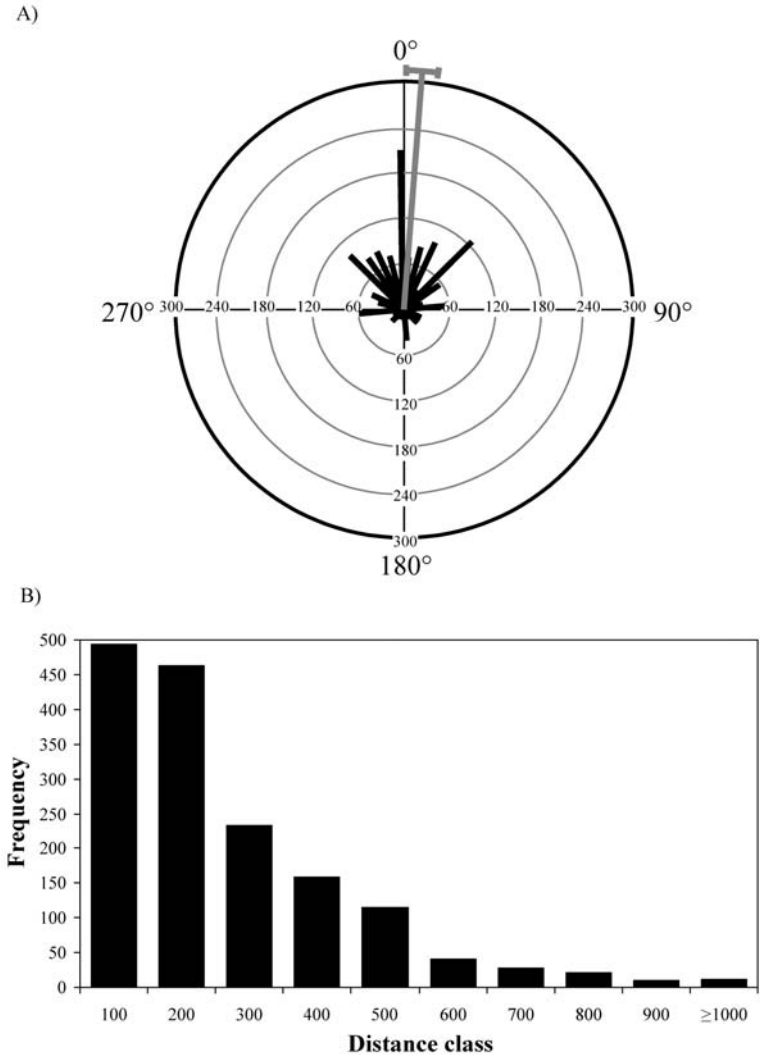


Fig. 2. (A) Frequency distribution of circular deviation angles for movements ≥100 m ($n$ = 1,536) for 10 female and 7 male cougars during 44 radiotracking sessions in southern California, USA, 1988–1992. An angle of 0° indicates an animal did not deviate from a straight line. Mean deviation angle and +/– 95% confidence intervals are shown. (B) Frequency distribution of distance moved per 15 min; abscissa is lower bound of each 100-m distance class ($n$ = 1,572).

km (SD = 3.0). Average time in static positions during a session was 10.8 hrs (SD = 5.1) for females and 7.9 hrs (SD = 3.5) for males, excluding the static intervals (of unknown duration) that occurred at the start and end of each session.

Movement segments between 50 and 100 m probably approached the resolution of triangulation. Because these short segments comprised only 0.4% of all movement segments, including these segments introduces little if any error to our analyses.

For 1,536 movement segments ≥100 m, cougars tended to move in a straight-line; the mean circular angle of deviation was 4.4° +/– 3.8 (95%CI; Fig. 2A), and the circular distribution of deviation angles was not uniform ($U$ = 351.8, $P$ < 0.001). During consecutive 15-min movement intervals, cougars often turned to the right or left; the average deviation angle during a session was 52.8° (SD = 47.8, $n$ = 1,536). Distance traveled per 15 min (Fig. 2B) averaged 288 m (SD = 192, range = 100 – 2,059 m, $n$ = 1,572), with 61% of movements <300 m. The distance moved was not correlated with turning angle ($nr^2_{al}$ = 4.13, $r$ = 0.34, $P$ > 0.10, $n$ = 36 angle classes of 10° each).

## Influence of Vegetation Type

The habitat composition of travel paths used by cougars differed from the habitat composition of alternative segments ($-N\ln\Lambda$ = 15.00, $P$ < 0.025, df = 5, $n$ = 9 females and 7 males; Fig. 3). Because forested, agricultural, and disturbed vegetation types were not available to some individuals, these types were dropped from all compositional analyses. Although riparian types ranked highest in the compositional analysis of habitat use during movements, use was statistically significant only in contrast with urbanized types. Chaparral and scrub types also were ranked above urbanized types. However, other contrasts were more ambiguous and difficult to interpret.

During intervals of stasis, cougar use of vegetation types was not statistically different from the habitat composition through which they traveled

during movement intervals ($-N\ln\Lambda = 4.76$, $P > 0.25$, df = 4, $n = 8$ females and 7 males with ≥7 static locations). Urbanized vegetation types were available to only a few individuals and were excluded from this analysis. Although neither the omnibus test nor pairwise contrasts were significant ($P > 0.05$), chaparral (10%) and riparian vegetation types (27%) ranked higher than scrub, grassland, and woodland types during periods of stasis, and they were used as stopping points more often than they were encountered on travel paths.

Cougars moved slowest through riparian vegetation (grand mean = 1.07 km/hr), which was the type ranked highest in the compositional analysis of movements and fastest through urbanized types (1.49 km/hr), the lowest ranking type (Table 1; Fig. 4A). In all vegetation types, females moved faster than males ($t = 5.52$, $P < 0.001$, $n = 9$). There was a significant negative correlation between ranks for travel speed and selection for a vegetation type ($r_s = -0.89$, $P < 0.05$, $n = 6$; Fig. 4B).

## Influence of Topography

During monitored intervals of movement, all cougars used maximum slopes that were more gentle than those available ($t = 7.38$, $P < 0.001$, $n = 17$). For indi-

Table 1. Mean travel speeds in 9 vegetation types for 10 female and 7 male cougars in the Santa Ana Mountain Range, California, USA, 1988–1992. "—" indicates vegetation type was not encountered on travel path.

| Animal ID | Total no. of sessions monitored | Total no. of movement segments | Travel speed (km/hr) | | | | | | | | Mean travel speed (+/– 1SD) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Scrub | Chaparral | Grassland | Riparian | Woodland | Forest | Agriculture | Urbanized | Disturbed | |
| F1 | 4 | 164 | 1.17 | 1.33 | 1.30 | 1.22 | 1.29 | 2.42 | 1.30 | 1.43 | 1.85 | 1.48 (0.41) |
| F2 | 4 | 142 | 1.22 | 1.06 | 1.42 | 1.11 | 1.30 | — | 1.19 | 1.23 | 1.29 | 1.23 (0.12) |
| F3 | 4 | 146 | 1.05 | 1.04 | 0.98 | 0.92 | 1.04 | 1.10 | — | 3.50 | 1.60 | 1.40 (0.87) |
| F4 | 2 | 68 | 0.84 | 0.87 | 0.79 | 0.77 | 0.48 | 0.90 | — | 0.60 | 0.74 | 0.75 (0.14) |
| F8 | 1 | 34 | 1.23 | 0.98 | 1.86 | 0.72 | 2.58 | 2.01 | — | — | — | 1.56 (0.70) |
| F10 | 1 | 28 | 0.78 | 0.99 | — | 0.98 | 1.03 | — | 0.63 | 1.16 | — | 0.93 (0.19) |
| F11 | 1 | 27 | 1.55 | 0.71 | 1.33 | 1.38 | 0.83 | — | — | — | — | 1.16 (0.37) |
| F17 | 2 | 87 | 1.05 | 0.98 | 1.02 | 1.10 | 1.09 | 1.16 | 1.74 | 1.05 | 1.09 | 1.14 (0.23) |
| F18 | 1 | 47 | 1.47 | 1.67 | 2.04 | 1.19 | 2.12 | — | 1.67 | 1.79 | — | 1.71 (0.32) |
| F19 | 2 | 74 | 1.54 | 1.64 | 1.28 | 1.50 | 1.48 | 1.03 | — | 1.40 | — | 1.41 (0.20) |
| Female mean (+/- 1SD) | 2 | 82 | 1.19 (0.27) | 1.13 (0.32) | 1.34 (0.40) | 1.09 (0.25) | 1.32 (0.62) | 1.44 (0.63) | 1.31 (0.45) | 1.52 (0.87) | 1.32 (0.43) | 1.29 (0.14) |
| M2 | 5 | 154 | 1.29 | 1.45 | 1.25 | 1.14 | 1.20 | 2.54 | 2.13 | 1.83 | 1.44 | 1.59 (0.48) |
| M5 | 1 | 26 | 0.81 | 0.73 | 1.12 | 1.13 | 0.83 | — | — | — | 0.97 | 0.93 (0.17) |
| M6 | 3 | 126 | 0.87 | 0.96 | 1.09 | 1.02 | 0.79 | — | 0.80 | 1.34 | 0.75 | 0.95 (0.20) |
| M9 | 2 | 97 | 1.33 | 1.22 | 1.25 | 1.17 | 1.54 | 1.02 | — | 1.56 | 2.22 | 1.41 (0.37) |
| M10 | 4 | 140 | 0.77 | 0.90 | 0.79 | 0.64 | 0.44 | 0.44 | 0.50 | 0.58 | 0.40 | 0.61 (0.18) |
| M12 | 3 | 116 | 1.05 | 1.01 | 1.42 | 1.21 | 1.09 | 0.85 | 0.56 | 0.85 | 0.99 | 1.00 (0.24) |
| M13 | 4 | 171 | 0.96 | 0.94 | 0.99 | 1.01 | 1.18 | 1.17 | — | 2.47 | 1.28 | 1.25 (0.51) |
| Male mean (+/- 1SD) | 3 | 119 | 1.01 (0.22) | 1.03 (0.24) | 1.13 (0.20) | 1.04 (0.19) | 1.01 (0.36) | 1.20 (0.79) | 1.00 (0.77) | 1.44 (0.68) | 1.15 (0.58) | 1.11 (0.14) |
| Grand mean (+/- 1SD) | 3 | 97 | 1.11 (0.26) | 1.09 (0.28) | 1.25 (0.45) | 1.07 (0.22) | 1.19 (0.53) | 1.33 (0.68) | 1.17 (0.59) | 1.49 (0.77) | 1.22 (0.51) | 1.21 (0.31) |

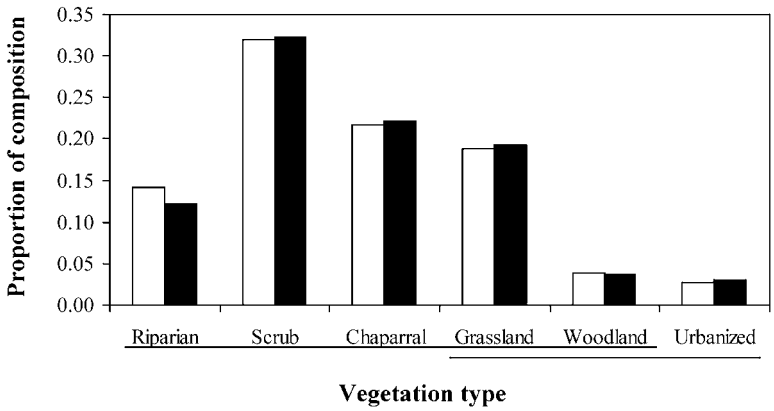


Fig. 3. Cougars ($n$ = 9 females, 7 males) in the Santa Ana Mountain Range, California, USA, 1988–1992, tended to avoid human-dominated vegetation types and areas lacking understory woody plants during 15-min intervals when the animal moved ≥50 m. White bars indicate mean proportional utilization and black bars indicate mean proportional availability. Vegetation types are arranged from highest to lowest rank; underlining under names of vegetation types on the $x$-axis indicates vegetation types for which rankings are not significantly ($P > 0.05$) different.

vidual cougars, the mean available maximum slopes exceeded the used slopes by 0.71° to 3.54° (mean difference = 1.49°, SD = 0.81).

### Influence of Roads

Total paved road density was about 21% lower on cougar travel paths (4.20 m/km$^2$, $\bar{x}$ = 0.10 +/– 0.20 m/km$^2$ [SD]) compared to available paths (5.30 m/km$^2$, $\bar{x}$ = 0.12 +/– 0.22 m/km$^2$; $t$ = –2.16, $P$ = 0.04, $n$ = 44). Density of dirt roads was slightly higher on paths used by cougars (62.50 m/km$^2$, $\bar{x}$ = 1.42 +/– 1.04 m/km$^2$) compared to available paths (59.17 m/km$^2$, $\bar{x}$ = 1.34 +/– 0.78 m/km$^2$; $t$ = 1.48, $P$ = 0.15, $n$ = 44). Buffered movement segments intersected dirt roads in all but 2 sessions, during which no dirt roads were available. All tracked individuals encountered or used dirt roads (368 occasions during 41 sessions).

Focal animals crossed 2-lane paved roads a total of 19 times; crossings involved 9 individual cougars and occurred during 11 of the 44 sessions, with a mean of 0.45 crossings per cougar per session (SD = 0.67, $n$ = 17 individuals). In contrast, simulated paths had a mean of 1.29 crossings per cougar per session (SD = 1.37), a difference that was statistically significant ($t$ = –2.50, $P$ = 0.012). The simulated travel paths of all individuals crossed paved roads. Only 3 individuals (F2, F10, M10) crossed paved roads more often (1 crossing each) than expected (0.37, 0.12, 0.87, respectively), based on simulated paths.

Three of 5,562 daybed locations, 0 of 855 nocturnal static locations, 0 of 85 deer killed by cougars, and 2 of 60 small mammal kills (opossum, raccoon in these cases) were within 300 m of a crossing structure under a major highway. All 5 of these locations reflected the activities of a single female (F2) during the last days before her death, when she was apparently keying in on garbage-eating animals near a housing development, not on animals using the crossing structure. These numbers are lower than the 42 documented crossings via such structures (Beier and Barrett 1993, Beier 1995). Because we required cougar tracks or unambiguous radio signals to confirm a crossing, these 42 crossings underestimate the true frequency of these events.

## DISCUSSION

Based on our observations, traveling cougars tended to continue moving in a consistent direction but often turned ~54° right or left, with few retrograde movements; movements averaged 288 m per 15-min interval and were not correlated with turning angle (Fig. 2). Our analysis of frequency of road crossings illustrates how these data can generate a null (random walk) model for hypothesis testing. These distributional data also can form the basis of more-sophisticated individually based movement models. Our results suggest that these advanced cougar movement models should reflect an aversion to paved roads and human-modified vegetation types, little differentiation among natural vegetation types, no aversion to dirt roads, and selection for gentle grades.

Our results support the assertion (Doak et al. 1992, Andren 1994, Dickson and Beier 2002) that habitat pattern has multi-scale impacts on the movement and distribution of animals. On the SAMR, Dickson and Beier (2002) identified strong patterns of selection by adult cougars for riparian areas at 2 spatial scales (based mostly on 1 static, diurnal location per animal per day). During the movement periods we analyzed here, riparian vegetation again ranked first, but several other natural vegetation types were statistically as

preferred as riparian vegetation. Additionally, grasslands ranked below riparian, scrub, and chaparral vegetation types for cougar movements, but not with the statistical significance Dickson and Beier (2002) observed for diurnal locations. Thus, traveling cougars monitored over nocturnal or diel periods used a broader range of habitats than used for diurnal locations alone (typically daybed sites; Beier et al. 1995). Our findings support the argument of Comiskey et al. (2002) that analysis of diurnal locations provides limited information about cougar patterns of selection during the times they are most active. We conclude that habitat use of cougars (and other nocturnal carnivores) estimated solely by analysis of diurnal locations may not accurately reflect habitat preferences of hunting and traveling animals. Movement studies of nocturnal carnivores should include data collected during those periods when the animal is most active.

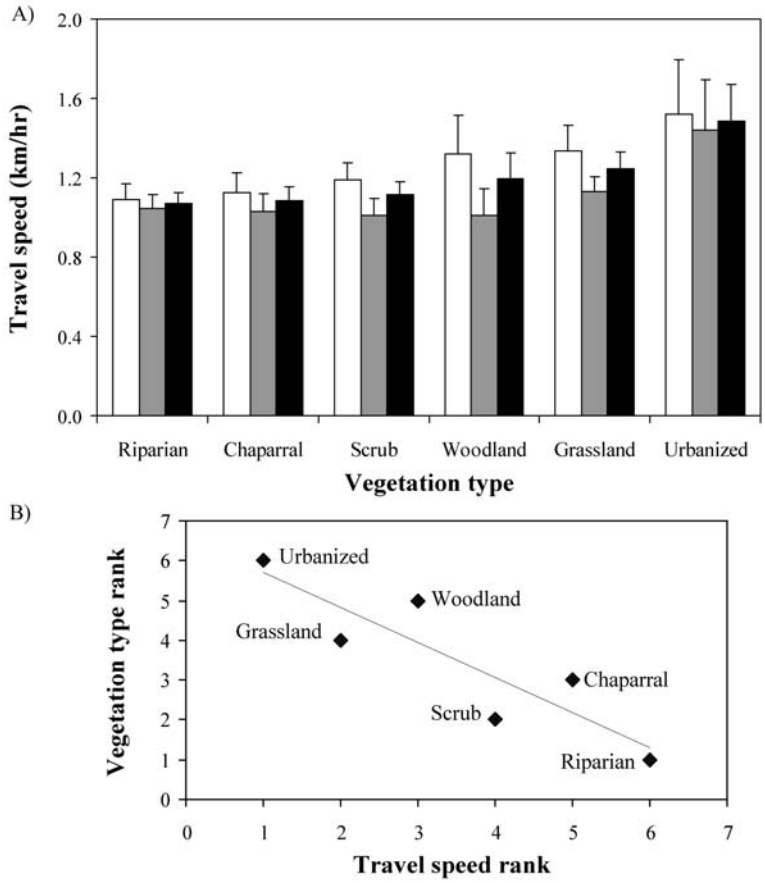


Fig. 4. Cougars in the Santa Ana Mountain Range tended to move more slowly through highly ranked vegetation types and more quickly through human-dominated types. (A) White bars indicate mean travel speed for females, gray bars indicate mean speed for males, and black bars indicate mean speed for the sexes combined. Error bars indicate +1 SE. Vegetation types are arranged from slowest to fastest based on the mean travel speed for the sexes combined. (B) The correlation between ranks for travel speed and vegetation type was statistically significant ($P < 0.05$).

Although previous research using diurnal locations suggested that cougars avoided grasslands due to lack of cover (Logan and Irwin 1985, Laing 1988, Williams et al. 1995, Dickson and Beier 2002), grasslands may play a more important role during cougar movement. Grassland vegetation constituted 19% of the composition of used movement segments. Perhaps grasslands provide cougars with the means to more readily permeate areas already known to them or to stalk and pursue prey. Grassland vegetation types were also a common (19%) characteristic of habitat mosaics used during intervals of stasis, which in some cases probably represented stalking or attempts to ambush prey (Beier et al. 1995).

If animals tend to move more rapidly through environments that make them uncomfortable or that offer few resources, our results on travel speed through various vegetation types is consistent with the rankings based on compositional analysis. An analysis of habitat selection based on travel speed, unlike other analyses of habitat use, does not require an estimate of habitat availability. Estimating habitat availability invariably requires making arbitrary assumptions. For instance, we made the reasonable assumption that habitat availability could be estimated by the average habitat composition in 35 buffered vectors with length equal to the average distance moved during a session. It would have been equally reasonable to estimate availability by buffered vectors with length equal to the actual distance moved in

a particular interval, or the average for all study animals. Our diligent search of the literature suggests that our study is the first attempt to make inferences about habitat use from travel speed for any terrestrial vertebrate, and we believe travel speed may offer an efficient tool for study of habitat selection patterns.

We found travel speed to be a useful complement to compositional analysis and other traditional methods of analyzing habitat selection. However, our single illustration of the method does not constitute a full exploration of its strengths and weaknesses. One important limitation of the travel speed method is that it cannot assess habitats the animal does not use at all. Similarly, travel speed cannot be used to assess animal response to fine-scale features such as paved roads.

Cougars consistently used travel paths that were less rugged than their general surroundings. This suggests that individuals consider the energetic cost of alternative paths and that they probably have a mental map of their surroundings. This is consistent with Beier's (1995) description of canyon bottoms and ridgelines as common travel routes for dispersing cougars. Hunting or traveling individuals minimize energetic expense by frequenting landscape features that cost the least.

The effectiveness of habitats to support cougars is reduced by human disturbance, particularly roads (Murphy et al. 1999). Our results indicate that 2-lane paved roads constrain cougar movement significantly but do not prevent movement. Indeed, vehicle collisions are the leading cause of mortality in this population, comprising 32% of all deaths of radiotagged cougars and their offspring (Beier and Barrett 1993). The problem is exacerbated by the placement of paved roads in preferred riparian habitats on the SAMR (Dickson and Beier 2002). Underpasses and other structures can facilitate cougar movements across paved roads (Beier 1993, Beier 1995, Foster and Humphrey 1995, Gloyne and Clevenger 2001), and we encourage efforts to construct or enhance crossing structures in preferred habitats.

Our data suggest that such structures are not exploited by predators in a way that creates a prey trap, supporting the conclusion of a recent review (Little et al. 2002). However, most crossings on our study area occurred where major roads crossed narrow, degraded habitat corridors, where cougars and their prey may not wish to linger. Cougars may behave differently where such crossing structures occur along roads passing through large blocks of intact habitat.

All individuals tracked during this study encountered or used dirt roads, and dirt road density was 8% higher on cougar travel paths than on available travel segments, suggesting that dirt roads do not inhibit, and may even promote, cougar movement. Back-tracking with hounds after our monitoring sessions confirmed that individuals frequently used dirt roads or trails to travel up to 2 km, especially in areas of dense scrub or chaparral (Beier 1995). In northern Florida, translocated cougars tended to cross light duty roads and trails in favor of all other road types (Belden and Hagedorn 1993). On study areas in northern Arizona and southern Utah, Van Dyke et al. (1986) reported that most cougars crossed most of the unimproved dirt roads within their home ranges. In addition to providing a path through dense scrub, dirt roads and trails may facilitate predator access to prey (James and Stuart-Smith 2000, Kinley and Apps 2001, Kerley et al. 2002). We believe that retaining or creating a dirt road or trail along the midline of a planned movement corridor would facilitate its use by cougars and minimize straying into adjacent human-dominated landscapes.

## MANAGEMENT IMPLICATIONS

Our results suggest that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in movement corridors, that dirt roads should not impede cougar use of corridors, that corridors should lie along routes with relatively gentle topography, and that cougars do not use road crossing structures to create prey traps. Managers and land-use planners are using these findings to design corridors to facilitate cougar movement in the South Coast ecoregion of California (Beier et al. 2005).

Because cougars will become extinct in even the largest core areas of this ecoregion if connectivity is severed (Beier 1996), cougars are an appropriate focal species for corridor design. However, because a corridor that serves cougars will not serve all species, we urge planners to consider a broad suite of focal species in designing landscape linkages (Beier et al. 2005).

Our frequency distributions of movement lengths and turning angles, in conjunction with the habitat preferences documented herein, are also being used to construct sophisticated individual-based movement models (in collaboration with J. Tracey and K. Crooks, Colorado State University). We hope these approaches can help quantify the influence of landscape features on

other, large carnivores used as umbrella species for conservation planning.

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# CONSERVATION THRESHOLDS FOR LAND USE PLANNERS

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*Encroachment, Gnatcatcher Habitat*
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# INTRODUCTION

While there are many threats to biological diversity in the United States, the loss and fragmentation of habitats and ecosystems have become the most significant (Wilcove et al. 1998). The survival of plant and animal species and whether our natural systems will continue to provide essential services—recycling of nutrients, flood and pest control, and maintenance of clean air, water, and soil—significantly depends upon where and how land is used, converted, and managed. Land use change resulting from development and associated human activities (e.g., agriculture, grazing, forest harvesting, and hunting) often alters the abundances and varieties of native species; introduces novel and potentially detrimental species to an area; and disrupts natural water and nutrient cycles, and natural disturbance patterns (e.g., fire) (U.S. Geological Survey 1998).

> *"Spatial planning is most significant in nature conservation when 10-40% of the natural vegetation has been removed from a landscape."*
>
> Forman and Collinge (1997), Landscape and Urban Planning 37, p. 129

Everyday, land use planners are faced with decisions regarding whether and how land is developed, parcelized, and used, and in what pattern. For the most part, such land use decisionmaking occurs without taking into account individual and cumulative impacts to biological resources. Implementing biologically sensitive spatial planning early in the development process will help preserve our natural heritage for the future, since the most crucial time for planning is when the first 10 to 40 percent of the natural vegetation is altered or removed from the landscape (Forman and Collinge 1997). A growing interest exists among land use planners and developers to use the tools at their disposal to better protect biological diversity. However, these professionals often lack the necessary information to incorporate ecological principles into their decisionmaking and to transform their traditional planning approaches into progressive, ecologically-based conservation tools.

To encourage and facilitate better integration of ecological knowledge into land use and land management decisionmaking, the scientific community needs to provide planners with applicable ecological information and guidance. To this end, the Ecological Society of America (ESA) convened a committee of leading scientists to identify principles of ecological science relevant to land use and to develop guidelines for land use decisionmaking.[1] The result was the development of eight general guidelines to assist land use planners in evaluating the ecological consequences of their decisions (*see* Box 1).

Conservation guidelines, such as those established by the ESA Land Use Committee, are designed to be flexible and to apply to diverse land use situations. As a result, they tend to be general in nature. For ecological principles to be put into practice, however, land use planners will need more specific information on potential threshold responses of species and ecosystems to development activities, particularly in relation to habitat fragmentation. To facilitate the adequate preservation of contiguous or connected natural areas, land use planners will need to know what science tells them about the minimum sizes of habitat patches species need to survive, or the amount of habitat necessary for the long-term persistence of native populations and communities in a region. In addition, they need information about the adequate size and placement of habitat corridors that would facilitate species movement and colonization among disjunct habitat patches, and about recommended widths of riparian buffers to protect water quality and provide wildlife habitat. Similarly, knowing the extent to which edges influence natural habitats would help land use professionals evaluate the effective area of any given habitat patch or corridor. Other fragmentation thresholds—such as the maximum distance between isolated patches tolerable in a landscape before ecological processes and patterns become disrupted—would arm decisionmakers with specific parameters that could be incorporated into land use design and modeling.

[1] "The Ecological Society of America (ESA) is a non-partisan, nonprofit organization of scientists founded in 1915 to: promote ecological science by improving communication among ecologists; raise the public's level of awareness of the importance of ecological science; increase the resources available for the conduct of ecological science; and ensure the appropriate use of ecological science in environmental decision making by enhancing communication between the ecological community and policy-makers."
*As cited in* Ecological Society of America. "About ESA." <www.esa.org> (31 July 2002).

Given the inherent complexity of ecological systems, scientists are understandably reticent about providing exact prescriptions for land use planning and design because answers vary depending on the species, ecosystem, or scale in question. Nevertheless, by not promoting the use of even partial knowledge about species or ecosystem responses to human disturbance and fragmentation, the result is that land use decisions—even the most well-intentioned—are being made completely uninformed by science.

**BOX 1. GUIDELINES FOR LAND USE PLANNING AND MANAGEMENT**

In the face of rapid land use change, the Ecological Society of America's Land Use Committee recommends that land use planners and developers take into consideration the following eight guidelines to evaluate the potential impact of their decisions on our natural systems (*see* Dale et al. 2000 for full discussion):

**1. Examine the impacts of local decisions in a regional context.**

The persistence of species and the sustainability of ecosystems are determined not only by immediate surroundings but also by larger landscape factors, such as how habitats are interspersed across the landscape. Thus, local land alterations may have broad-scale regional impacts. Land use planners should both identify the surrounding region that is likely to affect and be affected by a local project and examine how adjoining jurisdictions are using and managing their lands. Regional environmental data (e.g., land cover classes, hydrologic patterns, and habitats for species of concern) should be incorporated into the decision-making process to facilitate a regional assessment of impacts.

**2. Plan for long-term change and unexpected events.**

Ecological processes, such as nutrient cycling, energy flow patterns, and disturbance regimes, may function over lengthy and variable time scales. In addition, ecosystems change over time. As a result, impacts posed by land use decisions are often long-term and unpredictable. Impacts may be delayed and not fully realized until years or decades later, or they may be cumulative such that a "unique trajectory of events" results that could not have been predicted from any single event. The complexity and variability of ecosystem responses dictate that land use decisions consider potential occurrences and implications of unanticipated and long-term events (e.g., variations in weather and disturbance patterns).

**3. Preserve rare landscape elements and associated species.**

Rare landscape elements, such as wetlands, riparian and mountain zones, and old-growth forests, often provide critical habitats for rare and endangered species. To protect a region's biological diversity, the natural diversity within a landscape must be preserved. Land use planners should identify the location of rare and unique landscape elements, by methods such as inventory and analysis of vegetation types, geology, hydrology, and physical features, and by their associated species. Once such landscape elements are identified, development should be guided away from such areas and toward more common landscape features.

**4. Avoid land uses that deplete natural resources over a broad area.**

Depletion of natural resources over time will lead to the irreversible disruption of ecosystems and associated processes. Consequently, land use planning and development should strive to prevent the diminishment of natural resources (e.g., soil, water, and habitat types such as wetlands) in any given area by identifying vital or at-risk resources and by taking the necessary precautions to avoid actions that threaten resource sustainability. Certain land uses or land activities may be deemed altogether incompatible in particular settings.

**5. Retain large contiguous or connected areas that contain critical habitats.**

Large habitat patches typically support a greater diversity and abundance of plants and animals and can maintain more ecosystem processes than small patches. Large intact habitats provide more resources, allowing larger populations of a species to persist, thus, increasing the chance of survival over time. Parcelization of large habitats often decreases the connectivity of systems, negatively affecting the movement of species necessary for fulfilling nutritional or reproductive requirements. To counter such effects, large intact areas and small areas that are well connected to other critical habitats should be protected.

**6. Minimize the introduction and spread of non-native species.**

Non-native species often negatively affect the survival of native species and disrupt the functioning of ecosystems. The spread of non-natives is facilitated by the development of transportation infrastructure and by the creation of edge environments and artificial landscapes. Land use professionals should strive to minimize the potential introduction and spread of non-native species into natural environments.

**7. Avoid or compensate for effects of development on ecological processes.**

Development may not only cause site-specific impacts, but may also disturb regional ecological processes. Ecological processes, such as fire, grazing, dispersal patterns, and hydrologic cycles, help to sustain plant and animal populations across a landscape. Thus, land uses that could negatively affect other systems or lands through the disruption of these processes should be avoided while those that benefit or enhance ecological attributes should be encouraged.

**8. Implement land use and land management practices that are compatible with the natural potential of the area.**

The natural potential of a site, as determined in part by local physical and biologic conditions, should be factored into how land is used and managed. Land uses that do not take advantage of a site's natural potential or consider its limitations, will likely result in unnecessary resource loss and high economic costs.

For more information on ecological principles to guide land use planning decisionmaking, see Dale et al. (2000), Duerksen et al. (1997), and Dramstad et al. (1996).

# FROM GUIDELINES TO THRESHOLDS

The Environmental Law Institute (ELI) surveyed existing scientific literature to determine whether a body of knowledge has emerged within the scientific community relevant and applicable to national land use decisionmaking, specifically pertaining to biological conservation thresholds. A literature search of the major ecological, conservation, and land use journals was conducted using the Science Citation Index (ISI Web of Science) using search terms under the following categories: habitat fragmentation,[2] buffers,[3] corridors,[4] ecological thresholds,[5] and indicator species.[6] To increase applicability to current land use decisionmaking in the states, the search was confined to studies pertaining to the continental United States, as well as articles published between 1990-2001, and pre-1990 articles commonly cited within the scientific community. Only those articles containing quantitative information directly relevant to determining conservation thresholds for land use planning and land management were considered.[7] In addition to the literature search, review papers found in the gray literature (e.g., those produced by land management and regulatory agencies) were also included when possible and applicable.

ELI found adequate information on potential ecological threshold measures for the following areas: habitat patch area, percent of suitable habitat, edge effects, and buffers. Corridor design is reviewed in brief; however, specific guidance on corridor size was not feasible given inadequate available information within the scientific literature. This survey reflects scientific information largely related to habitat fragmentation and landscape ecology issues, with a focus on the spatial relationships (e.g., size, shape, location) and interactions of land attributes over large geographic areas.[8] This review does not cover other important conservation elements such as how to account for the biological integrity or ecological significance of habitat patches, which land use planners should consider when determining which parcels of land to protect. In addition, the thresholds presented in this review does not adequately address the conservation of species or habitat types that are naturally rare or localized (e.g., those with patchy distributions or limited ranges).

This report summarizes the Institute's findings and provides a platform for identifying gaps in existing knowledge to help guide more in-depth ecological research directly applicable to land use planning. This report in no way attempts to misrepresent the complexity of species and ecosystem response to land conversion, degradation, and fragmentation by providing simplified prescriptions. Land use planners should cautiously interpret the presented threshold values and ranges and tailor them to their unique circumstances and geographic settings.

First and foremost, land use planners need to establish their priorities for conservation—whether they be water quality or quantity, wildlife habitat, or biodiversity. In addition, conservation targets need to be established—whether they be regionally rare or endangered species or unique landscape elements (e.g., wetlands, old growth forests, riparian zones), or other targets—because this will directly influence the value and scale of any threshold.[9] Thresholds should be chosen or developed to meet the needs of the resources a locality is most concerned with managing and conserving. Planners should place great emphasis on evaluating site-specific and regional physical and biological conditions that influence the resiliency of particular systems to human disturbance.

The threshold values presented in this report should not detract from the larger goals of conserving or restoring indigenous species, rare and representative habitats, ecosystem functions, and natural connectivity. Where possible, the ESA land use guidelines should be followed. Land use planners should strive to protect large, intact parcels of land, high quality and ecologically important habitat, and where appropriate, should connect protected natural areas. When development is deemed necessary, land use planners should promote more compatible land uses and avoid or minimize fragmenting habitat patches wherever possible.

---

[2] To locate papers with potential habitat fragmentation threshold information, the following search terms were used: minimum habitat size, habitat size, habitat requirement, habitat fragmentation, patch size, minimum fragment size, island biogeography, landscape connectivity, habitat connectivity, and metapopulation theory.

[3] To locate papers with potential threshold information on buffer width, the following search terms were used: riparian buffer, wetland buffer, buffer zone, buffer distance, forest buffer, buffer width, and buffer size.

[4] To locate papers with potential threshold information on corridor width, the following search terms were used: fragment connectivity, boundary permeability, landbridge, highway overpass, highway underpass, stream cross, habitat corridor, corridor, migration corridor, riparian corridor, and underpass.

[5] To locate papers with potential ecological threshold information, the following search terms were used: ecological threshold, conservation threshold, environmental threshold, and landscape threshold.

[6] To locate papers with potential threshold information relevant to indicator species, the following search terms were used: indicator species, indicator species and habitat fragmentation, and indicator species and thresholds.

[7] The majority of the papers encountered and selected focus on terrestrial species and to a lesser extent freshwater aquatic communities.

[8] As defined by Risser et al. (1984), "Landscape ecology considers the development and dynamics of spatial heterogeneity, spatial and temporal interactions and exchanges across heterogeneous landscapes, influences of spatial heterogeneity on biotic and abiotic processes, and management of spatial heterogeneity."

[9] Thresholds presented in this report reflect a taxonomic bias in the scientific literature toward birds and mammals. Thus, for many of the recommended threshold values, these two animal groups are assumed to be the conservation targets.

## BOX 2. DEFINITION OF TERMS

**Biological diversity (or biodiversity)** – the variety of life and its processes, which includes the abundances of living organisms, their genetic diversity, and the communities and ecosystems in which they occur (The Keystone Center 1991). Diversity at all levels from genes to ecosystems need to be maintained to preserve species diversity and essential ecosystem services like climate regulation, nutrient cycling, water production, and flood/storm protection (Dale et al. 2000).

**Biological (or ecological) integrity** – refers to a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates, that is able to maintain itself through time (Angermeier and Karr 1994).

**Boundary** – a zone comprised of the edges of adjacent ecosystems or land types (Forman 1995).

**Corridor** – a linear strip of a habitat that differs from the adjacent land on both sides, connecting otherwise isolated larger remnant habitat patches (Forman 1995, Fischer et al. 2000).

**Buffers** – linear bands of permanent vegetation, preferably consisting of native and locally adapted species, located between aquatic resources and adjacent areas subject to human alteration (Castelle et al. 1994, Fischer and Fischenich 2000).

**Ecosystem** – a geographic area including all the living organisms (e.g., people, plants, animals, and microorganisms), their physical surroundings (e.g., soil, water, and air), and the natural cycles (nutrient and hydrologic cycles) that sustain them. Ecosystems can be small (e.g., single forest stand) or large (e.g., an entire watershed including hundreds of forest stands across many different ownerships) (USFWS 1994).

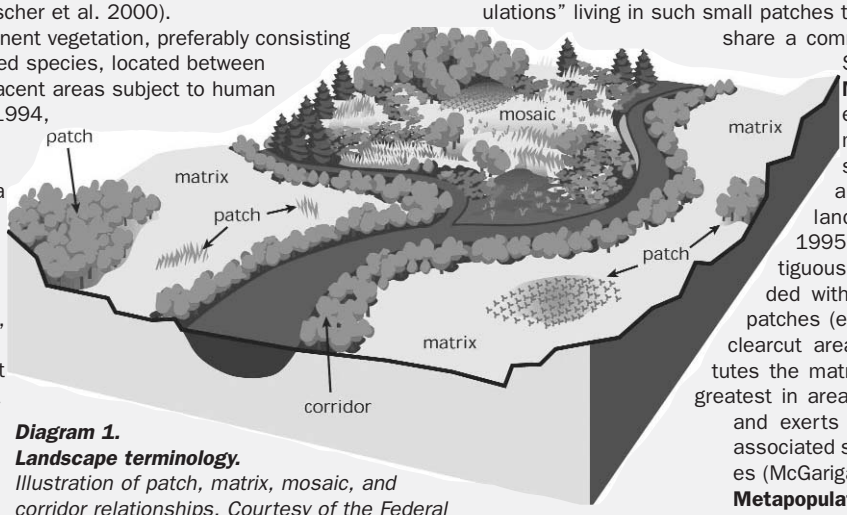


***Diagram 1. Landscape terminology.*** *Illustration of patch, matrix, mosaic, and corridor relationships. Courtesy of the Federal Interagency Stream Restoration Working Group (FISRWG), Stream Corridor Restoration: Principles, Processes, and Practices (10/98).*

**Ecosystem functions** – the biophysical processes that take place within an ecosystem, apart from any human context (e.g. nutrient, energy, and hydrologic cycling; or soil formation).

**Ecosystem services** – refer to the ecosystem goods (e.g., food, and medicine) and services (e.g., climate regulation, water purification, and flood control) that humans derive benefit, directly or indirectly, from ecosystem functions (Costanza et al. 1997).

**Ecosystem sustainability** – the tendency of a system to be maintained or preserved over time without loss of decline to elements such as its structure, function, diversity, and production. Sustainability is widely regarded as economically and ecologically desirable and the only viable long-term pattern of human land use (Dale et al. 2000).

**Edge** – the portion of an ecosystem or habitat near its perimeter, where influences of the surroundings prevent development of interior/core-area environmental conditions (Forman 1995).

**Edge effects** – the negative influence (e.g., such as the profound modifications of biological and physical conditions) of habitat or ecosystem edges on interior conditions of habitat or on associated species (Meffe and Carroll 1997, Lindenmayer and Franklin 2002).

**Habitat** – consists of the physical features (e.g., topography, geology, stream flow) and biological characteristics (e.g., vegetation cover and other species) needed to provide food, shelter, and reproductive needs of animal or plant species (Duerksen et al. 1997).

**Habitat fragmentation** – the breaking up of previously continuous habitat (or ecosystem) into spatially separated and smaller parcels. Habitat fragmentation results from human land use associated with forestry, agriculture, and settlement, but can also be caused by natural disturbances like wildfire, wind, or flooding. Suburban and rural development commonly change patterns of habitat fragmentation of natural forests, grasslands, wetlands, and coastal areas as a result of adding fences, roads, houses, landscaping, and other development activities (Dale et al. 2000).

**Landscape** – a large heterogeneous land area (e.g., multiple square miles or several thousand hectares) consisting of a cluster of interacting ecosystems repeated in similar form (e.g., watershed) (Forman 1995, Duerksen et al. 1997).

**Land use** – the purpose to which land is used by humans (e.g., protected areas, forestry for timber production, plantations, row-crop agriculture, pastures, or human settlement) (Dale et al. 2000).

**Local population** – set of individuals of a species that live in the same habitat patch and interact with each other; most naturally applied to "populations" living in such small patches that all individuals practically share a common environment (Hanski and Simberloff 1997).

**Matrix** – the background ecosystem or land use type in a mosaic, characterized by extensive cover, high connectivity, and/or major control over the landscape functioning (Forman 1995). For example, in a large contiguous area of mature forest embedded with numerous small disturbance patches (e.g., timber harvest patches or clearcut areas), the mature forest constitutes the matrix element type because it is greatest in areal extent, is mostly connected, and exerts a dominant influence on the associated species and ecological processes (McGarigal 2003).

**Metapopulation** – a network of semi-isolated populations with some level of regular or intermittent migration and gene flow among them, in which individual populations may be extinct but then be recolonized from other subpopulations (Meffe and Carroll 1997).

**Mosaic** – a pattern of patches, linear corridors, and matrix in a landscape (Forman 1995).

**Minimum viable population** - The minimum viable population size is the smallest number of individuals required to maintain a population over the long-term (Forman 1995).

**Non-native (or exotic) species** – organisms (plants, animals, insects, and microorganisms) that occur in locations beyond their known historical, natural ranges or have been brought in from other continents, regions, ecosystems, or habitats (National Invasive Species Council 2001).

**Patch** – a relatively homogeneous type of habitat that is spatially separated from other similar habitat and differs from its surroundings (Forman 1995).

**Remnant patch** – habitat patches that escape disturbance (e.g., development) and are left remaining from an earlier more extensive span of habitat (e.g., woodlots in an agricultural area) (Dramstad et al. 1996).

**Scale** – the relative size or degree of spatial resolution of an area of interest. Small areas of interest (e.g., area around a house of single subdivision) are considered to be fine scale; in contrast to a larger area (e.g., a county or watershed), which is considered to be of coarse scale (Forman 1995, Duerksen et al. 1997).

**Suitable habitat** – habitat that meets the survival and reproductive needs of a species, allowing for a stable or growing population over time (Lamberson et al. 1994).

# THRESHOLDS FOR LAND USE PLANNING: ADDRESSING HABITAT FRAGMENTATION

Habitat fragmentation severely threatens biodiversity and ecosystem functioning wherever humans dominate the landscape. Land use planners play a significant role in determining whether and how landscapes and ecosystems are fragmented or maintain natural connectivity.

*Varying shapes and configuation of habitat patches resulting from habitat fragmentation, Buchanan, Alabama. Courtesy of John R. Tolliver, USDA Forest Service, www.forestryimages.org.*

Habitat fragmentation is the process whereby contiguous natural areas are reduced in size and separated into discrete parcels. Fragmentation results from a reduction in the area of the original habitat due to land conversion for other uses, such as residential and commercial development. It also occurs when habitat is divided by roads, railroads, drainage ditches, dams, power lines, fences or other barriers that may prohibit the free movement and migration of plant and animal species (Primack 1993, Forman 1995). When habitat is destroyed, a patchwork of habitat fragments is left behind, often resulting in patches that are isolated from one another in a modified and inhospitable landscape matrix.[10] Fragmentation causes the microclimate to be altered due to changes in solar radiation, wind, and humidity; habitat patches become more isolated with a growing distance between remnant patches; and the resulting landscape is modified by changes in size and shape of the resulting patches (Saunders et al. 1991). These changes have varying impacts on species persistence and ecosystem sustainability.

Groups of organisms respond differently to habitat fragmentation. Some species, such as game species like white-tailed deer and bobwhite quail (referred to as edge species), may actually thrive under altered conditions (Bolger et al. 1997). However, many other species—often rare species and habitat specialists—are negatively affected. Species that depend upon the interior of forests, prairies, wetlands or other natural habitats will be absent from landscapes that lack sufficient natural areas containing true core habitat (Meffe and Carroll 1997). Although a fragmented landscape may enhance the abundance of certain generalist species, overall, fragmentation threatens the maintenance of biodiversity and the functioning of natural systems (Soulé 1991, Forman 1995).

To the detriment of many species, particularly those that are area-sensitive, habitat patches may lack the range of resources necessary to support permanent populations (Primack 1993, Forman 1995). Habitat fragmentation will reduce the foraging and nesting ability of animals and can lead to the rapid loss of species due to the creation of barriers to dispersal and colonization. In a fragmented landscape, normal dispersal will be disrupted when the land surrounding the remaining patches is inhospitable to species formerly thriving in the contiguous habitat (e.g., because it is degraded or is home to predators). For example, many bird species that dwell in the forest interior will not cross even short distances of open areas (Askins 1995). When species migration and dispersal is limited, new immigrants are less likely to supplement diminishing populations, thereby, increasing extinction vulnerability (Askins 1995).

The negative effects of habitat fragmentation are compounded by an altered physical environment (*see* "Edge Effects"). Land conversion and land transformation can cause major alterations in hydrologic regimes, mineral and nutrient cycles, radiation balance, wind and dispersal patterns, and soil stability (Harris 1984 as cited in Collinge 1996; Hobbs 1993 *as cited in* Forman 1995). Changes in such ecosystem properties and processes in turn affect native species composition, abundance, and long-term persistence, further degrading the biodiversity and the integrity of the affected natural areas.

[10] Matrix is the background ecosystem or land use type in a mosaic, characterized by extensive cover, high connectivity, and/or major control over the landscape functioning (Forman 1995) (see Box 2).

# UNDERSTANDING THE EFFECTS OF FRAGMENTATION

Over the past 25 years, the scientific community has devoted much energy to understanding the various components of fragmentation—the influence of fragment size, shape, configuration, heterogeneity, connectivity, among other factors—and how they effect the sustainability and persistence of species and natural processes in a landscape. Ideally, scientists would understand the influence and interaction of these characteristics on the continued survival of species and the integrity of ecosystems. Due to gaps in scientific knowledge, available information was only found within the literature to present potential threshold responses related to patch area, proportion of suitable habitat, edge effects, and buffers.

This paper provides land use decisionmakers with concrete information culled from the scientific literature in order to translate the land use guideline #5 offered by the Ecological Society of America (*see* Box 1) for on-the-ground practice. Recommendations on "how to retain large contiguous or connected areas that contain critical habitat" are presented, with specific information on how to best protect habitat patches and sufficient natural area, to minimize edge effects, and to design riparian buffers and habitat corridors.

## HABITAT PATCHES

A common consequence of land development is the fragmentation of an originally connected natural landscape into a mosaic of disconnected habitat patches.[11] The size of the remaining habitat fragments significantly influences the type, abundance, and diversity of species that can persist in the affected region. In general, large patches better sustain wildlife populations and ecosystem functions over time than small patches. Holding other factors constant—such as patch shape, condition, and configuration—larger areas of habitat tend to support larger population sizes and a greater number of interior, specialist, and native species due to increased habitat diversity and more core area (Harris 1984, Dramstad et al. 1996, Forman 1995). The probability of a species population being extirpated generally increases with decreasing patch size.[12] This is due to the tendency of larger patches to retain a greater array of the natural resources and ecological functions provided by healthy ecosystems than smaller patches with more edge, increased susceptibility to invasion by exotics or predators, and more disturbed conditions (Soulé 1991, Metro 2001) (*see* "Edge Effects"). Area-sensitive forest bird species in the mid-Atlantic United States, for example, have been found to exhibit lower species diversity and higher extinction and turnover rates in landscapes with smaller mean forest patch size (Boulinier et al. 2001).

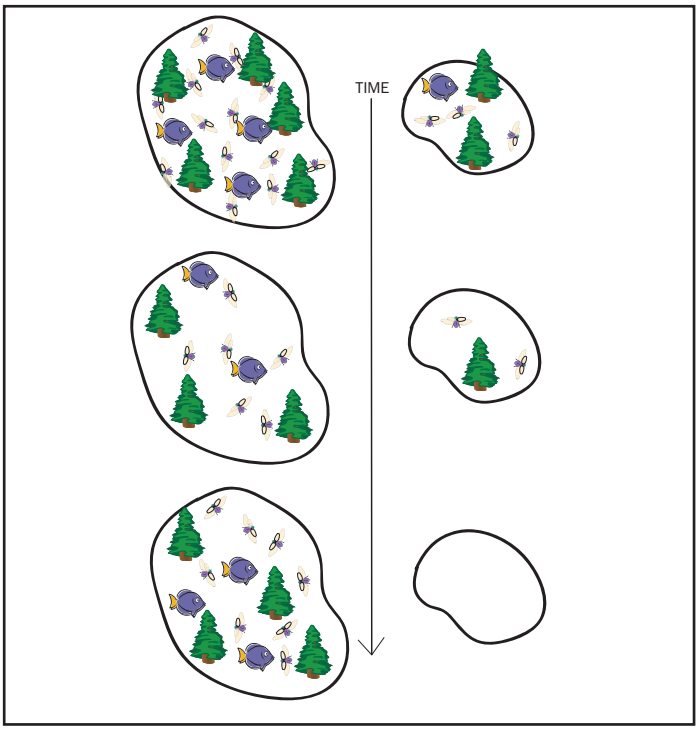


***Diagram 2. Patch size and local extinction.*** *Probability of a local species population going extinct increases with decreasing habitat patch size. A larger patch generally supports a larger population size for a given species than a smaller patch, making it less likely that the species will go locally extinct in the larger patch. Modified from Dramsted et al (1996), Landscape Ecology Principles in Landscape Architecture and Land-Use Planning, p. 20.*

In general, to ensure the survival of individual species, population levels must remain large enough to protect against extinction from random natural events (e.g., floods, fires, droughts) and to maintain sufficient genetic variation to adapt to changing environmental conditions (e.g., changes in rates of predation, competition, disease, and food supply) (Gilpin and Soulé 1986, Meffe and Carroll 1997). A common tool used to determine the size of a population(s) needed to ensure long-term survival is a Population Viability Analysis (PVA). A PVA uses quantitative methods to predict the likely future status of a population or set of populations of conservation concern—often those that are at risk of extinction (Morris et al. 2002). This technique can take into account the many environmental, demographic, and genetic variables that determine extinction probabilities for individual species (Meffe and Carroll 1997).

[11] A patch is a relatively homogeneous type of habitat that is spatially separated from other similar habitat and differs from its surroundings (Forman 1995).

[12] What is being discussed in this report is to the local extinction of a species population from a particular habitat or region (termed extirpation or population extinction), rather than the overall elimination of the species worldwide (termed global extinction).

Because plant and animal population size is the best predictor of extinction probability, habitat patches should be large enough to maintain viable populations of important species—including rare, endangered, and economically important species—and to maintain the ecological processes that support these communities. Based on Population Viability Analyses, general guidelines have been proposed for minimum viable population sizes:[13] 1) populations less than 50 individuals being too small and vulnerable to extinction due to their rapid loss of genetic variability and inability to withstand natural catastrophes; and 2) populations of 1,000 to 10,000 individuals being adequate to ensure long-term persistence (Meffe and Carroll 1997). Such numbers, however, should be viewed with scrutiny because much debate still exists about what size constitutes a minimum viable population for the many different species that make up natural systems (Saunders et al. 1991).

### Managing for Adequate Habitat Patch Size

For purposes of this review, minimum patch area is the smallest habitat patch that should be protected in order to sustain a species, a diversity of species or communities, or functioning of ecosystems. The literature suggests that, depending on the species or habitat in question, minimum critical patches range from as little as 0.0004 hectares (0.001 acres) (based on the needs of certain invertebrates) up to 220,000 hectares (550,000 acres) (based on the needs of certain mammals) to sustain target species or communities (*see* Appendix B). This wide range reveals that a generic "minimum" critical patch size or habitat requirement does not exist; thresholds are entirely dependent on the target species in question.

Ultimately, the amount of habitat necessary to maintain healthy wildlife populations varies according to many factors, such as taxonomic group, body size, foraging and resource requirements, and dispersal patterns of the species (Bender et al. 1998). Taxonomic groups, such invertebrates and plants, which have smaller dispersal ranges and tend to respond to their environment at smaller spatial scales, are reported to need less habitat area (e.g., less than 10 hectares or 25 acres) (McGarigal and Cushman 2002).

Larger patch areas are recommended to support bird, mammal, and fish species. Minimum habitat requirements for birds ranged from one hectare up to 2,500 hectares (6,250 acres), with the majority (75 percent) of the values found within the literature to be under 50 hectares (125 acres).[14] Minimum patch size required by mammals ranges from one hectare to 10 hectares for small mammals and up to 220,000 hectares for large-bodied or wide-ranging mammals (e.g., bears, cougars). Larger bodied vertebrates and wide-ranging predators tend to require larger territories to meet resource and reproductive needs (Soulé 1991). Minimum habitat area is greater for predators, such as bears, with recommended patch sizes greater than 900 and 2,800 hectares and cougars with 220,000 hectares (Mattson 1990, Mace et al. 1996, Beier 1993, respectively).[15] In contrast, estimates for habitat requirements for small mammals, such as rodents and rabbits, varied from one hectare to 10 hectares (Soulé et al. 1992, Barbour and Litvaitis 1993, Bolger et al. 1997). Only one study was found to provide evidence on possible watershed area needed to sustain fish species, finding that suitable patch sizes larger than 2,500 hectares might increase the chance of bull trout occurrence in Idaho (Rieman and McIntyre 1995).

Overall, the majority of the findings in this survey pertain to birds and mammals (*see* "A Closer Look at Habitat Patch Size" in Appendix A for specific information on numbers and trends). Few studies were found to recommend patch sizes to sustain plant, invertebrate, or fish populations. Keeping in mind this sample represents a narrow array of species and habitats, the protection of habitat patches of 55 hectares (137.5 acres) or more appears to capture 75 percent of species requirements reviewed in this select survey (*see* Figure 1). Such minimum land parcels, however, are not likely to capture particularly area-sensitive species, like wide-ranging predators or particularly sensitive interior bird species, found to need habitat patches greater than 2,500 hectares (or about 6,175 acres) (Trine 1998, Mattson 1990, and Beier 1993).

Given the great scientific uncertainty and gaps in the knowledge base on minimum habitat requirements of species and ecosystems, land use planners should adopt a conservative approach. The goal should be to maintain sufficiently large intact and well-connected habitat patches that would support the most area-sensitive species, species of greatest environmental concern (e.g., rare, threatened, or endangered species), or focal species, such as keystone species,[16] link species,[17] or umbrella species.[18] Declines in these groups of organisms may have wide ranging implications, negatively affecting the persistence of other associated species and ecosystems (Dale et al. 2000).

Land use planners should carefully consider the conservation needs of species with large-area or specialized life history requirements or that depend upon a combination of different habitats (e.g., large-ranging predators; interior species, or rare species); these species are likely to survive only in rel-

[13] The minimum viable population size is the smallest number of individuals required to maintain a population over the long-term (Forman 1995); for example, the size of a population that would have a 95 percent probability of persisting for 100 years (Boyce 1992).

[14] Recommended conservation threshold values are based on the goal of capturing 75 percent of the requirements found for species, communities, and habitats surveyed in this literature review; thus, the third quartile was used by calculating the value for which 75 percent of the threshold values lie below this value (after numerical ranking).

[15] One hectare is equal to approximately 2.5 acres.

[16] Keystone species are species that have greater effects on ecological processes than would be predicted by their abundance or biomass alone (Dale et al. 2000).

[17] Link species are species that exert critical roles in the transfer of matter and energy across trophic levels of a food web or that provide critical links for energy transfer within complex food webs (Dale et al. 2000).

[18] Umbrella species are species that either have large area requirements or use multiple habitats and thus overlap the habitat requirements of other species (Dale et al. 2000).

atively large areas or in very specific habitat types (potentially very small, localized areas), which should be actively targeted for protection (Saunders et al. 1991, Ruggierro et al. 1994, Collinge 1996). To help guide conservation planning, umbrella species (e.g., vertebrate mammals such as cougars and grizzly bears) have been proposed as targets for conservation, because their protection may ensure the protection of other secondary species (Franklin 1993). By protecting areas large enough to maintain viable populations of wide-ranging species, sufficient habitat may be maintained to ensure survival of other species dependent on the same habitat. Land use planning that allows for the persistence of focal species—like rare and endangered species, keystone or umbrella species—may help direct land conservation. Land use planners will need the help of local biologists to identify appropriate focal and area-sensitive species in their region to better implement habitat conservation strategies.

*Land use planners should strive to protection and maintain habitat patches larger than 55 hectares (137.5 acres).*

Even though protecting large expanses of connected habitat is the ultimate goal, this may not be practicable in the often highly developing landscapes in which land use planners often find themselves working. In these settings, land use professionals should try and conserve what habitat remains and, where possible, work with land management agencies and land trusts to identify potential areas for habitat restoration. Working to conserve even the smallest remaining natural areas is important, particularly in human-dominated landscapes. A series of small- or medium-sized reserves may capture a greater diversity of habitat types, environmental heterogeneity, and biological diversity than the preservation of one large fragment (Tscharntke et al. 2002) (*see* "Role of small patches"). Protecting natural habitats with the greatest conservation significance locally and regionally—regardless of size—is vital to preserving biological diversity and ecosystem services. No matter how small habitat patches may be, they still have ecological and/or aesthetic values, whether providing habitat for small organisms like amphibians or insects; providing green space for recreational activities; helping moderate temperature and provide shade in urban areas; or decreasing run-off from streets, pavements, and other impermeable surfaces.

### Other Patch Area Design Considerations

The size of any given habitat patch is only one factor determining whether or not the patch will support species persistence, biological diversity, and ecosystem functions. Other factors to consider are the shape, location/configuration, condition, and boundaries of patches, as well as the role of small habitat patches. The following is general guidance on ways to counteract the negative impacts of habitat fragmentation and habitat loss at a landscape scale.

- **Patch shape:** Patch size and shape determine the distance of the patch's edge to the habitat interior and the amount of core area remaining in any remnant habitat patch (*see* "Edge Effects") (Collinge 1996). Shape determines the edge to interior ratio of a habitat patch, which should be as low as possible to minimize edge effects (Wilcove et al. 1986, Saunders et al. 1991, Collinge 1996). Circular habitat reserves are recommended to minimize contact between the protected core habitat and adjacent environmental or human pressures (Wilcove et al. 1986). In contrast, long, thin remnants have proportionally more edge, and thus, more negative edge effects (Forman and Godron 1981, Saunders et al. 1991).

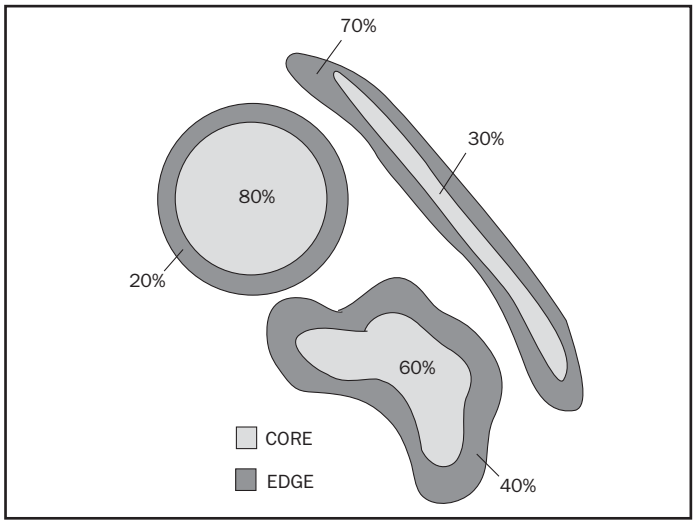


***Diagram 3. Patch shape and edge.*** *The edge to interior ratio of a habitat patch is affected by patch shape. A more convoluted, irregular, or linear patch will have a higher proportion of edge, thus, increasing the number of edge species and decreasing the number of interior species.*

- **Patch location/configuration:** The landscape context in which patches reside may have an even greater effect on the function and sustainability of a habitat fragment than the characteristics of the patch itself (Forman 1995). The distances between suitable habitat patches and the nature of the matrix between these patches will influence species survival (Ruggiero et al. 1994, Andren 1997). In general, more connected habitats are better than isolated habitats because patches in close proximity are likely to enhance species dispersal, recolonization, and persistence (Fahrig and Merriam 1994). Even where wildlife populations may decline or disappear in isolated patches due to random events or patch conditions, recolonization may occur if species are able to successfully disperse from nearby habitat (Pulliam et al. 1992). To maintain demographic linkages, suitable patches should be positioned to provide stop-over points or "stepping stones" for species dispersal (Forman and Godron 1981). The allowable distance between patches will depend

upon individual species' dispersal capabilities, which vary within and among species groups (Ruggiero et al. 1994, Bender et al. 1998). When making land use planning decisions, practitioners should consider the contribution of patches to the overall landscape structure and how well the location of any given patch relates or links to other patches (Dramstad et al. 1996).

- **Boundary zone:** The contrast between a patch edge and the surrounding landscape matrix (also referred to as the boundary zone) affects the severity of edge effects and the dispersal abilities of wildlife populations. The higher the contrast between patch types or patches and their surrounding matrix, the greater the edge effects (Franklin 1993). Boundaries in a landscape could be either "hard" or "soft." Hard boundaries usually result from human activities, such as clearcutting and development, and have linear borders with high vegetation contrast, such as between a forest and cultivated field. Soft edges, which dominate natural landscapes, tend to have varying degrees of structural contrast with curved habitat boundaries (Forman 1995). To minimize edge effects at the local scale and facilitate the movement of species between a patch and the surrounding matrix, land use planners should mimic naturally occurring edges and provide gradual thinning of vegetation (e.g., smaller shrubs grading into larger shrubs and taller trees at the edge of a wooded patch) rather than an abrupt transition from vegetated to denuded areas (Forman and Godron 1981, Forman 1995, Duerksen et al. 1997).

- **Patch condition:** The quality of the habitat patch itself will also influence the ability of remnant species and systems to persist or function over the long-term (Fahrig and Merriam 1994, Forman 1995). Large patches with degraded habitat—such as those dominated by non-native species, or with diminished biological diversity, severe erosion, or modified hydrologic patterns—may have less conservation value than small patches of high biological integrity.[19] The biological integrity of land parcels and whether or not they contain unusual or distinctive landscape features (e.g., cliffs, caves, meadows, thermal features, and vernal pools), old-growth forests or mature habitats, or rare, threatened, or endemic species, are also factors that land use planners should consider when selecting which lands to conserve (Dramstad et al. 1996, Duerksen 1997, Lindenmayer and Franklin 2002).

- **Role of small patches:** While large patches generally are recommended to provide sufficient habitat to sustain populations of species—particularly area-sensitive species—small patches also play a vital role in regional conservation. Although larger patches may contain greater habitat diversity than smaller ones, a collection of multiple small patches may capture a greater array of habitats, and perhaps more rare species, than a single large habitat patch (Forman and Godron 1981, Saunders et al. 1991, Forman 1995, Tschartnke et. al. 2002). Small wetlands of less than two hectares, for example, can support surprisingly high species richness of amphibians (Richter and Azous 1995 as cited in Metro 2001). Proximity to core habitat and local habitat heterogeneity, rather than riparian habitat area, may better predict reptile and amphibian richness (Burbink et. al. 1998). In addition, small isolated riparian habitat patches have been found to be vital stop-over sites for en-route migratory birds in the southeastern United States (Skagen et al. 1998). If strategically positioned between larger habitat patches, smaller patches can serve as "stepping stones" to allow for greater species dispersal and recolonization (Murphy and Weiss 1988; Burel 1989 and Potter 1990 as cited in Fahrig and Merriam 1994; Forman 1995).

Many of the above described factors influence not only the effective habitat patch size, but also other fragmentation thresholds, such as the proportion of suitable habitat or the amount of edge in a landscape. Thus, land use planners should keep these design considerations in mind when interpreting the thresholds presented below.

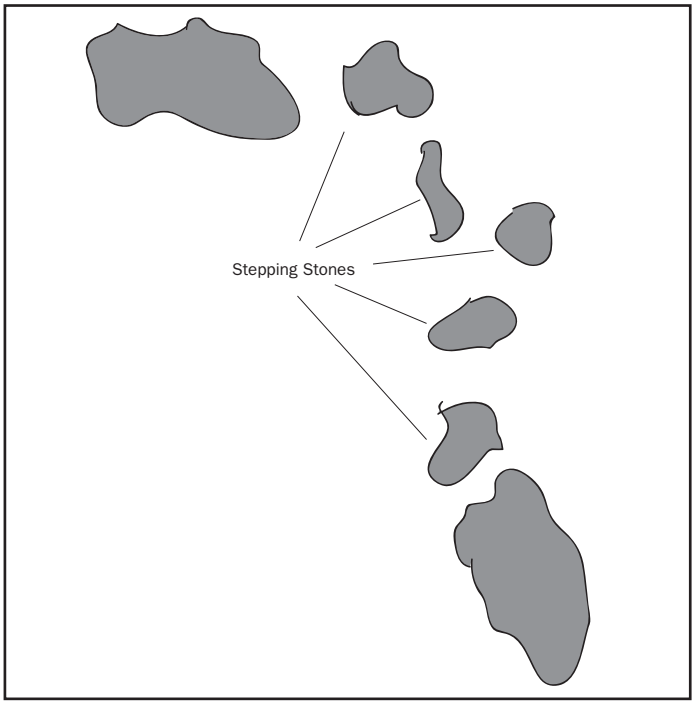


***Diagram 4. Stepping stone patches.*** *Protecting habitat patches strategically positioned between larger habitat patches can be a way to enhance species dispersal and colonization in a landscape, and to increase local species population persistence. Modified from Duerksen et al. (1997), Habitat Protection Planning: Where the Wild Things Are, p 14.*

[19] Biological integrity refers to "a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates" (as cited in Angermeier and Karr 1994).

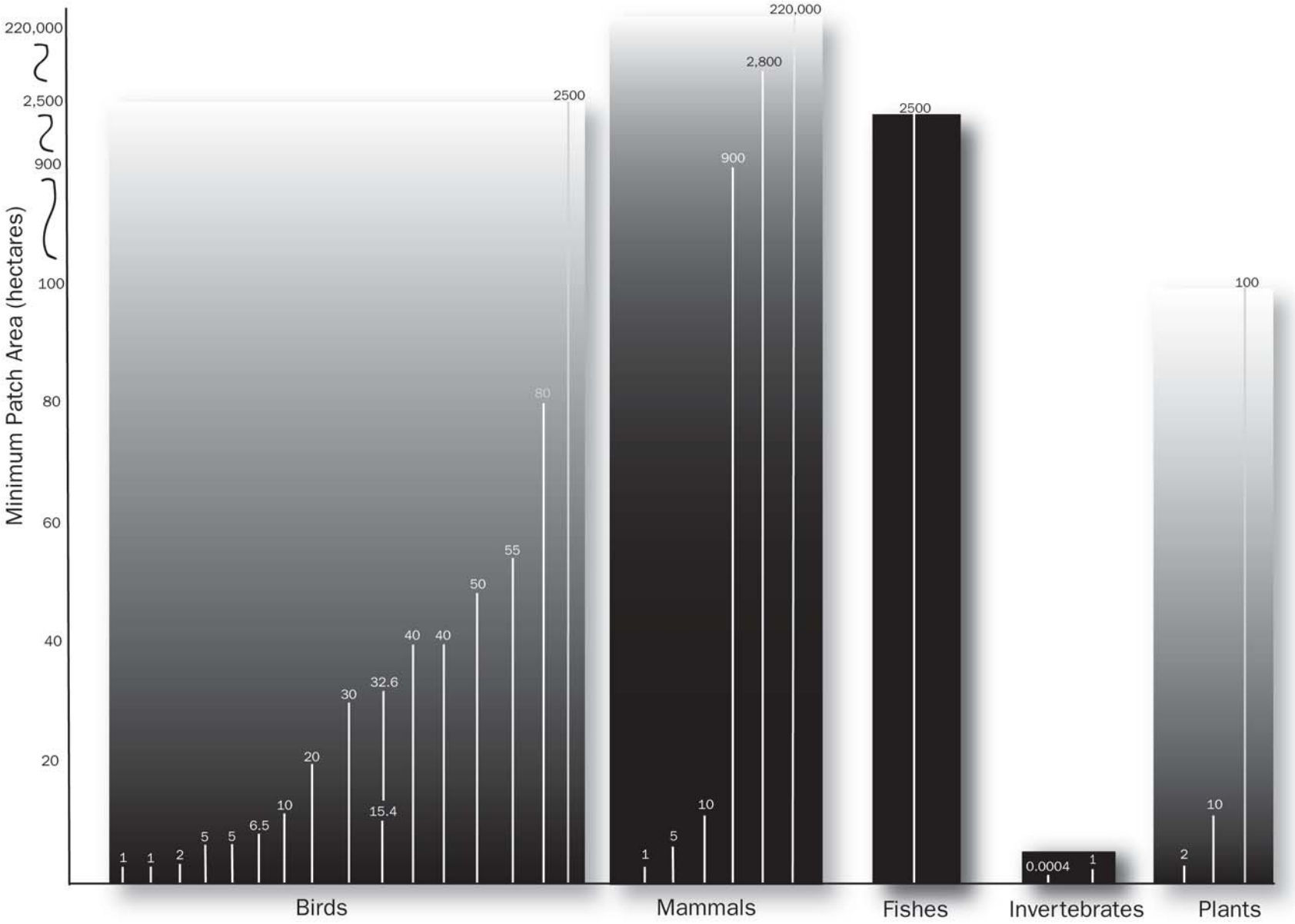


**Figure 1.** Minimum patch area requirements (in hectares) needed to maintain populations or communities of birds, mammals, fishes, invertebrates, or plants species in the United States, as cited in the scientific literature. Numbers represent the recommended minimum patch area sizes; two numbers along one line indicate a recommended range (*see* Appendix A for specific findings). Lines extend from zero to the recommended minimum patch area sizes to indicate the span of habitat needed for protection.

## SUITABLE HABITAT IN LANDSCAPE

Landscapes are complex assemblages of many habitat fragments that together help sustain large-scale biological systems. As a result, meeting minimum patch sizes for species in a given landscape may be inadequate to ensure their persistence (Fahrig 2001). The configuration and nature of the landscape surrounding a patch also greatly determine whether a region will support species persistence and diversity (Lindenmayer and Franklin 2002).

In addition to considering the size of patches, land use planners must consider the total amount of suitable habitat in a given landscape. Local populations of plants and animals are often linked together by dispersal, essentially forming a larger "metapopulation" (Hanski and Simberloff 1997).[20] Individual species from such subpopulations migrate between habitat patches, interacting and breeding with other individuals, which influences the overall survivorship of the species in a region. In addition, the quality and availability of habitat patches can greatly determine the viability of a metapopulation. Some habitat patches may be of higher quality allowing for the local species population to benefit from higher reproductive rates than death rates. These "source" populations produce excess individuals that could emigrate into neighboring patches to settle and breed, thus, expanding the overall population and helping to buffer it from local extirpation. On the other hand, some habitat patches may be of poor quality, where local productivity is less than mortality. Referred to as "sink" populations, these areas lack immigration of individuals from source populations, leading to the extirpation of the local population (Pulliam 1988). For species populations that exhibit a metapopulation structure, land use planners should strive to protect existing source habitat patches, as well as restore habitat that may serve to support future source populations. However, land use planners should be cautious not to designate critical habitat solely by the proportion of the local population present; a source habitat could support as little as 10 percent of the metapopulation, which is responsible for maintaining the other 90 percent of the total population (Pulliam 1988). Rather, land use planners should work with ecologists to identify source habitat by demographic characteristics (e.g., death and birth rates of species).

Metapopulation theory reveals that the local extinction of a subpopulation can be prevented by occasional immigration from neighboring patches, termed the "rescue effect," which is considered important in maintaining small populations and high levels of species diversity (Brown and Kodric-Brown 1977, Stevens 1989). Local extinctions may commonly occur within small habitat patches; about 10-20 percent of certain local populations of plants, arthropods, amphibians, birds, and small mammals within various habitat types have been found to go extinct per year (Fahrig and Merriam 1994). Thus, a set of interconnected habitat patches should be conserved to sustain sufficiently large metapopulations that would allow for regional species persistence.[21] Habitat patches must also be configured to facilitate dispersal and recolonization between patches, particularly those used for breeding and foraging (Saunders et al. 1991, Fahrig and Merriam 1994, Boulinier et al. 2001, Fahrig 2001). Land use planners should strive to identify particular subpopulations, habitat patches, or links between isolated patches that are critical for the maintenance of the overall metapopulation of priority species (Meffe and Carroll 1997).

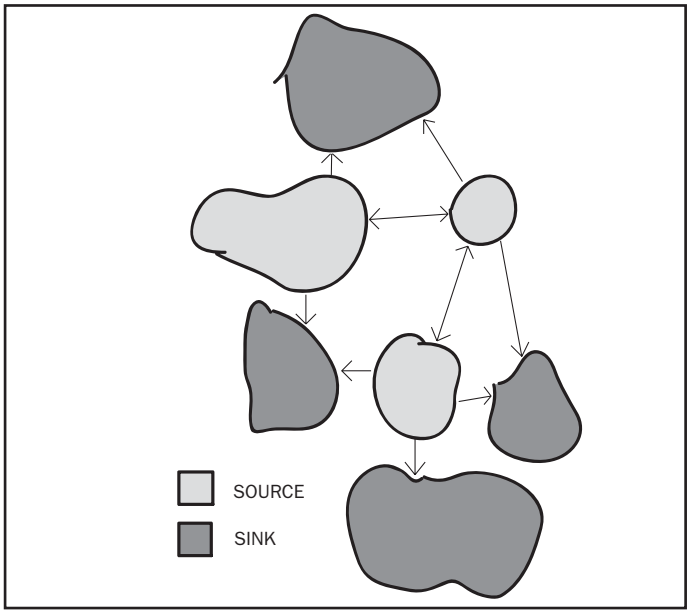


***Diagram 5. Metapopulation and Source/Sink Dynamics.*** *Local populations of organisms in different habitat patches may be linked demographically, forming an interdependent metapopulation. "Source" habitat patches, which supplement local populations in "sink" habitat patches, should be targeted for protection. Ideally, land use planners should protect entire metapopulations. Modified from Mette and Carroll (1994), Principles of Conservation Biology, p 188.*

Not only is the quality of the habitat patches themselves important, but also the condition of the matrix between isolated habitat patches. If the matrix is able to support populations of species present in the original contiguous habitat or allows for adequate species dispersal or migration between fragments, then communities in remnant patches may retain diverse and viable populations of native plants and animals (Askins 1995). Estimating the proportion of suitable habitat in a landscape is a larger scale method of determining how much suitable habitat should be conserved to ensure the persistence of species in a region.

### MANAGING FOR THE AMOUNT OF NECESSARY HABITAT IN A LANDSCAPE

Scientists generally offer recommendations on the proportion of suitable habitat that should be conserved in a

[20] A metapopulation is a set of local populations that interact by individuals moving between the local populations (or subpopulations) (Hanski and Gilpin 1991).

[21] A local extinction refers to the extinction of a single, local population in a given geographic area; a local extinction does not entail that the entire species has gone extinct within its known range.

landscape based on two scientific trends. First, species disappear in a landscape with the loss of a certain amount of habitat, and different species go extinct at different thresholds of habitat loss (Fahrig 2002). Thus, scientists have estimated extinction thresholds to determine the proportion of suitable habitat needed to sustain specific species.[22] The "extinction threshold" is the minimum amount of habitat required for a population to persist in a region below which the population will go extinct (Fahrig 2001, Fahrig 2002).[23] Extinction thresholds are essentially the converse of population viability estimates derived from PVAs (described above).

Second, threshold values may be based on the amount of habitat below, which the negative effects of habitat fragmentation may compromise species persistence. This is termed "habitat fragmentation thresholds" (Andrén 1994, Fahrig 1998). As the proportion of suitable habitat decreases in a landscape, the reduction in patch sizes and the increasing isolation of these fragments begins to significantly affect the abundance, distribution, or diversity of species in the landscape due to alterations in species movement or the spread of disturbance (e.g., wildfire, flooding, invasion by exotic species), among other factors (Gustafson and Parker 1992, Andrén 1994). The recommendations presented in this review are largely based on existing literature reviews of both extinction thresholds and habitat fragmentation thresholds (*see* Andrén 1994, Fahrig 2001).

Studies of suitable habitat range between 5 percent to 80 percent of the landscape depending on the species, geographic region, and parameters in question (*see* Appendix C). Seventy-five percent of the surveyed studies reported that suitable habitat should be up to 50 percent of the total landscape, whereas 50 percent of the studies reported at least 20 percent of habitat (*see* Figure 2). Given the constraints presented by the available literature (*see* "A Closer Look at Proportion of Suitable Habitat" in Appendix A for explanation on limitations), the conservation of greater proportions of habitat—such as a minimum of 60 percent—is recom-

[22] From a species perspective, suitable habitat has been interpreted as habitat utilized for nesting, with associated expected birth and death rates that allow for a stable or growing population (Lamberson et al. 1994).

[23] The extinction threshold may be estimated by: 1) the minimum amount of habitat below which the equilibrium population is zero; or 2) the minimum amount of habitat below which the probability of longterm population survival is less than one (Fahrig 2002).

**BOX 3. PLANNING AT THE RIGHT SCALE**

Natural communities vary greatly in the area in which they occur. In order to determine which land parcels and how much habitat to protect, land use planners should plan at the appropriate scale for the target system or species. Ideally, planning would occur across multiple scales to capture the greatest habitat and species diversity (*see* Box 2 for a definition of scale).

**1. Coarse scale**

Certain habitats and species, termed "matrix" habitats and "coarse-scale" species, will require planning to occur at a very large scale to capture their wide-ranging needs. Natural communities—such as spruce-fir forests (Northeast), longleaf pine forests (Southeast), tallgrass prairie (Midwest), and sagebrush (West)—can span as much as one million contiguous acres. Matrix communities are historically dominant habitat and exist across widespread physical gradients, such as broad ranges of elevation, precipitation, and temperature. Coarse-scale species (also termed wide-ranging species) require large areas to access the quantity of habitat or the different habitat types needed for survival (e.g., prairie chicken, fox, badger, marten, and pike minnow). Migratory species (e.g., migratory birds or salmon) and top-level predators (e.g., caribou, wolves, and bears) may depend upon not only matrix communities, but also associated habitat patches (described below), connecting corridors, and aquatic systems. To address the needs of such expansive communities and wide-ranging species, land use planners will need to take a landscape scale and regional approach; an area of several thousand acres up to one million acres may need to be conserved. This scale of planning will likely demand an inter-jurisdictional perspective and inter-municipal cooperation.

**2. Intermediate scale**

Planning may need to occur at a smaller scale—on the order of several hundred to a thousand acres—to conserve "large patch" community types and "intermediate-scale" species. Occurring in large patches, but not as vast an area as matrix types, are communities like red maple-black ash swamps or northern hardwood forests. Large patch communities may span a thousand acres but are bound by certain physical factors (e.g., coastal salt marshes being defined by low topographic position and predictable tides) or by a single dominant ecological process (e.g., fire, flooding, or drainage). Intermediate-scale species are those that depend on a single large patch or several different kinds of habitats (e.g., amphibians that depend on both wetland and upland complexes).

**3. Fine scale**

Land use planners will need to plan at a more "fine" or site-specific scale to ensure that "small patch" communities and local-scale species are protected. Small patch communities are communities that naturally occur in narrow, localized, or discrete areas (e.g., fens, bogs, glades, caves, or cliffs) or occur only where specific or narrow physical factors and local environmental conditions are present (e.g., seepages, outcrops, certain types of soil). Local-scale species are species with limited movement and dispersal abilities or specific habitat needs that restrict their populations to a single community or habitat type. Belonging to this category are many rare and threatened species, insects, and plants. Occurrences of small patch communities and local-scale species may be found in only a couple of acres up to several hundred acres.

Given the natural variability in occurrence of communities and species and their wide-ranging geographic needs land use planners will need to plan at multiple scales to capture the biological diversity of a region, as well as to plan at the right scale for designated conservation targets.

The conservation thresholds found within this literature survey are predominately based on matrix and large patch communities, as well as coarse- and intermediate-scale terrestrial species. Thus, the findings and recommendations in this report do not fully address the conservation needs for small patch communities, local-scale species, and aquatic environments. To ensure the protection of restricted communities and rare species, land use planners will need to collaborate with local ecologists to identify priority conservation areas for their region.

*The above information is based on research by The Nature Conservancy (TNC) (see Poiani and Richter 2000, and TNC 1998).*

mended to sustain long-term populations of area-sensitive species and rare species.

Scientists have proposed that more robust species (e.g., large dispersal range, high fecundity, high survivorship)—usually the more common widespread species—may persist in even the most extensively fragmented systems with only 25 to 50 percent of suitable habitat. In contrast, rare species and habitat specialists like the Northern spotted owl may require up to 80 percent of suitable habitat to persist in a region (Lande 1987, Lande 1988, Lamberson et al. 1992). Land use planners should take into account the more sensitive and rare species within their region to develop critical thresholds for proportions of suitable habitat relevant to their geographic setting (Mönkkönen and Reunanen 1999). Such an approach may also provide for the protection of more common and robust species that depend on similar habitat types.

*Land use planners should strive to conserve at least 20% to 60% of natural habitat in a landscape.*

In addition to the proportion of suitable habitat, other considerations should be factored into land use decisionmaking, such as the spatial arrangements of remaining habitat patches and the matrix between patches. In landscapes that are highly fragmented—including most urban, suburban, and even rural areas with less than 30 percent of remaining suitable habitat—the spatial arrangement of habitat patches greatly affects species survival (Andrén 1994). For example, wetland bird communities are found to depend not only on their local habitat, but also on the amount of wetlands within a surrounding three kilometer buffer (Fairbairn and Dinsmore 2001).

The condition of the surrounding matrix in which habitat patches are embedded also influences the effective size of the remaining fragments and the degree to which the patches are isolated (Andrén 1994, Lindenmayer and Franklin 2002). In turn, these factors affect whether or not species will be able to successfully disperse among habitat patches and whether important ecosystem processes, such as fire and hydrologic cycling, will occur on the landscape (Fahrig and Merriam 1994) (*see* "Patch location/configuration").

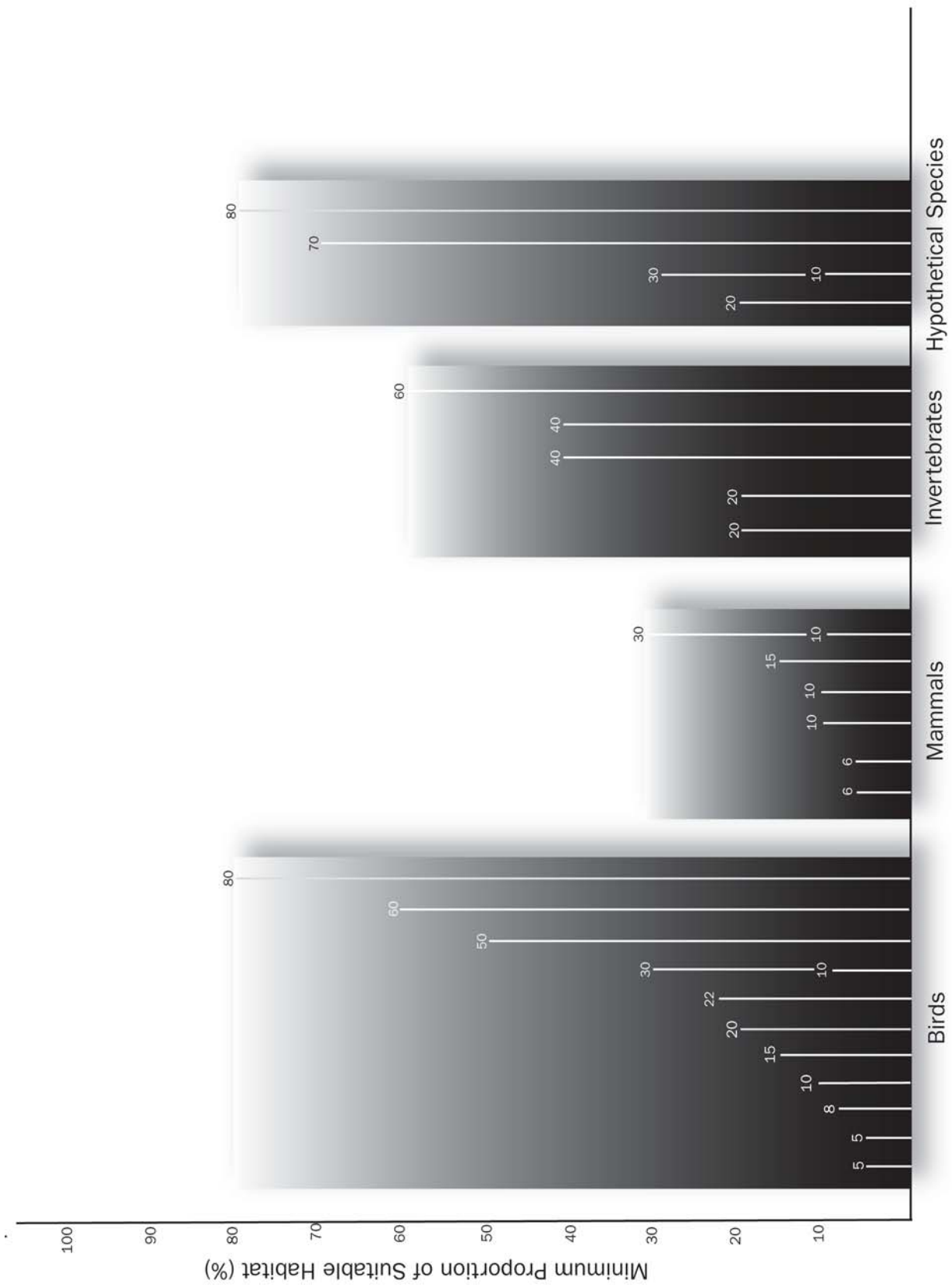


**Figure 2.** Recommended minimum proportions of suitable habitat (in percentages) needed to maintain populations or communities of birds, mammals, invertebrates, or hypothetical species (as determined by models) in the United States, as cited in the scientific literature. Numbers represent the recommended minimum proportions of habitat; two numbers along one line indicate a recommended range (*see* Appendix B for specific findings). Lines extend from zero to the recommended proportion to indicate the span of habitat needed for protection.

## EDGE EFFECTS

Habitat fragmentation inevitably results in the creation of edge environments. Edges occur where a habitat—such as a forest, prairie, or wetland—meets a road, clearcut, housing development, or some other natural or artificial transition or boundary (Soulé 1991). Habitat fragments differ from the original contiguous natural habitat in that they have a greater amount of edge per area and the habitat core is closer to an edge environment. Patch edges may have significantly different conditions than the contiguous system or habitat interior, with altered fluxes of wind, sun exposure, water, and nutrients that greatly affect animal and plant communities (Saunders et al. 1991, Murcia 1995). This change in energy, nutrient, or species flow results from increased amounts of edge and reduced interior habitat, and has been termed the "edge effect."

Increased amounts of edge along habitats create a disturbed environment that allows for the establishment of pest and predator species, which penetrate the fragment interior and adversely affect the diversity and abundance of interior species (Primack 1993). Mammalian predators (e.g., raccoons, foxes, coyotes, feral cats), egg-eating birds (e.g., crows and blue jays), and brood parasitizers (e.g., brown-headed cowbirds) concentrate their hunting along forest edges, thus, increasing the intensities of predation on native species (Soulé 1991).[24] Habitat fragmentation also increases the vulnerability of remnant patches to invasion by exotic and pest species (Soulé 1991, Askins 1995). Higher frequency and intensity of disturbances, like fire and wind damage, may also result due to increased edge (Soulé 1991). Edges like roads and trails introduce such disturbances as pedestrian, pet, and vehicular traffic, causing animals to avoid such areas (Duerksen et al. 1997). Each of these edge effects has significant impact on the vitality and composition of the species in the remaining habitat patch.

Information on environmental and species response to edges helps determine how large patch sizes should be designed to provide sufficient interior habitat, as well as how far development, such as roads, trails, and housing, should be from remnant core areas.

### Managing for Edge Influence

The intensity of edge effects has been measured by a number of different methods. The influence of an edge (termed "edge influence") may be defined as the distance between the border to the point where microclimate and vegetation do not significantly differ from the interior conditions of the habitat. From a species perspective, edge influence may be defined as the distance from an edge to the area where species densities, survival rates, or reproductive rates do not differ from those in the interior habitat (Forman 1995, Murcia 1995). Edge influence has also been measured by the behavioral response of animal movement, such as flushing distance, from a disturbance associated with edge environments.[25]

*Creation of edge by deforestation, Willamette National Forest, Oregon. Photo courtesy of Steve Holmer, American Lands Alliance.*

The intensity of edge effects is influenced by many physical factors, such as the shape and size of the patch, the direction the edge faces (i.e., aspect), and the structural contrast of its boundaries (Soulé 1991). As discussed earlier, larger, circular patches will have more interior habitat and less edge than a rectangular or oblong patch of the same size (Forman and Godron 1981) (*see* "Patch shape"). The orientation of edges affect the amount of exposure to solar radiation, with edges facing the equator tending to have wider edge influence (Forman and Godron 1981, Murcia 1995). The more structurally different the boundaries between different habitat types, the greater the edge effects.

To decrease the influence of edge, buffers are recommended to "soften" the transition between natural and artificial environments (*see* "Boundary zone"). A remnant forest patch directly abutting cropland or urban development will have significant edge effects in contrast to a forest adjacent to a buffer of small shrubs or secondary vegetation. In addition, some habitat types may be more susceptible to negative edge effects; for example, grasslands have been found to exhibit wider edges than forest edges (Forman 1995).

Scientists offer a wide range of findings on the distance edge effects penetrate into ecosystems in the United States, with results ranging from only eight meters up to five kilometers. Based on the response of birds to edge environments, edge effects may penetrate into a habitat patch from about 16 meters up to almost 700 meters; mammals may avoid edge environments from 45 meters up to 900 meters; and microclimate changes may extend from eight meters up to 240 meters into habitat (*see* Appendix E). The majority of the surveyed studies (75 percent) estimates edge influence to be approximately 230 meters or less (*see* Figure 3).

Based on this select review, land use planners should take a conservative approach to mitigating edge effects. To pro-

[24] Cowbird females lay their eggs in the nests of other bird species, relying on these hosts to incubate and raise their chicks. Brown-headed cowbirds have been found to parasitize over 220 host species. (see http://www.audubon.org/bird/research/cowbird-info.html).

[25] Flushing distance is the distance that an animal may flee in response to a disturbance, such as in response to pedestrian or pets on a trail or vehicular traffic on roads (Duerksen et al. 1997)

vide for sufficient suitable habitat, land use planners should buffer remnant patches by at least 300 meters from all edge peripheries, particularly for matrix and large patch community remnants; naturally small patch communities may not require such a wide buffer (*see* Box 3). The area within the buffer should not be counted as suitable habitat provided for species conservation. In addition, roads, trails, and other development should be placed at least 300 meters away from interior habitat to minimize impact. Ideally, land use planners and ecologists should work collaboratively to determine the intensity of edge effects by the response of species or groups of species that are most sensitive to patch size in the ecosystems or regions of concern (Forman 1995). Measuring edge distance by the most sensitive species—often vertebrates of conservation concern—would mean that the influence of edges may actually be hundreds or thousands of meters, thus, requiring much larger patch sizes to meet habitat requirements.

*To avoid the negative effects of edges, land use planners should consider buffering up to 230 to 300 meters around edge peripheries.*

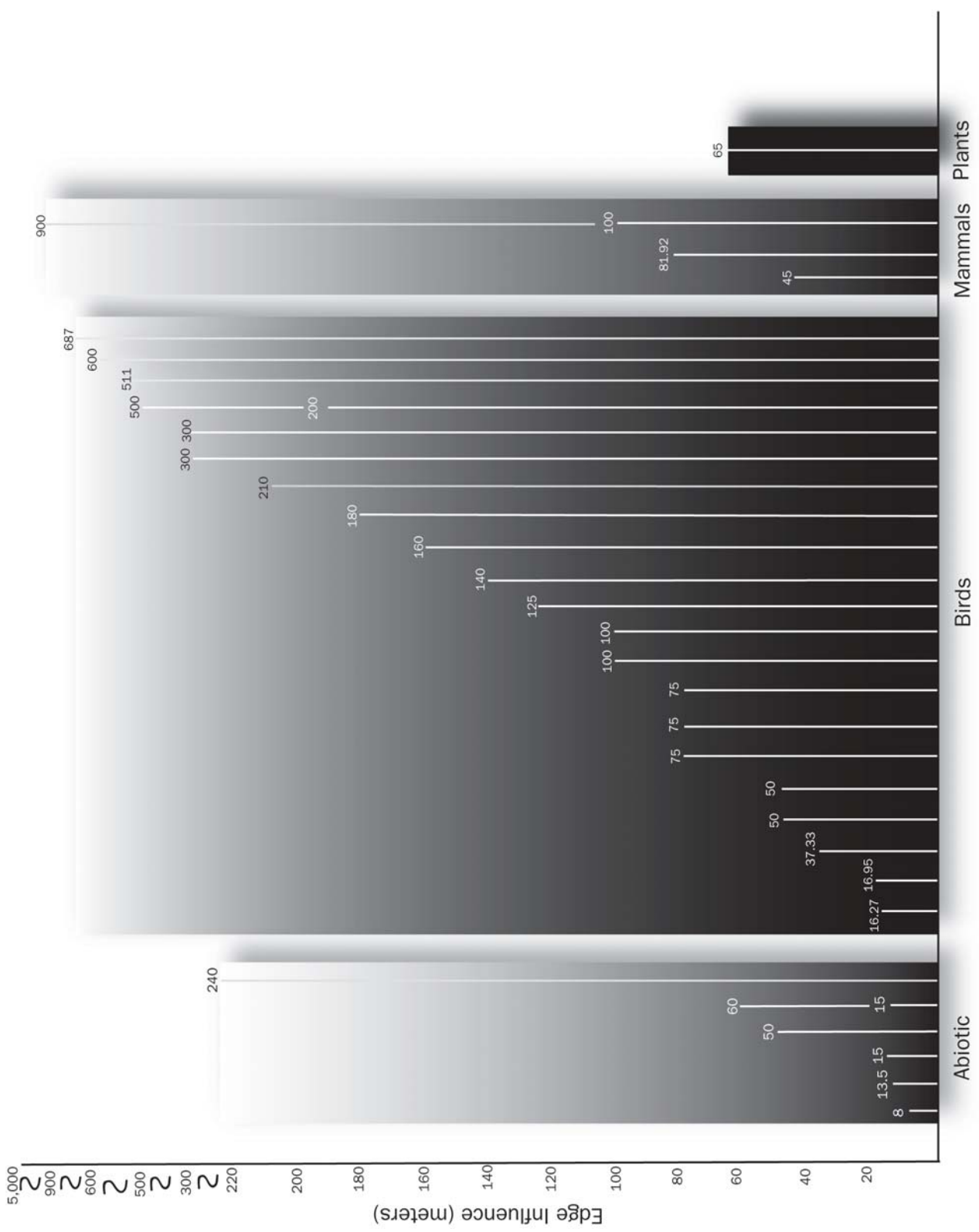


**Figure 3**. Distances (in meters) that edge effects penetrate into habitats in the United States, as cited in the scientific literature. Edge width is measured by abiotic, bird, mammal, or plant responses; abiotic responses include microclimate changes, such as changes in temperature, humidity and light. Numbers represent edge width distance findings; two numbers along one line indicate a range of edge width distance (*see* Appendix C for specific findings). Lines extend from zero to the determined edge widths to indicate the span of habitat that is affected by edge effects.

## RIPARIAN BUFFERS

Although generally comprising a small proportion of the landscape—often less than 1 percent—riparian areas are regional hot spots that support a disproportionately high number of wildlife species and provide a wide array of ecological functions and values (Naiman et al. 1993, Fischer and Fischenich 2000, National Research Council 2002). The support of high levels of species diversity and ecological processes in these areas is due in part to regular disturbance events, like floods, as well as to climatic and topographic variation and the availability of water and nutrients (Naiman et al. 1993).

Riparian areas are ecosystems adjacent to or near flowing water, such as rivers, lakes, shorelines, and some wetlands. They are transitional areas between aquatic and upland terrestrial systems and exhibit gradients in environmental conditions, ecological processes, and living organisms (National Research Council 2002). Unfortunately, riparian systems are continuously threatened by adjacent or upstream human activities. For example, agricultural, industrial, or urban development can increase levels of light, temperature, stormwater runoff, sedimentation, pollutant loading, and erosion, which degrade water quality and diminish suitable aquatic habitat (Castelle et al. 1994). In the last 200 years, over 80 percent of riparian land in North America and Europe has disappeared (Naiman et al. 1993).

To ameliorate the negative impacts of adjacent land uses, a common regulatory and management practice is to establish protected areas, or buffers, around aquatic resources like rivers, streams, lakes, and wetlands. At least 15 states and seven local jurisdictions in the United States have adopted riparian buffer regulations, protecting widths ranging from six meters to over 300 meters in size (Johnson and Ryba 1992).

Buffers are vegetated zones, usually linear bands of permanent vegetation, preferably native species, located between aquatic resources and adjacent areas subject to human alteration (Castelle et al. 1994, Fischer and Fischenich 2000). Buffers can help regulate riparian microclimate and provide necessary shading for the in-stream growth and reproduction of aquatic life; stabilize stream banks and prevent channel erosion; provide organic litter (e.g., leaf litter) and woody debris, which are important sources of food and energy for fish and aquatic invertebrate communities; remove or regulate sediment, nutrients, or other contaminants (e.g., pesticides, herbicides) from runoff; provide flood attenuation and storage to decrease damage to property; and provide wildlife habitat (Castelle et al. 1994, O'Laughlin and Belt 1995, Wenger 1999, Fischer and Fischenich 2000, National Research Council 2002).

*Riparian buffer establishment, North Hather Creek, Innoko, Alaska. Courtesy of U.S. Fish and Wildlife Service.*

### Managing for Adequate Buffer Width

Recommended buffer widths are commonly determined by one of two methods: uniform versus variable widths. Uniform-width buffers are commonly adopted because they are easier to enforce, require less specialized knowledge, time, and resources to administer, and allow for greater regulatory predictability (Castelle et al. 1994). Uniform widths are often based on a single resource protection goal, usually related to water quality. In contrast, with variable-width buffers, the size or width of the strip is adjusted along its length to account for multiple functions, adjacent land use, and site and stream conditions. The width of the strip may be adjusted depending on the value of the aquatic resources, the intensity of surrounding land use, and the type and condition of vegetation, topography, soils, or hydrology, among other variables. For example, a larger width may be required for buffers surrounding more pristine or highly valued wetlands or streams; in close proximity to high impact land use activities; or with steep bank slopes, highly erodible soils, or sparse vegetation (Castelle et al. 1994, Fischer and Fischenich 2000).

*Land use planners should strive to establish 100-meter wide riparian buffers to enhance water quality and wildlife protection.*

Although the method of varying buffer width is generally believed to provide more adequate protection for aquatic resources, it may be less efficient because variable strips can retain less material than a uniform-width buffer of equivalent average width (Weller et al. 1998). Thus, providing policymakers with scientific guidance on uniform buffer widths allows for the implementation of practicable land management practices that protect aquatic resources.

For this report, riparian buffer widths are measured from the top of the bank or level of bankfull discharge of one side of a water body;[26] therefore, a 50 meter buffer on a 10 meter stream would create a zone at least 110 meters wide (Wenger 1999, Fischer and Fischenich 2000).

As with other conservation thresholds, the scientific literature does not support an ideal buffer width applicable in all circumstances. This survey found recommended buffer widths ranging from one meter up to 1600 meters, with 75 percent of the values extending up to 100 meters (*see* "A Closer Look at Buffer Width" in Appendix E for further discussion). At minimum, a riparian buffer should encompass "the stream channel and the portion of the terrestrial landscape from the high water mark towards the uplands where vegetation may be influenced by elevated water tables or flooding, and by the ability of soils to hold water" (Naiman et al. 1993).

The necessary buffer size varies considerably based on the specific management goal. In general, recommended buffer sizes are significantly greater if the intent is to protect ecological functions, such as providing wildlife habitat and supporting species diversity, as opposed to water quality functions.

Based on the majority of scientific findings, land use practitioners should plan for buffer strips that are a minimum of 25 meters in width to provide nutrient and pollutant removal; a minimum of 30 meters to provide temperature and microclimate regulation and sediment removal; a minimum of 50 meters to provide detrital input and bank stabilization; and over 100 meters to provide for wildlife habitat functions.[27] To provide water quality and wildlife protection, buffers of at least 100 meters are recommended (*see* Figure 4).

### Other Buffer Design Considerations

The width of any given buffer is just one aspect, albeit important, which determines its ability to provide a variety of functions. Other factors to consider are the linear extent, vegetation composition, and level of protection of buffers. The following is general guidance on the design and development of buffers.

- **Vegetation:** Buffers should have diverse vegetation that is both native and well-adapted to the region. Maintaining a diverse array of species and vegetation structure (e.g., herbaceous ground cover, understory saplings, shrubs, and overstory trees) is recommended to allow for greater tolerance to possible fluctuations in environmental conditions (e.g., water levels, temperature, herbivory), and to provide for greater ecological functions (e.g., wildlife habitat) (see Fischer and Fischenich 2000 for further guidance on vegetation type, diversity, and propagation techniques).
- **Extent:** In part, the effectiveness of a buffer in meeting management objectives is a function of the linear extent of the aquatic system that is protected (Wenger 1999). Protection efforts should prioritize the establishment of continuous buffer strips along the maximum reach of stream, rather than focusing on widening existing buffer fragments (Weller et al. 1998). Protection of the headwater streams as well as the broad floodplains downstream is also recommended. Headwater streams and downstream floodplains generally encompass less than 10 percent of total landmass; thus, this level of protection is practicable (Naiman et al. 1993). Ideally, buffers

[26] The bankfull discharge is the maximum level of discharge that a stream channel can convey without flowing onto its floodplain. This stage plays a vital role in forming the physical dimensions of the channel because the flows near the bankfull stage move the most sediment over the long-term and the processes of sediment transport and deposition are the most active in forming the channel (Dunne and Leopold 1978).

[27] While a 100-meter buffer is recommended to provide for adequate wildlife values, some natural riparian habitat is too narrow to support such an area. In these cases, land use planners should consider the utility of narrower buffers, especially where they might function as wildlife corridors (see "Habitat Connectivity").

should extend along all perennial, intermittent, and ephemeral streams, lakes, shorelines, and adjacent wetlands (Weller et al. 1998, Wenger 1999), so long as such buffering would not create detrimental upland habitat fragmentation as might be the case in areas of high stream densities (Lindenmayer and Franklin 2002).

- **Buffer protection:** To ensure that buffers function adequately, all major sources of disturbance and contamination should be excluded from the buffer zone, including dams, stream channelization, water diversions and extraction, heavy construction, impervious surfaces, logging roads, forest clear cutting, mining, septic tank drain fields, agriculture and livestock, waste disposal sites, and application of pesticides and fertilizers (Wenger 1999, Pringle 2001). Another consideration is the level of legal protection afforded to the area. Whether the buffer is in preservation status or protected under a conservation easement that allows for some level of activity, for example, will also determine its ability to provide desired functions.

**BOX 4. UNDERSTANDING THE EFFECTS OF LAND USE**

The many different uses of land—whether for agriculture, silviculture, recreation/open space, or commercial or residential development—will have varying impacts on the ecosystems, habitats, and species in a region. The types, extent, and combinations of land uses within a matrix will affect the viability of habitat patch sizes, the amount of suitable habitat, the severity of edge effects, and the utility of buffers and corridors in a given landscape.

Certain land use types are likely to be more compatible with biodiversity conservation in certain landscapes, depending on the natural arrangement of physical features, habitats, and species, and the effect of previous land uses (Forman 1995). A study on breeding bird communities in central Pennsylvania, for example, found that forests within agricultural landscapes had fewer forest-associated species, long-distance migrants, forest-canopy and forest-understory nesting species, and a greater number of edge species than forest landscapes primarily disturbed by silviculture, irrespective of the effect of disturbance (Rodewald and Yahner 2001). In Colorado, ranchlands and protected reserves were found to be more compatible with species of conservation concern (including songbirds, carnivores, and plant communities) than exurban developments, which tended to support only human-adapted species (Maestas et al. *in press*).

To plan for long-term sustainability, land use planners will need more guidance on the level of compatibility of different land uses in various regions and ecosystems. As a general rule, a landscape mosaic should be planned first according to its ecological constraints (e.g., water availability, forest and soil productivity, natural flooding/fire cycles) and natural site potential (e.g., natural potential for productivity and for nutrient and water cycling) (Dale et. al. 2000). In terms of hierarchical planning, a general recommendation is for land use planners to first plan "for water and biodiversity; then for cultivation, grazing, and wood products; then for sewage and other wastes; and finally for homes and industry" (Forman 1995 *as cited in* Dale et al. 2000, p.658).

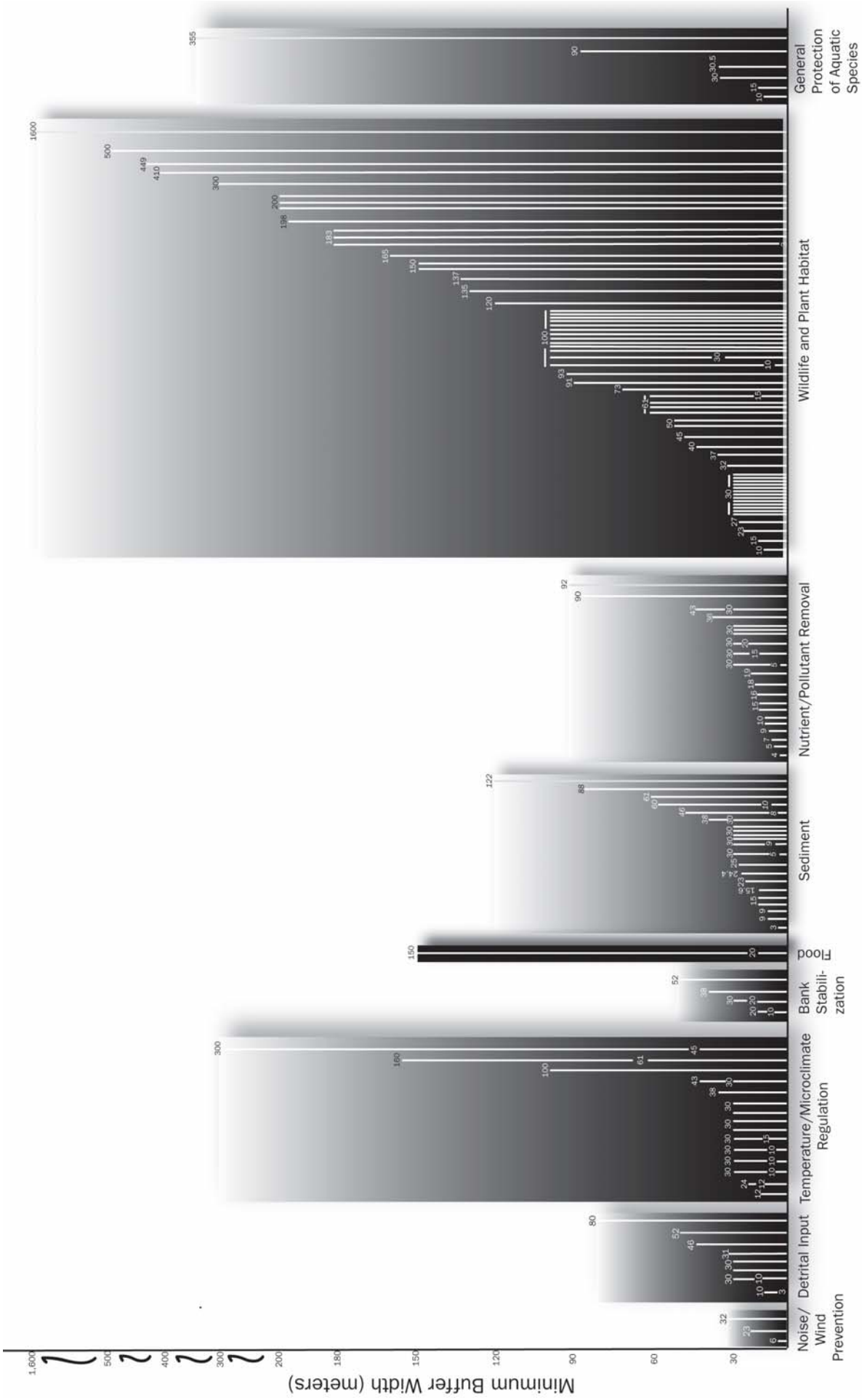


**Figure 4.** Recommended minimum riparian buffers (in meters) from each side of a water body (e.g. stream bank) needed to prevent noise/wind damage; provide detrital input; moderate temperature/microclimate; stabilize banks; provide flood attenuation; control sediment; reduce nutrients/pollutants; and provide wildlife habitat functions and general protection of aquatic systems in the United States, as cited in the scientific literature. Numbers represent the recommended minimum buffer widths; two numbers along one line indicate a recommended range (*see* Appendix D for specific findings). Lines extend from zero to the recommended buffer widths to indicate the span of habitat needed for protection.

## HABITAT CONNECTIVITY

Conservation biologists generally agree that species viability and diversity are enhanced by well-connected habitats (Fahrig and Merriam 1985, Gilpin and Soulé 1986, Primack 1993, Noss and Cooperrider 1994, Meffe and Carroll 1997, Beier and Noss 1998, Lehtinen et al. 1999). Because small, isolated reserves are unlikely to maintain viable populations over the long-term, and because climate change and disturbances require that organisms be able to move over large distances, corridors are recommended as one conservation measure to counter the negative effects of habitat fragmentation and patch isolation (Noss 1991).

Not only can riparian buffers help ensure water quality protection and habitat for plants and animals adjacent to waterbodies, but they can also act as dispersal routes for species and connect remnant patches.[28] Although riparian corridors are useful for some terrestrial wildlife, linkages outside riparian areas may be required to maintain connectivity for non-associated upland species (McGarigal and McComb 1992).

Corridors (also referred to as conservation corridors, wildlife corridors, or dispersal corridors) are intended to permit the direct spread of many or most taxa from one region to another (Brown and Gibson 1983 *as cited in* Noss 1991). They should facilitate foraging movements, seasonal migrations, dispersal and recolonization, and escape from disturbance (Saunders et al. 1991, Soulé 1991). Whether or not corridors actually provide connectivity will depend largely on the species in question and its dispersal capabilities and movement patterns across the landscape (Saunders et al. 1991). Given the species-specific nature of this issue, generalizations about the biological value of corridors are under debate among the scientific community (Noss 1987, Simberloff and Cox 1987, Simberloff et al. 1992, Franklin 1993, Beier and Noss 1998) (for further discussion *see* Appendix A "Further Analysis").

### Managing for Optimal Corridor Width

An important design consideration when maintaining or establishing habitat corridors is width. Corridor width can influence the dispersal behavior of species, resulting in changes in home range size, shape, and use. In addition, corridor width is positively correlated with the abundance and species richness for birds, mammals, or invertebrates (Lindenmayer and Franklin 2002). As is true for other conservation thresholds, in general, the wider the better. Wider corridor bands are recommended to provide interior habitat conditions, which allows for the movement and/or habitation of interior species. In addition, greater habitat area is more likely to provide sufficient cover for species from predators, domestic animals, or human disturbance (Forman and Godron 1981). Corridors that are too narrow may consist entirely of edge, thus, deterring the use by interior or area-sensitive species or causing an increase in mortality from predation (Wilcove et al. 1986).

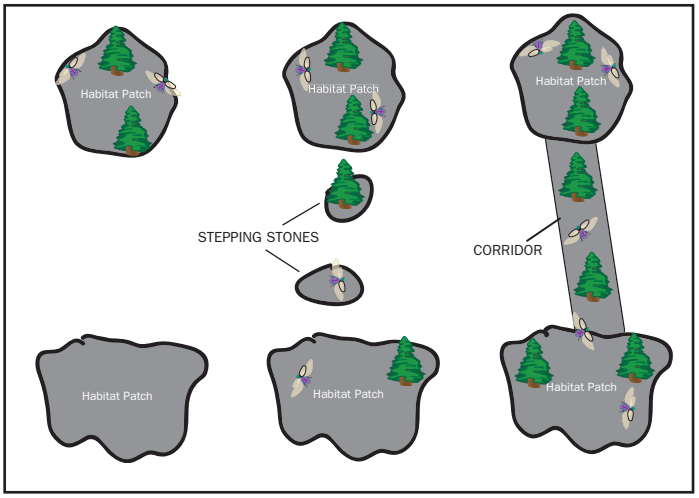


***Diagram 6. Habitat Connectivity.*** *Habitat connectivity can be increased by the protection of stepping stone patches or by the establishment of a corridor. Modified from Dramsted et al. (1996), Landscape Ecology Principles in Landscape Architecture and Land-Use Planning, p. 37.*

Although corridor width has been identified as an important design element, few studies explicitly examined minimum corridor width requirements. This survey found a limited number of studies that provide indirect evidence on effective corridor sizes, however, none of the reviewed studies explicitly tested different corridor widths with the goal of determining an optimal size. Although they did not directly examine recommended corridor width, three studies did find corridor widths of 32 meters and 100 meters to encourage the movement of butterflies and reduce species turnover rates for breeding birds, respectively (Haddad and Baum 1999, Haddad 1999 for butterflies; Schmiegelow et al. 1997 for birds).

Data limitations on the relationship between corridor width and species response prevent the development of recommendations on optimal corridor size. For any given set width, corridor effectiveness will vary with other attributes, such as length, habitat continuity, habitat quality, and topographic position in the landscape, among other factors (Lindenmayer and Franklin 2002) (*see* "Other Corridor Design Considerations").

First and foremost, land use planners should strive to limit the degree of isolation between existing habitat patches and optimize the natural connectivity to allow for the dispersal of sensitive native species through the most appropriate means. This may be done by establishing habitat corridors, maintaining specific structural conditions within the landscape, or setting aside stepping stone patches (Lindenmayer and Franklin 2002) (*see* "Inter-patch distance").

[28] A riparian corridor is a strip of vegetation adjacent to an aquatic system that connects two or more larger patches of habitat through which an organism is likely to move (Fischer et al. 2000). Corridors are not only riparian but also can be positioned in upland environments as well.

Simultaneously, land use planners should minimize the connectivity of artificial habitats like clearcuts, agricultural fields, and roadsides that tend to spread exotic and pest species (Noss 1991).

### Other Corridor Design Considerations

Corridor width is one important factor that determines whether a corridor will enhance landscape connectivity. Other factors to consider are the condition of the landscape matrix, the distances between remnant patches, and the extent and configuration of the corridors themselves.

- **Condition of landscape matrix:** The landscape matrix in which corridors are embedded greatly influences corridor use. If conditions in the matrix are suitable (e.g., sufficient original vegetation cover exists), then species reliance on corridors may be minimized. On the other hand, if matrix conditions are inhospitable or degraded (e.g., are highly developed or fragmented; have disrupted ecological processes or disturbed conditions; or are highly invaded by exotic species), then corridor systems linking remnant patches may be required to retain landscape connectivity (Rosenburg et al. 1997 *as cited in* Lindenmayer and Franklin 2002). Given that land use planners often work in extensively developed or developing areas, the latter case is the most likely. Understanding the relationship between the landscape matrix and the movements of target organisms will be fundamental in determining the best placement of corridors to enhance connectivity (Lindenmayer and Franklin 2002).

- **Inter-patch distance:** The distance between remnant patches will affect the conservation value of corridors. When distances between remnant patches are short as compared to the movement ability of target species, a stepping stone approach may be the most effective mechanism for promoting dispersal (*see* "Patch location/configuration"). On the other hand, if the distance separating habitat fragments is relatively far, corridors may be the right mechanism to provide landscape connectivity (Haddad 2000).

- **Corridor configuration and extent:** Networks of intersecting corridors may provide for more effective migratory pathways, allowing greater opportunities for animal foraging and predator avoidance (Forman and Godron 1981). Ideally, a corridor would "encompass the entire topographic gradient and habitat spectrum from river to ridgetop" (Noss 1991). Such an expansive corridor network may allow for the representation of different native habitat and land cover types in a region. In addition, having such a broad system of corridors would help enhance overall resiliency in case of the destruction of individual corridors by unexpected disturbances (Noss 1991).

**BOX 5. CONSERVATION THRESHOLDS: A STARTING POINT**

The following summarizes findings from a select sample of scientific papers pertinent to species and ecosystems in the United States on critical thresholds related to minimum habitat patch area, proportion of suitable habitat, edge influence, and riparian buffer width. Recommendations are based on the goal of capturing 75 percent of the requirements found for species, communities, and habitats surveyed; thus, the third quartile was used by calculating the value for which 75 percent of the threshold values lie below this value (after numerical ranking). These guidelines should be interpreted very cautiously because they are based on a small sample, and may not be applicable for specific species, habitats, and geographic settings of concern. Land use planners and land managers should consider these results as a baseline from which to launch more tailored and in-depth assessments.

**Habitat Patch Area**

In general, land use planners should strive to maintain and protect habitat patches greater than 55 hectares (137.5 acres). The goal should be to maintain larger parcels greater than 2,500 hectares (or about 6,175 acres) to protect more area-sensitive species.

**Proportion of Suitable Habitat**

In general, land use planners should strive to conserve at least 20 percent up to 50 percent of the total landscape for wildlife habitat, where possible.[†] The conservation of greater proportions of habitat—such as a minimum of 60 percent—may be needed to sustain long-term populations of area-sensitive species and rare species.

**Edge Influence**

In general, to avoid the negative effects of edges on habitats, land use planners should consider establishing buffer zones up to at least 230 to 300 meters from the periphery of edges.

**Riparian Buffer Width**

In general, land use planners should plan for riparian buffer strips that are a minimum of 25 meters in width to provide for nutrient and pollutant removal; a minimum of 30 meters to provide temperature and microclimate regulation and sediment removal; a minimum of 50 meters to provide detrital input and bank stabilization; and over 100 meters to provide for wildlife habitat functions. To provide water quality and wildlife protection, buffers of at least 100 meters are recommended.

**Landscape Connectivity**

Land use planners should strive to reduce the distances between habitat patches and to optimize the natural connectivity of the landscape. This may be done by establishing habitat corridors that connect previously isolated patches; by maintaining the natural, structural conditions within the landscape; or by setting aside stepping stone patches. Simultaneously, land use planners should minimize the connectivity of artificial habitats like clearcuts, agricultural fields, and roadsides.

‡ The 50 percent recommendation is based on capturing 75 percent of the threshold values surveyed; 20 percent is based on capturing 50 percent of threshold values surveyed. The latter recommendation is provided because land use planners are often working in highly developed regions where protecting 50 percent or more of the landscape is impractical.

# RECOMMENDATIONS FOR FUTURE RESEARCH AND ACTION

## THE ROLE OF THE SCIENTIFIC COMMUNITY

More scientific research is needed to help inform specific land use decisions being made everyday in the United States—decisions that significantly determine the future of domestic biodiversity. This survey of the scientific literature found that out of all land management strategies geared toward reducing the effects of urbanization and sprawl, the most substantial guidance available is on how to best develop riparian buffers. Conversely, science offers very little consensus opinion to land use planners on how to determine which habitat patches to conserve and where; the amount of habitat to protect in a region or conversely the maximum amount of impervious surface to allow; the ways in which to mitigate against the negative consequences of habitat edges; or how best to design and plan for corridors. In addition, because development will continue to occur and because private lands are increasing becoming more important in species conservation, more information is needed on the level of compatibility of the various types and combinations of land uses with biodiversity. To better inform decisionmaking, the scientific community needs to provide more specific information to land use practitioners on how to implement ecologically conscious growth.

> *"Fragmentation effects are difficult to translate into management rules-of-thumb for several reasons: (1) they tend to be highly specific to the taxa, spatial scales, and ecological processes considered; (2) they vary according to the landscape type and its structure; and (3) their influence on species distribution and abundance may be obscured by local effects such as changes to certain microhabitat features (e.g., habitat degradation)."*
>
> Villard (2002), Ecological Society of America, Ecological Applications 12(2), p.319

In addition, scientists should address the taxonomic bias in the literature. A recent review of 134 papers on habitat fragmentation found that over half of the research focuses on birds, the vast majority being songbirds. Mammals and plants come second, making up about 18 percent; invertebrates and reptiles/amphibians are the most understudied, with only 9 percent and 4 percent, respectively (McGarigal and Cushman 2002). Our survey found similar results. Most of the fragmentation research used for this study looks at the effects of fragmentation on bird species and, to a lesser extent, mammals. Sixty-six percent of the surveyed research on edge effects; 57 percent on patch area; 44 percent on proportion of suitable habitat; and 32 percent of the wildlife papers on buffers measured effects on bird species. Mammals made up 24 percent of the research on proportion of suitable habitat; 21 percent on patch area; 11 percent of research on buffers; and 9 percent on edge effects. Fish, invertebrate, and plant response made up anywhere from zero to 13 percent of the research. This focus has left particularly large gaps in research on reptiles and amphibians, invertebrates, and plants.

If the scientific community wishes to help curtail the loss and endangerment of species, then it will need to start addressing other taxonomic groups. The most at-risk species in the United States are flowering plants and freshwater species. In terms of species numbers, flowering plants have by far the greatest number of at-risk species (over 5,000 species are at-risk). In terms of the proportion, species that rely on freshwater habitats—mussels, crayfishes, stoneflies, amphibians, and fishes—exhibit the highest level of risk. With only 14 percent of bird species being at risk and 16 percent of mammal species, these groups are the least threatened (Master et al. 2000).

Above all else, this literature search reveals the inadequacy of the information currently available for land use planners to use in their day-to-day decisions, which have profound effects on biological diversity. The scientific community should be commended for developing theories, such as metapopulation concepts, which have important implications for applied management like endangered species recovery. However, due to the simplified assumptions implied within metapopulation models, their application to real landscapes is severely limited (Fahrig and Merriam 1994). In addition, whether metapopulations are actually common in real landscapes is largely unknown (Lindenmayer and Franklin 2002). Similarly, the SLOSS debate on whether a single large reserve is better than a group of small ones, which consumed the academic community for many years, failed to produce concrete management recommendations (Forman 1995).[29] In order for ecological principles to be put into practice, land use professionals will need general rules of thumb and specific guidelines to implement on-the-ground.

[29] SLOSS stands for Single Large Or Several Small, which refers to whether conservation reserves are best designed as one large tract of protected land versus several smaller tracts of the equivalent area (Meffe and Carroll 1997).

Only about 10 percent of the papers reviewed in this survey provided quantitative information useful for developing conservation thresholds relevant to land use planning. Similarly, most of the papers published in the Journal of Applied Ecology during a large proportion of the last 30 years have been devoid of practical applications or management recommendations (Pienkowski and Watkinson 1996). Given the complexity surrounding habitat fragmentation, it is understandable that the scientific community is apprehensive about presenting or extrapolating research findings such that they can be easily applied to land use planning and management. Scientists even warn that providing general thresholds "may be more dangerous than useful because many species can be lost if the threshold is determined by averaging over the requirements of many species" (Mönkkönen and Reunanen 1999).

Without adequate information on land use thresholds, land use decisionmaking will continue to be uninformed by the best available science. Although reaching consensus in the scientific community on these thresholds may be an impractical goal, if enough resources are directed to answer specific land use threshold questions, research results may begin coalescing on some general range of values, which would provide useful guidance. Hopefully, this literature review will prompt scientific research that is relevant to and usable by everyday land use practitioners.

## THE ROLE OF THE POLICY COMMUNITY

Although more scientific study is needed to provide ecologically-based and scientifically defensible advice on land use planning and land management thresholds, substantial research has already been conducted. The policy community could play a more active role as a conduit between the scientific community and land use planners—to help interpret the available research, help with dissemination, and communicate back to scientists on research gaps and needs. Periodical reviews of the literature, such as this survey, should be conducted to provide land use planners and land management practitioners with the most up-to-date and best available scientific information. In addition, where possible, scientific research will need to be translated into easily applied management recommendations. To ensure that land use decisions are well-informed, mechanisms should be in place to communicate current scientific understanding to the general public. Scientific institutes, such as the National Academy of Sciences, among others, should conduct or commission studies on areas where particular research gaps are found. Clear arguments, particularly those that are economically based, need to be conveyed to the land use community so that they understand why they should make land use decisions with biodiversity in mind.

## THE ROLE OF THE LAND USE PLANNING COMMUNITY

The failure of land use planners to communicate their needs to the scientific community may be another reason that science inadequately addresses land use planning concerns. Land use practitioners should be encouraged to better communicate with scientists about the type of information that they need and in what format it would be most useful. An exchange about what is working on-the-ground and what is not, and about public concerns regarding land use alteration and biodiversity, would be of great benefit.

However, given the diverse habitat requirements of species and the great uncertainty and unpredictability of species and ecosystem response to habitat alteration, land use planners should not wait for the development of *the magical threshold value* before applying known general ecological guidelines, such as those presented by the Ecological Society of America's Land Use Committee. To ensure that our natural resources will be conserved for future generations, spatial planning needs to proceed immediately using the best available information.

Land use planners should err on the side of caution and adopt the most conservative threshold ranges, particularly since factors, such as global climate change, are likely to intensify land use impacts. The future change of our climate —predicted to rise globally by an average about 4° Fahrenheit (2° Celsius) by the year 2100—is likely to alter the level and timing of temperature and precipitation and to increase the frequency of environmental disturbances (like floods, droughts, hurricanes, and fires), causing shifts in suitable ecosystem and species ranges, as well as the composition of species and flows of energy and nutrients (Field et. al. 1999). For species and ecosystems to be able to withstand such drastic environmental perturbations, sufficient intact and well-connected habitat will be essential. Thus, larger patch sizes, greater habitat area, wider buffers, and more corridors are likely required under future global warming than presented in this review.

Land use planners should realize that, ultimately, there is no replacement for site-specific assessments. It is both difficult and often misleading to develop thresholds that generalize across landscapes and across ecoregions (Mönkkönen and Reunanen 1999). Since thresholds will fail to be meaningful when generalized across landscapes, ecosystems, and states, thus unable to capture the unique variation in nature, land use planners and managers need to work in close collaboration with ecologists (Mönkkönen and Reunanen 1999). Land use professionals should use the articles and research highlighted in this review only to the extent that they are appropriate for their region and to launch more in-depth analyses. This review predominately covers thresholds and guidelines for planning at a large (coarse) scale. This report,

however, does not focus on the conservation of rare or localized species or habitat types, and species other than birds and mammals. It does not provide guidance on how to protect lands of greatest biological value. Rather than simply adopting the types of measures discussed in this review, land use planners should collaborate with scientists to better protect small patch communities and local-scale species and to better identify site-specific and regional conservation needs.

Although land use planners are asked to make local, site-specific decisions on a daily basis, it is still vital to maintain a landscape perspective. Numerous, small development projects that independently may not contribute to significant habitat loss, degradation, or fragmentation, may cumulatively have devastating consequences. Site-specific land use decisions would be more ecologically mindful if better informed by scientific information. Yet, to really make a difference for biodiversity, land use planners will need to begin considering their cumulative and landscape-scale impacts.

Biodiversity needs to be a central component directly considered in all land use and community planning projects. An overarching land use vision with a statewide or county-wide blueprint for protecting ecosystems, representative and rare species, and broader patterns of biodiversity would serve as an important framework to guide the implementation of the specific thresholds outlined in this report. For example, Florida developed a model that identifies areas with priority conservation significance and landscape linkages (i.e., corridors) captures most of the major ecological communities and known occurrences of rare species for the entire state (Hoctor et al. 2000). Conserving regional biodiversity and accounting for land use impacts over a large scale—both spatially and temporally—will likely require inter-municipal cooperation and state-level leadership, as in the case of Florida.

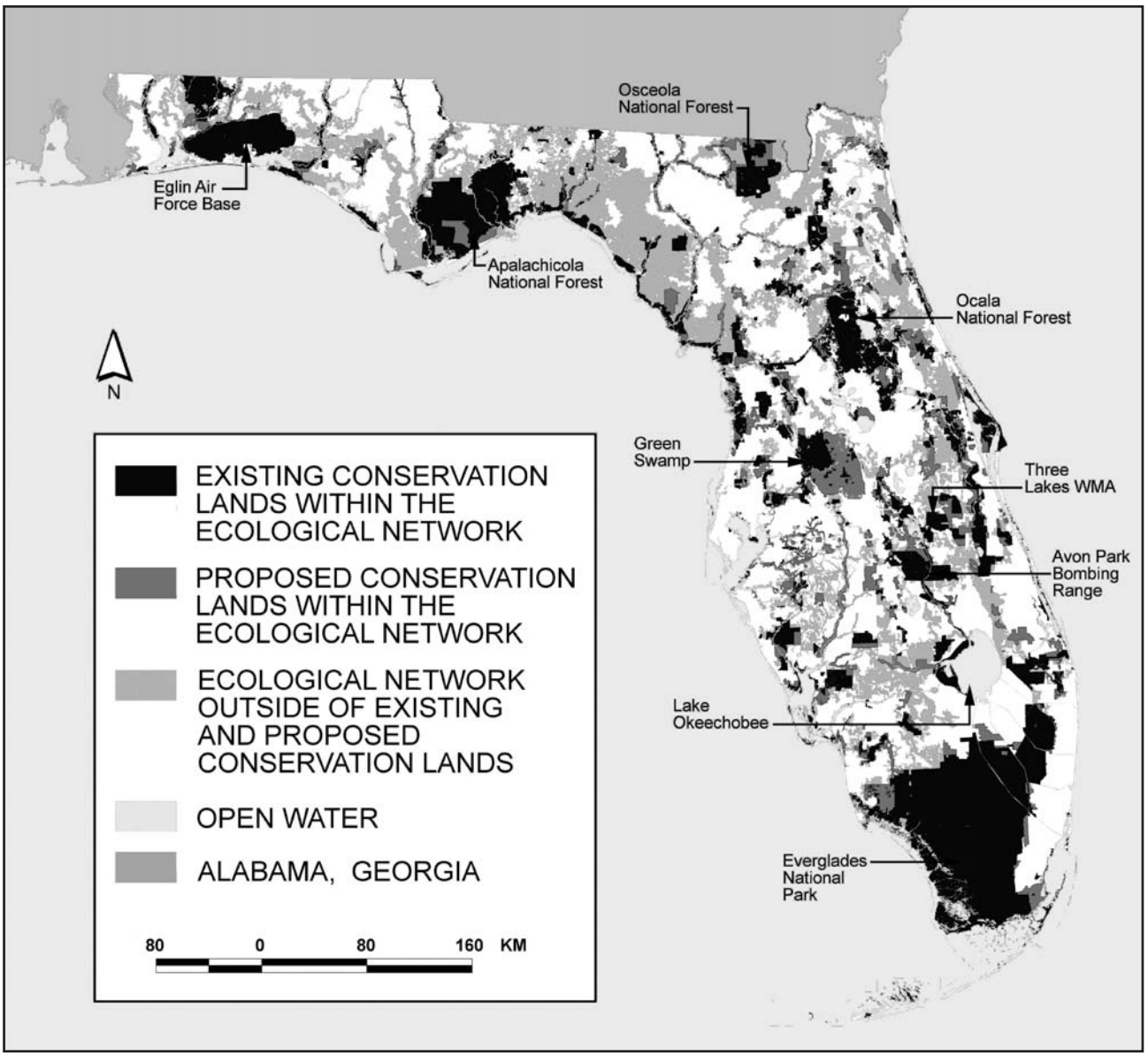


***Diagram 7. Florida Ecological Network.*** *Results from the Florida Statewide Greenways GIS decision support model. Courtesy of the University of Florida.*

# CONCLUSION

Land use decisions have profound effects on biological diversity. Land use planners, however, have many opportunities to tailor their traditional land use tools to better address biodiversity conservation. To the extent possible, planning decisions should be based on the best available science. Although the current scientific literature provides much guidance to land use planners on how to incorporate ecological knowledge into their actions, significant gaps exist in the information provided by the scientific community. The more that is known about how human mediated fragmentation impacts ecosystems, the more it is revealed that species and communities interact in complex, dynamic, and often unpredictable ways on multiple temporal and spatial scales. For science to meet the needs of local land use planners, on-going and dedicated collaboration needs to exist between the scientific, policy, and land use planning communities. Although a consensus may never develop in the scientific community on broad conservation thresholds, more effective and targeted guidance can be developed to help land use planners make more ecologically informed decisions. Without this information, little incentive exists for land use planners and land managers to factor biodiversity considerations into their decisions at all.

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# APPENDIX A. FURTHER ANALYSIS

Titles and abstracts of 1,458 papers within scientific and land use planning journals were reviewed to determine whether they provide specific information on conservation thresholds that could help guide land use planning in the United States. A total of 160 papers (11 percent) were selected for inclusion in this study: 20 papers with quantitative information on minimum patch area; 27 papers on minimum proportion of suitable habitat; 25 papers on edge width distance; and 88 papers on minimum buffer width.[30]

## A CLOSER LOOK AT HABITAT PATCH SIZE

Only 20 papers were found in the scientific literature to provide specific information on minimum patch area requirements pertaining to ecoregions within the United States; these papers provided 28 citations on threshold patch size.[31] The majority of papers that address habitat patch size focus primarily on estimating the area of habitat needed to sustain specific target species—as measured by species occurrence, population densities, or breeding success—and to a lesser extent species diversity or community assemblages. As reported in previous literature reviews, little is known about the amount of patch area needed to maintain essential ecosystem functions, such as primary productivity, nutrient and hydrologic cycling, or disturbance regimes (Forman 1995).

This survey reveals a taxonomic bias in scientific literature. Out of the total 28 citations, 16 citations (57 percent) pertain to birds and six citations (21 percent) to mammals. Minimum patch area requirements reported in the literature ranged from one hectare to over 2,500 hectares for birds, and from one hectare to over 220,000 hectares for mammals. Only two studies provide three relevant citations on patch size requirements for plant species: an estimated two hectares needed to sustain a representative tree community type (Elfstrom 1974), and at least 10 hectares needed to conserve an old growth forest if surrounded by secondary forest, or 100 hectares if surrounded by clearcuts (Harris 1984). Two additional studies provide patch area information for invertebrates, which indicate that habitat requirements for invertebrates may range from a minimum of 0.0004 hectares (four meters squared) up to one hectare. One study provides information for fishes, predicting a 50 percent chance of bull trout occurrence in watershed patches larger than 2,500 hectares (Rieman and McIntyre 1995).

Reported habitat patch size thresholds vary widely, even within the same taxonomic group and for the same species. This lack of convergence on minimum critical patch size reflects the large range of habitat needs exhibited by different species across different ecosystems and that species response to habitat fragmentation is very complex. This natural and inherent complexity is compounded by the lack of consistency in methodology researchers used to measure minimum habitat requirements—with differing study designs as well as parameters measured. Minimum patch area is commonly determined for target species by measuring species occurrence on a site, species densities, or nesting/breeding success. To a lesser extent studies evaluate the persistence of species diversity or community assemblages. Since different parameters are measured, different results are produced. For example, according to this survey, neotropical wood thrushes require anywhere from one hectare up to greater than 2,500 hectares of habitat depending on the variable measured (evidence of breeding versus nesting success and occurrence of nesting predation) (Robbins et al. 1989 and Trine 1998).

By in large, this review reiterates a viewpoint expressed by the scientific community several years ago: simply not enough is known about minimum critical size that should be protected in order to maintain species diversity and species composition in any given ecosystem (Lovejoy and Oren 1981 *as cited in* Saunders et al. 1991; Noss and Harris 1986). Given the lack of information on the habitat patch size requirements of species, communities, or ecosystems in the United States, land use planners should work with land and natural resource agencies and local scientists to identify the habitat patches most in need of protection.

## A CLOSER LOOK AT PROPORTION OF SUITABLE HABITAT

Twenty-seven papers were encountered within the scientific literature reporting extinction or habitat fragmentation thresholds on the proportion of suitable habitat needed for an array of species. The papers surveyed provide 26 different estimates of the amount of habitat needed, depending on the species and taxa in question, and the parameter measured. The majority of findings—42 percent (11 citations)—relate to the amount of habitat recommended to maintain bird

[30] These numbers only include papers that provided specific threshold information, which was factored into the assessment (see Appendices). Review papers and background papers are not included in these figures if they failed to provide relevant quantitative information.

[31] Because papers provide multiple findings/recommendations related to minimum patch area size requirements, the number of papers does not necessarily equal the number of citations.

species or populations. Based on this review, bird species in the United States may require anywhere from 5 percent to 80 percent of suitable remaining habitat.

The second most commonly researched group is mammals. About 23 percent of the findings (six citations) pertained to mammalian response to habitat loss and habitat isolation, which suggests that this taxonomic group may require anywhere from 6 percent to 30 percent of suitable habitat. This range, however, should not be considered representative for all mammalian groups, because it only includes small mammals (e.g., chipmunks, rabbits, squirrels) (*see* Appendix C). An important focal group—wide-ranging predators and large-bodied mammals—failed to be represented in this select review, thus, the proportions are skewed to the smaller range relevant to smaller bodied mammals.

Four studies (five citations) provide thresholds for invertebrates, ranging from 20 percent up to 60 percent of required protected habitat. Additionally, four studies base their findings on models predicting response by hypothetical species, which reveal that threshold responses may occur anywhere from as large a range as 20 percent to 90 percent of habitat loss.

As revealed by the diverse range of values offered by scientists, it is clear that no common threshold exists for the amount of habitat needed to support different populations of species or needed to minimize the negative effects of habitat fragmentation in a landscape. The lower range of proportions (e.g., 5 to 30 percent) tend to be habitat fragmentation thresholds, as determined by evidence that species are in some way negatively affected by habitat loss or habitat isolation. A significant proportion of these studies is based on predicted species response to habitat loss and fragmentation by models (at least seven of the citations). The larger proportions (e.g., 60 to 80 percent) tend to be based on models that predict the amount of habitat needed to sustain long-term species persistence or to prevent the consequences of extensive habitat fragmentation in a landscape.

Given the sparse and diverse findings, land use planners should apply these thresholds with great caution. As reported in earlier reviews, most of the habitat fragmentation studies are performed during short time periods (e.g., one or two seasons), and only provide a snap shot of how species may respond to habitat loss and isolation (Andrén 1994). In these studies, the damage to populations resulting from habitat alteration could have occurred previously (Mönkkönen and Reunanen 1999)—particularly for historically modified landscapes like eastern deciduous forests (Meier et al. 1995, Mitchell et al. 2002). Thus, the long-term consequences of fragmentation are likely not revealed in this select review because a time lag often exists between the fragmentation of a landscape and the associated response by species, populations, or systems (Andrén 1994).

## CLOSER LOOK AT EDGE INFLUENCE

Twenty-five studies surveyed provide 32 findings on the distance that edges might affect habitats in the United States. Like the other conservation thresholds, the focal species of choice is birds. Sixty-six percent of the findings (21 citations within 12 articles) measure the influence of edges related to bird response, revealing that edge influence for birds extends anywhere from about 16 meters to up to almost 700 meters. Studies measuring bird or bird nest abundance report that edge effects extend between 180 and 687 meters where as those measuring predation and nesting success range from 50 to beyond 600 meters. Bird response (e.g., flushing distance) to disturbances such as roads and human traffic extends from 16.27 meters to 300 meters.

Secondarily, the influence of edges is measured by abiotic responses. Edge effects based on microclimate conditions —such as changes in light, temperature, humidity, nutrients, and moisture—are found to extend from eight meters up to 240 meters based on five studies (six citations) (Ranney et al. 1981, Laurance and Yensen 1991, Brothers and Spingarn 1992, Matlack 1993, and Chen et al. 1995).

To a lesser extent, the scientific literature provides information on the effects of edges on mammals and plants. Three studies have found that mammals avoid edge environments from at least 45 meters to 900 meters. For example, studies reveal that wide-ranging grizzly bears are displaced from 100 to 900 meters due to traffic along roadways (Mills 1996, Miller et al. 2001, and Weaver et al. 1996). One study provides evidence on the influence of edges on plant communities, finding that almost no recruitment of seedlings occurs within 65 meters of forest clear-cut edges in Oregon (Jules 1998).

Within this review, no single study is found to report edge influence in relation to invertebrate communities in the United States. As is true for the other thresholds, research has been conducted more extensively in tropical forests outside of the United States, and may serve to address knowledge gaps. For example, a study in Brazil reveals that edge effects may be more intense for invertebrate groups. Edge effects may penetrate up to 50 meters as measured by bird density; 80 meters as measured by soil moisture; 100 meters as measured by canopy height, foliage density, and leaf-litter invertebrate abundance and richness; 200 meters as measured by leaf-litter invertebrate species composition and invasion of disturbance adapted beetles; and 250 meters for invasion of disturbance-adapted butterflies (Laurance et al. 1997).

To get a better handle on the intensity of edge influence in the United States and, consequently, the amount of habitat needed to reduce the effects of edges and related disturbances, land use planners will need more site-specific guidance from ecologists. Land use planners and land managers

will also need more information on effective measures that can be taken to better "soften" the many different types of edges affecting the large array of habitat types in the United States.

## A CLOSER LOOK AT BUFFER WIDTH

Eighty-eight papers (156 citations) are found to provide recommendations on riparian buffer widths.[32] Of all the conservation thresholds surveyed, buffer prescriptions are the most studied and best documented. Substantial research has been conducted on the effective size of buffers, particularly related to water quality considerations, to assist regulatory and land management agencies in developing scientifically sound minimum buffer width (Castelle et al. 1994). Several literature reviews have been conducted to help inform state and local governments in developing riparian protection plans and ordinances (*see* Johnson and Ryba 1992, Furfey et al. 1997, Wenger 1999, Fischer 2000, Fischer et al. 2000, and Metro 2001). In April 2000, the U.S. Army Corp of Engineers released national recommendations for riparian buffer strip and riparian corridor design (Fischer and Fischenich 2000). This baseline research significantly informed the buffer width recommendations in this report.

One review offers the following buffer prescriptions: a three to 10 meter buffer to provide detrital input; 10 to 20 meters for stream stabilization; five to 30 meters for water quality protection; 20 to 150 meters for flood attenuation; and 30 to 500 meters or more for riparian habitat (Fischer and Fischenich 2000). The Institute's review reveals wider buffer ranges to provide a variety of functions, with a range of six to 32 meters to reduce noise and wind damage; 10 to 52 meters to stabilize stream banks; three to 80 meters to provide detrital input; four to 92 meters to remove nutrients and pollutants; three to 122 meters to remove sediments; 20 to 150 meters to provide flood attenuation; 10 to 300 meters to regulate temperature and microclimate; and three to 1600 meters to provide wildlife habitat (*see* Appendix E).

Findings in this review primarily relate to river and stream systems, however, a small number of papers explicitly address wetlands (*see* Buhlmann 1998 and Joyal et al. 2001). Although not all wetlands lie within riparian zones (e.g., isolated wetlands), they serve as vital resources and provide essential functions, such as flood storage, water purification, sediment trapping, and wildlife habitat (Mitsch and Gosselink 1993). Thus, placing buffers around these areas to protect them from nearby development activities is also advised.

Predicting the adequacy of a buffer strip to provide sufficient wildlife habitat and to protect natural species diversity is quite challenging. The width recommendations primarily focus on birds and are based on various methods—ranging from determining species presence or nesting within the area to determining species abundance, diversity, or community assemblages. Few studies attempt to measure species survival over time; thus, it is questionable whether the recommended buffers will ensure persistence of the target species and communities over the long-term.

As mentioned above, the actual effective size and adequacy of any given buffer is determined by the management target, as well as other site-specific factors, such as site and watershed conditions; intensity of adjacent land use; slope steepness; stream order; soil characteristics (depth, texture, erodibility, moisture, pH); floodplain size and frequency of inundation; hydrology; buffer characteristics (e.g., type, density, and structure of vegetation, and buffer length); and landowner/manager objectives (Naiman et al. 1993, Castelle et al. 1994, Wenger 1999, Todd 2000). For example, larger buffers may be necessary when the buffer strip is in poor condition (e.g., comprised of sparse exotic vegetation, disturbed/erodible soils); is located on steep bank slopes (e.g., greater than 10 percent to 15 percent);[33] is surrounded by intense land uses; or is located within watersheds with increased impervious surfaces that results in high nutrient, chemical, and sediment inputs, and runoff (e.g., adjacent to urban/suburban areas or intensive agricultural farmland). Such factors should be considered when evaluating the applicability of the general recommended buffer sizes (*see* Wenger 1999, Fischer and Fischenich 2000, Metro 2001). In addition, management decisions should not only be based on site-specific characteristics but also on basin or watershed level needs to maintain the hydrologic connectivity and natural variability of these systems (Naiman et al. 1993, Pringle 2001). [34]

## A CLOSER LOOK AT CORRIDORS

To determine whether or not corridors are effectively enhancing species conservation, scientists evaluate whether (and how) patch occupancy, species abundance and diversity, colonization, and immigration rates change with and without the presence of corridors (Beier and Noss 1998).

Many studies lend support to the premise that corridors retain important species or provide faunal habitat (Bennett 1998). Few studies, however, provide clear evidence that corridors are required for species movement in landscapes (Hobbs 1992). Many species simply do not respond or require corridors (Rosenburg et al. 1997, Bowne et al. 1999, Hannon and Schmiegelow 2002). For example, male-hooded warblers preferentially travel across open areas, even in

[32] Some papers recommend multiple buffer widths, for example, they may suggest different widths for different species or functions of concern. Thus, the number of papers does not equal the number of citations.

[33] Herson-Jones et al. 1995 (found that greater than 10 percent slopes are steep slopes) and Nieswand et al. 1990 (found that greater than 15 percent slopes are steep) (as cited in Wenger 1999).

[34] Hydrologic connectivity refers to water-mediated transfer of matter, energy, or organisms within or between elements of the hydrologic cycle (Pringle 2001).

landscapes with corridors connecting habitat patches (Norris and Stutchbury 2001). For species like the Northern spotted owl, which has been found to disperse randomly, the presence of corridors will likely not enhance its survival (Murphy and Noon 1992 *as cited in* Lindenmayer and Franklin 2002). Because of the complexity of animal behavior, land use planners should not assume that establishing corridors between habitat patches in a region will automatically guarantee enhanced and effective dispersal and recolonization among the separated wildlife populations.

The benefits of corridors should be weighed against their potential repercussions. Scientists warn that corridors may potentially transmit diseases, fires, or other catastrophes among habitats and populations, as well as increase invasions by non-native invasions or exposure to predation (Simberloff and Cox 1987, Noss 1991, Noss and Cooperrider 1994). To add to the complexity of this issue, many corridor studies—both those that claim corridor benefits and those that claim costs—suffer from design flaws that limit their ability to discern the real conservation value of corridors (Beier and Noss 1998).

A recent scientific review is able to shed some light on the corridor controversy; a review by Beier and Noss (1998) presents evidence from well-designed studies that suggest that corridors seem to be providing sufficient connectivity to enhance the viability of wildlife populations. Conversely, a lack of evidence backs the assertion that the presence of corridors actually has a greater adverse impact than their absence (Beier and Noss 1998, Hobbs 1992). Although wildlife corridors should not be automatically assumed to be an essential component of all land conservation strategies (Lindenmayer and Franklin 2002), planners should consider corridors as one potentially valuable conservation tool (Beier and Noss 1998, Hobbs 1992).

# APPENDIX B. MINIMUM PATCH AREA

Minimum patch area requirements (in hectares) found within the scientific literature (as of December 2001) to maintain populations or communities of animal or plant species in the United States. One hectare is about 2.5 acres.

| TAXA | PATCH AREA | FINDING | STATE | CITATION |
|---|---|---|---|---|
| **Birds** | | | | |
| | ≥ 1 ha | Minimum area requirement for breeding wood thrushes is 1 ha, although nesting success on fragments of that size would be extremely low. | MD, PA, VA, WV | Robbins et al. 1989 |
| | > 1 | Five species of chaparral-requiring birds were supported by census plots larger than 1 ha. | CA | Soulé et al. 1992 |
| | ≥ 2 ha (seed-eating birds) ≥ 40 ha (insect-eating birds) | The minimum area point[1] for insect-eating birds was estimated to be at least 40 ha, in contrast to 2 ha for seed-eating birds. This is interpreted as the habitat size needed to support a representative bird community. | NJ | Forman et al. 1976[2] Galli et al. 1976[2] |
| | ≥ 5 ha (marsh) | Ten of the 25 species did not occur in marshes less than 5 ha. | IA | Brown and Dinsmore 1986 |
| | ≥ 5, ≥ 30, ≥ 40, ≥ 50, ≥ 55 ha | Estimates of minimal area requirements for five area-sensitive species ranged from 5 to 55 ha. | IL | Herkert 1994 |
| | ≥ 6.5 ha, 15.4 -32.6 ha | Black tern required 6.5 ha in heterogeneous landscapes, but required 15.4 - 32.6 ha in homogeneous landscapes. | SD | Naugle et al. 1999 |
| | ≥ 10 ha (forest) | Forest patches ≥ 10 ha had much greater bird diversity than patches < 3.25 ha | GA | McIntyre 1995 |
| | > 80 ha | In fragments < 80 ha, nesting success was low (43%), and nest predation was high (56%). | PA | Hoover et al. 1995 |
| | < 20 ha, >2500 ha | Based on a study of cowbird parasitism and nest predation on 3 large forest tracts (1100 - 2200 ha) in southern Illinois, maintaining wood thrush populations in the midwest might require > 2500 ha reserves. In the east even a small woodlot (< 20ha) may sustain a population. | IL | Trine 1998 |
| **Mammals** | | | | |
| | > 1 ha | Control plots larger than 1 ha supported most species of rodents. | CA | Soulé et al. 1992 |
| | ≥ 5 ha | Cottontails may become vulnerable to extinction if large patches ≥ 5.0 ha are not maintained. | NH | Barbour and Litvaitis 1993 |
| | ≥ 10 ha | Fragments < 10 ha did not support populations of native rodents. | CA | Bolger et al. 1997 |

| TAXA | PATCH AREA | FINDING | STATE | CITATION |
|---|---|---|---|---|
| | ≥ 900 ha (9 km2) | More than 80% of bear sitings occurred in blocks of undisturbed habitat ≥ 9 $km^2$. | MT | Mace et al. 1996[3] |
| | ≥ 2800 ha (28 km2) | Grizzly bears in the Yellowstone ecosystem should have security blocks 28 $km^2$ in size. | MT, ID, WY | Mattson 1990[3] |
| | ≥ 220,000 ha (2200 km2) | Model predicts low extinction risk for cougars in areas as small as 2200 $km^2$, but w/ increasing risk with little immigration. | CA | Beier 1993 |
| **Fishes** | | | | |
| | > 2500 | Found support that suitable patch size (as defined by watersheds above 1600 m elevation) influences the occurrence of bull trout. Predicted probability of occurrence is 0.5 for patches larger than 2500 ha. | ID | Rieman and McIntyre 1995 |
| **Invertebrates** | | | | |
| | ≥ .0004 ha (4m2) | Vegetation patches ≥ $4m^2$, as well as open areas, were important to the distribution and abundance of carabid beetles. | OH | Crist and Ahern 1999 |
| | ≥ 1 ha | Observed minimum patch size for occupancy by populations of 3 butterfly species is 1 ha. | model | Hanski 1994 |
| **Plants** | | | | |
| | ≥ 2 ha (5 acres) | Minimum area point[1] for tree communities was estimated to be about 2 ha. | NJ | Elfstrom 1974[2] |
| | ≥ 10, ≥ 100 ha | Conserving an old-growth forest might require 10 ha if surrounded by comparable forest, but 100 ha if surrounded by a clearcut. | — | Harris 1984[4] |

— Indicates that the geographic location was not determined because the recommendation was cited secondarily from another review article.

**model** indicates that the research was conducted through modeling and therefore is not specific to any geographic area.

[1] Minimum area point is the point on a species-area curve, which shows the relationship between species number and habitat area, where there is an abrupt change in the slope. The minimum area point has been considered an index of how large a community must be to representative of the community type (Forman 1995).

[2] *As cited in* Forman 1995

[3] *As cited in* Weaver et al. 1996

[4] *As cited in* Franklin 1993

# APPENDIX C. PROPORTION OF SUITABLE HABITAT

Recommended minimum proportions of suitable habitat found within the scientific literature (as of December 2001) to maintain long-term persistence of viable populations or communities of species or to minimize the negative consequences of habitat fragmentation in the United States.

| TAXA | PROPORTION OF SUITABLE HABITAT | FINDING | STATE | CITATION |
|---|---|---|---|---|
| **Birds** | | | | |
| | ≥ 5% | When < 5% of area was covered by habitat, there was an effect on bird density. | WI | Ambuel and Temple 1983[1] |
| | ≥ 5% | When < 5% of area was covered by habitat, there was an effect on bird community. | — | Howe 1984[1] |
| | > 8% | When 8% of area was covered by habitat, there was an effect on land bird community. | — | Nilsson 1978[1]<br>Nilsson 1986[1] |
| | ≥ 10% | When < 10% of area was covered by habitat, there was an effect on species richness. | — | Soulé et al. 1988[1]<br>Bolger et al. 1991[1] |
| | >10-30% | The negative effects of patch size and isolation on native species may not occur until the landscape consists of only 10-30% of the original habitat. | review | Andrén 1994 |
| | > 15% | When 15% of area was covered by habitat, there was an effect on bird density. | — | Askins et al. 1987[1] |
| | > 20% | When 20% of area was covered by habitat, there was an effect on bird community. | MD | Lynch and Whigham 1984[1] |
| | > 22% | When 22% of area was covered by habitat, there was an effect on land bird community | — | Whitcomb et al. 1981[1] |
| | > 50% | Numerous species were more likely to inhabit wetlands in landscapes where less than 50% of the upland matrix was tilled. | SD | Naugle et al. 2001 |
| | ≥ 60% | A model assuming 60% suitable habitat suggests a high likelihood for the longterm persistence of Northern spotted owls. | model | Lamberson et al. 1994 |
| | > 80% | Metapopulation model predicted that the Northern spotted owl population would go extinct if the proportion of old-growth forest was reduced to less than 20% of landscape. | model | Lande 1988[4]<br>Lamberson et al. 1992[4] |
| **Mammals** | | | | |
| | > 6% | When 6% of area was covered by habitat, there was an effect on chipmunk density. | — | Henderson et al. 1985[1] |
| | > 6% | When 6% of area was covered by habitat, there was an effect on pika abundance. | — | Smith 1974[1]<br>Smith 1980[1] |
| | ≥ 10% | When < 10% of area was covered by habitat, there was an effect on mammal species richness. | — | Soulé et al. 1992[1] |
| | > 10% | When 10% of area was covered by habitat, there was an effect on Columbian ground squirrel presence/absence. | — | Weddell 1991[1] |
| | > 10-30% | The negative effects of patch size and isolation on the native species may not occur until the landscape consists of only 10–30% of the original habitat. | review | Andrén 1994 |
| | > 15% | When 15% of area was covered by habitat, there was an effect on small mammal presence. | — | Lomolino et al. 1989[1] |

| TAXA | PROPORTION OF SUITABLE HABITAT | FINDING | STATE | CITATION |
|---|---|---|---|---|
| **Invertebrates** | | | | |
| | ≥ 20% | The threshold for changes in movement patterns of beetles occurred at 20% coverage of cells. | CO | Wiens et al. 1997 |
| | ≥ 20% | Clover patches became significantly more isolated below 20% habitat, which disrupted the predator foraging behavior of ladybird beetles, decreasing their ability to serve as biocontrol agents of aphids. | model | With et al. 2002 |
| | ≥ 40% | Habitat specialists of grasshoppers exhibited limited movement and disjunct populations—which can affect population persistence—when preferred habitat occupied less than 40% of the landscape. | model | With and Crist 1995 |
| | ≥ 40, ≥ 60% | Rare species were disproportionately affected by fragmentation and did not occur in patches with less than 40% habitat. Over half of the species were never observed in plots with less than 60% habitat remaining. | OH | Summerville and Crist 2001 |
| **Hypothetical Species** | | | | |
| | > 10-30% | As habitat loss continues beyond the threshold (occurring somewhere in the range of 70-90% habitat loss) decline in population performance should become much more severe. But model predicts that habitat fragmentation begins to occur when about 60% of original vegetation remains. | model | Gardner et al. 1987[2] |
| | ≥ 20% | The threshold value of habitat amount is 20% habitat, below which the effects of habitat fragmentation on population persistence may become evident. | — | Andrén 1994[3]<br>Fahrig 1998[3] |
| | > 70% | Models of forest landscapes forecast that patches of old-growth forest can become fragmented even when about 70% of the landscape cover remains. | model | Franklin and Forman 1987 |
| | > 80% | Terrestrial species with low demographic potential could not persist in landscape even with 80% of suitable habitat in landscape. | model | Lande 1987[4] |

— Indicates that the geographic location was not determined because the recommendation was cited secondarily from another review article.

**model** indicates that the research was conducted through modeling and therefore is not specific to any geographic area. review indicates papers that base recommendation on a survey of the literature.

1 As *cited in* Andrén 1994

2 As *cited in* Dooley and Bowers 1998

3 As *cited in* Fahrig 2001

4 As *cited in* With and Crist 1995

# APPENDIX D. EDGE INFLUENCE

Distances (in meters) that edge effects penetrate into habitats in the United States as found within the scientific literature (as of December 2001), according to abiotic, bird, mammal, and plant response.

| TAXA/SUBJECT | EDGE INFLUENCE | FINDING | STATE | CITATION |
|---|---|---|---|---|
| **Abiotic** | | | | |
| | 8 m | Microclimatic differences ceased to exist beyond 8 m into forest fragments. | IN | Brothers and Spingarn 1992 |
| | 13.3 m | Model indicated that elevated soil temperatures may extend up to 13.3 m from edge. | model | Laurance and Yensen 1991 |
| | ≥ 15 m | In deciduous forest patches, microclimate changes were estimated to extend at least 15 m from the forest edge to the interior. | WI | Ranney et al. 1981[2] |
| | 50 m | Significant edge effects were detected in light, temperature, litter moisture, vapor pressure deficit, humidity, and shrub cover, affecting the forest microenvironment up to 50 m from the edge. | PA, DE | Matlack 1993 |
| | 15-60 m (solar radiation) > 240 m (humidity and wind speed) | Solar radiation gradients extend 15–60 m into upland old-growth forest and humidity and wind speed gradients at > 240 m. | — | Chen et al. 1995[9] |
| **Birds** | | | | |
| | 16.27 m, 16.95 m, 37.73 m | Maximum flushing* distance in response to pedestrians and dogs was 16.27 m (American robin), 16.95 m (vesper sparrow), and 37.73 m (western meadowlark). | CO | Miller et al. 2001 |
| | 50 m | Predation and parasitism rates are often significantly greater within 50 m of an edge. | — | Paton 1994[3] |
| | 50 m | Murrelet nest success was higher when nests were more than 50 m from the forest edge. | — | Nelson and Hamer 1995[4] |
| | 75 m | Estimated that edge-related nest predation extended 75 m into forested buffer strip. | ME | Vander Haegen and Degraaf 1996 |
| | 75 m, 100 m | For the majority of species found to have reduced numbers near trails due to nest predation and brood parasitism by brown-headed cowbirds, the zone of influence of trails appears to be around 75 m; however, Townsend's Solitaires exhibited reduced numbers as far as 100 m away from trail. | CO | Miller et al. 1998 |
| | 75 m, 125 m, 140 m, 160 m, 210 m, 300 m | Buffer zones that would prevent flushing by approximately 90% of the wintering individuals of a species are: American kestrel, 75 m; merlin, 125 m; prairie falcon, 160 m; rough-legged hawk, 210 m; ferruginous hawk, 140 m; and golden eagle, 300 m. | CO | Holmes et al. 1993 |
| | 100 m | Flushing distances of waterbirds in response to pedestrians, all-terrain vehicles, automobiles, and boats, indicate that human disturbance extends up to 100 m. | FL | Rodgers and Smith 1997 |

| TAXA/SUBJECT | EDGE INFLUENCE | FINDING | STATE | CITATION |
|---|---|---|---|---|
| | 180 m | Avian densities were altered up to 180 m away from homes on the perimeter of ex-urban developments. | CO | Odell and Knight 2001 |
| | 200–500 m | The abundance of interior habitat bird species was reduced within 200 to 500 m of an edge. | CA | Bolger et al. 1997b[1] |
| | ≥ 300 m | Nest parasitism by brown-headed cowbirds decreased with distance away from forest edge but extended ≥ 300 m into the forest. | — | Brittingham and Temple 1983[5] |
| | 511 m, 687 m | Most Cooper hawk nests occurred 511 m from paved roads and 687 m from human habitation. | Northeast | Bosakowski et al. 1992 |
| | 600 m | Effect of increased predation extends 600 m into habitat. | — | Wilcove et al. 1986[1] |
| **Mammals** | | | | |
| | ≥ 45 m | The influence of a clearcut on small mammals (California red-backed vole and deer mouse) extends at least 45 m into the forest from its edge. | — | Mills 1996[6] |
| | 81.92 m | Maximum flushing distance of mule deer in response to pedestrians and dogs was 81.92 meters. | CO | Miller et al. 2001 |
| | 100–900 m | Human traffic along open roads displaces most grizzly bears from 100–900 meters. | — | Mattson et al. 1987[7]<br>McLellan and Shackleton 1988[7]<br>Aune and Kasworm 1989[7]<br>Kasworm and Manley 1990[7]<br>Mace et al. 1996[7] |
| **Plants** | | | | |
| | 65 m | Populations in forest remnants within 65 m of forest clear-cut edges have almost no recruitment of young plants. | OR | Jules 1998 |
| **General** | | | | |
| | 5000 m | In different habitats and for different taxa, edge effects may penetrate up to 5 km. | — | Janzen, 1986[8] |

* Flushing distance is the distance that an animal may flee in response to a disturbance, such as in response to pedestrian or pets on a trail or vehicular traffic on roads.
— Indicates that the geographic location was not determined because the recommendation was cited secondarily from another review article.
**model** indicates that the research was conducted through modeling and therefore is not specific to any geographic area.

1 *As cited in* Metro 2001.

2 *As cited in* Collinge 1996

3 *As cited in* Hartley and Hunter 1998

4 *As cited in* Meyer and Miller 2002

5 *As cited in* Robbins et al. 1989

6 *As cited in* Lidicker 1999

7 *As cited in* Weaver et al. 1996

8 *As cited in* Laurance and Yensen 1991

9 *As cited in* Brosofske et al. 1997

# APPENDIX E. RIPARIAN BUFFER WIDTH

Recommended minimum riparian and wetland buffer widths (in meters) to maintain water quality and wildlife functions within ecoregions of the United States, as found within the scientific literature (as of December 2001).

| FUNCTION | TAXA/SUBJECT | BUFFER WIDTH | CITATION |
|---|---|---|---|
| **Miscellaneous** | | | |
| | Noise | ≥ 6 m (mature evergreen) | Harris 1985[3] |
| | Wind damage prevention | ≥ 23 m | Pollock and Kennard 1998[3] |
| | Noise | ≥ 32 m (heavily forested) | Groffman et al. 1990[5] |
| **Detrital Input** | | | |
| | Organic litterfall | 1/2 SPTH | FEMAT 1993[3] |
| | Large Woody Debris | 1 SPTH | FEMAT 1993[3] |
| | Large Woody Debris | 1 SPTH | Spence et al. 1996[3] |
| | Woody Debris | 3–10 m | Fischer and Fischenich 2000 |
| | Woody Debris | 10–30 m | Wenger 1999 |
| | Organic litterfall | ≥ 30 m | Erman et al. 1977[3] |
| | Woody Debris | ≥ 30 m (forested watersheds) | Pollock and Kennard 1998[3] |
| | Woody Debris | ≥ 31 m | Bottom et al. 1983[4] |
| | Woody Debris | ≥ 46 m | McDade et al. 1990[3] |
| | Organic litterfall | ≥ 52 m | Spence et al. 1996[3] |
| | Woody Debris | ≥ 80 m | May 2000[3] |
| **Temperature and microclimate regulation** | | | |
| | Microclimate | 3 SPTH | FEMAT 1993[3] |
| | Shade | 10–30 m | Osborne and Kovacic 1993[3] |
| | Temperature control | 10–30 m | Wenger 1999 |
| | Water temperature | 10–30 m | Castelle et al. 1994 |
| | Shade | 11–24 m | Brazier and Brown 1973[5] |
| | Water temperature | ≥ 12 m | Corbett and Lynch 1985[4] |
| | Water temperature | 15–30 m | Hewlett and Fortson 1982[4] |
| | Shade | 23–38 m | Steinblums et al. 1984[5] |
| | Shade | ≥ 30 m | Spence et al. 1996[3] |
| | Shade | ≥ 30 m | FEMAT 1993[3] |
| | Shade | ≥ 30 m | May 2000[3] |
| | Maintenance of water temperature within 1°C of former mean | ≥ 30 m | Lynch, Corbett, and Mussalem 1985[1] |
| | Water temperature | 30–43 m | Jones et al. 1988[4] |
| | Air temperature, solar radiation, wind, humidity | ≥ 45–300 m | Brosofske et al. 1997 |
| | Microclimate regulation | ≥ 100 m | May 2000[3] |
| | Microclimate regulation | 61–160 m | Knutson and Naef 1997[3] |
| **Bank Stabilization** | | | |
| | Bank Stabilization | 1/2 SPTH | FEMAT 1993[3] |
| | Bank Stabilization | 10–20 m | Fischer and Fischenich 2000 |

| FUNCTION | TAXA/SUBJECT | BUFFER WIDTH | CITATION |
|---|---|---|---|
| | Stream/channel stabilization | 20–30 m | Corbett and Lynch 1985[4] |
| | Stream stabilization/sediment control | ≥ 38 m | Cederholm 1994[3] |
| | Bank Stabilization | ≥ 52 m | Spence et al. 1996[3] |
| **Flood Attenuation** | | | |
| | Floodplain storage | 20–150 m | Fischer and Fischenich 2000 |
| **Sediment Removal** | | | |
| | Sediment removal | ≥ 3m (sand), ≥ 15 m (silt), ≥ 122m (clay) | Wilson 1967[5] |
| | Sediment removal | 5–30 m | Fischer and Fischenich 2000 |
| | Sediment removal | 8–46 m (depending on slope) | SCS 1982[4] |
| | Sediment (85% removal) | ≥ 9 m (grass filter strips, 7%, 12% slopes) | Ghaffarzadeh et al. 1992[4] |
| | Suspended solids (84% removal) | ≥ 9 m (vegetated filter strip) | Dillaha et al. 1989[1] |
| | Sediment removal | 9–30 m | Wenger 1999 |
| | Sediment removal | 10–60 m | Castelle et al. 1994 |
| | Sediment removal | ≥ 15 m | Budd et al. 1987[4] |
| | Sediment removal | ≥ 15.6 m | Broderson 1973[4] |
| | Sediment removal | ≥ 23 m | Schellinger and Clausen 1992[4] |
| | Suspended sediment (92% removal) | ≥ 24.4 m (vegetated buffer) | Young et al. 1980[4] |
| | Sediment removal | ≥ 25 m | Desbonnet et al. 1994[4] |
| | Sediment removal | ≥ 30 m | Erman et al. 1977[3] |
| | Sediment removal | ≥ 30m | Moring 1982[3] |
| | Sediment removal | ≥ 30 m | May 2000[3] |
| | Sediment (75% removal) | 30–38 m | Karr and Scholosser 1977[4] |
| | Sediment (75–80% removal) | ≥ 30 m | Lynch, Corbett, and Mussalem 1985[1] |
| | Sediment (80% removal) | ≥ 61 m (grass filter strip and vegeated buffers) | Horner and Mar 1982[1] |
| | Sediment (50% removal) | ≥ 88 m | Gilliam 1988[4] |
| **Nutrient/Pollutant Removal** | | | |
| | Nitrogen, Phosphorus, Potassium, and Fecal Bacteria | ≥ 4 m (grass filter strip and forested buffers) | Doyle et al. 1997[1] |
| | Nitrates and Phosphates (90% removal) | ≥ 5 (grass filter strip) | Madison et al. 1992[1] |
| | Nutrient removal | 5–30 m | Fischer and Fischenich 2000 |
| | Nitrates (almost complete removal) | ≥ 7 m | Lowrance 1992[1] |
| | Removal of Phosphorus (79%) and Nitrogen (73%) | ≥ 9 m (vegetated filter strip) | Dillaha et al. 1989[1] |
| | Nitrogen and Phosphorus | ≥ 10 m | Corley et al 1999[1] |
| | Nutrient and Metal | ≥ 10 m | Petersen et al. 1992[4] |
| | Nutrient removal | 10—90 m | Castelle et al. 1994 |
| | Nitrate Concentrations | 15–30 m | Wenger 1999 |

| FUNCTION | TAXA/SUBJECT | BUFFER WIDTH | CITATION |
|---|---|---|---|
| | Nutrient and metal | ≥ 15 m | Castelle et al. 1992[4] |
| | Phosphorus | ≥ 15 m (hardwood buffer) | Woodard and Rock 1995[1] |
| | Nutrient and metal | ≥ 16 m | Jacobs and Gilliam 1985[4] |
| | Estradiol (98% decrease) | ≥ 18 m (grass filter strip) | Nichols et al. 1998[1] |
| | Nitrogen and Phosphorus (80 and 89% removal, respectively) | ≥ 19 m (riparian forest buffer) | Shisler, Jordan, and Wargo 1987[1] |
| | Nitrates (up to 100%) | 20–30 m | Fennessy and Cronk 1997[3] |
| | Fecal coliform reduction | 23–92 m | SCS 1982[5] |
| | Pollutant removal | ≥ 30 m | May 2000[3] |
| | Fecal coliform reduction | ≥ 30 m | Grismer 1981[5] |
| | Nutrient reduction to acceptable levals | ≥ 30 m | Lynch, Corbett, and Mussalem 1985[1] |
| | Nutrient and metal removal | 30–43 m | Jones et al. 1988[5] |
| | Nutrient and metal removal | ≥ 36 m | Young et al. 1980[4] |
| **Wildlife and Plant Species** | | | |
| | General wildlife | 3–183 m | FEMAT 1993[3] |
| | General wildlife habitat | ≥ 10 m | Petersen et al. 1992[5] |
| | General species diversity | 10–100 m | Castelle et al. 1994 |
| | General bird habitat | ≥ 15 m | Milligan 1985[5] |
| | Fish (Cutthroat trout, rainbow trout, and steelhead) | 15–61 m | Knutson and Naef 1997[3] |
| | Birds | ≥ 15–200 m | Stauffer and Best 1980 |
| | Aquatic wildlife habitat | 20–150 m | Fischer and Fischenich 2000 |
| | General wildlife habitat | ≥ 23 m | Mudd 1975[5] |
| | General wildlife habitat | ≥ 27 m | WDOE 1981[5] |
| | Invertebrates (aquatic insects) | ≥ 30 m | Erman et al. 1977[3] |
| | Invertebrates (macroinvertebrate diversity) | ≥ 30 m | Gregory et al. 1987[3] |
| | Fish (cutthroat trout) | ≥ 30 m | Hickman and Raleigh 1982[3] |
| | Invertebrates (benthic communities) | ≥ 30 m | Newbold et al. 1980[5] |
| | Amphibians (frogs and salamanders) | ≥ 30 m (riparian forest buffer) | NRCS 1995[3] |
| | Fish (brook trout) | ≥ 30 m | Raleigh 1982[5] |
| | Fish (rainbow trout) | ≥ 30 m | Raleigh et al. 1984[3] |
| | Fish (chinook salmon) | ≥ 30 m | Raleigh et al. 1986[5] |
| | Invertebrates (benthic communities) | ≥ 30 m | Roby et al. 1977[5] |
| | Amphibians, Reptiles, Vertebrates | ≥ 30 m (riparian forest buffer) | Rudolph and Dickson 1990[1] |
| | Fish (salmonid egg development) | ≥ 30 m | Spackman and Hughes 1995[1] |
| | Plants (vascular plant diversity) | ≥ 30 m | Spackman and Hughes 1995[1] |
| | Fish (fish diversity and densities) | ≥ 30 m | Stewart et al. 2000 |
| | Mammals (beavers) | 30–100 m | Jenkins 1980[9] |
| | General wildlife habitat | ≥ 32 m | Groffman et al. 1990[5] |
| | Birds (Willow flycatcher nesting) | ≥ 37.5 m | Knutson and Naef 1997[3] |

| FUNCTION | TAXA/SUBJECT | BUFFER WIDTH | CITATION |
|---|---|---|---|
| | Birds (diversity and assemblages) | ≥ 40 m | Hagar 1999 |
| | Birds (assemblages and persistence) | ≥ 45 m | Pearson and Manuwal 2001 |
| | Mammal (gray squirrel) | ≥ 50 m | Dickson 1989[1] |
| | Birds (neotropical migrants, interior species) | ≥ 50 m | Tassone 1981[3] |
| | Birds (raptors) | 50–1600 m | Richardson and Miller 1997[7] |
| | Fish (trout, salmon) | ≥ 61 m | Castelle et al. 1992[3] |
| | Mammals (deer) | ≥ 61 m | NRCS 1995[3] |
| | General wildlife | ≥ 61 m | Zeigler 1988[5] |
| | Mammals (small) | 67–93 m | Jones et al. 1988[5] |
| | Reptiles (gravid mud turtles, Florida cooters, slider turtles) | ≥ 73 m (90% protection) | Burke and Gibbons 1995 |
| | Birds | 75–200 m | Jones et al. 1988[3] |
| | Mammal (beaver) | ≥ 91 m | NRCS 1995[3] |
| | Mammals (large) | ≥ 100 m | Jones et al. 1988[5] |
| | Birds (neotropical migrants) | ≥ 100 m | Fischer 2000 |
| | Wildlife habitat | ≥ 100 m | Fischer, Martin, and Fischenich 2000; and Fischer and Fischenich 2000 |
| | Birds (yellow-billed cuckoo breeding habitat) | ≥ 100 m | Gaines 1974[2] |
| | Birds (neotropical migrant diversity and functional assemblages) | ≥ 100 m | Hodges and Krementz 1996 |
| | Birds (forest bird nesting habitat) | ≥ 100 m | Keller et al. 1993 |
| | Reptiles (Western pond turtle nesting habitat) | ≥ 100 m (stream buffer) | Knutson and Naef 1997[3] |
| | Aquatic wildlife | ≥ 100 m | May 2000[3] |
| | Birds (red-shouldered hawk and forest bird breeding habitat) | ≥ 100 m | Mitchell 1996[2] |
| | Birds (pileated woodpecker nesting habitat) | ≥ 100 m | Small 1982[3] |
| | Birds (neotropical migrant abundance) | ≥ 100 m | Triquet, McPeek, and McComb 1990[2] |
| | Terrestrial riparian wildlife communities | 100–300 m (300 m for forest interior species) | Wenger 1999 |
| | Reptiles (spotted turtles nesting habitat) | 120 m (wetland buffer) | Joyal et al. 2001 |
| | Reptiles (turtles) | ≥ 135 m (wetland buffer) | Buhlmann 1998[1] |
| | Birds (Pileated woodpecker) | ≥ 137 m | Castelle et al. 1992[3] |
| | Birds (species diversity) | ≥ 150 m | Spackman and Hughes 1995[2] |
| | Birds (reduce edge-related nest predation) | ≥ 150 m | Vander Haegen and DeGraaf 1996 |
| | Amphibians (salamanders) | ≥ 165 m | Semlitsch 1998 |
| | Birds (Bald eagle, nesting ducks, herons, sandhill cranes) | ≥ 183 m | Knutson and Naef 1997[3] |
| | Mammals (fawning of mule deer) | ≥ 183 m | Knutson and Naef 1997[3] |

| FUNCTION | TAXA/SUBJECT | BUFFER WIDTH | CITATION |
|---|---|---|---|
| | Plants (minimize non-native vegetation) | ≥ 198 m | Hennings 2001[3] |
| | Birds (Rufous-sided towhee) | ≥ 200 m | Knutson and Naef 1997[3] |
| | Reptiles (Blanding's turtles nesting habitat | ≥ 410 m (wetland buffer) | Joyal et al. 2001 |
| | Reptiles (False map turtles, slider turtles, lotic turtles dispersal) | ≥ 449 m | Bodie and Semlitsch 2000 |
| | Birds (complete assemblages) | ≥ 500 m | Kilgo et al. 1998[1] |
| **General Protection of Aquatic Systems** | | | |
| | Multiple functions | 1–90 m | Todd 2000 |
| | Multiple functions | ≥ 10 m | Fischer and Fischenich 2000 |
| | Multiple functions | ≥ 15 m | Fischer, Martin, and Fischenich 2000 |
| | Multiple functions | 30 m | Furfey et al. 1997 |
| | Sediment/contaminant control, general water quality maintenance | 30.5 m (+0.61 m per 1% slope) | Wenger 1999 |
| | Wetland and river integrity | ≥ 335 m | Schaefer et al. 1991[6] |

**SPTH**, or site potential tree height, is used as a standard measurement to allow for multiple riparian functions. SPTH is measured in various ways. FEMAT (1993) defines SPTH the height of a site potential tree as the average maximum height of the tallest dominant trees of 200 years or more of age for a given site class (*For further discussion, refer to Metro 2001*).

1 *As cited in* Fischer and Fischenich 2000.

2 *As cited in* Fischer 2000.

3 *As cited in* Metro 2001.

4 *As cited in* Furfey et al. 1997

5 *As cited in* Johnson and Ryba 1992

6 *As cited in* Burke and Gibbons 1995

7 *As cited in* Fischer, Martin, and Fischenich 2000

8 *As cited in* Hagar 1999

9 *As cited in* Allen 1983

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# Fractured Genetic Connectivity Threatens a Southern California Puma (*Puma concolor*) Population

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## Abstract

Pumas (*Puma concolor;* also known as mountain lions and cougars) in southern California live among a burgeoning human population of roughly 20 million people. Yet little is known of the consequences of attendant habitat loss and fragmentation, and human-caused puma mortality to puma population viability and genetic diversity. We examined genetic status of pumas in coastal mountains within the Peninsular Ranges south of Los Angeles, in San Diego, Riverside, and Orange counties. The Santa Ana Mountains are bounded by urbanization to the west, north, and east, and are separated from the eastern Peninsular Ranges to the southeast by a ten lane interstate highway (I-15). We analyzed DNA samples from 97 pumas sampled between 2001 and 2012. Genotypic data for forty-six microsatellite loci revealed that pumas sampled in the Santa Ana Mountains (n = 42) displayed lower genetic diversity than pumas from nearly every other region in California tested (n = 257), including those living in the Peninsular Ranges immediately to the east across I-15 (n = 55). Santa Ana Mountains pumas had high average pairwise relatedness, high individual internal relatedness, a low estimated effective population size, and strong evidence of a bottleneck and isolation from other populations in California. These and ecological findings provide clear evidence that Santa Ana Mountains pumas have been experiencing genetic impacts related to barriers to gene flow, and are a warning signal to wildlife managers and land use planners that mitigation efforts will be needed to stem further genetic and demographic decay in the Santa Ana Mountains puma population.

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**Data Availability:** The authors confirm that all data underlying the findings are fully available without restriction. All relevant data have been deposited to Dryad, and can be accessed with the DOI:10.5061/dryad.dp0qj.

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## Introduction

Genetic diversity, demography, and abundance – biological characteristics that influence population viability – can vary across a species' distribution. Species that are generally perceived as wide-ranging and abundant are sometimes relegated to status as "least conservation concern", in spite of indicators signaling concern and frequently, lack of data. Pumas (*Puma concolor*; also known as mountain lion, cougar, and in Florida, panther) epitomize this dilemma. Although pumas in California have not been subjected to hunting since 1972, and were designated as a Specially Protected Mammal in 1990 [1], there is minimal active management and little scientifically validated data on statewide or regional population numbers. Pumas in southern California have one of the lowest annual survival rates among any population in North America, on par with rates seen in hunted populations (unpublished data). They are under increasing threats from habitat loss and fragmentation, and mortality from vehicle strikes, depredation permits, poaching, public safety kills, wildfire, and poisoning [2,3]. Timely evaluation of potential threats to population viability is imperative in order to prioritize conservation activities to prevent collapse of some populations.

The human population of southern California is over 20 million [4] and expected to exceed 30 million by 2060 [5]. This increasing population will likely result in further loss, fragmentation, and degradation of natural habitats in the region. Habitat fragmentation south of greater Los Angeles has effectively turned the Santa Ana Mountain range in mostly Orange and Riverside counties into a 'mega-fragment' of habitat, surrounded to the west, north, and east by dense urban land uses. The only remaining montane and foothill habitat linkage connecting the Santa Ana Mountain range to other mountains of the Peninsular Range is a southeasterly swath of habitat bisected by a very heavily traveled 10-lane highway, Interstate 15 (I-15) (Figure 1).

Population viability of pumas in the Santa Ana Mountains (a geography henceforth referred to as distinct from the broader Peninsular Ranges to the east) has been of conservation concern

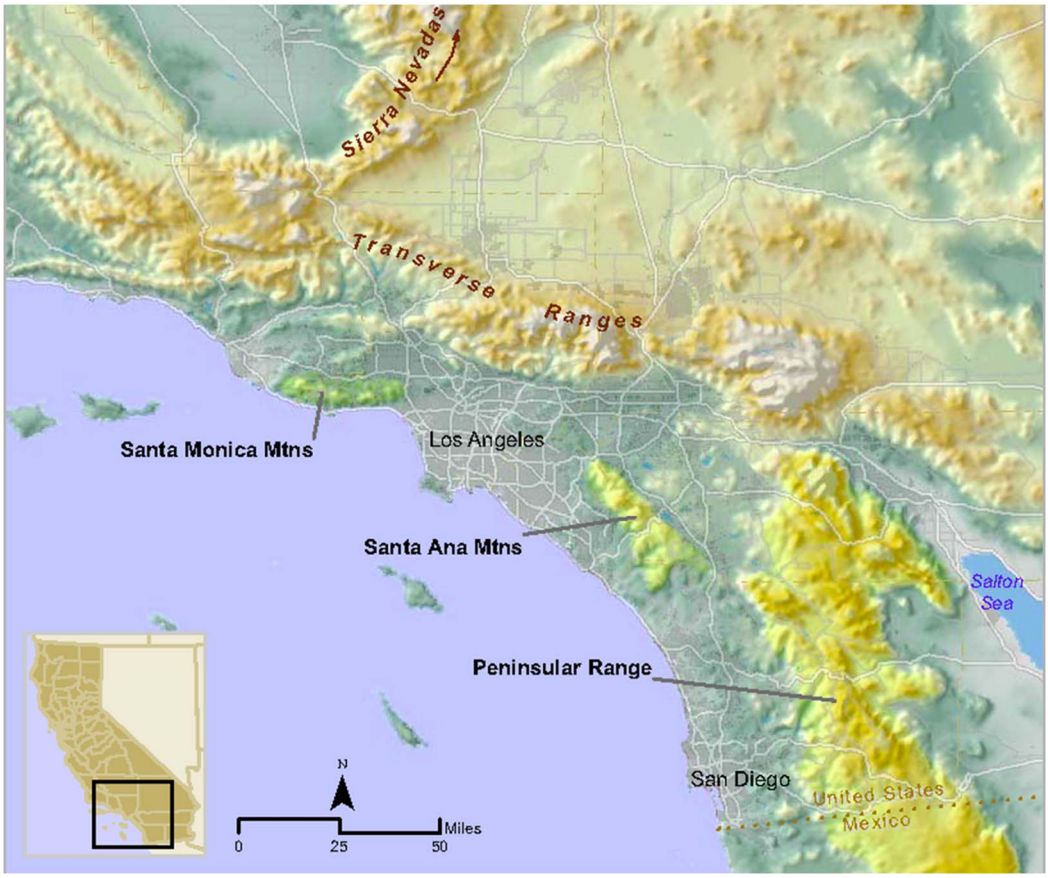


**Figure 1. Topographic map depicting location of Santa Ana Mountains, eastern Peninsular Ranges in southern California, and adjacent regions.** Inset shows location in the state of California.
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for decades. Population monitoring and modeling in the 1980s highlighted that urbanization and highways were fragmenting puma habitat (e.g., [6]), and that in turn motivated efforts to protect habitat connectivity in the region (e.g., [7,8]). As part of a statewide assessment of puma genetic diversity and population structure, Ernest et al. [9] employed an 11-locus microsatellite panel and found that, for a limited sample size (n = 14) Santa Ana pumas had lower genetic diversity than other populations in California. Since 2001, pumas in the region have been the subject of an ongoing study by the Karen C. Drayer Wildlife Health Center of the University of California, Davis (UCD) School of Veterinary Medicine. Telemetry data from 74 pumas in the UCD study has confirmed that minimal connectivity (only one GPS-collared puma over ten years was documented to transit successfully; unpublished data) exists between the Santa Ana Mountains and the eastern Peninsular Ranges across I-15, confirming that previous connectivity concerns were warranted.

We conducted a detailed appraisal of the genetic diversity, relatedness, and population structure of southern California puma populations. Using 97 samples collected over 12 years as part of the UCD study, and a 46-locus microsatellite panel, we evaluated levels of genetic diversity, estimated effective population sizes and tested whether genetic data supported a hypothesis of recent bottleneck in the populations. We assessed whether genetics reflected our telemetry observations of infrequent puma crossings of I-15 between the Santa Ana Mountains and the Peninsular Ranges to the east. Additionally we explored inter-population gene flow at multiple time scales by employing methods that reflect recent (a few generations) and more historical (tens or more generations). Finally, we tested our hypothesis that the Santa Ana population had lower genetic diversity than those sampled from other regions in California.

## Materials and Methods

### Samples

We obtained blood or tissue samples for analysis of nuclear DNA from pumas captured for telemetry studies, and from those found dead or killed by state authorities for livestock depredation or public safety in San Diego, Orange, Riverside, and San Bernardino counties of southern California (n = 97) during 2001–2012 (Figure 2). Pumas captured for telemetry were captured and sampled as detailed in [10]. Forty-two samples were collected to the west of I-15 in the Santa Ana Mountains, and 55 samples were collected in the Peninsular Ranges to the east of I-15. A small number of additional samples were collected from deceased animals in San Bernardino County just to the north of the Peninsular Range across Interstate Highway 10. For population genetic comparisons with pumas sampled elsewhere throughout California, a 257 sample subset of our statewide puma DNA data archive was employed (regions and sample sizes detailed in Table 1 and depicted in Figure 1 in [9])

### Ethics Statement

Animal handling was carried out in strict accordance with the recommendations and approved Protocol 10950/PHS, Animal

**Table 1.** Genetic diversity summary statistics for southern California pumas (n = 97) relative to other populations in California (n = 257).

| Sampling Region | Abbrev. | | N | Na | AR | Ho | He | I | %P |
|---|---|---|---|---|---|---|---|---|---|
| **North Coast** | **NC** | **Mean** | 29 | 3.6 | 2.0 | 0.41 | 0.44 | 0.80 | 98% |
| | | **SE** | | 0.2 | 0.1 | 0.03 | 0.03 | 0.05 | |
| **Modoc Plateau & Eastern Sierra Nevada** | **MP-ESN** | **Mean** | 51 | 4.2 | 2.4 | 0.52 | 0.54 | 0.98 | 100% |
| | | **SE** | | 0.3 | 0.1 | 0.03 | 0.03 | 0.05 | |
| **Western Sierra Nevada** | **WSN** | **Mean** | 47 | 4.2 | 2.4 | 0.47 | 0.51 | 0.95 | 98% |
| | | **SE** | | 0.2 | 0.2 | 0.03 | 0.03 | 0.06 | |
| **Central Coast: north** | **CC-N** | **Mean** | 83 | 3.2 | 1.9 | 0.41 | 0.41 | 0.70 | 98% |
| | | **SE** | | 0.2 | 0.1 | 0.03 | 0.03 | 0.06 | |
| **Central Coast: central** | **CC-C** | **Mean** | 21 | 3.4 | 2.1 | 0.43 | 0.46 | 0.81 | 96% |
| | | **SE** | | 0.2 | 0.1 | 0.03 | 0.03 | 0.05 | |
| **Santa Monica Mountains** | **CC-S** | **Mean** | | 2.2 | 1.7 | 0.38 | 0.33 | 0.53 | 76% |
| **Central Coast: South** | | **SE** | 26 | 0.1 | 0.1 | 0.04 | 0.03 | 0.05 | |
| **Peninsular Range-East** | **PR-E** | **Mean** | 55 | 3.1 | 2.0 | 0.43 | 0.41 | 0.74 | 87% |
| | | **SE** | | 0.2 | 0.2 | 0.04 | 0.04 | 0.07 | |
| **Santa Ana Mountains** | **SAM** | **Mean** | 42 | 2.3 | 1.6 | 0.33 | 0.32 | 0.54 | 80% |
| | | **SE** | | 0.2 | 0.1 | 0.03 | 0.03 | 0.05 | |

Abbrev. = region abbreviations used in Tables and Figures. Mean with standard error (SE). N = sample size. Na = average number of different alleles per locus. AR = allelic richness, standardized to sample size. Ho = observed heterozygosity. He = expected heterozygosity. I = Shannon's information index (Sherwin et al 2006). %P = percent of polymorphic loci. Regions are detailed further in text and generally follow California Bioregions designations. (http://biodiversity.ca.gov/bioregions.html).

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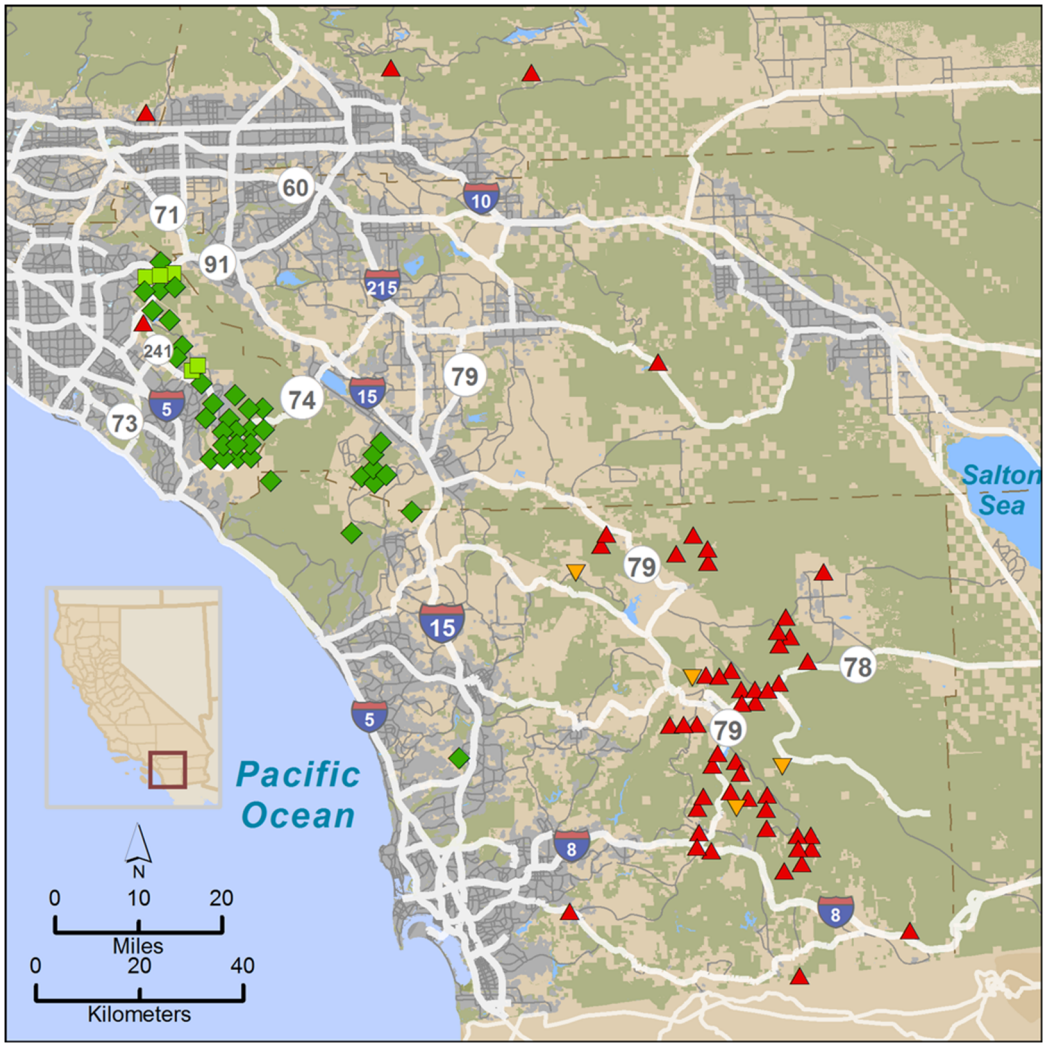


**Figure 2. Map of puma capture locations in the Santa Ana Mountains and eastern Peninsular Ranges of southern California.** Colors of symbols represent genetic group assignment inferred from Bayesian clustering analysis (STRUCTURE analysis, see Figure 4). Genetic group A-1 = green diamonds; A-2 = red triangles (apex at top). One male puma (M86) captured in the Santa Ana Mountains had predominant genetic assignment to the A-2 (red) genetic group. Five individuals (light green squares) captured in the Santa Ana Mountains had partial assignment to the A-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) captured in the Santa Ana Mountains were parents of pumas M91, F92, and M93 (captured in the Santa Ana Mountains). Puma M97 assigned in parentage to M86 and F61, while F102 had unknown parentage (no parentage assignments; due possibly to her death early in project prior to collection of most of the samples). Three individuals (orange triangles, apex at bottom), had partial assignment (however, less than 20%) to A-1.
doi:10.1371/journal.pone.0107985.g002

Welfare Assurance number A3433-01, with capture and sampling procedures approved by the Animal Care and Use Committee at the University of California, Davis (Protocol #17233), and Memoranda of Understanding and Scientific Collecting Permits from the California Department of Fish and Wildlife (CDFW). Permits and permissions for access to conserved lands at puma capture and sampling sites were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (US) Fish and Wildlife Service, US Forest Service, US Bureau of Land Management, US Navy/Marine Corps, Orange County Parks Department, San Diego County Parks Department, San Diego State University, Vista Irrigation District, Rancho Mission Viejo/San Juan Company, Sweetwater Authority, California Department of Transportation (CalTrans), and the City of San Diego Water Department.

## DNA Extraction and Microsatellite DNA data collection

Whole genomic DNA was extracted using the DNeasy Blood & Tissue Kit (QIAGEN, Valencia, CA, USA). Fifty microsatellite DNA primers were initially screened for this project. Forty-six loci that performed well in multiplex PCR (using the QIAGEN Multiplex PCR kit; QIAGEN) and conformed to expectations for Hardy-Weinberg and linkage equilibria were selected for ultimate analysis [11,12,13]. One sex-identification locus (Amelogenin) was used to confirm sex in samples from degraded puma carcasses [14].

PCR products were separated with an ABI PRISM 3730 DNA Analyzer (Applied Biosystems Inc., Foster City, CA, USA) with each capillary containing 1 μL of a 1:10 dilution of PCR product and deionized water, 0.05 μL GeneScan-500 LIZ Size Standard and 9.95 μL of HiDi formamide (both products Applied Biosystems Inc.) that was denatured at 95°C for 3 min. Products

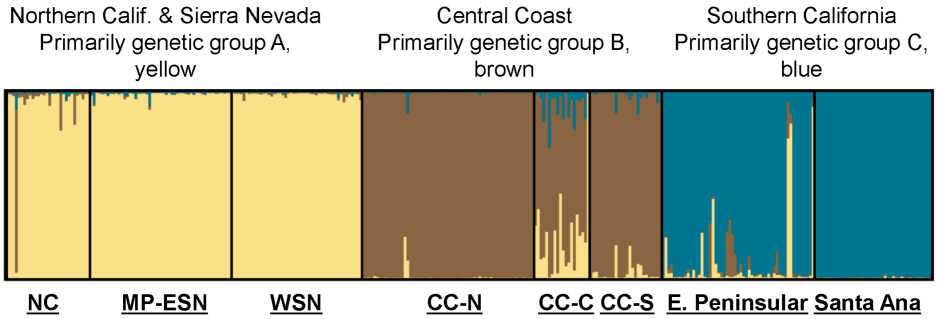


**Figure 3. California puma population genetic structure.** STRUCTURE bar plot displaying the genetic clustering relationship of southern California pumas relative to others in California. Three major genetic groups, A (blue, on right), B (brown, in center), and C (yellow, on left), are evident for analysis of 354 individuals sampled throughout California. Abbreviations: NC = North Coast, MP-ESN = Modoc Plateau & Eastern Sierra Nevada, WSN = Western Sierra Nevada, CC-N = Central Coast: north, CC-C = Central Coast: central, CC-S = Central Coast: South (Santa Monica Mountains), PR-E = Peninsular Range-East, SAM = Santa Ana Mountains. The plot is organized by grouping individuals in order of their geographic region sampling source. Proportional genetic assignment for each puma is represented by a vertical bar, most easily visualized for pumas that genetically assigned to a group different from most others sampled in its region (for example one individual with over 80% brown and 8% blue near far left of group A). Pumas primarily from the Sierra Nevada Range and northern California are represented by group A (yellow), group B (brown) includes primarily Central Coast pumas and group C (blue) represents primarily southern California pumas (Santa Ana Mountains and eastern Peninsular Ranges).
doi:10.1371/journal.pone.0107985.g003

were visualized with STRand version 2.3.69 [15]. Negative controls (all reagents except DNA) and positive controls (well-characterized puma DNA) were included with each PCR run. Samples were run in PCR at each locus at least twice to assure accuracy of genotype reads and minimize risk of non-amplifying alleles. For >90% samples, loci that were heterozygous were run at least twice and homozygous loci were run at least three times.

## Genetic diversity

The number of alleles (Na), allelic richness (AR; incorporates correction for sample size), observed heterozygosity (Ho), expected heterozygosity (He), Shannon's information index [16], and tests for deviations from Hardy-Weinberg equilibrium were calculated using software GenAlEx version 6.5 [17,18]. Shannon's information index provides an alternative method of quantifying genetic diversity and incorporates allele numbers and frequencies. Testing for deviations from expectations of linkage equilibrium was conducted using Genepop 4.2.1 [19], and we tested for the presence of null alleles using the program ML RELATE [20]. We assessed significance for calculations at alpha = 0.05 and used sequential Bonferroni corrections for multiple tests [21] in tests for Hardy-Weinberg and linkage equilibria.

The average probability of identity (PID) was calculated two ways using GenAlEx: 1) assuming random mating ($PID_{RM}$) without close relatives in a population [22], and 2) assuming that siblings with similar genotypes occur in a population ($PID_{SIBS}$) [23]. Probability of identity is the likelihood that two individuals will have the same genetic profile (genotype) for the DNA markers used. $PID_{SIBS}$ is considered conservative since it probably conveys a higher likelihood; however, we recognized that siblings occurred in these populations.

## Assessing population structure and genetic isolation

We used a Bayesian genetic clustering algorithm (STRUCTURE version 2.3.4 [24,25]) to determine the likely number of population groups (K; genetic clusters) and to probabilistically group individuals without using the known geographic location of sample collection. We used the population admixture model with a flat prior and assumed that allele frequencies were correlated among populations, and ran 50,000 Markov chain Monte Carlo repetitions following a burnin period of 10,000 repetitions. First,

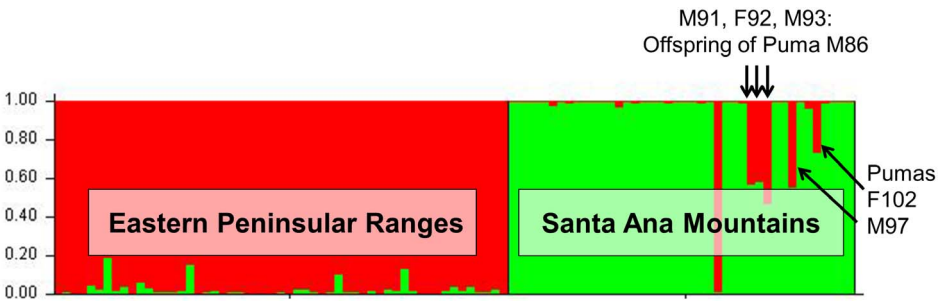


**Figure 4. Southern California puma population genetic structure.** Bar Plot displaying results of STRUCTURE analysis focused on genotypic data from 97 southern California pumas (the blue block from Figure 3). With removal of the strong genetic signal from northern California and Central Coast samples (see Figure 3), two distinct southern California groupings were inferred, C-1 (green, on right) and C-2 (red, on left). These reflect the two regions: Santa Ana Mountains to the west of I-15 (predominantly genetic group C-1) and eastern Peninsular Ranges to the east of I-15 (predominantly genetic group C-2). Genetic clustering is dependent on genetic variance among samples included in the analysis. One male puma (M86) captured in the Santa Ana Mountains has predominant genetic assignment to the C-2 (red) genetic group (the predominant genetic cluster for PR-E), and five others had partial assignment to the C-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) assigning to the C-1 genetic group were parents of pumas M91, F92, and M93 (all were captured in the Santa Ana Mountains).
doi:10.1371/journal.pone.0107985.g004

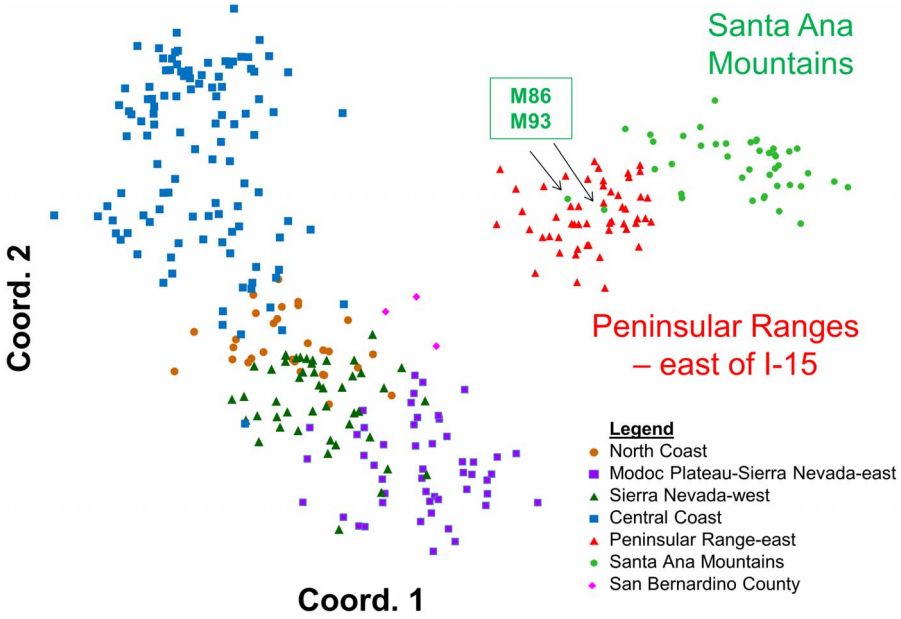


**Figure 5. Principal Coordinates analyses (PCoA) constructed using genetic covariance matrices (GenAlEx) for 354 California puma genetic profiles including 97 from southern California.** Patterns displayed for first two axes of variation within the genetic data set. Each point, color-coded to its sampling region, represents an individual puma. Note that colors in PCoA diagrams reflect geographic source of samples and not STRUCTURE genetic cluster assignment. Abbreviations and sample sizes per Table 1. Arrows denote pumas described in Figure 4.
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an analysis including 354 statewide puma genotypes (97 from southern California and 257 from other regions) was run to estimate the probability of one through 10 genetic clusters (K), with each run iterated three times. Second, given the output of the statewide run, we ran an analysis using only the 97 southern California puma genotypes to estimate the probability of one through five K, with each run iterated three times. Employing STRUCTURE HARVESTER [26] we averaged log probability

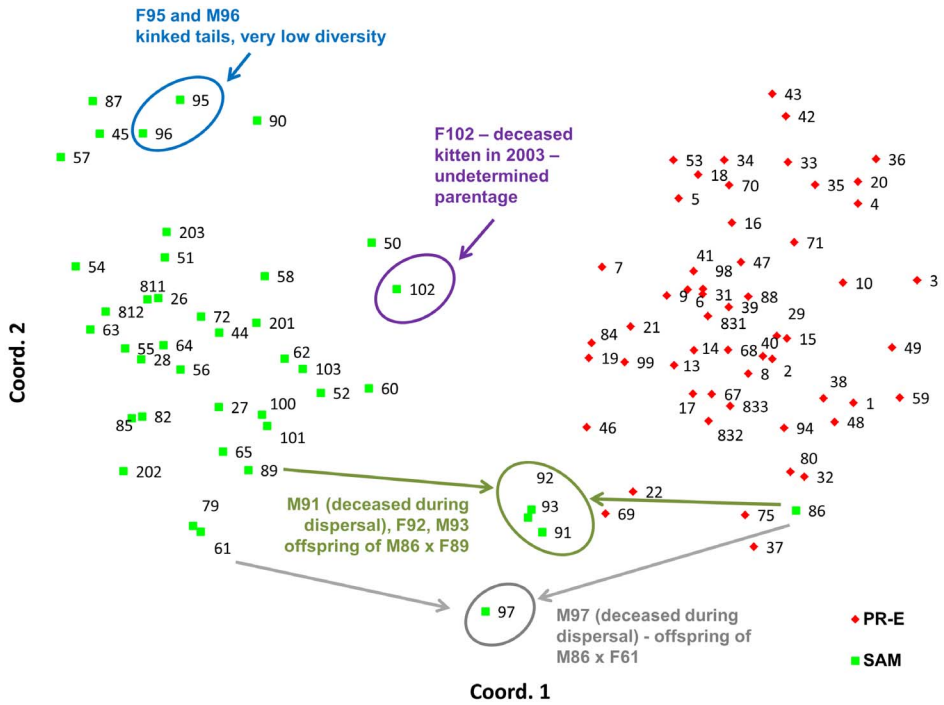


**Figure 6. Principal Coordinates analyses (PCoA) via covariance matrices for 97 southern California puma genetic profiles as conducted in GenAlEx.** Patterns displayed for first two axes of variation within the genetic data set. Each point represents an individual puma, and has sample identification number and color-coding to sampling region. Note that colors in PCoA diagrams reflect geographic source of samples and not STRUCTURE genetic cluster assignment. Abbreviations and sample sizes per Table 1.
doi:10.1371/journal.pone.0107985.g006

**Table 2.** Wright's $F_{ST}$ values indicate that southern California mountain lion populations are genetically distinct from other populations in California.

| | NC | MP-ESN | WSN | CC-N | CC-C | CC-S | PR-E | SAM |
|---|---|---|---|---|---|---|---|---|
| **North Coast (NC)** | 0 | | | | | | | |
| **Modoc Plateau & Eastern Sierra Nevada (MP-ESN)** | 0.09 | 0 | | | | | | |
| **Western Sierra Nevada (WSN)** | 0.05 | 0.03 | 0 | | | | | |
| **Central Coast: north (CC-N)** | 0.13 | 0.14 | 0.12 | 0 | | | | |
| **Central Coast: central (CC-C)** | 0.08 | 0.09 | 0.06 | 0.07 | 0 | | | |
| **Santa Monica Mountains (CC-S)** | 0.17 | 0.15 | 0.12 | 0.14 | 0.10 | 0 | | |
| **Peninsular Range-East (PR-E)** | 0.13 | 0.08 | 0.09 | 0.12 | 0.09 | 0.16 | 0 | |
| **Santa Ana Mountains (SAM)** | 0.18 | 0.16 | 0.17 | 0.19 | 0.17 | 0.27 | 0.07 | 0 |

Note that one of the geographically closest puma populations, Santa Monica Mountains, has highest $F_{ST}$ with the Santa Ana population, evidence of high genetic isolation for both regions. Probability, P(random>= data) based on 9999 permutations for all values are <0.001. Abbreviation definitions and sample sizes are included in Table 1.

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of the data given K, log Pr(X|K), statistics across the multiple runs for each of the K estimates. In each case (statewide and southern California), we selected the K value of highest probability by identifying the set of values where the log Pr(X|K) value was maximized and subsequently selected the minimum value for K that did not sacrifice explanatory ability [27,28,29]. We defined membership to a cluster based upon the highest proportion of ancestry to each inferred cluster.

To further assess and visualize genetic relationships among regions and individuals, we performed principal coordinates analyses (PCoA) via covariance matrices with data standardization [30] using GenAlEx. This is a technique that allowed us to explore and plot the major patterns within the data sets. The PCoA process located major axes of variation within our multidimensional genotype data set. Because each successive axis explains proportionately less of the total genetic variation, the first two axes were used to reveal the major separation among individuals. Employing Genalex software, a pairwise, individual-by-individual genetic distance matrix was generated and then used to create the PCoA.

Wright's F-statistic, $F_{ST,}$ was calculated to appraise how genetic diversity was partitioned between populations. As implemented in GenAlEx, we used Nei's [31] formula, with statistical testing options offered through 9999 random permutations and bootstraps.

## Detecting migrants

We used GENECLASS2 version 2.0.h [32] to identify first-generation migrants, i.e. individuals born in a population other than the one in which they were sampled. Genetic clusters identified during STRUCTURE analysis were treated as putative populations. GENECLASS2 provides different likelihood-based test statistics to identify migrant individuals, the efficacy of which depends on whether all potential source populations have been sampled. We first calculated the likelihood of finding a given individual in the population in which it was sampled, $L_h$, assuming all populations had not been sampled. We then calculated $L_h/L_{max}$, the ratio of $L_h$ to the greatest likelihood among the populations [33], which has greater power when all potential source populations have been sampled. The critical value of the test statistic ($L_h$ or $L_h/L_{max}$) was determined using the Bayesian approach of Rannala and Mountain [34] in combination with the resampling method of Paetkau et al. [33]; i.e., Monte Carlo simulations carried out on 10,000 individuals with the significance level set to 0.01.

## Testing for bottlenecks and inferring effective population size

We tested for evidence of recent population size reductions in Santa Ana Mountains and eastern Peninsular Range regions with one-tailed Wilcoxon sign-rank tests for heterozygote excess in the program BOTTLENECK version 1.2.02 [35]. The program evaluates whether the reduction of allele numbers occurred at a rate faster than reduction of heterozygosity, a characteristic of populations which have experienced a recent reduction of their effective population size (Ne) [35,36]. This bottleneck genetic signature is detectable by this test for a finite time, estimated to be less than 4 times Ne generations [37]. These tests were performed using the two-phase (TPM, 70% step-wise mutation model and 30% IAM) model of microsatellite evolution and 10,000 iterations.

We then estimated contemporary Ne for each of the two regions based on gametic disequilibrium with sampling bias correction [38] using LDNE version 1.31 [39]. Ne is formally defined as the size of the ideal population that would experience the same

**Table 3.** Effective population size estimations and indications of recent genetic bottlenecks in southern California pumas.

| | Mode | TPM | Ne (P-CI; JK-CI) |
|---|---|---|---|
| Santa Ana Mtns | Shifted mode | 0.009 | 5.1 (3.3–6.7; 3.3–6.6) |
| Peninsular Range, East | Normal L | 0.19 | 24.3 (21.7–27.3; 20.6–28.8) |

Listed by column are p-values for population bottleneck tests (Wilcoxon sign-rank test; BOTTLENECK) assuming the two-phase (TPM) model of microsatellite evolution. Effective size (Ne) estimations (95% CI) based on data from 42 microsatellite loci. The Santa Ana Mountains population exhibited clear evidence of a population bottleneck. Effective population size estimate using the point estimate linkage disequilibrium method of (LDNE, Waples 2006) with 95% confidence intervals (CI) for both parametric (P) and jackknifed (JK) estimates.
doi:10.1371/journal.pone.0107985.t003

amount of genetic drift as the observed population [40]. These analyses excluded alleles occurring at frequencies ≤0.05, and we used the jackknife method to determine 95% confidence intervals [38].

### Relatedness analyses: pairwise coefficient and internal

Molecular kinship analysis was conducted using a number of software packages. Pairwise relatedness among individuals was evaluated using the algorithm of Lynch and Ritland [41], with reference allele frequencies calculated and relatedness values averaged within each southern California population, as implemented in GenAlEx. Partial molecular kinship reconstruction was conducted using a consensus of outputs from the GenAlEx pairwise relatedness calculator, ML Relate [20], CERVUS version 3.0.3 [42], and Colony version 2.0.3.1 [43,44]. Individual genetic diversity (also called internal relatedness) was assessed using Rhh [45] as implemented in R statistical software [46]. This is a measure of genetic diversity within each individual (an estimate of parental relatedness [47], and we averaged over individuals for each of the two regions of southern California. Significance of differences between means was evaluated using t tests.

## Results

Forty-two of the 46 loci that we employed were polymorphic in southern California and selected for the subsequent analyses. The average probabilities of identity with assumptions of either random mating ($PID_{RM}$) or mating among sibs ($PID_{SIBS}$) across the 42 loci for the eastern Peninsular Ranges were ($PID_{RM}$) $6.3\times10^{-22}$ and ($PID_{SIBS}$) $3.1\times10^{-10}$, and for the Santa Ana Mountains were ($PID_{RM}$) $2.8\times10^{-15}$ and ($PID_{SIBS}$) $1.1\times10^{-7}$ respectively. These very small values indicate that the panel of genetic markers provided very high resolution to distinguish individuals. For example, given this data the probability of seeing the same multi-locus genotype in more than one puma was less than one in nine million for Santa Ana Mountains pumas.

### Genetic diversity

Measures of genetic variation including allelic diversity, heterozygosity, Shannon's information index, and polymorphism, were lower for Santa Ana pumas than most of those tested from other regions of California (Table 1). Such low genetic diversity indicators were approached only by pumas in the Santa Monica Mountains (Ventura and Los Angeles Counties), a neighboring remnant puma population in the north Los Angeles basin (Figure 1).

### Population Structure

Bayesian clustering analysis (STRUCTURE; Figure 3 of statewide puma genetic profiles (n = 354), including 97 from southern California, also support genetic distinctiveness of Santa Ana Mountains and eastern Peninsular Range pumas from other populations in the state. Three main genetic groups (A, B, and C) were evident in the analysis (Figure 3) The 97 pumas sampled in southern California (right-hand set of bars in Figure 3, with samples from Santa Ana and eastern Peninsular Range pumas labeled) predominantly cluster within genetic group C. The Santa Ana pumas assign very tightly to group C (0.996 average probability assignment), while pumas of the eastern Peninsular Ranges showed more variable assignment (0.93 average probability assignment), with 9 individuals (16%) having less than 0.90 assignment. Pumas sampled in the Central Coast of California (which included Santa Monica Mountains pumas) make up the central set of bands, and those individuals predominantly assign to the genetic group B. Pumas sampled in the other regions of California (North Coast Ranges, Modoc Plateau, western Sierra

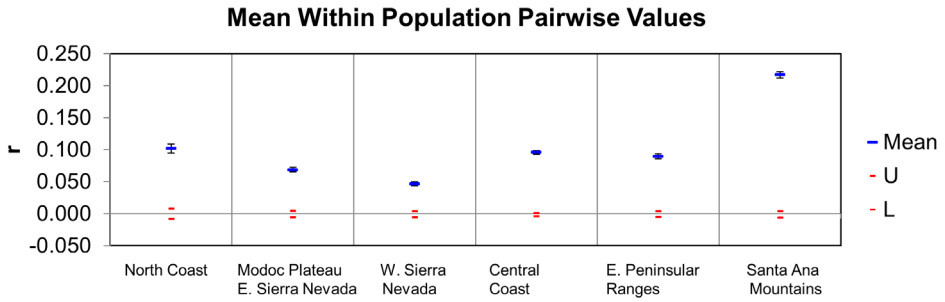


**Figure 7. Average pairwise relatedness (r; blue bars with confidence intervals) for pumas sampled in southern California relative to other regions in California. Algorithm of Lynch and Ritland (1999) as implemented in GenAlEx.** Expected range for "unrelated" is shown as red bars with confidence intervals. The average relatedness of Santa Ana Mountain pumas is higher than those sampled in Peninsular Ranges east of I-15 and for any other region tested in California. Relatedness in the Santa Ana Mountains pumas approaches second order family relationship (half sibs, niece-aunt, grandparent-grandchild, etc.). Abbreviations listed in Table 1.
doi:10.1371/journal.pone.0107985.g007

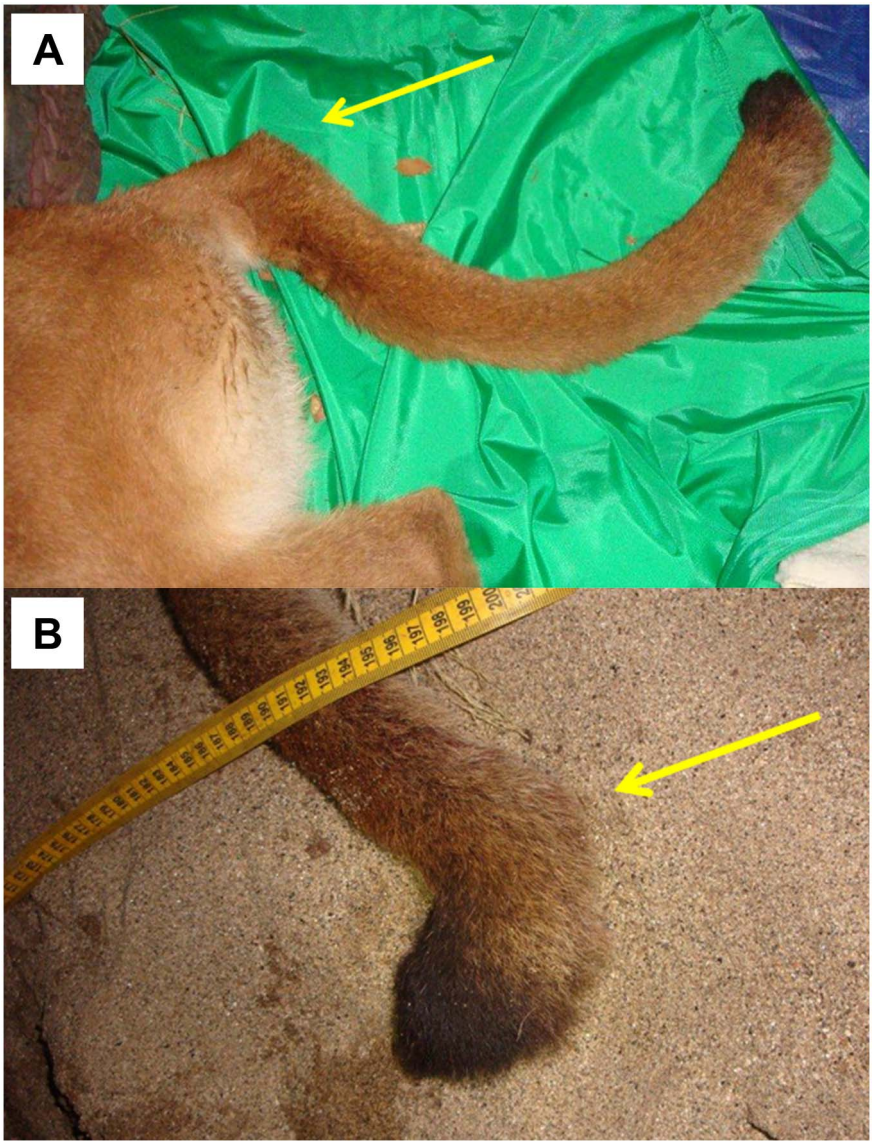


**Figure 8. Photographs of kinked tails of pumas F95 (a) and M96 (b).** Arrows indicate kink sites. Puma F95 had tail kink at base of tail and Puma M96 had tail kink near distal tip of tail. These two pumas had among the lowest genetic diversity measured in this study.
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Nevada, and eastern Sierra Nevada) predominantly cluster with the genetic group A. Notably, there are individuals sampled in each geographic area which cluster with a genetic group that is not the dominant one in that area, suggesting dispersal events and/or genetic exchange that have occurred to varying degrees in each region.

A STRUCTURE analysis focused only on genetic data from the 97 southern California pumas indicated two distinct genetic groups (C-1 and C-2 shown in Figure 4). Pumas sampled in the eastern Peninsular Range region east of I-15 group primarily with C-2 and those of the Santa Ana Mountain region on the west side of I-15 group with C-1. An exception to the consistent genetic clustering was an adult male (M) puma (M86), that was captured in the Santa Ana Mountains but clustered with pumas from the eastern Peninsular Ranges (primarily genetic group C-2). Five other pumas captured in the Santa Ana Mountains had a 30–50% assignment to the C-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) captured in the Santa Ana Mountains and assigned to the C-1 genetic group were the likely parents of three of these pumas (M91, F92, and M93) (results of relatedness and kinship analyses). M86 also was the likely parent of another puma in the group (M97), an offspring of another female (F61) that was sampled in Santa Ana Mountains and clustered with the C-1 genetic group. F102 was a $<1$ year old female killed by a vehicle in 2003 prior to collection of the majority of samples from adults in the Santa Ana Mountains.

Principal coordinates analysis of statewide puma genetic profiles ($n = 354$) (PCoA; Figure 5) allowed graphical examination of the first two major axes of multivariate genetic variation, and confirmed and added detail to the genetic distinctiveness of southern California pumas relative to others in California. The PCoA also reinforced the distinctiveness of pumas sampled in the Santa Ana Mountains from those sampled in the eastern Peninsular Ranges. Most pumas sampled in the Santa Ana Mountains align in a cloud of data points distinct from the eastern

Peninsular Range pumas, and were the most genetically distant from all other pumas tested in California (Figure 5). The analysis also confirms the STRUCTURE findings that M86 who was sampled in the Santa Ana Mountains genetically aligns with the pumas sampled in the Peninsular Ranges, as does one of his offspring, M93 (see Figure 6 for additional detail). The PCoA position of data points for three pumas sampled in the San Bernardino Mountains north of Peninsular Ranges (pink diamonds in Figure 5) illustrates an intermediate genetic relationship between pumas from the rest of California and pumas sampled in the eastern Peninsular Ranges and Santa Ana Mountains, and suggests that they may represent transitional gene flow signature between southern California and regions to the north and east.

PCoA analysis of only the samples collected in the Santa Ana and Peninsular Ranges (Figure 6) confirms the findings from the STRUCTURE analysis indicating genetic distinctiveness of these two populations despite geographic proximity. Siblings M91, F92, and M93 (offspring of F89 and M86 according to our kinship reconstructions) as well as M97 (likely offspring of a female puma captured in the Santa Ana Mountains, F61, and M86, according to kinship reconstructions) are located graphically midway between their parents' PCoA locations.

### Genetic isolation

Wright's $F_{ST}$ calculations (Table 2) indicate that Santa Ana Mountains pumas are the most isolated of those tested throughout California ($p = 0.0001$). Despite the short distance (as short as the distance across the I-15 Freeway) between the Santa Ana Mountains and the eastern Peninsular Range region, $F_{ST}$ was surprisingly high (0.07) given the very close proximity of the two regions (separated only by an interstate highway). The Santa Monica Mountains pumas and Santa Ana Mountains pumas had the highest $F_{ST}$ (0.27; lowest gene flow) of all pairwise comparisons in the state, demonstrating a high level of genetic isolation between these regions.The Santa Monica Mountains and Santa Ana Mountains are less than 100 km direct distance apart, through the center of Los Angeles. However the more likely distance for puma travel between these two mountain ranges, avoiding urban areas and maximizing upland habitat, would likely exceed 300 km (estimated using coarse measurements on Google Earth, Google, Inc.).

### Detection of migrants

GENECLASS2 identified four individuals as first-generation migrants ($P<0.01$), four with the $L_h$ method (pumas F75, M80, M86, and M99), and one with the $L_h/L_{max}$ ratio (M86, which was detected using both likelihood methods). Pumas F75, M80, and M99 were all captured from the San Bernardino Mountains (Figure 2) at the northern extent of the study region, yet clustered with individuals from the Eastern Peninsular Range during STRUCTURE analysis. Their migrant designation may suggest immigration from populations north of Los Angeles and/or a distinct genetic population within the San Bernardino region. Puma M86 was captured in the Santa Ana Mountains, but assigned strongly to the eastern Peninsular Range genetic cluster, indicating a seemingly clear population of origin. This individual assignment is in accord with the clustering results from STRUCTURE (Figure 4).

### Evidence of genetic bottlenecks

The Santa Ana Mountains population exhibited clear evidence of a population bottleneck (Table 3; Wilcoxon sign-rank test for heterozygote excess, and detection of a shift in the allele frequency distribution mode [36]; BOTTLENECK software). The eastern Peninsular Range mountain lions did not show a strong signature of a bottleneck.

### Effective population size

Effective population size (Ne) estimations using the linkage disequilibrium method (LDNe program) were 5.1 for the Santa Ana Mountains population and 24.3 for mountain lions in the eastern Peninsular Ranges. Statistical confidence intervals for both regions, given the genetic data, were tight (Table 3).

### Relatedness: pairwise coefficient and internal

The average pairwise coefficient of relatedness (r, Figure 7) was highest in Santa Ana Mountains pumas relative to all others tested in California (0.22; 95% confidence interval of 0.22–0.23), a level that approaches second order kinship relatedness (half-sibs, grantparent/grandchild, aunt-niece, etc). The value for the eastern Peninsular Ranges was 0.10 (confidence interval of 0.09–0.10), less than that of third order relatives (first cousins, great-grandparent/great grandchild). Other regions of California averaged similar or lower values to those of eastern Peninsular Ranges (Figure 7).

Among pumas sampled in the Santa Ana Mountains, the population average (0.14) for internal relatedness as implemented in rHH software was significantly higher (t test; $p = 5.8\times10^{-6}$) than for those sampled in the eastern Peninsular Ranges (0.001). Of a group of six pumas which clustered near one another in PCoA (Figure 6), five have among the lowest individual genetic diversity measured in southern California (Puma ID [Internal Relatedness value: F45 [0.37], F51 [0.37], M87 [0.28], F90 [0.21], F95 [0.38], and M96 [0.33]). Notably, pumas F95 and M96 (highest internal relatedness) were observed with kinked tails at capture in the Santa Ana Mountains (Figure 8).

## Discussion

Pumas of the Santa Ana Mountains are genetically depauperate, isolated, and display signs of a recent and significant bottleneck. In general, coastal California puma populations have less genetic diversity and less gene flow from other populations than those farther inland [9] (Table 1). This study showed that two coastal populations (Santa Ana Mountains and Santa Monica Mountains) had particularly low genetic variation and gene flow from other regions. Lack of gene flow is likely due in part to natural barriers to puma movement: geography and habitat (Pacific Ocean to the west; less hospitable desert habitat bounding certain regions, etc.). However, our data suggest that anthropogenic developments on the landscape are playing a large role in genetic decay in the Santa Ana Mountains puma population. As large solitary carnivores with sizable habitat requirements, pumas are extremely sensitive to habitat loss and fragmentation [48,49].

The genetic bottleneck in the Santa Ana Mountains pumas is estimated at less than about 80 years, depending on definitions of effective population size (Ne) and puma generation time. Luikhart and Cornuet [37] state that the bottleneck signatures decay after "4 times Ne [here estimated to be 5.1] generations". Logan and Sweanor [50] estimated generation time for their New Mexico population of pumas to be 29 months (2.4 years) for females. If an allowance of 2.4–4.0 years is made for generation times (unknown) in the Santa Ana Mountains population, the maximum estimated time since a bottleneck would be about 40–80 years. This was a period of tremendous urban development and multi-lane highway construction in southern California, particularly I-15 [51]. It is likely that the potential for connectivity between the Santa Ana Mountains and the Peninsular Range-East region will continue to be eroded by ongoing increases in traffic volumes on I-15, and

conversion of unconserved lands along the I-15 corridor by development and agriculture [8,48,52].

An isolated population of pumas in the Santa Monica Mountains to the north of the Santa Ana Mountains also exhibit low values relative to other western North American populations (see Table 2 in [53]. Santa Monica pumas are isolated by urbanization of a megacity and busy wide freeways (Ventura county, including greater Los Angeles region [53]. Multiple instances of intraspecific predation, multiple consanguineous matings (father to daughter, etc.), and lack of successful dispersal highlight a suite of anthropogenic processes also occurring in the Santa Ana Mountains. Our collective findings of kinked tails *and* very low genetic diversity in Santa Ana pumas F95 and M96 may portend manifestations of genetic inbreeding depression similar to those seen in Florida panthers [54,55]; however recognizing that kinked tails can have non-genetic etiologies.

Our analyses suggest that the Santa Ana Mountains puma population is highly challenged in terms of genetic connectivity and genetic diversity, a result hinted at in Ernest et al. [9] and now confirmed to be an ongoing negative process for this population. This compounds the demographic challenges of low survival rates and scant evidence of physical connectivity to the Peninsular Ranges east of I-15 (unpublished data). Beier [6] documented these same challenges during the 1990's, and data from the ongoing UCD study suggest the trends have accelerated. Substantial habitat loss and fragmentation has occurred and is continuing to occur; Burdett et al. [10] estimated that by 2030, approximately 17% of puma habitat that was still available in 1970 in southern California will have been lost to development, and fragmentation will have rendered the remainder more hazardous for pumas to utilize. Riley et al [53] document a natural "genetic rescue" event: the 2009 immigration and subsequent breeding success of a single male to the Santa Monica Mountains. This introduction of new genetic material into the population was paramount to raising the critically low level of genetic diversity, as also exemplified by the human-mediated genetic augmentation of Florida Panthers with Texas puma stock [56].

These findings raise concerns about the current status of the Santa Ana Mountains puma population, and the longer-term outlook for pumas across southern California. In particular, they highlight the urgency to maintain – and enhance – what connectivity remains for pumas (and presumably numerous other species) across I-15. Despite warnings [6,9] about potential serious impacts to the Santa Ana Mountains puma population if concerted conservation action was not taken, habitat connectivity to the Peninsular Ranges has continued to erode. We are hopeful that these new genetic results will motivate greater focus on connectivity conservation in this region. Indeed, the Santa Ana Mountains pumas may well serve as harbingers of potential consequences throughout California and the western United States if more attention is not paid to maintaining connectivity for wildlife as development progresses.

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## Author Contributions

Conceived and designed the experiments: HBE TWV WMB. Performed the experiments: HBE TWV MRB WMB. Analyzed the data: HBE TWV MRB. Contributed reagents/materials/analysis tools: HBE TWV SAM WMB. Contributed to the writing of the manuscript: HBE TWV SAM MRB WMB.

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# California Red-Legged Frog (*Rana draytonii*) Movement and Habitat Use: Implications for Conservation

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ABSTRACT.—**Nonbreeding habitats are critically important for *Rana draytonii*, especially for individuals that breed in temporary bodies of water. We radiotracked 123 frogs to evaluate seasonal habitat use. Individual frogs were continuously tracked for up to 16 months. Some individuals remained at breeding ponds all year, but 66% of female and 25% of male frogs moved to nonbreeding areas, even when the breeding site retained water. Frogs at our main study site moved 150 m (median), roughly the distance to the nearest suitable nonbreeding area. The greatest straight-line distance traveled was 1.4 km, although the presumed distance traveled was 2.8 km. Females were more likely than males to move from permanent ponds (38% of females, 16% of males), but among dispersing frogs, males and females did not differ in distance moved. Some frogs left breeding sites shortly after oviposition (median = 12 days for females, 42.5 days for males), but many individuals remained until the site was nearly dry. Fog provided moisture for dispersal or migration throughout the summer. Our data demonstrate that maintaining populations of pond-breeding amphibians requires that all essential habitat components be protected; these include (1) breeding habitat, (2) nonbreeding habitat, and (3) migration corridors. In addition, a buffer is needed around all three areas to ensure that outside activities do not degrade any of the three habitat components.**

*Rana draytonii* (California Red-Legged Frog) was once an abundant frog throughout much of central and southern California and is believed to have inspired Mark Twain's fabled story "The Celebrated Jumping Frog of Calaveras County." Now this frog is rare in both the Sierra Nevada foothills and the southern portion of its range (Jennings and Hayes, 1994). In parts of the central Coast Range, there are still large, vigorous populations, some of which probably rival those present 200 years ago (Fellers, 2005). *Rana draytonii* was federally listed as a Threatened species on 24 June 1996, and the recovery plan states that it ". . . has been extirpated from 70 percent of its former range . . . Potential threats to the species include elimination or degradation of habitat from land development and land use activities and habitat invasion by non-native aquatic species" (U.S. Fish and Wildlife Service, 2002:iv).

*Rana draytonii* use ponds or pools for breeding during the wet season (December through March) and ponds, riparian areas, or other aquatic habitats during the rest of the year. In Marin County, stock ponds are the most commonly used breeding sites. There is only one published report on migration or nonbreeding habitat requirements for this frog. Bulger et al. (2003) described movements of 56 *R. draytonii* in a coastal area about 100 km south of San Francisco. They found that 80–90% of the frogs remained at one breeding site all year. Frogs radiotagged at nonbreeding sites often moved in a straight-line between breeding and upland habitats without apparent regard to intervening vegetation or topography. Frogs traveled overland up to 2,800 m, and Bulger et al. (2003) recommended a 100 m buffer zone around breeding sites.

The California Red-Legged Frog recovery plan outlines the necessary actions for recovery. One task is to "conduct research to better understand the ecology of the California Red-Legged Frog including the use of uplands, dispersal habits, and overland movements" (U.S. Fish and Wildlife Service, 2002:84). This is a concern not only for *R. draytonii*, but also for many endangered and nonendangered vertebrates that migrate between breeding and nonbreeding areas. This includes salamanders (*Ambystoma*; Madison, 1997; *Triturus*; Joly et al., 2001), frogs (*Rana*; Richtor et al., 2001; Pope et al., 2000), snakes (*Farancia*; Gibbons et al., 1977), turtles (Burke and Gibbons, 1995; Bodie, 2001), and many species of passerine birds (Keast and Morton, 1980). Lamoureux and Madison (1999) made the point that studies need to examine amphibian habitat requirements at all times of the year not just during the breeding season. We designed our study to address this concern for *R. draytonii*.

## MATERIALS AND METHODS

*Study area.*—Our study was conducted in Marin County, California, 45 km northwest of

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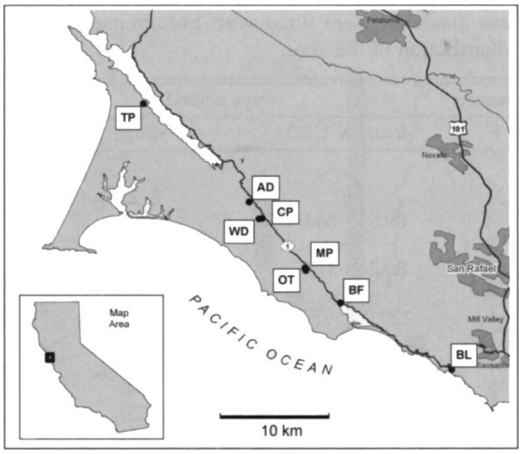


FIG. 1. Sites where California Red-Legged Frogs (*Rana draytonii*) were radiotagged at Point Reyes National Seashore and Golden Gate National Recreation Area, Marin County, California. Site descriptions are listed in Table 1.

San Francisco. All sites were within 6 km of the ocean and located at either Point Reyes National Seashore or Golden Gate National Recreation Area (Fig. 1). The local climate is Mediterranean, with an average annual rainfall of 100 cm that largely occurs between November and March. Mean monthly temperatures range from 8.6°C (December) to 16.6°C (August/September) at the headquarters of Point Reyes National Seashore in Olema Valley (National Park Service weather records). Most frogs ($N$ = 112) were tagged in the Greater Olema Valley (Olema Valley and Pine Gulch Valley; 38°01′41″N, 122°46′50″E). To evaluate movement and habitat use in areas with contrasting habitats, nine frogs were tagged at Big Lagoon (37°51′36″N, 122°34′29″E), and two were tagged at Tomales Point (38°09′19″N, 122°54′43″E; Fig. 1).

Most of the Greater Olema Valley was characterized by a mixture of grazed and ungrazed grasslands interspersed with seasonal drainages with California bay (*Umbellularia californica*) and coast live oak (*Quercus agrifolia*). The west side of the valley was predominantly a Douglas fir forest (*Pseudotsuga menziesii*). Olema and Pine Gulch Creeks had well-defined riparian zones composed of California bay, red alder (*Alnus rubra*), willow (*Salix* spp.), big-leaf maple (*Acer macrophyllum*), and Douglas fir, with an understory dominated by blackberry (*Rubus discolor*), poison oak (*Toxicodendron diversilobum*), stinging nettles (*Urtica dioica*), and western sword fern (*Polystichum munitum*). Within the valley, there were 24 *R. draytonii* breeding sites. Fourteen of these were artificial stock ponds, and the others were naturally occurring ponds or marshes. Aquatic vegetation was predominantly cattails (*Typha* spp.), pennywort (*Hydrocotyle verticillata*), and rushes (*Juncus* spp.). About half of the ponds were seasonal, whereas the others usually held water all year. Study sites within the Olema Valley were selected to represent a range of habitats and because there was a sufficiently large *R. draytonii* population at each of the study sites.

The Big Lagoon study site consisted of a cattail marsh with a seasonal creek (Green Gulch Creek) that flowed into it. The marsh had several small areas where water depth was 1.0–1.5 m during the winter, but most of the marsh was covered by $< 0.25$ m of water, even during the wet season. A levee on the north side separated the marsh from a permanent creek (Redwood Creek), but a set of culverts allowed water to enter the marsh during higher winter flows. Water retention in the marsh varied with rainfall but was also influenced by how much water the National Park Service allowed to pass through flood gates on the culverts. The Tomales Point study site was a nonbreeding site at a seasonal seep. The dominant vegetation was coyote brush (*Baccharis pilularis*), with a few wax myrtle (*Myrica californica*). The nearest breeding pond was 650 m away.

*Field methods.*—Frogs were caught at night either with a dip net or by hand. We marked each frog with a passive integrated transponder (PIT) tag (TX1400L, Biomark, Meridian, ID; www.biomark.com) for individual identification and recorded sex, snout–vent length (SVL), and mass. Each frog was radiotagged by attaching a transmitter (model BD-2G, Holohil Systems Ltd., Carp, Ontario, Canada; www.holohil.com) to a belt of aluminum beaded chain that was slipped over the frog's extended rear legs and up onto the waist (Rathbun and Murphey, 1996). The transmitters were either a dull green or light brown color. The aluminum belt was painted flat black to eliminate reflections. The smallest frog we radiotagged was 32 g, and the mass of the transmitter and belt was approximately 2.1 g (6% of the frog's mass). When possible, we recaptured frogs before the battery died (20-week life) and fitted a new transmitter. We tagged frogs during all months of the year except August, with most being tagged just prior to, or during, the December to March breeding season.

A total of 123 individual frogs was radiotagged (47 females, 76 males) between 5 November 1997 and 1 May 2003 at eight sites (Table 1). Twenty-three frogs were consecutively fitted with two transmitters, six frogs with three transmitters, and one frog wore six

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TABLE 1. Sites where California Red-Legged Frogs (*Rana draytonii*) were fitted with radiotransmitters in Marin County, California. Figure 1 shows the geographic distribution of the sites.

| Site name | Habitat | Number of frogs tagged | | Days tracked | |
|---|---|---|---|---|---|
| | | M | F | Median $\bar{x}$ ± SD | Range |
| Greater Olema Valley | | | | | |
| CP | Permanent pond | 44 | 31 | 86<br>89.6 ± 56.0 | 2–229 |
| MP | Seasonal pond | 19 | 9 | 76<br>80.5 ± 47.3 | 12–191 |
| AD | Seasonal pond | 2 | 4 | 127<br>139.0 ± 75.0 | 63–253 |
| BF | Seasonal pond | 2 | 2 | 112<br>109 ± 74.9 | 28–184 |
| WD | Permanent pond | 0 | 1 | 134 | 134 |
| OT | Permanent pond | 1 | 0 | 121 | 121 |
| All sites | – | 68 | 47 | 83<br>91.3 ± 56.1 | 5–253 |
| Big Lagoon | | | | | |
| BL | Permanent marsh | 9 | 0 | 68<br>66.8 ± 36.8 | 16–130 |
| Tomales Point | | | | | |
| TP | Seasonal seep and ditch | 0 | 2 | 283 | 68–498 |

consecutive transmitters. Seventy-eight percent of all transmitters ($N$ = 166) were recovered. Three frogs (two females, one male) lost their transmitters but were subsequently recaptured and outfitted with new transmitters 54, 244, and 493 days later. This yielded 126 telemetry histories. We generally located radiotagged frogs twice weekly; more often when the frogs were making regular movements. We recaptured frogs every 3–4 weeks to check for injuries and ensure proper fit of the transmitter belt. Frogs were radiotagged for 91 days (median) at the Olema Valley study sites and for 67 and 283 days at the Big Lagoon and Tomales Point sites, respectively.

Frogs were located using a TR-2 receiver (Telonics, Mesa, AZ; www.telonics.com) or an R-1000 receiver (Communication Specialists, Inc., Orange, CA; www.com-spec.com) with a directional "H" or three-element yagi antenna. Fine scale location of transmitters was accomplished with a partially stripped coaxial cable inserted into a length of PVC pipe that was used as a probe (Fellers and Kleeman, 2003). Radio locations were only determined during the day.

Frog locations were plotted on a 7.5′ USGS topographic map by noting proximity to a mapped feature or permanent local landmark (e.g., dead snag, fence corner). On a few occasions, locations were initially determined using a Garmin 12XL GPS unit (Garmin International Inc., Olathe, Kansas, www.garmin.com), but these locations were later visited and mapped on a topographic map using local landmarks. Telemetry data were analyzed by plotting coordinates on digitized USGS topographic maps (1:24,000 scale) using Topo! software (National Geographic TOPO! Maps, San Francisco, California; maps.nationalgeographic.com/topo). Unless otherwise noted, movements represent straight-line distances between successive locations. For some frogs, we also calculated a longer distance moved based on locations between breeding and nonbreeding sites. For example, frogs found at several successively further distances along a riparian corridor were presumed to have followed the creek between sites. This typically resulted in a longer distance moved than would be obtained using a straight-line distance and is referred to as presumed distance. Statistical analysis was conducted using Statistix (Version 7, Analytical Software, Tallahassee, Florida; www.statistix.com/home.html). We used $\alpha$ = 0.05 to evaluate statistical significance.

Olema Creek passed within 110 m of our main study site (CP) in Olema Valley (Fig. 1). To evaluate use of nonbreeding habitat, we conducted nocturnal surveys along all or part of a 4.8-km segment of Olema Creek where it flowed past our study area. One or two observers walked the creek while carefully searching both pools and stream banks for frogs. Observers used a combination of spotlights and binoculars to locate animals (Corben and Fellers, 2001). Radiotelemetry was not used as part of these nocturnal surveys. We believe that most of the frogs we located used the adjacent pond (CP) for breeding because (1) it

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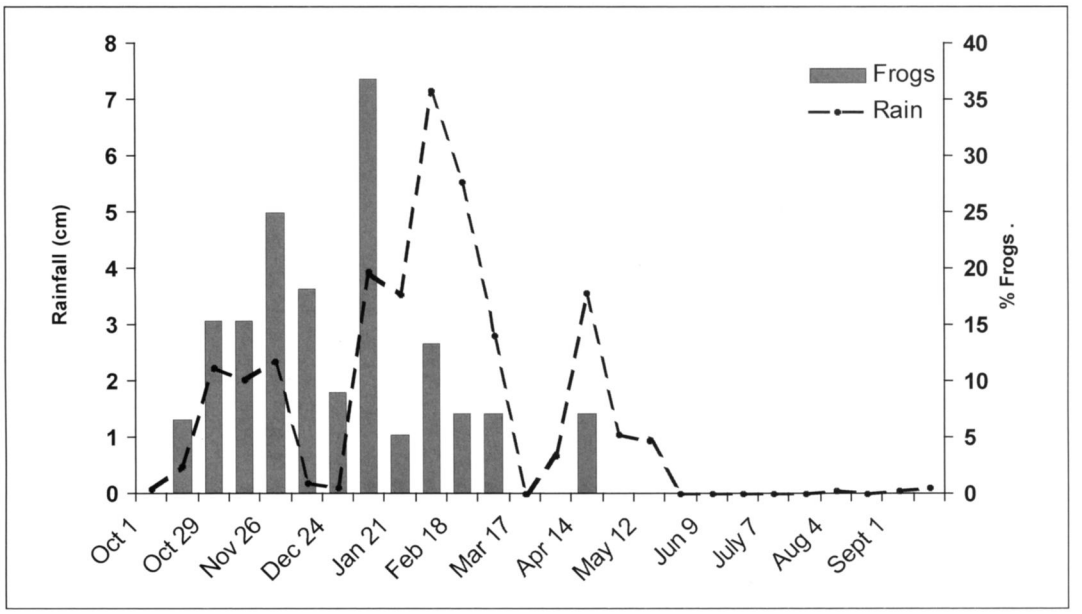


FIG. 2. Biweekly rainfall and the percent of radiotagged *Rana draytonii* that moved ≥30 m between October 1999 and September 2000.

was the closest breeding site and (2) some of the frogs found along the creek had been fitted with radiotransmitters at the pond.

## RESULTS

Frogs made small-scale movements (<30 m) throughout the year. Movements of <30 m could be made without leaving the breeding sites; hence, they were considered local, non-dispersal. Movements ≥30 m generally coincided with winter rains, although some frogs did not move until their seasonal habitat was on the verge of completely drying. In general, frogs moved toward breeding ponds with the onset of heavy winter rains. Frogs departed from breeding ponds at varying times throughout the rainy season, with some frogs remaining at permanent ponds all year. Some frogs made large-scale movements during the dry season (May through October), as seasonal breeding sites dried. A regression of the percent of frogs that moved ≥30 m versus rain showed that more frogs moved with higher amounts of rain ($P$ = 0.006). We show rainfall and movements for the 1999–2000 season (Fig. 2), the year we had the most frogs simultaneously radiotagged.

*Frog movements in the greater Olema Valley.*—One hundred fifteen frogs were tracked for a mean of 91 days each (range = 5–253, Table 1). Median distance moved from the breeding site was 0 m, but for the 36 frogs that moved ≥30 m, the median was 150 m (range = 30–1400 m, Table 2, Fig. 3). In many cases, frogs almost certainly moved more than the straight-line distance between sites. This was confirmed with individuals that were located in transit. Presumed distance moved for those frogs that moved ≥30 m was 185 m (median, range = 30–1400 m).

A higher proportion of radiotagged females moved ≥30 m than males (13 of 68 males, 23 of 47 females, $\chi^2$ = 11.49, df = 1, $P$ < 0.01). For frogs that moved ≥30 m, distance traveled was not significantly different for males ($N$ = 13) and females ($N$ = 23; median = 210 vs. 140 m, respectively; Wilcoxon rank sum $T$ = 1.22, $P$ = 0.22). Because some frogs lost their transmitters or were killed by predators (see below), the median distance moved might be greater than what we measured. Of the 36 frogs that moved ≥30 m, 22 (11 males, 11 females) reached a destination where they remained for at least two weeks. For these frogs, median distance traveled was 175 m. The median for these males and females was not significantly different (210 vs. 120 m; Wilcoxon rank sum $T$ = 0.56, $P$ = 0.58), in part because of the large variability in distance traveled.

A higher proportion of females left breeding sites than males. At our main study site (CP), nine of 21 (43%) females left the breeding site, whereas only four of 25 (16%) males departed. Females left the breeding site sooner than males (1, 5, 5, 5, 12, 55, 60, 76, 92 days for females [median = 12]; 31, 38, 47, 69 days for males

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TABLE 2. Distance moved for 110 California Red-Legged Frogs (*Rana draytonii*) with radiotransmitters at three study sites in Marin County, California. Sixteen frogs radiotagged at nonbreeding sites are not included in this tabulation.

| | | Distance moved for frogs that moved ≥30 m | | | | | | Frogs that moved <30 m |
|---|---|---|---|---|---|---|---|---|
| | Sex | Minimum | Median | Maximum | Mean | SD | *N* | *N* |
| Olema Valley | | | | | | | | |
| CP | Males | 200 | 240 | 490 | 293 | 135 | 4 | 31 |
| CP | Females | 100 | 320 | 1400 | 421 | 416 | 10 | 14 |
| MP | Males | 270 | 270 | 270 | 270 | – | 1 | 18 |
| MP | Females | 150 | 150 | 150 | 150 | 0 | 2 | 7 |
| AD | Males | – | – | – | – | – | 0 | 2 |
| AD | Females | 30 | 80 | 90 | 70 | 28 | 4 | 0 |
| BF | Males | 80 | 80 | 80 | 80 | – | 1 | 1 |
| BF | Females | 40 | 95 | 150 | 95 | 78 | 2 | 0 |
| WD | Males | – | – | – | – | – | 0 | 0 |
| WD | Females | – | – | – | – | – | 0 | 1 |
| OT | Males | 560 | 560 | 560 | 560 | – | 1 | 0 |
| OT | Females | – | – | – | – | – | 0 | 0 |
| Big Lagoon | | | | | | | | |
| BL | Males | 30 | 105 | 390 | 158 | 136 | 6 | 3 |
| | Females | – | – | – | – | – | 0 | 0 |
| Tomales Point | | | | | | | | |
| TP | Males | – | – | – | – | – | 0 | 0 |
| TP | Females | 30 | 40 | 50 | 40 | 14 | 2 | 0 |

[median = 42.5]), but the sample size was small, and the difference was not significant ($T = 0.61$, df = 11, $P = 0.55$).

Some of the dispersing frogs moved well away from the breeding site. One female (10.7 cm SVL) left the pond at our main study area (CP), crossed Olema Creek (the primary nonbreeding area) and stopped at a pond 320 m from the breeding pond. Two females (10.9 and 10.1 cm SVL) moved from CP, across Olema Creek and eventually resided in marshes, 0.88 and 1.02 km from the breeding site. Another female (10.6 cm SVL) moved down Olema Creek and up a small tributary for a total distance of 2.8 km (see individual case histories below).

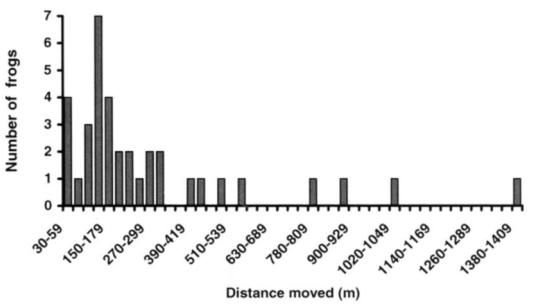


FIG. 3. Straight-line distance moved for all radiotagged Greater Olema Valley frogs that traveled ≥30 m. Median = 185 m, $N = 36$.

Fourteen of the breeding sites in the Greater Olema Valley were stock ponds surrounded by pastures. At these sites, all frogs that left the breeding site had to cross heavily grazed grassland to reach another pond or the riparian area. Frogs moved directly across these fields, typically traveling the most direct route to their destination. Movements of 100–200 m across open grasslands were common. With one exception, movements taking more than one night were along riparian corridors. One frog, however, spent five days sitting in a small clump of rushes in an open grassland (45 m from the breeding pond) before moving another 100 m to a small riparian area where it spent the next 50 days.

In two instances, we radiotagged females that appeared to have recently laid eggs (i.e., gaunt sides, conspicuously loose skin). Both frogs left the breeding pond within two days and moved to a seasonal marsh 800 m away. One frog took 32 days (5 December 1997 to 5 January 1998), whereas the other took five days (14–19 January 2000). A gravid female was fitted with a transmitter at a seasonal pond on 29 January 2001. By 8 February 2001, she had moved to an adjoining swale dominated by rushes. When captured on 28 February 2001, she had laid her eggs, as indicated by a sudden drop in mass. By 3 April 2001, she had moved 150 m to a riparian area where she remained until the transmitter was removed on 1 August 2001.

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*Frog movements at Big Lagoon.*—The nine male frogs at this site moved a median distance of 70 m (0–390 m, Table 2). Frogs made small-scale movements (<30 m) throughout the time they were radiotagged (26 December 2002 through 3 June 2003). Most movements were between three of the deeper parts of the marsh, but one frog moved 390 m up Green Gulch Creek (when part of the marsh dried), to a seasonal creek that flowed into the marsh system. The other frogs moved to the only remaining pool at the west edge of the marsh, 50–75 m away. Most frogs did not use the riparian zone along the adjacent Redwood Creek. One individual spent four weeks there, and another frog moved to the riparian zone just before it lost its transmitter. We found frogs in the riparian area during only one nocturnal survey, although we regularly found them in the marsh or adjacent cattails.

*Frog movements at Tomales Point.*—The two female frogs radiotagged at this site (6.7 and 10.6 cm SVL) were relatively sedentary and apparently did not move to a breeding site. They had transmitters for an average of 283 days (68 and 498 days). Both frogs moved >30 m, with a mean of 65 m (Table 2). Although it might have been possible for the female that we tracked for 498 days to have moved to a breeding pond, laid eggs, and returned to her nonbreeding site without our noticing her absence, the gradual increase in mass throughout the time we tracked her indicated that this did not happen, and she apparently did not breed during the time we radiotracked her.

*Use of riparian habitat.*—On six of the 21 nocturnal stream surveys, there were ≥4 frogs per 100 m of stream, and one survey located seven frogs per 100 m (2 September 1999). Because radiotagged frogs known to be present (i.e., located during the same day by telemetry and also found along the creek on subsequent days) were frequently not seen during nocturnal surveys, the number of frogs along the creek was greater than what we observed, but it is not possible to determine by how much. For example, during a nocturnal survey on 5 July 2000, we observed one of the radiotagged frogs known to be along the creek, but we did not find two other radiotagged frogs whose presence had been confirmed earlier that day. Similarly, a nocturnal survey on 3 August 2000 did not detect either of two radiotagged frogs known to be present earlier that day; however, two untagged adults and nine subadults (<5.5 cm SVL) were observed. Nocturnal surveys also suggested that frogs tended to concentrate along portions of the creek nearest the breeding sites (Fig. 4).

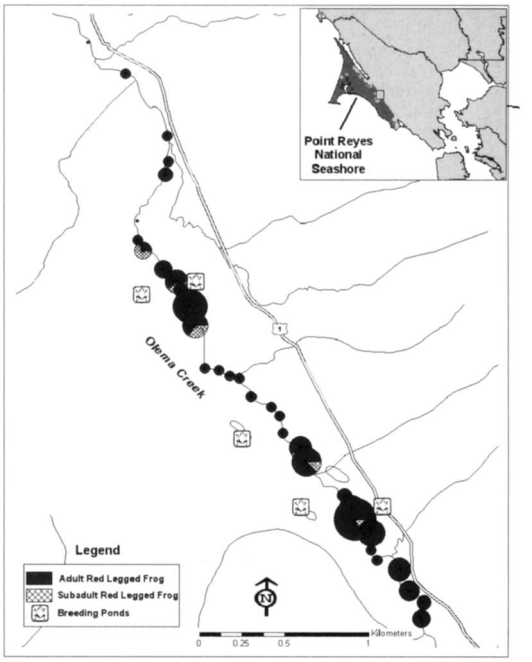


FIG. 4. Distribution of *Rana draytonii* along Olema Creek as detected during nocturnal surveys 4–6 October 1999. The distribution of frogs was similar during other surveys. Circles represent frogs, and size of each circle indicates relative number of frogs.

*Diurnal behavior.*—We conducted our radiotracking during the day and were frequently able to confirm visually the exact location of frogs with transmitters. This allowed us to evaluate diurnal microhabitat use. It was not unusual to find California Red-Legged Frogs basking in full sun, immediately adjacent to the water. Although we observed this behavior primarily at breeding ponds, occasionally frogs were found in similar situations in nonbreeding riparian areas.

Frogs that were not basking used a variety of cover. In permanent ponds, they sat entirely underwater in the deeper portions of the pond (>0.75 m), usually in association with the emergent vegetation. At sites with deeper water, *R. draytonii* sat on the bank in close proximity to the water. In shallow, seasonal ponds (<0.4 m deep), frogs were usually under vegetation (e.g., rushes, blackberries, hedge nettles [*Stachys ajugoides*]) at the edge of the pond. In seeps or seasonal streams, frogs were found under blackberry thickets interspersed with poison oak, coyote brush, hedge nettles, stinging nettles, and mats of rushes. Along permanent streams, frogs were found in or near pools with a depth of >0.5 m and associated with structurally complex cover (e.g., root mass, logjam, or overhanging bank). When on stream

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banks, frogs sat under dense vegetation as far as 2 m from the water's edge. Vegetation was predominantly western swordfern, blackberry, hedge nettle, and giant horsetail (*Equisetum telmateia*).

*Predation.*—We documented two predation events and had circumstantial evidence for three others. A Great Blue Heron (*Ardea herodia*) ate two radiotagged frogs sometime between 4 and 18 January 2000 (Fellers and Wood, 2004). Three other frogs appeared to have been killed by predators. The skin, bones, and transmitter of one frog were found at the base of a guano-stained fence post, along with a number of raptor pellets. Two frogs appeared to have been killed by mammalian predators, although we have no definitive proof. We found the skin, internal organs, PIT tag, and transmitter of a frog in a riparian corridor, and we found pieces of skin, internal organs, and the transmitter of another frog. One frog appeared to have been stepped on by a large, hoofed animal, probably one of the cows that grazed in the pasture. We found the anterior two-thirds of the frog in a pasture; the posterior portion of the frog had been crushed into the ground. Although we did not observe any predation during our nocturnal surveys along Olema Creek, we regularly observed raccoons (*Procyon lotor*), Black-Crowned Night Herons (*Nycticorax nycticorax*), river otters (*Lutra canadensis*), and nonnative rats (*Rattus* spp.). At breeding sites, we observed Great Blue Herons, but other potential predators probably visited the ponds and marshes at times.

*Injuries from transmitters.*—Twenty frogs had injuries from transmitter belts (17% of radiotagged frogs). The most common injury consisted of small abrasions on the dorsum or, less frequently, a midventral abrasion. The wounds generally healed within two weeks if frogs were fitted with transmitter belts with one additional bead. Eleven of the injured frogs were reweighed at the time the wound was noticed, and all frogs had gained mass since their initial capture. We reweighed 23 uninjured frogs with transmitters; 18 (78%) gained mass after initial capture, two (9%) had no change, and three (13%) lost mass. The mean mass gain for these frogs was 21%, and mean mass loss was 8.5%. Overall, we do not believe that the minor injuries caused by the transmitter belt interfered with frog behavior.

*Individual case histories.*—The frog that was radiotagged for the longest time had a transmitter for 16 months. When first caught on 12 May 1999, the female frog weighed 42.5 g and was 7.3 cm SVL. It grew steadily and was 77.7 g and 8.9 cm when last captured on 14 June 2000.

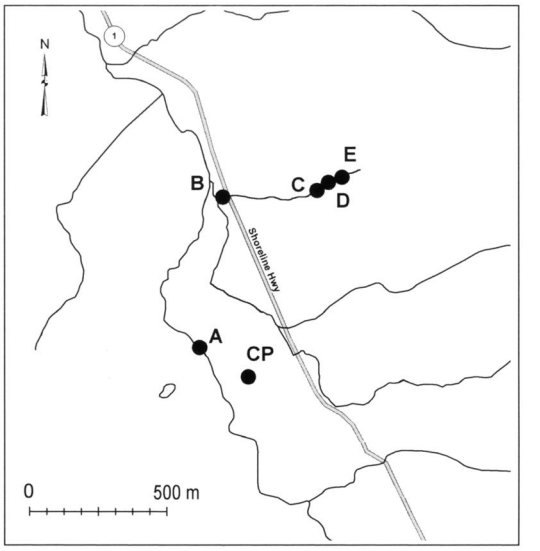


FIG. 5. Movements of a female radiotagged *Rana draytonii* that was captured at a breeding pond (CP) and subsequently moved to sites A–E. The frog was 10.5 cm (SVL) and was tagged during the breeding season (19 January 1999). The straight-line distance from CP to E was 1.4 km, but the presumed distance moved was 2.8 km.

The frog was caught in a puddle (1.0 × 0.3 m, 15 cm deep) that had formed in a rut created by a roadside seep along an abandoned dirt road on Tomales Point (site TP, Fig. 1). For 16 months, this frog made frequent, small (2–10 m) movements, within a 200-$m^2$ area surrounding the seep. The furthest the frog moved was 110 m. It used a variety of microhabitats: underwater in the puddle, underground in small mammal burrows, partially buried in duff beneath wax myrtle and coyote brush, and sitting in small clumps of grass. Although this frog was an adult female, it did not move to the nearest known breeding pond (650 m away) during the winter of 1999–2000. On 1 September 2000, the transmitter was found in the grass beneath a coyote brush, 6 m from where the frog had last been found. We could not determine whether the transmitter had fallen off or whether the frog had met a predator.

One frog moved at least 1.4 km. This was a female (10.5 cm SVL) tagged at a breeding pond (CP) during the breeding season (19 January 1999). On 23 January 1999, she was located under a fallen tree, 240 m away in Olema Creek. On 30 January 1999, she had moved a minimum of 650 m to a pool in a small tributary of Olema Creek (Fig. 5). It is quite likely that the frog followed Olema Creek to the tributary, which would have required a move-

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ment of 1.0 km to reach that point. By 14 February 1999, the frog had moved either across a two-lane, paved country road or under the road through a culvert. She then moved up a small, seasonal drainage, 430 m from her previous location. The presumed distance traveled by this frog was 2.8 km. The frog stayed in this drainage and was often found under blackberry brambles and thickets of poison oak along the stream. The transmitter and remains of the frog were found on 14 June 1999, apparently the victim of avian predation (see Predation above).

## Discussion

The California Red-Legged Frog recovery plan emphasizes protection and recovery of breeding habitat (U.S. Fish and Wildlife Service, 2002), and most protection efforts have focused on breeding sites. One challenge in managing *R. draytonii* has been the paucity of data on habitat use beyond the breeding site, thus making it difficult to evaluate requirements for nonbreeding habitat and connecting migration corridors. Our study provides insights into *R. draytonii* movement and habitat use in a coastal environment and establishes a basis for making decisions about habitat protection.

Migration of *R. draytonii* from the breeding sites we studied was highly variable. Some frogs remained at breeding ponds all year, whereas others spent only a few days. Two-thirds of female frogs and 25% of male frogs moved from breeding areas. Bulger et al. (2003) found that 80–90% of *R. draytonii* remained at one breeding site all year. In our study, frogs at sites that held water only seasonally often lingered until the site was on the verge of drying completely. Because all our study sites were in an area where summer fog is the norm (E. J. Null, NOAA Technical Memorandum, NWS WR-126, 1995; Lundquist and Bourcy, 2000), frogs could move throughout much of the summer with little risk of desiccation. Once along the riparian corridor, frogs used a range of microhabitats that provided both cover and moisture, especially blackberry thickets, log-jams, and root tangles at the base of standing or fallen trees. Regular summer dispersal across open grassland is in contrast to what Rothermel and Semlitsch (2002) reported for juvenile *Ambystoma* and *Bufo* in Missouri where desiccation appeared to be a significant factor affecting amphibian dispersal across fields adjacent to their artificial pools.

There was a wide range of migration distances (30–1400 m, straight-line). Our main study pond was 110 m from a riparian zone that provided suitable nonbreeding habitat (CP, Fig. 1). For frogs that moved at least 30 m from the pond, the median movement was 150 m. Relatively short movements from breeding sites was also suggested by the nocturnal surveys of riparian vegetation along Olema Creek (Fig. 4) where we found more frogs in areas adjacent to breeding sites. At Big Lagoon, where nonbreeding habitat was immediately adjacent to breeding sites in the marsh, the median distance moved was 68 m, and none of the frogs went more than 390 m. These short movements were similar to Columbia Spotted Frogs (*Rana luteiventris*); Pilliod et al. (2002) found no significant difference between males ($\bar{x}$ = 367 m moved) and females ($\bar{x}$ = 354 m). Bartelt et al. (2004) reported that male Western Toads (*Bufo boreas*) traveled shorter distances from breeding ponds than females (581 m ± 98 and 1105 m ± 272, respectively). Because there is relatively little data on these species, it is not possible to determine whether the differences are species-specific or dependent on the local landscape.

When frogs moved beyond the minimum distance to reach a suitable nonbreeding area, some followed riparian corridors, whereas others moved directly toward sites where they stayed through the nonbreeding season. Because most frogs moved from a breeding pond, across a grazed pasture, to a riparian area, they did not have the option of following a waterway during their initial movement. This is similar to Bulger et al. (2003), where frogs mostly moved in a straight line without apparent regard to intervening vegetation or topography. However, there were a few individuals in each study that moved primarily along a creek.

During our nocturnal surveys of Olema Creek, some frogs were well hidden by cover, whereas others sat fully exposed on top of logs or even on the sandy edge of the creek, places where California Red-Legged Frogs were rarely seen during the day. It is unclear why some individuals spent hours exposed to predation when good cover was only 1–2 m away. A frog in the open would have a wider field of view to detect and capture prey, perhaps partially mitigating the risk of predation. We documented predation by a Great Blue Heron, had evidence of predation by a raptor, and suspect that two other frogs succumbed to mammal predators. Additionally, we occasionally observed predators along Olema Creek including raccoons, Black-Crowned Night Herons, river otters, and nonnative rats (*Rattus* spp.). At a marsh that was not part of this study, we regularly observed night herons, and *R. draytonii* were so skittish that we have never been able to capture a single individual.

Based on their findings that 60% of the radiotagged frogs stayed within 30 m of their

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breeding sites, Bulger et al. (2003) recommend a 100-m buffer with an array of suitable habitat elements around breeding sites. Although that might work well at their study area, we do not believe that a simple, symmetrical buffer is typically adequate. At our main study site, a 100-m buffer would not include any suitable nonbreeding habitat. Because the pond completely dries every 4–5 years, such a buffer would result in the elimination of the local population. By contrast, the Big Lagoon site has suitable nonbreeding habitat immediately adjacent to the marsh. At that site, maintaining the marsh habitat and the natural water levels would likely be adequate for long-term survival.

Three important conclusions from our study are that (1) most frogs move away from breeding sites, but only a few move farther than the nearest suitable nonbreeding habitat; (2) the distance moved is highly site-dependent, as influenced by the local landscape; and (3) land managers should not use average dispersal or migration distances (from our study, or any other) to make decisions about habitat requirements. A herpetologist familiar with *R. draytonii* ecology needs to assess the local habitat requirements.

*Recommendations.*—Maintaining populations of pond-breeding amphibians, such as *R. draytonii*, requires that all essential habitat components be protected. These include (1) breeding habitat, (2) nonbreeding habitat, and (3) migration corridors. In addition, a buffer is needed around all three areas to ensure that outside activities do not degrade any of the three habitat components.

For *R. draytonii*, nonbreeding habitats must have several characteristics: (1) sufficient moisture to allow amphibians to survive throughout the nonbreeding season (up to 11 months), (2) sufficient cover to moderate temperatures during the warmest and coldest times of the year, and (3) protection (e.g., deep pools in a stream or complex cover such as root masses or thick vegetation) from predators such as raptors (hawks and owls), herons, and small carnivores.

Breeding habitat has been well described (U.S. Fish and Wildlife Service, 2002; Stebbins 2003) and receives most of the management attention (US Fish and Wildlife Service, 2002). However, nonbreeding areas are equally important because some *R. draytonii* spend only a week or two at breeding sites, yet nonbreeding habitat is frequently ignored and is generally not well understood. Aside from our study, Bulger et al. (2003) are the only ones to publish details on the use of nonbreeding habitat by *R. draytonii*. Additional research on nonbreeding habitat is needed, especially in other parts of range where *R. draytonii* occupy a diversity of ecotypes.

Migration corridors are frequently not considered in management planning for California Red-Legged Frogs. Our work and that of Bulger et al. (2003) indicate that *R. draytonii* migration corridors can be less ''pristine'' (e.g., closely grazed fields, plowed agricultural land) than the other two habitat components. Bulger et al. (2003) observed that *R. draytonii* did not avoid or prefer any landscape feature or vegetation type. They tracked frogs that crossed agricultural land, including recently tilled fields and areas with maturing crops. Our study site did not encompass such a diversity of habitats, but frogs readily traversed pastureland that surrounded the breeding sites. While conducting other research, we observed five frogs crossing a recently burned field as they moved toward a breeding pond during the first rain of the season (25 October 2004). Both our study and that of Bulger et al. were conducted at study sites near the Pacific Ocean where summer fog and high relatively humidity reduce the risk of desiccation for dispersing amphibians (E. J. Null, NOAA Technical Memorandum, NSW, WR-126, 1995; Lundquist and Bourcy, 2000). Though desiccation was probably not a problem for frogs in our study, amphibians are often faced with a variety of hazards including roads (Gibbs, 1998; Vos and Chardon, 1998), degradation of habitat (Vos and Stumpel, 1995; Findlay and Houlahan, 1997; Gibbs, 1998), and predation (Gibbs, 1998), as well as desiccation (Rothermel and Semlitsch, 2002; Mazerolle and Desrochers, 2005).

Buffers are often described as the area that frogs use near breeding sites. Such usage combines migration corridors and nonbreeding habitat, as well as the adjacent area necessary to protect these areas. We believe that it is important to identify each habitat component separately and then include a buffer that is sufficiently large to maintain the integrity of each habitat type. Such a buffer cannot be defined as a standard distance but rather as an area sufficient to maintain the essential features of the amphibian habitat. Hence, a riparian area adjacent to a forest undergoing clear-cut logging would need a relatively large buffer to protect it from increased sedimentation and the increased temperature fluctuations that occur after logging. Less severe habitat modifications adjacent to amphibian habitat could be accommodated with a narrower buffer (deMaynadier and Hunter, 1995, 1999; Gibbs, 1998).

Buffers are typically described as a fixed-width boundary around breeding sites (Semlitsch and Bodie, 2003). However, the distribution of habitat components is rarely symmetrical

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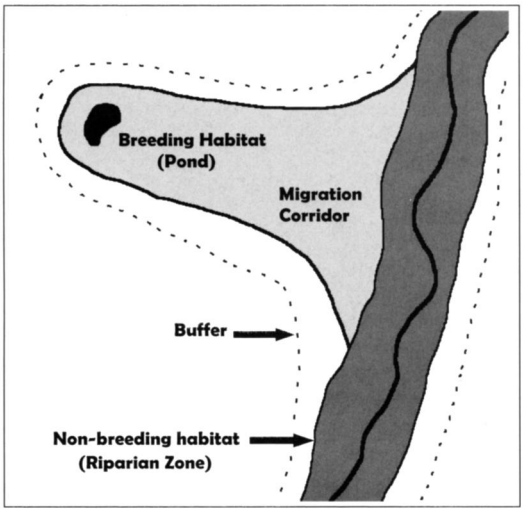


FIG. 6. Stylized diagram of typical *Rana draytonii* habitat showing the critical habitat components and the required asymmetrical buffer.

(e.g., a pond with frogs dispersing in all directions to surrounding nonbreeding area). At all of our study sites, frogs moved primarily in one direction, often toward the nearest riparian area, similar to what Rothermel and Semlitsch (2002) reported. As suggested by Regosin et al. (2005), protecting frog habitat in these situations requires an asymmetrical conservation area (Fig. 6). Because it is often not obvious from casual inspection what areas frogs are relying upon, delineating each habitat component and determining the size of a suitable buffer requires either an expert opinion from a field biologist with extensive experience with the species of interest or a field study to monitor radiotagged frogs.

The design of protected areas is often developed with the unstated assumption that only the most sedentary frogs can or need to be protected. The resulting systematic loss of individuals that move the farthest can have unexpected and unwanted effects (Gill, 1978; Berven and Grundzien, 1990). Long-distance dispersers are the individuals most likely to reach distant breeding sites and, hence, provide the genetic diversity that is important for survival of small populations. Additionally, those same dispersers are the individuals that would colonize sites where frogs have been lost because of random events that periodically extirpate local populations. By consistently selecting against frogs that disperse the greatest distances, the effective size of a metapopulation is reduced and the size of the effective breeding population is smaller; smaller breeding populations have a greater likelihood of extirpation (Gill, 1978; Sjogren, 1991).

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CALIFORNIA

# Gov. Newsom slams PG&E over ‘unacceptable’ power outages and failure to fix systems

Residents pick up meals Wednesday from one of the few food trucks operating in the Sonoma, Calif., area after Pacific Gas & Electric Co. initiated widespread power outages. (Brittany Hosea-Small / AFP/Getty Images)



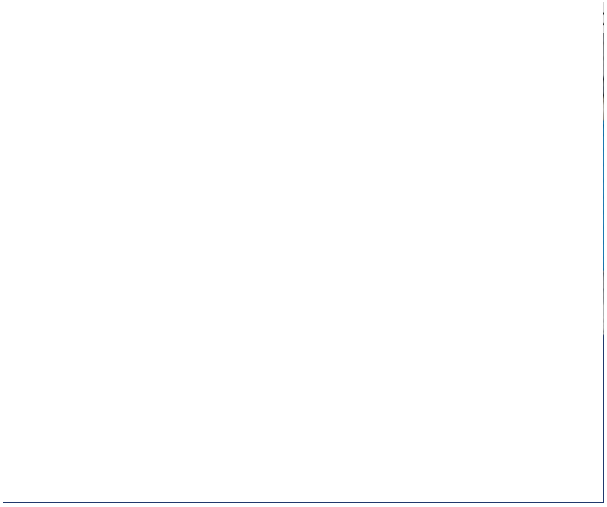
OCT. 10, 2019
8:26 PM

Gov. Gavin Newsom tore into Pacific Gas & Electric Co. on Thursday, calling the mass power outages “unacceptable” and the result of the bankrupt utility’s own long legacy of mistakes.

“What’s happened is unacceptable. And it’s happened because of neglect. It’s happened because of decisions that were deferred, delayed or not made by the largest investor-owned utility in the state of California and one of the largest in the nation,” he said at a news conference. “This current operation is unacceptable. The current conditions and circumstances are unacceptable.”

For parts of Thursday, more than 1 million Californians remained without power after the state’s largest utility shut off electricity in an attempt to prevent windblown power lines from sparking devastating wildfires. PG&E said late Thursday that 738,000 customers remained without power and that it was restoring service in many areas.

Newsom said PG&E’s failure to maintain its system created the need for the outages.



“It’s decisions that were not made that have led to this moment in PG&E’s history and the state of California as it relates to our major investor-owned utility,” Newsom said. “This is not, from my perspective, a climate change story as much as a story about greed and mismanagement over the course of decades. Neglect. A desire to advance not public safety but profits.”

Responding to widespread criticism over the blackouts, the utility’s chief executive, Bill Johnson, said he was focused on PG&E’s future, not it’s past. He joined the company in April.

“I didn’t come here to deal with the past. I came here to help improve the future,” he said. “I haven’t delved into all those matters.”

He added: “There are many things we need to do better than we did this time. Communicate better, with as much notice as possible, as much clarity as frequently as possible. We did not deliver on that commitment at this time. Our website crashed. Maps were inconsistent or incorrect.”

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By Visit Huntington Beach

Residents had already rushed to empty store shelves looking for batteries and water and had lined up for gas to prepare for the looming outage. They did laundry, ran dishwashers and vacuumed, fearful they would not have power for several days. Some stuffed refrigerators and freezers with ice so they would stay colder longer. Others emptied food into coolers.

But their lights stayed on, while their frustrations mounted.

The steady alerts that power would be shut off at specific times — only to have it remain on — proved more unnerving than the actual loss of electricity for some.

Mary Carey, a lawyer who lives in a wooded East Bay community, compared the situation to knowing a “meteorite is on the way, but it won’t hit for 12 hours.”

Kevin Marker, 66, a retired businessman, had another take: “I think PG&E is just getting back at people.”

By Thursday morning, the utility had turned off power to customers in Alameda, Alpine, Contra Costa, Mariposa, San Joaquin, San Mateo, Santa Clara, Santa Cruz, Stanislaus and Tuolumne counties.

It also had restored power to about 125,000 customers across the state, including 74,000 in Humboldt County. Still, officials warned, more areas could see blackouts, depending on weather conditions. The utility is still considering cutting off about 4,000 customers in the southern portion of its coverage area in Kern County.

Fierce winds blew through several counties in Northern California on Thursday, the kind of gusts that bend treetops and cause cars to swerve.

In response, the National Weather Service issued a red-flag warning for much of the region, cautioning residents to expect northerly winds between 15 and 30 mph, with gusts up to 50 mph, and very low daytime humidity. The warning is in effect through Friday.

**Where PG&E may shut off power**

The high winds and dry weather create ideal fire conditions, authorities warn, with the potential to transform a spark into a raging inferno. PG&E fears windblown electrical lines could spark fires if power is not cut.

About two hours northwest of Sacramento in Clearlake, residents entered their second full day without power. At the local Safeway, which had a generator to provide electricity, customers searched for ice and charcoal hoping to save or cook the groceries in their refrigerators.

At a nearby senior center, PG&E set up a charging station in a back room for cellphones and medical equipment. At least 150 people had visited Wednesday, said representative Conrad Asper. By lunchtime Thursday, there had been more than 250.

Paul Spillane, 79, expressed what was a common sentiment at the center: frustration with PG&E.

“I think it’s an outrage,“ he said of the blackouts. “I say it’s the three most miserable days I’ve had since I’ve been up here. I haven’t been eating properly or anything.“

Amee Peterson, 66, said she feels so dirty from a lack of hot showers that she's considering boiling water on the barbecue to wash her hair. On Wednesday night, she ate cake for dinner because she couldn't cook. Peterson, who has post-traumatic stress disorder, fibromialgia and other conditions, said she received automated calls warning her of the blackout, but they were not specific. When the power cut out at 1 a.m. while she was reading a book, she was surprised. Even more frustrating, she said, has been the lack of clarity on when power might return.

"There is no idea when it's coming back on," she said.

The utility has warned that some customers may be in the dark for up to five days, even after the winds subside, as crews check equipment and repair fallen lines before restoring electricity.

CALIFORNIA

**Full coverage: California power outages**

Oct. 9, 2019

The PG&E blackout marks the largest power shut-off to date as California utilities attempt to reduce the risk of wildfires that have charred thousands of acres, caused billions of dollars in damage and spurred cries for widespread change in how electricity is delivered over the state's aging grid.

Equipment malfunctions have been tied to some of the state's most destructive and deadliest fires, including the 2017 wine country blazes and last year's Camp fire, which devastated the town of Paradise and killed 85 people.

In January, PG&E filed for Chapter 11 bankruptcy protection, anticipating multibillion-dollar legal claims stemming from the Camp fire, which also destroyed nearly 14,000 homes. A month later, officials at the utility acknowledged that its equipment probably sparked that blaze.

At a news conference Wednesday evening, PG&E officials signaled that these types of massive shut-offs during fire season might be the new normal.

Sumeet Singh, vice president of PG&E's community wildfire safety program, said customers should anticipate similar shutdowns in the future until the utility has finished its wildfire safety plan, "unless the weather changes significantly and the vegetation condition and the fuel-loading condition, and land and the forest management, changes significantly within the state."

"We understand that this power shut-off is difficult for our customers and communities. Please check on your neighbors, friends and family and know that we will work safely, and quickly as possible, to restore power across the region," Singh said.

The power shut-offs have prompted backlash, with some residents saying they create a whole new set of dangers as they try to keep up with news about fires. Critics worry that communications and evacuations will be hampered when the power is out, especially if traffic signals don't work and cellphone service is affected.

There also was concern about how those with health issues who rely on electrically powered medical equipment to stay alive would cope without power.

State Sen. Jerry Hill (D-San Mateo) said Thursday that he sent a letter to the California Public Utilities Commission asking the panel to conduct a review of how PG&E decided which areas should lose power and how the blackouts were rolled out.

"Many questions remain unanswered as the state reels from the consequences of this decision by PG&E, chief among them why is PG&E alone in making this decision?" Hill wrote to the commission.

The outage prompted UC Berkeley to cancel classes for a second consecutive day. University officials say some buildings are running on generator power for "life safety, animal care and support of critical research infrastructure." However, the generators cannot power the entire campus.

The Oakland Zoo also remained closed after the region lost power overnight. The zoo had closed ahead of the planned blackout, and staff rushed out to purchase additional generators to power exhibits for animal safety. The gas they have will power the generators for about four days, Darren Minier, assistant director of animal care, told the San Francisco Chronicle.

In Southern California, residents have anxiously watched how the power shutdowns have affected other parts of the state, wondering if it was a glimpse of what was to come for them.

Southern California Edison on Thursday began preventive power outages across its service area. Given the strong Santa Ana winds forecast for the area, the utility said, power could be cut off to more than 173,000 customers in parts of nine counties in Southern and Central California: Los Angeles, San Bernardino, Riverside, Orange, Ventura, Kern, Tulare, Inyo and Mono.

*Times staff writers Jaclyn Cosgrove, Anita Chabria and Patrick McGreevy contributed to this report.*

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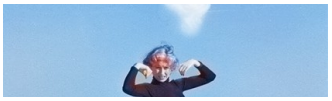

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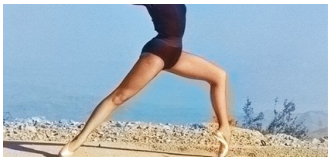

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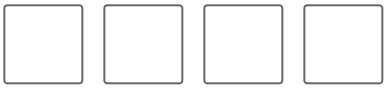

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CALIFORNIA

# Saddleridge fire explodes to 4,700 acres, burns 25 homes in San Fernando Valley

By HANNAH FRY, LEILA MILLER, MATTHEW ORMSETH, JOSEPH SERNA

OCT. 11, 2019

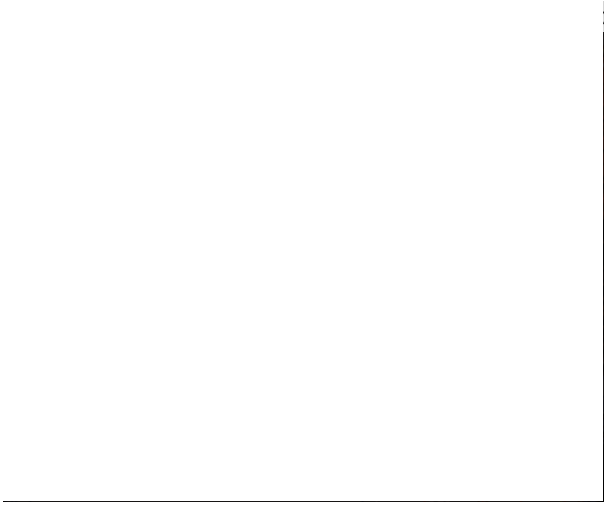
9:41 AM

A fast-moving brush fire continued its destructive march into the northern foothills of the San Fernando Valley on Friday, burning at least 25 homes, closing freeways and forcing thousands to flee.

The Saddleridge fire, which broke out late Thursday in Sylmar amid strong Santa Ana winds, spread rapidly overnight west into Porter Ranch and other communities, burning more than 4,700 acres at a rate of roughly 800 acres per hour, Los Angeles Fire Department Chief Ralph Terrazas said early Friday.

“These weather conditions are significant,” Terrazas said. “You can imagine the embers from the wind have been traveling at significant distances, which cause other fires to start.”

Mandatory evacuations have been issued to roughly 23,000 homes making up a huge swath of neighborhoods north of the 118 Freeway from Tampa Avenue all the way to the Ventura County line — an area covering 100,000 residents.



**L.A. County Fire Department**
@LACoFDPIO

#SaddleridgeFire Los Angeles County Firefighters working all out! A physical and mental delivery from Camp 12 personnel creating a fuel break in an extreme fire behavior environment.

This highlights the challenges of night firefighting @LACOFD @Angeles_NF @LAFD @LASDHQ @LAPDHQ

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One firefighter suffered a minor injury to his eye, and a man in his late 50s died after suffering a heart attack while talking with firefighters early Friday, Terrazas said. Authorities could not confirm reports that the man was trying to fight the fire from his home before he was stricken.

---

## Saddleridge fire resources

Evacuation zones, evacuation centers, school and road closures

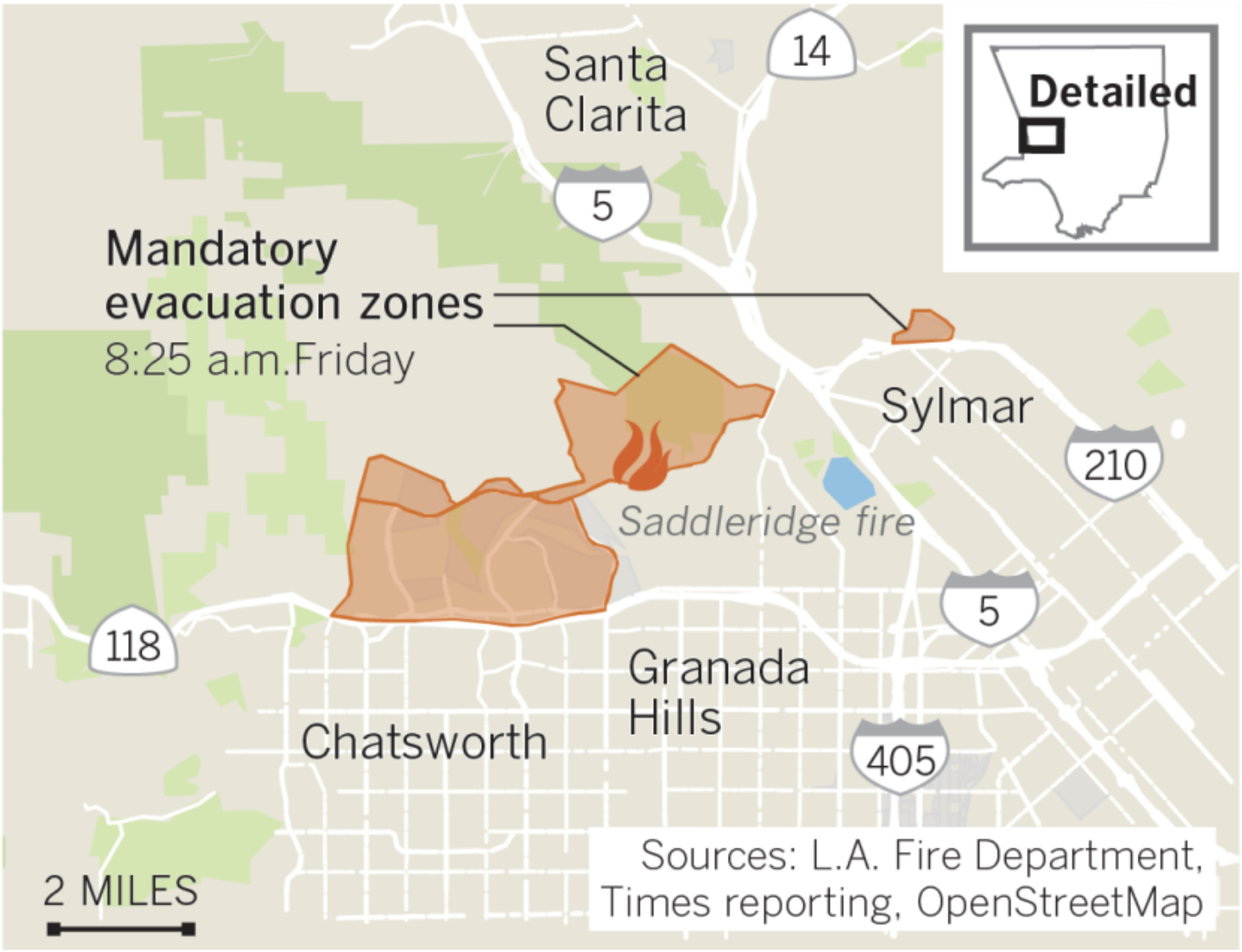
Map: Wildfires currently burning in California

More than 1,000 firefighters from multiple agencies were attacking the blaze Friday from the air and ground. Officials deployed helicopters and amphibious firefighting aircraft known as Super

Scoopers, while ground crews manned bulldozers to cut containment lines into nearby hillsides in an effort to slow the fire's spread. At least one air tanker blanketed fire retardant across the ridges.

However, unrelenting winds gusting up to 50 mph, low humidity and rising temperatures — which can dry out brush that fuels the fire — put crews at a disadvantage. Officials said they expect it will take days to get the blaze under control.

"Nobody is going home right away," Terrazas said.




The L.A. Fire Department has established these evacuation zones for the Saddleridge fire near Sylmar. They are current as of 5 a.m. Friday Oct. 11. (Chris Keller / Los Angeles Times)

The fire was first reported in Sylmar about 9 p.m. Thursday on the north side of the 210 Freeway, but wind-driven firebrands soared over the 210 and 5 freeways and ignited more dry brush. A 30-acre spot fire broke out west of Balboa Boulevard and pushed westward, officials said.

There are few options for firefighters against a wind-whipped fire with a lot of fuel, Los Angeles firefighter John Ferrer said.

“Because of the wind-driven factor, it creates a more defensive posture for firefighters,” Ferrer said. “We wait until the wind dies down and can deploy adequate resources to contain the flanks of the fire and an early-morning attack on the fire.”

The blaze moved so quickly that it jumped into neighborhoods overnight before firefighters and police could warn residents.

In Porter Ranch, a man stared as waves of embers crested against a two-story home abutting a hillside on Sheffield Way and flames lapped at the back of the structure.

“That’s my home,” he said. He had gotten out 15 minutes earlier.

Flames had already reached a second home on the cul-de-sac, which was choked with thick gray smoke, punctured only by the high beams of fleeing cars speeding through the small streets that crisscross the hillsides.

CALIFORNIA

## Saddleridge fire: Residents flee flames, worry whether their homes survived

Oct. 11, 2019

Kuriakose Chaz watched flames scale the side of the canyon, thinking about his Porter Ranch home of six years just a few blocks from the houses that by 2:30 a.m. were beginning to be devoured.

“If it goes,” he said, “it goes.”

Chaz, who’d gone to sleep at 10:30 p.m. Thursday, was awakened by a call around midnight from his nephew, who works for Southern California Edison and was monitoring the fire.

His nephew said, “You need to go.”

Chaz watched, dismayed, as flames charred the canyon he often enjoys hiking. Thick brush that had been watered by the winter’s plentiful rains stoked the blaze.

“I’ve watched fires on the news,” Chaz said. “But this hits home. I live here.”

CALIFORNIA

## Saddleridge fire approaches Aliso Canyon natural gas facility, site of massive 2015 blowout

Oct. 11, 2019

Cece Merkerson first noticed an orange glow from the living room of her third-story apartment in Porter Ranch about 11:30 p.m. Thursday. She had heard a fire was raging in nearby Granada Hills but figured it was a safe distance away.

“That can’t be that fire,” she thought. “That can’t be it.”

She checked the TV news, but there wasn't an evacuation order for Porter Ranch. To calm her nerves, Merkerson started packing anyway: medication, a small safe with important papers, a change of clothes and a couple of bananas.

Around 2 a.m., Merkerson looked through her window and saw flames. The mandatory evacuation order was issued minutes later.

"I started knocking on all my neighbors' doors because I knew they were sleeping," she said. "I'm banging and banging and I woke up about eight of them — and they all looked at me like I was crazy."

**Saddleridge fire: Residents flee flames, worry whether their homes survived**



Several major highways were closed because of the blaze, snarling morning traffic across the region, the California Highway Patrol said. The 210 Freeway was shut down in both directions between the 5 and 118 freeways. The 5 Freeway was closed between Roxford Street and Calgrove Boulevard. The 14 Freeway was closed at Newhall Avenue. Authorities have not said when the roads will reopen.

Evacuations have been ordered for Oakridge Estates, Glenoaks, the Foothill area and into neighborhoods in Granada Hills and Porter Ranch. Officials warned that other communities near the fire need to be ready to leave at a moment's notice.

Evacuees included hundreds of teenagers incarcerated at the Barry J. Nidorf Juvenile Hall facility in Sylmar, not far from the fire's edge.

The facility holds 278 teenagers, most of them 15 to 18, along with dozens of facility officers and workers. They all were being relocated to Los Padrinos Juvenile Hall in Downey, said facility spokesman Kerri Webb. It was an hours-long process to move them all.

“It’s very methodical. We have to utilize a lot of security,” Webb said. “Right now, getting everyone out safely is our highest priority.”

CALIFORNIA

**Numerous Riverside County homes destroyed by fire; SoCal Edison cuts power to thousands**

Oct. 10, 2019

About 1 a.m. Friday, several Sylmar residents stood about three miles from Oakridge Estates, which was under a mandatory evacuation order, watching the fire burn in the mountains beyond.

Iván DeGuzman, 34, said he had packed his car hours before after receiving a text message from a friend alerting him to the fire. He loaded up passports, clothes and some other items.

He recalled how the neighborhood was overwhelmed by smoke and ashes during a massive 2008 fire in Sylmar. He had evacuated then, but said it was still too early to go now.

“We’re waiting for mandatory evacuations,” he said.

Kim Thompson, who lives at the intersection of Sesnon Boulevard and Jolette Avenue in Granada Hills, said she took her dog out at 10 p.m. Thursday and immediately smelled smoke.

After reading about the fire on Twitter and realizing it was a danger,Thompson evacuated her home about midnight, taking just her dog. The flames by then were “bright orange, terrifying to look at,” she said at a strip mall downhill from her neighborhood on Balboa where other displaced residents had gathered to await news.

Later, she admitted, she doubled back to retrieve a bottle of wine. Her neighbors were less willing to leave: “Up here, we’re stubborn. My neighbors are spraying their roofs right now.”

A little after 1 a.m., Thompson heard from a friend that fire crews were allowing two homes on Jolette Avenue to burn to the ground. She thought back to the Aliso Canyon and Sayre fires, which

burned to the very edge of her cul-de-sac.

“We’ve been through a lot, but we choose to live here,” she said.

“You’re on edge. You think you get used to it,” Thompson said, the wind whipping eye-stinging smoke and ash through the air, “but you can’t really get used to this.”

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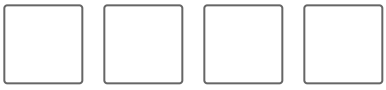

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# Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands

M. Goverde*, K. Schweizer, B. Baur, A. Erhardt

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**Abstract**

We examined visiting patterns of pollinators of *Betonica officinalis* L. (Lamiaceae) in experimentally fragmented calcareous grasslands and corresponding control plots at two study sites (Movelier and Nenzlingen) in the north-western Swiss Jura mountains. Fragments (1.5×1.5 m) were isolated by a 5-m wide strip of frequently mown vegetation while the control plots were situated in the adjacent undisturbed vegetation. The most common pollinator, the bumblebee *Bombus veteranus* (Apidae), visited fragments 53.7% less frequently than control plots. Furthermore, a change in foraging behaviour of *Bombus veteranus* was observed. In fragments the bumblebees visited more inflorescences, flew longer total visiting distances and the visiting time per patch tended to be higher than in control plots. The distribution of angles between arrival and departure direction (turning angles) differed from a uniform distribution in fragments but not in control plots. The increased directionality of bumblebee flight might be due to a decrease in floral rewards. Our results show that small-scale habitat fragmentation can affect plant pollination at two levels both relevant for plant fitness. First, lower visitation rates indicate a limitation of pollinators which might result in reduced seed set of the pollinated plant. Second, changes in pollinator behaviour might reduce pollen dispersal among flowers, increase inbreeding and hence reduce genetic variability in populations of this bumblebee pollinated plant. © 2002 Elsevier Science Ltd. All rights reserved.

*Keywords:* *Betonica officinalis*; *Bombus veteranus*; Bumblebee; Gene flow; Plant–pollination interaction

## 1. Introduction

Nutrient-poor, calcareous grasslands are among the habitats with the highest species richness in western Europe (Zoller, 1954; Ellenberg, 1982; Willems, 1982). However, industrialisation and changes in agricultural land use since the 1950s caused a dramatic decline of this once common type of grassland, and the remaining remnants are often small, fragmented and isolated (e.g. Willems, 1982; Zoller et al., 1986; Fischer and Stöcklin, 1997). Fragmentation of these natural habitats has especially negative biological consequences for ecosystem functions (Saunders et al., 1991; Kearns et al., 1998), such as plant–pollinator interactions, the subject of the present study.

The ecological importance of pollinators in their communities is crucial (Kearns et al., 1998). The entire structure of biotic communities will be dramatically changed when keystone plant species lose their pollinators. A cascade of changes including a decline in biodiversity may follow (Allen-Wardell et al., 1998; Kearns et al., 1998). Habitat fragmentation can affect pollinator behaviour, population size of animals and plants, and even pollinator morphology (Phillips, 1997; Berwaerts et al., 1998; Thomas et al., 1998; VanDyck and Matthysen, 1999). These chances might in turn influence community structure, population dynamics, trophic levels and genetic diversity in natural ecosystems. Plants experience lower fitness if pollinators are missing or reduced in numbers (e.g. Jennersten, 1988; Pavlik et al., 1993; Fischer and Matthies, 1997; Robertson et al., 1999). Furthermore, habitat fragmentation can change the spatial distribution of plants, which in turn changes foraging patterns of pollinators (Cresswell, 1997). If the distance between plants to be pollinated is too large, pollination is limited (Schmitt, 1983; Klinkhamer et al., 1989) and plant fitness may be reduced due to inbreeding and/or outbreeding depression caused by increased genetic drift (Waser and Price, 1983; Van Teuren et al., 1991; Holsinger, 1993; Percy and Cronk, 1997; Gigord et al., 1999). Thus, a change in pollinator behaviour might strongly affect plant reproductive success and plant fitness.

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There is empirical evidence that habitat fragmentation can influence pollinator populations directly or indirectly, and may cause declines of pollinators (Allen-Wardell et al., 1998). However, little attention has been given to the effect of fragmentation on pollinator behaviour. The aim of this study was to investigate under natural conditions the influence of experimental small-scale fragmentation on the pollinator behaviour of *Bombus veteranus* (Apidae), the most common pollinator of *Betonica officinalis* L. (Lamiaceae), a typical perennial forb in calcareous grasslands of the Swiss Jura mountains.

## 2. Methods

### 2.1. Fragmentation experiment and sampling

The study was carried out from 22 July to 7 August 1998 in the experimental habitat fragmentation study site of the University of Basel in the Swiss Jura mountains (Baur and Erhardt, 1995; Baur et al., 1996). The original design, established in spring 1993, consists of three field sites with a total of 12 blocks (Fig. 1) on nutrient-poor, dry calcareous grasslands belonging to the Teucrio-Mesobrometum type (Ellenberg, 1988). In the present study the medium-sized fragments (1.5×1.5 m) and control plots of equal size from six blocks at two sites were used (three blocks at Movelier and three blocks at Nenzlingen). These field sites are situated near Nenzlingen (10 km south of Basel) and near Movelier (5 km north of Delémont).

In each block, fragments were separated by a 5-m wide strip of frequently mown vegetation (6–12 times per year). Corresponding control plots of equal size were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Because the original control plots varied largely in occurrence of *Betonica officinalis*, we placed control plots in the undisturbed vegetation so as to contain approximately the same number of *Betonica officinalis* inflorescences as in the fragments. Thus, in the surroundings of the control plots numerous other *Betonica officinalis* inflorescences were present, whereas those in the fragments were separated by at least 5 m from other *Betonica officinalis* inflorescences.

In each patch (fragment or control plot) all *Betonica officinalis* inflorescences and open flowers were counted. The positions of all flowering *Betonica officinalis* inflorescences were mapped in 36 cells measuring 25×25 cm. Pollinators were observed in each patch for 20 min on three separate days. We recorded the visitation pattern of every flower visitor entering the plot during the survey. We measured for each insect the visiting distances between successively visited inflorescences, the total flying distance in the patch and the turning angles. Flower visitors that were already in the patch at the beginning

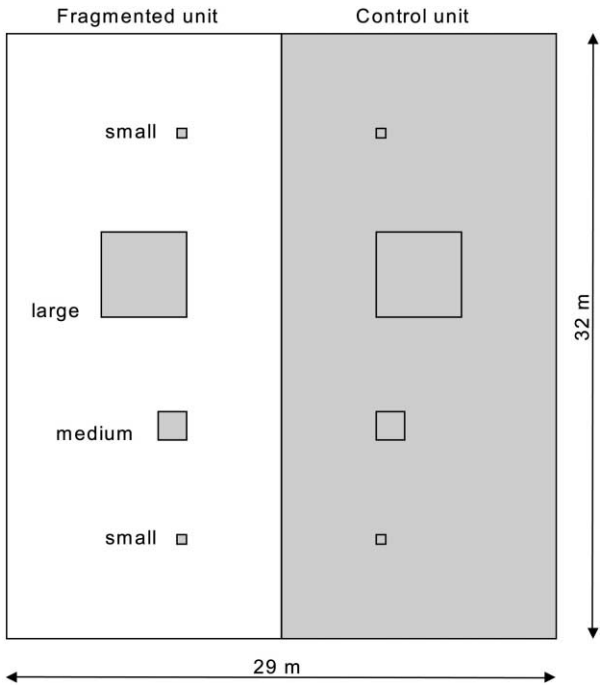


Fig. 1. Experimental layout for one of 12 experimental blocks of 29×32 m established in spring 1993. Each unit contained one large (4.5×4.5 m), one medium (1.5×1.5 m) and two small fragments (0.5×0.5 m), all of them separated by a 5-m wide strip of mown vegetation (white area), as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (grey area).

of the survey were not considered. Additionally, the duration of the visit in the plot of each flower visitor was assessed using a DAT-recorder. Observations were performed between 10:00 and 16:00 in sunny and warm weather. To avoid any time effect the order of surveys in fragments and their control plots were randomised on each observation day. Fragments and control plots of each site were surveyed on three different days (Nenzlingen on 22 and 30 July and on 8 August 1998, Movelier on 24 July and on 6 and 7 August 1998).

The distance between nesting sites of *Bombus veteranus*, the most frequent visitor, and the experimental patches could potentially have affected our observations. However, the fact that bumblebees can forage several hundred metres away from their nesting sites (Osborne et al., 1999), and the design of our experiment (random distribution of fragments and control plots) suggest that positions of nesting sites do not affect the results of the present study.

### 2.2. Data analyses

To compare the number of visits between fragments and control plots a chi-square goodness of fit test with a hypothesised ratio of 1:1 was used for each site (Zar, 1999). We used pooled data from the three survey days for each fragment and control plot.

To prevent spatial pseudoreplication, data from visiting patterns were averaged per fragment or control plot, respectively, for each survey day. To prevent temporal pseudoreplication we used the average of the three survey days per site, thus, resulting in 12 independent replications (six fragments and six control plots). Three-way analyses of variance (ANOVA, type III model, using JMP 3.1, SAS, 1995) with the fixed factors site and treatment and the random factor block nested by site were used to examine effects on the following parameters (patches refer to fragments or control plots):

Percent of visited inflorescences

$$= \frac{\text{Mean of visited inflorescences per bumblebee}}{\text{Total number of inflorescences in patch}}$$

Visiting time per patch related to inflorescence number (= "Visiting time per patch")

$$= \frac{\text{Mean time spent in patch per bumblebee}}{\text{Total number of inflorescences in patch}}$$

Ratio of mean visiting distances

$$= \frac{\text{Mean distance flown between two successively visited inflorescences}}{\text{Mean nearest neighbour distance between inflorescences}}$$

Ratio of total visiting distances

$$= \frac{\text{Total distances between visited inflorescences in patch per bumblebee}}{\text{Total nearest neighbour distances between inflorescences in patch}}$$

As a measure of the pollinators' flight directionality, turning angles between the arrival and departure directions were assessed from visiting patterns of single bumblebees. For data analysis angles were assigned to 18 classes each of 20°. The distributions of angles recorded in fragments and those from the control plots were compared with a uniform distribution using chi-square goodness of fit test (Zar, 1999). Furthermore, a $2\times18$ contingency table (G-test) was used to compare the distribution of angles in fragments with those in control plots (Zar, 1999).

## 3. Results

The number of inflorescences per patch as well as the number of open flowers were not affected by the experimental fragmentation but differed between sites (Table 1). Furthermore, the number of open flowers per inflorescence did not differ between sites ($F_{1,4}=0.44$, n.s.) or treatments ($F_{1,5}=0.17$, n.s.).

In total, the visiting pattern of 314 flower visitors was recorded. Among them, 218 belonged to the most common species, *Bombus veteranus*. The remaining flower visitors were other Hymenoptera (34), *Zygaena* spp. (42), other Lepidoptera (12) and Diptera (eight). Individuals of *Bombus veteranus* visited the fragments less frequently (69 individuals) than the control plots (149 individuals; Fig. 2) which means 53.7% fewer visits in the fragments.

Fragmentation significantly influenced the behaviour of the pollinator *Bombus veteranus* (Fig. 3). The percentage of visited inflorescences and the ratio of total visiting distances was significantly higher in fragments than in control plots (Fig. 3A,D). Thus, flying longer distances and especially visiting more inflorescences within a fragment indicate more near-neighbour pollination, which may result in increased inbreeding in pollinated plants in the fragments. Furthermore, the "visiting time per patch" tended to be longer in fragments than in control plots (Fig. 3B), while the ratio of mean visiting distances did not differ between fragments and control plots (Fig. 3C). A significant site effect on

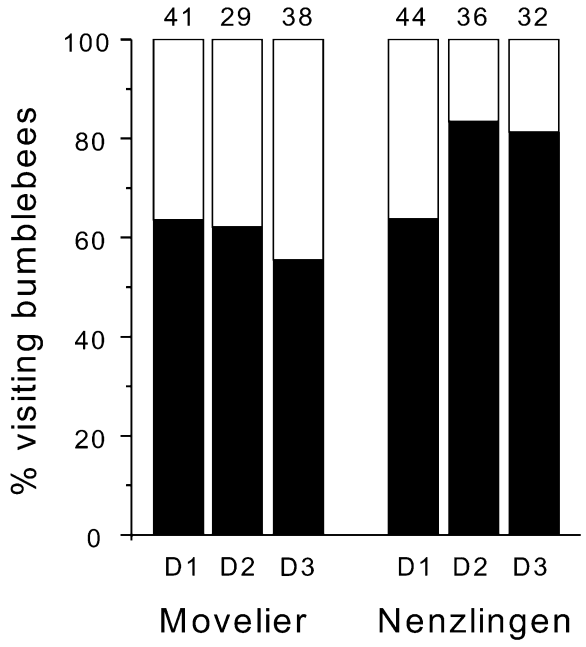


Fig. 2. Percentage of visits of *Bombus veteranus* in fragments (open bars) and corresponding control plots (black bars) at the two different sites, separated per day (D1, D2, D3 = first, second and third observation day, respectively). The numbers above the bar indicate the total number of observed bumblebees at this day. The difference between fragments and control plots was significant for both sites (Movelier: $\chi^2=4.48$, d.f. = 1, $P=0.034$; Nenzlingen: $\chi^2=28.00$, d.f. = 1, $P<0.001$).

Table 1
(a) Mean number (±1 S.E.) of inflorescences and open flowers of *Betonica officinalis* in fragments ($n=3$) and control plots ($n=3$) at the two study sites in Movelier and Nenzlingen. (b) Three-way analyses of variance (ANOVA) for effects of site and fragmentation treatment

(a)

| Site | Treatment | Number of inflorescences per patch (2.25 $m^2$) | Number of open flowers per patch (2.25 $m^2$) |
|---|---|---|---|
| Movelier | Fragments | 9.9±3.3 | 85.8±36.7 |
| | Control plots | 7.4±1.7 | 64.2±24.5 |
| Nenzlingen | Fragments | 22.9±1.3 | 146.0±8.4 |
| | Control plots | 21.7±0.5 | 176.8±14.5 |

(b)

| | d.f. | SS | *F* | *P* | d.f. | SS | *F* | *P* |
|---|---|---|---|---|---|---|---|---|
| Site | 1 | 630.18 | 35.58 | 0.004 | 1 | 30959.51 | 15.40 | 0.017 |
| Treatment | 1 | 17.17 | 3.87 | 0.11 | 1 | 163.33 | 0.12 | 0.75 |
| Block (site) | 4 | 70.84 | 3.99 | 0.08 | 4 | 8041.43 | 1.43 | 0.35 |
| Error | 5 | 22.20 | | | 5 | 7036.28 | | |

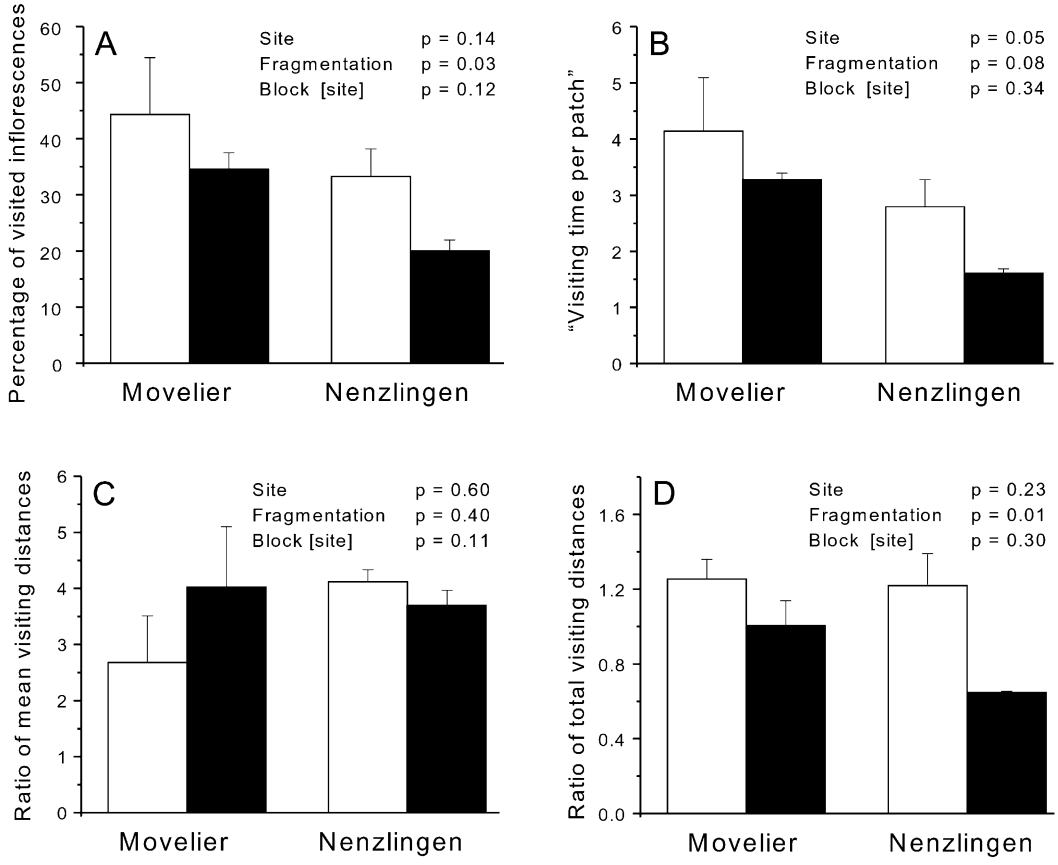


Fig. 3. Effect of habitat fragmentation on the behaviour of the pollinator *Bombus veteranus* visiting *Betonica officinalis* (mean±1 S.E.; open bars = fragments, black bar = control plots) at the sites Movelier and Nenzlingen. (A) percentage of visited inflorescences, (B) visiting time per patch related to inflorescence number ("visiting time per patch"), (C) ratio of mean visiting distances, and (D) ratio of total visiting distances.

the behaviour of *Bombus veteranus* was only found in "visiting time per patch" (Fig. 3B).

The distribution of turning angles of foraging *Bombus veteranus* differed significantly from a uniform distribution in fragments (Fig. 4, $\chi^2=48.28$, d.f. = 17, $P<0.001$), but not in the control plots (Fig. 4, $\chi^2=23.79$, d.f. = 17, $P=0.12$). There is thus a stronger tendency towards directionality in fragments than in control plots. However, a direct comparison of the distributions of turning angles in fragments and control plots revealed no significant difference ($G=14.14$, d.f. = 17, $P=0.66$).

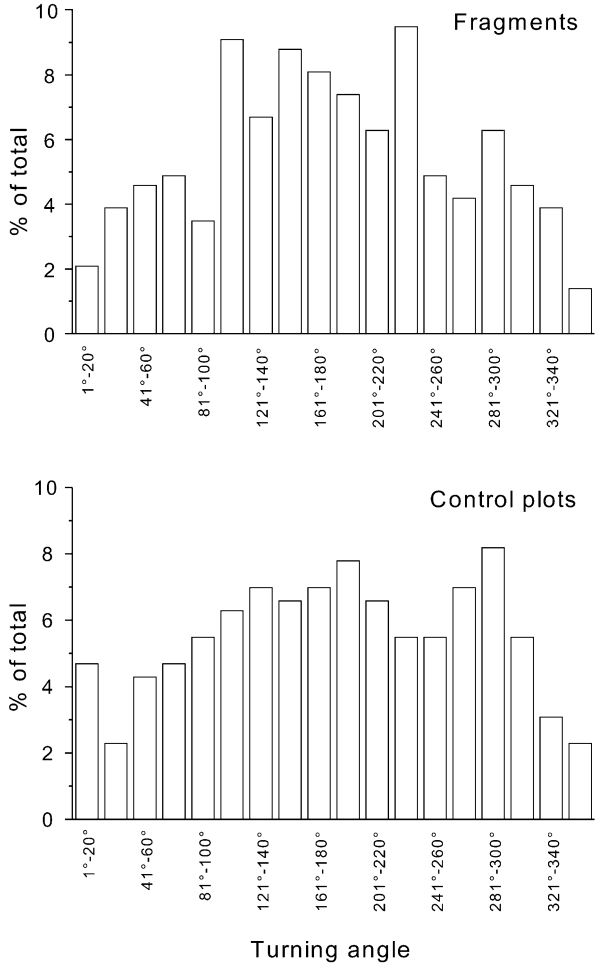


Fig. 4. Distribution of turning angles for *Bombus veteranus* visiting *Betonica officinalis* inflorescences in fragments ($n=285$) and control plots ($n=256$).

## 4. Discussion

The present study shows that the behaviour of the most common pollinator of *Betonica officinalis*, the bumblebee *Bombus veteranus*, was altered by small-scale fragmentation of calcareous grasslands. Bumblebees visited more inflorescences, flew longer total distances and tended to stay longer in fragments than in control plots (Fig. 3A,B,D). Thus, *Bombus veteranus* preferred to stay within the fragment rather than flying a long distance to reach the next inflorescence outside the fragment. Rasmussen and Brodsgaard (1992) examined visiting patterns of *Bombus lapidarius* in *Lotus corniculatus* patches, which were of different sizes and interspersed with dry areas dominated by mosses, lichens and short grass. Most flights of *Bombus lapidarius* were restricted to single patches (97.4%), although the animals had no difficulty to cross the distance of 10–40 m between patches. Since long distance flying is energetically expensive, the higher visitation rate within patches can be explained by the attempt of pollinators to optimise net energetic gain during foraging (Zimmerman, 1982; Price, 1997). In the present study, fragments were 53.7% less frequently visited than control plots. As a consequence, nectar rewards of inflorescences in fragments might be higher and pollinators might probe more thoroughly because movement decisions are based on the amounts of nectar encountered in flowers (Heinrich, 1979; Cresswell, 1990). However, measurements of nectar samples of *Betonica officinalis* did not support this assumption. The nectar quantity was smaller in fragments than in control plots, whereas the nectar concentration was higher in fragments than in control plots (H.-P. Rusterholz, unpublished data). These differences could be a result of lower soil moisture in fragments than in control plots resulting from frequent mowing of the surroundings (H.-P. Rusterholz, personal communication). In spite of this, bumblebees visiting fragments could have a more economic net energetic gain if they properly probe all available inflorescences in fragments.

The bumblebees' attempt to achieve the highest net energetic gain is confirmed by the observed difference in "visiting time per patch" between the two study sites (Fig. 3B). At Movelier, where there were fewer inflorescences per patch, bumblebees spent more time in a particular patch relatively to the total number of inflorescences, i.e. they visited more intensively all available inflorescences. This finding is supported by other studies in which bumblebees probed fewer flowers per plant and bypassed more plants with increased plant aggregation (e.g. Zimmerman, 1982; Cresswell, 1997). Furthermore, the directionality of foraging movement of bumblebees decreases with increasing plant aggregation (Cresswell, 1997). Additionally, edge plants in isolated patches provoke more reversals of flight than plants in the centre of patches (Rasmussen and Brodsgaard, 1992). Therefore, we assumed that foraging pollinators show less distinct directionality in their flights in fragments, while in the control plots pollinators would rather pass through the patch and, consequently show a directionality in their flight. Directionality in foraging flight decreases revisitation and results in decreased self-pollination, which in turn may affect the genetic structure of the plant population (Cartar and Real, 1997). In the present study bumblebees tended to fly more directly in fragments than in control plots (Fig. 4). A possible explanation could be an adjusted behaviour pattern of foraging strategy. The directionality of flights between inflorescences is random when rewards are high but approaches 180° when rewards are intermediate or poor (Heinrich, 1979; Richards, 1997). Thus, the lower nectar volume of flowers in fragments mentioned earlier might explain the observed tendency towards directionality in fragments.

Most relevant for plant fitness are the lower visitation rates in fragments and the tendency of bumblebees to

remain in isolated patches. Pollinator limitation may reduce seed set while the frequent neighbour visits may reduce the exchange of pollen between distant plants. Thus, gene flow is reduced between fragments which may decrease the probability of outcrossing. Indeed, genetic investigations conducted in the same fragmentation experiment revealed that offspring of *Betonica officinalis* had a lower genetic diversity and an increased self-fertilisation rate in fragments (H.P. Rusterholz, personal communication). These findings illustrate general processes in fragmented landscapes, which in turn might lead to an Allee effect followed by the extinction of small plant populations (Allee et al., 1949; Courchamp et al., 1999).

We showed that experimental small-scale fragmentation reduced flower visitation and changed the behaviour of a common pollinator. Other pollinator species might be affected in a similar way. The reproductive success of pollinated plants might be reduced in fragments due to higher geitonogamy and increased rate of inbreeding. However, any extrapolation of the findings to large-scale fragmentation should be made with caution.

## Acknowledgements

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# Wildfires and Climate Change: California's Energy Future

A Report from Governor Newsom's Strike Force

April 12, 2019

# Executive Summary

**Climate change has created a new wildfire reality for California.** The state's fire season is now almost year round. More than 25 million acres of California wildlands are classified as under very high or extreme fire threat. Approximately 25 percent of the state's population – 11 million people – lives in that high-risk area.

Wildfires are not only more frequent but far more devastating. **Fifteen of the 20 most destructive wildfires in the state's history have occurred since 2000; ten of the most destructive fires have occurred since 2015.** The results are visible to all: lives lost, grave fire damage to homes and communities, rising gas and electricity rates, pressure on the home insurance market, and the threat of insolvency for California's utilities. The largest investor-owned utility in the state has filed for bankruptcy protection and two other major investor-owned utilities in southern California have had their credit ratings downgraded. Financial experts have opined that these utilities are likely one major fire away from bankruptcy. Making matters worse, this year has all the conditions for devastating fires, with a very wet season leading to high vegetation density. During fire season, that vegetation dries out and becomes fuel.

Since the first days of his administration, the Governor has taken decisive action to strengthen California's emergency preparedness and response capabilities to mitigate wildfires and build community resilience. In response to instability in the energy sector and to PG&E's decision to file for bankruptcy, the Governor created a strike force to coordinate the state's efforts relating to the safety, reliability, and affordability of energy, as well as to continue progress to achieve the state's climate commitments. As part of these efforts, sixty days ago, the Governor directed the strike force to develop a comprehensive roadmap to address the issues of wildfires, climate change, and the state's energy sector. That roadmap is attached.

The strike force report sets out steps the state must take to reduce the incidence and severity of wildfires, including the significant wildfire mitigation and resiliency efforts the Governor has already proposed. It renews the state's commitment to clean energy. It outlines actions to hold the state's utilities accountable for their behavior and potential changes to stabilize California's utilities to meet the energy needs of customers and the economy.

It is imperative that utilities not put profits ahead of safety and service. That is why the state has and will continue to advocate in PG&E's bankruptcy proceeding for fair treatment of fire victims, for California consumers, and for California policies and values.

## Preventing and Responding to Catastrophic Wildfires

The report begins by setting out steps that the administration, the CPUC, local communities, and utilities must take to reduce the incidence and severity of wildfires and to step up both community resilience and the state's response capabilities. To accomplish this, it is critical that the state:

- **Expand fire prevention activity** by improving forest and vegetation management, accelerating fuel reduction projects on both public and private land, training the workforce needed to scale up these projects, investing in new technologies to model and monitor fire risk, and strengthening utility oversight so that they invest more in safety.
- **Make communities more resilient** by considering updating codes that govern defensible space, encouraging cost-effective hardening of homes, strengthening evacuation, encouraging other emergency planning, and improving land use practices to reduce the damage to life and property from wildfires.
- **Invest in fire suppression and response** by investing in new fire engines and aircraft, re-deploying National Guard personnel from the border to support fire suppression initiatives, purchasing detection cameras to provide advanced data to firefighters, and investing in a statewide mutual aid system to pre-position resources in high-risk areas.
- **Call on the Federal Government to Better Manage Federal Forest Land.** As the owner of 57 percent of California's forestland, the federal government must also do its fair share to reduce fire risk. Specifically, the Governor has joined the governors of Washington and Oregon to call for the federal government to double the investment in managing federal forestlands in our states due to the high risk of wildfires.

## Renewing California's Commitment to Clean Energy

Given that climate change is a core driver of heightened wildfire risk, California must continue its transition to clean energy. California has established ambitious greenhouse gas reduction targets and the utility sector has been critical to the significant progress our state has made. But, an unstable energy market presents new risks, and temperatures keep rising. Any solution must adapt to the changing market landscape while maintaining the state's commitment to mitigating climate change. To do this, the state should consider:

- **Evaluating state-level resource backstop options** to reduce gaps and inefficiencies that can result from an increasingly fragmented energy market – including the option of creating a state power procurement entity.
- **Increasing transparency and reliability protections for customers** by establishing standards to make energy provider information more transparent and facilitate statewide planning.

## Allocating Responsibility for Wildfire Costs

An honest assessment of the realities of current and future climate change tells us that no matter how committed we are to preventing and fighting fires and to reducing carbon emissions over the long-term, the state will experience further fire damage in the coming years. If we continue on our current legal and regulatory path, we will get similar results – more deadly and destructive fires that put utilities near insolvency. That is unacceptable for fire victims and utility customers and is incompatible with an economy that requires safe, reliable, and affordable power. Any real plan must allocate costs resulting from wildfires in a manner that shares the burden broadly among stakeholders,

including utilities (ratepayers and investors), insurance companies, local governments, and attorneys. Taxpayers have substantially increased their contribution to mitigating fire risk and fighting fires when they ignite.

Any successful approach for allocating responsibility for wildfire costs should be based on the following principles: (1) maintaining safe and affordable power, (2) holding utilities accountable to prioritize safety, (3) treating wildfire victims fairly, (4) requiring equitable stakeholder contributions, (5) reducing overall costs from wildfire damage, (6) promoting California's clean energy goals, and (7) recognizing the contribution of California taxpayers.

The strike force has identified the following three concepts for evaluation against these principles:

- A **liquidity-only fund** that would provide liquidity for utilities to pay wildfire damage claims pending CPUC determination of cost recovery potentially coupled with modification of cost recovery standards.
- Adopting a **fault-based standard** that would modify California's strict liability standard to one based on fault to balance the need for public improvements with private harm to individuals.
- Creation of a **catastrophic wildfire fund** coupled with a revised cost recovery standard to spread the cost of catastrophic wildfires more broadly among stakeholders.

These concepts should be publicly debated, as each has impacts, tradeoffs, and consequences that must be addressed. Some concepts rely on voluntary contributions from utility investors, who in exchange will demand more clarity in the regulatory standard for cost recovery from ratepayers.

The choices are difficult, the future is uncertain and the solutions are imperfect. But legislative action is necessary for the stability of the state's energy market to meet the needs of Californians, and to achieve the state's clean energy goals.

**Under the status quo, all parties lose – wildfire victims, energy consumers, and Californians committed to addressing climate change.** Victims face a great deal of uncertainty and diminished ability to be compensated for their losses and harm. Customers face rising rates and instability. California's ability to achieve its climate goals is frustrated. Utility vendors and employees face uncertainty and likely significant losses. The bottom line is that utilities either in or on the verge of bankruptcy are not good for Californians, for economic growth, or for the state's future.

## Strengthening Utility Market Regulation

Utilities must be active participants in the quest for safe, reliable, and affordable power. This report recommends strengthening utility regulation by reforming the California Public Utilities Commission (CPUC) to:

- **Expand safety expertise** by improving the CPUC's ability to review wildfire mitigation plans, conduct inspections and audits, and enforce safety standards at investor-owned utilities.
- **Clarify cost recovery standards** by setting clear guidelines in statute for when the CPUC can pass on the costs of claims from wildfire damage to ratepayers.
- **Improve decision-making** by overhauling procedures, delegating more decisions to technical staff so that judges and commissioners focus on core questions of rate-setting, and improving enforcement.
- **Review high-risk industry regulatory models** and explore options for incorporating the latest climate impact research, in concert with the Governor's Office of Planning & Research, as well as academic and industry experts in risk reduction.

## Holding PG&E Accountable for Safety

PG&E is a textbook example of what happens when a utility does not invest in safety after numerous deadly reminders to do so over many years. Even today, PG&E is taking advantage of the bankruptcy process to promote the interests of investors over fire victims and other stakeholders. California will advocate for fair treatment of victims and employees, as well as to uphold the state's clean energy commitments in the bankruptcy process. The state will:

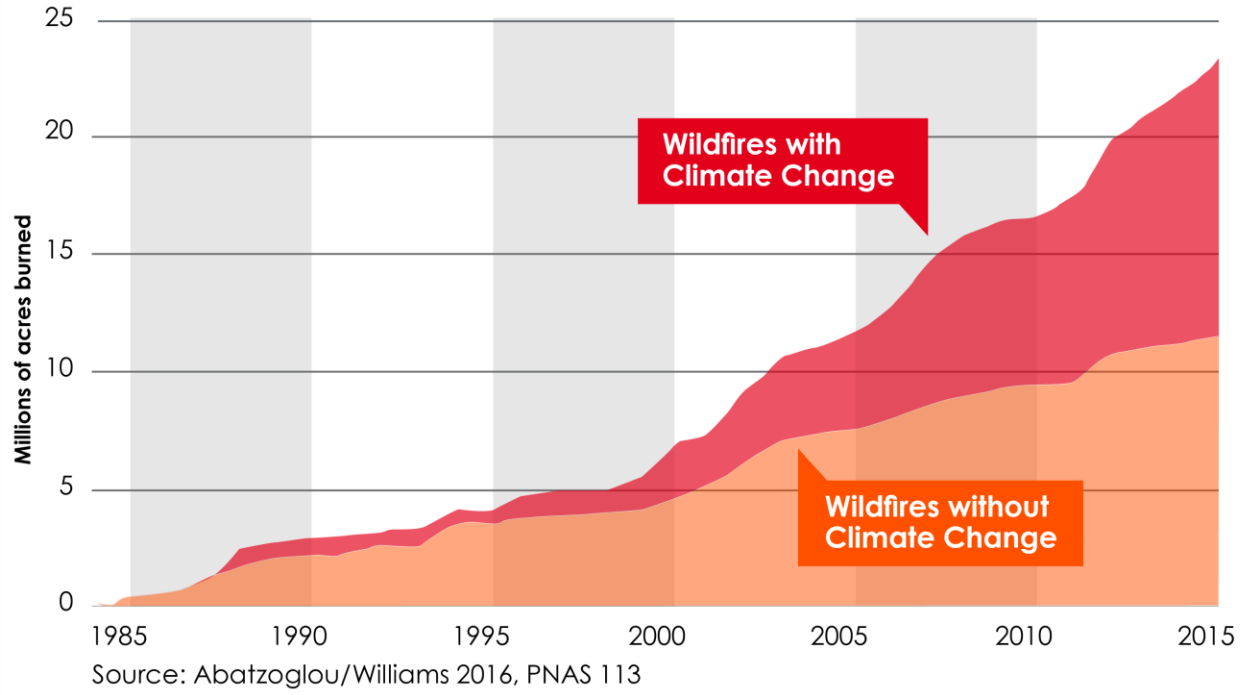
- **Monitor – and intervene – in the bankruptcy proceedings** to protect California's interests. PG&E is a private entity, but its misconduct has had grave consequences for the state and its people.
- **Evaluate options to satisfy wildfire claims** from the last two years so fire victims are treated fairly.
- **Demand that a reorganized PG&E serve the public interest**. After years of mismanagement and safety failures, no options can be taken off the table to reform PG&E, including municipalization of all or a portion of PG&E's operations; division of PG&E's service territories into smaller, regional markets; refocusing PG&E's operations on transmission and distribution; or reorganization of PG&E as a new company structured to meet its obligations to California.

The status quo is unsustainable. A better future is possible – one grounded in clear rules, effective regulation, and a new emphasis on safety so every Californian can access safe, reliable, affordable power. As the climate changes and risks rise, California must once more lead the way.

# Introduction

California faces a dramatic increase in the number and severity of wildfires. Fifteen of the 20 most destructive wildfires in the state's history have occurred since 2000; ten of the most destructive fires have occurred since 2015.[1] While wildfires are a natural part of California's ecology, the fire season is getting longer every year—with most counties now experiencing fire season from mid-May to mid-December and several counties facing fire danger year-round.[2] Warmer temperatures, variable snowpack, and earlier snowmelt caused by climate change make for longer and more intense dry seasons, leaving forests more susceptible to severe fire.

**Figure-01[3]**




At the same time that our climate is changing and fueling the devastating force of wildfires, increased development in the wildland-urban interface (WUI) has placed more

[1] *See generally*, CAL FIRE, *Top 20 Most Destructive California Wildfires*, (Mar. 2019), http://www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Destruction.pdf) (last visited Apr. 10, 2019) ("Top 20 Most Destructive California Wildfires").

[2] *See generally*, CAL FIRE, 2018 Fire Season Incident Information, http://cdfdata.fire.ca.gov/incidents/incidents_seasondeclarations?year=2018 (last visited Apr. 10, 2019).

[3] Eberhard Faust & Markus Steuer, CLIMATE CHANGE INCREASES WILDFIRE RISK IN CALIFORNIA | MUNICH RE MUNICHRE.COM (2019), https://www.munichre.com/topics-online/en/climate-change-and-natural-disasters/climate-change/climate-change-has-increased-wildfire-risk.html (last visited Apr 11, 2019) ("Climate Changes Increases Wildfire Risk").

residents in the potential path of destruction. Today, approximately 25 percent of the state's population (over 11 million people) lives in high fire-risk areas, including the WUI.[4]

The combination of more powerful wildfires and more Californians living in their paths has resulted in enormous, incomprehensible loss. Last year, 85 people died in the Camp Fire alone and 19,000 homes and other structures were damaged or destroyed.[5] According to data from Butte County, more than 60 percent of those victims were over 60 years old.[6] Paradise and other towns were devastated. The Camp Fire was only one of approximately 7,600 wildfires in 2018. Damage estimates for the 2018 wildfire season are staggering, with insured losses alone exceeding $12 billion.[7] Thousands of Californians who lost their homes, and their livelihoods in these fires, are still without permanent homes and struggling to rebuild their lives.

The damages caused by wildfires are unsustainable for the directly impacted victims, for the state, which is spending hundreds of millions of dollars to respond, and for local communities trying to rebuild. In response to climate change and heightened wildfire threat, California is expanding resilience efforts through increased investments in fire mitigation and response, community hardening, and emergency preparedness.

California's electric utilities must be part of the solution to this problem. In the past four years, equipment owned by California's three largest investor-owned utilities sparked more than 2,000 fires.[8] Utility-caused fires tend to spread quickly and be among the most destructive. Hundreds of thousands of miles of electrical transmission and distribution lines snake across the California landscape, often igniting fires during extreme wind events and in remote areas, making early detection and fire suppression extremely challenging. Longer fire seasons make utility-caused fires even more likely. Hardening the electrical grid is thus a critical component to overall wildfire risk management.[9] Our utilities—public and private—must make needed investments to reduce the risk of utility-ignited fires and, with the new reality of climate change, must do so now.

At the same time, the current system for allocating costs associated with catastrophic wildfires—often caused by utility infrastructure, but exacerbated by drought, climate change, land-use policies, and a lack of forest management—is untenable both for

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[4] LEVENTHAL CENTER FOR ADVANCED URBANISM, *Cataloguing the Interface: Wildfire and Urban Development in California,* (Spring 2018), http://lcau.mit.edu/project/cataloguing-interface-wildfire-and-urban-development-california (last visited Apr. 10, 2019).

[4] Top 20 Most Destructive California Wildfires.

[5] Cal Fire, *Top 20.*

[6] *Los Angeles Times, Many victims of California's worst wildfire were elderly and died in or near their homes, new data show,* (Dec. 13, 2018) (archived from the original on Dec. 14, 2018).

[7] CAL. DEP'T. INSUR., *CALIFORNIA DEPARTMENT OF INSURANCE INSURED LOSSES FROM THE 2018 CALIFORNIA WILDFIRES*, (Jan., 28, 2019), http://www.insurance.ca.gov/0400-news/0100-press-releases/2019/upload/nr14-2019Insured-Losses-2018-Wildfires.pdf (last visited Apr. 10, 2019).

[8] *Carolyn Kousky, et. al., Wildfire Costs In California: The Role of Electric Utilities* Wharton Risk Management and Decision Processes Center (Sept. 2018), riskcenter.wharton.upenn.edu/wp-content/uploads/2018/08/Wildfire-Cost-in-CA-Role-of-Utilities-1.pdf (last visited Apr. 10, 2019).

[9] Measures commonly used to harden the electrical grid include using insulated electrical lines in high-risk areas, replacing wood poles with steel, installing specialized monitoring equipment, and using new technologies that can reduce sparks or undergrounding lines when necessary in extreme high-fire areas.

utility customers and for our economy. Multi-billion dollar wildfire liabilities over the last several years have crippled the financial health of our privately and publicly owned electric utilities. Pacific Gas & Electric Company (PG&E) filed for bankruptcy in the face of massive potential liability for wildfire damages. Other investor-owned and public utilities have experienced recent credit ratings downgrades, with San Diego Gas & Electric (SDG&E) and Southern California Edison Company (SCE) now precipitously hovering just above junk status. Utilities rely on credit to finance ongoing infrastructure investments, including fire mitigation. As utilities' credit ratings deteriorate, their borrowing costs increase and those costs for capital necessary to make essential safety improvements are passed directly tto customers. These downgrades, and the prospect of additional utility bankruptcy filings, directly impact Californians' access to safe, reliable and affordable electricity.

In his State of the State Address, the Governor directed a strike force to develop a comprehensive strategy, within 60 days, to address the destabilizing effect of catastrophic wildfires on the state's electric utilities. He charged the strike force with developing a strategy to ensure California's "continued access to safe affordable power" and to "seek justice for fire victims, fairness for employees and protection for consumers."[10]

As the Governor stated, the crisis confronting California's electric utilities comes "at a time when the entire energy market is evolving" and is exacerbated by "regulations and insurance practices created decades ago [that] didn't anticipate these changes." The Governor recognized the need to "map out longer-term strategies, not just for the utilities' future, but for California's future, to ensure that the cost of climate change doesn't fall on those least able to afford it."

The Governor directed his strike force to develop a comprehensive strategy that achieves the following objectives:

1. Assure access to safe, reliable and affordable power for all Californians.
2. Reduce the severity of wildfires through continued investments in fire mitigation, vegetation management and other strategies to reduce fuels.
3. Develop and implement technologies to more quickly identify and respond to wildfires.
4. Reduce the number of utility-sparked wildfires through smart investments in increased safety, prevention, grid-hardening, and vegetation management around electrical lines.
5. Facilitate fair and prompt treatment for wildfire victims and allocate the burden of wildfire damage responsibly and fairly across all stakeholders.
6. Ensure that California continues to make progress toward its clean energy goals.

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[10] OFFICE OF GOV. GAVIN NEWSOM, *Governor Newsom Delivers State of the State Address*, (Feb. 12, 2019), https://www.gov.ca.gov/2019/02/12/state-of-the-state-address/ (last visited Apr. 10, 2019).

7. Provide sufficient certainty to investors and credit ratings agencies to avoid downgrades of utilities that could cause further bankruptcies and/or drive up borrowing costs, each of which raises prices for utility customers.
8. Hold utilities accountable for improving safety and preventing wildfires and for damages if their misconduct causes a wildfire.
9. Avoid a band-aid approach and instead set a path for the energy market of the future.
10. PG&E serves 40 percent of California electricity customers and has an egregious safety record. The state must hold PG&E accountable and demand systemic reforms and a commitment to safety.

This Report provides a roadmap to confront the challenges of catastrophic wildfires:

Part 1: Catastrophic Wildfire Prevention and Emergency Response

Part 2: Mitigating Climate Change through Clean Energy Policies

Part 3: Fair Allocation of Catastrophic Wildfire Damages

Part 4: A More Effective CPUC with the Tools to Manage a Changing Utility Market

Part 5: Holding PG&E Accountable & Building a Utility that Prioritizes Safety

It will take a comprehensive approach to mitigate and prepare for wildfires, as well as to advance our climate goals. That said, the most vexing public policy challenge addressed in this Report is the equitable distribution of wildfire liability. The Report sets forth three concepts to address this central question--the imminent wildfire liability issues facing California's utilities--each as described further in Part 3:

- **Concept 1:** Liquidity-Only Fund. This concept would create a fund to provide liquidity for utilities to pay wildfire damage claims pending CPUC determination of whether or not those claims are appropriate for cost recovery and may be coupled with modification of cost recovery standards.
- **Concept 2:** Changing Strict Liability to a Fault-Based Standard. This concept would involve modification of California's strict liability standard under inverse condemnation to one based on fault to balance the need for public improvements with private harm to individuals.
- **Concept 3:** Wildfire Fund. This concept would create a wildfire fund coupled with a revised cost recovery standard to spread the cost of catastrophic wildfires more broadly among stakeholders.

California needs to think creatively to find new ways to apportion the cost of catastrophic wildfires—ones that treat victims fairly and compassionately, that are sustainable for consumers, and that spread the burden equitably.

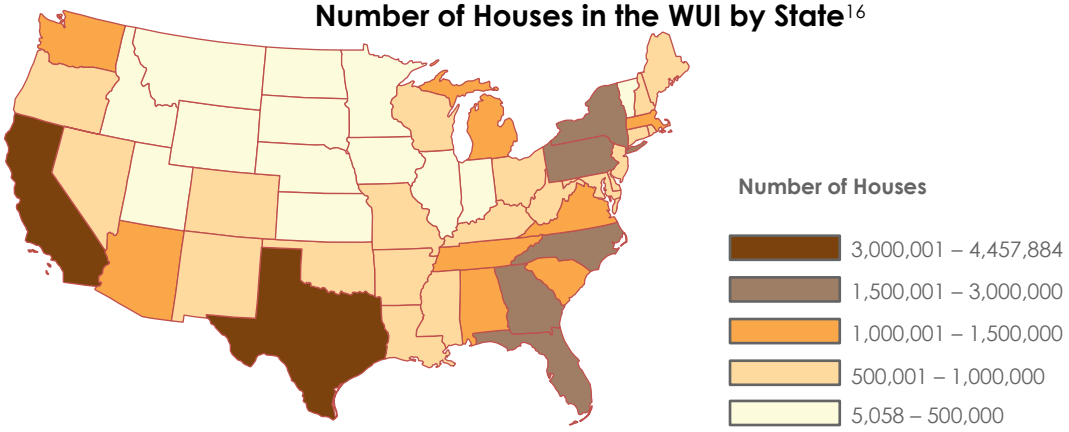
# Part 1: Catastrophic Wildfire Prevention and Response

Catastrophic wildfires pose an urgent threat to lives, property, and resources in California. The 2017 and 2018 wildfire seasons were the most destructive in California's history.[11] More than 9,000 wildfires ignited across California in 2017 and 7,571 wildfires ignited in 2018, burning more than 2.8 million acres combined.[12] These fires caused the loss of 139 lives and destroyed tens of thousands of homes and businesses.[13] They also poisoned the air across vast swaths of the state and harmed public health.[14] Additionally, catastrophic wildfires compounded the challenge of reducing our greenhouse gas emissions by emitting millions of carbon particles into the air.[15]

Climate change, widespread tree mortality, weak utility infrastructure, and the proliferation of homes in the WUI magnify the wildfire threat and place substantially more people and property at risk than ever before.

Today, as illustrated in Figure-02 below, California's WUI is home to approximately 4.5 million homes and 11 million people.

**Figure-02**
**Number of Houses in the WUI by State**[16]




[11] CAL FIRE, Incident Information as of Jan. 24, 2018, http://cdfdata.fire.ca.gov/incidents/incidents_stats?year=2017 (last visited Apr. 10, 2019).

[12] Id.

[13] CAL FIRE, *Top 20 Most Destructive California Wildfires,* (Mar. 14, 2019), http://www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Destruction.pdf (last visited Apr. 10, 2019); CAL FIRE, *Top 20 Deadliest California Wildfires,* (Feb. 19, 2019), http://calfire.ca.gov/communications/downloads/fact_sheets/Top20_Deadliest.pdf (last visited Apr. 10, 2019); CAL FIRE, *Top 20 Largest California Wildfires,* (Mar. 14, 2019), http://www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Acres.pdf (last visited Apr. 10, 2019).

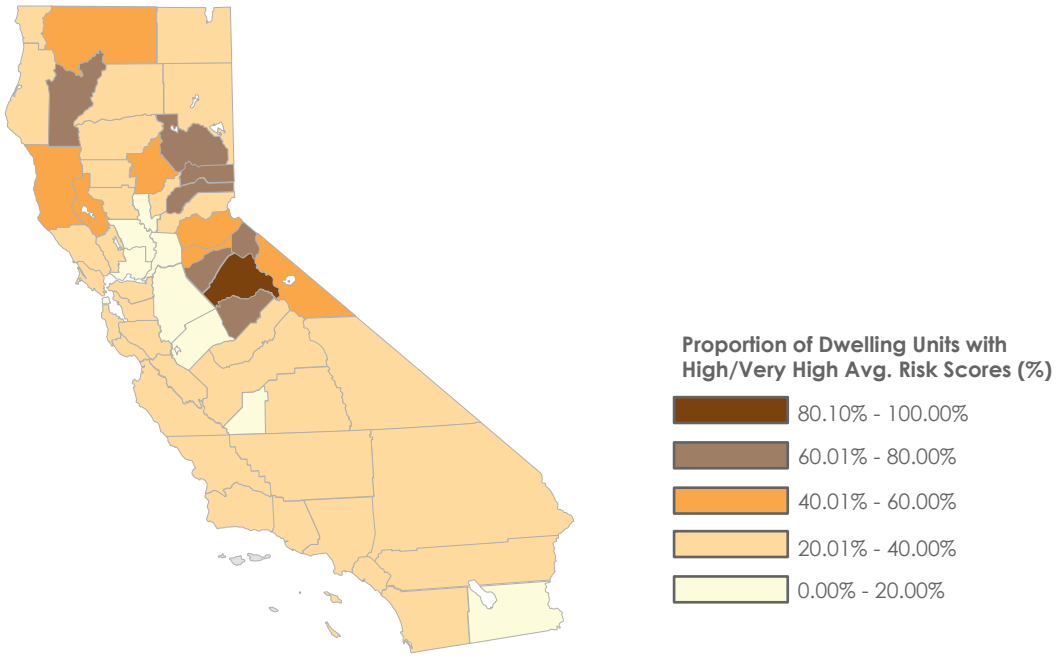
[14] STATE OF CALIFORNIA GOVERNOR'S OFFICE OF PLANNING AND RESEARCH, et al., *California's Fourth Climate Change Assessment: Statewide Summary Report* at 38, http://www.climateassessment.ca.gov/state/docs/20190116-StatewideSummary.pdf) (last visited Apr. 10, 2019).

[15] CALIFORNIA DEPARTMENT OF INSURANCE, *New Analysis Shows 2018 California Wildfires Emitted as Much Carbon Dioxide as an Entire Year's Worth of Electricity* (Nov. 30, 2018), https://www.doi.gov/pressreleases/new-analysis-shows-2018-california-wildfires-emitted-much-carbon-dioxide-entire-years) (last visited Apr. 10, 2019) ("Fourth Climate Assessment").

[16] CAL. DEP'T. INSUR., *The Availability and Affordability of Coverage for Wildfire Loss in Residential Property Insurance in the Wildland-Urban Interface and Other High-Risk Areas of California: CDI Summary and Proposed Solutions,* (Dec. 2017), http://www.insurance.ca.gov/0400-news/0100-press-releases/2018/upload/nr002-2018AvailabilityandAffordabilityofWildfireCoverage.pdf (last visited Apr. 10, 2019).

More than 25 million acres of California wildlands are now classified as under very high or extreme fire threat, extending that risk to over half the state--a high-risk area that will likely grow over time.[17] Decades of fire suppression have disrupted natural fire cycles and added to increased wildfire risk.

**Figure-03**
**Proportion of Dwelling Units with High / Very High Average Risk Scores[18]**




The state's major study on climate impacts, the Fourth Climate Assessment, projects that California's wildfire burn area likely will increase by 77 percent by the end of the century.[19] The growing risk of catastrophic wildfires has created an imperative for the state to act urgently and swiftly to expand preemptive fire prevention and bolster wildfire response efforts to help protect vulnerable communities and reduce the severity of wildfires in our state.

All levels of government, communities, utilities, and residents must share in this responsibility in order to better defend California from this devastating threat.

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[17] *See* California Department of Forestry and Fire Protection, *Community Wildfire Prevention & Mitigation Report* (Feb. 22, 2019), http://www.fire.ca.gov/downloads/45-Day%20Report-FINAL.pdf (last visited Apr. 10, 2019).

[18] Ibid.

[19] Fourth Climate Assessment at 9.

## Wildfire Reduction and Mitigation Action Plan

Recognizing the need for urgent action, the Newsom administration has placed a high priority on fire prevention and recovery measures, as well as on identifying ways the state can become more resilient in the face of future fires.

On January 9, the Governor issued Executive Order N-05-19, directing CAL FIRE to recommend immediate, medium and long-term actions to help prevent destructive wildfires. With an emphasis on taking immediate actions to protect vulnerable populations, and recognizing a backlog in fuels management, the Executive Order called for a strategic approach to focus actions on California's most vulnerable communities to realize the greatest returns on reducing risk to life and property in the most fire-prone areas of the state.

To further augment fire prevention, the Governor signed a General Order in February rescinding previous authorization for California National Guard operations at the U.S.-Mexico border and redeploying personnel to prepare for the upcoming fire season by supporting CAL FIRE in fire prevention and fire suppression efforts.

The state needs to continue to build on this work with a focus on four specific areas:

11. General Prevention and Fire Suppression
12. Building Safer Utilities
13. Emergency Response
14. Land Use, Building Codes and Community Resilience

## General Prevention and Fire Suppression

In response to Executive Order N-05-19, CAL FIRE released the Community Wildfire Prevention and Mitigation Report (CAL FIRE Report) on March 5. The CAL FIRE Report outlined a suite of actions to substantially reduce wildfire risk to 200 of California's most vulnerable communities this fire season.

On March 22, the Governor, citing the extreme peril posed by wildfire risk, issued an Emergency Proclamation directing CAL FIRE to immediately implement 35 emergency projects identified to protect lives and property. CAL FIRE will utilize existing funding totaling $30 million from the Forest Health and Fire Prevention Program to immediately execute the priority fuel reduction projects.

The proclamation suspends certain requirements and regulations. To ensure environmental protection, CAL FIRE requested input from regulatory agencies, and will employ a set of best management practices designed to identify and avoid sensitive natural and archaeological resources.

As discussed below, the state has numerous new initiatives to prevent and suppress fires.

### Improving Vegetation Management and Forest Health

After decades of disinvestment, the state has committed hundreds of millions of dollars in recent years to improve the health and resiliency of the state's forests.
Despite these increases, much work remains to be done. Over the next five years, the state will commit over $1 billion for critical fuel reduction projects, to support prescribed fire crews, forest thinning, and other forest health projects. In addition, the Governor redeployed the National Guard to support fire prevention efforts and is proposing to expand the California Conservation Corps to focus on forest management.

Since 2010, California has nearly doubled the number of acres treated annually by fuel reduction, and has tripled the number of acres treated by prescribed burning. However, these efforts—less than 33,000 treated acres in 2017-18—are dwarfed by the number of acres that require attention. California's Forest Carbon Plan sets a goal of treating 500,000 acres of private land every year.

As the owner of 57 percent of California's forestland, the federal government must do its fair share to reduce fire risk. Specifically, the Governor has joined the governors of Washington and Oregon to call for the federal government to double the investment in managing federal forestlands in our states due to the high-risk of wildfires.[20]

### Support for Regional Projects

In March 2019, the California Natural Resources Agency and Department of Conservation announced the award of $20 million in block grants for regional projects to improve forest health and increase fire resiliency. The Regional Forest and Fire Capacity Program helps communities prioritize, develop and implement projects that strengthen fire resiliency.

### Suppression

In recent years, the state has added additional year-round fire engines and firefighters to address longer, more severe fire seasons. The state has also launched a major initiative to replace Vietnam War-era helicopters with new state-of-the-art helicopters with enhanced firefighting capabilities. The Governor's Budget proposes to further expand the state's firefighting surge capacity by adding additional crews and engines. The Budget also includes funding to operate C-130 federal air-tankers.

To spur engagement from innovators in fire safety technologies and more effectively fight fires, Governor Newsom signed Executive Order N-04-19 to modernize the state contracting process for goods and technology systems. The "Innovation Procurement Sprint" will enable CAL FIRE to identify solutions to more effectively detect wildfire starts and predict the path of wildfires.

[20] Letter from Gov. Gavin Newsom to Pres. Donald J. Trump (Jan. 8, 2019), https://www.gov.ca.gov/wp-content/uploads/2019/01/1.8.19-Joint-Letter.pdf

**Figure-04**
**Additional Recommendations on Prevention[21]**

***Implement Additional Recommendations from the Community Wildfire Prevention and Mitigation Report:*** The strike force recommends that the following additional actions from the CAL FIRE Report be considered and, when appropriate, expedited.

A. Create Incentives for Fuel Reduction on Private Lands

- Small non-industrial private landowners make up approximately 25 percent of California's forestland owners and managers, almost twice as much as private industrial forestlands. These private landowners may not have the resources to actively manage their forests and are subject to the same fire risk as other Californians.
- The Board of Forestry and Fire Protection should consider changes in regulations, through an emergency rule-making process as needed, to encourage private landowners to engage in fuel reduction projects.

B. Develop Methodology to Better Assess At-Risk Communities

- The methodology used to identify priority projects provides a robust assessment of near-term projects that can be implemented before the 2019 fire season. This methodology should serve as the basis for ongoing assessment methods to evaluate short- and long-term wildfire risk reduction strategies across the state, with specific attention to identifying vulnerable communities noting that long-term planning and decision-making efforts to reduce wildfire risk require consideration of additional factors, including more robust integration of climate risk factors into fire vulnerability assessments.
- The Forest Management Task Force should establish an interagency team with experience in spatial analysis, technology support, environmental management, public health, climate change, and social vulnerability to develop the methodology enhancements needed to inform the long-term planning needs of both state and local agencies.

C. Jumpstart Workforce Development for Forestry and Fuel Work

- The California Natural Resources Agency should identify specific opportunities to develop and encourage workforce training programs.
- The goal should be to increase the number of properly trained and compensated personnel, with an emphasis on providing opportunities for local residents, available to perform fuel reduction and forest management and restoration work in the private sector. These training programs should be implemented before the end of 2019.

D. Develop a Mobile Data Collection Tool for Project Reporting

- The California Natural Resources Agency should procure a mobile fuel reduction data collection application to be used by all land management departments and agencies to increase accuracy and ease of data collection in the field.

[21] *See* CALIFORNIA DEPARTMENT OF FORESTRY AND FIRE PROTECTION, *Community Wildfire Prevention & Mitigation Report* (Feb. 22, 2019), http://www.fire.ca.gov/downloads/45-Day%20Report-FINAL.pdf (last visited Apr. 10, 2019.

E. Develop a Scientific Research Plan for Wildfire Management and Mitigation, with Funding Recommendation

- The Forest Management Task Force should develop a research plan with prioritized funding.
- Topics that should be considered include:
  - Leverage the Governor's Request for Innovative Ideas (RFI2).
  - Best management practices in the face of a changing climate and developing an understanding of forest health and resilience.
  - Use of LIDAR, satellite, and other imagery and elevation data collection, processing and analysis for incorporation into state management plans and emergency response.
  - Funding for collaborative research to address the full range of wildfire-related topics. Important research investments could include both basic and applied research as well as social science to better understand social vulnerability, human behavior, land use, and policies that support resilience in communities that coexist with fire and mitigate impacts on life and property.
  - Research and development on new WUI building test standards in future research programs including the use of damage inspection reports from recent fires.

F. Develop Models and Best Management Practices for Evacuation Planning

- CAL FIRE and the Governor's Office of Emergency Services (Cal OES) and the Standardized Emergency Management System Advisory Committee should develop robust local evacuation planning models for high or very high Fire Hazard Severity Zones based upon best practices from within California.

***Explore Public Private Partnerships and Capital Investment in Forest Waste Management Businesses:*** Public-private partnerships that find secondary uses for forest waste and increase fuel reduction can be a constructive part of the solution. Fostering innovation and entrepreneurship, these could include biomass facilities, especially those that use the energy on-site or as an "alternate fuel" for electric vehicles, cross-laminated timber using beetle kill wood, wood chips or pellets, or composting practices for soil restoration.

Expanding small scale businesses around forest waste, like micro-mills or carpentry using "Alpine Blue" (beetle kill) wood, will help scale-up forest treatment on small, private land. The strike force recommends that the Natural Resources Agency explore how best to facilitate these types of partnerships, recognizing the critical role they play in both forest management and community economic development.

## Building Safer Utilities

The state's most destructive wildfires have been sparked by utilities. Electrical fires tend to ignite during extreme wind events in remote areas with limited access for first responders. To reduce the overall risk of catastrophic wildfires for vulnerable communities, public and private utilities must make needed investments in grid hardening, vegetation management, and fire detection technologies.

### Current Process for Utility Safety Investment

Regulatory review of safety investments follows the same general approach as discussed in Part 4 of this Report. Historically, this meant that investment in fire safety and mitigation was driven largely by the utilities. The California Public Utilities Commission (CPUC) adopted safety regulations for overhead electrical systems in Rule 35 of CPUC General Order 95. Utilities were required to comply with those regulations but set their own priorities for safety investment.

This largely utility-defined fire mitigation program resulted in inconsistencies in investment among the state's investor-owned utilities. SDG&E engaged in a robust fire mitigation and safety program after experiencing devastating fires in its service territory in 2007 and has become a recognized leader in wildfire safety.

More recently, SCE implemented a wildfire safety program designed to mitigate the challenges of wildfires, including the development of operational practices and inspections, vegetation management activities, and community outreach.

PG&E has begun to implement wildfire safety measures, but its efforts lag behind the other IOUs, which is particularly troubling given that it serves 40 percent of California's utility customers and many counties in high-risk areas.

### CPUC and Wildfire Mitigation Plans

As the scale of utility-sparked wildfires increased, the CPUC, through statutory changes and on its own initiative, increased oversight of utility wildfire mitigation efforts. Each IOU is now required to prepare and submit a wildfire mitigation plan (WMP) annually to the CPUC for review and approval.[22] The CPUC, in consultation with CAL FIRE, will evaluate the WMPs.[23] As part of this process, the CPUC held a public workshop and two days of technical workshops on wildfire mitigation. A comparison of the WMPs submitted by PG&E, SCE and SDG&E is attached as Annex A to this Report. The CPUC expects to approve the WMPs in May 2019 and thereafter oversee compliance with the WMPs. The CPUC intends to develop and refine the content of and process for review and implementation of wildfire mitigation plans to be filed in future years.

While substantial efforts are underway to build safer utilities, the strike force has identified areas for immediate improvement.

## Recommendations

**Establish a More Rigorous WMP Process:** The WMP requirements should be revised to include a section on long-term fire management and a process to ensure faster compliance with the proposed plan. WMPs should also include specific performance-based risk mitigation metrics that are independently and scientifically verified as well as

[22] Cal. P.U.C. § 8386.

[23] The IOUs that are required to submit WMPs are PG&E, SCE, SDG&E, Liberty Utilities/CalPeco Electric, Bear Valley Electric Service, and Pacific Power.

cost-effective. Further, to hold IOUs accountable, California should consider putting in place an auditing system tied to financial incentives.

- **Safety Incentives:** Consider other CPUC reforms to better align IOU incentives with safety, including:
  - Adjust the allowed return on equity (ROE) based on wildfire safety performance
  - Align compensation and stock options of executives with wildfire safety performance
  - Make Board composition contingent on wildfire safety performance
  - Require Board-level reporting to CPUC on wildfire safety issues
- **Invest in Technology and Innovation:** New technologies, including weather stations, drones, and artificial intelligence have tremendous potential as tools to more effectively prevent, detect and respond to wildfires. The CPUC convened the state's first Wildfire Technology Innovation Summit in March 2019 to gather national and international thought leaders and practitioners from state and local governments, academia, industry and other areas to inform and collaborate as to innovative technological solutions to wildfire risk, including:
  - Statewide deployment of weather stations and cameras paired with meteorology and fire behavior modeling
  - Artificial Intelligence-based visual recognition technology to analyze satellite imagery to determine fuel conditions and vegetation risks in proximity to utility lines
  - Fire modeling tools to support all fire departments and emergency responders across the state
  - Machine learning and automation inspections for increased safety assurance and regulatory compliance
  - Widespread adoption of aerial patrols, LIDAR and advanced imaging for vegetation management and utility infrastructure inspections
- **Update Models to Reflect Climate Change:** Climate change has rendered many assumptions about California's climate outdated. Historical records for humidity, wind, rain, and temperature are regularly broken. CPUC regulations—such as General Order 95 governing electrical lines—are premised on historical climate trends which may no longer be accurate. The state should work with experts to update their models on climate change, using the existing Adaptation Clearinghouse and Climate Assessment process as a central location for data, maps, and information. The state should also facilitate cross-learning with utilities, which often make capital investments in physical infrastructure over decades.
- **More Cost-Effective Financing for Wildfire Mitigation Safety Investments:** A critical element of mitigating utility-sparked wildfires is substantial and immediate investment in electrical grid safety. The state may be able to mitigate the rate impact of this investment by offering a lower cost financing alternative through a dedicated rate

stream. Where IOUs fall behind on making needed investments, a reduced return on equity for this deferred maintenance can further reduce ratepayer impact.

## Emergency Response

In a matter of hours, 52,000 people from rural Paradise and surrounding communities evacuated onto roads built for a fraction of that capacity and converged on Chico, overwhelming the recovery system. The scale and speed of catastrophic, wind-driven wildfires, like the Camp Fire, incapacitate existing emergency response systems, local infrastructure and planned recovery efforts. Many California communities designed their fire emergency response and recovery systems decades ago, using old technology and outdated fire modelling. A clear overhaul of the California emergency response systems and the underlying infrastructure is needed.

The lack of broadband in rural communities and access to cell service make it difficult to communicate clear emergency evacuation orders to residents or locate residents who are in trouble. Roads in rural counties were often designed around old gold-rush tracks that were not designed to accommodate the number of residents using those roads, the ability of emergency vehicles to access the roads, or the need for defensible space. Evacuation plans assume that residents can evacuate and do not identify safe havens and shelter-in-place options for residents.

The state should partner with local government to encourage updates to local emergency plans, to increase resident awareness of those plans, and to otherwise improve emergency prevention and response efforts. Further, the state should encourage local governments to adopt recently issued guidelines to improve communications during an emergency.

On February 13, the Governor signed AB 72 (Assembly Committee on Budget, Chapter 1, Statutes of 2019), which appropriated $50 million for an emergency preparedness campaign focused primarily on California's most vulnerable populations, including the elderly, disabled, and those in disadvantaged communities. The California for All Emergency Preparedness Campaign—a joint initiative between California Volunteers and Cal OES—will augment the efforts of first responders by ensuring at least one million of the most vulnerable Californians are connected to culturally and linguistically competent support.

The Emergency Preparedness Campaign will provide:

- $24.25 million in grants to community-based organizations across the state to prepare residents for natural disasters through education and other resources designed to bolster resiliency.
- $12.6 million to support community efforts to build resiliency and respond to disasters by dispatching expert disaster teams to key regions and expanding citizen emergency response teams (CERT).
- $13.15 million to assist community groups in the development of a linguistically and culturally appropriate public awareness and outreach campaign, directed specifically at the most vulnerable California communities.

### Recommendations

- **Governor's Emergency Preparedness Summit:** By the end of June 2019, Cal OES, in partnership with the League of California Cities and the California State Association of Counties, will convene first responders, government agencies, local governments, community residents, and technical experts to develop plans for the state's emergency preparedness. The summit will highlight best practices of local communities, share resources that have worked around the world, and develop the networks necessary for ongoing preparedness improvements.
- **Develop Models and Best Management Practices for Evacuation Planning:** Cal OES, in collaboration with CAL FIRE, the Standardized Emergency Management System Advisory Committee, and local governments should develop evacuation planning models for high or very high Fire Hazard Severity Zones based upon best practices. These models can be a tool for local governments to use when developing location specific evacuation plans. Cal OES should consider how adoption of these models can be incorporated into County Operational Area plans of jurisdictions that also receive FEMA program grant dollars.
- **Develop Methodology to Better Assess Communities At-Risk:** The Forest Management Task Force should establish an interagency team with experience in spatial analysis, technology support, environmental management, public health, climate change, and social vulnerability to develop methodology improvements to inform the long-term planning needs of both state and local agencies.

## Land Use, Building Codes, and Community Resilience

According to the Fourth Climate Assessment, the average area burned statewide will increase by an estimated 77 percent by 2100. At the same time, the housing affordability crisis is forcing more Californians to move farther from urban areas, and often into high-risk areas. An additional outcome of these land use patterns is the year-by-year increase in driving, or "vehicle miles traveled" (VMT), which in turn increases carbon emissions and vehicle pollution across the states. California's housing affordability crisis is increasingly fueling the dangers of climate change and wildfire. Reducing fire risk to these areas will require changes in how higher-risk areas are designed, planned, built, served by utilities, and allowed to grow, and will require people across the state to participate in the solution.

The Governor has made housing production and affordability a key priority. California already has strong standards to reduce VMT. The strike force recommends that at the state and regional level, governments and planners incorporate CAL FIRE's fire risk projections and the fire projection information in the Adaptation Clearinghouse and Fourth Climate Assessment into short-term and long-term planning, and begin to de-prioritize new development in areas of the most extreme fire risk. In turn, more urban and lower-risk regions in the state must prioritize increasing infill development and overall housing production.

California has made progress in developing and adopting stringent wildland building codes. Since 2008, new construction in California's wildlands must use ember-resistant building materials. For homes built before the 2008 standards, CAL FIRE is working to

develop a list of low-cost retrofit steps homeowners can take. In addition, the Office of the State Fire Marshal (OSFM) maintains an advisory committee of fire and building officials that continuously considers building code updates to improve fire safety. Most recently, OSFM advanced building code changes including sealing of garage door gaps, sealing skylights and safety improvements to outbuildings.

Developing new housing in Very High Fire Hazard Severity Zones presents challenges. Since 2015, CAL FIRE has assisted local governments in land use planning. CAL FIRE is working to identify subdivisions at significant fire risk without secondary evacuation routes and to make recommendations to improve access.

Homeowners are encouraged to actively maintain defensible space, which is defined as a minimum 100-foot area around a home. Maintenance is an ongoing task. California inspected more than 217,600 homes for defensible space compliance in 2017-2018 alone.

It is critical that roads and other infrastructure be more fire defensible and evacuation ready for the populations in the WUI. All levels of government must establish clear contingency plans with local communities to identify and create temporary refuge areas and shelter-in-place procedures to help fire evacuees survive when unable to escape a wildfire.

Cal OES, in coordination with local communities and the Standardized Emergency Management System Advisory Committee, should consider developing local evacuation planning models for high or very high fire hazard severity zones based on best practices in California.

### Recommendations

- **Prioritize Building In Less Fire-Prone Areas:** The strike force recommends that at the regional level, governments and planners incorporate CAL FIRE's fire risk projections and the fire projection information in the Adaptation Clearinghouse and Fourth Climate Assessment into short- and long-term planning, and consider how to encourage more urban and lower-risk regions in the state to provide an alternative for those otherwise shut out of the state's housing market.
- **Local General Planning:** The strike force recommends that the safety element of local general plans be strengthened in high-risk areas, specifically for local governments to include fire risk projections into general and specific plans, including through zoning and design standards. Additionally, OPR should prioritize providing technical assistance support to these communities, many of which are rural and lack planning resources.
- **Cost-Effective Home Retrofits**: While California has stringent building standards and requirements for defensible space, the intensity of the wildfire threat in California now warrants higher levels of fortitude.
    - CAL FIRE should consider options to encourage cost-effective home hardening to create fire resistant structures within the WUI and with a focus on vulnerable communities.

  - The Forest Management Task Force should work with the Department of Insurance to seek input from the insurance industry on potential rebates or incentives for homeowners.
  - CAL FIRE and the Department of Housing and Community Development should develop a list of low-cost retrofits that provide comprehensive fire risk reduction to protect structures from fires spreading from adjacent structures or vegetation and to prevent vegetation from spreading fires to adjacent structures.
  - Consideration should be given to implementing a funding mechanism to assist individuals with cost-effective home retrofits. The model used by the California Earthquake Authority provides an example of such a mechanism.

- **Defensible Space and Forest and Rangeland Protection:** Compliance and enforcement is key to ensure that defensible space standards are met. CAL FIRE should review and make recommendations to increase defensible space.

# Part 2: Mitigating Climate Change through Clean Energy Policies

California's recent experience with catastrophic wildfires confirms the critical importance of climate change mitigation efforts. As discussed in Part 1 of this report, the devastating impacts of climate change, predicted for years, are now a reality. As the state moves quickly to respond to these impacts and become more resilient, we must remain focused on addressing climate change through clean energy policy.

The state's IOUs have played a significant role in moving California away from fossil fuels—from enabling the renewable energy markets to mature with continuing decreasing costs to carrying out energy efficiency mandates and demand response and storage programs. While other retail providers have entered the energy market and helped advance clean energy, IOUs still play a critical role in the state's efforts to address climate change. To continue the state's progress in reducing greenhouse gas emissions in the energy sector, California needs investment-worthy IOUs.

California's efforts to mitigate and adapt to climate change must remain an overarching priority for the state and for the IOUs. Action must be taken to facilitate progress toward a 100 percent clean energy grid. We also must ensure that the state's current system of oversight keeps up with the evolving energy market so that reliability, affordability, and continued progress toward California's climate goals is not compromised.

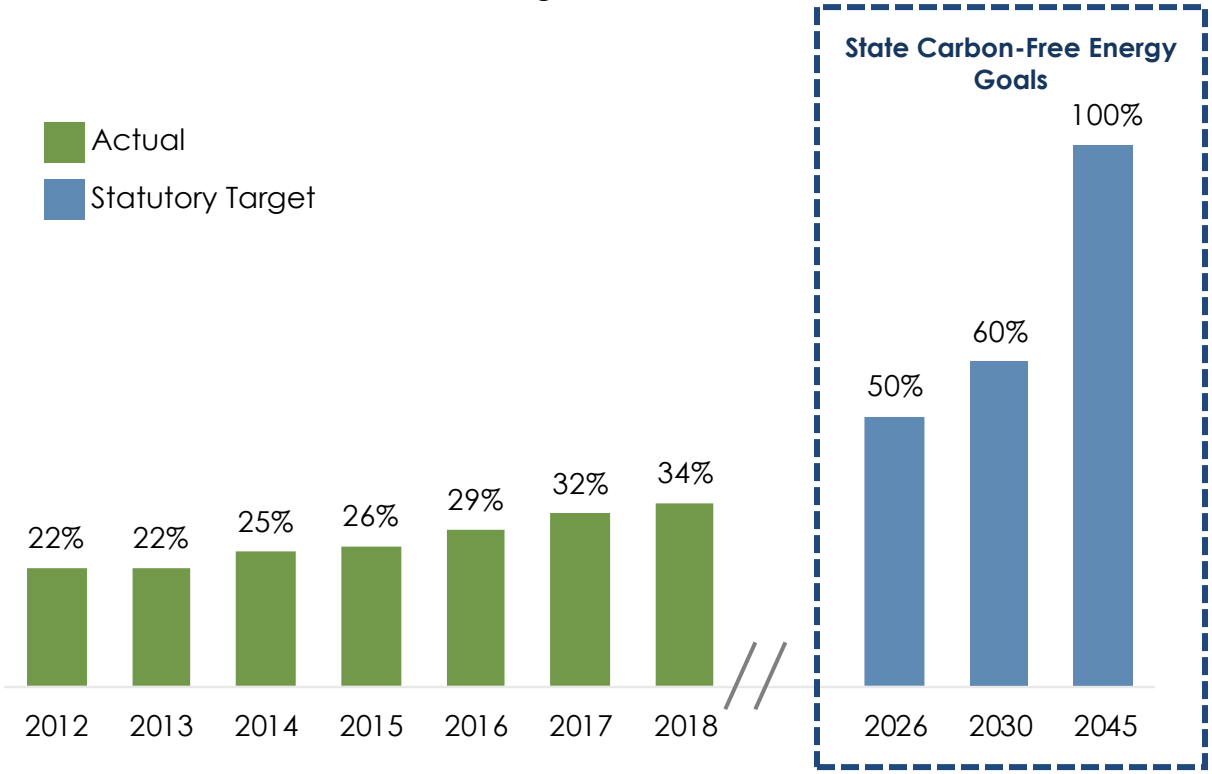
While working to increase carbon-free energy resources, utilities are also improving wildfire prevention and safety planning practices. Investments in safety at a level necessary to stay ahead of volatile climate conditions come at a cost, and this cost is being incurred at a time when maintaining low electricity rates is vital to meeting California's climate goals, as the next steps in carbon reduction involve electrifying the transportation and building sectors of the economy.

Safety investments have many benefits. A modern transmission and distribution system will create high-quality jobs and long-term economic stability, in addition to making us more resilient to the impacts of climate change and protecting the millions of residents living in fire-prone areas.

## Renewable Energy Development

California has made extraordinary progress in meeting its energy sector climate goals. The state is a leader in replacing conventional forms of electric generation with cleaner sources using wind, solar, and other renewable resources instead of fossil fuels. Currently approximately 34 percent of retail electric sales are served by renewable resources and over 55 percent of sales are covered by carbon-free resources, including hydroelectric and nuclear energy. Figure-05 illustrates the progress toward renewable and carbon-free energy development.

**Figure-05**




California's renewable energy industry is a powerful economic force in the state. Wind and solar energy projects brought over $70 billion in capital investments to California, establishing the state as a leader in renewable generation and spurring broader innovations.[24] Future electrification of buildings and transportation offers even more benefits, as those sectors represent the most cost-effective opportunities to decarbonize.[25]

Over $22 billion in clean technology venture capital funding was invested in California from 2007 to 2017.[26] One 2015 study shows that from 2003-2014, approximately 52,000 jobs were created in California due to the construction of renewable energy facilities.[27] The construction of those facilities also created and facilitated a number of indirect jobs and opportunities. In total, approximately 130,000 jobs were created. The study also projected that increasing California's renewable portfolio standard to 50 percent could

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[24] AMERICAN WIND ENERGY ASSOCIATION, *Wind Energy in California,* https://www.awea.org/Awea/media/Resources/StateFactSheets/California.pdf (last visited Apr. 10, 2019); SOLAR ENERGY INDUSTRIES ASSOCIATION, *Solar State By State,* https://www.seia.org/states-map (last visited Apr. 10, 2019).

[25] California Energy Commission, *Deep Decarbonization in a High Renewables Future,* (June 2018), https://www.ethree.com/wp-content/uploads/2018/06/Deep_Decarbonization_in_a_High_Renewables_Future_CEC-500-2018-012-1.pdf (last visited Apr. 10, 2019).

[26] NEXT 10, 2018 California Green Innovation Index (10th Ed.), (2016) (https://www.next10.org/sites/default/files/2018-ca-green-innovation-index.pdf (last visited Apr. 10, 2019).

[27] UC BERKELEY LABOR CENTR., INST. FOR RESEARCH ON LABOR AND EMPLOY'T., *Job Impacts of California's Existing and Proposed Renewables Portfolio Standard*, (Aug. 2015), laborcenter.berkeley.edu/pdf/2015/job-impacts-ca-rps.pdf (last visited Apr. 10, 2019).

create an additional 354,000 to 429,000 direct jobs from the construction of new renewable generation, and hundreds of thousands of indirect jobs and opportunities.

Today, we have both a challenge and an opportunity: a challenge to continue progress toward 100 percent carbon-free energy generation and an opportunity to transform the state's economy. During this transition period, we need to make sure we have effective tools and protections to manage costs to consumers, ensure reliability, and reduce risks.

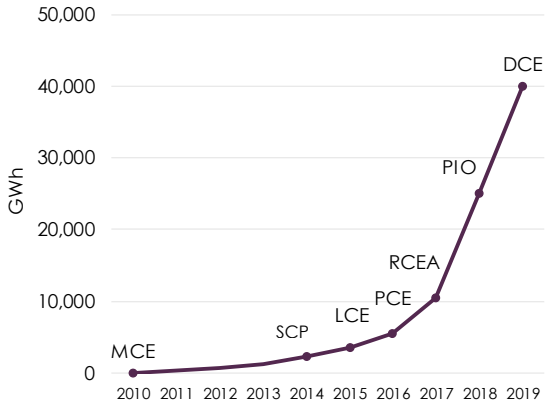
## Challenges in the Evolving Electric Sector

### Maintaining Reliability with Less Centralized Control

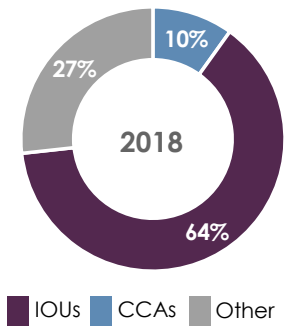
As more IOU customers install rooftop solar and storage, migrate to community choice aggregators (CCAs) and purchase energy from energy service providers (ESPs), IOUs are focusing on providing electric transmission and distribution service. New CCAs and ESPs are entering the market, acquiring energy in the wholesale market from electric generating companies, and selling energy to customers at retail. As a result, IOUs increasingly are becoming "poles and wires"--companies that are responsible for constructing, maintaining, and operating the facilities over which electric energy is delivered to customers. Figure-06 illustrates the CCA load growth over time.

**Figure-06**

**CCA Load Growth Over Time[28]**




**Market Share by LSE Type[28]**




MCE: MCE Clean Energy
SCP: Sonoma Clean Power
LCE: Lancaster Choice Energy
RCEA: Redwood Coast Energy
PIO: Pioneer Community Energy
DCE: Dessert Community Energy

Between rooftop solar, Community Choice Aggregators (CCAs) and Direct Access providers (ESPs), as much as 85% of Investor Owned Utility (IOU) retail electric load will be effectively unbundled and served by a non-IOU source or provider by the middle of the 2020s".

The IOUs delivery electricity and perform other important functions, such as metering and billing (including collecting fees from consumers to fund certain public-interest programs). CCAs typically do not have credit ratings which can limit their ability to

[28] See UCLA Luskin Center for Innovation's The Growth in Community Choice Aggregation, dated July 2018. CCA annual load data from each CCA's respective implementation plan. "Other" category represents the difference between the California Energy Commission's statewide load estimation and the IOU and CCA loads.

obtain the financing necessary to enter into long-term contracts at the scale needed to achieve a zero-carbon grid by 2045 and to meet Resource Adequacy (RA) requirements.

### Meeting Provider of Last Resort (POLR) Obligations

Customers who choose not to obtain retail service from a CCA or an ESP, or who may be subject to a failure by a CCA or ESP to provide service, currently are protected by the requirement that an IOU must step in to provide energy under the IOUs' POLR obligation.[29] If IOUs become primarily "poles and wires" businesses, it raises the question as to whether the IOUs should continue to provide POLR service or whether another entity should assume this responsibility.

### Avoiding Significant Rate Increases and Addressing the Need for Investment

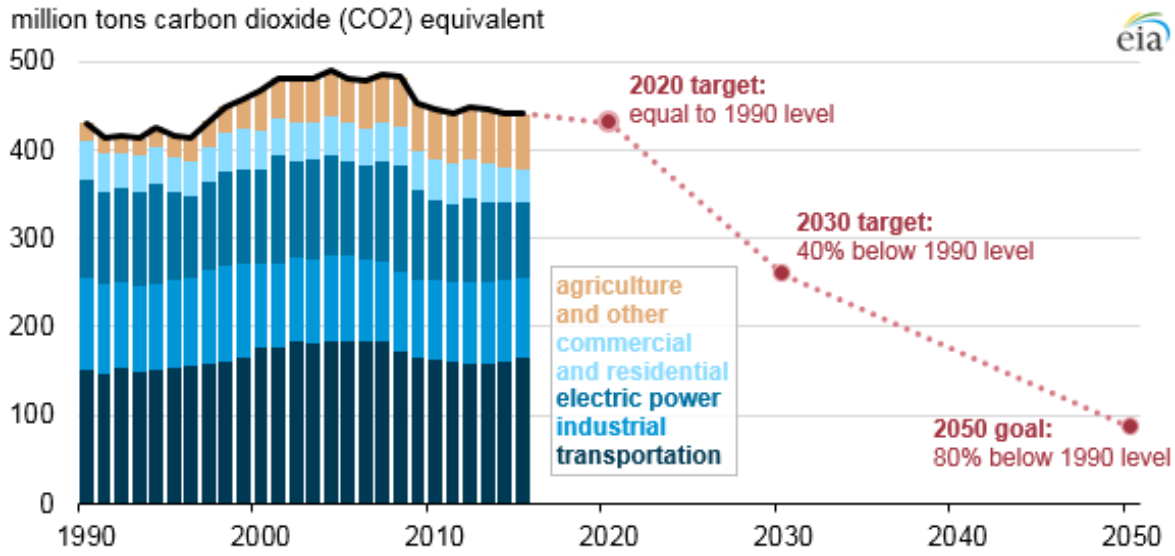
Major investments will be needed in the electric transmission and distribution system in California to make the system less susceptible to wildfires, to otherwise modernize it, and to accommodate changes in generation and demand. It will be important to have financially strong utilities so they can attract the capital necessary to make these investments at low rates (since the cost of capital is passed along to consumers). Keeping capital costs down is particularly important in light of potential increases in other costs, including the cost of large wildfire liabilities.

### Continuing Progress in Reducing Certain Carbon Emissions

As shown in Figure-07 below, California has made significant progress in reducing carbon emissions. In the energy sector, the IOUs have been instrumental in reducing carbon emissions. Their long-term contracts for renewable energy resources have driven prices down as new technologies have been deployed at commercial scale. Some CCAs have more aggressive renewable targets than the IOUs, and benefit from the early IOU renewables projects because they are benefitting from today's lower solar and wind energy prices. New CCAs are required to collect an adjustment charge from their customers to reflect the cost of older, long-term contracts that IOUs entered into on their behalf.

[29] The IOUs have a duty to provide distribution service on a non-discriminatory basis to the customers in their service territory. This currently includes the POLR obligation to sell energy at retail to those customers who opt out of obtaining service from a CCA. This POLR obligation also would extend to any situation in which a CCA or ESP were to cease providing service for some reason such as in the case of a bankruptcy.

**Figure-07**
**California Greenhouse Gas Emissions by Sector[30]**




## Distributed Resources

California utilities provide a means to implement various Distributed Energy Resources (DER) initiatives throughout the state.[31] California has experienced phenomenal growth in electric generation by customers on a distributed basis (in contrast to obtaining energy from large, central generating stations), particularly in the form of rooftop solar generation. In the future, it is expected that more customers will install battery storage on a distributed basis.

Many of these programs grew as a result of state mandates carried out by IOUs. Few of the programs (with the notable exception of net energy metering) directly involve CCAs, ESPs or publicly-owned utilities (POUs). Additionally, the California Independent System Operator (CAISO) has developed an innovative mechanism to allow distributed resources to join together and bid into the wholesale market, providing revenue for distributed resources as well as a benefit to the electrical system. Distributed resources, however, contribute to the fragmentation of the energy supply, and need to be managed to ensure they continue to benefit the electricity system.

## Adapting to Intermittent Electric Generation

Today, almost two-thirds of California's renewable energy generation capacity is from intermittent sources such as wind and solar. The output from these sources vary

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[30] *See* U.S. Energy Information Administration, based on California Air Resources Board data.

[31] Those initiatives include (i) providing rebates to customers that install self-generation facilities or storage; (ii) these are funded by a charge that the IOUs collect from their consumers; mandating that IOUs (and to a lesser extent CCAs and POUs) directly procure battery storage technologies that connect at the distribution grid level; and (iii) developing pilot projects to test the ability of DER to offset the need to build new distribution lines; and developing programs within the RPS that target distributed solar resources.

depending on the weather, season, and time of day. This imposes challenges on electric grid operations. Generation output from wind and solar sources is not controlled by the grid operator and can increase or decline rapidly, which requires adjustments in generation from other sources (or adjustments in demand) to keep supply in balance with demand. In particular, large amounts of low-cost solar electric generation during the middle of the day has created a situation where on some days there can be an overproduction of electricity and on many days generation from other sources must ramp up rapidly in the afternoon.

Overproduction can be a good problem to have since that energy, coupled with the right policies, can be harnessed to electrify other parts of the economy, such as transportation and buildings. A diverse portfolio of renewable resources and policies, including time-of-use rates, demand response programs, storage, energy efficiency, increased regional coordination, and electric vehicle charging, will continue to be critical to reduce the need for the carbon-intensive resources generally used to meet the afternoon ramp and overnight demand.

### Reliability

Several factors, including flat demand for electricity and growth in renewable energy generation, have contributed to substantial retirements of fossil-fueled electric generation (mainly natural gas). Stricter environmental standards have accelerated this trend. Yet flexible resources continue to be needed in the near term to quickly ramp up as solar generation resources go off-line or load increases, and during extended cloudy periods. Over the long-term, it will be critical to ensure that cost-effective clean energy resources are available for reliability and other grid services.

### Resource Adequacy Requirements

California has responded to energy shortages in the past by requiring that load-serving entities (LSEs) contract to purchase sufficient electric generation (or distributed resources or storage) to meet their forecasted peak demand plus a pre-set reserve margin. Several factors caused some LSEs to experience difficulty meeting their RA requirements.[32] Some LSEs have had to obtain temporary waivers from the CPUC and others have been penalized. Additionally, IOUs have taken on procurement of some resources needed for reliability that other LSEs may not want to procure. In some cases, the CPUC required IOUs to enter into long-term contracts needed for reliability, including contracts for battery storage. This option is less effective as IOUs have fewer and fewer retail customers.

### Maintaining Public Purpose Programs; Promoting Energy Efficiency and Demand Response.

California has been a leader in energy efficiency, with electricity use per capita remaining virtually flat over the past four decades despite substantial economic growth

[32] Challenges in the RA market include (i) a growing number of LSE competing to buy the same existing resources, (ii) a shrinking pool of resources LSE can procure as the planned retirement dates of older natural gas plants approach, and (iii) the inability/unwillingness of LSEs to enter into long-term contracts for some needed resources.

during that period.[33] The state has had success with programs that align the incentives of utilities and consumers in using less energy, including programs providing financial incentives or rebates, incorporating efficiency requirements in various codes and standards, and providing education and technical assistance.

Demand response programs, which provide incentives for customers to adjust their consumption during certain periods, have also been successful. Similarly, time-of-use rates provide incentives for customers to adjust their energy use to optimize renewable resources. New demand response programs are being developed that can increase loads at times when there is an abundance of solar generation.

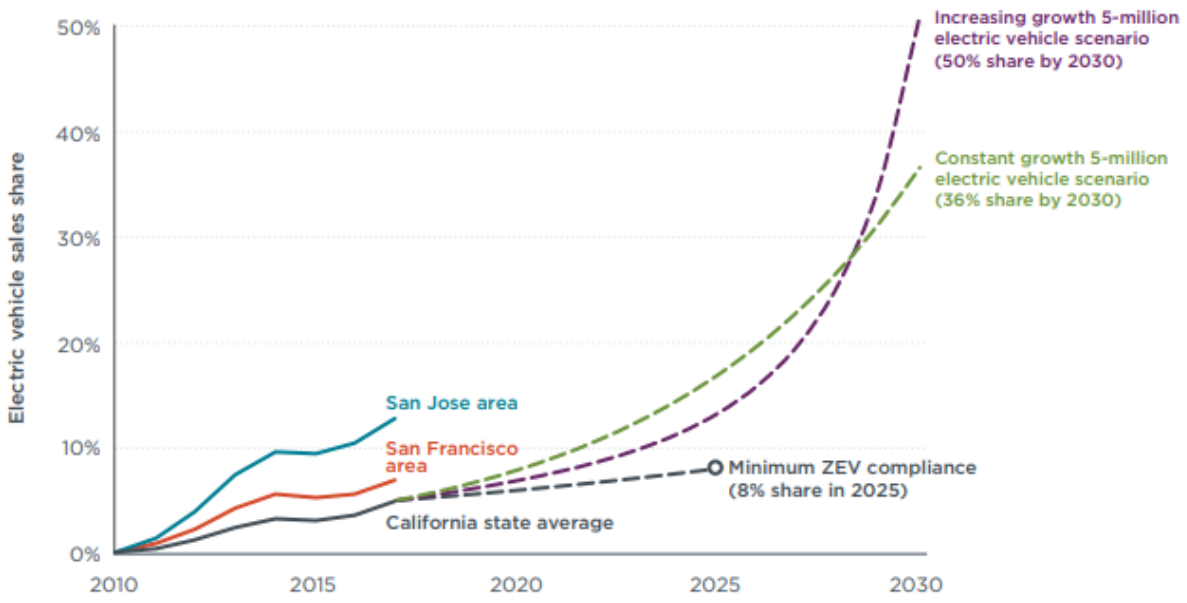
California has relied on the IOUs to implement public-purpose programs to fund energy efficiency and demand response, as well as reducing rates for low-income customers and renewable energy incentives. If the IOUs become "poles and wires" companies, it will be important to ensure that this change does not threaten these public-purpose programs.

### Electric Vehicle Integration

A critical component of California's efforts to meet its goals to reduce carbon emissions is to replace vehicles that use gasoline or diesel fuel with electric vehicles or hydrogen vehicles. The CPUC and other agencies in California support this effort by promoting deployment of charging stations, providing rate incentives (encouraging charging at off-peak hours), and other programs. Growth in vehicle electrification will result in increases in electric consumption over time and further increase the dependence of Californians on the electrical grid and the utilities that own and operate it. Over half of California's greenhouse gas emissions are from the transportation sector. Thus, the success of transportation electrification programs is essential to meeting the state's climate goals, and will depend on electricity being clean and available, and a less expensive option to fuel vehicles than gasoline. This provides one justification, among many, for efforts to minimize increases to electric rates. Figure-08 illustrates the California vehicle forecast.

[33] Energy efficiency helps to reduce the need for electric generation, including from sources that emit carbon and other greenhouse gases. Targeted energy efficiency, as well as programs such as demand response and time-of-use pricing, to reduce energy use at periods of high prices or demand, contributes to a more reliable electric grid with less need for physical improvements to the grid.

**Figure-08**
**California Electric Vehicle Adoption Forecast[34]**




## Recommendations

- **Evaluate Resource Adequacy Back-Stop Options Through the Legislative Process***:* Procurement by the IOUs, under supervision by the CPUC, has been effective over time. But as the state transitions to more LSEs, gaps and inefficiencies could emerge. To manage this transition, new procurement support models, including a new state procurement entity that could enter into long-term contracts, provide credit support or otherwise facilitate purchases of electric energy, should be explored. Procurement support could have a number of benefits, including providing back stop resource adequacy procurement and ancillary services needed to support reliability. To maintain cost-effectiveness and achieve rate benefits, it will be important to continue to focus on procurement through integrated resource planning or a similar framework. In addition, the POLR obligation discussed above and the responsibility for implementing public purpose programs could also be examined.
- **Increase Transparency for Load-Serving Entities and State Coordination of Procurement:** Customers in California should have access to complete and accurate information about the energy they are procuring, regardless of whether the procurement is from an IOU, POU, CCA, or ESP. This should include transparent information about prices, compliance with resource adequacy requirements, and the sources of energy being procured (including reliance on renewable energy sources). To the extent that customers have a choice regarding their retail electric provider, transparency is required so that they are able to make informed choices. Of course, transparency also is required for the appropriate government agencies to

[34] *See* International Council on Clean Transportation, May 2018 Briefing.

ensure compliance with applicable RPS, resource adequacy, and other requirements. Additionally, new programs or legislation may be needed for coordination of purchasing by CCAs and ESPs to ensure they continue to meet California's standards for integrated resource planning, resource adequacy, clean energy progress, consumer protection, and hedging risk.

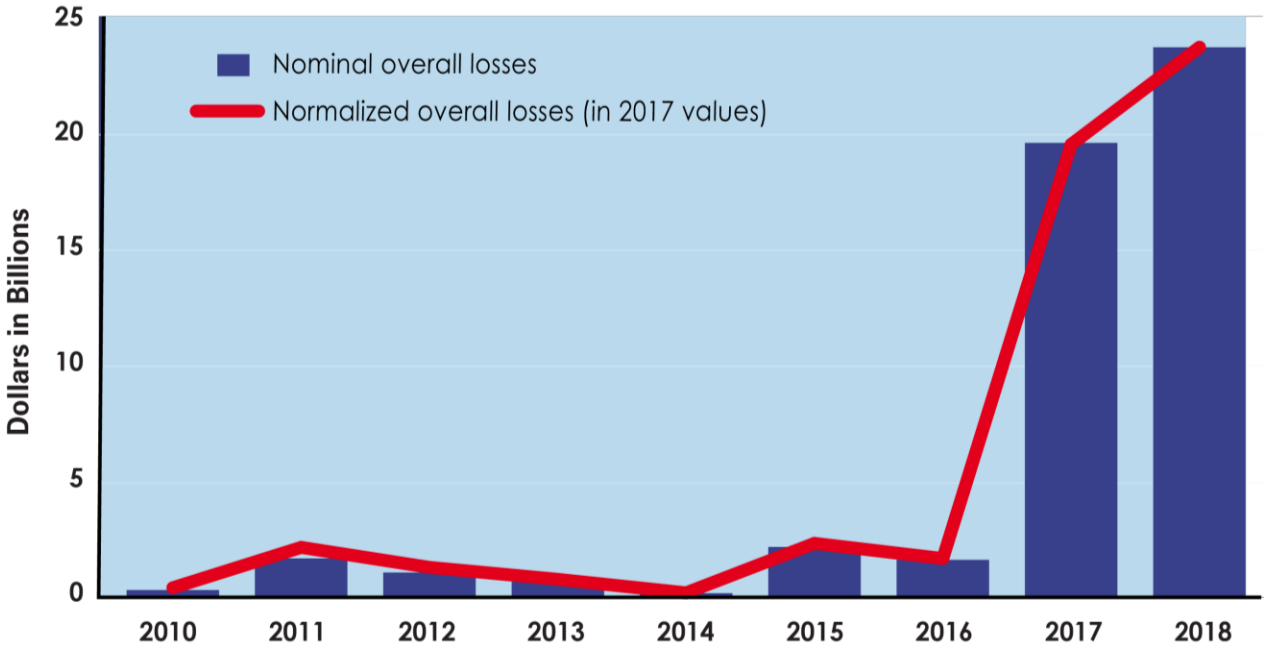
- **Addressing Variability in Generation and Consumption:** Addressing variability in electric generation and consumption will require efforts on a number of fronts. The afternoon ramp—the period when solar and wind energy decline and demand goes up—is increasing. Traditionally, flexible resources, such as natural gas-fired generators, have been used to provide a reserve margin, to ensure that generation and consumption stay in balance, and to provide other ancillary services needed for reliability. In the near term, a limited number of natural gas resources are still needed. In the longer term, more innovative solutions will be required. Further progress in time-of-use rates, demand response programs, storage, energy efficiency, increased regional coordination, and electric vehicle charging can help to ensure that demand at any given moment is at a level that can be accommodated by the amount of available electric generation. Proper infrastructure and incentives can be developed to facilitate and encourage integration of electric vehicles into the electric system in a manner that can enhance reliability and reduce costs. The strike force recommends that the CPUC use its Integrated Resource Planning process and other related proceedings to address these issues.

## Part 3: Fair Allocation of Catastrophic Wildfire Damages

Climate change, forest management practices, and real estate development patterns in the WUI have dramatically increased the risk and magnitude of wildfire damage. All stakeholders, public and private, must invest in mitigation, suppression and emergency response to reduce the incidence of catastrophic fire and to protect lives and property. At the same time, communities need electricity—including communities in remote, high fire-risk areas. As long as electrical lines run through tinder-dry forests, California can mitigate but not eliminate utility-sparked fires. California also must support wildfire victims and communities as they work to rebuild. These often competing imperatives require a new policy framework to responsibly and fairly allocate the cost of wildfire damage in an era of climate change. No single stakeholder created this crisis, and no single stakeholder should bear its full cost.

Developing workable solutions to equitably share the burden of compensating victims for wildfire damages is made more challenging by uncertainty regarding the future effects of climate change and the efficacy of mitigation efforts. The staggering wildfire damages of 2017 and 2018 highlight the potential severity of wildfires in the future.

**Figure-09**
**Wildfire Damages[35]**




We do not know whether this magnitude of damage is a new normal, or if recent years were aberrational. Experts consulted by the strike force believe climate change, development patterns, deferred utility equipment maintenance, and other factors suggest much heightened risk going forward but predicting how much risk and how

[35] Climate Changes Increases Wildfire Risk

consistently is more difficult. There is also uncertainty about the level of success we can expect in reducing the frequency and severity of wildfires.

Another challenge to a durable solution is that liability for wildfires ignited by utility equipment is governed by California's inverse condemnation law, which holds a utility strictly liable for wildfire damages if the utility's equipment ignites a wildfire, even if the utility's design and maintenance of infrastructure were not unreasonable or negligent. While a utility faces strict liability for all damages caused by its equipment, it can recover those costs through rates only by proving to the CPUC that its conduct was prudent. This regime—strict liability for wildfire damage coupled with uncertain ability to recover those damages in rates—increases the risk of bankrupt utilities, which in turn drives up costs for consumers, threatens fair recoveries for fire victims, undermines the state's ability to mitigate and adapt to climate change, and creates uncertainty for utility employees and contractors.

Under the status quo, all parties lose – wildfire victims, energy consumers, and Californians committed to addressing climate change. Victims face a great deal of uncertainty and diminished ability to be compensated for their losses and harm. Customers face rising rates and instability. California's ability to achieve its climate goals is frustrated. Utility vendors and employees face uncertainty and likely significant losses. Bottom line --- utilities in or on the verge of bankruptcy are not good for Californians, for economic growth or for the state's future.

## Strike Force Deliberations

The strike force has identified and intensively researched several approaches to address wildfire liabilities. Each of the approaches evaluated by the strike force has benefits and tradeoffs.

Much work remains to be done to evaluate these concepts and determine which alternative or combination of alternatives will best support safe, reliable, and affordable energy for Californians, further clean energy goals, and enable fair treatment for wildfire victims. The strike force recommends that the Commission on Catastrophic Wildfire Cost and Recovery (SB 901 Commission) jointly appointed by the Governor and the Legislature, evaluate these concepts and report back to the Governor and the Legislature on its findings.

## Principles Underlying a New Approach to Stabilizing and Sharing Costs

California's approach to wildfire mitigation must be grounded in principles that further the imperative to provide safe, reliable, and affordable power on a sustainable basis. To that end, the strike force has identified the following principles against which any proposal must be measured:

1. *Maintaining Safe, Reliable, and Affordable Power.* California residents and businesses require a safe and reliable electrical system, the achievement of which requires ongoing investment in new equipment, systems, and workforce. At the same time, steep rate increases would have adverse consequences for consumers, businesses, and California's climate goals. Thus, rate increases must be mitigated.

2. *Hold Utilities Accountable to Prioritize Safety.* Any changes in the liability rules should provide incentives for utilities and their management to prioritize and invest in safety and impose penalties for failure to do so. Any changes also must continue to hold a utility's shareholders—not its customers—responsible for failures to operate safely.
3. *Treat Wildfire Victims Fairly*. California wildfire victims deserve fair disposition of their claims so that they can move forward with their lives.
4. *Require Equitable Stakeholder Contributions*. The burdens of wildfire damages brought on by climate change are too great to be borne by any one stakeholder. A fair distribution of the burden requires utilities (ratepayers and investors), insurance companies, local governments, and attorneys representing victims to contribute.
5. *Reduce Overall Costs.* We must reduce wildfire damages as well as the financial claims that arise from them. This means prioritizing and paying for safety. It also means structuring the process by which claims are made and paid to assure the highest proportion of resources to pay for the actual losses victims suffer. And it means not creating a "free rider" problem or creating incentives for people not to act responsibly (e.g. by not properly insuring property against the risk of fire damages).
6. *Promote California's Clean Energy Goals.* Any solution must be consistent with California's long-term climate and clean energy goals and minimize the risk that wildfire liabilities will prevent utilities from having the resources to advance those goals, both in the near-term and over time.
7. *Recognize the Contribution of Taxpayers.* As described elsewhere, taxpayers have substantially increased their contribution to mitigating fire risk and fighting fires when they ignite. Any consideration of a fair burden of costs must recognize the substantial contribution the state and its taxpayers have already made and are continuing to make.

**Current Framework for Allocating Costs of Utility-Caused Wildfires**

In California, when a utility's equipment causes a wildfire, the utility may be held liable to pay for damages through (1) inverse condemnation lawsuits for property damages[36] brought by property owners or insurance companies (which seek compensation for payments they make to insured property owners); (2) tort lawsuits by a harmed party; and/or (3) recovery of fire suppression costs from third parties.[37] California's application

[36] Inverse condemnation is limited to property damage caused by utility equipment, so not all utility wildfire liabilities are actionable under inverse condemnation. For example, wildfire liabilities caused by a utility company employee, rather than utility equipment, are not recoverable under inverse condemnation. In practice, litigation pursuing subrogation recovery will include multiple liability theories, including inverse condemnation, some of which apply a strict liability standard and some of which apply other standards, such as negligence.

[37] When a utility is found to be a cause of a wildfire, the utility can be required to pay for three primary types of losses: (i) property damage and damages for personal injury, death, and related impacts, (ii) suppression expenditures incurred by government entities, including Cal FIRE and the United States Forest Service, and (iii) other economic and natural resource damages. The first two categories are direct costs (e.g. damage to structures, fire-fighting expenditures, injury and mortality) and are well defined, whereas the third category represents indirect damages (e.g. business interruption, temporary housing costs).

of inverse condemnation to utilities places 100 percent of the cost of wildfire property damage on a utility if its equipment caused the fire—regardless of fault and without consideration of the contributing role of climate change, forest management, land-use policies and other factors.

California is unique in extending the concept of inverse condemnation to IOUs.[38] Nonetheless, California courts have reasoned that "the nature of the California regulatory scheme demonstrates that the state generally expects a public utility to conduct its affairs more like a governmental entity than a private corporation."[39] The primary purpose of inverse condemnation is to spread costs to relieve individuals from bearing a disproportionate share of the economic burden of a governmental action.

Inverse condemnation claims have two unique features that create challenges for California's IOUs:

1. *Fault is Irrelevant.* In an inverse condemnation claim, the plaintiff need not allege or prove that the utility behaved unreasonably or negligently. An entity may be held strictly liable for damages so long as the plaintiff proves that the utility was a substantial cause of such damage--even if it was only one of several concurrent causes.
2. *Attorney's Fees and Expenses are Part of the Claim.* The California Code of Civil Procedure provides that in any inverse condemnation proceeding the plaintiff is entitled to recover the reasonable costs, disbursements, and expenses, including reasonable attorney's fees and expert costs.[40] These costs can be substantial.

The combination of strict liability and statutory attorney's fees exposes California utilities to significant potential liabilities.

Insurance companies play an important role in the practical application of inverse condemnation to utilities in California. Insurance companies write insurance and collect premiums to cover property owners for fire losses. In the event of a fire, the insurance company pays an insured property owner's claim and absorbs the loss. If the fire was ignited by a utility's equipment, the insurance company seeks reimbursement from the utility for the damage claim it paid to homeowners, typically through an inverse

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[38] Only Florida and Alabama have applied the doctrine of inverse condemnation to utility companies and only Alabama has extended the doctrine to privately-owned utilities. Similar to California, under Alabama law, a non-governmental entity can be subject to a claim for inverse condemnation. As such, in Schultz v. SE. Supply Header, LLC, No. CA 09-0055-KD-C, 2009 WL 3075671 (S.D. Ala. Aug. 20, 2009), the property owners' claim for inverse condemnation against the private utility company did not fail by virtue of the utility company's non-governmental status. In that case, the property owners gave the utility company a permanent easement to their property for the installation of a natural gas pipeline to run underground, but in the process of construction, the utility company flooded the property and caused the property owners' septic system to malfunction, reducing the property to a swamp. Since the utility company was expressly authorized to exercise the power of eminent domain for installation of the natural gas pipelines, the property owners could avail themselves of the remedy of inverse condemnation for damage of the property by the company.

[39] *Barham v. Southern California Edison Company*, 74 Cal. App. 4th 744, 753 (1999).

[40] CA Civ. Pro. Code § 1036 (2017).

condemnation claim.[41] These claims from the insurance company are known as subrogation claims.[42]

### Cost Recovery and Wildfire Damages

While a public utility found liable under inverse condemnation spreads the costs by using its rate-setting power to pass the costs to customers, investor-owned utilities can recover inverse condemnation damages in rates only if the CPUC separately determines that they may do so. California law requires that any rates charged by a utility must be "just and reasonable". [43] A utility may pass through and recover non-routine costs as a result of third-party litigation or inverse condemnation only if the IOU demonstrates to the CPUC that it acted reasonably and prudently (i.e., met a "prudent manager" standard).[44]

To meet this prudent manager standard in the context of extraordinary wildfire expenses, the CPUC requires that a utility affirmatively prove that it: (1) behaved reasonably and prudently in managing its facilities before and during the fire and (2) behaved reasonably and prudently in settling any litigation claims, if applicable. The CPUC has wide latitude as to the applicable evidentiary standard—typically applying a preponderance of the evidence standard—which generally requires evidence that "when weighed with that opposed to it, has more convincing force and greater probability of truth."[45]

### Recent Application of Utility Wildfire Cost Recovery Standards

In October 2007, three large wildfires occurred in the service area of SDG&E. The ignition of those fires was attributed to the company's equipment. After 7 years of litigation, SDG&E settled legal claims for $2.4 billion in costs and legal fees to resolve third-party damages arising from the fires. After collecting from other responsible parties and under liability insurance policies, SDG&E sought recovery from ratepayers for the remaining

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[41] Inverse condemnation is limited to property damage caused by utility equipment, so not all utility wildfire liabilities are actionable under inverse condemnation. For example, wildfire liabilities caused by a utility company employee, rather than utility equipment, are not recoverable under inverse condemnation. In practice, litigation pursuing subrogation recovery will include multiple liability theories, including inverse condemnation, some of which apply a strict liability standard and some of which apply other standards, such as negligence.

[42] Generally, insurance company subrogation recoveries are not 100 percent reimbursement for claims paid to property owners. Limited public information suggests that subrogation settlements equal about 50 percent of the claim. Specifically, SCE's general auditor stated that wildfire subrogation claims have in the past settled at "historical levels" of "around 50 percent" at a meeting of the Commission on Catastrophic Wildfire Cost and Recovery on April 3, 2019.

[43] CAL. P.U.C § 451.

[44] The prudent manager standard means that "at a particular time any of the practices, methods, and acts engaged in by a utility follow the exercise of reasonable judgment in light of facts known or which should have been known at the time the decision was made." The prudent manager standard is a standard of care that demonstrates all actions were well planned and properly supervised and all necessary records are retained. *See See In re: San Diego Gas & Electric Co.*, Order Denying Application for Decision 17-11-033 at p.5 (Cal. Pu. Util. Comm'n) (Nov. 30, 2017).

[45] Decision Implementing a Safety Enhancement Plan and Approval Process, Decision 14-06-007 [D.14-06-007]

$379 million in damages it had paid. In October 2017, the CPUC denied SDG&E's request, ruling that the utility had not met required standards of prudency.[46]

The CPUC decision in the San Diego case was the first time a utility had incurred costs that exceeded its insurance coverage. The decision raised concerns in the capital markets that investors in California utilities were more exposed to wildfire liabilities than previously thought.

In late 2017, shortly after the CPUC's decision in the San Diego fires, California suffered one of its worst wildfire seasons on record. Combined, these events created uncertainty in the capital markets regarding the safety of investing in California utilities.

### Senate Bill 901 (Dodd, Chapter 626, Statutes of 2018) (SB 901)

After the utility market destabilization, California enacted SB 901, which requires the CPUC to consider "conduct of the electric grid and relevant information submitted into the commission record" when determining whether a utility is permitted to recover costs related to wildfires. The statute outlines 12 categories of information for consideration, which are set forth on Annex B. SB 901 also incorporated a "stress test" that provided the CPUC additional flexibility to allow utilities to recover their costs in respect of wildfire liabilities from ratepayers where the denial of cost recovery could negatively impact the IOUs' financial condition.

In a cost recovery action, the CPUC must first find that utility equipment ignited the wildfire. Then the CPUC must determine whether the utility acted prudently both in the behavior causing the wildfire and in the settlement of any claims. If it acted prudently, the utility may recover the costs by charging higher rates to customers. If it did not act prudently, the utility would be required to bear those costs itself, in effect by reducing the returns paid to its equity investors. SB 901 attempted to provide the CPUC guidance on application of the cost recovery rules that would create more certainty around cost recovery.

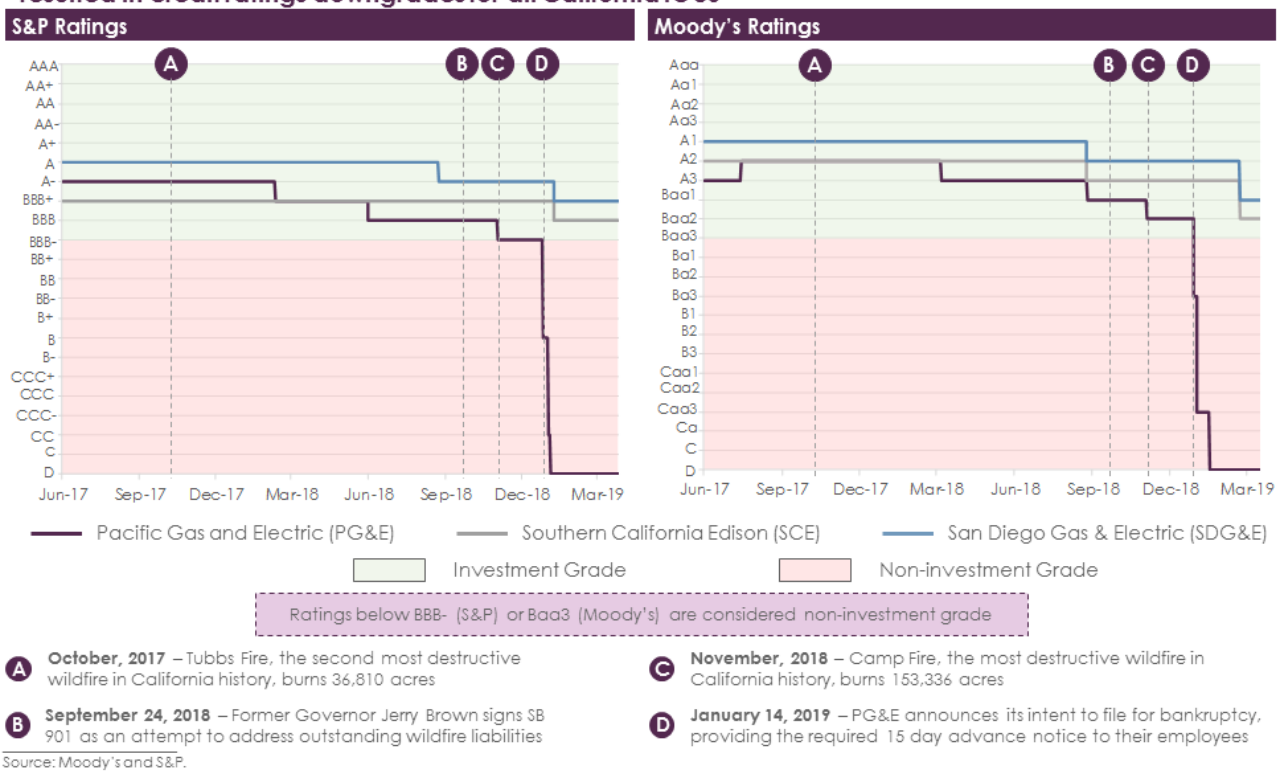
After passage of SB 901, the credit rating agencies (Moody's, Standard & Poor's and Fitch) immediately began to downgrade California's three large IOUs, opining that the measure failed to adequately address the risks to the utilities' financial health posed by inverse condemnation. Two months later, the Camp Fire occurred. Two months after that, PG&E stated its intention to seek chapter 11 bankruptcy protection.

The rating agencies followed with an additional series of downgrades that now leave SCE and SDG&E with close to non-investment grade ratings.

[46] See Order Denying Application [D. 17-11-033] (Cal. Pu. Util. Comm'n) (Nov. 30, 2017); Order Denying Rehearing of Decision (D.) 17-11-033 [D. 18-07-025] (Cal. Pub. Util. Comm'n) (July 12, 2018); Order Denying Writ for Review, No. D074417, Cal. Ct. of Appeal, 4th District, Div. 1 (Nov. 13, 2018)

**Figure-10**

**Increasing wildfire risk coupled with uncertainty surrounding cost recovery for wildfire liabilities has resulted in credit ratings downgrades for all California IOUs**




Source: Moody's and S&P.

Ratings downgrades increase utilities' cost of capital (including capital raised for investment in fire mitigation and safety) and those additional costs are generally passed on to consumers.

The capital markets concluded that too much uncertainty regarding cost recovery remained following passage of SB 901. Their key concerns were that it left the CPUC with extensive discretion to determine whether catastrophic wildfire damages could be passed through to the ratepayers.[47] In addition, investors raised concerns that SB 901 did not address the significant time period between the occurrence of a catastrophic wildfire, the payment of damages arising from that wildfire, and the CPUC's final

[47] California's cost recovery process contrasts with the framework employed for federally-regulated transmission rates by the Federal Energy Regulatory Commission (FERC). Pursuant to section 205 of the Federal Power Act (FPA), public utility rates for transmission services in interstate commerce must be "just and reasonable," which includes a requirement that the utility is prudent in incurring costs. This statutory standard is similar to the standard in the California Public Utilities Code, however, FERC applies the standard differently than the CPUC applies its similar statutory standard. In practice, FERC generally presumes that a utility's expenditures have been prudent unless a third party raises a formal complaint that casts a serious doubt on the utility's prudency, in which case the utility has the burden to prove that its conduct and expenditures were prudent. FERC will consider a utility's conduct prudent if the utility acted as any other reasonable utility in its position would have acted, given the same circumstances and the same facts known to the company at the time. FERC precedent in evaluating the prudency standard affords considerable latitude as FERC, in reviewing a decision, does not look for a single correct result or require the evaluation of every possible alternative. Thus, the FERC standard is far more predictable.

determination of whether those payments can be recovered in rates. Under current timelines, a utility does not file an application for cost recovery until after it resolves all litigated claims, which in the case of San Diego took more than seven years from the time of the fires. The CPUC's cost recovery process can take 18 months to two years. This time lag creates financial stress on a utility which may need to raise additional capital to pay billions of dollars of wildfire claims without knowing whether it will be able to recover the costs of that capital in future rate increases. This can lead to lower credit ratings, higher borrowing costs and, therefore, higher rates paid by utility customers. Ultimately, as we have seen with PG&E, it can lead a utility to seek protection under the federal bankruptcy laws.

### Consideration of Insurance Impacts

Before discussing potential concepts, it is important to consider the current impact of climate change and catastrophic wildfire damage on the availability and affordability of insurance and the risk that any proposed changes to liability for wildfire damage could exacerbate those impacts.

Insurance pricing and availability is responsive to a very basic principle: as risk increases, the cost of insurance increases and the availability of insurance coverage decreases. With record high losses from catastrophic wildfires, insurers are responding by filing for rate increases and retrenching their coverage eligibility standards. According to the California Department of Insurance (CDI), many regions of the state face insurance availability and affordability constraints. This is evidenced by increasing non-renewals and significant insurance premium increases in the areas of the state affected by wildfires. Investments that increase resiliency to climate-related catastrophes will add stability to insurance options. Without affordable insurance, regions throughout the state will find homes decreasing in value.

### Current Trends in Insurance Availability and Affordability

Insurance rates are principally based on recent loss experience. According to CDI, in California, the loss experience resulting from catastrophes is not loaded directly into the rates but instead placed in a catastrophe load that is an average of at least 20 years of catastrophe experience. Despite that fact, rates are beginning to increase.

According to the CDI:

- Carriers have submitted applications to CDI for over 100 rate increases for homeowners insurance in the last two years, more than double the filings in the previous two years;
- Homeowners in areas with heightened wildfire risk are receiving double-digit rate increases;

- There has been a significant uptick in policy counts at the California Fair Access to Insurance Requirements Plan (FAIR Plan)[48] for homes located in areas of high wildfire risk, by 50 percent in the last five years (from 22,000 policies for homes with wildfire risk exposures to 33,000 such policies), although the FAIR Plan only insures about 130,000 homes in total out of approximately 13 million residences in the state;
- The number of homeowners who have purchased insurance from surplus lines insurers has also increased, though the total remains fewer than 60,000 statewide. Surplus lines coverage is available only to consumers who cannot find coverage with an admitted insurer. The rates are not regulated nor is the coverage backed by the California Insurance Guarantee Association; and
- Consumer complaints about non-renewals in high risk counties have also doubled in the last two years.

According to CDI, the overall number of adverse actions that are reflected in available data are relatively low compared to the California homeowners' insurance market as a whole. After two consecutive years of massive homeowners insurance loss ratios of insurers—201 percent in 2017 and 170 percent in 2018–there is a sense of urgency about the decreasing availability and affordability in 2019, especially for regions with high wildfire risk.

The strike force recommends that the Governor and Legislature, in consultation with the Insurance Commissioner, consider the following:

- Should all insurers be obligated to offer insurance to homeowners living in the WUI if the insured conducts specific wildfire mitigation?
- Should all insurers be obligated to offer reduced rates for those homeowners and communities that implement prescribed wildfire mitigation measures?
- Should insurers be obligated to offer consumers who are ineligible for a homeowners' policy either a "difference in conditions" policy or a "premises liability policy" as complementary coverage for a FAIR Plan fire policy?
- The California Insurance Guarantee Association policy limits have not been increased for at least two decades. Is it time to increase the current limit of $500,000 to recognize current construction costs?

### Concepts for a Solution

The strike force heard from experts and stakeholders about alternative approaches. Based on this input, research and evaluation of the strengths and weaknesses of alternative approaches, we identified three concepts for consideration:

- **Concept 1:** Liquidity-Only Fund. This concept would create a fund to provide liquidity for utilities to pay wildfire damage claims pending CPUC determination of

[48] The FAIR Plan was created in July 1968 as an insurance pool established to assure the availability of basic property insurance to people who own insurable property in the State of California and who, beyond their control, have been unable to obtain insurance in the voluntary insurance market. *See* https://www.cfpnet.com.

whether or not those claims are appropriate for cost recovery and may be coupled with modification of cost recovery standards.

- **Concept 2:** Changing Strict Liability to a Fault-Based Standard. This concept would involve modification of California's strict liability standard under inverse condemnation to one based on fault to balance the need for public improvements with private harm to individuals.
- **Concept 3:** Wildfire Fund. This concept would create a wildfire fund coupled with a revised cost recovery standard to spread the cost of catastrophic wildfires more broadly among stakeholders.

Given the inherent uncertainty we face and the number of foundational policy questions that must be addressed, the strike force recommends that the Commission on Catastrophic Wildfire Cost and Recovery, the Legislature, and the Governor's strike force continue working over the next two months to develop a solution for consideration by the Governor and the Legislature that most effectively addresses wildfire liability consistent with the principles that the strike force has outlined.

Each of the three concepts requires statutory changes to clarify the prudent manager standard and the requisite burden of proof related to when an IOU is permitted to recover costs and expenses of wildfires from its customers. To achieve a result that meets the principles outlined in this Report, utilities will have to make significant contributions to the benefit of ratepayers.

Concepts 1 and 3 rely on voluntary contributions from utility investors to different extents. The larger the contribution required, the more clarity utility investors will demand in the regulatory standard for cost recovery from ratepayers.

## Concept 1: Liquidity-Only Fund

The liquidity-only fund involves a modest modification to the current SB 901 framework to address the delay between when a utility pays wildfire claims and when the CPUC makes its rate recovery determination. This concept would create a fund to provide bridge financing for utilities to pay wildfire liability claims pending the CPUC's decision on cost recovery under a modified standard. The liquidity-only fund does not reduce the burden on utility customers or re-distribute the costs of wildfires among stakeholders. As such, it does not address certain principles set forth above. In combination with changes to the CPUC cost recovery process, a liquidity-only fund could stabilize the credit ratings of utilities.

The liquidity-only fund could be capitalized by utility investors and ratepayers, potentially through a continuation and securitization of the Department of Water Resources (DWR) charge implemented during the power crisis in 2001 and expected to be fully repaid before the end of 2020. All or a portion of that securitization charge could be extended and dedicated to the liquidity-only fund.

The fund would then be available to provide funds for utilities to pay claims after a determination of cause and before a determination of cost recovery. When the CPUC makes a cost recovery determination, the fund then works as follows:

- If the CPUC determines that the utility met the cost recovery standard and therefore can recover the costs in rates, then the utility would charge the ratepayers and reimburse the fund for the amounts drawn.
- If the CPUC determines that the utility did not meet the cost recovery standard and therefore cannot recover costs in rates, then the utility would be required to repay the amounts drawn from the fund such that ratepayers would not bear the cost of such amounts.

This concept does not shield utility customers from uncapped liability for wildfire damages. In fact, if cost recovery changes increase the certainty that utilities can recover damages from their customers, ratepayers will pay more.

### Further Research.

Several questions and policy considerations must be addressed to evaluate the liquidity-only fund and the impact it would have on reducing and socializing costs, and its ultimate impact on consumers:

- Can the fund provide sufficient liquidity to pay claims in a timely manner while allowing the CPUC to evaluate wildfires?
- Can this concept, in combination with necessary changes in the CPUC rate recovery process, provide enough certainty to the capital markets to stabilize ratings and the perception of a utility's credit quality?
- How durable can the liquidity fund be while the utilities address their safety deficiencies?
- How much can we expect from this simplified solution if we don't address the factors that turn massive wildfires into massive damage claims?
- What does this option mean for rates and affordability?
- What shareholder contribution, if any, would be required to capitalize the fund?

## Concept 2: Changing Strict Liability to a Fault-Based Standard

A second concept is to change California's strict liability standard to one based on fault. Applying a fault-based standard—utilities pay for damage if caused by their misconduct—would balance the need for public improvements (i.e. an electrical distribution system) with the private harm to individuals occasioned by those improvements. This change would impact only claims for property damage, since California already applies a negligence standard to personal injury, wrongful death, and other tort claims.

Moving to a fault-based standard would shift the risk of property loss to insurance companies and uninsured or underinsured property owners in cases where the utility was not a bad actor. Where the utility acted negligently, recklessly, or with intentional misconduct, it would still be responsible for paying damages, including possible punitive damages.

As with Concepts 1 and 3, a solution that changed to a fault-based liability standard would be accompanied with modifications to clarify the prudent manager standard and the requisite burden of proof related to when an IOU is permitted to recover costs and expenses of wildfires from its consumers.

Shifting more of the direct financial burden of wildfires to insurance companies may also affect the cost and availability of property insurance in the WUI. Whether a reform of inverse condemnation would affect the cost and availability of insurance is unclear. If such an impact occurred, a variety of policy responses might be considered, including creating a catastrophic pooled insurance fund or reforms to the FAIR Plan, which provides last-resort fire insurance when homeowners or dwelling coverage is unavailable in the voluntary market of admitted insurers.[49] Admitted insurers are obligated to share in any losses suffered by the FAIR Plan.

### Further Research.

Several questions and policy considerations must be addressed to evaluate the impact moving to a fault-based system would have on reducing and spreading costs, and its ultimate impact on consumers:

- How much would moving to a fault-based system reduce the settlements that utilities pay for wildfire claims?
- Would availability and affordability of property insurance in the state, particularly in the WUI be affected? If so, are there policy options to mitigate that impact?
- Would this approach yield certainty in the needed timeline given the potential legal risks and challenges?

## Concept 3: Wildfire Fund

A third concept is to establish a well-capitalized wildfire fund that would create a buffer to absorb a significant portion of the wildfire liability costs that might otherwise be passed on to ratepayers under existing law and regulation while providing time for mitigation efforts to be advanced. The wildfire fund would also provide the utilities a source of immediate funding for the claims asserted against them for catastrophic wildfire damages and ensures prompt payment of those claims.

This concept could accomplish each of these objectives if utility shareholders were prepared to make a substantial contribution to the fund's claims-paying resources and if insurers were willing to accept a cap on their subrogation claims (their claims for reimbursement from the utilities of the payments to their insurance policyholders). If the wildfire fund is not sufficiently capitalized and/or the other stakeholders are not willing to

[49] The Commission on Catastrophic Wildfire Cost and Recovery is tasked with, among other matters, evaluating the impact of wildfire damage on insurance availability and affordability. The Commission is expected to deliver its report by July 1.

compromise their claims, then the wildfire fund will be exhausted more quickly and ratepayers will be responsible for costs thereafter.

The CPUC would retain jurisdiction to impose penalties on utilities that fail to prudently manage their wildfire risks, and those penalties would be paid to the fund to enhance its claims paying resources. Like the liquidity-only fund, an extended DWR charge could be dedicated to support the claims paying resources of the wildfire fund.

The following are reasonable elements of a wildfire fund that, depending on additional research, analysis, and development, may warrant consideration in the future.

3. **Pooled Capital:** The wildfire fund would include pooled capital from all IOUs including each of SDG&E, SCE and PG&E and be accessible by each of those utilities to pay catastrophic wildfire claims. Municipally owned utilities may participate at their option.
4. **Only Catastrophic Fires:** The fund would be limited to paying claims of utility-caused catastrophic wildfire liabilities only (as such fires would be defined in legislation establishing the fund). Smaller utility-caused fires and the first-dollar costs of catastrophic wildfires would be paid by a utility's commercial liability insurance policy and/or self-insurance reserve.
5. **Claims Administration Trust.** A wildfire fund could use a trust for the administration of claims. The trust could pay all subrogation claims to insurance companies and reimburse utilities for the costs of judgments on or settlements of uninsured and underinsured victims' claims. All insurance companies writing insurance in the state could be required to agree that subrogation claims arising out of catastrophic wildfire claims will be asserted against the trust. A potentially valuable feature of the wildfire fund could be that subrogation claims will receive settlements at a stated percentage of the validated amount of their claim. Utilities could be responsible for litigating or settling claims brought by uninsured and underinsured victims. They could then seek reimbursement from the trust for the settlement amounts or final judgments. The reimbursement process could provide incentives for the utilities to settle promptly with victims, while also ensuring that they settle for fair, but not excessive, amounts.
6. **Automatic Access to the Fund.** A utility could seek to pay wildfire claims from the fund upon determination that the fire was a catastrophic utility-caused wildfire without pre-determination by the CPUC whether or not the utility acted prudently, reasonably, or without negligence.
7. **Penalties to Discourage Behavior by Fund Participants that Violates Regulatory Requirements or is Imprudent:** Regulatory reforms could incorporate penalties that would create disincentives for negligent or unreasonable behavior by fund participants. Penalties could be paid into the fund to further extend claims paying capacity.

**Further Research.**

- How large would the fund need to be to be durable over the anticipated period of time necessary for utilities to make material progress in containing catastrophic wildfire risk?
- How can we design a fund that provides the proper incentives for utilities to invest in prevention to reduce wildfire damages and claims and for property owners to protect themselves by purchasing adequate insurance?
- After emerging from bankruptcy and providing for adequate compensation to its pre-petition wildfire victims, how will PG&E raise the necessary capital to make its contribution to the fund?
- How much time will it take to form and capitalize a wildfire fund? How should liability for wildfires that may occur in 2019 prior to the fund's formation be treated? Can the fund be established before PG&E emerges from bankruptcy?
- Capping subrogation claims moves the upper range of risk from the utility to the insurers, who will pass it on to customers. What would be the long-term impact on the availability of insurance?
- Would the subrogation cap apply to both property claims and casualty claims, which are different rights under the law?
- Should insurers or insureds contribute to fund capitalization?

# Part 4: A More Effective CPUC with the Tools to Manage a Changing Utility Market

California's changing energy market and the need to mitigate and adapt to climate change require a state utility regulator that is effective in today's reality.

The CPUC has a long history as a regulator of rates. It manages complex, participatory, and time-consuming proceedings to set energy rates for the state's utilities. Its structure and deliberative processes flow from the California Constitution, which authorizes the CPUC to fix rates and charges and allows utilities to raise rates or charges if justified.[50] The CPUC has an imperative to balance the financial health of utilities and the need to keep rates as low as possible.

The current structure of the CPUC does not align with California's need for a regulator that can effectively address wildfire safety and can be nimble in today's changing energy market. The CPUC has assumed a greater role in safety regulation, as well as in protecting consumers. However, its structure has not fundamentally changed. Further, its other obligations, including regulation of some transportation industries, telecommunications, and other industries has grown as the demands on the Commission as the state's regulator of utilities have increased and become more complicated.

The Commission needs to strengthen its efforts as an evaluator of risk reduction and as a key line of defense to prevent wildfires caused by utility infrastructure. It must also be more nimble and provide necessary certainty more quickly than it does today in light of the changing energy market and heightened fire risk. Implementing a comprehensive strategy to improve safety, keep costs down and reach California's clean energy goals requires a regulator that applies and enforces regulation in a predictable, timely, and fair way.

## The Current CPUC Process

The CPUC has three primary roles: quasi-legislative, rate-setting, and adjudicatory disputes. Under current law and practice, the CPUC uses different processes depending on the role it is performing. All types of proceedings are record based and governed by either an Assigned Commissioner or an Administrative Law Judge (ALJ). All involve extensive consultation and public input.

The CPUC typically addresses policy issues and capital expenditures in separate proceedings. For example, the issue of wildfire mitigation is being handled in two separate proceedings in front of the CPUC--one specific to the WMPs and the second as part of the general rate case (GRC). As wildfires become more frequent and larger, and as the state's energy market changes, the CPUC needs a decision-making process that is responsive to these developments.

[50] Article XII Public Utilities, CAL. CONS. [SECTION 1 - SEC. 9].

IOUs file GRCs with the CPUC every three years for prospective costs. Between GRC proceedings, the IOUs often file for approval for recovery of unexpected costs incurred. Except for certain minor matters, a highly structured legal process applies to decisions on these filings. The process insures that the filing party and opposing parties have an ability to be heard, including by submitting pleadings and testimony. The testimony and filings are important because the Commission must base its decisions on evidence in the record. The process provides other parties the ability to present views that are contrary to those of the IOUs. While it has value, the existing process can be time-consuming.[51]

If the Assigned Commissioner is not the presiding officer, the statutory structure of the CPUC's decision-making process often leaves ALJs with more control over the timing of the process than the Commissioners. That can lead to delays in proceedings even when the Commissioners wish to prioritize the decision-making.

In its rate-setting mode, the CPUC faces a difficult balancing act. On the one hand, the CPUC wants the IOUs to make appropriate investments and expenditures so they can provide safe and reliable service to their customers. On the other hand, an IOU's only source of income is its customers. Consumers have an interest in avoiding unnecessary costs and investments and keeping borrowing costs down. IOUs operate their business by collecting a return on investment, but the investments and the return are closely regulated by the CPUC. When the IOUs are financially healthy, utility customers benefit from lower cost of capital. When utilities are financially unhealthy, the inverse occurs as evidenced today in the case of PG&E.

In rate-setting and cost recovery cases, the burden falls on the utility to prove that its requests or its past actions were reasonable or prudent. In some instances, the utility may face difficulty proving that past actions meet this burden, which can create financial uncertainty for the utility. To avoid this, utilities may elect not to make expenditures unless the cost recovery was pre-approved by the CPUC.

The CPUC sometimes is tasked with new responsibilities that fall outside its traditional function of ensuring that rates are just and reasonable. After the San Bruno and Aliso Canyon events, safety has become a much more significant issue for the CPUC. The recent expansion of the Commission's role into reviewing WMPs under SB 901, as described above, is a further example of the CPUC's expanded role.

The CPUC's statutory and Constitutional responsibilities go beyond the rate-making cases. In developing and overseeing clean energy programs and in its role in

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[51] As an example, SCE filed its most recent GRC on September 1, 2016, and it is still pending today, more than 2 years later. *See In re: San Diego Gas & Electric Co.*, Test Year 2018 General Rate Case Application of So. Cal. Edison Co A 16-09-001 (Cal. Pu. Util. Comm'n) (Sept. 1, 2016); When SDG&E filed to recover its third-party damage claims in connection with its 2007 wildfires, it took 2 years for the CPUC to issue its decision denying recovery, and it took 6 months for the CPUC to issue its rehearing order after SDG&E filed its rehearing request. *See* Application of San Diego Gas & Elec. Co. (U 902 E) for Authorization to Recover Costs Related to the 2007 Southern California Wildfires Recorded in the Wildfire Expense Memorandum Account, *In re: San Diego Gas & Electric Co.*, Decision Denying Application, A 17-11-033 (Cal. Pu. Util. Comm'n) (Dec. 6, 2017); *In re: San Diego Gas & Electric Co.*, Order Denying Rehearing of Decision 17-11-033 (Cal. Pu. Util. Comm'n) (Jul. 13, 2018).

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developing and enforcing safety regulations, the CPUC can also be a policy-setting body and a quasi-judicial body. At times, the ALJ-led process the CPUC utilizes does not lend itself to public accessibility or speedy development of new policies. This may contrast with the public's expectation that the Commissioners be the ultimate decision makers who should be held accountable for the timing of developing new rules and programs.

While there is merit in existing CPUC processes, the lack of flexibility and inefficiency frustrates the ability of the CPUC to effectively regulate utilities in a way that best meets the needs of Californians from a safety and financial standpoint. To more effectively meet the state's needs in today's environment, the CPUC must be reformed. The recommendations set forth below represent near-term steps that can be taken to improve CPUC efficiency and effectiveness. Longer-term, the state should evaluate a more comprehensive overhaul of the CPUC in an effort to better serve the changing needs of California.

### Recommendations

- **Expand Safety Expertise:** Provide resources to the CPUC for meaningful review of WMPs or alternatively create a wildfire safety division in another agency. The CPUC must—on a priority basis—develop appropriate processes and expertise to handle matters involving safety. This should cover the CPUC's responsibilities for setting safety standards, conducting inspections and audits, and enforcing the standards. A good starting point would be to look at safety-related programs used by regulators in other industry sectors that involve high risks to property and human health and safety, such as the nuclear, aviation, and refinery industries. While the 2016 reforms made a small step toward an increased focus on safety, more is needed. Building the CPUC's capabilities related to safety may require organizational changes, budget increases, and a concerted effort to hire, contract for, or obtain through cooperative efforts with other agencies, the expertise needed to handle these new responsibilities. If experts are not available, then the CPUC should consider entering into grants or contracts with universities or consulting firms that could conduct research and develop standards and training programs to create the necessary expertise.
- **Overhaul Decision-Making Processes.** The CPUC should overhaul and reform its procedures to implement safety related initiatives and requirements more efficiently. Given the potentially large financial implications of such determinations as related to wildfire-related costs, it is particularly important that the CPUC put in place a process that is both timely and fair, while maintaining public input and transparency as appropriate. To achieve this goal, the strike force recommends that the Legislature consider directing the CPUC to do the following:
  - Streamline procedural designations for simpler cases. Many proceedings that could be quasi-legislative are currently subject to full rate-setting procedures.
  - Increase authority to delegate lower-level decisions to technical staff to free up time for administrative law judges and commissioners to focus on traditional rate-setting matters.
  - Eliminate unnecessary steps in proceedings and provide Commissioners with discretion to shorten timelines.

  - Streamline enforcement procedures and increase enforcement authority, including delegating more enforcement authority to the Commission's safety division staff.

- **Review of High-Risk Industry Regulatory Models.** The Governor's Office of Planning and Research, in consultation with experts from academia, industry, and other research institutions, should review models of agencies that regulate high-risk industries, such as nuclear power and refineries, and summarize best practices that could be applied to the CPUC. These practices could include structural or procedural models and necessary expertise.
- **Industry Best Practices.** The CPUC should develop and adopt industry best practices for utilities as a resource. It should regularly monitor and update those practices to reflect learning, changing technology, and the latest assessment of climate change.

# Part 5: Holding PG&E Accountable and Building a Utility that Prioritizes Safety

On January 29, PG&E filed voluntary chapter 11 petitions in the United States Bankruptcy Court for the Northern District of California--PG&E's second bankruptcy filing in the last 18 years.[52] PG&E attributed its chapter 11 filing to claims resulting from the 2018 wildfires, including the Camp Fire which PG&E has since stated was likely ignited by its equipment.[53] PG&E justified the filing, in part, by citing the need to provide fair compensation for fire victims. Yet consistent with its historic culture, PG&E failed to honor scheduled settlement payments to victims of the Butte Fire in the days leading up to its bankruptcy. PG&E's willingness to use the bankruptcy process to the advantage of its investors, and at the expense of Californians, cannot be repeated.

PG&E's decision to voluntarily seek the protection of a chapter 11 bankruptcy court punctuates more than two decades of mismanagement, misconduct, and failed efforts to improve its safety culture. Prior to its filing, PG&E already was on criminal probation, having been convicted of five felony counts for safety violations in connection with the San Bruno gas explosion in 2010. That explosion resulted in eight deaths, approximately 58 injuries and 38 homes destroyed.[54] PG&E was also convicted of obstruction of justice, fined over $4.6 million, and sentenced to substantial community service as a result of the same incident.

In addition to the incidents described above, PG&E has been investigated in connection with or settled claims related to numerous wildfires and explosions in the last 25 years including:

- The Trauner Fire (1994)
- The Pendola Fire (1999)
- The Sims Fire (2004)
- Fred's Fire (2004)
- The Rancho Codova gas explosion (2008)
- The 2009 San Francisco electrical explosion
- The 2014 Carmel gas explosion
- The Butte Fire (2015)
- Numerous electrical and substation fires (*e.g.* 1996, 1999, 2003).

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[52] PG&E previously filed for bankruptcy in 2001 in an effort to undermine the jurisdiction of the CPUC. That multi-year bankruptcy resulted in substantial rate increases for PG&E customers.

[53] PG&E, *PG&E Publicly Releases Supplemental Report on Electric Incidents Near the Camp Fire," the Camp Fire*, (Dec. 11, 2018) https://www.pge.com/en/about/newsroom/newsdetails/index.page?title=20181211_pge_publicly_releases_supplemental_report_on_electric_incidents_near_the_camp_fire (last visited Apr. 10, 2019).

[54] *See* CAL. PUB. UTILITIES COMM., *The San Bruno Catastrophe and Its Aftermath*, (May 2012), https://www.in.gov/iurc/files/Zeller_-_San_Bruno_Catastrophe_Aftermath.pdf (last visited Apr. 10, 2019).

Despite repeated assurances from management that the company would change, PG&E has failed to implement the fundamental management and cultural reforms to prioritize safety and reliable service.

Californians deserve better, and we will demand better. The state simply will not accept a situation where 40 percent of Californians are served by a company that cannot be trusted to provide safe and affordable power. PG&E must be radically restructured and transformed into a responsible and accountable utility.

PG&E's bankruptcy proceedings will have direct and profound impacts on the people of California. The state must participate in the proceedings to protect its interests, including those of wildfire victims who have claims against the company that must be resolved fairly and equitably, PG&E employees who are vital to maintain energy delivery and protect the safety of communities, and the company's customers who deserve clean, safe, reliable, and affordable energy. We expect and demand that PG&E will, as it is obligated to do, comply with state law, including CPUC safety directives and renewable energy mandates.

## Recommendations

PG&E's stakeholders have the primary responsibility for filing a plan of reorganization or otherwise formulating an exit from chapter 11. For a plan of reorganization to be confirmed in the bankruptcy proceedings, it must meet the criteria set forth in the Bankruptcy Code, including that the plan be feasible and that PG&E be in compliance with law. To meet those standards, PG&E will have to demonstrate that it has sufficient funds available to make fund distributions provided under the plan and comply with its WMP and demonstrate that is in compliance with state and federal laws, rules and regulations, including laws and regulations related to clean energy. Given the importance of PG&E to California, the state must work to assure that any resolution of that proceeding achieves the near, medium and long-term goals of the state and its people over opportunistic investors.

The strike force recommends that the state actively monitor and evaluate the PG&E bankruptcy proceeding to assure that the state's interests are being protected. Where appropriate and necessary, the state should participate in the bankruptcy proceedings and be heard on particular issues of interest to California. The strike force specifically recommends the following:

- **Evaluate Any Proposals to Satisfy 2017-2018 Wildfire Claims.** PG&E must satisfy the claims against it from the 2017-2018 wildfires. To that end, the state should evaluate the structure and amount of any trust or other mechanism to satisfy those claims to assure victims are fully and fairly treated. In addition, the state must evaluate any plan of reorganization to assess whether provisions of that plan could disadvantage existing and future wildfire victims.
- **Assure that PG&E Treats Its Employees Fairly.** PG&E's employees are a critical part of the future of the company and must be treated fairly in the bankruptcy proceeding. The state should monitor the bankruptcy proceedings to assure that employees are treated fairly.

- **Require that PG&E's Investors Contribute to a Solution.** Part 3 of this report identified certain conceptual approaches to the wildfire liability framework applicable to IOUs. While PG&E would be a beneficiary of any of those constructs, PG&E's investors must contribute to any solution adopted by the state to address wildfire liabilities in a way that benefits consumers. Those contributions could take a variety of forms, including investing in wildfire mitigation and safety or providing funding for other solutions.
- **Require PG&E Meet Conditions to Participate in Changes to the Wildfire Liability Structure for IOUs.** PG&E must meet conditions to participate in any approach to address wildfire liabilities, including fully remaking its corporate and safety culture and prioritizing governance that recognizes the public trust placed in PG&E.
- **Assure That PG&E Meets Its Obligations to Decommission Diablo Canyon.** PG&E must move forward with plans to safely and expeditiously decommission the Diablo Canyon Nuclear Power Plant. Trust funds and other moneys collected by consumers must not be diverted from that effort and additional funds must be provided by PG&E as needed. The state should evaluate the filings in the PG&E bankruptcy proceeding including the plan to assure that such filings require PG&E to meet its obligations with regard to Diablo Canyon.
- **Evaluate the Impact of PG&E Bankruptcy on Clean Energy Goals**. PG&E is party to numerous power purchase agreements that could be impacted by the chapter 11. The state should evaluate the impact of any decisions made by PG&E in its chapter 11 with regard to those agreements in light of California's clean energy goals.
- **Assure Plan is Compliant with Law and Feasible.** The state should evaluate any plan of reorganization to assure that the emerging company will be in compliance with law and that the plan will be feasible.
- **Continue Appropriate Regulatory Oversight.** Although PG&E is in chapter 11, the CPUC also has a substantial say in the future of PG&E (as it does for all IOUs). For example, the CPUC has the power to review PG&E's WMP and its compliance with that plan, as well as to review PG&E's safety culture assessment. The CPUC also has the authority to impose substantial penalties on PG&E for failure to comply with applicable regulations. Moreover, through the rate-setting function, the CPUC may provide incentives for PG&E to make prudent expenditures on, and investments in, safety. This can include actions, such as adjusting the allowed return on equity, that directly affect investors and management. The CPUC should continue to provide appropriate regulatory oversight.

While regrettable, the company's chapter 11 filing offers an opportunity to build a new, responsible, and accountable utility for Northern California.

Given the long history of safety failures and the critical interests at stake, the state can take no options off the table, including municipalization of all or a portion of PG&E's operations; division of PG&E's service territories into smaller, regional markets; refocusing PG&E's operations on transmission and distribution; or reorganization of PG&E as a new company structured to meet its obligations to California..

# Conclusion

Catastrophic wildfires present tremendous challenges for California. The Governor's strike force makes numerous recommendations throughout this report to address those challenges. The strike force recommended immediate next steps are below.

**Figure-11**

| Next Steps | |
|---|---|
| ***Catastrophic Wildfire Prevention and Response*** | ✓ Publicize the Ready, Set, Go app – Wildfire prevention depends on each of us. To help educate property owners and residents in areas most at risk, CALFIRE has developed an app called "Ready, Set, Go!" that breaks down actions needed to be ready for wildfire. CALFIRE should work with leaders in vulnerable communities on outreach and provide technical assistance. Every Californian should download the Ready Set Go App. |
| | ✓ Monitor and assess mitigation efforts – CALFIRE is pursuing a number of aggressive wildfire mitigation efforts, including distributing local community grants for mitigation. Metrics will be developed to measure the effectiveness of these programs and the community reach for local grant recipients. |
| | ✓ Convene Governor's 2019 Emergency Preparedness Summit – The Governor's Office of Emergency Services will, by June 2019, convene first responders, government agencies, local governments, community residents, and technical experts to develop plans for the state's emergency preparedness. The summit will highlight best practices of local communities, share resources that have worked, and develop the networks necessary for ongoing preparedness improvements. |
| | ✓ Prepare for state response to utilities reducing fire risks – Utilities are reportedly considering expanded de-energization of specific areas during high-risk periods to reduce the risk of wildfires. OES and the CPUC will lead an effort to assess utility plans to de-energize and will work with utilities, local governments, first responders, critical providers, businesses and residents to manage the potential of de-energization. |
| | ✓ Implement emergency preparedness campaign and continue to pursue necessary resources for wildfire prevention and response. |
| ***Mitigating Climate Change through Clean Energy Policies*** | ✓ Work with the Legislature, Cal ISO, and the CPUC on a legislative and regulatory agenda to ensure that California simultaneously addresses the impacts of climate change, including increased wildfires, and the root causes of climate change. Such work must include review of emissions from the electricity and transportation sectors. We must plan for a multi-year reform agenda, working in collaboration with the Legislature. |

| | |
|---|---|
| | ✓ Convene academics, private foundations, stakeholders, and government to assist in the development of a multi-year agenda to ensure that California simultaneously addresses the impacts of climate change. |
| ***Fair Allocation of Catastrophic Wildfire Damage*** | ✓ Significant policy development work, legal analysis, and financial simulations have all informed the liability concepts included in the report. However, additional analysis is needed. Request the SB 901 commission to review and analyze major liability concepts presented in report and solicit public comment regarding the different options. |
| | ✓ Direct the Governor's Strike Force to continue its work developing these options for consideration by the Governor and the Legislature by no later than this summer. |
| | ✓ Request the Department of Insurance to monitor, study, and issue recommendations to maintain an accessible and affordable insurance market throughout the state. |
| ***Increasing Capacity of the CPUC with the Tools to Effectively Manage a Changing Utility Market*** | ✓ Focus on building internal CPUC capacity to evaluate and help strengthen the IOU's wildfire mitigation plans immediately. |
| | ✓ Direct the CPUC to immediately assess regulatory and legislative changes to make their proceedings more expeditious. Identify and draft regulations and legislation needed to expedite their administrative proceedings. Such proposals should be reviewed with stakeholders and pursued as soon as possible. |
| ***Holding PG&E Accountable by Building a Utility that Prioritizes Safety*** | ✓ Push for Safety Changes. The CPUC should continue to provide appropriate regulatory oversight on utility safety. The CPUC has the power to review PG&E's wildfire mitigation plan and its compliance with that plan, as well as to review PG&E's safety culture assessment. The CPUC also has the authority to impose substantial penalties on PG&E for failure to comply with applicable regulations. These tools should be actively used to help create the safest utility possible. |
| | ✓ Actively Monitor and Appear in the Bankruptcy Proceedings. The state will actively monitor the PG&E bankruptcy proceedings to assure that California's interests are being protected. Where appropriate and necessary, the state will participate in the bankruptcy proceedings and be heard on particular issues of interest to California, including fair treatment of fire victims and employees, issues relating to safety, and factors affecting the state's progress to achieve climate commitments. |
| | ✓ Require PG&E's investors to contribute to any solution adopted by the state to address wildfire victim claims. Those contributions could take a variety of forms including investing in wildfire mitigation and safety or providing funding for the wildfire fund. |

Wildfires have always plagued California. Climate change has made--and will continue to make--the fires hotter, bigger, more frequent, and more destructive. The costs of these fires is unbearable. The loss of human life, property, economic opportunities, community life, exacerbated by the costs to rebuild communities – cannot be sustained.

Yet, we know we cannot avoid all fire risks. This level of disaster touches every Californian. All Californians must share in the responsibility to mitigate wildfires. Paying for the costs of wildfires is also a problem that requires shared responsibility and shared sacrifice. All stakeholders must come together to address the cumulative liability of uncontrolled fires. The status quo is not an option. Doing nothing is unacceptable.

# Annex A

# Comparison of Wildfire Mitigation Plans

### **Estimated 2019 Costs** ($ in millions)

| PG&E | SCE | SDG&E |
|---|---|---|
| O&M: $849<br>Capital: $1,623<br>**Total: $2,472** | O&M: $507<br>Capital: $1,027<br>**Total: $1,535** | O&M: $24<br>Capital: $178<br>**Total: $202** |

### **Plan Priorities**

| PG&E | SCE | SDG&E |
|---|---|---|
| • Vegetation Management & Enhanced Inspections<br>• Wildfire Response<br>• System Hardening<br>• Situational Monitoring<br>• Operational Practices (*e.g.*, de-energization)<br>• Tech Research / Development | • Ignition Reduction in High-Risk Areas<br>• Fire Suppression<br>• System Hardening<br>• Communication | • Ignition Reduction in High-Risk Areas<br>• Fire Suppression<br>• Wildfire safety and recovery |

### **High-Risk Exposure** (% of Service Territory)

| PG&E | SCE | SDG&E |
|---|---|---|
| 52% | 35% | 54%[55] |

### **System Hardening** (Est. 2019 % of Circuit Miles Hardened in High-Risk Threat District)

| PG&E | SCE | SDG&E |
|---|---|---|
| 0.6% | 0.5% | N/A[56] |

### **Vegetation Management** (Est. 2019 removals / % of total trees)

| PG&E | SCE | SDG&E |
|---|---|---|
| 375,000 trees<br>*(0.375%)* | 7,500 trees<br>*(0.500%)* | 9,000 trees<br>*(1.935%)* |

[55] Percentage of SDG&E's overhead circuit miles that reside in High Fire Threat Districts. Percentage of Service Territory figures were not available.

[56] SDG&E uses an execution metric which expects that 90-100 percent of its system will be hardened by the end of 2019. This includes system miles hardened and percentage of poles replaced

### Weather Stations in High-Risk Threat District

| PG&E | SCE | SDG&E |
|---|---|---|
| 2019 Install: 400<br>*(1.10 per 100 mi²)* | 2019 Install: 315<br>*(1.70 per 100 mi²)* | N/A |
| Cumulative: 600<br>*(1.65 per 100 mi²)* | Cumulative[57]: 440<br>*(2.38 per 100 mi²)* | Cumulative: 175<br>*(6.21 per 100 mi²)* |

### Cameras in High-Risk Threat District

| PG&E | SCE | SDG&E |
|---|---|---|
| 2019 Install: 71<br>*(0.20 per 100 mi²)* | 2019 Install: 62<br>*(0.34 per 100 mi²)* | N/A |
| Cumulative: 79<br>*(0.22 per 100 mi²)* | Cumulative[58]: 160<br>*(0.87 per 100 mi²)* | Cumulative: 107<br>*(3.79 per 100 mi²)* |

### De-Energization

| PG&E | SCE | SDG&E |
|---|---|---|
| • PG&E has implemented the Wildlife Reclosing Disable program to manage circuit breakers if necessary<br>• PG&E targets an increase in its Public Safety Power Shutoff program from ~7,000 mi of lines to ~25,000 mi of lines in 2019 | • SCE has broadly outlined its plans to install additional remote automatic reclosers<br>• SCE will conduct Public Safety Power Shutoffs based on the judgement of the incident management team and has a contingency operating plan in place | • SDG&E has deployed overhead distribution reclosers focusing on High-Risk Threat Districts<br>• To determine whether to employ a Power Shutoff, SDG&E considers multiple variables such as weather conditions, vegetation, field observations, flying debris, expected duration of conditions and location of existing fires/wildfire activity |

[57] Weather stations reflect 2018 + 2019E installations.
[58] Cameras reflect 2018-2020E installations.

# Annex B

# SB 901 Factors

1. The nature and severity of the conduct of the electric grid and its officers, employees, contractors, and other entities with which the electric grid forms a contractual relationship, including systemic corporate defects.

2. Whether the electric grid disregarded indicators of wildfire risk.

3. Whether the electric grid failed to design its assets in a reasonable manner.

4. Whether the electric grid failed to operate its assets in a reasonable manner.

5. Whether the electric grid failed to maintain its assets in a reasonable manner.

6. Whether the electric grid's practices to monitor, predict, and anticipate wildfires, and to operate its facilities in a reasonable manner based on information gained from its monitoring and predicting of wildfires, were reasonable.

7. The extent to which the costs and expenses were in part caused by circumstances beyond the electric grid's control.

8. Whether extreme climate conditions at the location of the wildfire's ignition, including humidity, temperature, or winds occurring during the wildfire, contributed to the fire's ignition or exacerbated the extent of the damages. The electric grid shall provide the CPUC with specific evidence and data demonstrating the impact of climate conditions on the severity of the wildfire.

9. The electric grid's compliance with regulations, laws, CPUC orders, and its wildfire mitigation plans prepared pursuant to Section 8386 of the PUC, including its history of compliance.

10. Official findings of state, local, or federal government offices summarizing statutory, regulatory, or ordinance violations by any actor that contributed to the extent of the damages.

11. Whether the costs and expenses were caused by a single violation or multiple violations of relevant rules.

12. Other factors the CPUC finds necessary to evaluate the reasonableness of the costs and expenses, including factors traditionally relied upon by the CPUC in its decisions.

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# California Firefighters Battle Exhaustion

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August 8, 2018 · 5:19 AM ET
Heard on Morning Edition

Firefighters continue to battle blazes in California. NPR's David Greene talks with Ventura County Fire Captain Steve Kaufmann about how crews are holding up.

DAVID GREENE, HOST:

Wildfires raging here in the state of California have now burned some 600,000 acres. And this includes the so-called Mendocino Complex, which is now officially the largest wildfire in California history. Earlier, I spoke to Steve Kaufmann. He's a fire captain in Ventura County. He joined me from Mendocino County and the community of Ukiah. He told me how people are doing in one of the many shelters in the area that have filled up with hundreds of evacuees.

STEVE KAUFMANN: Some of them, it's been up to a week now. And just, you know, trying to explain why we still have them out of their home and in the evacuation shelter, that's probably the most vivid memory that I have of this fire.

GREENE: Are these families you're talking to - I mean, how are they getting by? Are they getting the food and support they need?

KAUFMANN: They are getting along fairly well. The Red Cross takes very good care of them and provides them, you know, a place to sleep, a shelter, meals. They try to, you know, accommodate most of their needs. In these shelters - not only do they have the

family in the shelters, but a lot of the shelters are accommodating the family pets. And there's a whole variety of family pets that are in the shelters from bunny rabbits to dogs, cats, birds, stuff like that.

GREENE: I guess having your pets around might be one sort of memory of what it's like to be home and give you a sense of being home.

Captain, can I just ask you - I know that in one of these fires in California - the Carr Fire, not the one you're fighting - two firefighters were killed. How much does knowing that loom over the work you're doing?

KAUFMANN: Well, I mean, it definitely affects our firefighters. And we think about that every single day. And even at the camps that we don't have firefighter fatalities at, there are little, you know, memorials that the firefighters will go and sign to send up to the Carr Fire or the Ferguson Fire or any other fire that we have a firefighter fatality. It definitely - yeah, we think about it. And, you know, our families back home think about it. And you can tell when they're calling you, and they're concerned about you. And they want to know, you know, what your status is. And they, you know, want that daily check-in. It's definitely something that we think about. It weighs heavy on our hearts.

GREENE: Who are you checking in with? Who's calling you to make sure you're doing OK out there?

KAUFMANN: Actually, my parents. I make sure I check in with them and let them know when I get there and how things are going. And yeah, they're definitely concerned.

GREENE: The governor of California, Jerry Brown, suggested that this just is going to become a way of life in California, these types of fires. And I know there have been some reports that suicide rates have been going up among firefighters with all of these blazes, with the limited resources. Does that surprise you? And are you feeling pressures that are getting worse in this line of work?

KAUFMANN: You know, I don't know that I personally am feeling pressures. I know that - you know, I've heard those statistics. And I know that we're, you know, really trying to reach out. And the firefighter community is a tight-knit community. And one of the things - I don't like speaking on behalf of other people very often, but one of the things I do feel comfortable telling you is that for firefighters, this isn't a job for us. This is truly a passion or a calling. And so we take what we do every single day very seriously. And so when I go up to a community like this - there's going to be 3,900 firefighters on the Mendocino Complex. For all intents and purposes, we're the Mendocino and Lake County firefighters as long as we're here.

GREENE: Steve Kaufmann is a fire captain in Ventura County. But as he says, he feels like he's part of the fire community where he is fighting now in Mendocino County.

Captain Kaufmann, thank you so much.

KAUFMANN: Thank you, David.

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# Best Management Practices for Mitigating the Effects of Roads on Amphibian and Reptile Species at Risk in Ontario

April 2016

Written by Kari Gunson, David Seburn, Julia Kintsch and Joe Crowley

ontario.ca/speciesatrisk

Ontario

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Cover photo provided by Joe Crowley

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# 1 INTRODUCTION

## 1.1 Purpose

The purpose of the Ontario Ministry of Natural Resources and Forestry (OMNRF) Best Management Practices for Mitigating the Effects of Roads on Amphibian and Reptile Species at Risk in Ontario (hereafter referred to as the best management practice (BMP) document) is to provide information on designing, implementing and monitoring mitigation measures to restore connectivity and reduce road mortality for species at risk (SAR) amphibians and reptiles. This information will assist in providing information on mitigation planning for amphibians and reptiles at risk in Ontario in order to meet the requirements of the *Endangered Species Act, 2007* (ESA) or its associated regulations. The intended audience includes planning authorities (local or provincial government), individuals applying ESA requirements on the landscape, consultants working on their behalf and conservation organizations involved in the planning and design of impact mitigation for all new roads and road rehabilitation (improvement) projects.

The focus of this BMP document is on crossing structures and fencing. While there is no singular solution for mitigating road effects on amphibians and reptiles, this document offers information for developing site-specific mitigation based on best practices and findings from current peer-reviewed and grey literature (e.g., websites and conference proceedings), government documents, academic theses and personal communication surveys with experts in road ecology and other areas of relevance (e.g., engineering, species biology). When knowledge gaps were identified, the recommendations are based on the best available information and expert opinion, as well as logical interpretation from species-specific needs and life-history traits.

This document presents current information as of the date of publication and is meant to be updated through time as improved information becomes available. If you are interested in providing pertinent information for consideration in updates of this document, please email esapermits@ontario.ca.

## 1.2 Endangered Species Act, 2007 (ESA)

The ESA provides the legislative framework for the protection of species at risk in Ontario. Section 9 of the ESA includes prohibitions against activities such as killing, harming, harassing, capturing or taking a living member of a species that is listed as extirpated, endangered or threatened on the Species at Risk in Ontario (SARO) List. Section 10 of the ESA includes prohibitions against damage or destruction of the habitat of an endangered or threatened species.

The ESA contains provisions that enable the Minister to issue permits and enter into agreements to authorize activities that would otherwise be prohibited and Ontario Regulation 242/08 sets out conditional exemptions from prohibitions under the Act for certain activities. For additional information, visit the government website or read the full text of the legislation on e-Laws using the links provided below.

How species at risk are protected:
https://www.ontario.ca/page/how-species-risk-are-protected

Endangered Species Act, 2007 on e-Laws:
http://www.ontario.ca/laws/statute/07e06

Ontario Regulation 242/08 on e-Laws:
http://www.ontario.ca/laws/regulation/080242

## 1.3 Document Outline

This document is organized into the following sections:

**Section 1 (Introduction)** provides background information on the threats of roads to amphibian and reptile species and the overall objectives of the document.

**Section 2 (The Impacts of Roads)** details background information on the impacts of roads on amphibians and reptiles and the need for road mitigation measures.

**Section 3 (Mitigation Planning)** provides information about considerations for developing a mitigation plan in a landscape context within project planning processes.

**Section 4 (Road Mitigation BMPs)** addresses design variations and applications of three crossing systems for amphibians and reptiles, in addition to detailed considerations for siting, designing, enhancing and maintaining crossing structure and fencing systems.

**Section 5 (Supplementary Measures)** provides recommendations about using mitigation measures other than crossing structures and fencing systems to reduce road impacts on amphibians and reptiles. These measures may be used when crossing structures are not required, or as a complement to an effective mitigation plan.

**Section 6 (Temporary Mitigation During Road Construction)** provides considerations for reducing impacts from construction activities, including timing construction activities to avoid construction-related impacts, and considerations regarding the use of temporary mitigation measures to minimize impacts during construction.

**Section 7 (Monitoring)** highlights where there are knowledge gaps about effectiveness of mitigation measures for reducing road impacts on amphibians and reptiles. Study design and monitoring techniques for measuring crossing structure and fencing effectiveness, in an adaptive approach, are discussed.

## References

**Appendix A (SAR Amphibian and Reptile Habitat Use and Movement)** provides a general summary of seasonal habitat use, general movement distances within and between habitat and when this occurs for species at risk amphibians and reptiles in Ontario.

**Appendix B (Definitions)** provides a glossary of terms used throughout the document.

**Appendix C (Crossing Structure Summary from Literature)** summarizes the findings from the literature-based review that informed the recommendations throughout the document.

**Appendix D (Links and Other Resources)** contains a list of useful references, which may be cross-referenced when developing a mitigation plan for SAR amphibians and reptiles.

**Appendix E (Sample Tunnel Cost Table (2014)** contains the cost per metre for round and box tunnels, as well as special installation considerations.

## 2 IMPACTS OF ROADS

Globally, there are significantly more amphibian and reptile species at risk than either mammals or birds (IUCN 2010). Amphibians and reptiles were the most negatively affected species groups in a meta-analysis using data from 75 studies that quantitatively measured the relationship between roads or traffic and population size (Rytwinski and Fahrig 2012). The threats of roads to amphibian and reptile populations in Ontario are well-documented, and primarily include direct mortality of animals as well as habitat loss, degradation and fragmentation (e.g., Fahrig et al. 1995, Ashley and Robinson 1996, Findlay and Houlahan 1997, Vos and Chardon 1998, Haxton 2000, MacKinnon et al. 2005, Crowley 2006, Seburn 2007, Eigenbrod et al. 2008a, Eberhardt et al. 2013).

In southern Ontario the network of major roads increased from 7000 km to over 35 000 km from 1935 to 1995 (Fenech et al. 2001). Consequently, there is no point in southern Ontario that is further than 1.5 km from a road (Gunson et al. 2012), and remaining natural habitat is isolated into patches. In addition, human population growth is projected to increase by at least 30% over the next 20 years in the Greater Golden Horseshoe, increasing traffic volume and pressure for road expansions and rehabilitation. With properly planned and implemented road ecology solutions, these impacts can be lessened across Ontario.

Monitoring has documented significant levels of road mortality (van Gelder 1973, Rosen and Lowe 1994, Ashley and Robinson 1996, Aresco 2005) and road barrier effects (Andrews and Gibbons 2005) for amphibians and reptiles. Snakes are particularly vulnerable to road mortality because some species immobilize in response to a passing vehicle (Andrews and Gibbons 2005), or may bask on the roadway for thermoregulation (Andrews et al. 2008). Snakes may also avoid crossing roads altogether, which may disrupt normal behaviours, prevent access to key habitats, and lead to reduced genetic diversity (Shine et al. 2004, Rouse et al. 2011, Robson and Blouin-Demers 2013). Road mortality of more than three adult females per year can lead to declines for some long-lived snake populations such as the Gray Ratsnake (Row et al. 2007).

Modelling studies suggest that populations of many turtle species are declining because of the high rates of annual traffic mortality in some areas (Gibbs and Shriver 2002). Turtles are particularly vulnerable to traffic mortality because their life history strategy is characterized by long life spans, delayed maturity (sometimes taking more than 20 years), and very high adult survivorship. As a result even small, but ongoing, increases in adult mortality can lead to population declines (Congdon et al. 1993) and recovery is slow (Brooks et al. 1991). Females are threatened by traffic mortality because of overland movements to nesting areas (Steen et al. 2012) and populations of some species have been found to be male-biased in wetlands in areas with high road density (Marchand and Litvaitis 2004, Steen and Gibbs 2004).

Amphibians are subject to road mortality when migrating to wetland breeding sites and this can range from 19% (Gibbs and Shriver, 2005) to as high as 98% (Hels and Buchwald, 2001) depending on traffic volumes (Bouchard et al. 2009). Road mortality of just 10% of the adult population can lead to population extinctions (Gibbs and Shriver, 2005), resulting in lower species richness and abundance of individuals near roads (e.g., Carr and Fahrig, 2001; Eigenbrod et al., 2008). In addition, Karraker and Gibbs (2011) found road mortality reduced the life expectancy of Spotted Salamanders (*Ambystoma maculatum*) next to roads, and

because younger salamanders lay smaller egg masses this also reduced reproductive output. In addition to road mortality, roads also inhibit movements of amphibians (deMaynadier and Hunter 2000) which can potentially restrict gene flow (Marsh et al. 2008).

# 3 MITIGATION PLANNING

## 3.1. Project-Level Impact Avoidance and Mitigation

Project planning and design for roads is a stepwise process that begins with defining the study area for new road construction or other major road rehabilitation projects. Meese et al. (2009) identifies the potential impacts of different types of road projects on wildlife species in general (Table 1). The list of project types is not meant to be exhaustive but rather to include major road improvements and rehabilitations within the scope of this document. There are other impacts to SAR during road operations and maintenance activities such as shoulder grading and paving that are not covered in this document. Projects should be designed to avoid impacts whenever possible, and this is best achieved by locating roads to avoid species at risk habitat altogether. When impacts are unavoidable, appropriate authorizations need to be obtained and the necessary mitigation measures incorporated into the project design.

## 3.2 Project Planning Considerations and Sources of Information

The information in this document outlines considerations for devising and integrating a mitigation plan into the road planning process in situations when avoidance cannot be achieved. New roads or road improvements present opportunities to lessen the impacts on SAR by integrating mitigation measures. These mitigation measures include specialized tunnels for wildlife passage as well as modifying or retrofitting existing drainage crossings for both water and wildlife use.

**Table 1: A summary of project types during road improvement and rehabilitation activities, and potential impacts on amphibians and reptiles (adapted from Meese et al. 2009).**

| Road Activity | Project Type | Impacts on SAR |
|---|---|---|
| Road improvement | New road alignment or extension | Bisection of existing habitat and movement routes; genetic isolation of populations; road mortality; habitat loss |
| Road improvement | Road widening | Increased traffic volumes and road width increase risk of road mortality (Gibbs and Shriver 2002); habitat loss |
| Road improvements | Creation of median and installation of shoulder barriers | Increased barriers and road corridor width increase risk of road mortality |
| Road rehabilitation | Culvert or bridge improvements | May provide opportunities or barriers to movement, depending on resulting permeability of structure (Kintsch and Cramer 2011); risk of destroying turtle nests if work is carried out during the nesting period |
| Road rehabilitation | Improved road pavements | Increased risk of road mortality and disturbance of animals |

Implementation of the mitigation plan begins during the construction phase, and particular attention to design details is important for amphibians and reptiles. It is important for all individuals involved in construction projects, including road crews, to be aware of the mitigation measures to be implemented for the project. Oversight by individuals with the greatest understanding of the mitigation measures is imperative to ensure that effective road mitigation solutions are implemented. For example, a fence with a gap or a fence buried improperly can render the mitigation measures ineffective. Quality assurance and adherence to the mitigation specifications needs to be practiced for each project. Routine quality checks to ensure that implementation of mitigation measures is not misinterpreted during construction, and routine maintenance of mitigation measures following construction is required.

Compiling field and geographic information system (GIS) data can support the development of an effective mitigation plan. Standard data compilations include species occurrence data obtained from the MNRF or other sources; these data are best

supplemented with additional road survey data and species presence data collected in the project study area using standard survey techniques (see section 7.2.1). In the case of larger road projects, the duration of the environmental assessment (EA) process can last up to ten years, especially if there are time lapses between the preliminary assessment, detail design and construction. This provides opportunities for formal data collection within the project study area that can inform both mitigation planning and assessments of the effectiveness of mitigation.

Georeferenced data that may be available to support project planning and design may include the following:

- Existing and future land use and ownership maps,
- Habitat mapping (e.g., Southern Ontario Land Resource Information System, or Ecological Land Classifications),
- Species at risk occurrence information (Natural Heritage Information Centre),
- Terrain features,
- Natural Heritage Systems, and
- Existing and future road network and other infrastructure (i.e., existing barriers or passageways, including culverts, median and shoulder barriers, and adjacent railroads, local or private roads).

## 3.3 Recommended Process

The recommended steps for developing a comprehensive mitigation plan for SAR amphibians and reptiles are outlined in Figure 1 and described below.

**Step 1:** Identify and prioritize sections of roads that will impede connectivity and/or pose mortality risk to amphibians and reptiles using field data collections and additional landscape information (see section 3.4). Defined road impacts and objectives for mitigation will provide the content and scope of the mitigation plan.

**Step 2:** Design and determine the location of mitigation measures such as crossing structures and fencing by combining ecological data (e.g., species, habitat and landscape information) with engineering data (e.g., geomorphological, hydrological and topographical). This step requires collaboration between the ecological and engineering design team to ensure fluid integration of information into the mitigation plan. For a road rehabilitation project, there may be opportunities to retrofit existing infrastructure. Through careful evaluation, existing bridges and drainage culverts may be used or adapted for amphibians and reptiles (see section 4.1.4).

**Step 3:** Consider a multi-species perspective to ensure that a strategy for an individual species does not create unintended impacts for other wildlife species. Supplementary measures such as warning signs at fence ends may complement a multi-species strategy (see section 5).

**Step 4:** Identify temporary mitigation measures. This could include carrying out road construction when animals are not active, timing construction at particular road sections when animal activity is minimal (see section 6.1) and installing temporary mitigation measures (see section 6.2).

**Step 5:** Develop a monitoring plan for evaluating the effectiveness of the mitigation. Refer to section 7 for information on developing a complete monitoring plan that addresses the uncertainty with respect to mitigation design.

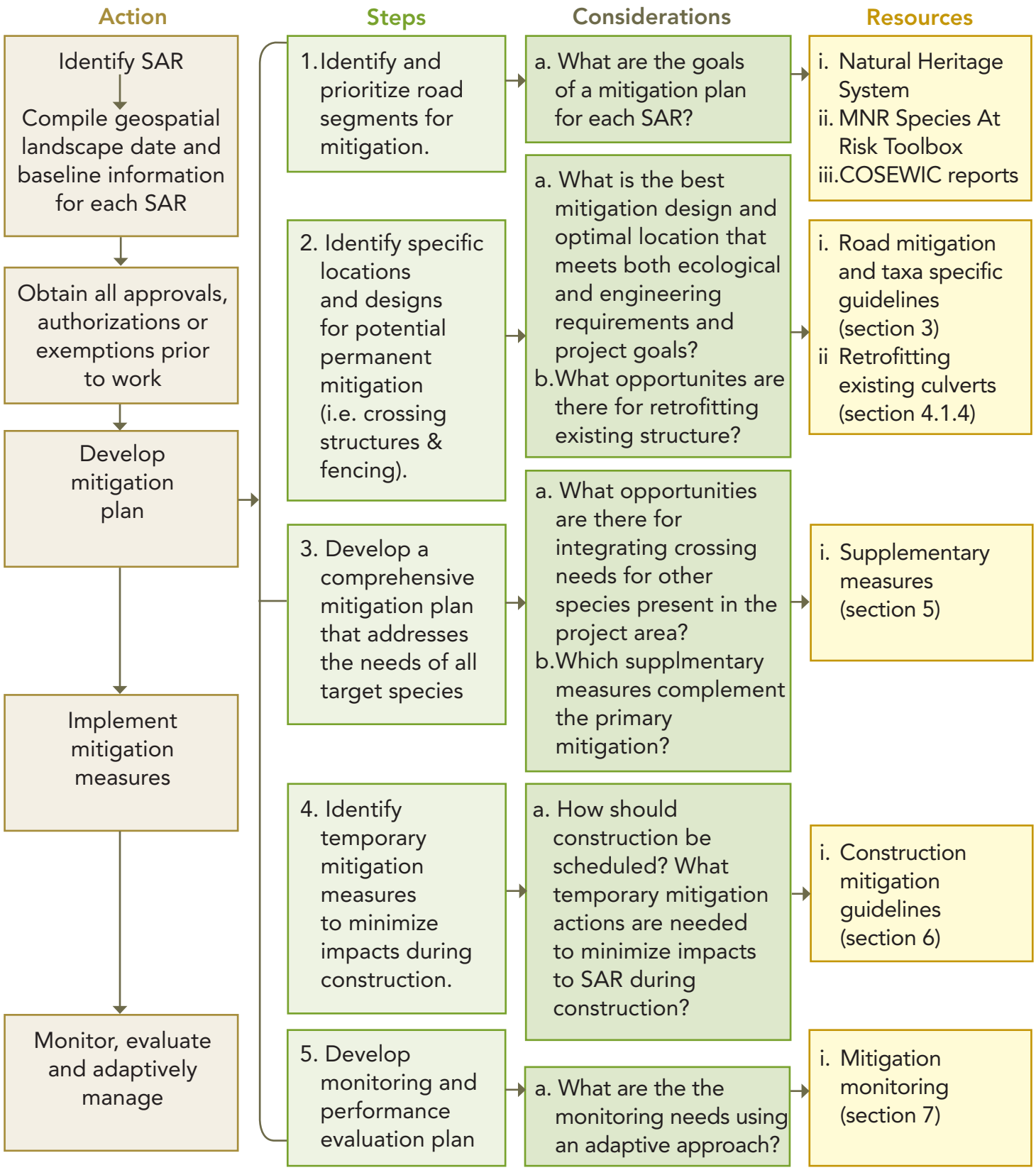


Figure 1: Flowchart summarizing the development of a mitigation plan (individual steps, considerations and supporting resources) within the established authorization processes for major road activities.

## 3.4 Landscape Considerations

Consideration of the larger landscape context is a vital component of effective mitigation planning for transportation projects because amphibians and reptiles require protection from adverse impacts at both the local and landscape scales (Semlitsch 2008). In other words, animals need to move within habitat patches to access resources (local scale), but also between habitats at different times of year, when habitat becomes inhospitable or to maintain genetic interchange (regional metapopulation scale).

In Ontario, natural heritage systems (NHS) have been developed at a variety of scales. Some are local in scale, while others span multiple jurisdictions, such as the systems in the Greenbelt Plan which span multiple regional municipalities. Natural heritage systems will often include a variety of habitat types including important amphibian and reptile habitat. The natural heritage system identified in the Greenbelt Plan 2005 is an example of a landscape level system approach to cores and linkages for natural heritage conservation. NHS can connect important natural heritage features and areas used by amphibians and reptiles, such as wetlands and upland habitat. Applicable conservation planning efforts, such as NHS, can be refined with taxa specific models for amphibians and reptiles (Gunson et al. 2012) and identified SAR habitat. This information can be used to identify where roads will pose the highest risk for road mortality and isolation of habitat, and should be integrated into early phases of mitigation plan development.

Consideration of the broader landscape context is required because impacts to wildlife are rarely caused by transportation alone (Clevenger 2012). The following landscape level considerations will contribute to the development of a comprehensive mitigation plan:

- Identifying the location of SAR populations and their habitat, including seasonal habitat usage and movement routes (described in Appendix A);
- Identifying connectivity at a regional scale that integrates an ecosystem approach (e.g., natural heritage systems);
- Understanding adjacent land security (i.e., the condition and ownership of land adjacent to a project, and the potential for land-use change); and
- Coordination with other jurisdictions (e.g., municipalities and conservation authorities that own adjacent infrastructure and land).

# 4 ROAD MITIGATION BMPS

This section provides a summary of BMPs specific to crossing structures and fencing (see sections 4.1 and 4.2). The focus is on the best structural design for all amphibians and reptiles, with species-specific considerations noted when relevant. Following these BMPs, taxa specific (turtles, snakes and lizards, salamanders, frogs and toads; see section 4.1.5) considerations are summarized and supplemented with a rationale section based on a comprehensive literature review. All BMPs are further illustrated and supported with relevant examples, photos, references, and caveats specified throughout. Although SAR amphibians and reptiles found in Ontario are the focus for this document, information also derives from research on related species in other regions for each taxa. This document provides the minimum recommended design specifications (e.g., height, length and width for crossing tunnels and fencing) based on the best available information. All mitigation plans will be subject to trade-offs as presented by engineering, budget, public safety, and site specific constraints.

To date, crossing structures (see section 4.1) combined with fencing (see section 4.2) offer the most effective mitigation of road impacts for amphibians and reptiles by facilitating landscape connectivity and reducing road mortality by excluding animals from the road (Dodd et al. 2004, Aresco 2005). Crossing structures and fencing integrated into road improvement and rehabilitation projects provide the greatest opportunity for creating functional passages, although, in some cases, existing structures may be retrofitted to facilitate wildlife passage (see section 4.1.4). The recommendations herein focus primarily on crossing structure tunnels less than 3 m wide because these structures are typically used for amphibians and reptiles and are available as precast or prefabricated structures. When a tunnel exceeds 25 m in length, a larger structure such as an overpass, multi-span bridge, or viaduct should be considered (see section 4.1.1). Larger structures can be integrated into a multi-species design strategy to increase effectiveness for both large and small species. Multi-species considerations are provided in this document, in addition to approaches for combining mitigation measures to achieve an overall mitigation plan.

## 4.1. Crossing Structures

Crossing structures can play an integral role in mitigating the impacts of roads on SAR amphibian and reptiles in Ontario. Recommendations regarding the use of different types of crossing structures, design considerations, location and spacing of crossing structures and taxa specific guidelines are provided. The retrofitting of existing drainage culverts and associated considerations are also covered.

In this document, the term tunnel is used to differentiate between crossing structures intended for amphibian and reptile use as opposed to culverts that are designed to transport water under the road. Box tunnels with natural substrate, arch tunnels and round tunnels buried 0.3-0.4 m into the ground are the primary recommended tunnel types because they meet essential criteria, such as providing natural substrate bottoms and a flat crossing surface.

### 4.1.1 Types of Crossing Structures for Amphibians and Reptilesa

<table>
<tr><th colspan="2">BOX TUNNEL</th></tr>
<tr><td colspan="2">
<ul>
<li>Traditionally used for drainage, but also increasingly being placed and modified specifically for amphibian and reptile passage.</li>
<li>Tunnels up to 3 m wide or high typically made from precast concrete (Photo 1).</li>
<li>Maximum recommended tunnel length of 25 m.</li>
<li>Variations include open-top (Photo 2) or open-grate (Photo 3), open-bottom (Photos 4) or variations of these (Photos 5 - 7).</li>
<li>Straight walls may be perceived by target species as increased openness.</li>
<li>Provide more cross sectional area or openness than round or elliptical culverts with the same width.</li>
</ul>
</td></tr>
<tr><td rowspan="2">STRUCTURAL VARIATIONS</td><td>OPEN-TOP<ul><li>Achieved with slots or grooves along the top (Photo 2), or open-grate set upon two concrete footings (Photo 5).</li><li>Allows for more consistent ambient conditions, including moisture, light and temperature (Photo 8).</li><li>Possible concerns with influx of road debris, pollutants, or traffic noise.</li><li>Installation at a downward incline from middle of road to road edge to allow for drainage and natural cleaning of the tunnel.</li></ul></td></tr>
<tr><td>OPEN-BOTTOM<ul><li>Three-sided structures (Photo 4).</li><li>Allows natural substrate conditions to be retained (e.g., streambed or grass floor) (Photo 9).</li></ul></td></tr>
<tr><td>APPLICATION</td><td><ul><li>A smaller sized open-top tunnel may increase crossing success or provide microhabitat conditions equivalent to the openness created by larger tunnels.</li><li>Open-top grate tunnels have previously been used on low-use cottage roads or roads in protected areas (e.g., Wild Rice Trail, Algonquin Provincial Park, Killbear Provincial Park (Photos 5 and 6)).</li><li>For divided highways with two structures that end in the median, tunnels should be connected with a fence (Photo 10).</li><li>Headwalls may be used at entrance to shorten length of structure or for a seamless join to a concrete guide wall (Photo 11).</li><li>For box culverts, the tunnel floor should be buried with natural substrate and cover objects (Photos 12 and 13).</li><li>An open-top in the road shoulder and a closed-top along the road pavement may be more suitable for high volume roads (Photo 7).</li></ul></td></tr>
</table>

| BOX TUNNEL | |
|---|---|
| **ENGINEERING CONSIDERATIONS** | • Open-top tunnels must be at grade with road surface.<br>• Design variations may require special design drawings if not prefabricated.<br>• Size of tunnel must fit within the vertical road profile so that top load is adequate for structural stability. |
| **MAINTENANCE CONSIDERATIONS** | • Smaller tunnels will be more difficult to keep clear of debris.<br>• Open-top tunnels may have to be periodically flushed with water (e.g., with a fire hose) to clean build-up of road pollutants.<br>• Larger structures allow better maintenance accessibility while having relatively minor cost increases relative to cost of road project.<br>• Open-top tunnels are thought to interfere with snow removal; however, this has not been the case in other tunnel installations in cold countries and the top of the tunnel wears away with the road surface (see review in Langton 2014).<br>• Natural substrate and other cover objects must be maintained. |
| **COST (relative material comparison in 2014)** | • Costs/m vary from CAN $800.00 for prefabricated open-top ACO tunnel (0.5 m x 0.5 m) to CAN $3,000 for enclosed box tunnel (1.8 m x 1.8 m). |

Photo 1. Precast box culvert along highway 69, Ontario. © K. Gunson

Photo 2. Open-top tunnel in Waterton Lakes National Park, Alberta. © K. Gunson

## BOX TUNNEL

Photo 3. Open-grate tunnel at Killbear Provincial Park, Ontario. © K. Gunson

Photo 4. Open-bottom tunnel along highway 69, Ontario. © K. Gunson

Photo 5. Open-bottom and open-top grate tunnel at Killbear Provincial Park, Ontario. © K. Gunson

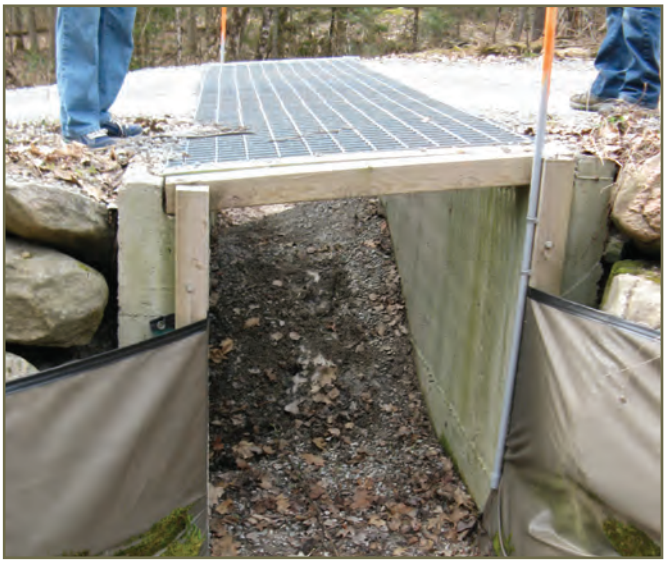

Photo 6 Open-top and open-bottom at Wild Rice Trail, Six Mile Lake. © K. Gunson

## BOX TUNNEL

Photo 7. Open- and closed-top variation, Germany. © ACO International

Photo 8. ACO open-top tunnel allowing light into tunnel. © Kari Gunson

Photo 9. Open-bottom box tunnel with natural stream on Trans Canada Highway in Banff National Park, Alberta. © K. Gunson

Photo 10. Box tunnels in median that should be connected with a fence when intended for wildlife passage. © K. Gunson

## BOX TUNNEL

Photo 11. Tunnel with headwalls connected to concrete guide fencing in Cuba. © G. Barrett

Photo 12. Adding soil to box tunnel near Ucluelet, B.C. © Barb Beasely

Photo 13. Soil and branches inside tunnel bottom, Ucluelet, B.C. ©Barb Beasley

| ARCH/ROUND TUNNEL | |
|---|---|
| • Arch tunnels have natural bottoms (Photos 14 and 15) and are recommended for tunnels greater than or equal to 1.5 m diameter (common widths 1.8, 2.4 and 3.0 m).<br>• Round tunnels work well in aquatic conditions for turtles and semi-aquatic snakes.<br>• In terrestrial conditions, round tunnels should be filled 0.3-0.4 m with local soil/debris to create a level crossing surface, and it is recommended that the size be increased from the minimum recommendations in section 4.1.5 to compensate for this area that is lost due to infilling.<br>• Maximum recommended tunnel length of 25 m.<br>• Terrestrial pathways alongside stream or creek bed are possible with additional structural width.<br>• Recommended design specifications for arch tunnels are slightly larger than box tunnels to compensate for the loss of openness as a result of tunnel shape. | |
| **STRUCTURAL VARIATIONS** | **OPEN-TOP**<br>• Slotted open-top (Photos 16 and 17) or vertical skylight risers along the length of the tunnel to provide natural light. |
| | **OPEN-BOTTOM**<br>• Achieved by burying round tunnels (0.3 to 0.4 m) to accommodate natural terrestrial floor (Photo 18). |
| **APPLICATION** | • Arch structure may be preassembled and dropped in place or assembled at site (Photo 19).<br>• Corrugated steel arch or concrete side slabs are placed on footings (Photo 15). |
| **ENGINEERING CONSIDERATIONS** | • Footings required for arch tunnels.<br>• Buried tunnels may be more suitable when tall footings are required. |
| **MAINTENANCE CONSIDERATIONS** | • Larger structures allow better maintenance accessibility while having minor cost increases relative to cost of road project.<br>• Natural substrate and other cover objects must be maintained. |
| **COST (relative material comparison in 2014)** | • Costs/m vary from CAN $145.00 for corrugated steel pipe (CSP) (1.2 m) to CAN $990.00 for arch (0.6 m rise; 1.22 m span).<br>• Costs/m vary from CAN $500.00 for CSP (3.0 m) to $1500.00 for arch (1.45 m rise; 2.99 m span). |

## ARCH/ROUND TUNNEL

Photo 14. Arched tunnel allowing natural stream crossing. © D. Seburn

Photo 15. Aluminum arch culvert on metal footings. © K. Williams

Photo 16. Pipe culvert with slotted top installed for Timber Rattlesnakes in Illinois, U.S. © S. Ballard

Photo 17. Zoom-in of open-top pipe culvert at road for Timber Rattlesnakes in Illinois, U.S. © S. Ballard

Photo 18. Buried plastic round culvert allowing terrestrial flat floor in Sweden © K. Gunson

Photo 19. Arch culvert preassembled off site © K. Williams

## LARGE UNDERPASS OR WILDLIFE OVERPASS

- Larger multi-species crossing structures greater than 3 m wide such as tunnels (Photo 20) and bridges, viaducts or overpasses (Photo 21) that are generally not prefabricated or precast.
- Possible to maintain natural landscape if road is tunneled, (e.g., Herb Gray Parkway in Windsor) or elevated (e.g., viaduct).
- Consider when tunnel length will exceed 25 m.
- Integrated as a multi-species strategy for both large and smaller animals.

| | |
|---|---|
| **STRUCTURAL VARIATIONS** | **UNDERPASS**<br>• Designs include crossing structures that are below grade (e.g., tunnel, single or multi-span bridge, arches, and viaducts).<br>• Larger multi-span bridge, arches and viaducts have opportunity to maintain natural ecosystem and physical properties.<br>Allows for the integration of dry pathways at creek and river crossings.<br>• Two structures that open in median allow more openness (Photo 22). |
| | **OVERPASS**<br>• Design includes bridge deck spanning over road.<br>• Requires natural landscape planting strategy and drainage system on top of structure.<br>• Slope on approach ramps should be minimized for greatest visibility.<br>• Overpass width has varied from 20 m to > 70 m. |
| **APPLICATION** | • Large structures provide greater opportunity to provide cover objects such as flat rocks, vegetated mounds composed of branches and logs and covered with sod, or rock piles (Photos 23 and 24).<br>• Design enhancements for amphibians and reptiles include small ponds as 'stepping-stones' along or through the length of a structure. Natural or artificial substrate may be used to retain pond water or natural rainfall (Van der Grift et al. 2003; Figure 2).<br>• For multi-use structures, wildlife and human use should be separated or human use should be mitigated. For example, the Rt. Hon. Herb Gray Parkway, which leads to the international crossing between Ontario and Michigan, incorporates a crossing structure for Butler's Gartersnake and Eastern Foxsnake into the multi-use trail system to minimize disturbance impacts from recreational trail users.<br>• Multi-species fencing designs should be used. For example, the Highway 69 fencing combines ¼ inch mesh with 2.4 m high, large animal mesh fence (Photo 25). |

| LARGE UNDERPASS OR WILDLIFE OVERPASS | |
|---|---|
| **ENGINEERING CONSIDERATIONS** | • Overpass decks can integrate natural footings such as rock cliffs (Photo 26).<br>• Engineering measurements and road design will determine best options for large crossing structure type in the road. |
| **MAINTENANCE CONSIDERATIONS** | • Require maintenance checks for initial establishment of vegetation on overpass structures; may require irrigation for pools and vegetation. |
| **COST (relative material comparison in 2014)** | • Approximately CAN $7,800 for large concrete box culvert (2.8 m x 3.3 m, Appendix E); range from CAN $2-4 million for installation, design, and materials of wildlife overpass. |

## LARGE UNDERPASS OR WILDLIFE OVERPASS

Photo 20. 3.4 x 2.4 m concrete box culvert connecting wetland habitat used by turtles on highway 69. © K. Gunson

Photo 21. 30 m wide overpass installed near Sudbury on highway 69. © K. Gunson

## LARGE UNDERPASS OR WILDLIFE OVERPASS

Photo 22. 3.4 m x 2.4 m tunnel on Highway 69. © K. Gunson

Photo 23. Brush piles on top of overpass on highway 69. © K. Gunson

Photo 24. Rock and wood piles on top of overpass in Brandenburg, Germany. © K. Gunson

Photo 25. Small animal fence attached to the base of large animal barrier fence. © K. Gunson

Photo 26. Wildlife overpass on highway 69 showing rock footing K. Gunson.

## LARGE UNDERPASS OR WILDLIFE OVERPASS

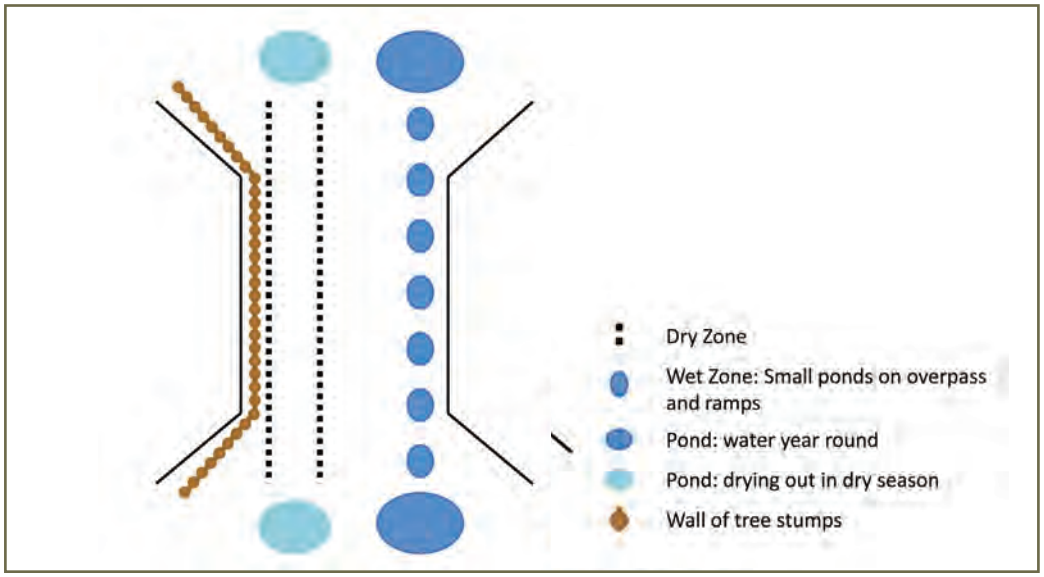


**Figure 2:** Example of a series of pools created along one side of an overpass (50 m long x 65 m wide). Amphibian passage was at least 1.5 times higher through the wetland zone than the dry zone. Adapted from van der Grift et al. 2009

### 4.1.2 Crossing Structure Design

Design of effective crossing structures must account for the ecology, behaviour and movement patterns of amphibians and reptiles. For example, amphibians and reptiles possess a number of physiological vulnerabilities that require particular microhabitat conditions when using tunnels to cross roads (Andrews et al. 2008). High skin permeability and vulnerability to water loss necessitates warm and damp conditions in tunnels for amphibians. These microhabitat specializations require additional design modifications (e.g., natural substrate, cover) in and near crossing structures. General recommendations based on the literature and expert opinion for tunnel design (<3 m wide), to facilitate amphibian and reptile use, are outlined below:

**Design Specifications**

- Refer to minimum design specifications and tunnel types summarized in structural (see section 4.1.1) and taxa recommendations (see section 4.1.5) for each species group; where existing culverts are being replaced, upsize tunnels to at least minimum design specifications and tunnel type.
- Tunnels should be as open as possible to maximize air flow and light inside the tunnel. This may be achieved by designing tunnels with larger (typically wider) openings, using two structures connected with fencing when a median is present (Photo 22), or with an open-top or partial open-top tunnel (Photos 2 and 7).
- Artificial and ambient lighting inside a culvert has been shown to encourage tunnel use by turtles (Yorks et al. 2011) and entry by salamanders (Jackson et al. 2006).
- Generally, larger tunnel dimensions are more effective for amphibians and reptiles. For example, Smith (2003) showed amphibians and reptiles in Florida used tunnels more often that were at least 1.5 m wide and 0.6 m high as compared to smaller tunnels. See section 4.1.5 for additional information on tunnel dimensions for each taxa group.

- In general, the recommended tunnel length for SAR amphibians and reptiles is less than 25 m. There is reduced crossing success as tunnels get longer (e.g.,Yorks et al. 2011) and other jurisdictions suggest tunnels are less effective beyond 20-25 m in length (e.g., British Columbia Ministry of Forests, Lands and Natural Resource Operations 2004).
- In locations where tunnels will be longer than 25 m, consider the following:
- A large underpass (> 3 m) or overpass
- Elevating or tunneling the road
- Using two separate, shorter tunnels under each of the opposing traffic lanes with head walls; ensure the tunnels are connected with appropriate fencing in the median (Photo 22).
- On divided highways, crossing structures should never end in the center median (Photo 27) unless they are connected to other structures through fencing.
- When possible include skylights, or fenced gaps at medians and shoulders (Photos 28 and 29).

**Microhabitat and Cover:**

- All terrestrial crossings should have a natural substrate that consists of soil, sand, branches and other natural materials on the tunnel floor to increase structure use (Photos 13 and 35). The use of local soil in crossing structures is widely recommended for amphibians (e.g., Jackson 2003, Smith 2003, Schmidt and Zumbach 2008, Amphibian and Reptile Conservation 2009, Beasley 2013). For example, salamanders will cross through tunnels with or without natural substrate, but fewer individuals cross through bare concrete tunnels (Patrick et al. 2010). Considerations for substrates:
- Soils should be from the local area
- Soils that consist of large stones should be avoided
- Sediment baffles such as open plate may be used to 'hold' natural substrate in place (Photo 36).
- Cover objects (flat rocks and/or woody debris) should be placed in larger tunnels along the sides to provide shelter and escape from predators. These cover objects should not block sightlines or impede individuals from crossing straight through the tunnel. Sufficient cover objects (1 large or 2-3 small per 10 $m^2$) should be present near the entrances to all terrestrial crossing structures to provide shelter and cover. Cover objects should be used for all crossing structures to encourage multi-species use. Retain as much natural vegetation as possible during construction; where needed, additional planting should occur after construction.

**Other Design Considerations:**

- Terrestrial tunnels should be as level as possible for the entire length of the structure. One exception to this is that open-top tunnels should be installed with the highest point in the middle of the tunnel to allow for drainage and natural cleaning of the tunnel.
- Tunnel entrance bottoms should be at ground-level so animals do not need to 'step up' or 'step down' to enter the structure (Photo 30).
- At terrestrial tunnels, water should be diverted away from the entrances with drainage ditches or sloped excavation (Photo 31).
- If culverts are intended for drainage, or tunnels are large enough, a dry bench placed above the water mark can be integrated into the tunnel, in which case the bench must access dry ground at both entrances to be effective (Photo 32).
- When new highway alignments will bisect provincially significant wetlands and SAR habitat, consider elevating or tunneling the

road (e.g., Rt. Hon. Herb Gray Parkway road mitigation project for Butler's Gartersnake and Eastern Foxsnake).

- When arch tunnels are used at road-stream crossings, terrestrial pathways can be created along the stream by using wider tunnels (Photo 14). This design can better accommodate seasonal high water and flooding events (Lesbarrères and Fahrig 2012).
- When dealing with multi-species issues and variable site conditions, a mixed array of structure types and sizes should be provided along the site (see section 4.1). Structural diversity can compensate for landscape variations, such as land use change, and can also provide an experimental setting to test species-specific crossing preferences (see section 7).

Photo 27. Drainage box tunnel left open in median along highway 69 © K. Gunson

Photo 28. Open grate skylight in median on Terry Fox Extension, Ottawa, Ontario. © D. Seburn

Photo 29. Zoom-in of skylight in median on Terry Fox Extension, Ottawa, Ontario. © D. Seburn

- Aquatic crossing structures should never be fully submerged (e.g., Caverhill et. al. 2011, Photo 37).
- Water in aquatic tunnels should be standing or have low flow rates.
- Many crossing structures are no longer effective due to a lack of maintenance (Iuell et al. 2003). Regular maintenance is required for long-term effectiveness of all tunnels to ensure the microhabitat is intact, passageways are clear of debris, and that suitable substrate remains.

Photo 30. Earth excavated to allow at grade entrance to tunnel. © D. Filip

Photo 31. Water accumulation at tunnel entrance. © K. Gunson

Photo 32. Dry bench in drainage culvert for small animals, could be modified for snakes. © K. Foresman

**BOX 1. OPENNESS OR OPENNESS RATIO**

Openness Ratio (OR) was first conceived by Reed et al. (1979) as a threshold measure for comparing the relative openness of box culverts for use by Mule Deer (*Odocoileus hemionus*), given their preference for a clear line of site through a structure. This measure has since been extrapolated beyond this original use and applied to a variety of species and structure shapes; see review of OR application to small mammals, deer, and amphibians and reptiles in Gartner Lee and Ecoplans (2009). The ratio is defined as the cross-sectional area of a structure (square metres) divided by the length of the tunnel (metres) ([rise x span] / length). The intent of OR is to provide a measure of the tunnel effect of a structure, which may influence use by various wildlife species.

**BOX 1. OPENNESS OR OPENNESS RATIO**

The use of OR as a sole measure to inform road mitigation design should be used with caution, especially for amphibians and reptiles, because of the following:

- Cross sectional definition needs to be modified to account for shape.
- OR does not account for the effect that a structure's width versus its rise has on openness and whether this influences wildlife use (Jacobson 2007). For example, once a minimum height has been achieved, wider rather than taller structures may be recommended to enhance openness for some wildlife, such as turtles (Smith 2003) and elk (Kintsch and Cramer 2011).
- Tunnel effectiveness may be improved beyond manipulating structural dimensions by providing natural cover, substrate and light via open-tops into the tunnel design (Woltz et al. 2008, Yorks et al. 2012).
- Openness may be less important for tunnel use when animals become more familiar with new structures then when encountering a structure for the first time (Clevenger et al. 2002).

### 4.1.3 Crossing Structure Location and Spacing

Species that need to move between different habitats are also particularly susceptible to road mortality and landscape fragmentation by roads. Amphibian and reptile species need to move among breeding sites, summer foraging areas and overwintering sites during their active seasons. When these habitats are not adjacent, animals must move up to several kilometers to find necessary habitat. In areas with high road density, it is likely these movements will cross roads, putting animals at higher risk of road mortality (Gibbs and Shriver 2002, Beaudry et al. 2008).

An effective crossing structure should function as a movement corridor connecting suitable habitat on both sides of a road. Tunnels and fencing are best located where SAR movement paths cross existing and planned roads as determined from field surveys or spatial analyses (see examples in Gunson et al. 2012, Patrick et al. 2012). Examples of predictable movements include an annual spring migration of amphibians from upland forest to breeding ponds (Patrick et al. 2010, Faggyas and Puky 2012, Pagnucco et al. 2012) or an annual snake migration to and from overwintering hibernaculum (e.g., Fortney et al. 2012). Turtles are likely to interact with roads during terrestrial nesting migrations and inter-wetland movements (Gunson et al. 2012).

Amphibians and reptiles have specific microhabitat needs, smaller home ranges and restricted movement capabilities relative to larger fauna (Jochimsen et al. 2004). The following considerations are outlined below to assist with siting the optimal placement and number of crossing structures along a road improvement or rehabilitation project:

- In general, crossing structures should be considered when the road bisects habitat used by the target species (photo 33), when the road is between seasonal habitat used by a species (e.g., wetland and upland forested habitat for Jefferson Salamanders), or when the road bisects a movement corridor (e.g., riparian pathway, hedgerow, or ridge valley). Appendix A provides a general summary of movement distances, home range areas, and habitat used by each species, but more detailed species-specific information should be used to inform mitigation plans.

- When roads bisect large expanses of continuous habitat (e.g., forest), crossing structures should generally be spaced 300 m apart for small animals depending on species, budget, and site-specific engineering and ecological considerations (Carsignol 2005). This is generally applicable to most turtles and snakes; however, Schmidt and Zumbach (2008) recommend that tunnels be spaced no more than 50 m apart for amphibians.
- Species with smaller home ranges usually require crossing structures to be placed closer together and the numbers of crossing structures will depend upon the road length where animals are interacting with the road (preferably measured with road encounter data, see section 7.2.1). The approximate distance between crossing structures can be determined based on the average home range size of the species in question. Another, similar approach is to use the square root of the home range area (Bissonette and Adair 2008).
- Man-made features (e.g., ditches, retaining walls) in the right-of-way may influence species movement and access to crossing structures (Gartner Lee and Ecoplans 2009).
- Likely crossing locations for turtle and amphibian SAR are where aquatic features and wetlands intersect with roads (Photo 34).
- Hydraulic and engineering information should be used to determine the amount of water and flow through the tunnel and whether this is appropriate for the target species. Refer to taxa specific BMPs for aquatic and terrestrial crossing types in section 4.1.5, in addition to site-specific conditions measured in the field.
- Vertical alignment and location of the tunnel should be based on environmental conditions at the site, such as water level. For example, terrestrial tunnels should be above high water marks defined by wetlands and riparian corridors.
- Integrate crossing structures with the natural landscape. For example, take advantage of valleys for crossings under roads and incorporating fencing into natural landscape features, such as existing steep rock faces.

Photo 33. Road bisecting open water wetlands, Victoria Street, Whitby, Ontario. © K. Gunson.

Photo 34. Where drainage meets road would be likely location for tunnel for SAR amphibians and reptiles. © K. Gunson.

Photo 35. Turtle using open-grate tunnel with natural substrate at bottom© A. Mui

Photo 36. Tunnel structure with sediment baffles at bottom © B. Steinberg

### 4.1.4 Retrofitting Existing Drainage Culverts

Historically, culverts have been used to convey water under roads, and these structures have also been used by some species of amphibians and reptiles (e.g., Caverhill et al. 2011). Road improvement and rehabilitation projects provide opportunities to retrofit or enhance existing drainage culverts to facilitate use by amphibians and reptiles. When replacing a culvert, consider implementing a tunnel-fencing system with specifications for the target species (see section 4.1.5). In some cases, existing drainage culverts may already be sited and designed correctly for use by the target species and may only require

Photo 37. Large 1.8 m drainage culvert partially filled with standing water allows light into tunnel, Highway 24, Aurora, Ontario. © K. Gunson

guide fencing to facilitate crossing use and reduce road mortality (Caverhill et al. 2011). A formal evaluation of existing wildlife crossing structures for wildlife passage for the intended species is recommended (Kintsch and Cramer 2011, Central Lake Ontario Conservation Authority 2015).

### 4.1.5 Taxa-specific Recommendations

In addition to the general design considerations for reptiles and amphibians that are outlined in section 4.1.2, the following are specific recommendations that are unique to each taxa group. The following sections focus on the threatened and endangered SAR in each taxa group; however, the information is generally applicable to all other reptile and amphibian species in Ontario. In general, these recommendations make the assumption that as tunnels get longer an increase in width is more important than an increase in height (see Box 1).

The salamander section only addresses the Jefferson Salamander. The Jefferson Salamander is the only SAR salamander that

is likely to be affected by road development in Ontario. In Ontario, the Small-mouthed Salamander and the two Dusky Salamanders have extremely small distributions (only a few isolated sites) and are unlikely to be affected by road construction. To date, the Fowler's Toad is the only endangered or threatened frog or toad species in Ontario, so the information in this section is specific to that species.

**SPECIFICATIONS FOR TURTLES**

**Structure type and minimum size based on tunnel length**

| Tunnel Length | Box Tunnel (w x h) | Arch Tunnel (w x h) | Round Tunnel (diameter) | Overpass |
|---|---|---|---|---|
| 15 m | 1.5 x 1.0 m | 1.8 x 0.9 m | 1.5 m | NA |
| 15-25 m | 1.8 x 1.0 m | 2.0 x 1.0 m | 1.8 m | NA |
| > 25 m | NA | NA | NA | Yes |

**ADDITIONAL DESIGN CONSIDERATIONS**

- Terrestrial and aquatic structures are suitable for most turtle species; terrestrial crossing structures are not appropriate for Eastern Musk Turtle or the Spiny Softshell, which are highly aquatic and rarely move over terrestrial areas.
- Open and closed top tunnels have been used by turtles; open-top tunnels may increase crossing success.

**RATIONALE**

- Turtles have used a variety of crossing structures under roads (e.g., Dodd et al. 2004, Aresco 2005, Caverhill et al. 2011)
- Several studies have demonstrated relatively high use of large (>1.5 m width) crossing structures by turtles:
  - A drainage culvert 1.8 m in diameter in Ontario that was approximately half full of water (Caverhill et al. 2011) was used regularly by Blanding's Turtles and was also used by an unknown number of Snapping Turtles
  - Multiple Spotted Turtles were confirmed to cross through a tunnel 1.8 x 1.8 m (Kaye et al. 2005)
  - Aresco (2005) documented over 200 turtle crossings through a 3.5 m diameter drainage culvert

## SPECIFICATIONS FOR TURTLES

### RATIONALE

- Wood Turtles continued to use a stream that passed through a culvert that was 3 m in diameter and 26 m long (Parren 2013).
- In a simulated tunnel experiment, more turtles crossed through a tunnel that let in at least 75% ambient light through the top (Yorks et al. 2011).
- Turtles will cross through tunnels 25 m long (Caverhill et al. 2011), although crossing success may be lower as length increases (Yorks et al. 2011).
- Turtles have used closed-top tunnels (e.g., Dodd et al. 2004, Aresco 2005, Kaye et al. 2005, Caverhill et al. 2011) and Wood Turtles (Photo 54) and Snapping Turtles (Whitelock 2014) have crossed through open-top tunnels in Ontario).
- Substrate type may not be as important in terrestrial tunnels for turtles as with other taxa. Blanding's and Spotted Turtles have been documented to cross through tunnels with natural substrates (e.g., Kaye et al. 2005, Caverhill et al. 2011), but in a simulated crossing structure experiment, Painted and Snapping Turtles did not demonstrate a substrate preference (Woltz et al. 2008).

Photo 54. Wood Turtle using open-grate tunnel © A. Mui

## SNAKE AND LIZARD SPECIFICATIONS

**Structure type and minimum size based on tunnel length**

| Tunnel Length | Box Tunnel (w x h) | Arch/Round Tunnel (w x h) | Round Tunnel (diameter) | Overpass |
|---|---|---|---|---|
| 15 m | 1.0 x 1.0 m | 1.5 x 0.75 m | 1.0 m | NA |
| 15-25 m | 1.5 x 1.0 m | 1.8 x 0.9 m | 1.5 m | NA |
| > 25 m | NA | NA | NA | Yes |

### ADDITIONAL DESIGN CONSIDERATIONS

- Open and closed-top tunnels have been used by snakes; open-top tunnels may increase crossing success.
- Open-top tunnels should not be used for lizards because they may be able to crawl onto the road surface.
- Aquatic tunnels will likely be used by highly aquatic SAR, such as Eastern Ribbonsnake, Queensnake, and Lake Erie Watersnake; however, they are unlikely to be used by other snake and lizard SAR and are not recommended for those species.

### RATIONALE

- Snakes (e.g., Taylor and Goldingay 2003, Laidig and Golden 2004, Roberts 2010, Eads 2013) and lizards (e.g., Taylor and Goldingay 2003, Painter and Ingraldi 2007, Arizona Game and Fish 2010) have used a variety of crossing structures under roads. However, compared to other taxa, there is less certainty about crossing structure design preference for snakes and lizards, particularly for the species that occur in Ontario.
- Snakes have crossed through tunnels as small as 0.25 m in diameter (Roberts 2010), but tunnels 1.0 m in diameter had a greater crossing success than smaller tunnels for the Eastern Gartersnake and Eastern Ribbonsnake in an experimental set-up (Eads 2013).
- Both closed-top (Taylor and Goldingay 2003, Laidig and Golden 2004, Roberts 2010, Eads 2013) and open-top (Pagnucco et al. 2011, M. Colley pers. comm.) crossing structures have been used by snakes.
- Open-bottom box tunnels with cross-sectional dimensions of 1.0 x 1.0 m in Killbear Provincial Park were used by many (11) Massasaugas and 2 Eastern Foxsnakes in 2014 (M. Colley pers. comm.).
- Timber Rattlesnakes have crossed through concrete-bottom structures without natural substrate bottoms (Laidig and Golden 2004), but natural substrate or habitat conditions may enhance use (Laidig and Golden 2004; M. Colley pers. comm.).

## SALAMANDER SPECIFICATIONS

**Structure type and minimum size based on tunnel length**

| Tunnel Length | Box Tunnel (w x h) | Arch Tunnel (w x h) | Round Tunnel (diameter) | Overpass |
|---|---|---|---|---|
| 15 m | 1.0 x 1.0 m | 1.5 x 0.75 m | 1.0 m | NA |
| 15-25 m | 1.5 x 1.0 m | 1.8 x 0.9 m | 1.5 m | NA |
| > 25 m | NA | NA | NA | Yes |

### ADDITIONAL DESIGN CONSIDERATIONS

- Terrestrial tunnels should be used for salamanders; high moisture content and even small pools of standing water may be beneficial but the tunnel should not be flooded with water.
- Open or closed-top tunnels can be effective. Open-top tunnels allow more light into the tunnel and may increase moisture levels; the latter being important in longer tunnels where salamanders are at risk of desiccation. Consequently, open-top tunnels may offer suitable conditions for salamanders even when the dimensions are smaller than those listed above.
- Despite the potential advantages of open-top tunnels, they may result in higher levels of road salt and other pollutants in the tunnel, but these may be washed away with storm events.
- Soils and leaf litter substrates should be used as opposed to larger gravel or stone substrates.
- Mole salamanders make focused migrations to breeding ponds, and it is important to have multiple tunnels where migration paths cross roads. Tunnels for salamanders should not be more than 50 m apart (Schmidt and Zumbach 2008) as salamanders will not follow a fence for long distances (e.g. Pagnucco et al. 2012).

### RATIONALE

- The best size of tunnel to encourage crossing by Jefferson Salamanders is not known, although there have been studies of crossing structures used by other salamanders in the same family (mole salamanders), which share similar life history traits.
- All documented use of tunnels by salamanders has been in terrestrial tunnels.
- Both closed-top (Patrick et al. 2010, Beasley 2013, Bain 2014) and open-top (Jackson and Tyning 1989, Allaback and Laabs 2002, Pagnucco et al. 2012) crossing structures have been used by other mole salamanders.
- Rectangular box culverts with local damp soil conditions are recommended for amphibians (see Jackson 2003, Smith 2003, Schmidt and Zumbach 2008, Amphibian and Reptile Conservation 2009, Beasley 2013).

## SALAMANDER SPECIFICATIONS

### RATIONALE

- Other mole salamanders have crossed through round tunnels as small as 0.25 m in diameter (Bain 2014) and 0.2 m wide; however, salamanders demonstrate hesitancy entering into small tunnels (Jackson 1996) and the percentage of salamanders that successfully cross through small tunnels may be low (e.g., Allaback and Laabs 2002, Pagnucco et al. 2012). Larger tunnels are required to ensure there is space for natural substrate and cover objects. In general, tunnels for amphibians are recommended to be at least 1 x 1 m in size (Schmidt and Zumbach 2008).
- Salamanders will cross through tunnels with or without natural substrate, but fewer individuals cross through bare concrete tunnels (Patrick et al. 2010). Natural soil substrate will retain moisture longer, lessening the risk of salamanders dehydrating or not entering structures.

## FROG AND TOAD SPECIFICATIONS

**Structure type and minimum size based on tunnel length**

| Tunnel Length | Box Tunnel (w x h) | Arch Tunnel (w x h) | Round Tunnel (diameter) | Overpass |
|---|---|---|---|---|
| 15 m | 1.0 x 1.0 m | 1.5 x 0.75 m | 1.0 m | NA |
| 15-25 m | 1.5 x 1.0 m | 1.8 x 0.9 m | 1.5 m | NA |
| > 25 m | NA | NA | NA | Yes |

### ADDITIONAL DESIGN CONSIDERATIONS

- Terrestrial tunnels should be used for frogs and toads; high moisture content and even small pools of standing water may be beneficial but the tunnel should not be flooded with water.
- Open or closed-top tunnels may be used.
- Open-top tunnels will provide moisture and air flow in the tunnel; however road salt or other pollutants may also enter into the tunnel but are most likely washed away during storm events.
- Soils and leaf litter substrates should be used as opposed to larger gravel or stone substrates.

### RATIONALE

- There is no documented information available for crossing structure preferences for Fowler's Toads, however there is literature available for other species of toads and amphibians. Frogs and toads have used a wide variety of crossing structures under roads (reviewed in Schmidt and Zumbach 2008; Puky et al. 2013).
- Wide crossing surfaces with local soil are recommended for amphibians (e.g., Jackson 2003, Smith 2003, Schmidt and Zumbach 2008, Amphibian and Reptile Conservation 2009, Beasley 2013).

| FROG AND TOAD SPECIFICATIONS |
| --- |
| **RATIONALE** |
| • Although toads have been documented to use tunnels <1.0 m wide (e.g., Lesbarrères et al. 2004, Ottburg and van der Grift 2013, Puky et al. 2013, Wind 2014), larger tunnels tend to be more effective (e.g., Puky et al. 2013). There was very high toad crossing rates through tunnels 1.8 m wide (Biolinx (2013).<br>• Guidelines for road crossing structures in England have been developed for the Common Toad (*Bufo bufo*). These guidelines recommend a rectangular crossing structure at least 1.0 x 0.75 m (w x h) for tunnels up to 20 m long and 1.5 x 1.0 m (w x h) for longer tunnels (Amphibian and Reptile Conservation 2009).<br>• Both closed-top (Biolinx 2013, Puky et al. 2013, Wind 2014) and open-top (Pagnucco et al. 2012, Ottburg and van der Grift 2013) crossing structures have been used successfully by other toads. |

## 4.2 Fencing for Reptile and Amphibian Crossings

Fencing in conjunction with crossing structures serves two purposes: 1) directing animals towards structure entrances and 2) providing a barrier to exclude animals from the road. Fencing can be used with crossing structures or as a stand-alone measure to prevent mortality along roads where connectivity is not a concern; this may include situations such as when suitable habitat is adjacent to, but not bisected by the road, or where animals are unlikely to cross successfully due to high traffic volumes (Jackson et al. 2015).

The following BMPs are divided into fencing design, placement, and maintenance considerations and are applicable to all amphibian and reptile SAR. For additional best practices for amphibian and reptile exclusion fencing, refer to Reptile and Amphibian Exclusion Fencing: Best Practices (OMNR 2013).

### 4.2.1 Fence Design

The primary objective of a fence design is to minimize fence breaches because animals that get through a fence can be trapped on the road and killed (e.g., Wilson and Topham 2009). Therefore these BMPs focus on providing recommendations for designing and installing a gap-free, permanent fence. Permanent fencing may have higher initial costs; however, when ongoing maintenance of temporary fencing is considered, permanent fences are less expensive in the long-run. A number of projects have experimented with fencing effectiveness for amphibians and reptiles (e.g., Woltz et al. 2008; Langen 2011; Smith and Noss 2011), and it is important to recognize that new cost-effective designs are continually being engineered and tested, and are strongly encouraged.

Fencing design should consist of a solid durable framework (stakes, posts, and sheeting) that is able to withstand weight and impact from snow removal and effectively exclude the target species. Recommended durable fencing materials include hardware cloth, chain link fencing, concrete barriers, and heavy-duty plastic fencing designed for wildlife (Table 2; Photos 38-44). Light-duty geotextile fence (lifespan up to 1 year; Photo 45), heavy-duty geotextile fence (2-3 years), or wood lath snow fencing (< 3 years), are not recommend for long-term use.

Standard chain link large animal fencing (e.g., 2.5 m high wildlife exclusion fencing with 4" mesh) does not work for many amphibians and reptiles as individuals can pass through the large mesh holes. In locations requiring guide or barrier fencing for both large animals and amphibians and reptiles, additional fencing material, such as hardware cloth at the appropriate height, can be attached to the base of the large animal fencing (Photo 25). When more than one species is targeted for mitigation, fencing height should be the tallest height recommended for all target species.

Table 2: **Summary of fence materials that have been used for long-term projects to exclude amphibians and reptiles from the road and/or guide animals to tunnels. For additional fencing specifications, refer to OMNR 2013.**

| Fence Type | Benefits | Drawbacks | Considerations |
|---|---|---|---|
| Hardware mesh cloth (Photos 38 and 39) | Relatively durable; relatively low maintenance; allows drainage; available in rolls. | Susceptible to rust in seasonally wet areas unless heavy gauge wire used. | Use ¼" or smaller gauge to reduce the risk of small snakes getting stuck; requires attachment to post at regular intervals to avoid collapse. |
| Chain link fence (Photo 40) | Very durable; low maintenance; allows drainage; available in rolls. | Mesh size typically larger than species specifications. | Use buried hardware cloth with recommended mesh at the base of the fence to provide multi-species use for large and small animals (Photo 25); lip extension may increase effectiveness for some species (Photos 39 and 40). |
| Concrete (Photo 41), corrugated steel (Photo 43), aluminum sheeting (Photo 44), or vinyl walls | Very durable; low maintenance; vertical smooth surfaces prevent climbing. | Inhibits drainage and may cause pooling. | Aluminum sheeting and vinyl walls are less durable than concrete; corrugated steel can be obtained from corrugated steel pipes cut in half and are curved providing lip extension. |

| Fence Type | Benefits | Drawbacks | Considerations |
|---|---|---|---|
| Prefabricated plastic sheeting fence (Photo 42) | Very durable designs available, e.g., ACO fencing, available in 1 metre sections OR Animex fencing, available in rolls depending on thickness. | Inhibits drainage and may cause pooling. | Back-fill at road-side of fence to provide escape route for animals (Photo 49); fencing best suited for flat dirt terrain such as in drainage ditch (Photo 42); 1 m sections may not be suitable for long fences greater than 1 km. |

Photo 38. Animex plastic sheeting made from post-consumer products ©K. Gunson

Photo 39. Hardwire cloth with ¼ inch mesh, wood frame, and top lip © K.Gunson

Photo 40. Chain link guide fencing and lip extension, Terry Fox Extension, Ottawa, Ontario © D. Seburn.

Photo 41. Concrete wall in Aurora, Ontario © K. Gunson

Photo 42. ACO fencing on highway near, Oliver, B.C. © R. Guse

Photo 43. Angled fence for salamanders at Waterton Lakes National Park© K. Gunson

Photo 44. Example of aluminum sheet fencing © K. Gunson

Photo 45. Fence end U design to deter animals following fence line from entering roadway in Haliburton County © K. Gunson

General considerations for fence design are as follows (see Figure 4 for further illustration):

- Steel posts will not break with snow load.
- Posts that are closer together (e.g., between 2-3 metres) will prevent fence sag and collapse during severe weather events and snow removal along roads.
- Stakes or posts should be placed along the road-side of the fence to deter climbing and be buried 30 cm into the ground (OMNR 2013).
- Use of materials that allow drainage at wet sites to avoid pooling at or near a crossing structure (Smith and Noss 2011; Photo 46).
- Mesh size needs to be appropriate for the target species (Photo 47). Refer to Table 3 for species-specific fence types. Many snakes can pass through ½" mesh fencing and some small snakes can even pass through or get stuck in ¼" mesh (Smith and Noss 2011, S. Marks pers. comm. 2014). A mesh size of ¼" or smaller should be used to help reduce the risk of small snakes getting stuck in the fence (Photo 47). The fence should be buried to deter animals from digging; the recommended depth is 10-20 cm where feasible. If rock cannot be avoided, the bottom of the fence can be folded and covered with gravel to hold it in place (Photo 48).
- The fence height should be higher than the high water level in spring.
- For reptiles, the fence should include an overhang lip extended away from the road to deter climbing (Photo 40).
- Backfill on the road-side of the fence can be used as escape ramps to assist trapped animals to climb to the safe side (e.g., ACO wildlife fence; Photo 49).
- Nylon mesh fencing or erosion materials should not be used along the right-of-way as snakes can become entangled and die in this material.
- Fence end treatments can be used to deter amphibians and reptiles from accessing the road at the fence ends:
  - The fence can be extended away from the road in a curved or 90 degree U design (Photo 45; Figure 4) to redirect animals away from the road
  - The fence should extend along the entire habitat and end at a point where habitat types transition (e.g., wetland-forest edge)
  - Rocks or other inhospitable materials at the fence end can help deter movement onto the road.

Photo 46. Pooling at culvert entrance that should be avoided at terrestrial wildlife tunnels © K. Gunson

Photo 47. Snake caught in ½ inch wire mesh; © M. Patrikeev

Photo 48. Fence along rock with gravel used to hold bottom of fence in place © K. Gunson

Photo 49. Backfill along ACO wildlife fence that can provide an escape ramp for animals on the roadside of the fence © V. D'elia

Table 3: **Fence design specifications for SAR reptile and amphibian species are based on OMNR 2013, Woltz et al. 2008 and expert advice.**

| Taxonomic Group | Species | Fencing | |
|---|---|---|---|
| | | Fence/wall Material | Minimum Height (above ground) |
| Salamanders, Frogs, Toads | Jefferson Salamander | • Hardware cloth with ¼ " mesh or smaller, concrete, aluminum, prefabricated plastic fence, or vinyl wall.<br>• Salamanders are generally poor climbers (T. Bain pers. comm.) so a small mesh fence will work and also allow some drainage. | 30 cm |
| | Fowler's Toad | • Solid, permanent material (e.g., cement, plastic panels), or hardware cloth with ¼" mesh or smaller.<br>• Avoid using netted fencing because they can climb (Smith and Noss 2011). | 50 cm |
| Lizards | Five-Lined Skink | • Aluminum flashing; skinks can easily climb most other fencing materials. | 50 cm |

| Taxonomic Group | Species | Fencing | |
|---|---|---|---|
| | | Fence/wall Material | Minimum Height (above ground) |
| Snakes | Eastern Foxsnake, Gray Ratsnake | • Concrete, aluminum, or vinyl wall. | 200 cm |
| | Blue Racer, Milksnake | • Hardware cloth (¼" mesh or smaller), concrete, aluminum or vinyl walls. | 100 cm |
| | All other snake species | • Hardware cloth (¼" mesh or smaller), concrete, aluminum or vinyl walls. | 60 cm |
| Turtles | All species | • Hardware cloth, chain link fence (½" mesh or smaller), concrete, aluminum, vinyl wall, or prefabricated plastic wildlife fence<br>• Combining chain link and hardware cloth will be effective for adults, juveniles, and hatchlings.<br>• When fencing is used for both turtles and snakes, mesh size larger than ¼" is discouraged as snakes can become entrapped. | 60 cm |

### 4.2.2 Fence Placement

**Right-of-way considerations:**

- Fencing should be placed as far as possible from the road edge to minimize impacts from snow removal, mowing or other road-side maintenance practices.
- Fencing cannot interfere with road interchanges or driveway access.
- Permissions and permits must be obtained from the road authority.
- When the fence will extend beyond the right-of-way, permission must be obtained from property owners, or in the case of Crown land, from the Ministry of Natural Resources and Forestry.

**Fence Length and Placement:**

Fence length depends on the species' movement abilities as well as the interface of the surrounding habitat with the road. Spatial analyses of where species are found on the road, in the road shoulder and in the road verge can help determine how much fencing is required and where it should be placed (Gunson and Teixeira 2015). However, when roads bisect continuous expanses of SAR habitat, fencing is often required along the entire stretch of a road to prevent mortality. The following should be considered when evaluating fence and crossing structure placement:

- Data collected from field and on-road surveys, expert opinion and other sources such as the NHIC to understand species presence, habitat use, and movements in relation to the road (see Appendix A).
- Maximum and mean movement distances of the target species should be used to inform fencing length. For example, salamanders generally will not move distances greater than a couple hundred metres, while turtles and snakes may move several kilometers (see Appendix A). Some species will move considerable distances along the fence and access the road at the fence ends; this can only be avoided if the fence is longer than the distances that the species will move.
- Gullies, uneven terrain and solid rock areas should be avoided when possible; if rocky areas cannot be avoided, gravel can be used to hold fence in place (Photo 50).
- When multiple crossing structures are used, fencing should span between structures (and angle away from the tunnel opening in a 'V' pattern: Photo 43 and Figure 4).
- To be effective, fencing must connect to the tunnel entrances without gaps (Photo 51) or go over top of the tunnel (Photo 52) in a 'V' pattern (Photo 53; Figure 3).

Photo 50. Fence with gap at bottom due to erosion from water draining under fence © K. Gunson

Photo 51. Fence tying into tunnel at Rice Lake Trail, Note shadecloth not recommended for permanent fencing © K. Gunson

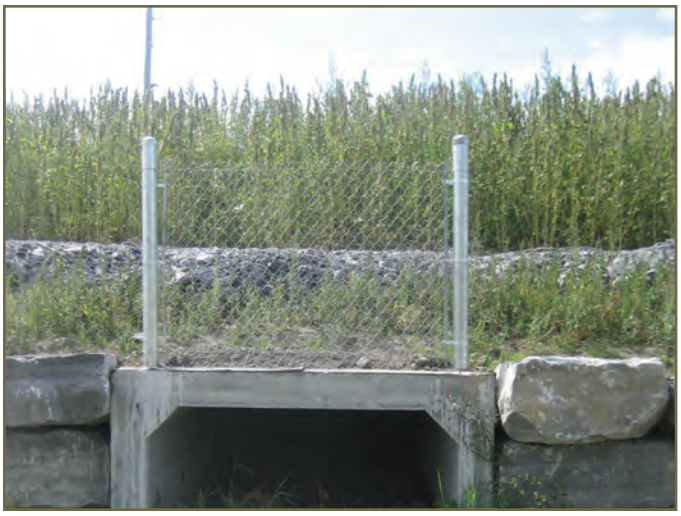

Photo 52. Fencing above tunnel, Terry Fox Drive extension © K. Gunson

Photo 53. Fencing approaching tunnel entrance in a 'V' pattern © K. Gunson

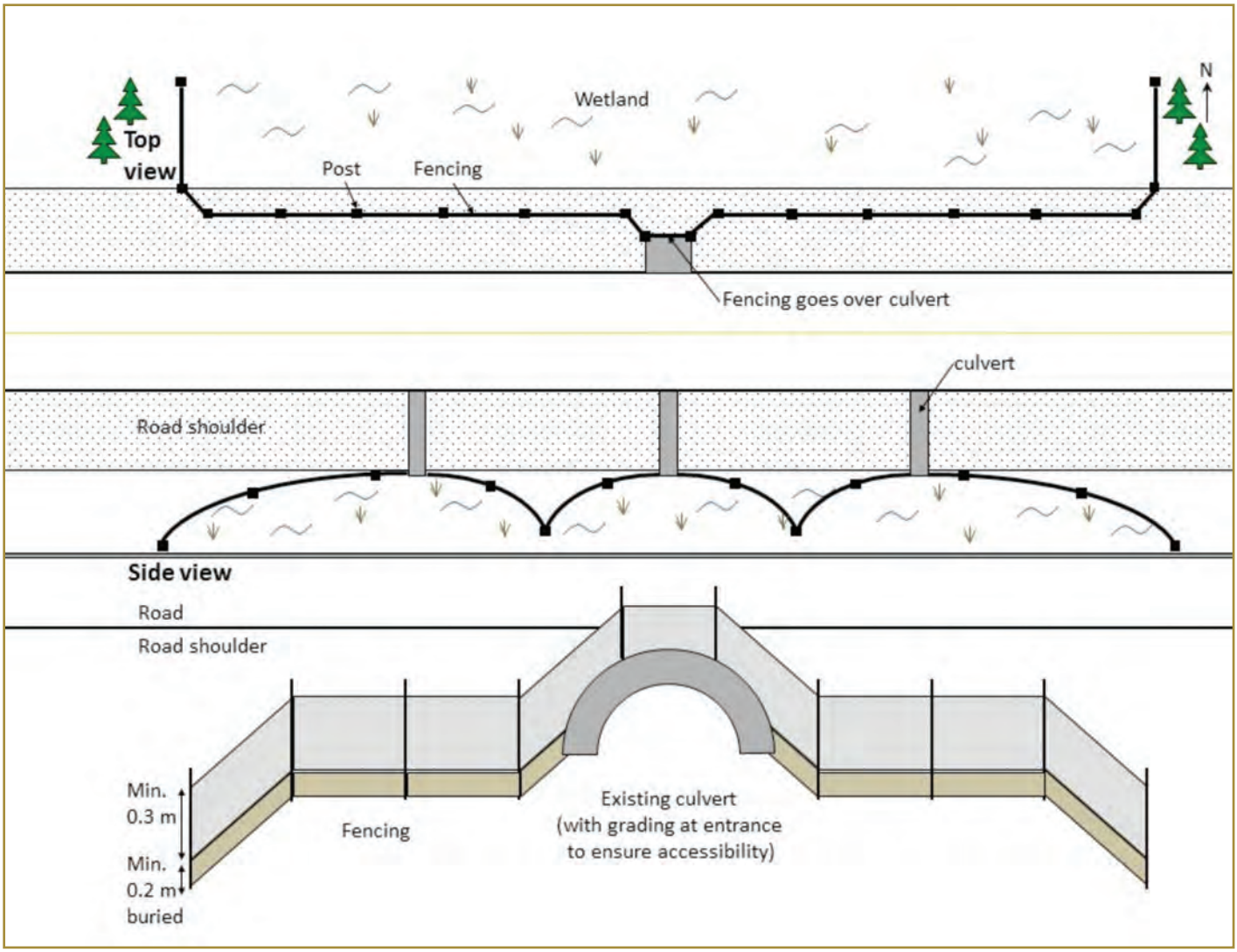


Figure 3. **Top view and side view of fencing design and siting options along the right-of-way. Figure adapted from Nature Conservancy Canada schematic.**

### 4.2.3 Fence Maintenance

All fencing requires routine survey checks and subsequent maintenance repairs and this should be planned and budgeted for. The frequency of maintenance checks and repairs will vary with the durability of the fence. After snowmelt, a thorough survey and follow-up fence repairs are essential prior to animals emerging from hibernation. The following are recommended considerations for fence maintenance:

- Woody vegetation, leaves, thick grasses, and other debris that pile up along fence may provide a `ladder` or puncture the fence allowing animals access to the road. Regular maintenance is required to clear vegetation from all fences.
- Fences should be marked with long posts and flagging tape to warn maintenance crews about its presence, especially where mowing will occur.
- Routine fence surveys should be done using a checklist approach to identify where repairs are required, including a description of the damage and the location. Checklist items should include that the fence has not collapsed, fence is still in the ground, fence abuts crossing tunnels, vegetation is not near the fence, and that there are no holes in the fence. Repair crews need to fix the fence in a timely manner to minimize fence breaches during the active season for amphibians and reptiles.

# 5 SUPPLEMENTARY MEASURES

Specifically designed crossing structures, combined with fencing, are the most effective mitigation strategy to reduce road mortality and enhance habitat connectivity (Dodd et al. 2004, Aresco 2005); however supplementary mitigation measures may be used in association with crossing structures and fencing (i.e., installing signage or reduced speed zones at fence ends). In addition, supplementary measures may be used as temporary measures during construction, or prior to road upgrade and rehabilitation projects, or on existing roads where there would otherwise be no mitigation. The effectiveness of some of these strategies at reducing road mortality and improving connectivity is difficult to measure and largely unknown; therefore implementation of these measures should proceed with caution using an adaptive management approach.

This section classifies each measure as those that influence driver behaviour, and those that influence wildlife movement as defined by Huijser et al. 2007. The following list of measures is not exhaustive, but instead summarizes what has been used in Ontario and elsewhere, with specific consideration for how each strategy may be applied to amphibians and reptiles.

## 5.1 Influencing Driver Behaviour

The strategies outlined in this section have relatively low effectiveness when used in isolation and several of these approaches should be used concurrently whenever possible. For example, a good strategy may include a reduced speed limit, traffic calming measures to reinforce the low speed limit, high quality signage to warn drivers, and a public education program to help drivers understand the measures that have been put in place.

With the exception of road closures, strategies that influence driver behavior rarely result in a significant reduction in road mortality. This is in part because, despite these measures, many reptiles and amphibians are small and difficult to see and/or avoid. Further, Ashley et al. (2007) found that approximately 2.7% of drivers intentionally ran over reptiles, and such behavior severely limits the success of these strategies.

**Reduced speed zones** allow drivers more time to react to an animal on the road, and subsequently safely avoid a collision. They have been implemented in Banff National Park to reduce collisions with larger wildlife, such as Grizzly bears (Banff National Park, unpublished data 2011-2014). Speed limits may be reduced seasonally and/or at specified times of day. This methodology is only suitable for amphibians and reptiles on low volume roads or roads in protected areas. A reduced speed zone is typically combined with a public awareness strategy and/or signage to educate motorists about the need to minimize road mortality for amphibians and reptiles. Enforcement or traffic calming mechanisms (see below) are usually necessary for the effective implementation of lower speed limits. This strategy can have a high cost given the need for regular enforcement.

**Seasonal road closures** offer an effective mechanism for reducing road mortality by eliminating vehicles from a road. Although this is a very effective solution, such closures are typically only feasible for a few days per year and they must be timed precisely to coincide with amphibian and reptile migrations. This method is most easily implemented in protected areas, on low volume roads where access to residences or businesses is minimal, or on roads where alternate access exists. A good example is King Road on the Niagara escarpment (Photo 55), where a seasonal road closure has been implemented for several years for the endangered Jefferson Salamander. Salamanders typically move across a defined road segment within a 2-3 week time period in early spring during a warm, rainy period. This type of strategy requires both buy-in from the road authority as well as the community using the roads. A public relations campaign is a useful tool to inform and gather support from local residents. This strategy has a relatively low cost.

**Traffic calming** refers to the installation of road features designed to decrease vehicle speeds without interfering with the flow of traffic. Some traffic calming methods, such as speed bumps (Photo 56), traffic circles, and raised medians, can only be implemented on low speed roads; whereas other methods, such as narrow lane widths, and rumble strip patches may be used on moderate to high speed roads. In some cases, speed bumps may interfere with snow removal; however installations can be used seasonally. This strategy has low to moderate costs dependent on the measure used.

**Signage** is a low-cost, widespread method of road-side messaging that is relatively easy to implement (Photo 57). The key objective for sign use is to instill awareness so motorists can avoid hitting wildlife along roads where the signs are placed. Effectiveness may be improved with a well thought-out strategy that avoids driver habituation and includes the following criteria (see Gunson and Schueler 2012; Kintsch et al. 2015):

- Seasonal placement of signs, or use of text indicating when target animals are likely crossing;
- Enhancement of signs with flags, flashing lights, or unique art work (Pojar et al. 1975, Hardy et al. 2006);
- Use of science and data to inform effective placement;

- Use of signs on moderate to high volume roads to deter theft;
- Strategic placement of signs and at the ends of exclusion fencing;
- Use of signs as temporary measures and markers in advance of more permanent mitigation measures (Ontario Ministry of Transportation 2012).

As with all of the other measures in this section, the effectiveness of signage can also be increased by combining it with other measures (e.g. reduced speeds, traffic calming). Benefits of signage for SAR amphibians and reptiles include driver awareness of wildlife on the road and heightened understanding of the importance of conservation efforts when used with a public awareness and education campaign (see example in Joyce and Mahoney 2001). In Ontario, signage has commonly been used on municipal and provincial park roads (Photo 58), and more recently on provincial roads (Ontario Ministry of Transportation 2012; Photo 59).

**Public awareness and education campaigns** are designed to inform drivers about wildlife and road issues and how they can help minimize or avoid wildlife road collisions. For amphibians and reptiles, public awareness campaigns typically target local communities near known high-risk road mortality locations, such as at Heart Lake Road in Brampton, Ontario. Local media attention generated awareness of the issue from local residents and subsequently a volunteer task force of 20-40 individuals was used to conduct on-road mortality surveys in 2011 and in 2013 (TRCA 2014).

While it is difficult to draw a direct correlation between heightened driver awareness and a decrease in road mortality, this strategy has the potential to improve effectiveness and public acceptance of other mitigation efforts, such as signage, reduced speed zones, or traffic calming measures. The cost of conducting a local-based public awareness campaign is comparable to that of the other strategies discussed; however, a regional, coordinated, long-term strategy (i.e. similar to the well-known Drinking and Driving Campaign) would entail greater funding and long-term commitment.

## 5.2 Influencing Wildlife Movement

**Ramped curbs and escape gaps** are used along roads (typically local, municipal roads) to replace vertical curbs that are too high for amphibians and reptiles to climb over. A good example is in Waterton Lakes National Park, where right-angle curbs were replaced with sloped curbs to allow Long-toed Salamanders to successfully escape the road (Photo 60). Additionally, escape gaps can be used where the structures meet the road (e.g., Banff National Park; Photo 61). Escape gaps would work well along high volume roads where continuous sections of jersey barriers divide opposing lanes of traffic and animals that enter the right-of-way cannot cross the road (e.g. Highway 401 and 417). This strategy has a relatively low cost.

**Assisted migration** can be used where a concentrated amphibian migration crosses a defined stretch of road. Temporary traps (typically drift fencing and buckets) may be used to prevent animals from crossing the road, which are then collected and moved across the road by volunteers. Alternatively, volunteers can survey the road during peak times and move any animals that are encountered. This strategy is labour-intensive and relies on having local volunteers to monitor traps during a migration event, and it requires safety precautions for the volunteers. However, if timed and coordinated effectively, facilitated migrations can be effective in reducing road mortality for amphibians (Photo 62).

**Habitat creation** can be used to reduce the need for individuals to access habitat close to the road or cross the road to access habitat on the other side. Since reptiles and amphibians often show high fidelity to specific habitats, many individuals will continue using historical habitat features and a population-level transition to the new habitat can take decades. Consequently, road-side barrier fencing is still necessary to prevent dispersing animals from accessing the road. The cost, feasibility and effectiveness of creating new habitat is variable and will be site and species specific (B.C. Ministry of Forests, Lands and Natural Resource Operations 2004).

New habitat creation may include wetlands as breeding sites for amphibians (e.g., Merrow 2007), artificial nesting sites for turtles; (Clarke and Gruenig 2002; Paterson et al. 2013); or gestation sites (Rouse 2005; Parent and Black 2006) and hibernacula (Willson 2005) for snakes. The B.C. Ministry of Forests, Lands and Natural Resource Operations BMP document (2004) describes the applicability of habitat restoration (or creation in this case) for amphibians and reptiles. General recommendations are as follows:

- A thorough understanding of the habitat use and movements of the target species is necessary.
- New habitat should be in close proximity and on the same side of the road as other habitat used by the target species.
- The created microhabitat should be suitable for the target populations.
- Other important habitats should not be manipulated to create new habitat.

Photo 55. Road Closure on King Road, Halton Region. © N. Finney

Photo 56. Speed bumps used to reduce speed on Cyprus Lake Road, Bruce Peninsula, Ontario. ©K. Gunson

Photo 57. Awareness sign on provincial park road in Point Pelee National Park. ©K. Gunson

Photo 58. Turtle signs used on municipal roads in Ontario. ©K. Gunson

Photo 59. Provincial Wildlife Habitat Awareness Sign on Highway 654. ©K. Gunson

Photo 60. Sloped curve in Waterton Lakes National Park, ©B. Johnstonh

Photo 61. Jersey barrier with gaps at the road surface ©K. Gunson

Photo 62. Assisted migration of toadlets in British Columbia. © E. Winde

# 6 TEMPORARY MITIGATION DURING ROAD CONSTRUCTION

This section provides general considerations for mitigation during construction when working in areas with SAR amphibians and reptiles. The following considerations address two components, timing construction activities to avoid construction-related impacts, and installing mitigation measures to minimize interactions with amphibians and reptiles and their habitat during construction.

Effective implementation of construction mitigation BMPs requires both oversight and consultation with experts. Regular consultation with local species experts is strongly recommended because active times for the target species will vary annually with changing climatic conditions and is site-specific especially in a landscape as large as Ontario.

## 6.1 Timing of Construction Activities

When road construction will occur within or near amphibian and reptile habitat, some impacts can be minimized by carefully scheduling the timing of the work to avoid habitats when they are occupied or during sensitive periods. Construction during the overwintering periods should avoid wetlands and other sites that are used for hibernation. This includes direct disturbance as well as indirect disturbance such as decreasing water levels in overwintering wetlands. Construction during the active season should avoid key habitat features or times when the species is most sensitive (see Appendix A). For example, avoiding work at breeding wetlands being used by Jefferson Salamander and Fowler's Toad in late March to June. Amphibian and reptile populations are active from March to October in southern Ontario and this time period lessens for more northern populations (Appendix A). Consultation with a local species expert and the district MNRF office may be required to assess annual variations of site-specific movements for the target species during construction activities.

## 6.2 Mitigation Measures for Construction Activities

On-site, temporary measures for all road projects that occur within, or adjacent to amphibian and reptile habitat help to avoid harming or killing individuals. BMPs for temporary measures include:

- Installation of exclusion fencing between the road construction zone and SAR habitat;
  - Use fencing that will last the duration of the road construction project (i.e., light-duty geotextile fence with a lifespan of up to one year)or, for longer projects, heavy-duty geotextile fence should be used (see section 5.2, OMNR 2013);
  - If permanent fencing is going to be installed as part of the mitigation plan (i.e. along roads), the permanent fence can be installed instead of temporary construction fence to avoid extra costs (Photo 63);
  - Fencing should be inspected and repaired daily to maintain effectiveness and avoid potential breaches; and
  - Fencing should be installed so that construction sediment does enter into wetlands or aquatic systems.
- When possible, alternative measures (e.g., rock barriers) should be integrated to create a sufficient barrier between construction sites and adjacent SAR habitat;
- Blast mats and other measures to control blast size and vibrations should be used within or adjacent (up to 250 m) to snake habitat (OMNR 2011);

- A qualified species expert should be present or available at all times to conduct searches, handle encounters, and translocate animals during construction;
- Searches should be conducted daily prior to and during construction activities;
- When SAR amphibians and reptiles are found on a construction site, proper handling, translocation and reporting protocols should be followed. Specific protocols for SAR encounters are available in the Ontario Species at Risk Handling Manual in addition to the Georgian Bay Biosphere Reserve BMP document (Clayton and Bywater 2012); and
- Project-specific reporting and handling protocols should be developed in coordination with the appropriate agency personnel. Observation records should include the observer's name, date and time, species, location (descriptive and georeferenced), photographs, and action taken.

Photo 63. Temporary fencing installed prior to installation of more permanent fencing along highway 69, note permanent fencing completed in Photo 48. © W. Kowbasniuk

# 7 MONITORING

Substantial research has been conducted to monitor the effectiveness of mitigation for large animals (e.g., Ford et al. 2010; Dodd et al. 2007); however, there exists a significant knowledge gap for amphibians and reptiles, and many mitigation projects have had no monitoring at all (Paulson 2010). This section provides recommendations for monitoring the effectiveness of road mitigation projects.

## 7.1 Study Design

Most studies that have evaluated the effectiveness of mitigation structures to-date are of low inferential strength due to poor study design, and this has resulted in results with high uncertainty (van der Grift et al. 2013). This uncertainty impedes implementation of mitigation measures and leads to inefficient use of limited financial resources.

Many monitoring plans only consider whether a specific species uses a structure at a specific location. However it is essential to monitor the viability of populations affected by a mitigated road (Figure 4). For example, if particular individuals, such as breeding females do not use a crossing structure to access breeding sites, this will lead to reduced breeding success and population declines, even though traffic mortality has been reduced and some individuals were observed using the tunnel.

Ideally, the population size (or density) of the target population should be measured at or near the road mitigation project to assess how the species responds (van der Grift et al. 2013). The population may increase, decrease or show no change in abundance after the road construction project (Rodenbeck et al. 2007). For example, Torres et al. (2011) performed visual census surveys for the Great Bustard

(*Otis tarda*), a globally threatened bird in Spain, and compared population trends in a Before-After-Control-Impact (BACI) design (see description below).

When it is not possible to measure a change in population size, the research questions should ask, "Is the current rate of road mortality sufficiently low, and/or is the rate of crossing sufficiently high to ensure a viable population?" If the answer to that question is no or possibly not, the next question is, "Which parameter of the road, traffic, or mitigation structure should be modified to improve viability to an acceptable level?" This question is more easily answered by assessing crossing and road mortality rates at different mitigation designs while controlling for habitat and road conditions.

Up to three years of monitoring data (from both before and after a road mitigation project) is likely necessary to measure changes in the ecological response (e.g. population size or road mortality rate) of the target species and reduce the influence of random, one-time events. The appropriate time-frame will depend on the ecological response and target species characteristics (e.g. longer-term monitoring for species that have longer generation times). This requires an understanding of the research goals among both the road planners and monitoring team early in the planning process to ensure the study design is adequately implemented in the road construction phase.

The optimal study design consists of data collected before and after the impact at sites where the impact has occurred and at control sites which have not been affected by the impact (Rodenbeck et al. 2007). This study design is referred to as a Before-After-Control-Impact (BACI) design and provides the highest level of inferential strength to measure the ability of the study to detect a change in the parameter of interest (e.g. population size, and rate of wildlife mortality on roads). A properly implemented BACI design allows the monitoring objectives to change from, "Are animals using crossing structures?" to "Has the mitigation prevented population decline?".

Other considerations for a study design are to select specific mitigation treatments at each monitoring site as well as carrying out consistent and repeatable sampling to ensure results are broadly applicable (van der Ree et al. 2015). Design elements are described below as well as in Figure 4:

- Treatments that can be manipulated allow for different structural features to be assessed (e.g. open-top vs. closed-top or varied fencing type and length) while controlling for other variables.
- Replication of treatments and controls among sites is important, as is monitoring each treatment in more than one location.
- Treatments that are randomly assigned will help to reduce bias and allow for a rigorous statistical analysis.
- Appropriate covariates need to be selected and controlled for. Examples of covariates include spatial and temporal variability in road design and traffic levels, mitigation structure design and the features of the surrounding landscape (van der Grift et al. 2013).
- Sampling and field protocols that are repeatable and consistent at monitoring locations before and after road mitigation help to ensure unbiased data collection.
- Inclusion of impact (mitigated) and control sites is essential to ensure that the apparent effects of mitigation (reduced mortality or increased permeability) are due to the mitigation and not a confounding variable such as weather, differences in habitat or road and terrain conditions.
- The variables being monitored (e.g. relative abundance) should be clearly identified prior to the commencement of the project.

**Research Questions**

**Monitoring Goal**
1. Maintain and restore population viability
   a. Measure trend in population size/density

**Fencing**
1. Reduce road mortality
   a. Ask is the reduced mortality sufficient to maintain or restore population viability?

**Crossing Structures**
1. Crossing use by population (e.g. male and females)
   a. Ask is use enough to maintain or restore population viability?

**Planning**

**Long-term Monitoring**
1. Multiple seasons
2. Multiple years (3 or more) prior to AND after mitigation measures have been installed or modified, e.g. Beofre, after and control impact (BACI studies).
   a. To reduce influence of random, one-time events

**Expertise & Collaboration**
1. SAR biologist
2. Road authority
3. Road developer
4. Monitoring team

**Other**
1. Obtain funds
2. Obtain permits
3. Start collaborating early!

**Study Design**

**Treatments**
1. Measure trend in population size/density
2. Vary crossing structure design
3. Combination of both

**Site Selection**
1. Obtain pool of potential treatment and control sites
2. Random assignment of treatment at impact sites
3. Replication of treatments and controls among sites
4. Include before, after, and control sites

**Sampling**
1. Repeatable
2. Consistent

Figure 4. **Study design recommendations for developing research questions, and a rigorous study design that will inform road mitigation effectiveness for amphibians and reptiles.**

## 7.2 Monitoring Techniques

This section outlines monitoring techniques that are used to evaluate crossing structure and fencing effectiveness for amphibians and reptiles. All techniques may be combined in a monitoring plan depending on budget, timelines, and the specific objectives.

### 7.2.1 Road Surveys

Road surveys are the most common method used to evaluate where amphibians and reptiles road mortality and interactions occur along roads (see Langen et al. 2007 for a description of methods). This information can be used to evaluate road impacts on wildlife, where animals are interacting with roads, and the effectiveness of crossing structures and fencing systems.

Data is collected by driving, cycling, or walking along a selected length of road looking for alive or dead individuals. The sampling method will vary depending on the objectives, road conditions, and the degree of detectability desired (Langen et al. 2007, Collinson et al. 2014). Driving surveys allow greater distances of road travelled over a sampling period, however the detectability of small vertebrates may be underestimated (Slater 2002; Langen et al. 2007).

General monitoring considerations for documenting amphibian and reptile SAR on roads include the following:

- Surveys should be conducted at least three years prior to the construction phase of a road improvement or rehabilitation project:
  - When a species is common, road surveys may generate a lot of data in 1 or 2 seasons (Ashley and Robinson 1996), however for SAR that are inherently rare, more time will be required to understand movements in relation to the project area.
- Surveys should take place during the active season or movement period for the target species (Appendix A).
- The frequency of surveys will depend on the goal of the study, the target species, traffic volume, rates of scavenging, carcass persistence, and when the species is moving (Slater 2002; Barthelmess and Brooks 2010; Santos et al. 2011). When the goal is to survey the majority of species on a road in an active season, the following recommendations should be considered for each taxon:
  - For species that move in well-defined time periods such as salamanders and toads that migrate to breeding ponds, surveys should be timed during peak movements (e.g., rainy, warm spring nights) because carcasses will be obliterated with rain and from traffic in a few hours even on low traffic roads.
  - Greater than 50% of snake carcasses will disappear in 24 hours so surveys should be conducted daily during peak movements in spring and fall (Antworth et al. 2006).
  - Dead turtles persist the longest on roads, so surveys two to three times a week during nesting season are recommended.
- Weather conditions, time of day and traffic volumes will all impact detectability of carcasses. For animals that move on rainy nights, such as the Jefferson Salamander, surveys must be conducted at night before rainfall and morning traffic obliterates carcass remains.
- Note that road surveys may not detect rare species where road mortality has already depleted the number of individuals adjacent to the road (Fahrig and Rytwinski 2009), or species that avoid crossing roads all together (Andrews and Gibbons 2005):
  - Other visual encounter survey techniques may be required to detect rare and elusive animals surrounding roads (Konze and McLaren 1997). Examples include cover boards for snakes (Patrick and Gibbs 2009), pit-fall traps for amphibians and toads (Gibbs and Shriver 2005), and hoop-net traps for turtles (Beaudry et al. 2009).
  - When information is lacking for rare species, data from common species (e.g. Painted Turtles) may supplement sample size.
- Surveys should be conducted with consistent and repeatable methods so the road can be surveyed the same way in a before and after mitigation design. Smith et al. (2015) discusses methods as well as how to avoid observer bias.
- Each specimen should be carefully examined and photographed to determine the species and, if possible, the sex and length of the animal should be recorded (e.g. plastron of a turtle, total length of snakes) (Photos 82 and 83). Depending on the project, it may also be important to collect a DNA sample or to mark live individuals.

Photo 64. Identifying amphibian specimen peeled off the road. ©K. Gunson

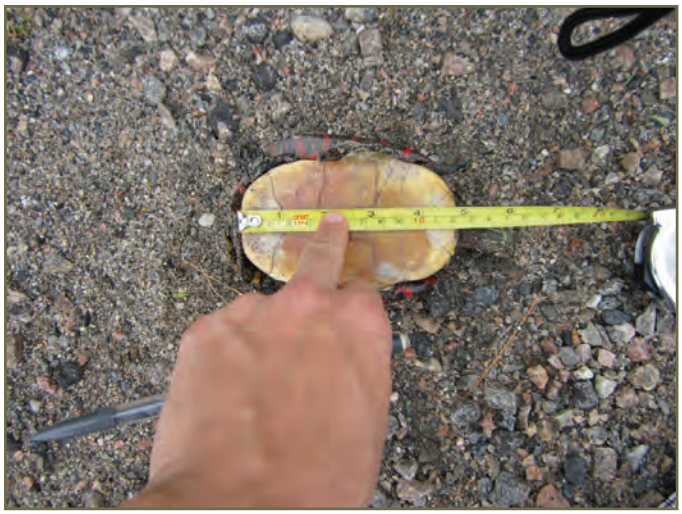

Photo 65. Measuring mid-plastron length for dead Painted Turtle found on the road. © K. Gunson

### 7.2.2 Crossing Structure and Fencing Effectiveness

This section focuses on monitoring techniques for measuring whether crossing structures and fence designs are effective at providing connectivity across roads. Previously the majority of studies that have monitored crossing structures have assessed use of tunnels by amphibians and reptiles (see review in Appendix C). Studies that assess fence-efficiency (proportion of animals encountering the fence that enter into the tunnel) and tunnel-efficiency (proportion of animals that enter tunnels and go through them) are needed to better inform mitigation designs (Jackson and Tyning 1989).

Smith et al. (2015) offer information for developing a monitoring plan to measure mitigation effectiveness for small vertebrates including reptiles and amphibians, and Clevenger and Huijser (2011) provide information on monitoring techniques based on mark-recapture methods. Further information regarding methods for surveying amphibians and/or reptiles can be found in Heyer et al. (1994), Konze et al. (1997) and McDiarmid et al. (2012). The Canadian Council on Animal Care (CCAC 2004) provides an excellent manual for handling and capturing amphibians and reptiles that can be integrated into the following monitoring techniques (http://www.ccac.ca/Documents/Standards/Guidelines/Add_PDFs/Wildlife_Amphibians_Reptiles.pdf)

**Digital cameras** are currently the most commonly used technique for measuring crossing structure use for animals in Ontario. Motion-activated cameras work well for large and medium-sized animals; however, they are not very effective at capturing pictures of ectothermic animals, such as amphibians and reptiles. This is because motion-triggered cameras only take a photograph when there is a temperature differential between the animal and the ambient temperature (Reconyx 2010). For example, Pagnucco (2012) found Reconyx infra-red motion triggered cameras only documented approximately 19% of salamanders in a 0.5 m by 0.5 m ACO tunnel. Since the motion-activated feature is not effective, the time lapse setting should be used instead to take pictures at regularly spaced intervals (e.g. every minute). Approximately 20,000 images are taken in a

two week period with a one-minute interval and camera detection software can help to efficiently find wildlife in images (Dillon et al. 2011). Setting the camera to take photos over shorter intervals (e.g. every 10 seconds) will improve the quality of the data but would require the cameras to be checked more regularly. Cameras should be placed at both ends of the tunnel, securely fastened and locked to the undersurface of the tunnel top (photo 84). At larger tunnels, cameras can be mounted close to the ground to capture snakes and turtles.

Pitfall Traps: Pitfall traps consist of buckets, cans, or other containers that are buried flush with the ground and are set up along a fence that directs animals to the traps. Pitfall traps need to be large enough so that the target species cannot climb or jump out of the containers. In addition, once traps are set they need to be checked regularly (at least every day) to avoid drowning, desiccation or predation of individuals. They can be used at or near amphibian habitat to assess where animals are moving in relation to a road. For example, Gibbs et al. (2005) used metal cans

Photo 66. Camera securely fastened to top of culvert; note difficult to capture animals when water in culvert or tunnel. © K. Gunson

Photo 67. Using hand-held receiver to locate Blanding's turtles around highway 24 © K. Gunson

Photo 68. Blanding's turtle with radio transmitter on back of shell. © K. Gunson

Photo 69. Passive data logger receiver used to record turtle passage at culvert on highway 24. ©K. Gunson

50 cm deep and 7.5 cm in circumference to assess movements of salamanders across a road. Furthermore, pitfall traps have been used at entry and exit points of crossing structures to assess use of structures (Pagnucco et al. 2012). This also provides a useful technique to capture and mark individuals.

**Mark-recapture:** This technique involves capturing, marking and recapturing animals to determine if they cross the road. Several methods exist for marking amphibians and reptiles, including inserting Passive Integrated Transponders (PIT), notching scutes on turtles, marking salamanders with visible implant elastomer (e.g., MacNeil et al. 2011) and using image-recognition software. Some of these techniques are discussed in more detail in the CCAC (2004) manual. Mark-recapture methods for turtles are discussed in detail in Robertson et al. (2013) and for all reptiles in McDiarmid et al. (2012).

**Radio-Telemetry and passive data loggers/ PIT tag readers:** Radio-telemetry can be used to monitor animal movements using a hand-held receiver (photos 85 and 86) without the need to recapture the animals. Further, passive data loggers (photo 87) or PIT tag readers can be mounted near crossing structure entrances (James et al. 2011; Caverhill et al. 2011) to record the movement of marked individuals through them.

Table 4 provides a comparison of the advantages and disadvantages of these methodologies. A combination of several methods will provide the most robust data set and eliminate most of the disadvantages of any one method. For example, using both hand-held radio telemetry and passive receivers mounted in the crossing structures will provide high quality data on crossing events as well as the detailed movements of the individuals in relation to the crossing structures/road.

Table 4: **Advantages and disadvantages of the techniques used to monitor road crossing structures**

| Technique | Advantages | Disadvantages |
|---|---|---|
| Mounted digital cameras | • Provides information on the time and date of the crossing event<br>• Provides direct evidence that the structures are used<br>• Should detect most individuals using the crossing structure if cameras are set to take photos regularly (e.g. every minute) | • Does not provide information on the individuals using the structure (e.g. sex)<br>• Effective cameras are expensive, and there is a risk of theft<br>• It can be very time-consuming to review photographs and maintain cameras (downloading pictures, adjustments, batteries, water levels, etc.)<br>• Cameras typically do not work under aquatic conditions |

| Technique | Advantages | Disadvantages |
|---|---|---|
| Pitfall traps | • Provides information on the individuals using the structure (e.g. sex) and the date of the crossing event<br>• Provides direct evidence that the crossing structures are used<br>• Should detect most individuals using the crossing structure<br>• Can use trapped animals for genetic sampling and mark-recapture | • Labour-intensive for set up and sampling as the traps should be checked a minimum of every day<br>• Risk of animals dying in traps<br>• Method is less suitable for reptiles |
| Mark-recapture | • Provides information on the individuals using the structure (e.g. sex)<br>• Allows for estimates of population abundance (with enough sampling) | • May not provide information on the time and date of crossings<br>• Does not provide direct evidence that animals used crossing structures (e.g. it is not possible to rule out crossing through holes in fence or at fence ends)<br>• Detection of individuals crossing the road is limited to the number of animals captured and subsequently recaptured |
| Radio-telemetry and passive data loggers | • Provides information on the individuals using the structure (e.g. sex) and the time and date of crossing<br>• Passive data loggers and PIT tag readers in the structure provide direct evidence that the structures are used<br>• Hand held radio-telemetry receiver can track movements in relation to the road (e.g. home range size, etc.)<br>• Will work under aquatic conditions | • Considerable field time, effort and cost can be required to capture, handle and monitor animals<br>• Detection of individuals crossing the road is limited to the number of animals that are captured and tagged or tracked<br>• Radio-telemetry with a hand-held receiver is unlikely to provide direct evidence that the structure is used, so it is ideal to combine this with passive readers mounted in the structure |

### 7.2.3 Population Estimates

Monitoring that measures changes in population abundance, animal distribution, and genetic relatedness before and after a road mitigation project can answer questions related to how new road mitigation maintained or improved the long-term persistence of wildlife populations, especially when used in a BACI design. This section generally outlines inventory and survey techniques to measure whether a population is stable, increasing or decreasing as a result of the road mitigation measures and road construction project.

**Mark-recapture studies** may be used to estimate population size, but a large number of individuals need to be marked to produce statistically significant estimates.

**Relative Abundance surveys** are carried out using standardized methods, such as timed searches, grids or transects, that allow for comparisons over time or between sites. In addition to free searches, these surveys may consist of cover boards for snakes and salamanders or pit-fall traps for toads and frogs along. Abundance surveys (counts of animals per area and standardized by search effort) require a systematic study design with regular surveys by the same trained volunteers to reduce observer bias.

**Call surveys** may be used to collect relative abundance data for toads and frogs near roads, and do not require direct observation of the animals (Eigenbrod et al. 2008b). With respect to SAR amphibians and reptiles in Ontario this monitoring technique would only be applicable to the Fowler's Toad.

**Genetic Sampling** involves taking from blood or tissue samples from live or dead individuals to compare genetic relatedness and structuring (e.g. sex and age ratios) before and after a road mitigation project (e.g. James et al. 2011). For example, Clark et al. (2010) found roads have an effect on the genetic structure, connectivity and gene flow on Timber Rattlesnakes. In another study, Row et al. (2010) genetically analyzed blood samples from Eastern Foxsnake populations bisected by highways in Ontario, Ohio and Michigan. Notably, some populations bisected by Highway 401 were not genetically distinct, possibly because of underpasses that allowed snake passage.

## 7.3 Adaptive Management

Adaptive management consists of using the results from monitoring to inform decision making with regard to planning and designing subsequent phases of a project (Holling 1978). The Environmental Impact Assessment (EIA) process is meant to be a flexible, iterative and adaptive process that can adjust for uncertainty and preferences that emerge during the process (Lawrence 2003). With this in mind, and the typical long-term nature of road projects, there is an opportunity to integrate long-term and adaptive monitoring into the road planning processes.

Road construction and the implementation of mitigation strategies typically occurs in phases. The phased construction process allows for mitigation designs to be implemented in the initial section of highway so that lessons learned via monitoring can be integrated into subsequent phases of the road project. For example, the improvement of the Trans-Canada Highway in Banff National Park was conducted in 4 phases over 30 years, and long-term monitoring of crossing structures enabled lessons learned to be applied in each subsequent phase to improve crossing structure designs (Ford et al. 2010). Adaptive management of the project design based on monitoring results requires

regular and close communication between the people conducting the monitoring and the transportation agency. Ongoing communication will permit timely changes to design plans that reflect the most current results from monitoring activities (Clevenger and Ford 2010).

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# 9 APPENDICES

## Appendix A: SAR Amphibian and Reptile Habitat Use and Movements

General summary of seasonal habitat use, general movement distances within and between habitat and when this occurs for species at risk amphibians and reptiles in Ontario. Bold text indicates high risk of road mortality for the species during months indicated. Summary based on review of COSEWIC reports, Recovery Strategies, ESA Habitat Regulations, and ESA Habitat Descriptions. All of the COSEWIC reports that were used to inform this table are listed in the references section of the document. In some cases information was obtained from other sources and is indicated. More detailed summaries should be conducted for each target species on a project specific basis.

| Species | Scientific name | Habitat | | Home range | Movement | When movement occurs |
|---|---|---|---|---|---|---|
| | | Spring and Summer | Winter | | | |
| **Salamander** | | | | | | |
| Jefferson Salamander | *Ambystoma jeffersonianum* | Spring Breeding habitat: ephemeral ponds or other ponds without fish (Helferty 2002); Summer: Deciduous or mixed upland forest | Deep rock fissures and burrows below the frost line in upland forest habitat | Generally within 300 m of wetland | Adults may move up to 1 km, usually 300 m from breeding habitat; Juveniles up to 100 m | Explosive adult breeding migration from late March to late April; juvenile dispersal in July and August |
| **Toad** | | | | | | |
| Fowler's Toad | *Anaxyrus fowleri* | Spring Breeding habitat: shallow ponds, sandy lakeshore bays and wetlands, ephemeral ponds, bedrock pools; Summer: Sand dunes, sand bars and beaches along Lake Erie shore | Burrows in moist sand along Lake Erie shore to just above water table and below frost line | Within a few hundred metres during summer; seasonal migrations up to 1 km are typical | Usually only move a few hundred metres of of Lake Erie shoreline | Adult breeding migration in May and June; juvenile dispersal in August and September |
| **Turtles** | | | | | | |
| Blanding's Turtle | *Emydoidea blandingii* | Eutrophic, shallow lakes, ponds, slow-flowing rivers, streams, marshes, bog, open fens with basking sites and thick vegetation, upland woods; nest in loose soils (including road shoulders) | Permanent wetlands and other bodies of water, occasionally temporary ponds (Glenside Ecological Services 2011) | Up to 3 $km^2$ | Typical adult movement to and from hibernation and nesting sites is 2 km, although longer migrations have been documented; hatchlings move 400m to water (M. Gartshore, F. Schueler pers. comm.) | Spring migration from hibernation sites to summer habitat (April – early May); Adult nesting migration from late May to early July; Inter-wetland movements in the summer; hatchling and adult overwintering movements in fall months |

| Species | Scientific name | Habitat | | Home range | Movement | When movement occurs |
|---|---|---|---|---|---|---|
| | | Spring and Summer | Winter | | | |
| Eastern Musk | *Sternotherus odoratus* | Shallow water with abundant floating and submerged vegetation; nest near water in direct sun | Similar to summer; buried in 30 cm of mud | Confined to single bodies of water | Overland movement limited; tend to nest at shorelines | Adult nesting migration from June to early July |
| Snapping Turtle | *Chelydra serpentina* | Slow-moving water with soft mud substrate and dense vegetation; nest on sand and gravel banks, roads (Patrick et al. 2012, M. Karch, F. Schueler pers. comm.) | Under floating vegetative mats, logs, overhanging banks in streams and lakes, or buried in mud | Up to 0.09 $km^2$ | Adults move from 0.5km up to 5 km to and from hibernation site and in search of nesting sites | Spring migration from hibernation sites to summer habitat in April – early May; Adult nesting migration from late May to early July; hatchlings move to water in early fall |
| Spiny Softshell | *Apalone spinifera* | Rivers or lakes with shallow water and muddy or sandy substrate, deep pools, riffles, and inlets; nest in sunny areas with fine gravel or sandy substrate close to water | deep pools in rivers (>1 m in depth) | Confined to one body of water | Rarely leave water; nest close to water | Adult nesting from June to early July |
| Spotted Turtle | *Clemmys guttata* | Slow-moving or still shallow water wetlands with aquatic vegetation (fens, bogs, marshes and rocky pools); upland woods used for aestivation and movement; Mate in woodland pools connected to hibernacula; nest in sunny upland locations (Glenside Ecological Services 2011, Patrick et al. 2012) | Rock caverns in lakes, under hummocks and in burrows in sphagnum-rich wetlands, and in root cavities in swamps | Home range: 0.04 $km^2$ | Adults can move on average 1120 m to and from hibernation site, in search of nesting site, and during inter- wetland movements; move on average 250 m from wetland to nest (Joyal et al. 2001). | Adult nesting migration from late May to June; inter-wetland movements in summer; spring and fall migration from and to hibernation sites |

| Species | Scientific name | Habitat | | Home range | Movement | When movement occurs |
|---|---|---|---|---|---|---|
| | | Spring and Summer | Winter | | | |
| Northern Map Turtle | *Graptemys geographica* | Well-oxygenated, shallow rivers, streams, creeks, and lakes with basking sites adjacent to deep water; nest in soft sand beaches or soil in full sun | Bottom of lakes or rivers in deep hollows | Home range: 1.2 – 13.5 $km^2$ (usually within waterways) | Travel inland in search of nesting sites 35-100 m from water | Adult nesting season in early June – late July; Migration to and from hibernation sites in April - early May and late August - October |
| Wood Turtle | *Glyptemys insculpta* | Clear-water streams with sand or gravel substrate, alder thickets, upland forested areas; nest on sand or gravel-sand beaches and farm fields, road shoulders (Glenside Ecological Services 2011) | Bottom of deep pools in streams | Home range up to 1.5 $km^2$ | Female adults move to nesting sites; typical home range length of 2 km; extensive movement in upland habitats throughout active season, typically within 300 m of water (K. Barrett pers. comm.) | Adult nesting migration from late May to early July |
| **Snakes** | | | | | | |
| Blue Racer | *Coluber constrictor foxii* | Edge habitat, open fields, woodlands with sunny vegetation piles or rocks; nests in decaying organic matter, logs and under rocks in full sun | Crevices in Pelee Island's limestone plain and in piles of rock and soil | Confined to Pelee Island | Adults travel up to 2.7 km from hibernacula to find mates, nesting locations; hatchlings cross roads from nests | Adult mating season in April and May; neonate dispersal in July and August; movement to hibernaculum in September and October |
| Butler's Garter-snake | *Thamnophis butleri* | Open prairies, grasslands, old fields and other open habitats; bask on roads; live birth under cover | Small mammal burrows, ant mounds, rocky dikes, possibly crayfish burrows (M. Gartshore pers. comm.) | Within specialized habitat confined by roads | Most adults only move a few hundred metres from hibernacula in active season, but some move > 1 km | Adult mating season in April and May; neonate dispersal in July and August; movement to hibernaculum in September and October |

| Species | Scientific name | Habitat | | Home range | Movement | When movement occurs |
|---|---|---|---|---|---|---|
| | | Spring and Summer | Winter | | | |
| Eastern Foxsnake, Georgian Bay population | *Pantherophis gloydi* | Open rock barrens, coastal meadow marshes, woodlands and forest clearings; nest in decaying vegetation piles, rock crevices | Granite or limestone fissures | 3.5 km linear home range | Move extensively throughout active season to foraging, nesting and hibernation sites; Carolinian snakes move through vegetated corridors to find habitat | Adult mating season in April and May; neonate dispersal in July and August; movement to hibernaculum in September and October |
| Eastern Foxsnake, Carolinian population | *Pantherophis gloydi* | Wetlands complexes, unforested, early successional lands, hedgerows, riparian zones, woodlands; nest in decaying vegetation piles and fallen trees, road-side burrows, under concrete slabs | limestone bedrock fissures, mammalian burrows, tree root crevices, various man-made features | Up to 1.5 km linear home range, but varies with extent of habitat available | | |
| Eastern Hog-nosed Snake | *Heterodon platirhinos* | Sandy areas or well-drained soil in open forests, forest edges or brushy habitats; sometimes wetlands close to conifer plantations; nest in south-facing open areas, under driftwood, or rock crevices in Shield (Glenside Ecological Services 2011) | Hibernate in upland burrows excavated by the snake, root cavities or abandoned mammal burrows (Glenside Ecological Services 2011) | Home range > 1 $km^2$ | Very mobile throughout season; adults can move >4 km from hibernacula; max. adult movement 6.2 km | Adult mating season in spring and late summer; neonate dispersal and movement to hibernaculum in fall |
| Eastern Ribbon-snake | *Thamnophis sauritus* | Wetlands, shorelines, sloughs, and swamps. Sometimes give birth or seek cover in upland areas. Live-bearing. | Underground animal burrows and cracks and crevices ranging from well-drained to completely | Home range small, e.g. < 0.007 $km^2$ within their wetland | Typically found within 10 m of water; may move up to 200 m from water for birthing and hibernation | Adult mating season in spring, and birthing in July and August; neonate dispersal and movement to hibernacula in September and October |

| Species | Scientific name | Habitat | | Home range | Movement | When movement occurs |
|---|---|---|---|---|---|---|
| | | Spring and Summer | Winter | | | |
| Gray Ratsnake | *Pantherophis spiloides* | Forest edge and open forests; hide in hollow logs and trees, under rocks and in rock crevices; Gravid females prefer large trees; nest communally in standing snags, stumps, logs and compost piles (S. Thompson pers. comm.) | Moist hibernacula (rock fissures) below the frost line | On average 0.18 $km^2$ | Adults move up to 4 km to and from hibernacula | Adult mating season late May to early June; neonate dispersal and movement to hibernacula in fall |
| Lake Erie Water-snake | *Nerodia sipedon insularum* | Limestone shorelines with ledges and cracks, cobblestone beaches, gravelly or sandy areas with debris. Will also use flooded quarries and drainage ditches in summer. Live-bearing. | Inland communal hibernacula are used: cavities and crevices in quarries, soil and rock piles, cracks in bedrock, tree root masses and animal dens | Generally found along shorelines | Generally restricted to the shoreline during the active season, but may travel several hundred metres inland to hibernacula | Adult mating season early May to early June; neonate dispersal and movement to hibernacula in fall |
| Massa-sauga, Great Lakes population | *Sistrurus catenatus* | Habitats with low canopy cover (rock barrens, forest clearings, alvars, beaver meadows, fens, bogs and shorelines); Live-bearing: gestation sites are in open habitat (e.g. rock barren), often with large table rocks and low vegetation | Forested areas on the Northern Bruce Peninsula; Wetlands on the Eastern Side of Georgian Bay; mammal burrows, old roots and rock crevices that extend below the frost line with access to the water table | Home range: 0.25 $km^2$ | Can move >1 km to and from hibernacula; max. adult movement: 4 km; max. juvenile movement: 400 m | Mating season from July - August; Neonate dispersal in July - August; Movement to and from hibernacula in early May and September |
| Massa-sauga, Carolinian population | *Sistrurus catenatus* | Open shrubby areas and man-made piles of woody debris. Will also use grassy, prairie-like fields, wetlands and hedgerows in summer. Live-bearing. | Mammal burrows tree root cavities below the frost line with access to the water table | | | |

| Species | Scientific name | Habitat | | Home range | Movement | When movement occurs |
|---|---|---|---|---|---|---|
| | | Spring and Summer | Winter | | | |
| Milksnake | *Lampropeltis triangulum* | Forests, woodlands, fields, rocky outcrops, forest clearings and edges of wetlands | Mammal burrows, old foundations, old wells, gravel and dirt banks, hollow logs, rotting stumps | Home range up to 0.02 $km^2$ | Adult movement: 400 m or more within the active season | Mating season in the spring; Neonate dispersal in July and August; Movement to hibernacula in September and October |
| Queen-snake | *Regina septemvittata* | Rocky streams, rivers and lake shorelines, wetlands, ponds, meadow marshes with full sun exposure | Underground and close to water | Linear home range (along waterways) 250m | Movement along waterways typically no more than 250m, but longer dispersal movements of > 1 km may occur; found within 15m of water during active season, but inland movements to hibernacula may be several hundred metres | Migrate to and from hibernacula in early April - mid-May and again in fall |
| Lizard | | | | | | |
| Five-lined Skink | *Plestiodon fasciatus* | Great Lakes: open rocky areas in forests Carolinian: woody debris-strewn stable sand dunes, open forests, wetlands | same as spring, hibernate in rock crevices or buried in soil | Home range 270 – 578 $m^2$ | Generally move short distances and adults move up to 210 m and juveniles up to 110 m | Breed in May or early June |

## Appendix B: Definitions

**Connectivity** - the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993)

**Corrugated Steel Pipe (CSP)** - round or elliptical culvert made with corrugated steel

**Crossing Structure** - general term for mitigation measures placed in roads to allow wildlife to cross safely

**Culvert** - general term for underpass structure type, traditionally used for conveyance of water under a road; in context of this document can be box or round
- **Arch Culvert** - portion of round culvert that allows natural bottom
- **Drainage Culvert** - a drain or pipe that allows water to flow under a road or railroad

**Field-based information** - Information measured within or near (few hundred metres) the road corridor used to inform impacts

**Landscape scale** - larger study area that may include an entire jurisdiction where information is available for an entire jurisdiction that is typically available in a GIS and informs broader level impacts of roads

**Major road improvements** - include road extensions, new alignments, and upgrades such as twinning from two to four lanes.

**Population viability** - the ability of a population to persist and avoid local extinction

**Range length** - maximum distance within animal's home range

**Regional assessment** - Integrate all multi-jurisdictional stakeholders and landscape information within the impact study area to develop a mitigation plan

**Road-habitat interface** - suitable habitat used by target species that is adjacent to the road

**Road rehabilitation project** - includes replacing bridges and pavements which are done under our capital program as opposed to our maintenance program

**Skylight** - structure on tunnel that permits ambient light to enter the structure

**Target species** – the species that the road mitigation measures are designed for; may include one, two or several species that are impacted by roads

**Tunnel** - type of crossing structure that is placed under the road surface for wildlife passage; in context of this document specifications are < 3 m width
- **Closed-bottom tunnels** - tunnel bottom is structural material
- **Open-bottom tunnels** - tunnel bottom is not structural material, provided by 3-sided concrete structure, arch pipe aluminum or corrugated steel
- **Open-grate tunnels** - provide ambient light through traditional metal grate structure that is placed on footings
- **Open-top tunnels** - provide ambient light through openings or slots at the top of the tunnel; openings must be at grade with road surface
- **Terrestrial tunnels** - dry tunnels installed for amphibians and reptiles undergoing overland movements

**Underpass** - general term for structural measures, e.g., culverts, bridge, viaducts, placed under roads to allow wildlife to cross safely

## Appendix C: Crossing Structure Summary from Literature

| Mole Salamander Crossing Structure and Fencing Review | | | |
|---|---|---|---|
| **Species** | **Comments** | **Crossing Structure** | **Crossing Structure Reference** |
| Projects with confirmed crossings | | | |
| Long-toed Salamander (*Ambystoma macrodactylum*) | No salamander >16 m from a tunnel was confirmed to cross. Tunnels ~200 m apart. Fences not angled to tunnels. | Six structures installed, two monitored. Two sizes of open-topped ACO Polymer tunnels: 0.47x0.32m (WxH); 0.23 x 0.21 (WxH). Did not indicate which size they monitored. Tunnels 11.1 m and 12.0 m long. | Allaback and Laabs 2002 |
| California Tiger Salamander (*Ambystoma californiense*) | Salamanders readily used tunnels. Some individuals showed hesitancy to enter tunnels. | Three 0.25 m dia steel pipes, ~20 m long. Tunnels ~35 m apart. | Bain 2014 |
| Northwestern Salamander (*Ambystoma gracile*), Rough-skinned Newt (*Taricha granulosa*), and Western Redback Salamander (*Plethodon vehiculum*) | Known Red-legged Frog (Rana aurora) migration route but also used by these spp. Juvenile newts and Redbacks could climb fence. | Concrete box culvert 1.8 x 0.9m (WxH). Half filled with soil and downed woody debris. | Beasley 2013 |
| Spotted Salamander (*Ambystoma maculatum*) | At least 76% of salamanders that reached the tunnel entrances successfully crossed. Dark tunnel entrances may keep some salamanders from entering tunnels. | Two ACO open-topped tunnels, size not specified. Tunnels 7m long and ~60 m apart. | Jackson and Tyning 1989, Jackson 1996 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Long-toed Salamander | More than 100 salamanders caught in tunnel exit traps in 2009, but only 23% of salamanders marked at the drift fence were caught exiting the tunnels. | Four open-topped ACO tunnels, 0.5 x 0.33m (WxH) and ~12 m long. Tunnels 80-110 m apart. | Pagnucco et al. 2011, 2012 |
| Projects with no confirmed crossings | | | |
| Jefferson Salamander (*Ambystoma jeffersonianum*) | Not detected crossing through tunnels. Very few detected away from roads as well. Guidewalls not angled toward tunnel entrances. | 5 tunnels installed. Four 1.2 m diameter CSP or concrete, and one 1.7m wide elliptical culvert. Tunnels 25-31 m long. | Gartshore et al. 2005 |
| Spotted Salamander | Three years of monitoring failed to confirm usage by any amphibians. Migration routes not confirmed before construction. | 2 bridges, 1 concrete box culvert 1.2 x 1.2m. Structure 17 m long and lined with soil. | Merrow 2007 |
| Outdoor lab experiments | | | |
| Spotted Salamander | Found no major statistical differences in culvert crossing comparing the lengths, diameters and substrates tested. Thirty percent more salamanders crossed through the largest tunnel compared with the smallest. | Experimental culverts along migration route, not under road. Tested 0.3, 0.6, and 0.8 m diameter corrugated PVC pipes, 3, 6, or 9 m long. Also tested three kinds of substrate: bare plastic, sand/ gravel and concrete. | Patrick et al. 2010 |

| Toad Crossing Structure and Fencing Review | | | |
|---|---|---|---|
| **Species** | **Comments** | **Crossing Structure** | **Crossing Structure Reference** |
| Projects with confirmed crossings | | | |
| Western Toad (*Anaxyrus boreas*) | Tunnel used by 1700-7000+ toadlets leaving breeding pond. Significant road kill at fence ends. | One semi-circular, closed-topped culvert with earthen floor. 1.8 x 0.5 m (WxH) x 3.7 m long. | Biolinx 2013 |
| American Toad (*Anaxyrus americanus*) | Confirmed tunnel crossing by American Toads. | 5 closed-topped tunnels, mainly 1.2 m diameter CSP or concrete, but one 1.7 m wide elliptical culvert; 25-31 m long. | Gartshore et al. 2005 |
| Common Toad (*Bufo bufo*) | Marked all toads. 40% used tunnels, 27% got around fence, 33% did not cross. | 2 ACO open-topped concrete tunnels, ~0.5 m wide on bottom, 0.33 m high. No soil on bottom. | Ottburg and van der Grift 2013 |
| Western Toad | 7 caught in exit traps. | 4 ACO open-topped box culverts, 0.5 m wide and 0.33 m high and ~12 m long. Slots along the top. Tunnels 80-110 m apart. | Pagnucco et al. 2012 |
| Common Toad (*Bufo bufo*) | Greater usage of larger rectangular culverts than smaller round culverts. | 4 types. 0.4 and 0.6 m diameter concrete culverts; box culverts 1.6 and 1.7 m high (width not given, but appears variable in photos). | Puky et al. 2013<br>Wind 2014 |
| Western Toad | Dispersing toadlets from breeding pond crossed through culverts in the thousands. | 2 CSP culverts, both 0.4 m in diameter. | |
| Outdoor lab experiments | | | |
| Frogs and Toads of France | Toads showed no difference in use of tunnels with or without soil. | 0.5 m diameter concrete culvert. Compared bare concrete with layer of soil. | Lesbarrères et al 2004 |

| Turtle Crossing Structure Research | | | |
|---|---|---|---|
| **Species** | **Comments** | **Crossing Structure** | **Crossing Structure Reference** |
| Projects with confirmed crossings | | | |
| Florida Cooter (*Pseudemys floridana floridana*), Slider (*Trachemys scripta*), and Florida Softshell (*Apalone ferox*) | Primarily Cooters and Sliders crossed through culvert. | Drainage culvert 3.5 m in diameter (46.6 m long). | Aresco 2005 |
| Blanding's Turtle (*Emydoidea blandingii*), Snapping Turtle (*Chelydra serpentina*) | Individual Blanding's Turtles used culvert up to 13 times. Snapping Turtles also crossed using the culvert, no numbers provided. Virtually no roadkill (2 in 2 years). | 1.8 m diameter corrugated steel culvert, 25 m long, pre-existing, with sediment and year round water. | Caverhill et al. 2011 |
| Spotted Turtle (*Clemmys guttata*) | At least 7 turtles confirmed to cross through tunnel. Other turtles likely crossed as well. | 1.8 x 1.8m concrete box tunnel, ~13m long; 0.1-0.15 m organic substrate in culvert. | Kaye et al. 2005 |
| Blanding's Turtle | Blanding's Turtles showed no strong preference for culvert size. Turtles more apt to cross through culvert when light visible at end of culvert. | Tested 1.0 and 1.2 m diameter corrugated steel culverts and 1.1 m diameter arch culverts; length unspecified. Culverts tested in pairs along known in outdoor lab. | Lang 2000 |
| Snapping Turtle | Crossed through culvert. No details on amount of usage. Fence end roadkill. Hatchling could get through 5x10cm mesh fence. Effectiveness of fence increased after first yr or two, as vegetation held bottom of fence better. | 1.3 m diameter corrugated steel culvert. | Langen 2011 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Wood Turtle (*Glyptemys insculpta*) | Long term study found turtles moved along a stream that passed through the culvert . | 3 m diameter culvert, 26 m long. | Parren 2013 |
| Wood Turtle | At least one Wood Turtle observed to cross through tunnel. | Open-top (grate) tunnel ~1.5 x 1.0 m (WxH) on dirt logging road. | Steinberg pers. comm. |
| Projects with unconfirmed crossings | | | |
| Painted Turtle (*Chrysemys picta*), Snapping Turtle | 6 Painted Turtles, 1 Snapping Turtle photographed in culverts. Plus Snapper tracks in culverts observed but no photos. Crossing not confirmed. | 3 crossing structures, each consisting of 2 culverts connected with fenced open area between. Size: 3.4 x 2.4 m box culvert, 24.1 m long, then 15.3 m fenced opening and then another culvert 24.1 m long. | Baxter-Gilbert 2014 |
| Snapping Turtle and Painted Turtle | No turtles detected in dry culvert with trail camera. | 1 dry culvert 1.2m diameter CSP; 2 wet culverts, one was 4m wide concrete box culvert, second unspecified. | Buchanan and Basso 2007 |
| Blanding's Turtle, Painted Turtle | Turtles could climb over 0.2 m high curb. Tunnel used by at least 1 Painted Turtle. | Three 4.6 x 0.9m (WxH) and 17.1 m long, open-top, 3-sided box culverts. | Compton and Seivert 2002 |
| Blanding's Turtle, Snapping Turtle, Painted Turtle | Blanding's Turtles commonly observed in dry and wet culverts. Snapping Turtles used wet culverts mainly, but one dry. Only 1 Painted found in a wet culvert. | 4 dry and 6 wet culverts, multiple sizes, with skylights. Minimum size 1.8 x 0.9m (WxH) and ~50 m long. | Dillon 2011, 2013 |
| Eastern Musk Turtle (*Sternotherus odoratus*), Florida Softshell | 1 Musk Turtle and 3 Softshells detected in 0.9m culvert. No turtles detected in other tunnels. | 3 sizes of tunnels: 0.9m diameter; 1.8x1.8 m box culvert, with 3 light boxes; 2.7 x 2.7m box culvert. All tunnels 44 m long. | Dodd et al. 2004 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Turtles | Monitored culverts in area with little roadkill before mitigation. Turtle roadkill went from 1 to 0. No turtles photographed in culverts. | 1 and 2 m diameter culverts (although described as square sometimes). | Garrah 2012 |
| Painted Turtle | No sex difference in climbing ability. In trials ~4% of turtles climbed over 0.45m tall fence with no flashing, while no turtles climbed fence with flashing. | n/a | Griffin 2005 |
| Eastern Box Turtle (*Terrapene carolina carolina*) | At least 3 turtles used pre-existing drainage culverts. | No details. | Hagood and Bartels 2008 |
| Snapping Turtle, Painted Turtle | Snapping Turtle photographed in both 0.8 and 0.9m culverts. Painted Turtle photographed in 0.8 m culvert. | Two culverts: 0.8 and 0.9 m diameter CSP. | Gunson et al. 2013 |
| Spotted Turtle | Review of other crossing structures. Reported Spotted Turtles using an arch culvert and a box culvert at two sites in Mass. | Arch culvert: 11 x 3.4m (WxH) and 12m long; Box culvert: 1.8 x 1.8 m and 16.8 m long. | Paulson 2010 |
| Blanding's Turtle | No mitigation. Studied roadill hotspots and movement patterns. Suggested crossing structures be an average of 500 m apart and no more than 1.5 km apart. | n/a | Riley et al. 2013 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Snapping Turtle | Detected by trail camera in at least one tunnel. No details on which tunnel. | 4 sizes, from 1.5 x 0.9m (WxH) to 2.7 x 1.8m. ~5 cm soil spread in bottom of culverts. | Rogers et al. 2009 |
| Snapping Turtle and other herps | Pooled use of all frogs, snakes, lizards and turtles. Most use of culverts 1.5m or more in width and 0.6-1.5m high. | Variety of existing culverts. | Smith 2003 |
| Snapping Turtle, Painted Turtle, Map Turtle (*Graptemys geographica*)(?) | At least 7 Snapping and 1 Painted Turtle used culverts. Map Turtle may have been seen swimming in one culvert. All but one reptile detected in ACO tunnel. | 1.8 m x 0.9 m concrete box culvert; 0.5 x 0.48 open-top ACO tunnel. | Whitelock 2014 |
| Outdoor lab experiments | | | |
| Painted Turtle | Tunnel placed on path of females on nesting forays. All turtles that reached the tunnel crossed through. Mean crossing time 113 sec (range: 60-197 sec). | 0.6 x 0.6m wooden tunnel, ~6 m long in field. | Jackson and Marchand 1998 |
| Painted Turtles | >85% of turtles used all tunnels. Largest tunnel had highest success rate and fastest crossing times. Turtles more hesitant to enter tunnels below grade. | Outdoor lab with 3 types of culverts: 0.6 x 0.6m, 0.6 x 1.2m, 1.2 x 1.2 m all 12.2 m long. Plywood with soil bottom. | Paulson 2010 |
| Snapping Turtle, Painted Turtle | Outdoor lab. No turtle climbed 0.6m fence. Turtles more apt to use tunnels at least 0.5m dia. All substrates used about equally. Longest tunnel had slightly less usage. Light did not affect usage. | Black PVC pipe culverts. Varied length (3-9.1 m), aperture size (0.3-0.8 m), substrate (bare, soil, gravel, concrete) and light permeability (0-4%). | Woltz et al 2008 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Painted Turtle, Blanding's Turtle, Spotted Turtle | Outdoor lab. Increased light increased crossing success. In closed-topped tunnels, the percentage of turtles crossing increased with increased culvert size. Low crossing rate (54% or less) with 80' culverts. | 3 tunnels sizes: 0.6 x 0.6m, 1.2 x 1.2m, 2.4 x 1.2m; two lengths: 40' and 80'. Varied light through ceiling (0, 75, 100%). | Yorks et al. 2011 |
| **Snake Crossing Structure Research** | | | |
| Projects with confirmed crossings | | | |
| Eastern Massasauga (*Sistrurus catenatus*) | 4 snakes detected under crossing structures (likely crossing) in 2013. | 4 open-grate crossing structures. ~1 x 1m (WxH) under 2-lane gravel roads. | Colley pers. comm. |
| Eastern Garter Snake (*Thamnophis sirtalis sirtalis*), Ribbon Snake (*Thamnophis sauritus sauritus*) | Outdoor lab. At least 70% of Ribbons and 90% Garters crossed at all widths. All Garters crossed whether substrate was soil or water. In 1.3m culvert >90% of Ribbons crossed regardless of substrate. In 0.33 m culverts Ribbons had lower crossing success with soil (50%), compared with water (70%). In real culverts, Ribbons had low crossing success (<30%) in small culverts but high success (~80%) in large culverts. | Outdoor lab box culverts 0.66 m high and variable width (0.33-1.33m) and 5 m long. Also examined crossing of real culverts ~1 m and ~0.5 m in diameter and 10 m long. Some culverts dry (soil bottom) and some with liner with ~7 cm of water. | Eads 2013 |
| Northern Watersnake (*Nerodia sipedon sipedon*) | >80% crossing success with both size culverts. | 0.5 and 1.0 m culverts. No other detail. | Eads et al. 2012 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Timber Rattlesnake (*Crotalus horridus*), Ratsnake (*Pantherophis spiloides*) | Two radio-tracked rattlesnakes used one culvert during the culvert's first year. Snakes spent 10-14 days near fence before crossing through culvert. Some snakes went around fence and others used gaps in fence. 1 possible Ratsnake (or Racer) was also detected in one culvert. | 5 concrete closed-top box culverts 0.91 x 0.41 m (WxH) and 15 m long. | Laidig and Golden 2004 |
| Eastern Garter Snake | Tunnels used commonly. Fence end roadkill, some snakes got over fence. | 0.25-0.30 m diameter steel pipe. | Roberts 2010 |
| Unidentified snakes | 3 crossings by a snake detected in sand tracking. | Concrete box culvert 2.74 (W) x1.83 (H)m and 30.5 m long. | Rogers et al. 2009 |
| Snakes | Used sand tracking to detect usage. 1 snake crossing over 8 days in spring, and 1 crossing over 8 days in summer. | 9 concrete box culverts, 2.4 x 1.2m and 18 m long. Culvert bottoms scattered with small stones and a thin layer of silt. | Taylor and Goldingay 2003 |
| Milos Viper (*Macrovipera schweizeri*) | No snakes found on roads in areas with barriers. Snakes crossed through underpasses. Mean of 77% of snakes that encountered an underpass crossed through. | 6 underpasses, 4 types. No details. | Yannis 2011 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Projects with unconfirmed crossings | | | |
| Various species | Snakes found in both sizes of round culvert. | looked at use of existing culverts: 0.6 m and 1.0 m diameter CSP, concrete box culverts (size not given). | Arizona Game and Fish 2010 |
| Snakes and lizards pooled; no species named | In general, reptile use of culverts was negatively correlated with culvert length. | Existing drainage culverts, no specs provided. | Ascensão and Mira 2007 |
| Northern Watersnake, Red-bellied Snakes (*Storeria occipitomaculata*) | 3 Watersnakes photographed in culvert, 1 juvenile Red-bellied observed in culvert. | 3 crossing structures, each consisting of 2 culverts connected with fenced open area between: 3.4 x 2.4 m box culvert, 24.1 m long, then 15.3 m fenced opening and then another culvert 24.1 m long. | Baxter-Gilbert 2014 |
| Eastern Garter Snake | No confirmed crossing by any snake, and very few captures away from road. | 2 bridges, 1 culvert 1.65m wide. | Bellis et al. 2007 |
| Unspecified species of Garter Snake | 20 detected under bridge via sand tracking. Culverts not well monitored. | Bridge 5-9'aboveground, 400' long; multiple size tunnels, as small as 0.5m diameter culverts. | de Rivera and Bliss-Ketchum 2010 |
| Unidentified snakes (likely Garter and Northern Watersnake) | 39-50 snakes per yr (3 yr) in wet and dry culverts. Largest percentage in dry culverts, but may have been easier to photograph in those culverts. Snakes photographed basking in light from skylights. | 4 dry and 6 wet culverts, multiple sizes, with skylights. Smallest tunnel 1.8 x 0.9m (WxH). | Dillon 2011, 2013 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Eastern Racer (*Coluber constrictor*), Eastern Ratsnake (*Pantherophis alleghaniensis*), Eastern Ribbonsnake, plus other non SAR spp | 1 Racer, 1 Ratsnake and 4 Ribbonsnakes detected in 1.8 x1.8m tunnels but crossing not confirmed. Not detected in other size culverts. | 3 sizes of tunnels: 0.9m diameter; 1.8 x 1.8 m box culvert, with 3 light boxes; 2.7 x 2.7m box culvert. All tunnels 44 m long. | Dodd et al. 2004 |
| Snakes | Monitored culverts in an area with little road kill before mitigation. No change in roadkill. Snakes not photographed in culverts. | 1 and 2 m diameter culverts (although described as square sometimes). | Garrah 2012 |
| Northern Watersnake, Eastern Gartersnake, Black Ratsnake | Watersnake found in association with 6 culverts, Ratsnake with 3, and Gartersnake with 2 (sizes of culverts not given). | Monitored 265 culverts of various sizes. | Gates and Sparks 2011 |
| Timber Rattlesnake | Used by some snakes. | ~0.3m diameter culvert. | Jacobson pers. comm. |
| Snakes | To prevent snakes getting through fence attached a fine mesh (0.6x0.6 cm) to turtle fencing. 30 cm high mesh did not prevent all passage, but 60 cm high mesh was more successful. No monitoring of culvert for snakes. | 1.3 m diameter corrugated steel culvert. | Langen 2011 |
| Northern Watersnake, Eastern Gartersnake | Watersnake entered and turned around in 0.9 m culvert. Gartersnake observed in 0.9 m culvert. | Two culverts: 0.8 and 0.9m diameter CSP. | Lesbarrères Gunson et al. 2013 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Massasauga | No proof of crossing, but no DOR snakes in 4 years of monitoring road. | 6 open-topped structures, with rock substrate, ~1.0 x 1.5m (WxH) and ~6 m long. | Lewis pers. comm. |
| Wandering Garter Snake (*Thamnophis elegans vagrans*) | Photographed in tunnels 48 times. | 4 ACO box culverts, 0.5 m wide and 0.33 m high and ~12 m long. Slots along the top. Tunnels 80-110 m apart. | Pagnucco et al 2011, 2012 |
| Grass Snake (*Natrix natrix*) | Detected in culverts. Believed to be hunting frogs in wet culvert. | Three 1m dia concrete culverts, 34 m long. Opening in middle of culvert to allow in light and water. | Puky et al. 2007 |
| Grass Snake | Shed skins found in tunnels. | Eight 0.6-0.9 m diameter culverts, 8-9 m long. Five culverts had light shafts. | Puky et al. 2007 |
| Massasauga, Eastern Hog-nosed Snake, Milksnake (*Lampropeltis elapsoides*), Northern Ribbonsnake (*Thamnophis sauritus septentrionalis*) | Milksnake and Northern Ribbonsnake confirmed in tunnels. Possible Hog-nosed, but photo blurry. | Concrete box culvert 1.8 x 1.2 m (WxH). | Rouse 2005 |
| Eastern Garter Snake and other herps | Pooled use of all frogs, snakes, lizards and turtles. Most use of culverts 1.5m or more in width and 0.6-1.5m high. | Variety of existing culverts. | Smith 2003 |
| Eastern Garter, unidentified snakes | At least 2 Garter and 2 unidentified snakes used culverts. All but one reptile detected in ACO tunnel. May have been more use but trail cameras set to shoot every 15 min. | 1.8 m x 0.9 m concrete box culvert; 0.5 x 0.48 open-top ACO tunnel. | Whitelock 2014 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Outdoor lab experiments | | | |
| Small (<20g) and medium-sized (75-250g) snakes | No snake able to climb over any fence. Medium-sized snakes could escape through ½" mesh. Small snakes could escape through ½ and ¼" mesh. Some snakes got caught in ½" mesh and had to be cut free. | n/a<br>Tested fencing types. | Smith and Noss 2011 |
| **Lizard Crossing Structure and Fencing Review** | | | |
| Projects with confirmed crossings | | | |
| Various lizards (no skinks) | Lizards found in all 3 types of culverts. More spp in smallest size culvert. Highest crossing rate (0.4) in box culverts. | looked at use of existing culverts: 0.6m and 1.0m dia CSP, concrete box culverts (size not given). | Arizona Game and Fish 2010 |
| Flat-tailed Horned Lizards (*Phrynosoma mcallii*) | Experimental tests of simulated culverts. 12 of 54 lizards crossed. All size tunnels used, but the 1.0m CSP without skylights was used by more lizards. Dark culverts were used more frequently than culverts with skylights. | tested 3 sizes of tunnel: 0.6 m and 1.0 m CSP, and 2.6 x 1.3m (WxH) plywood box culverts. Two of each culvert size, one with skylights and one without. All tunnels were ~13 m long and had 2.5-7.5 cm of sand in the bottom of the tunnels. | Painter and Ingraldi 2007 |
| Lace Monitor (*Varanus varius*) and other unidentified lizards | Australian study. 11 crossings by lizards during limited monitoring. | 9 concrete box culverts, 2.4 x 1.2m and 18 m long. Culvert bottoms scattered with small stones and a thin layer of silt. | Taylor and Goldingay 2003 |

| Species | Comments | Crossing Structure | Crossing Structure Reference |
|---|---|---|---|
| Projects with unconfirmed crossings | | | |
| Snakes and lizards pooled; no species named | In general, reptile use of culverts was negatively correlated with culvert length. | Existing drainage culverts, no specs provided. | Ascensão and Mira 2007 |
| Five-lined Skink (*Plestiodon fasciatus*) | Skinks observed around the entrance of 5 culverts (sizes not given). Apparently used culvert entrances for basking and foraging but did not appear to cross through culverts. | Monitored 265 culverts of various sizes. | Gates and Sparks 2011 |
| Northern Fence Lizard (*Sceloporus undulatus hyacinthinus*) | Detected in culverts 12 times during two month period. | 5 concrete closed-topped box culverts 0.91 x 0.41m (WxH) and 15 m long. | Laidig and Golden 2004 |
| Sand Lizard (*Lacerta agilis*) | Lizards lived on overpasses, using them for hiding places, basking sites and foraging habitat. | Wildlife overpass. Details not provided. Shrubs planted at side of overpass. | Puky et al. 2007 |
| Five-lined Skink and other herps (pooled all amphibians and reptiles) | In general, amphibians and reptiles made most use of culverts 1.5m or more in width and 0.6-1.5m high. | Variety of existing culverts. | Smith 2003 |
| Outdoor lab experiments | | | |
| Five-lined Skink | Skinks able to crawl through ¼ mesh fence. The aluminum flashing was the only fence that stopped all skinks from escaping. | n/a<br>Tested fencing types. | Smith and Noss 2011 |

## Appendix D: Links and Other Resources

### Applicable Legislation and MNRF policies

General Regulation under the Endangered Species Act, 2007: Ontario Regulation 242/08
https://www.e-laws.gov.on.ca/html/regs/english/elaws_regs_080242_e.htm

Permits under the Endangered Species Act
http://www.ontario.ca/environment-and-energy/endangered-species-permits-and-authorizations

Overall Benefit Permit
http://www.ontario.ca/environment-and-energy/endangered-species-act-overall-benefit-permits

Step-by-step guide to applying for an overall benefit permit
http://www.ontario.ca/environment-and-energy/endangered-species-act-overall-benefit-permits (click link on right side of above page: "How to apply")

Streamlined approvals under the Endangered Species Act
(also known as Registering online for Natural Resources activities)
https://www.ontario.ca/environment-and-energy/natural-resources-registration-guide

Development and infrastructure projects and endangered or threatened species
http://www.ontario.ca/environment-and-energy/development-and-infrastructure-projects-and-endangered-or-threatened-species

### Ontario Species at Risk Information

Ontario Species at Risk website
http://www.ontario.ca/environment-and-energy/species-risk

Species at Risk Reference Toolbox
http://www.ontario.ca/environment-and-energy/species-risk-guides-and-resources

### Best Practices and Guidance

Reptile and Amphibian Exclusion Fencing: Best Practices
http://files.ontario.ca/environment-and-energy/species-at-risk/mnr_sar_tx_rptl_amp_fnc_en.pdf

Passage Assessment System for Evaluating the Permeability of Existing Structures
http://www.wsdot.wa.gov/research/reports/fullreports/777.1.pdf

### Design Examples

Amphibian Tunnel Project in Waterton Lakes National Park, Vancouver
http://naturevancouver.ca/sites/naturevancouver.ca/VNHS%20files/Amphibian%20Tunnel%20Project.pdf

## Appendix E: Sample Tunnel Costs Table (2014)

| Tunnel type | Model Number | Provider | Size of culvert | Length (m) (estimate) | Cost | Installation costs (very approximate) | Cost/m (culvert only) |
|---|---|---|---|---|---|---|---|
| Terrestrial concrete box culvert | Reinforced non-standard concrete box culvert | M-CON Pipe and products Inc. | 1.8m x 0.9m | 16.3 | $25,000 | $15,000 | $1,533 |
| Terrestrial open-top culvert | ACO AT500 | ACO Systems Ltd. | 0.50m x 0.48m | 16.2 | $13,000 | $11,000 | $802 |
| Hydraulic Concrete Box culvert | Reinforced non-standard concrete box culvert | M-CON Pipe and products Inc. | 3.0 m x 2.1m | 18.3 | $65,000 | $45,000 | $3,551 |
| Concrete Box culvert | Includes all materials | MTO | 1.8m x 1.8m | 48 | $225,000 | | $4,687 |
| Concrete Box culvert | Considered a structure, so includes only the cost of culvert | MTO | 3.3m x 2.8m | 48 | $375,000 | $325,000 | $7,812 |
| Concrete Box culvert | | MTO | 1.0m x 1.0m | 48 | $150,000 | | $3,125 |

| Cost/m (installed) | Comments (installation limitations) | Additional information: | Source |
|---|---|---|---|
| $2,453 | | Additional fixed costs associated with each mobilization, special environmental precautions and insurances -Soil conditions play a crucial part in costs; -Generally, add 20% per project over $150,000, add 30% for smaller projects- Add $250,000 per site for special shoring-. | Rick Levick, Longpoint Improvement Committee |
| $1,481 | | | |
| $6,010 | Cost about 30% more than typical installation reflected in table due to digging to connect channels to marsh on one side and the bay on the other. | | |
| | | Actually for 2 culverts (= 1 eco-passage) for 4-lane hwy 69: each culvert is 24m long (spanning 2 lanes of highway, plus shoulders), and they're separated by a 15.3m gap (the median) | Andrew Healy, MTO |
| $14,583 | True cost is much greater than structure alone due to blasting, footings etc., costs could be up to 700 K with installation | | |
| $3,125 | This is a guess and can range from 100 - 200 K | | |

| Tunnel type | Model Number | Provider | Size of culvert | Length (m) (estimate) | Cost | Installation costs (very approximate) | Cost/m (culvert only) |
|---|---|---|---|---|---|---|---|
| Corrugated steel Pipe culverts | | Atlantic Industries Ltd. | 1.2 m round | 16.5 | $2,392 | + | $145.00 |
| Corrugated Metal Arch c/w metal footings | | Atlantic Industries Ltd. | 0.6 m rise x 1.22 m span | 16.5 | $16,360 | + | $991.56 |
| Corrugated steel Pipe culverts | | Atlantic Industries Ltd. | 3 m round | 16.5 | $9,240 | + | $560.00 |
| Corrugated Metal Arch c/w metal footings | | Atlantic Industries Ltd. | 2.99 m span x 1.45 m rise | 16.5 | $24,024 | + | $1,456 |

| Cost/m (installed) | Comments (installation limitations) | Additional information: | Source |
|---|---|---|---|
| + | Minimal assembly required. | Various coatings available. Price based on a coating common on low volume roads. Pipe material is subjective to enviornmental conditions. Reference Ontario Gravity Pipe Study for more specific detail. | Kevin Williams, Atlantic Industries Ltd. |
| + | Available preassembled or assembled in place. Can be assembled by person (no hoisting equipment) for a rough estimated cost of $50/m. | Open-bottom which can be constructed to maintain a more natural environment. Pricing based on low to moderate covers (0.6 m to 2 m cover). Greater covers are permitted but price will vary. | Kevin Williams, Atlantic Industries Ltd. |
| + | Minimal assembly required. | Various coatings available. Price based on a coating common on low volume roads. Pipe material is subjective to environmental conditions. Reference Ontario Gravity Pipe Study for more specific detail. | Kevin Williams, Atlantic Industries Ltd. |
| + | Available preassembled or assembled in place. Can be assembled by person (no hoisting equipment) for a rough estimated cost of $50/m. | Open-bottom which can be constructed to maintain a more natural environment. Pricing based on low to moderate covers (0.6 m to 2 m cover). Greater covers are permitted but price will vary. | Kevin Williams, Atlantic Industries Ltd. |

| Tunnel type | Model Number | Provider | Size of culvert | Length (m) (estimate) | Cost | Installation costs (very approximate) | Cost/m (culvert only) |
|---|---|---|---|---|---|---|---|
| Corrugated Metal Arch c/w concrete footings and headwall | Includes headwall costs. Shorter lengths conduits required with headwalls. | Atlantic Industries Ltd. | 2.99 m span x 1.45 m rise | 10 | $29,617 | + | $2,961 |

| Cost/m (installed) | Comments (installation limitations) | Additional information: | Source |
|---|---|---|---|
| + | Available preassembled or assembled in place. Hoisting equipment required for headwalls and footings. | Open-bottom which can be constructed to maintain a more natural environment. Price/m value is inflated by inclusion of headwalls but headwalls permit shorter length conduits. Pricing based on low to moderate covers (0.6 m to 2.5 m cover). Greater covers are permitted but price will vary. Headwalls are intended for more aesthetically pleasing requirements. | Kevin Williams, Atlantic Industries Ltd. |

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RESEARCH ARTICLE

# Genetic source–sink dynamics among naturally structured and anthropogenically fragmented puma populations

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## Abstract

Fragmentation of wildlife populations is increasing on a global scale and understanding current population genetic structure, genetic diversity, and genetic connectivity is key to informing wildlife management and conservation. We genotyped 992 pumas (*Puma concolor*) at 42 previously developed microsatellite loci and identified 10 genetic populations throughout the states of California and Nevada, USA. Although some genetic populations had large effective population sizes, others were small and inbred. Genetic diversity was extremely variable (heterozygosity, uHe = 0.33–0.53), with some populations nearly as low as an endangered subspecies, the Florida Panther (*P. c. coryi*, uHe = 0.24). Specifically, pumas in the Sierra Nevada were genetically diverse and formed the largest genetic source population in the region. In contrast, coastal and southern populations surrounded by urbanization had low genetic diversity, fragmented gene flow, and tended to be genetic sinks. The strong population genetic structuring of pumas across California ($F_{ST}$ = 0.05–0.39) is vastly different than other genetic studies in less-urbanized states, including our analysis in Nevada, where pumas had few barriers to gene flow and weak population differentiation. Our results have far-reaching conservation and management implications for pumas and indicate large-scale fragmentation in one of North America's most biodiverse and rapidly-urbanizing regions.

**Keywords** Mountain lion · Cougar · *Puma concolor* · Population genetics · Genetic structure

## Introduction

Fragmentation of wildlife habitat and resultant impacts to populations are increasing worldwide and urbanization is one of the primary contributors (Crooks et al. 2017; Fahrig 2003; Haddad et al. 2015; Newbold et al. 2016). Unlike

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natural barriers that have impacts over a geological timescale (Albert et al. 2016), urbanization can have more immediate effects on gene flow among populations (Balkenhol and Waits 2009; Karlson et al. 2014). Gene flow is critically important to individual fitness and to the evolutionary potential of populations because successful migrants can diversify gene combinations (i.e., increase heterozygosity) and introduce new genetic material (i.e., increase allelic richness) (Caballero and García-Dorado 2013; Chapman et al. 2009; Frankham 2015). Without receiving gene flow, small populations are especially subject to inbreeding, genetic drift, and increased extinction risk (Carlson et al. 2014; Wootton and Pfister 2015).

Population fragmentation is increasingly evident for species located in the urbanized western United States (Buchalski et al. 2016; Delaney et al. 2010; Fisher and Shaffer 1996; Tuma et al. 2016), including the puma (*Puma concolor*) (Beier 1995; Gray et al. 2016), which is becoming a model for studying genetics of isolated populations (Ernest et al. 2014; Gustafson et al. 2017; Johnson et al. 2010; Riley et al. 2014). Despite the long-distance dispersal ability of pumas (Hawley et al. 2016; Newby et al. 2013; Pierce et al. 1999; Thompson and Jenks 2005), gene flow among adjacent puma populations has been nearly negated by freeways in densely populated Southern California (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014). Consequently, some California puma populations have become functionally isolated and have experienced rapid population divergence and inbreeding (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014; Vickers et al. 2015) with concerns for extinction (Benson et al. 2016). Given that *P. concolor* and other wide-ranging species serve as umbrella species (Carroll et al. 2001; Maehr et al. 2002; Thorne et al. 2006)—the conservation of which indirectly provides protection for many other species (Roberge and Angelstam 2004)—the low genetic diversity of puma populations in human-fragmented habitats suggests that a large-scale ecological problem may be occurring in some of the most biologically-diverse regions of North America (Calsbeek et al. 2003; Dobson et al. 1997).

During the late Pleistocene, pumas were extirpated from North America and repopulated by migrants from South America (Culver et al. 2000). As a result, pumas in North America compose a single phylogenetic group (based on mtDNA) and exhibit founder effects (i.e., reduced population genetic diversity based on mtDNA and microsatellites) compared to pumas in South America and Central America (Culver et al. 2000). Therefore, it is critical to understand effects of fragmentation on populations from this North American lineage. A previous genetic analysis along the west coast of the United States indicated that pumas in California did not exist as a single population and suggested urbanization may have led to genetically-depauperate, fragmented populations (Ernest et al. 2003). In addition, a population genetic analysis in Nevada indicated there were asymmetric migration rates between the two states, and that pumas from Nevada were a genetic source for genetic-sink populations in California (Andreasen et al. 2012). However, these previous reports relied on a limited number of genetic loci ($\leq$13 microsatellites) and investigators did not sample across the two states. In this study, we attempted to address these limitations and provide a more comprehensive view of puma genetic diversity and gene flow within and among California and Nevada.

Our aim was to identify the number and spatial structure of puma populations across California and Nevada and the extent of gene flow among the populations. In doing so, we were able to identify genetic source and sink populations as well as isolated populations with limited gene flow. We expected pumas would exhibit genetic structure associated with both natural geographic features and anthropogenic development. Given the complex structure of ecoregions and large human population in California (> 39 million people; 92.5/km$^2$; US Census Bureau 2016), we hypothesized pumas in California would exhibit more population divergence and less interpopulation gene flow relative to pumas in Nevada, which have access to more contiguous ecoregions with fewer humans (< 3 million people; 10.3/km$^2$; US Census Bureau 2016). To address these hypotheses, we genotyped 992 pumas at 42 microsatellite loci across California and Nevada. We then identified regional populations using population assignment models and evaluated functional connectedness of puma populations by modeling population divergence and computing bi-directional migration rate estimates.

## Materials and methods

### Sampling and extractions

We obtained tissue or blood samples from 992 pumas captured alive, found dead, or legally killed by authorized agencies for livestock depredation, public safety, or sport hunting (Nevada only) during 1992–2016 (Fig. 1). Approximately 49% of individuals sampled were legally killed, 31% were from captures, 11% were hit by vehicles, and the rest were found dead of other causes. We isolated genomic DNA using QIAGEN DNeasy Blood & Tissue kits (QIAGEN Inc., Valencia, CA, USA).

### Genotyping

We genotyped each individual puma at 42 previously developed microsatellite loci, plus a single sex-linked locus (Ernest et al. 2003, 2014; Riley et al. 2014) and ran polymerase chain reactions on ABI 2720 thermocyclers (Life Technologies, Carlsbad, CA, USA) using QIAGEN

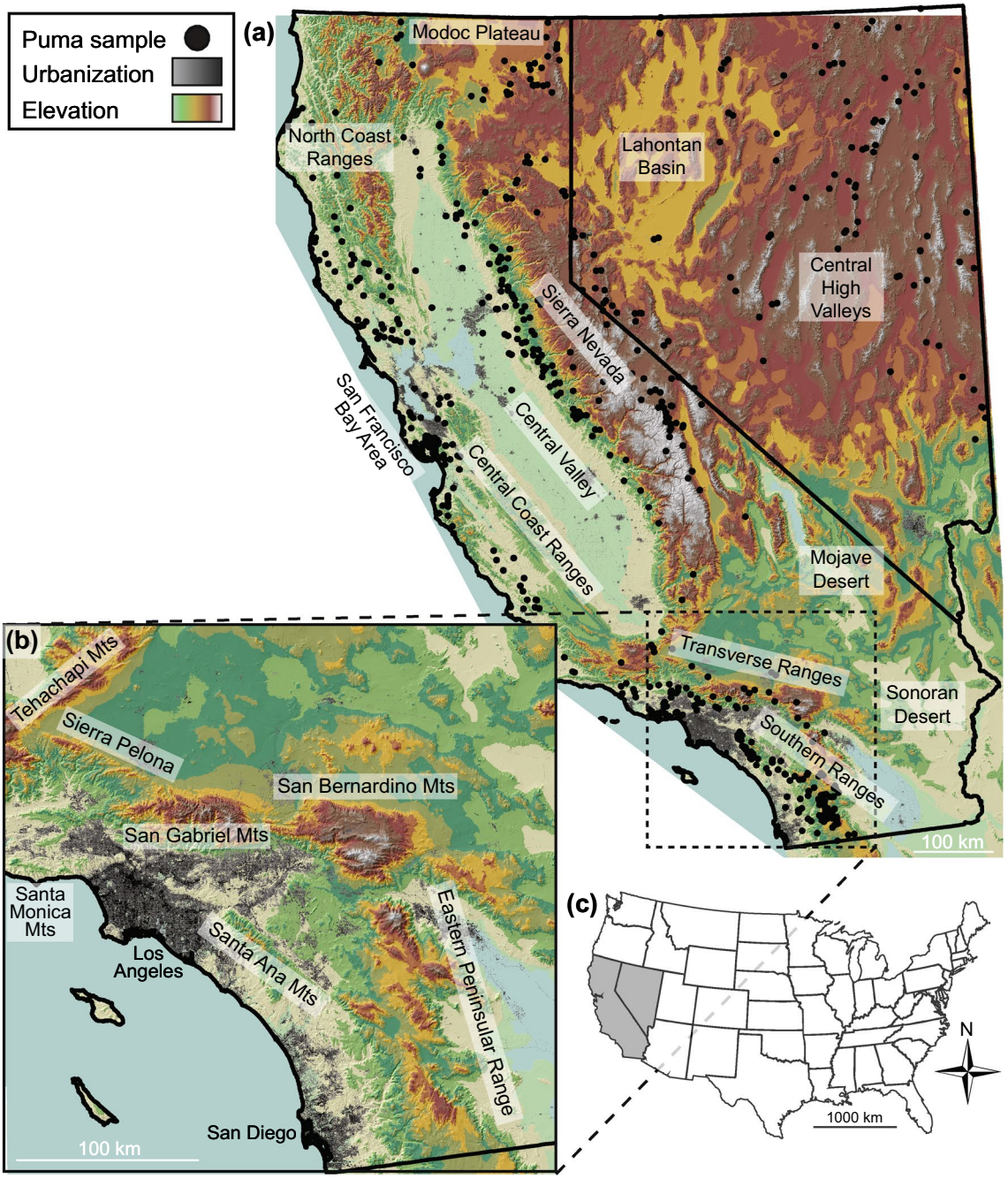


**Fig. 1** Map of our study system, including **a** sampling locations of 992 pumas and ecoregions, **b** specific mountain ranges within the Transverse and Southern Ranges, and **c** an inset map of the United States of America showing the locations of California and Nevada. Elevation data source: USGS national elevation dataset (http://nationalmap.gov). Dark circles indicate locations where pumas were sampled, the gray to black scale indicates low to high urbanization, and the blue to white scale indicates 0 m elevation (sea level) to 4,421 m elevation

Multiplex PCR kits with Q solution (Table S1) following the protocols of Gustafson et al. (2017). We included negative and positive controls in each PCR run and visualized fragments with STRand version 2.3.69 (Toonen and Hughes 2001). For each locus, we confirmed heterozygous genotypes at least twice and homozygous genotypes at least three times.

## Population genetic structure

The spatial arrangement of sample locations can confound population genetic analyses (Meirmans 2012; Schwartz and McKelvey 2009). Thus, we used spatially-explicit hierarchical Bayesian clustering programs TESS 2.3 (Durand et al. 2009a) and GENELAND 4.0 (Guillot et al. 2005b). We tested for consistency among programs because TESS has been shown to identify finer-scale hierarchical puma population genetic structure compared to GENELAND (Gustafson et al. 2017). In general, TESS outperforms GENELAND in the presence of isolation-by-distance (Safner et al. 2011) whereas GENELAND outperforms TESS at detecting genetic barriers to dispersal (Blair et al. 2012; Safner et al. 2011).

In TESS, the number of populations (K) must be specified and tested over a range of possible values. Model selection must be used to determine the K with the best fit to the data. We followed developer instructions for determining K and population assignments. First, we ran 10 non-admixture models for each K from 2 to 20. For model comparisons, TESS computes a deviance information criterion (DIC). We ran 10 spatially-conditional auto-regressive admixture models for each K to the DIC plateau of non-admixture models (Figs. S1, S2). All models included pairwise great circle geographic distances for weighting the Voronoi neighborhood, 100,000 iterations, and a 25,000 iteration burn-in period. We retained 20% of the models exhibiting the lowest DIC scores and used CLUMPP 1.1.2 to perform model-averaging (Jakobsson and Rosenberg 2007).

In GENELAND, K is optimized by the model. We followed developer recommendations for determining K and individual population assignments (Guillot et al. 2005a). First, we identified a distribution of K from initial models, and then we ran correlated allele frequency models allowing K to vary within its distribution from the initial models (Fig. S1). Finally, we ran 5 spatial, correlated allele frequency models with K fixed at the mode and selected the model with the highest negative log-likelihood value for further inference. Each run included an uncertainty on GPS coordinates of 0.1 decimal degrees (~ 11 km), 1,000,000 iterations, a thinning interval of 10,000, and a 25% burn-in period prior to extracting model output. We assigned individuals to populations based on their highest assignment probability. To visualize the probability of population membership across the study area, we used package POPSutilities 1.0 in R 3.3.0, which interpolates admixture coefficients using geospatial kriging (Jay et al. 2012).

Temporal variation in sampling can bias spatial population genetic analyses; however, spatially-explicit Bayesian clustering models should account for most temporal variation (Durand et al. 2009b; François and Durand 2010). Populations did not group based on sampling date in TESS or GENELAND. Additionally, isolation-by-distance was significant across our study area ($R^2 = 0.15$, $P < 0.001$). Although TESS and GENELAND showed nearly identical results, we used TESS admixture models for analyses and inferences because TESS outperforms GENELAND in the presence of isolation-by-distance.

## Genetic diversity

We tested for linkage disequilibrium, deviations from Hardy–Weinberg proportions, and null alleles in GENEPOP 4.5.1 (Rousset 2008). For each identified population, we calculated standard measures of genetic diversity and used 1000 permutations to test for significant genetic isolation-by-distance in GenAlEx 6.502 (Peakall and Smouse 2006, 2012). To measure the number of alleles, we calculated allelic richness using rarefaction methods which correct for sample size in FSTAT 2.9.3.2 (Goudet 1995). To assess inbreeding, we calculated internal relatedness using package Rhh 1.0.2 in Program R 3.3.0 (Alho et al. 2010). We calculated effective population size ($N_e$) for each population using NeEstimator 2.01 using the linkage disequilibrium method assuming random mating (Do et al. 2014). Because the inclusion of low-frequency alleles can upwardly bias estimates of $N_e$ (Waples and Do 2010), we ran two separate models including alleles with frequencies $\geq 5\%$ or $\geq 1\%$. To test for evidence of recent reductions in $N_e$ (i.e., genetic bottlenecks), we used program BOTTLENECK 1.2.02 to determine if a population exhibited a significant number of loci with heterozygote excess (Piry et al. 1999). For each population identified by assignment models, we performed bottleneck analyses using two-phase (70:30 step-wise:infinite-alleles) microsatellite mutation models for 100,000 iterations.

We used biotools 3.1 (da Silva et al. 2017) in R to obtain spatial unbiased genetic diversity estimates [uHe: unbiased expected heterozygosity; (Nei 1978)] based on the interpolation of individual estimates (Manel et al. 2007). We minimized spatial extrapolation by using a radius of 500 m and reduced bias by setting the neighborhood size (i.e., minimum number of individuals used to calculate uHe) to 2. The mean size of each neighborhood was 14.6 and 42.5% of the neighborhoods contained at least 10 individuals.

## Population differentiation and genetic source–sink dynamics

We used three complementary approaches to assess functional population connectivity, including a discriminant analysis of principal components (DAPC), pairwise estimates of population divergence ($F_{ST}$), and pairwise estimates of bi-directional migration rates ($m$). The DAPC uses linear combinations of alleles to maximize between-population genetic variation and provides a graphical representation

of functional connectivity among genetic clusters (Jombart et al. 2010).

We implemented the DAPC in program R using package adegenet 2.0.1 (Jombart 2008). The identified number of genetic clusters in adegenet agreed with TESS and GENELAND (Fig. S3). Because the algorithm for individual assignments in adegenet is not as powerful as Bayesian population assignment algorithms (Jombart et al. 2010), we defined populations in the DAPC using results from the Bayesian population assignments. Because we were not assigning individual membership probabilities in the DAPC, we retained all information (i.e., 344 PCA axes and all 9 discriminant functions) in the analysis. Our results from retaining all information did not differ from results when only retaining an estimated optimal number of PCA axes using the α-score method. Pairwise population divergence estimates ($F_{ST}$) were calculated in GenAlEx using 999 permutation tests for significance. To conform to the expectations of genetic isolation-by-distance, rather than an island model, we also calculated Rousset's $F_{ST}/(1-F_{ST})$ (Rousset 1997).

We used program BayesAss 3.0 to estimate migration rates (*m*) among populations identified by population assignment models (Wilson and Rannala 2003). We used 10 randomly-seeded runs each with 5,000,000 iterations, a burnin of 1,000,000, and thinning interval of 1000. Posterior mean parameter estimates were nearly identical among runs, and all trace files indicated convergence of model parameters (Meirmans 2014). We tested the hypothesis of Andreasen et al. (2012) that Nevada pumas were a genetic source for California pumas by summing emigration rates and subtracting the sum of immigration rates for each population (Andreasen et al. 2012). Positive numbers indicate the population was a genetic source whereas negative numbers indicate a sink. We used package circlize 0.3.7 in program R to visualize bi-directional migration rates estimated in BayesAss (Gu et al. 2014).

## Results

### Population genetic structure and diversity

Our analyses revealed that pumas in California exhibited strong population genetic structure and some California populations had extremely low levels of genetic diversity. We identified nine genetic clusters in California and one genetic cluster in Nevada (Figs. 2, S1, S2, S4). We classified these 10 genetic clusters as genetic populations, including the Nevada (NV), Eastern Sierra Nevada (ESN), Western Sierra Nevada (WSN), North Coast (NC), Northern section of the Central Coast (CC-N), Central section of the Central Coast (CC-C), Southern section of the Central Coast (CC-S), San Gabriel/San Bernardino (SGSB), Santa Ana (SA), and Eastern Peninsular Range (EP) populations (Fig. 2).

The genetic diversity of California puma populations exhibited a large amount of variation with some populations having estimates similar to other large populations and some exhibiting estimates nearly as low as the endangered Florida Panther. The NV, ESN, and WSN populations had the highest estimates of genetic diversity compared to other populations (Table 1). Regionally, the Modoc Plateau and Sierra Nevada contained individuals that had consistently high genetic diversity (Fig. 3). Although the NV population had high genetic diversity, the individual-based analysis indicated spatially-heterogenous genetic diversity across Nevada with low levels occurring near the Lahontan Basin (Fig. 3). The CC-C population had relatively intermediate levels of genetic diversity (Table 1). The SA population had the lowest genetic diversity observed across all estimates, followed by the SGSB, NC, CC-S, and CC-N populations. SA also had the highest measure of internal relatedness. WSN had the largest effective population size ($N_e$), followed by NV, NC, and CC-C (Table 2). All other populations had an $N_e$ of $< 50$ (often given as a desirable minimum from a conservation genetics point of view; Frankham 1995; Mace et al. 2008), and CC-S and SGSB had extremely low effective population sizes ($\leq 5$). All populations except NV and NC exhibited evidence of a prior genetic bottleneck (Table 2).

### Population differentiation and genetic source–sink dynamics

Our discriminant analysis of principal components (DAPC) revealed that puma populations in California had low connectivity compared to pumas in Nevada which were composed of a single genetic population that exhibited high connectivity with several California populations. The first axis (x-axis; 33.3% of total variation) of the DAPC broadly corresponded to a latitudinal population separation with north to the left and south to the right (Fig. 4a). The second axis (y-axis; 24.4%) separated populations longitudinally and primarily separated central coast populations from southern populations (Fig. 4a). The NV, ESN, WSN, and NC populations grouped together, as did the CC-N, CC-C, and CC-S populations. The SA and EP populations grouped slightly but were separated from all other populations (Fig. 4a). Lastly, the SGSB was intermediate relative to all other populations, but was most closely-related to the WSN population (Fig. 4a).

Bi-directional migration rate models indicated there were 5 genetic source populations (i.e., ESN, WSN, CC-N, CC-C, EP) and 5 genetic sink populations (i.e., NV, NC, CC-S, SGSB, SA), however, there was only weak evidence indicating CC-N and NC were source and sink populations, respectively. Bi-directional migration

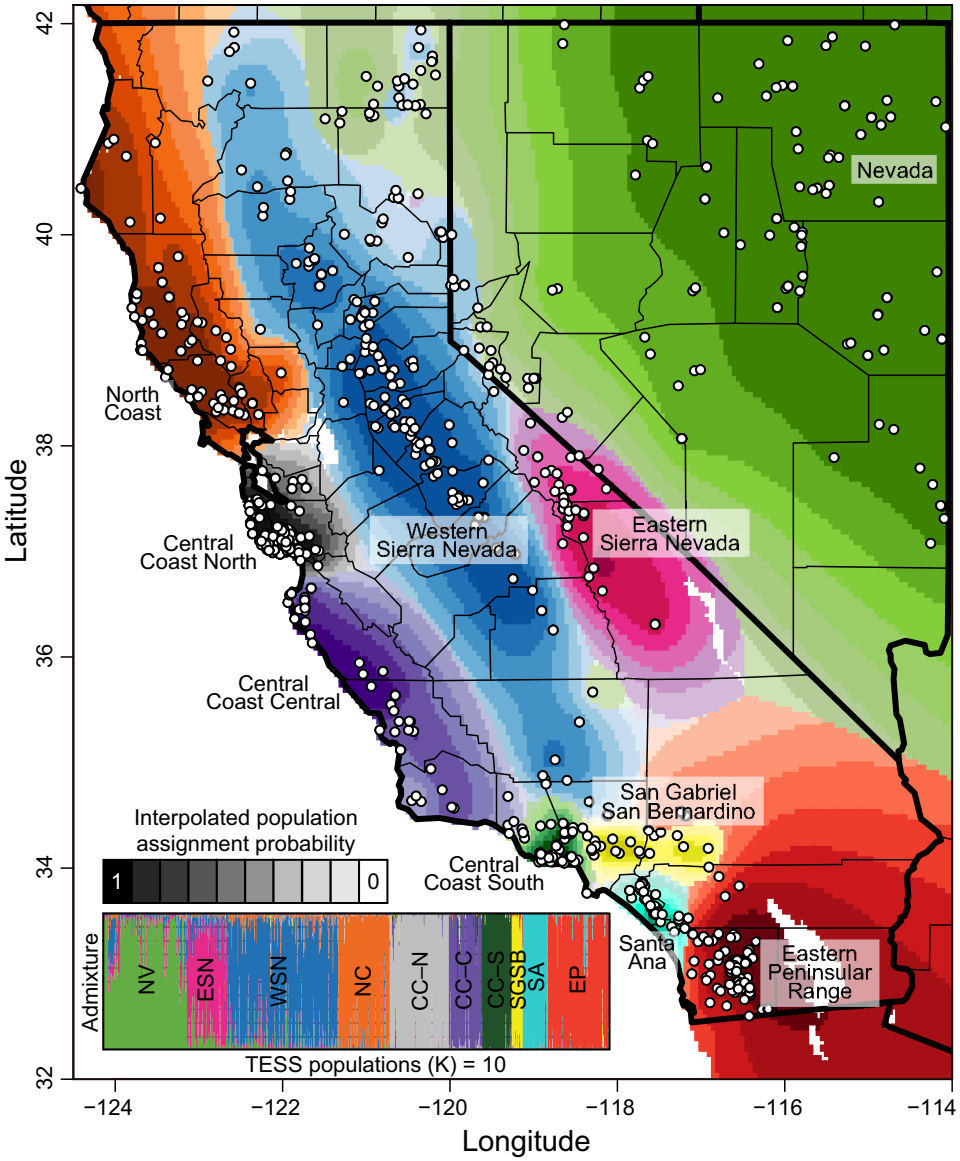


**Fig. 2** Population genetic structure of pumas across California and Nevada. Individual admixture proportions from TESS (inset barplot) were spatially-interpolated. Each color represents a genetic population. The decay in color intensity on the map represents lower probabilities of population assignment and indicates areas with admixture between populations. State and county borders are displayed for reference. *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range

rate estimates showed connectivity patterns similar to the DAPC (Fig. 4). Although there was gene flow among the NV, ESN, and WSN populations based on bi-directional migration rates, the NC population primarily exchanged migrants with the ESN and WSN populations (Fig. 4b). The populations in the Sierra Nevada (ESN, WSN) were the greatest genetic source populations but exhibited limited gene flow with the populations along the central coast of California (CC-N, CC-C, CC-S), and neither NV nor NC exhibited appreciable gene flow with central coast populations (Fig. 4b; Table S2). The SA population exhibited gene flow only with the EP population, and the EP population had low connectivity with the SGSB population (Fig. 4b). The puma population in the Transverse Ranges (SGSB) was the largest genetic sink but exchanged some genetic material with the WSN, CC-C, and EP populations (Fig. 4b). Populations in the Southern Ranges (SA, EP) were largely disconnected from all other populations (Fig. 4b).

**Table 1** Allelic and genetic diversity of puma populations, including sample-size corrected allelic richness, the number of private alleles, the percent of polymorphic loci, observed heterozygosity, unbiased expected heterozygosity, and average internal relatedness (a measure of inbreeding)

| Population | N | Allelic richness | Private alleles | Polymorphic Loci (%) | Observed heterozygosity | Expected heterozygosity | Internal relatedness |
|---|---|---|---|---|---|---|---|
| NV | 166 | 3.47 (0.09) | 9 | 100 | 0.50 (0.03) | 0.52 (0.03) | 0.15 (0.01) |
| ESN | 79 | 3.46 (0.13) | 5 | 100 | 0.52 (0.03) | 0.53 (0.03) | 0.11 (0.01) |
| WSN | 217 | 3.63 (0.08) | 5 | 100 | 0.51 (0.03) | 0.52 (0.03) | 0.09 (0.01) |
| NC | 101 | 3.06 (0.10) | 5 | 97.6 | 0.40 (0.03) | 0.41 (0.03) | 0.28 (0.01) |
| CC-N | 116 | 2.62 (0.08) | 1 | 97.6 | 0.41 (0.03) | 0.42 (0.03) | 0.27 (0.01) |
| CC-C | 63 | 3.00 (0.12) | 1 | 95.2 | 0.45 (0.03) | 0.46 (0.03) | 0.19 (0.02) |
| CC-S | 60 | 2.63 (0.13) | 1 | 92.9 | 0.41 (0.04) | 0.41 (0.03) | 0.27 (0.02) |
| SGSB | 22 | 2.75 (0.17) | 0 | 95.2 | 0.40 (0.03) | 0.42 (0.03) | 0.29 (0.03) |
| SA | 48 | 2.27 (0.12) | 0 | 85.7 | 0.34 (0.03) | 0.33 (0.03) | 0.39 (0.02) |
| EP | 120 | 3.07 (0.11) | 3 | 100 | 0.44 (0.03) | 0.44 (0.03) | 0.21 (0.01) |

*NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range. Standard errors are presented in parentheses

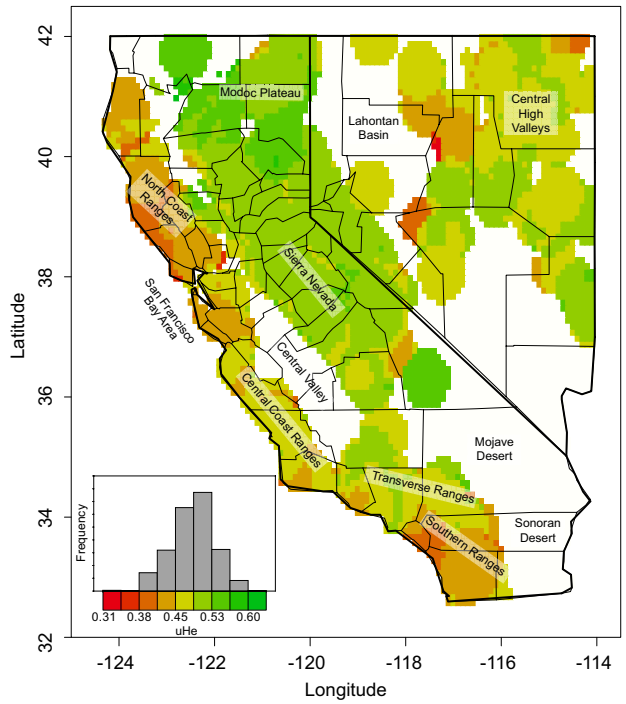


**Fig. 3** Gene diversity (uHe: unbiased expected heterozygosity) heat map of pumas in California and Nevada. Neighborhood size was not significantly related to uHe ($R^2 = 0.005$, $P < 0.001$)

## Discussion

We identified 10 genetically-distinct puma populations within California and Nevada that varied considerably in genetic diversity (uHe range 0.33–0.53) and effective population size ($N_e$ range 5–157). Some of our previous analyses identified family-level genetic structure which was not observed here (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014), indicating these genetic populations are not the result of sampling related individuals. The large number of populations (N = 9) and the strong genetic differences among neighboring puma populations in California differed from other studies at similar spatial scales (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005), including Nevada (Andreasen et al. 2012). Most state-wide studies have been conducted in less-developed locations with more continuous habitat and showed that geographic distance and natural landscape components were the most common factors associated with the broad-scale genetic structure of puma populations (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005; Wright 1943). In contrast, mountain ranges in California are variable in size and arrangement and there are vast areas of inter-mountain anthropogenic development throughout the state. Previous local studies in California have identified individual roadways and associated human development as major barriers to puma movements (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014; Vickers et al. 2015), and our study confirms, on a broad geographic scale, strong population structure among adjacent puma populations. The considerable variation in genetic diversity and effective population size among California and Nevada populations is likely attributable to the variation in the amount of suitable habitat and their degree of isolation. The Western Sierra Nevada population had the largest effective size and was closely related (i.e., lowest $F_{ST}$ values) to every population except for the Northern Central Coast population and populations south of Los Angeles (Santa Ana, Eastern Peninsular Range), suggesting puma populations form a

**Table 2** Summary of effective population size and bottleneck analyses for each population

| Population | Sample size | Effective population size ($N_e$) $N_e$ with AFs ≥ 0.05 | Bottleneck $N_e$ with AFs ≥ 0.01 | P-value |
|---|---|---|---|---|
| NV | 166 | 92.2 (84.2–101.4) | 107.2 (98.5–117.1) | 0.123 |
| ESN | 79 | 22.6 (20.8–24.5) | 26.5 (24.7–28.5) | < **0.001** |
| WSN | 217 | 157.5 (141.2–176.8) | 180.6 (164.1–199.7) | **0.038** |
| NC | 101 | 82.5 (71.3–96.8) | 66 (59.3–73.9) | 0.256 |
| CC-N | 116 | 16.6 (15.1–18.2) | 15.5 (14.2–16.8) | **0.001** |
| CC-C | 63 | 56.6 (47.4–69.0) | 63 (53.3–75.8) | **0.018** |
| CC-S | 60 | 2.7 (2.5–2.9) | 3.6 (3.4–3.9) | **0.008** |
| SGSB | 22 | 5 (3.3–6.4) | 7.5 (6.2–9.1) | **0.046** |
| SA | 48 | 15.6 (13–18.7) | 21.7 (18–26.4) | **0.007** |
| EP | 120 | 31.6 (29.1–34.4) | 37.4 (34.5–40.5) | **0.021** |

*AF* allele frequencies, *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range. Parametric 95% confidence intervals are presented in parentheses. Bottleneck P-values from standardized differences tests are presented

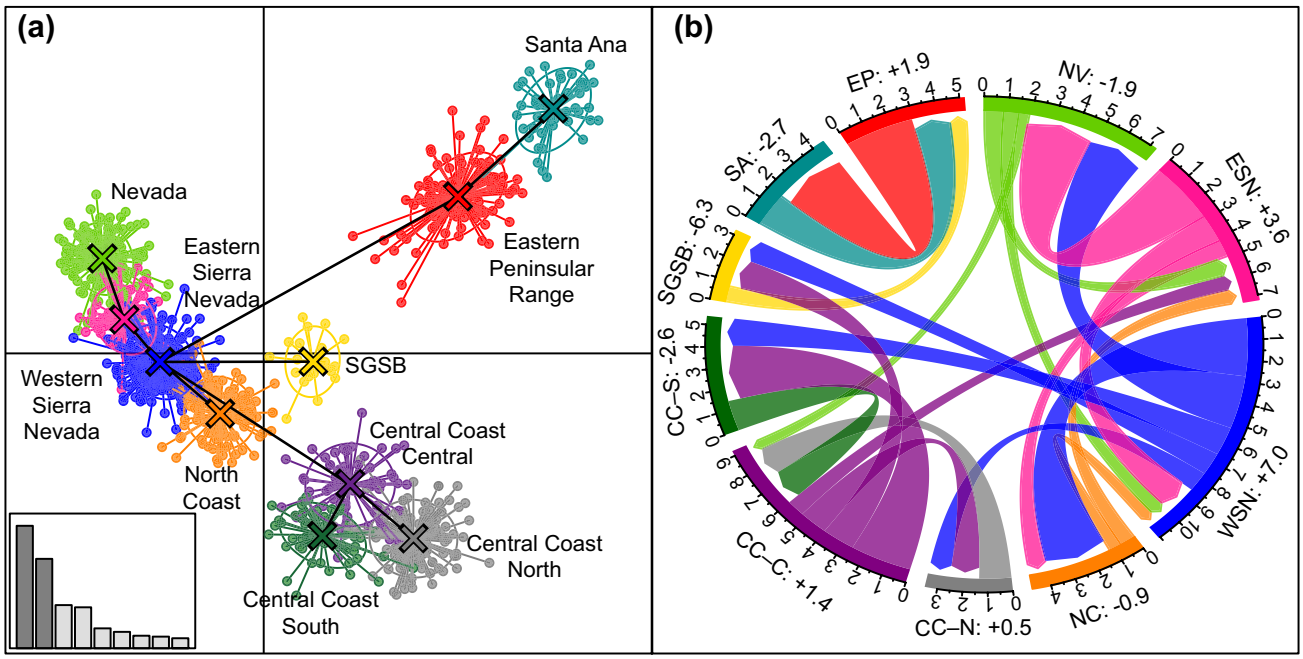


**Fig. 4** Functional connectedness of puma populations, based on **a** a discriminant analysis of principal components and **b** bi-directional migration rate estimates (multiplied by 100 for visualization). Each dot represents an individual (**a**). Each color **a, b** represents a population. Black lines **a** indicate the most closely-related population based on genetic dissimilarities. The inset barplot **a** shows which axes are being displayed (i.e., discriminant functions 1 and 2) and the relative proportion of variation explained by each of the 9 discriminant functions. Two-thirds of the individuals in each population are contained within the corresponding ellipsoid. For a biologically meaningful interpretation, only estimates of interpopulation migration rates with 95% confidence intervals that do not cross 0 are presented (b; Table S2). Net genetic source–sink migration rates are presented next to population names with positive values indicating a net genetic source and negative values indicating a net genetic sink (e.g., WSN exported 9% of migrants and received 2%, so its net rate is +7.0). *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range

"horseshoe" network around the Central Valley with San Francisco Bay acting as a major barrier along the coast (Hooper 1944). The large National Parks and National Forests (e.g., Sequoia–Kings Canyon and Yosemite National Parks) in the Sierra Nevada provide contiguous habitat for pumas with minimal anthropogenic infrastructure (Ernest et al. 2000).

Our results are consistent with a previous report (Andreasen et al. 2012) indicating pumas from Nevada form a single genetic cluster and are distinct from pumas in the Sierra Nevada of California, but our results contrast with their suggestion that pumas from Nevada are a genetic source for pumas in California. There are several differences between the studies that could explain the inconsistencies. Andreasen et al. (2012) used considerably fewer genetic markers than the present study (9 microsatellites vs. 42). Because the number of loci used in bi-directional migration rate models has the largest effect on the accuracy of the estimates (Faubet and Gaggiotti 2008; Wilson and Rannala 2003), we expect the differences are driven by the different number of loci. Although we sampled fewer pumas from Nevada and more pumas from California, sample size differences generally only affect the variance and not the accuracy of the bi-directional migration rate estimates (Faubet and Gaggiotti 2008; Wilson and Rannala 2003). Further, sample size alone likely does not explain the contrasting results and the multiple lines of evidence supporting the Sierra Nevada populations as a genetic source for the surrounding populations, including Nevada.

Both our population-level and individual-based analyses clearly indicated that the Western Sierra Nevada population had the highest genetic diversity, which is likely being maintained by the large effective population size and not via migrants from the Nevada population, which had lower genetic diversity estimates. Further, instead of testing migration rates among the two populations (K = 2) which had the highest model support in their study, Andreasen et al. (2012) tested among five genetic clusters (K = 5) which had average within-cluster migration estimates of only 54% (and a large SD of 8.4%) compared to our within-population migration estimates of 94% (± 1.9%). Thus, their examination of genetic source–sink dynamics was based on significantly less distinct genetic units ($F_{ST}$ = 0.05–0.09 compared to our study where Rousset's $F_{ST}$ = 0.05–0.39), which is computationally problematic with a small number of loci (Faubet and Gaggiotti 2008; Wilson and Rannala 2003). Additionally, puma hunting is legal in Nevada but not California, and puma densities that have been reduced regionally from hunter harvest are known to be compensated by higher immigration rates from neighboring populations (Cooley et al. 2009; Robinson et al. 2008), which is biologically consistent with our observations.

The North Coast and inland populations (Nevada, Eastern Sierra Nevada, Western Sierra Nevada) appear to be large (i.e., high $N_e$), genetically diverse, and well-connected, and may form an evolutionary significant unit (ESU: a group of populations that have accumulated adaptive differences from other populations in part from reproductive isolation; Palsbøll et al. 2007). However, genome-wide data and gene–environment correlation studies will be needed to evaluate whether these population are exhibiting adaptations to specific habitats or ecoregions. Within this group of populations, we detected evidence for bottlenecks in the Eastern Sierra Nevada population and Western Sierra Nevada population. The bottleneck in the Eastern Sierra Nevada population is not surprising given that the puma abundance in this region may have been reduced by 50% after a severe decline in mule deer (Pierce and Bleich 2014; Pierce et al. 2000; Villepique et al. 2011). Besides the North Coast and Nevada populations, all of the other populations also exhibited evidence of genetic bottlenecks; however, we do not know if this was caused by urbanization, a decrease in prey abundance, or some other factor, because the demographic and genetic histories of these populations are not well-documented.

The Central population of the Central Coast exhibited intermediate levels of genetic diversity, and maintaining gene flow from this population to the genetically-depauperate Northern and Southern Central Coast populations is critically important for their long-term viability (Benson et al. 2016; Gray et al. 2016; Riley et al. 2014). A previous report examined the southern area of the central coast region specifically and observed extremely low genetic diversity in the Santa Monica Mountains, south of Highway 101 in the Los Angeles Area (Riley et al. 2014). At a statewide level, we found pumas in the Santa Monica Mountains to be part of a larger genetic population including pumas in the Simi Hills and Santa Susana Mountains; however, our larger sample from the Southern Central Coast population revealed only slightly higher estimates of genetic diversity than pumas sampled from the Santa Monica Mountains alone (Riley et al. 2014). Road-isolated pumas in the Santa Monica Mountains only receive rare migrants from the Simi Hills and Santa Susana Mountains and are at a high risk of extirpation from isolation and subsequent demographic and genetic stochasticity (Benson et al. 2016). These results emphasize the need to conserve within-population connectivity, specifically from the Coast Ranges and the Sierra Nevada through the Santa Susana Mountains and Simi Hills to the Santa Monica Mountains.

Despite being very close geographically, the puma populations around Los Angeles (Southern Central Coast, San Gabriel/San Bernardino, Santa Ana) are highly diverged. For example, the Santa Ana and Southern Central Coast population are among the closest populations geographically

(~ 100 km apart) but are among the most genetically distant populations we observed (Rousset's $F_{ST} = 0.32$). Additionally, the Southern Range populations (Santa Ana, Eastern Peninsular Range) are largely disconnected from all other populations in this study, including those just to the north of the Los Angeles Basin. These observations are consistent with the hypothesis of reduced connectivity from habitat fragmentation by human development (i.e., the Los Angeles metropolitan area), including major roads (i.e., I-10, I-15, I-210, etc.) (Ernest et al. 2003). The San Gabriel/San Bernardino population was most genetically similar to the Western Sierra Nevada, Central region of the Central Coast, and Eastern Peninsular Range populations, indicating it is an area of intersection between multiple populations. We suggest the small mountain ranges in this area (i.e., Tehachapi, Sierra Pelona, San Gabriel, and San Bernardino Mountains) are necessary for contiguous statewide genetic connectivity and that pumas occupying those ranges, and the wildlands habitat in those ranges, should be considered conservation priorities (Beier et al. 2009; Ernest et al. 2003; Wildlands 2008).

The Santa Ana population exhibited the lowest measures of genetic diversity and the highest measures of inbreeding among all populations, with levels nearing those of Florida panthers (most recent estimates of $He = 0.24$), which nearly went extinct from genetic factors prior to artificial genetic rescue (Johnson et al. 2010). It is important to note, however, that out of the 42 microsatellite loci used in this study, only 4 were shared with the 23 microsatellite loci used in the Florida panther study. A set of shared markers would be most appropriate for direct interpopulation comparisons (e.g., Culver et al. 2000). A single immigrant from the Eastern Peninsular Range recently enhanced the genetic diversity of Santa Ana pumas and is likely responsible for the higher effective population size than previously observed (Ernest et al. 2014). Nevertheless, genetic diversity of Santa Ana pumas will decline without additional immigration (Gustafson et al. 2017). The Eastern Peninsular Range population had the highest genetic diversity and effective size among the populations in the Los Angeles—San Diego area (Southern Central Coast, San Gabriel/San Bernardino, Santa Ana, Eastern Peninsular Range). Restoring connectivity with the Eastern Peninsular Range and reducing further impacts from development on gene flow among the adjacent populations, including pumas from Arizona and Mexico (Gustafson et al. 2017), are critically important to avoiding extirpation of genetically-depauperate populations (Benson et al. 2016).

By identifying puma populations and measuring gene flow among them, our analyses can help guide and inform puma conservation and management. Whenever possible, government agencies and other stakeholders should consider population connectivity and prevent further fragmentation by human development both within and among populations. In contrast to other studies in 7 western states that generally indicated weak puma genetic structure (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005), our study showed strong genetic structure. Although puma habitat in California is aggregated and separated by valleys, it is unlikely these valleys would have been such strong barriers to gene flow pre-development given that pumas have been documented to move across the entire Central Valley post-development (Ernest et al. 2003; McClanahan et al. 2017). Further, similar geographic features, such as the Wyoming Basin, have not been reported to structure puma populations (Anderson et al. 2004). Instead, we hypothesize that human-associated infrastructure within the valleys are artificially isolating pumas beyond what they would naturally experience among ecoregions.

Population-level conservation strategies are needed to reintegrate fragmented, at-risk populations into a connected multi-state, multi-landscape population network (Zeller et al. 2017). Gene flow via maintenance of existing occupied habitat combined with improved and additional networks of wildlife corridors (Bennett 2017; Gloyne and Clevenger 2001; Johnson et al. 2010; Sawaya et al. 2013) will ultimately be necessary to promote the long-term persistence of isolated populations (Benson et al. 2016; Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014). Without such measures, it is likely too late to expect a natural increase in genetic connectivity or selection for increased dispersal (Burdett et al. 2010; Cheptou et al. 2017), and assisted gene flow may be needed in perpetuity for several populations to remain viable (Benson et al. 2011, 2016; Ernest et al. 2014; Gustafson et al. 2017; Johnson et al. 2010; Vickers et al. 2015).

In some of these populations, individual migrants are of immediate conservation importance, and human-induced mortality should be avoided to the extent possible. The effects of fragmentation on multiple populations of this umbrella species are likely indicative of a larger ecological problem in one of the most biologically diverse regions of North America (Calsbeek et al. 2003; Dobson et al. 1997; Thorne et al. 2006). We strongly encourage land owners and managers to proactively consider broad-scale wildlife connectivity in future development proposals. However, in the absence of maintaining habitat of a spatial scale grand enough to ensure the persistence of prey and predator populations, the issue of connectivity will become a moot point.

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**Data availability** Through agreements with non-profit organizations, private landowners, and Native American Tribes, exact GPS locations of puma samples are not to be publicly shared. Thus, puma GPS locations are referenced to the nearest town or city. Sampling locations and microsatellite genotypes are available on Dryad: https://doi.org/10.5061/dryad.j76c4k4.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** Permission to carry out fieldwork and necessary permits were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (U.S.) Fish and Wildlife Service, U.S. Forest Service, U.S. Bureau of Land Management, U.S. Navy/Marine Corps, Orange County Parks Department, San Diego County Parks Department, Riverside County Parks Department, San Diego State University, University of California—Riverside, Audubon Starr Ranch, Vista Irrigation District, Rancho Mission Viejo/San Juan Company, Sweetwater Authority, California Department of Transportation, the City of San Diego Water Department and Parks Department, and the Irvine Ranch Conservancy.

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CALIFORNIA WILDFIRES

# As California burns, volunteer firefighters become harder to find

**Melody Gutierrez** and **Megan Cassidy** | Aug. 11, 2018 | Updated: Aug. 12, 2018 7:19 a.m.

Volunteer firefighter Dick Brown works with the Calaveras Consolidated Fire Protection District in Calaveras County.

Photo: Paul Chinn / The Chronicle

Dick Brown isn't sure how much longer he will be a volunteer firefighter. At 66 years old, he doesn't douse flames much anymore, instead driving the water tender to blazes in rural Calaveras County.

But he's worried about who will replace him. And who will replace thousands of volunteer firefighters in local departments across the state in the coming years as the number of residents willing to do the job dwindles and fires burn at record-breaking pace.

Hard numbers charting the decline of the volunteer firefighting force in California are hard to come by. But in rural county after rural county — including those hit hard by this summer's wildfires — local officials are sounding the alarm.

They say current volunteers are aging out of the job, and that with extensive training requirements having been put in place in recent years, fewer recruits are stepping up. That puts residents at risk in counties where there isn't enough money in the budget for a large, full-time force.

"Typically, volunteer fire departments exist because there isn't money for a paid one," said Brown, who is the California director for the National Volunteer Fire Council, an industry group representing nonpaid firefighters.

One-third of the 28,000 firefighters in California are volunteers, most of them in rural areas. Across the country, where 70 percent of firefighters are volunteers, departments say they are struggling to recruit new people for a dangerous job. The number of volunteer firefighters in the United States fell by 10 percent over the past three decades, even as the number of emergency calls tripled, according to the National Fire Protection Association, an industry trade group whose figures are often cited by the federal government.

“It’s becoming more difficult to recruit and retain volunteers because it’s a huge demand on your time,” Brown said. “People are busier. They commute longer, work more. Their kids are in sports.

“But, if not for volunteers, who will do it?” Brown said.

Volunteer firefighter Mike Beyer battles a Carr Fire flareup in July.
Photo: Paul Kitagaki Jr. / Sacramento Bee

That’s the question fire officials are asking as deadly fires rage from one end of California to the other, with 17 states and Australia sending crews to help.

There were 17 major wildfires burning in California at the end of last week, including the Mendocino Complex, which at more than 300,000 acres is the largest wildfire in state history. Five firefighters have died battling the blazes, making it the most lethal year for firefighters in the state since 2008.

“The new normal is we are busier than we’ve ever been,” said Cliff Allen, president of Cal Fire Local 2881, the union that represents paid firefighters with the state Department of Forestry and Fire Protection. “Demand is higher and staffing levels aren’t meeting those needs.”

Allen advocates for paid union firefighting jobs. But he said that in rural parts of the state, volunteers fill a critical need.

“It’s a necessary evil, so to speak,” he said.

Every minute counts after a fire breaks out — a quick response can be the difference between a small brushfire and a blaze that burns for

weeks. That means a rural community with a depleted volunteer firefighting force is at greater risk, said Fire Chief Kim Zagaris of the state Office of Emergency Services.

“We have hired more paid people, but we have less people in rural areas stepping up,” Zagaris said.

In Tuolumne County, impacted by the Ferguson Fire that has been raging for nearly a month, county officials and grand juries have been warning for years about the dwindling number of volunteer firefighters. The county contracts with Cal Fire for some services, but its local departments are primarily staffed with volunteers.

The fire warden for Tuolumne County told a grand jury last year that 250 to 300 volunteers are needed for stations to be adequately staffed. There were just 36 volunteer firefighters before an aggressive marketing campaign brought the total to 70 last year.

Under state law, volunteer firefighters have to undergo the same certification training as paid firefighters. Depending on their responsibilities, volunteers may have a long list of qualifications to satisfy.

“We just don’t have the number of people interested in doing it,” said Tuolumne County Supervisor John Gray. “I’m 70. When I was a young man, you could show up and help put out a fire. Now you have to be trained and certified. In a rural county like Tuolumne, the majority of our population is over 50, and you can’t find people who can do the physical tasks.”

Departments around the state offer various incentives to join, such as a

nominal stipend to help defray out-of-pocket costs. Some provide a retirement account depending on how long a person volunteers. In some cases, a retiree can receive $1,200 a month for life if they volunteered for 20 years.

The National Fire Protection Association says that nationwide, there were 1.2 million firefighters in 2015. Of those, 815,000 were volunteers, down from 897,750 in 1984.

There has been an uptick since 2011, when the ranks of volunteers bottomed out at 756,000. But the number isn't keeping up with the increased demand, said Curt Floyd of the fire protection association.

"This is a trend that is a concern," Floyd said. "Some communities have had to hire (paid firefighters). There is a cost involved, and some communities can't bear that weight."

Nearly every fire department in Lake County, center of the Mendocino Complex fire, and Shasta County, which has been devastated by the Carr Fire, is feeling the strain.

The Lake County Fire Protection District in Clearlake considers its volunteer roster filled when it has 55 volunteers. Lately the total has been around 20. The Lakeport Fire Department also has 20 volunteers, about 15 short of the ideal.

The Shasta County Fire Department is authorized to deploy 385 volunteers. Last month, when the Carr Fire burned into Redding, destroying more than 1,000 homes, the department had 149 volunteers. Among the homes burned were those of several volunteer firefighters, who continued to work, said Julia Haven, a staff services

analyst for Cal Fire/Shasta County Fire.

Lakeport Fire Chief Doug Hutchison said his department's force has dwindled as training standards became more rigorous and the economy improved.

"People just don't have the time to volunteer like they used to," he said. "We're actually pretty fortunate — we've had 10 new volunteers in the last year."

He added, "We did some outreach at high schools, to seniors, to get people interested in this as a career. Volunteering is a first step to it."

Mandi Huff, office clerk for South Lake County Fire Protection in Middletown, said the agency has about 30 volunteers on the books, but only about 16 show up consistently.

Huff said volunteer staffing plummeted after the 2015 Valley Fire. The blaze charred more than 76,000 acres, killed four people and destroyed more than 1,200 homes.

People who were volunteer firefighters "had to focus on themselves" and moved away to start over, Huff said. "We've been trying to rebuild the number ever since."

Some local officials brought their concerns to Sacramento this year, to push for a bill that would have offered volunteer firefighters a tax credit of up to $1,500 a year for expenses they incur.

The measure, AB2727, would have cost the state up to $30 million a year in lost revenue, according to the bill's analysis. It stalled in the Assembly Appropriations Committee.

"This isn't a partisan issue — this is a save-my-house issue," said Shasta County Supervisor Les Baugh, who testified before a legislative committee. "We have a need for this everywhere."

The bill's author, Assemblyman Heath Flora, R-Ripon (San Joaquin County), said he will introduce another incentive bill in January in hopes of drawing more interest in volunteer firefighting. Flora, who became a volunteer firefighter in Modesto in 2000, said he's watched as some agencies struggled to recruit new people.

"That's a public safety issue," he said. "People call 911 and they expect someone to show up and help them in their time of need."

It was a 911 call that originally sparked Brown's interest in volunteering in western Calaveras County. He said he called for help 29 years ago when his 10-year-old daughter was kicked in the face by her horse at their Valley Springs home.

Two dozen firefighters showed up to help. Each one was a volunteer. He still feels he owes the fire department that helped treat his daughter's broken nose and concussion.

"When I get to the point where I feel I paid my debt, I will retire," Brown said.

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CALIFORNIA WILDFIRES

# California blazes tax budgets, firefighters: ‘Fatigue is starting to set in’

**Melody Gutierrez**

July 31, 2018 | Updated: July 31, 2018 6:41 p.m.

Firefighters at the Mendocino Complex fire. California has been using inmate firefighters to fight a series of large and complex fires all over the state. A new program partially fixes a big problem with the practice -- the inmate firefighters haven't been allowed to work in fire departments after their release from prison.

Photo: AFP Contributor#AFP

SACRAMENTO — California’s firefighters are stretched as thin as they have ever been, state officials said Tuesday, with no indication that the wave of fires scorching the Golden State will ease in the

coming months.

It used to be that the fire season picked up at the end of August and ran through October. That changed with the state’s five-year drought, and this year’s outbreak in July has officials worried about firefighter fatigue.

It was an unprecedented month for fires, both in the number of acres burned and the cost of fielding crews to douse the flames.

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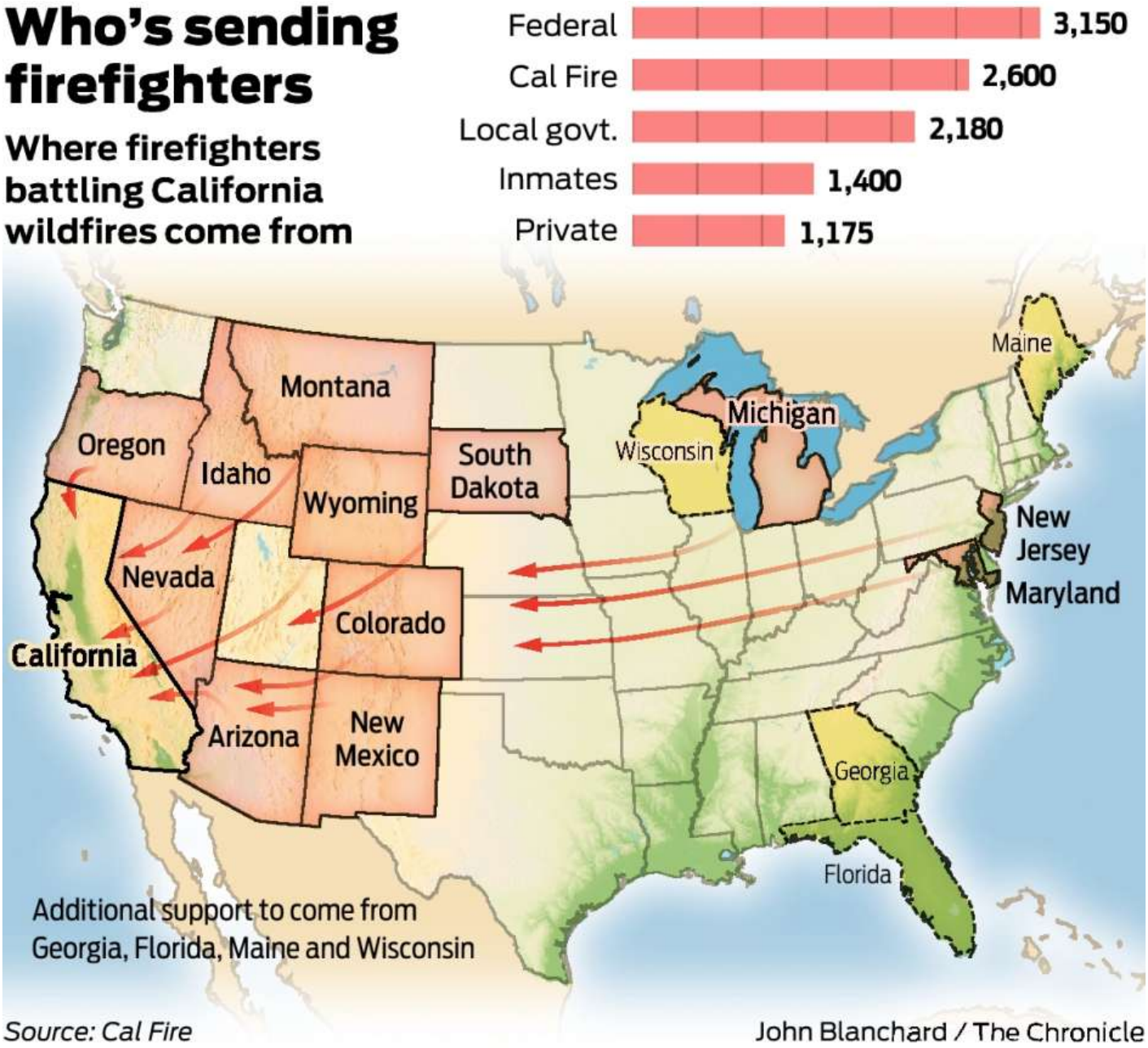
The state spent $125 million in July fighting wildfires. That was more than one-fourth of what was budgeted for the entire fiscal year, which began July 1 and won’t end until June 30, 2019.


Who's sending firefighters
Where firefighters battling California wildfires come from
Federal 3,150
Cal Fire 2,600
Local govt. 2,180
Inmates 1,400
Private 1,175
Montana
Oregon
Idaho
Wyoming
South Dakota
Nevada
Colorado
California
Arizona
New Mexico
Wisconsin
Michigan
Maine
New Jersey
Maryland
Georgia
Florida
Additional support to come from Georgia, Florida, Maine and Wisconsin
Source: Cal Fire
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It was also a tragic month for firefighters. Four died while battling blazes, two on the Ferguson Fire near Yosemite National Park and two on the Carr Fire as it threatened Redding.

"Unfortunately, no one is going home," said Mark Ghilarducci, director of the Governor's Office of Emergency Services. "There is no rest. ... We are literally moving firefighters and personnel from one fire to another, and will continue to do so until the threat is mitigated."

Cliff Allen, president of Cal Fire Local 2881, the union that represents employees with the state Department of Forestry and Fire Protection, said the workload is taking a toll.

"Fatigue is starting to set in," Allen said.

Nearly 300,000 acres of state and local lands have burned in California since January, 70,000 acres more than at this time last year and close to triple the five-year average for the date. Cal Fire has had to tap agencies in 12 other states to help build the force of 10,500 firefighters who are on the lines fighting the largest fires.

State officials even persuaded Australia and New Zealand to send firefighters. And Ghilarducci said his office is considering asking the Pentagon to deploy ground troops from the Marines or Army who can help clear brush to stop fires from spreading.

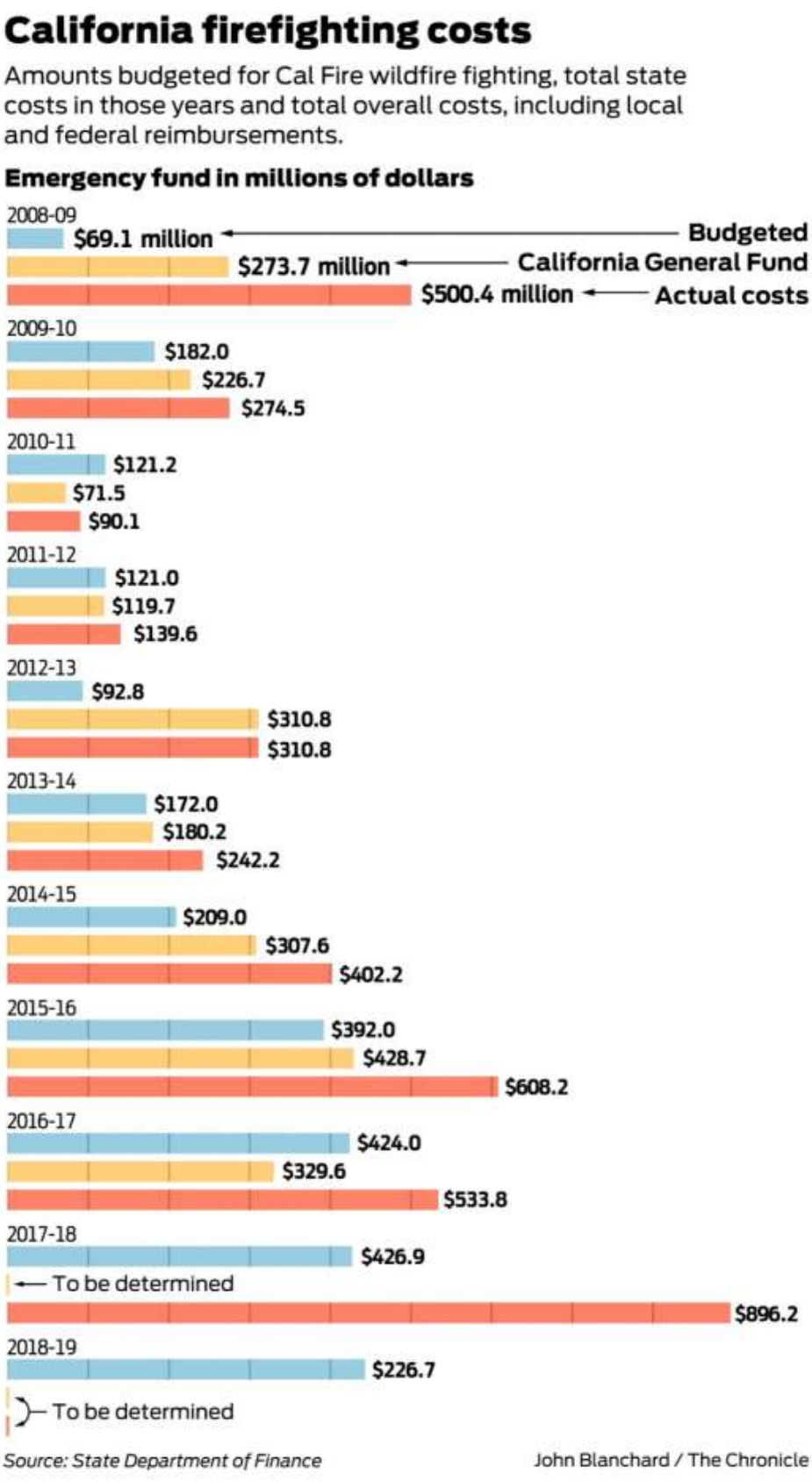
"We have fire literally from one end of the state to the other, and we have weather conditions that are making this an even more dynamic situation," Ghilarducci said. "We have to get resources to the right place at the right time. It's like a chess board."

Ghilarducci said that in recent days, state officials redirected fire crews from the Ferguson Fire near Yosemite to the Carr Fire as it threatened Redding and to the Mendocino Complex Fire when

it took aim at communities in Lake County.

When those fires are contained, Ghilarducci said, it’s unlikely firefighters will get a break. The way the summer is going, they’ll probably have another fire to put out.

“It’s really all hands on deck,” he said.




And that comes at a cost.

The state is likely to need to dip into reserves for the eighth time in the past decade to cover the cost of putting out wildfires. That's despite an ever-increasing budget for fighting fires.

Last year, the state budgeted $427 million. The outburst of fires in the North Bay and elsewhere in October, and then in Southern California in December, left the state, local governments and the federal government having to come up with another $470 million to cover costs.

California has budgeted $443 million for this fiscal year that began July 1, and has spent $125 million so far. That's more than the state spent during the entire 2010-11 fiscal year.

"This is why the governor has been so insistent over the years of having a healthy budget reserve because, as this year may very well show, Mother Nature doesn't always coordinate with the state budget," said H.D. Palmer, spokesman for the state Department of Finance. "The second thing it speaks to is that it underscores what the governor has talked about in terms of the kind of effect that climate change has had on conditions in California and how they set the state up for these kinds of catastrophic wildfires."

Edward Struzik, author of the book "Firestorm: How Wildfire Will Shape Our Future," said rising firefighting costs are going to put pressure on budgets across the U.S. in coming years. The only way to prevent that is to keep people from moving into wildland areas and investing in technology that predicts where fires are likely to happen, he said.

"There is no indication we will get cooler and wetter in the West," Struzik said. "Every study I've seen shows California and most of the American West will get hotter and drier. We have more people working and living in these forest areas, and that is increasing the likelihood of fires. I don't see any other future other than one with more fires."

And, he added, a future of "really stressed-out fire crews."

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APPLIED ECOLOGY

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# Habitat fragmentation and its lasting impact on Earth's ecosystems

Nick M. Haddad,[1]* Lars A. Brudvig,[2] Jean Clobert,[3] Kendi F. Davies,[4] Andrew Gonzalez,[5] Robert D. Holt,[6] Thomas E. Lovejoy,[7] Joseph O. Sexton,[8] Mike P. Austin,[9] Cathy D. Collins,[10] William M. Cook,[11] Ellen I. Damschen,[12] Robert M. Ewers,[13] Bryan L. Foster,[14] Clinton N. Jenkins,[15] Andrew J. King,[9] William F. Laurance,[16] Douglas J. Levey,[17] Chris R. Margules,[18,19] Brett A. Melbourne,[4] A. O. Nicholls,[9,20] John L. Orrock,[12] Dan-Xia Song,[8] John R. Townshend[8]

**We conducted an analysis of global forest cover to reveal that 70% of remaining forest is within 1 km of the forest's edge, subject to the degrading effects of fragmentation. A synthesis of fragmentation experiments spanning multiple biomes and scales, five continents, and 35 years demonstrates that habitat fragmentation reduces biodiversity by 13 to 75% and impairs key ecosystem functions by decreasing biomass and altering nutrient cycles. Effects are greatest in the smallest and most isolated fragments, and they magnify with the passage of time. These findings indicate an urgent need for conservation and restoration measures to improve landscape connectivity, which will reduce extinction rates and help maintain ecosystem services.**

## INTRODUCTION

Destruction and degradation of natural ecosystems are the primary causes of declines in global biodiversity (*1*, *2*). Habitat destruction typically leads to fragmentation, the division of habitat into smaller and more isolated fragments separated by a matrix of human-transformed land cover. The loss of area, increase in isolation, and greater exposure to human land uses along fragment edges initiate long-term changes to the structure and function of the remaining fragments (*3*).

Ecologists agree that habitat destruction is detrimental to the maintenance of biodiversity, but they disagree—often strongly—on the extent to which fragmentation itself is to blame (*4*, *5*). Early hypotheses based on the biogeography of oceanic islands (*6*) provided a theoretical framework to understand fragmentation's effect on extinction in terrestrial landscapes composed of "islands" of natural habitat scattered across a "sea" of human-transformed habitat. Central to the controversy has been a lingering uncertainty about the role of decreased fragment size and increased isolation relative to the widespread and pervasive effects of habitat loss in explaining declines in biodiversity and the degradation of ecosystems (*7*). Observational studies of the effects of fragmentation have often magnified the controversy because inference from nonmanipulative studies is limited to correlation and because they have individually often considered only single aspects of fragmentation (for example, edge, isolation, and area) (*8*). However, together with these correlative observations, experimental studies reveal that fragmentation has multiple simultaneous effects that are interwoven in complex ways and that operate over potentially long time scales (*9*).

Here, we draw on findings of the world's largest and longest-running fragmentation experiments that span 35 years and disparate biomes on five continents. Their rigorous designs and long-term implementation overcome many limitations of observational studies. In particular, by manipulating and isolating individual aspects of fragmentation while controlling for others, and by doing so on entire ecosystems, they provide a powerful way to disentangle cause and effect in fragmented landscapes. Here, we present experimental evidence of unexpected long-term ecological changes caused by habitat fragmentation.

Highlighting one ecosystem type as an example, we first present a global analysis of the fragmentation of forest ecosystems, quantifying for the first time the global hotspots of intensive historical fragmentation. We then synthesize results from the set of long-term experiments conducted in a wide variety of ecosystems to demonstrate consistent impacts of fragmentation, how those impacts change over time, and how they align with predictions from theory and observation. Finally, we identify key knowledge gaps for the next generation of fragmentation experiments.

## GLOBAL ANALYSIS OF THE EXTREME MAGNITUDE AND EXTENT OF FRAGMENTATION

New satellite data sets reveal at high resolution how human activities are transforming global ecosystems. Foremost among these observations are those of forest cover because of the high contrast between forest

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and anthropogenic land cover types. Deforestation, which was already widespread in temperate regions in the mid-18th to 20th centuries and increased in the tropics over the past half century, has resulted in the loss of more than a third of all forest cover worldwide (*10*, *11*). Beyond the direct impacts of forest loss and expanding anthropogenic land cover (for example, agricultural fields and urban areas), remnant forests are likely to suffer from being smaller, more isolated, and with a greater area located near the edge of the forest (*12*).

We analyzed the world's first high-resolution map of global tree cover (*13*) to measure the magnitude of forest fragmentation. This analysis revealed that nearly 20% of the world's remaining forest is within 100 m of an edge (Fig. 1, A and B)—in close proximity to agricultural, urban, or other modified environments where impacts on forest ecosystems are most severe (*14*). More than 70% of the world's forests are within 1 km of a forest edge. Thus, most forests are well within the range where human activities, altered microclimate, and nonforest species may influence and degrade forest ecosystems (*15*). The largest contiguous expanses of remaining forests are in the humid tropical regions of the Amazon and Congo River Basins (Fig. 1A). Large areas of more disjunct forest also remain in southeastern Asia, New Guinea, and the boreal biomes.

Historical data enable the study of the process of forest fragmentation over time. We reconstructed the historical forest extent and timing of fragmentation in two forested regions of Brazil that provide a stark contrast in land-use dynamics. The Brazilian Amazon is a rapidly changing frontier (*10*), yet most of its forests remain contiguous and far from an edge despite recent increases in fragmentation (Fig. 1, C and D). In contrast, the Brazilian Atlantic Forest is a largely deforested landscape, cleared for agriculture and logged for timber over the last three centuries (*11*). This remaining forest is dominated by small fragments, with most fragments smaller than 1000 ha and within 1000 m of a forest edge (Fig. 1, E and F) (*16*). In the Brazilian Amazon, the proportion of forest farther than 1 km from the forest edge has decreased from 90% (historical) to 75% (today), and in the Brazilian Atlantic, from 90% to less than 9%.

These two forested regions of Brazil define extremes of the fragmentation process and are representative of the extent of fragmentation in forested landscapes worldwide (Fig. 1), as well as many other biomes including temperate grasslands, savannas, and even aquatic systems (*17*). For example, although a spatial analysis similar to that of forest is not currently possible in grasslands, 37% of the world's grassland eco-regions are classified as "highly fragmented" (*18*, *19*).

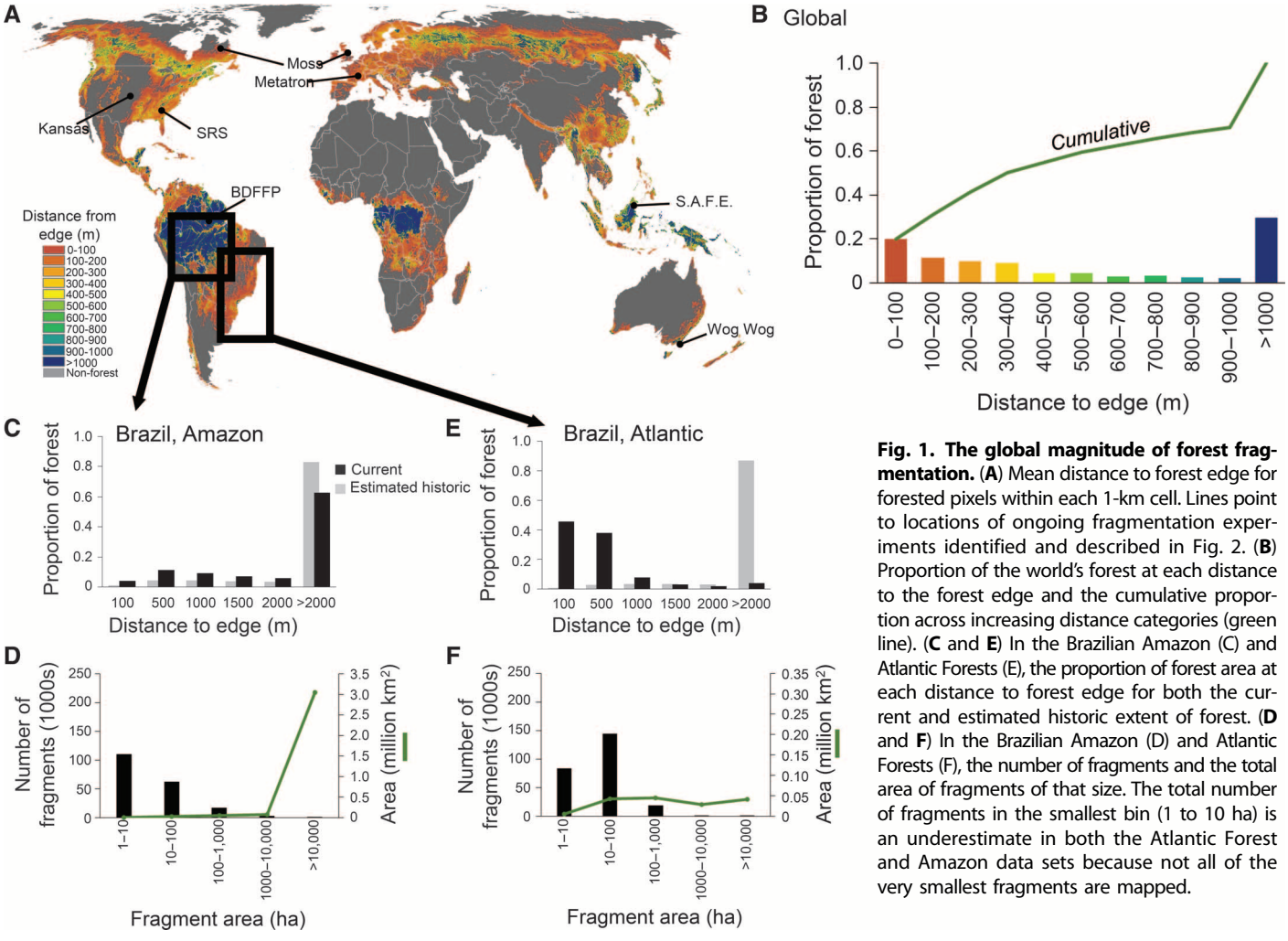


**Fig. 1. The global magnitude of forest fragmentation.** (**A**) Mean distance to forest edge for forested pixels within each 1-km cell. Lines point to locations of ongoing fragmentation experiments identified and described in Fig. 2. (**B**) Proportion of the world's forest at each distance to the forest edge and the cumulative proportion across increasing distance categories (green line). (**C** and **E**) In the Brazilian Amazon (C) and Atlantic Forests (E), the proportion of forest area at each distance to forest edge for both the current and estimated historic extent of forest. (**D** and **F**) In the Brazilian Amazon (D) and Atlantic Forests (F), the number of fragments and the total area of fragments of that size. The total number of fragments in the smallest bin (1 to 10 ha) is an underestimate in both the Atlantic Forest and Amazon data sets because not all of the very smallest fragments are mapped.

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Robust knowledge of how habitat fragmentation affects biodiversity and ecosystem processes is needed if we are to comprehend adequately the implications of this global environmental change.

## THE VALUE OF LONG-TERM FRAGMENTATION EXPERIMENTS

Long-term experiments are a powerful tool for understanding the ecological consequences of fragmentation (*20*). Whereas observational studies of fragmented landscapes have yielded important insights (*9*, *21*), they typically lack rigorous controls, replication, randomization, or baseline data. Observational studies have limited ability to isolate the effects of fragmentation from concomitant habitat loss and degradation per se (*4*, *7*, *22*). Remnant fragments are embedded in different types and qualities of surrounding habitat, complicating interpretation because the surrounding habitat also influences biodiversity and ecosystem productivity (*23*).

The long-term fragmentation experiments we analyze here comprise the entire set of ongoing terrestrial long-term experiments. They occur in several biomes (Fig. 2 and Supplementary Materials) and were designed to manipulate specific components of fragmentation—habitat size, isolation, and connectivity—while controlling for confounding factors such as the amount of habitat lost across a landscape (Fig. 2). The largest fragments across these experiments match the size of fragments commonly created by anthropogenic activities (Figs. 1 and 2). Distances to the edge of experimental fragments range to 500 m, encompassing edge distances found in more than half of forests worldwide (Fig. 1B). In each experiment, different fragmentation treatments with replication were established, starting from continuous, nonfragmented landscapes and controlling for background environmental variation either by experimental design (blocking) or by measurement of covariates for use in subsequent analyses. Tests were conducted within fragments that varied experimentally in area or edge, within fragments that were experimentally isolated or connected, or within experimental fragments compared to the same area within continuous habitat. All treatments were replicated. Experiments were created by destroying or creating precise amounts of habitat across replicate landscapes, allowing tests of fragmentation effects independent of habitat loss. The robust

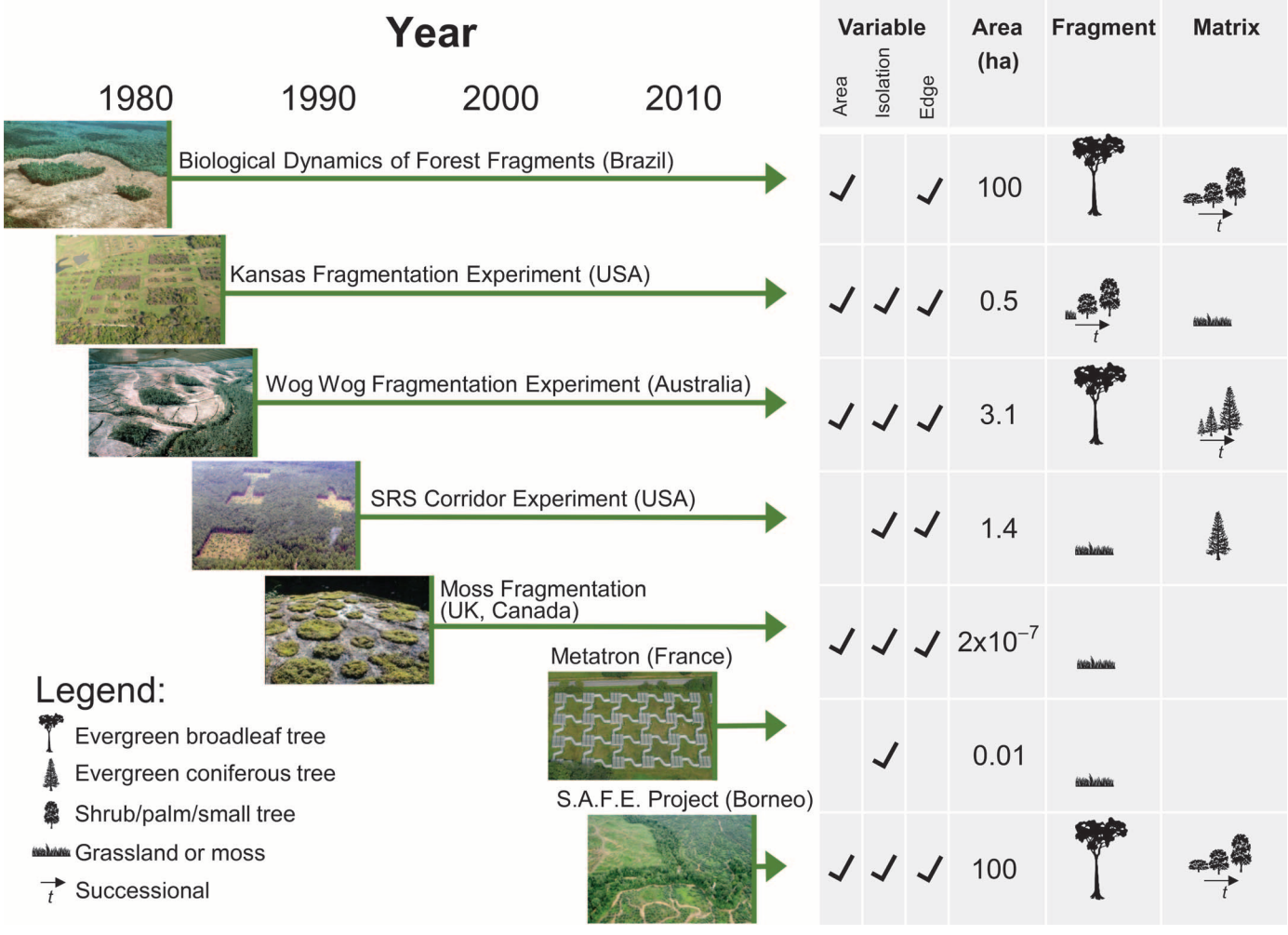


**Fig. 2. The world's ongoing fragmentation experiments.** All experiments have been running continuously since the time indicated by the start of the associated arrow (with the exception of the moss fragmentation experiment, which represents a series of studies over nearly two decades). The variables under study in each experiment are checked. The area is that of the experiment's largest fragments. Icons under "Fragment" and "Matrix" indicate the dominant community and its relative height, with multiple trees representing succession.

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and comparable experimental designs allow for powerful tests of the mechanisms underpinning the ecological impacts of fragmentation, and the long-term nature of ensuing studies has revealed consistent emergent effects.

These experiments mimic anthropogenic fragmentation; they are whole-ecosystem manipulations in which all species and processes experienced the same treatment (*24*). Emergent responses thus reflect the multiple direct and indirect effects of interacting species and processes. Further, because experimentally fragmented ecosystems are open to fluxes of individuals and resources, fragmentation effects can manifest across multiple levels of ecological organization (Fig. 3). Long-term experiments have the power to detect lagged and/or chronic impacts.

The first fragmentation experiments, now more than three decades old, were created to test effects of fragment area on both species persistence and patterns of immigration, reflecting concern in conservation biology about the role of fragmentation in reducing population sizes below viable levels (*25*) (Fig. 2). Subsequent experiments, created two decades ago, shifted focus to modifying habitat isolation, reflecting recognition of the potential to mitigate negative effects of fragmentation by recreating habitat—specifically with corridors—to increase connectivity among fragments (*26*) (Fig. 2). The newest experiments test emerging questions about potentially deleterious synergies between fragmentation and global changes in climate and land use (Fig. 2).

We synthesized results available 31 January 2014 for all studies within these experiments that were conducted in all treatments and replicates, and tested fragmentation effects on dispersal, abundance, extinction, species richness, community composition, and ecosystem functioning. We first calculated effect sizes of fragmentation as log response ratios (Fig. 3). Data from 76 different studies across the five longest-running experiments were drawn from published and unpublished sources (table S1). We synthesized results according to three fragmentation treatments: reduced fragment area [the focus of Biological Dynamics of Forest Fragments Project (BDFFP), Wog Wog, and Kansas; see Fig. 2 for identifiers of experiments], increased fragment isolation [Savannah River Site (SRS) and Moss], and increased proportion of edge (all experiments). Fragmented treatments were compared directly to non- or less-fragmented habitats that were either larger or connected via structural corridors (table S1).

## Strong, consistent, and accumulating effects of habitat fragmentation

Our synthesis revealed strong and consistent responses of organisms and ecosystem processes to fragmentation arising from decreased fragment area, increased isolation, and the creation of habitat edges (Fig. 3).

Community and ecosystem responses emerge from observed responses at the level of populations. Reduced area decreased animal

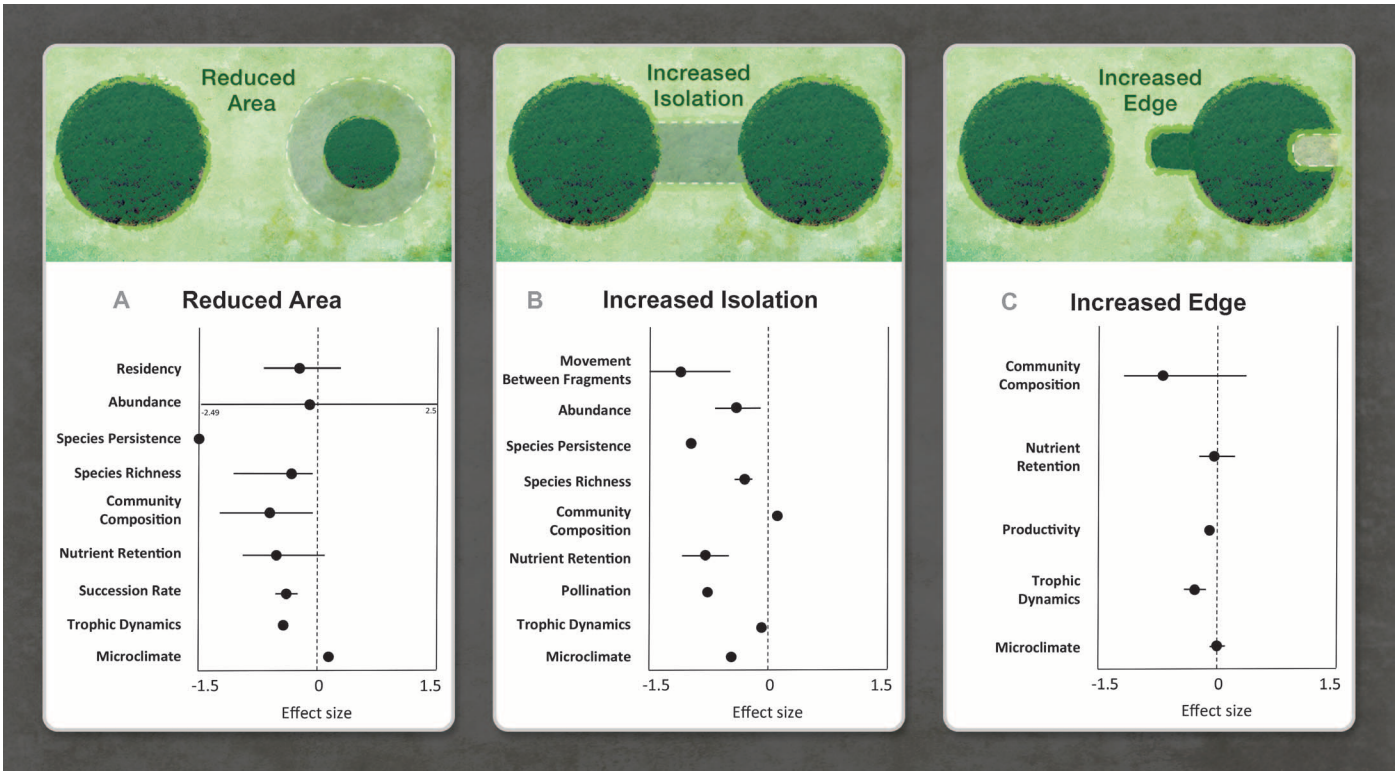


**Fig. 3. Fragmentation effects propagate through the whole ecosystem.** (**A** to **C**) For each fragmentation treatment [reduced area in BDFFP, Wog Wog, Kansas (A); increased isolation in SRS and Moss (B); and increased edge in all experiments (C)], we summarize major findings for ecological processes at all levels of ecological organization. Each dot represents the mean effect size [computed as log response ratio: ln(mean in more fragmented treatment/mean in non- or less-fragmented treatment)] for an ecological process. Effect sizes are statistical, such that negative or positive values could represent degrading function. Horizontal bars are the range when a dot is represented by more than one study. Details, including individual effect sizes for each study, are reported in table S1.

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residency within fragments, and increased isolation reduced movement among fragments, thus reducing fragment recolonization after local extinction (Fig. 3, A and B). Reduced fragment area and increased fragment isolation generally reduced abundance of birds, mammals, insects, and plants (Fig. 3, A and B). This overall pattern emerged despite complex patterns of increases or declines in abundance of individual species (Fig. 3A) with various proximate causes such as release from competition or predation, shifts in disturbance regimes, or alteration of abiotic factors (*14*, *27*–*29*). Reduced area, increased isolation, and increased proportion of edge habitat reduced seed predation and herbivory, whereas increased proportion of edge caused higher fledgling predation that had the effect of reducing bird fecundity (represented together as trophic dynamics in Fig. 3, A to C). Perhaps because of reduced movement and abundance, the ability of species to persist was lower in smaller and more isolated fragments (Fig. 3, A and B).

As predicted by theory (*6*, *30*, *31*), fragmentation strongly reduced species richness of plants and animals across experiments (Fig. 3, A and B), often changing the composition of entire communities (Fig. 3, A to C). In tropical forests, reduced fragment size and increased proportion of edge habitat caused shifts in the physical environment that led to the loss of large and old trees in favor of pioneer trees (Fig. 3, A and C), with subsequent impacts on the community composition of insects (*32*). In grasslands, fragment size also affected succession rate, such that increased light penetration and altered seed pools in smaller fragments impeded the rate of ecological succession relative to that of larger fragments (*33*) (Fig. 3A).

Consistently, all aspects of fragmentation—reduced fragment area, increased isolation, and increased edge—had degrading effects on a disparate set of core ecosystem functions. Degraded functions included reduced carbon and nitrogen retention (Fig. 3, A to C), productivity (Fig. 3C), and pollination (Fig. 3B).

In summary, across experiments spanning numerous studies and ecosystems, fragmentation consistently degraded ecosystems, reducing species persistence, species richness, nutrient retention, trophic dynamics, and, in more isolated fragments, movement.

## Long-term consequences of fragmentation

To synthesize all time series of species richness and ecosystem functioning gathered across experiments, we measured effects of fragmentation over the course of each study. The effect of fragmentation was calculated over time as the proportional change in fragmented relative to non- or less-fragmented treatments (Fig. 4).

In most cases, the large and consistent effects of fragmentation revealed by the experiments were predicted from theory. However, we were struck by the persistence of degradation to biodiversity and ecosystem processes and by the increase in many of the effects over time (Fig. 4). For example, extreme rainfall events at Wog Wog appeared to delay the decline in plant species richness for 5 years after fragmentation. In the Kansas Experiment, a lag of 12 years occurred before fragmentation effects on plant succession were detected. Our results thus reveal long-term and progressive effects of fragmentation and provide support for three processes proposed by recent studies in spatial ecology: extinction debt, immigration lag, and ecosystem function debt (Fig. 4).

First, we found strong evidence for temporal lags in extinction [that is, "extinction debt" (*30*)] in fragments. Species richness of plants, arthropods, and birds sampled in the experiments conducted in mature forest fragments and replicated moss landscapes showed decreases of

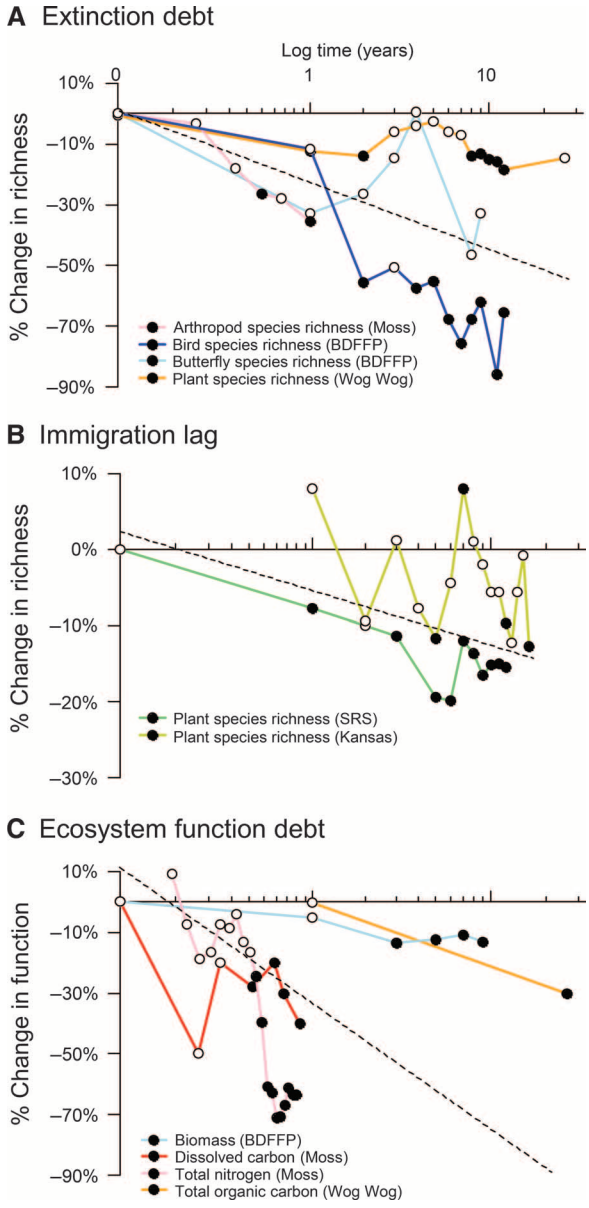


**Fig. 4. Delayed effects of fragmentation on ecosystem degradation.** (**A**) The extinction debt represents a delayed loss of species due to fragmentation. (**B**) The immigration lag represents differences in species richness caused by smaller fragment area or increased isolation during fragment succession. (**C**) The ecosystem function debt represents delayed changes in ecosystem function due to reduced fragment size or increased isolation. Percent loss is calculated as proportional change in fragmented treatments [for example, (no. of species in fragment − no. of species in control)/(no. of species in control) × 100]. Fragments and controls were either the same area before and after fragmentation, fragments compared to unfragmented controls, or small compared to large fragments. Filled symbols indicate times when fragmentation effects became significant, as determined by the original studies (see table S2). Mean slopes (dashed lines) were estimated using linear mixed (random slopes) models. Mean slope estimates (mean and SE) were as follows: (A) −0.22935 (0.07529); (B) −0.06519 (0.03495); (C) −0.38568 (0.16010).

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20 to 75% after fragmentation (Fig. 4A). Some declines were evident almost immediately after fragmentation, whereas others increased in magnitude over the experiment's duration. Across experiments, average loss was >20% after 1 year, >50% after 10 years, and is still increasing in the longest time series measured (more than two decades). The rate of change appears to be slower in larger fragments [in BDFFP, 50% decline in bird species after 5 years in 1-ha fragments, but after 12 years in 100-ha fragments; in Moss, 40% decline in arthropod species richness of small fragments and 26% reduction in large fragments after 1 year (*34*, *35*)]. As predicted by theory (*36*), the extinction debt appears to take longer to pay in larger fragments.

Second, we observed that reduced richness was coincident with an "immigration lag" (*37*), whereby small or isolated fragments are slower to accumulate species during community assembly (*33*, *38*) (Fig. 4B). Immigration lags were observed in experiments conducted in successional systems that were initiated by creating new habitat fragments, rather than by fragmenting existing habitats. After more than a decade, immigration lags resulted in 5% fewer species after 1 year, and 15% fewer species after 10 years in small or isolated fragments compared to large or connected fragments (Fig. 4B).

Third, we observed an ecosystem function debt caused by fragmentation (*39*) in forest and moss fragments (Fig. 4C). An ecosystem function debt is manifest both as delayed changes in nutrient cycling and as changes to plant and consumer biomass. Loss of function amounted to 30% after 1 year, rising to 80% after a decade in small and isolated fragments when compared to larger and more connected fragments (Fig. 4C). Functional debts can result from biodiversity loss, as when loss of nutrients and reduction in decomposition are caused by simplification of food webs. Alternatively, the impact is exhibited through pathways whereby fragmentation changes biotic (for example, tree density in successional systems) or abiotic conditions (for example, light regimes or humidity) in ways that alter and potentially impair ecosystem function [for example, biomass collapse in fragments; Figs. 3 and 4; altered nitrogen and carbon soil dynamics (*40*)].

### A new understanding of the effects of fragmentation

By testing existing theory, experiments play a pivotal role in advancing ideas and developing new theory. We draw on experimental evidence to highlight two ways that the understanding of fragmentation has been enriched by the interplay between long-term experiments and development of theory.

First, island biogeography (*6*) was among the earliest theories to predict extinction and immigration rates and patterns of species richness in isolated biotas, which were later used to predict the effects of fragmentation on these variables. Experiments in continental settings tested the theory and gave rise to fresh perspectives. For example, islands are surrounded by sea, a thoroughly inimical matrix for island-dwelling species. Habitat islands, or fragments, are surrounded by a matrix that may not be so unsuitable for some species. In terms of all of the ecological variables studied in our long-term experiments, our results support the conclusion that ecological dynamics in human-modified fragments are a stark contrast to the dynamics in intact habitats that remain. Observational studies that have devoted more detailed consideration to the countryside within which fragments are embedded explain the diversity of ecological responses in remaining fragments (*41*). At the same time as experiments supported the core predictions of classical theories about effects of fragment size and isolation (Figs. 3 and 4), they spurred and tested new theories such as metacommunity theory (*42*) to account for variation in connectivity and habitat quality within and between fragments (*33*, *43*–*45*), spatial dynamics (*14*, *46*), and spatially varying interspecific interactions (*47*).

Second, experiments have demonstrated that the effects of fragmentation are mediated by variation in traits across species. More realistic predictions of community responses to fragmentation emerged after explicit consideration of species traits such as rarity and trophic levels (*48*, *49*), dispersal mode (*50*–*52*), reproductive mode and life span (*29*, *53*), diet (*54*), and movement behavior (*55*, *56*). Increasingly, the simple theoretical prediction that fragmentation reduces species richness is being modified to account for species identity through models that focus on how species vary in their traits (*4*, *21*, *36*, *48*, *57*, *58*). Consideration of traits may help to interpret variation around the overarching pattern that fragmentation consistently reduces species richness across many species and biomes (Figs. 3 and 4).

## A NEW GENERATION OF FRAGMENTATION EXPERIMENTS

New foci are emerging for studying ecosystem fragmentation, including (i) synergies between fragmentation and global changes, (ii) eco-evolutionary responses of species to fragmentation, and (iii) ecological responses to fragmentation in production landscapes—that is, ecosystems whose services are under extreme appropriation by humans (*59*).

First, conclusions from experiments thus far are likely to have been conservative because impacts from other environmental changes have been mostly excluded. Most forms of global change known to reduce population sizes and biodiversity will be exacerbated by fragmentation (*58*, *60*), including climate change (*61*), invasive species (*62*, *63*), hunting (*64*), pollution [including light, noise, and chemicals (*65*)], and altered disturbance regimes (*66*).

More complex experiments with unparalleled control and capacity to simultaneously manipulate fragmentation and other global changes are now under way (*53*). The Metatron, created in 2011 in southern France (*67*), enables ecologists to assess effects of variation in temperature and other abiotic factors in addition to habitat isolation. The SAFE Project is being created in the rainforest of Borneo (*68*) and will embed a fragmentation experiment within a production agricultural plantation in which poaching will occur. Other synergies should be investigated experimentally, including the interaction between fragmentation and hunting, fire, infectious disease outbreaks, or nitrogen deposition. Within these experiments, fragmentation and loss of habitat can then be varied independently.

Second, current experiments have stopped short of examining how fragmentation drives evolution through genetic bottlenecks, ecological traps, changing patterns of selection, inbreeding, drift, and gene flow (*69*–*72*). Extensive fragmentation has occurred over many years, and in some regions over millennia (*11*). Changes caused by fragmentation undoubtedly lead to altered patterns of selection and trait evolution. Evolutionary responses to fragmentation have already been suggested (*73*, *74*), and it is likely that such changes will, in turn, feed back to influence population persistence and ecosystem resilience in fragmented landscapes. Linking long-term experiments with the tools of landscape genetics (*75*) may provide powerful insights into the evolutionary dynamics of species inhabiting fragmented landscapes.

Third, new experiments should address the management of natural habitats in production landscapes by monitoring vegetation, networks of interacting species, and ecosystem services at ecologically relevant

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spatial and temporal scales (*76*–*78*). Some ecosystem services have global consequences, for example, local carbon sequestration affects global atmospheric $CO_2$. However, in many cases the benefits obtained by people depend on their proximity to habitat fragments (*79*). For example, crop pollination and biological pest control from natural areas adjacent to farms are made available by the very process of habitat fragmentation, bringing people and agriculture closer to those services. Yet, further fragmentation reduces access to many services and ultimately may push landscapes past tipping points, beyond which essential ecosystem services are not merely diminished but lost completely (*80*). This complex relationship creates a double-edged sword, for which locally optimal levels and arrangements of habitat must be sought. New fragmentation experiments should consider how multiple fragments in a landscape interact, creating an ecological network in which the collective benefit of ecosystem services may be greater than the sum of services provided by individual fragments (*81*, *82*). Experimental inferences may then be tested beyond their spatiotemporal domains and, if successful, extrapolated across scales. Such research will be aided by satellite monitoring of ecosystems and human land use across the globe. The most powerful research programs will integrate experiments, observational studies, air- and space-borne imaging, and modeling.

## CONCLUSIONS

Fragmentation experiments—some of the largest and longest-running experiments in ecology—provide clear evidence of strong and typically degrading impacts of habitat fragmentation on biodiversity and ecological processes. The findings of these experiments extend to a large fraction of the terrestrial surface of the Earth. Much of the Earth's remaining forest fragments are less than 10 ha in area, and half of the world's forest is within 500 m of the forest edge—areas and distances matched to existing long-term experiments (Figs. 1 and 2) from which consistent effects of fragmentation have emerged (Figs. 3 and 4).

Reduced fragment area, increased isolation, and increased edge initiate changes that percolate through ecosystems (Fig. 3). Fragmentation has the capacity to generate persistent, deleterious, and often unpredicted outcomes, including surprising surges in abundance of some species and the pattern that long temporal scales are required to discern many strong system responses. In light of these conclusions and ongoing debates, we suggest that fragmentation's consistency, pervasiveness, and long-term degrading effect on biodiversity and ecosystem function have not been fully appreciated (*9*).

Without gains in yield and efficiency of agricultural systems (*83*), the expansion of human populations will inevitably continue to reduce and fragment natural areas. The area of Earth's land surface devoted to cropland already occupies 1.53 billion hectares (*83*) and may expand 18% by the middle of this century (*84*), and the area committed to urban centers is predicted to triple to 0.18 billion hectares by 2030 (*85*). The capacity of the surviving forests and other natural habitats to sustain biodiversity and ecosystem services will hinge upon the total amount and quality of habitat left in fragments, their degree of connectivity, and how they are affected by other human-induced perturbations such as climate change and invasive species. Long-term experiments will be even more needed to appreciate, explain, and predict long-term effects. New efforts should work in concert, coordinating a network of experiments across ecosystems and spatial extents.

The effects of current fragmentation will continue to emerge for decades. Extinction debts are likely to come due, although the counteracting immigration debts may never fully be paid. Indeed, the experiments here reveal ongoing losses of biodiversity and ecosystem functioning two decades or longer after fragmentation occurred. Understanding the relationship between transient and long-term dynamics is a substantial challenge that ecologists must tackle, and fragmentation experiments will be central for relating observation to theory.

Experimental results to date show that the effects of fragmentation are strong and markedly consistent across a diverse array of terrestrial systems on five continents. Increasingly, these effects will march in concert with other global changes. New experiments should be coupled with emerging technologies, landscape genetics, and detailed imagery of our planet, and should be coordinated with current ecological theory to understand more deeply the coupled dynamics of ecological and social systems. These insights will be increasingly critical for those responsible for managing and prioritizing areas for preservation and ecological restoration in fragmented landscapes.

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/1/2/e1500052/DC1

Materials and Methods

Fig. S1. Map of the BDFFP experiment and location within Brazil.

Fig. S2. Map of the Kansas fragmentation experiment.

Fig. S3. Map of the Wog Wog experiment and location within Australia.

Fig. S4. Map of the SRS experiment showing locations of the eight blocks in the second SRS Corridor Experiment within the SRS, South Carolina, USA.

Fig. S5. Design of the Moss experiment.

Fig. S6. Design of the Metatron experiment with 48 enclosed fragments and adjoining enclosed corridors.

Fig. S7. Map of the SAFE experiment and location within Borneo [after Ewers *et al.* (*68*)].

Table S1. Metadata for Fig. 3 in the main text.

Table S2. Metadata for Fig. 4 in the main text.

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Review

# Biodiversity management in the face of climate change: A review of 22 years of recommendations

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ABSTRACT

Climate change creates new challenges for biodiversity conservation. Species ranges and ecological dynamics are already responding to recent climate shifts, and current reserves will not continue to support all species they were designed to protect. These problems are exacerbated by other global changes. Scholarly articles recommending measures to adapt conservation to climate change have proliferated over the last 22 years. We systematically reviewed this literature to explore what potential solutions it has identified and what consensus and direction it provides to cope with climate change. Several consistent recommendations emerge for action at diverse spatial scales, requiring leadership by diverse actors. Broadly, adaptation requires improved regional institutional coordination, expanded spatial and temporal perspective, incorporation of climate change scenarios into all planning and action, and greater effort to address multiple threats and global change drivers simultaneously in ways that are responsive to and inclusive of human communities. However, in the case of many recommendations the how, by whom, and under what conditions they can be implemented is not specified. We synthesize recommendations with respect to three likely conservation pathways: regional planning; site-scale management; and modification of existing conservation plans. We identify major gaps, including the need for (1) more specific, operational examples of adaptation principles that are consistent with unavoidable uncertainty about the future; (2) a practical adaptation planning process to guide selection and integration of recommendations into existing policies and programs; and (3) greater integration of social science into an endeavor that, although dominated by ecology, increasingly recommends extension beyond reserves and into human-occupied landscapes.

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## 1. Introduction

Climate change poses major new challenges to biodiversity conservation. As atmospheric $CO_2$ increases over the next century, it is expected to become the first or second greatest driver of global biodiversity loss (Sala et al., 2000; Thomas et al., 2004). Global average temperatures have increased 0.2 °C per decade since the 1970s, and global average precipitation increased 2% in the last 100 years (IPCC, 2007a). Moreover, climate changes are spatially heterogeneous. Some locations, such as the Arctic, experience much larger changes than global means, while others are exposed to secondary effects like sea level rise (IPCC, 2007a). Climate change may have already resulted in several recent species extinctions (McLaughlin et al., 2002; Pounds et al., 2006). Many species ranges have moved poleward and upward in elevation in the last century (Parmesan and Yohe, 2003; Root et al., 2003) and will almost certainly continue to do so. Local communities are disaggregrating and shifting toward more warm-adapted species (Parmesan, 2005). Phenological changes in populations, such as earlier breeding or peak in biomass, are decoupling species interactions (Walther et al., 2002).

These changes raise concerns about the effectiveness of existing biodiversity protection strategies (Halpin, 1997; Hannah et al., 2002; Peters and Darling, 1985; Scott et al., 2002). Biodiversity conservation relies predominately on fixed systems of protected areas, and the mandated goals of many conservation agencies and institutions are to protect particular species assemblages and ecosystems within these systems (Lemieux and Scott, 2005; Scott et al., 2002). With the magnitude of climate change expected in the current century, many vegetation types and individual species are expected to lose representation in protected areas (Araujo et al., 2004; Burns et al., 2003; Lemieux and Scott, 2005; Scott et al., 2002). Reserves at high latitudes and high elevations, on low-elevation islands and the coast, and those with abrupt landuse boundaries are particularly vulnerable (Sala et al., 2000; Shafer, 1999). Landscapes outside of protected areas are hostile to the survival of many species due to human infrastructure and associated stressors, such as invasive species, hunting, cars, and environmental toxins. Such fragmentation directly limits species migration and gene flow. Projected rates of climate change are also faster than they were in the past – so rapid that in situ genetic adaptation of most populations to new climate conditions is not likely (Jump and Penuelas, 2005), nor is migration likely to be fast enough for many species (Davis and Shaw, 2001). Moreover, even if major global action reduced emissions significantly within the next years or capped them at year 2000 levels, the thermal inertia of the oceans will continue to drive climate change for decades and will require adaptive responses (Meehl et al., 2005; Wigley, 2005). A recent update of atmospheric $CO_2$ growth rate, which has more than doubled since the 1990s as global economic activity increases and becomes more carbon-intensive, makes clear that significant global emissions reductions are a distant goal at best (Canadell et al., 2007).

How should we modify our biodiversity protection strategies to deal with climate change? Here we focus on adaptation strategies. Adaptation is broadly defined as adjustment in human or natural systems, including structures, processes, and practices (IPCC, 2007b). Scientists have written about adaptation with increasing frequency over the last two decades, but developments in this area have progressed slowly. For years, emissions mitigation has largely been the only game in town, with little governmental or private support for climate change adaptation. For instance, the United States National Park Service (NPS) in collaboration with the Environmental Protection Agency (EPA) has created a 'Climate Friendly Park' program. It aims to reduce greenhouse gas emissions, but it does not include measures or incentives to park managers to build and test adaptation strategies to preserve biodiversity under climate change. In many ways, adaptation science has begun to develop only very recently in response to recent widespread acceptance by governments and private citizens of the certainty of climate change.

In this paper we review the growing, published literature specifically addressed at biodiversity management and adaptation in the face of climate change. We consider biodiversity to include all types of organisms at all scales, from genes to ecosystems. The genesis for our review was the 2006 annual meeting of the California Invasive Plant Council, where climate change was identified by both researchers and practitioners as a key issue for action. Discussions throughout the meeting, however, made clear that practitioners felt at a loss for practical steps to take. Managers working at local preserves were particularly uncertain about what, if anything, they could do to prepare for climate change. We use this review in order to highlight what actions and actors scientists have so far identified to address climate change, and to

explore how recommendations inform an adaptation planning process at various management scales. Scott and Lemieux (2005) reviewed a similar literature but focused on park management. Here we explore adaptation planning across scales and in both protected and unprotected areas.

## 2. Methods

We used Web of Science, including Science Citation Index Expanded, Social Science Citation Index, and Arts and Humanities Citation databases from 1975 to March 2007, to search for published journal articles on climate change and biodiversity management. We used the search terms "climate change", "global warming", "climatic change", "climate-change" and "changing climate" in all possible combinations with the search string "management OR biodiversity OR adaptation OR conservation OR restoration OR planning OR reserve design OR strategy OR land-use OR landuse OR landscape OR protected area OR park". Articles that discussed strategies for both biodiversity and related ecosystem services were included, but we excluded articles that only addressed ecosystem services such as management strategies for carbon stocks, human infrastructure, and food security. We also did not attempt to review studies that explore climate impacts on ecosystem components and processes without making explicit recommendations for biodiversity management. This literature is large and has been reviewed elsewhere (Kappelle et al., 1999; McCarty, 2001; Walther et al., 2002). From these searches, we identified and read 281 prospective articles, and from these culled those that provided explicit recommendations for management in the face of climate change. An additional four articles published after March 2007 were included, which were found through personal communication.

To analyze recommendations, we created a database in which we recorded every recommendation for action or information in the exact language used in the paper and answered a series of questions designed to synthesize recommendations and identify biases in the literature to date. We asked:

(1) *In what formal and informal contexts does action need to occur?* To answer this question, we categorized recommendations into broad spheres of activity: (1) policy reform, (2) science and technology effort and advances, (3) changes in conservation sector activity including restoration, or (4) changes in individual and community behavior, such as by farmers, ranchers, and other private landowners.

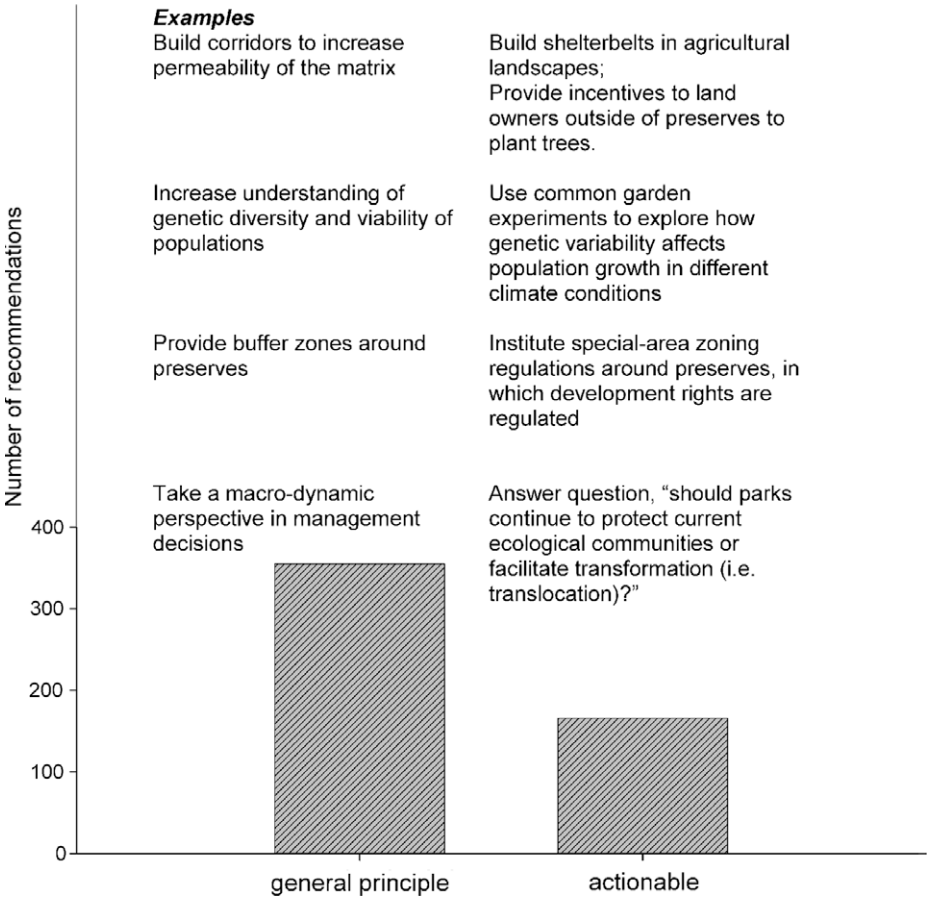


**Fig. 1 – Examples and distribution of recommendations classified as "general principle" and "actionable". Most recommendations offer general principles for climate change adaptation but lack specificity needed for implementation.**

(2) *What is the basis for the recommendation?* We recorded what information an author used to formulate their recommendation. Categories included empirical experimental data, simulation, literature review, case studies, interviews, or workshops. We also included the term 'ecological reasoning' to encompass studies based predominately on theory and opinion.
(3) *Is the recommendation a general principle or actionable?* A recommendation was considered a "general principle" if it provided a guiding concept, such as "build flexibility", but was generic open-ended and without example of who should act or what one should do (see Fig. 1). "Actionable" was given to those recommendations that identified a very clear who and what and often gave examples, such as, "[in restoration] use a broader range of species than prescribed solely on local basis to build system resilience (Harris et al., 2006)".
(4) *Is the recommendation for biodiversity or for biodiversity and related ecosystem services?*
(5) *Is there a geographic context for the recommendation?*
(6) *Does the article focus on a biome or ecosystem-type?*
(7) *Where in the landscape would the recommendation apply?* We categorized recommendations as applying to reserve (any public or private land-holding dedicated to biodiversity protection and maintenance, synonymous with protected area), or human-use lands (the matrix), or non-specific, meaning the recommendation could be enacted in either reserve or matrix land.
(8) *Does the recommendation describe an information need or a necessary action?* All recommendations for research were categorized as information needs, while the 'action' category included recommendations such as building corridors, reforming policy or buying more land.

To minimize variation in how articles were classified as a function of when they were read (i.e. the 1st paper entered compared to the 100th), records in the database were periodically shuffled by different criteria (i.e. year published or geographic context) and then re-classified. In addition, both authors coded a sub-sample of recommendations. After compiling the database, similar records were grouped into 'recommendation' categories. We tabulated the most common recommendations and ranked them by frequency cited overall.

## 3. Results and discussion

We recorded 524 recommendations from 113 papers, published in 57 different source journals and three books. Recommendations ranged from calls for specific types of modeling (e.g. inexact-fuzzy multiobjective programming (Huang et al., 1998) to broad shifts in governance structures (Tompkins and Adger, 2004) (Table 1). The number of papers published on this topic has increased dramatically in recent years (Fig. 2). Thirty-three percent of recommendations addressed biodiversity protection in conjunction with related ecosystem services, including forest products, fisheries and hunting, agriculture and grazing, and human health. Recommendations call for research, leadership and reform by a range of actors in several sectors; Emphasis in this set of literature is on science and nature conservation rather than on social or political adaptation measures (Fig. 3), with an emphasis somewhat more focused on reserve land over the matrix (Fig. 4a). Action is weighted more than information needs (Fig. 4b). When information needs were identified, they were overwhelmingly calls for more ecological rather than social scientific data (Fig. 4c). Recommendations are biased toward North America and Europe (Fig. 5a) and forests ecosystems (Fig. 5b).

Recommendations address various stages in an adaptation process, from research needs to methods for impact assessments to large-scale changes in policies by governmental, academic or non-governmental institutions (Table 1). About 70% of recommendations were classified as general principles under our classification scheme rather than specific, actionable strategies or tactics (Fig. 1). For example, seven authors suggest flexibility in management approaches, but only Millar et al. (2007) suggest flexibility and follow with a definition of what that means: willingness to change course, risk-taking including doing nothing, and capacity to reassess conditions frequently. Climate change adaptation work, at least in this literature, is still largely at the "idea" stage – it is based predominately on ecological reasoning rather than specific research, case studies, or empirical data (Fig. 5c), and it is largely nonspecific in the geographic areas or biome types that it targets (Fig. 5a and b). Many articles based on concrete modeling work or empirical studies of species responses to climate change tended either to not elaborate their results to management directives, or to present recommendations in vague terms such as, "restoration should be considered". Alternatively, very specific recommendations were proposed and not generalized for use outside of the target system. There appears to be a need for a happy medium between highly specific recommendations useful only in target areas and highly generalized recommendations that fail to inspire application (Halpin, 1997). This happy medium is likely to emerge rapidly as climate change adaptation science grows.

In the literature reviewed here, few recommendations suggested a process a manager could use to develop an adaptation plan and evaluate its usefulness (but see Hannah et al., 2002). More information on adaptation frameworks are developed in reports by Parks Canada (Welch, 2005), the NCEAS Conservation and Climate Change Working Group 2 (personal communication), and England's Department for Food Environment and Rural Affairs (http://www.defra.gov.uk/wildlife-countryside/resprog/findings/ebs-climate-change.pdf), which were not reviewed here. In practice, planners and managers could apply recommendations in at least three ways. At the broadest scale, long-term planning and policy formulation should tackle adaptation for whole landscapes and regions, with tools like reserve selection, ecosystem management, and landuse zoning schemes. Second, managers of individual reserves might want to know what they can do at their sites, individually or in concert with other sites. Third, rather than initially pursuing an idealized regional, landscape, or site-scale plan, the first practical step for many managers, conservation stakeholders and policymakers is to evaluate and adapt existing conservation plans. In the following

**Table 1 – List of recommendations for climate change adaptation strategies for biodiversity management assembled from 112 scholarly articles. 524 records were condensed into 113 recommendation categories and are ranked by frequency of times cited in different articles.**

| Rank | Recommendation | No. articles | References |
|---|---|---|---|
| 1 | Increase connectivity (design corridors, remove barriers for dispersal, locate reserves close to each other, reforestation | 24 | Beatley (1991), Chambers et al. (2005), Collingham and Huntley (2000), Da Fonseca et al. (2005), de Dios et al. (2007), Dixon et al. (1999), Eeley et al. (1999), Franklin et al. (1992), Guo (2000), Halpin (1997), Hulme (2005), Lovejoy (2005), Millar et al. (2007), Morecroft et al. (2002), Noss (2001), Opdam and Wascher (2004), Rogers and McCarty (2000), Schwartz et al. (2001), Scott et al. (2002), Shafer (1999), Welch (2005), Wilby and Perry (2006) and Williams (2000) |
| 2 | Integrate climate change into planning exercises (reserve, pest outbreaks, harvest schedules, grazing limits, incentive programs | 19 | Araujo et al. (2004), Chambers et al. (2005), Christensen et al. (2004), Dale and Rauscher (1994), Donald and Evans (2006), Dyer (1994), Erasmus et al. (2002), Hulme (2005), LeHouerou (1999), McCarty (2001), Millar and Brubaker (2006), Peters and Darling (1985), Rounsevell et al. (2006), Scott and Lemieux (2005), Scott et al. (2002), Soto (2001), Staple and Wall (1999), Suffling and Scott (2002) and Welch (2005) |
| 3 | Mitigate other threats, i.e. invasive species, fragmentation, pollution | 17 | Bush (1999), Chambers et al. (2005), Chornesky et al. (2005), Da Fonseca et al. (2005), de Dios et al. (2007), Dixon et al. (1999), Halpin (1997), Hulme (2005), McCarty (2001), Noss (2001), Opdam and Wascher (2004), Peters and Darling (1985), Rogers and McCarty (2000), Shafer (1999), Soto (2001), Welch (2005) and Williams (2000) |
| 4 | Study response of species to climate change physiological, behavioral, demographic | 15 | Alongi (2002), Chambers et al. (2005), Crozier and Zabel (2006), Dyer (1994), Erasmus et al. (2002), Fukami and Wardle (2005), Gillson and Willis (2004), Honnay et al. (2002), Hulme (2005), Kappelle et al. (1999), McCarty (2001), Mulholland et al. (1997), Noss (2001), Peters and Darling (1985) and Swetnam et al. (1999) |
| | Practice intensive management to secure populations | 15 | Bartlein et al. (1997), Buckland et al. (2001), Chambers et al. (2005), Chornesky et al. (2005), Crozier and Zabel (2006), Dixon et al. (1999), Dyer (1994), Franklin et al. (1992), Hulme (2005), Morecroft et al. (2002), Peters and Darling (1985), Soto (2001), Thomas et al. (1999), Williams (2000) and Williams et al. (2005) |
| | Translocate species | 15 | Bartlein et al. (1997), Beatley (1991), Chambers et al. (2005), de Dios et al. (2007), Halpin (1997), Harris et al. (2006), Honnay et al. (2002), Hulme (2005), Millar et al. (2007), Morecroft et al. (2002), Pearson and Dawson (2005), Peters and Darling (1985), Rogers and McCarty (2000), Schwartz et al. (2001), Shafer (1999) and Williams et al. (2005) |
| 5 | Increase number of reserves | 13 | Burton et al. (1992), Dixon et al. (1999), Hannah et al. (2007), Hughes et al. 2003, LeHouerou (1999), Lovejoy (2005), Peters and Darling (1985), Pyke and Fischer (2005), Scott and Lemieux (2005) (2007), van Rensburg et al. (2004), Wilby and Perry (2006) and Williams et al. (2005) |
| 6 | Address scale problems match modeling, management, and experimental spatial scales for improved predictive capacity | 12 | Chornesky et al. (2005), Da Fonseca et al. (2005), Dale and Rauscher (1994), Ferrier and Guisan (2006), Guisan and Thuiller (2005), Huang (1997), Hughes et al. (2003), Kueppers et al. (2004), Kueppers et al. (2005), Mulholland et al. (1997), Noss (2001), Root and Schneider (1995) and Root and Schneider (2006) |
| | Improve inter-agency, regional coordination | 12 | Bartlein et al. (1997), Cumming and Spiesman (2006), Da Fonseca et al. (2005), Grumbine (1991), Hannah et al. (2002), Lemieux and Scott (2005), Rounsevell et al. (2006), Scott and Lemieux (2005), Soto (2001), Suffling and Scott (2002), Tompkins and Adger (2004) and Welch (2005) |
| 7 | Increase and maintain basic monitoring programs | 11 | Chambers et al. (2005), Cohen (1999), Huang (1997), Rogers and McCarty (2000), Root and Schneider (1995), Schwartz et al. (2001), Shafer (1999), Staple and Wall (1999), Suffling and Scott (2002), Wilby and Perry (2006) and Williams (2000) |
| | Practice adaptive management | 11 | Allison et al. (1998), Chambers et al. (2005), Hulme (2005), Lasch et al. (2002), Maciver and Wheaton (2005), Millar et al. (2007), Scott and Lemieux (2005), Staple and Wall (1999), Suffling and Scott (2002), Tompkins and Adger (2004) and Welch (2005) |
| | Protect large areas, increase reserve size | 11 | Beatley (1991), Bellwood and Hughes (2001), Burton et al. (1992), Bush (1999), Halpin (1997), Hulme (2005), Morecroft et al. (2002), Peters and Darling (1985), Shafer (1999), Soto (2001) and Watson (2005) |

**Table 1 – continued**

| Rank | Recommendation | No. articles | References |
|---|---|---|---|
| 8 | Create and manage buffer zones around reserves | 10 | Bush (1999), de Dios et al. (2007), Halpin (1997), Hannah et al. (2002), Hartig et al. (1997), Hughes et al. (2003), Millar et al. (2007), Noss (2001), Shafer (1999) and van Rensburg et al. (2004) |
| 9 | Create ecological reserve networks large reserves, connected by small reserves, stepping stones | 8 | Allison et al. (1998), Collingham and Huntley (2000), de Dios et al. (2007), Gaston et al. (2006), Opdam et al. (2006), Opdam and Wascher (2004), Shafer (1999) and Welch (2005) |
| | Develop improved modeling and analysis capacity i.e. more effective software, integration with GIS, integrate greater complexity | 8 | Chornesky et al. (2005), Ferrier and Guisan (2006), Guisan and Thuiller (2005), Guo (2000), Huang et al. 1998, Mulholland et al. (1997), Peters and Darling (1985) and Rounsevell et al. (2006) |
| | Do integrated study of multiple global change drivers | 8 | Dale and Rauscher (1994), Desanker and Justice (2001), Donald and Evans (2006), Halpin (1997), Hannah et al. (2002), McCarty (2001), Watson (2005) and Williams (2000) |
| | Improve techniques for and do more restoration wetlands, rivers, matrix | 8 | Da Fonseca et al. (2005), de Dios et al. (2007), Dyer (1994), Hartig et al. (1997), Lovejoy (2005), Millar et al. (2007), Mulholland et al. (1997) and Shafer (1999) |
| | Increase interdisciplinary collaboration | 8 | Gillson and Willis (2004), Guisan and Thuiller (2005), Hannah et al. (2002), Hulme (2005), Kappelle et al. (1999), Root and Schneider 1995, Soto (2001) and Williams (2000) |
| | Promote conservation policies that engage local users and promote healthy human communities | 8 | Chapin et al. (2006), Desanker and Justice (2001), Eeley et al. (1999), Lovejoy (2005), Opdam and Wascher (2004), Ramakrishnan (1998), Tompkins and Adger (2004) and McClanahan et al. (2008) |
| | Protect full range of bioclimatic variation | 8 | Bush (1999), Eeley et al. (1999), McCarty (2001), Noss (2001), Pyke et al. (2005), Pyke and Fischer (2005), Shafer (1999) and Thomas et al. (1999) |
| | Soften landuse practices in the matrix | 8 | Beatley (1991), Burton et al. (1992), Da Fonseca et al. (2005), Franklin et al. (1992), Hannah et al. (2002), Noss (2001), Williams (2000) and Woodwell (1991) |
| 10 | Adopt long-term and regional perspective in planning, modeling, and management | 7 | Eeley et al. (1999), Ferrier and Guisan (2006), Franklin et al. (1992), Guo (2000), Lovejoy (2005), Millar and Brubaker (2006), Opdam and Wascher (2004), Peters and Darling (1985), Peterson et al. (1997), Scott et al. (2002) and Welch (2005) |
| | Re-asses conservation goals (i.e. move away from concepts of natural, embrace processes over patterns | 7 | Franklin et al. (1992), Hulme (2005), Millar et al. (2007), Scott and Lemieux (2005) (2007), Scott et al. (2002) and Suffling and Scott (2002) |
| | Study species dispersal across landuse boundaries, gene flow, migration rates, historic flux | 7 | Guo (2000), Halpin (1997), Hughes et al. (2003), Kappelle et al. (1999), Lovejoy (2005), Opdam and Wascher (2004) and Rice and Emery (2003) |
| | Study species distributions current and historic | 7 | Da Fonseca et al. (2005), Eeley et al. (1999), Erasmus et al. (2002), Guo (2000), Hannah et al. (2002), Kappelle et al. (1999) and Millar and Brubaker (2006) |
| 11 | Broaden genetic and species diversity in restoration and forestry | 6 | Burton et al. (1992), de Dios et al. (2007), Harris et al. (2006), Maciver and Wheaton (2005), McCarty (2001), Millar et al. (2007), Rice and Emery (2003) and Staple and Wall (1999) |
| | Develop adaptation strategies now; early adaptation is encouraged | 6 | Huang et al. (1998), Hulme (2005), Lemieux and Scott (2005), Scott and Lemieux (2005) (2007) and Welch (2005) |
| | Do not implement $CO_2$ emission mitigation projects that negatively impact biodiversity | 6 | Chambers et al. (2005), Klooster and Masera (2000), Koziell and Swingland (2002), Kueppers et al. (2004) and Streck and Scholz (2006), Welch (2005) |
| | Manage for flexibility, use of portfolio of approaches, maintain options | 6 | Eeley et al. (1999), Hulme (2005), Kappelle et al. (1999), Lovejoy (2005), Millar et al. (2007) and Welch (2005) |
| | Validate model results with empirical data | 6 | Dale and Rauscher (1994), Guisan and Thuiller (2005), Hulme (2005), Malcom et al. (2006), Opdam and Wascher (2004) and Watson (2005) |
| 12 | Do regional impact assessments | 5 | Cohen (1999), Desanker and Justice (2001), Lasch et al. (2002), Lindner et al. (1997) and Suffling and Scott (2002) |
| | Identify indicator species | 5 | Chambers et al. (2005), Hulme (2005), Noss (2001), Underwood and Fisher (2006) and Welch (2005) |
| | Initiate long-term studies of species responses to climate | 5 | Mulholland et al. (1997), Noss (2001), Opdam and Wascher (2004), Peters and Darling (1985) and Root and Schneider (2006) |
| | Model species ranges in the future | 5 | Allison et al. (1998), Da Fonseca et al. (2005), Hannah et al. (2002), Kerr and Packer (1998) and Kriticos et al. (2003) |
| | Protect refugia current and predicted future | 5 | Bush (1999), Chambers et al. (2005), Eeley et al. (1999), Noss (2001) and Scott et al. (2002) |
| | Study adaptive genetic variation | 5 | Harris et al. (2006), Hughes et al. (2003), Jump and Penuelas (2005), Kappelle et al. (1999) and Rice and Emery (2003) |

(continued on next page)

**Table 1 – continued**

| Rank | Recommendation | No. articles | References |
|---|---|---|---|
| 13 | Leadership by those with power senior management, government agencies | 4 | Scott and Lemieux (2005) (2007), Tompkins and Adger (2004) and Welch (2005) |
| | Limit $CO_2$ emissions | 4 | Hannah et al. (2007), Hannah et al. (2005), Mayer and Rietkerk (2004) and Rogers and McCarty (2000) |
| | Predict effects of directional climate change on ecosystems, communities, populations | 4 | Allison et al. (1998), de Dios et al. (2007), Kappelle et al. (1999) and Root and Schneider (2006) |
| | Preserve genetic diversity in populations | 4 | Chambers et al. (2005), de Dios et al. (2007) and Lovejoy (2005), Noss (2001) |
| | Represent each species in more than one reserve | 4 | Halpin (1997), Millar et al. (2007), Peters and Darling (1985) and Shafer (1999) |
| 14 | Create culturally appropriate adaptation/ management options | 3 | Dixon et al. (1999), Huang (1997), Tompkins and Adger (2004) |
| | Create education programs for public about landuse practices and effects on and with climate | 3 | Bush (1999) and Welch (2005), Williams (2000) |
| | Develop best management practices for climate change scenarios | 3 | Mulholland et al. (1997), Rogers and McCarty (2000) and de Dios et al. (2007) |
| | Institute flexible zoning around reserves | 3 | Halpin (1997), Peters and Darling (1985) and Soto (2001) |
| | Increase investment in climate related research | 3 | Lemieux and Scott (2005), Lovejoy (2005) and Peters and Darling (1985) |
| | Increase communication of knowledge about climate change impacts to policymakers and stakeholders | 3 | Erasmus et al. (2002), Opdam and Wascher (2004) and Welch (2005) |
| | Initiate dialogue among stakeholders | 3 | McKenzie et al. (2004), Rogers and McCarty (2000) and Scott et al. (2002) |
| | Institute government reform (i.e. adaptive governance) | 3 | Chapin et al. (2006), Tompkins and Adger (2004) and Williams (2000) |
| | Locate reserves in areas of high heterogeneity, endemism | 3 | Halpin (1997), Opdam and Wascher (2004) and Peters and Darling (1985) |
| | Maintain natural disturbance dynamics of ecosystems | 3 | Halpin (1997), Noss (2001) and Shafer (1999) |
| | Practice proactive management of habitat to mitigate warming | 3 | Halpin (1997), Mulholland et al. (1997) and Wilby and Perry (2006) |
| | Secure boundaries of existing preserves | 3 | Hannah et al. (2007), van Rensburg et al. (2004) and Welch (2005) |
| | Start strategic zoning of landuse to minimize climate related impacts | 3 | Bush (1999), Solecki and Rosenzweig (2004) and Tompkins and Adger (2004) |
| | Study and monitor ecotones and gradients | 3 | Halpin (1997), Lovejoy (2005) and Stohlgren et al. (2000) |
| | Study effectiveness of corridors | 3 | Graham 1988, Halpin (1997) and Williams et al. (2005) |
| | Use predictive models to make decisions on where to situate new reserves | 3 | Bush (1999), Hannah et al. (2007) and Pearson and Dawson (2005) |
| 15 | Anticipate surprises and threshold effects i.e. major extinctions or invasions | 2 | Bartlein et al. (1997) and Millar et al. (2007) |
| | Design biological preserves for complex changes in time, not just directional change | 2 | Bartlein et al. (1997) and Graham (1988) |
| | Locate reserves at northern boundary of species' ranges | 2 | Peters and Darling (1985) and Shafer (1999) |
| | Manage the matrix | 2 | Eeley et al. (1999) and Lovejoy (2005) |
| | Practice proactive research on climate change | 2 | Harris et al. (2006) and Williams (2000) |
| | Protect many small reserves rather than single large | 2 | Opdam and Wascher (2004) and Pearson and Dawson (2005) |
| | Provide education opportunities and summaries of primary literature for management staff to learn and network about climate change | 2 | Grumbine (1991) and Welch (2005) |
| | Study and protect metapopulations | 2 | Crozier and Zabel (2006) and Opdam and Wascher (2004) |
| | Study processes of change at multiple spatial and temporal scales | 2 | Dale and Rauscher (1994) and Watson (2005) |
| | Use GIS to study species distributions and landscape patterns | 2 | Brown (2006) and Da Fonseca et al. (2005) |

**Table 1 – continued**

| Rank | Recommendation | No. articles | References |
|---|---|---|---|
| 16 | Action plans must be time-bound and measurable | 1 | Welch (2005) |
| | Adjust park boundaries to capture anticipated movement of critical habitats | 1 | Welch (2005) |
| | Create institutional flexibility | 1 | Millar et al. (2007) |
| | Create linear reserves oriented longitudinally | 1 | Pearson and Dawson (2005) |
| | Establish cross-national collaboration | 1 | Desanker and Justice (2001) |
| | Establish neo-native forests plant species where they were in the past, but are not found currently | 1 | Millar et al. (2007) |
| | Experiment with refugia | 1 | Millar et al. (2007) |
| | Focus protection on sensitive biomes | 1 | Scott et al. (2002) |
| | Focus on annual plants rather than perennials near climate boundaries | 1 | Buckland et al. (2001) |
| | Increase wetland protection | 1 | Hartig et al. (1997) |
| | Institutional capacity enhancement to address climate change | 1 | Lemieux and Scott (2005) |
| | Institute reform to improve support for interdisciplinary, multi-institutional research | 1 | Root and Schneider (1995) |
| | Locate reserves so major vegetation transitions are in core | 1 | Halpin (1997) |
| | Locate reserves at core of ranges | 1 | Araujo et al. (2004) |
| | Manage for landscape asynchrony | 1 | Millar et al. (2007) |
| | Manage human-wildlife conflict as change occurs | 1 | Wilby and Perry (2006) |
| | Manage populations to reduce temporal fluctuations in population sizes | 1 | Rice and Emery (2003) |
| | Develop guidelines for climate sensitive restoration and infrastructure development | 1 | Welch (2005) |
| | Need to increase social acceptance of shared resilience goals | 1 | Tompkins and Adger (2004) |
| | Promote personal action plans among employees to reduce emissions | 1 | Welch (2005) |
| | Protect endangered species ex situ | 1 | Noss (2001) |
| | Protect functional groups and keystone species | 1 | Noss (2001) |
| | Protect mountains | 1 | Peterson et al. (1997) |
| | Protect primary forests | 1 | Noss (2001) |
| | Protect urban green space | 1 | Wilby and Perry (2006) |
| | Quantify environmental susceptibility versus adaptive capacity to inform conservation planning | 1 | McClanahan et al. (2008) |
| | Schedule dam releases to protect stream temperatures | 1 | Rogers and McCarty (2000) |
| | Study changes in populations at rear of range rather than only range fronts | 1 | Willis and Birks (2006) |
| | Study response of undisturbed areas to climate change | 1 | Mulholland et al. (1997) |
| | Study social agency and human decision making | 1 | Desanker and Justice (2001) |
| | Study time-series data on species dynamics | 1 | Erasmus et al. (2002) |
| | Substitute space for time to study the responses of species to climate change | 1 | Millar and Brubaker (2006) |
| | Train more taxonomists | 1 | Huber and Langor (2004) |
| | Use caution in predictive modeling because the responses of some species are not well predicted | 1 | Willis and Birks (2006) |
| | Use simple decision rules for reserve planning | 1 | Meir et al. (2004) |
| | Use social networks for education about climate change | 1 | Huang (1997) |
| | Use triage in short-term to prioritize action | 1 | Millar et al. (2007) |

sections, we discuss how recommendations in the literature to date inform these three scales of application.

## 4. Regional policy and planning

Species historically respond to changing climate with distributional shifts, and many species are expected to lose current habitat representation in the future. In light of this, many recommendations call for greater integration of species protection plans, natural resource management, research and development agendas across wider geographic areas, on longer time-scales, and involving more diverse actors than in current practice. (1) Long-term, regional perspective and (2) improved coordination among scientists, land managers, politicians and conservation organizations at regional scales are among the most frequently cited recommendations to protect biodiversity in the face of climate change (Rank 10 and 6 respectively, see references in Table 1 and for all ranks mentioned hereafter). Increased interdisciplinary collaboration (Rank 9) as well as regional-scale impact assessments are also frequently identified (Rank 12). Recommendations for adaptation to regional policy and planning focus on two comple-

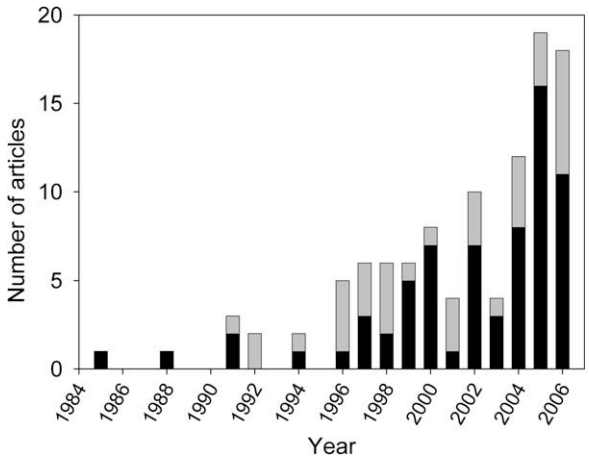


**Fig. 2 – Frequency distribution by publication year of papers included in this review, including articles addressing biodiversity only (black) or biodiversity in conjunction with ecosystem services (grey). Records from 2007 were only partially covered in this review and not included.**

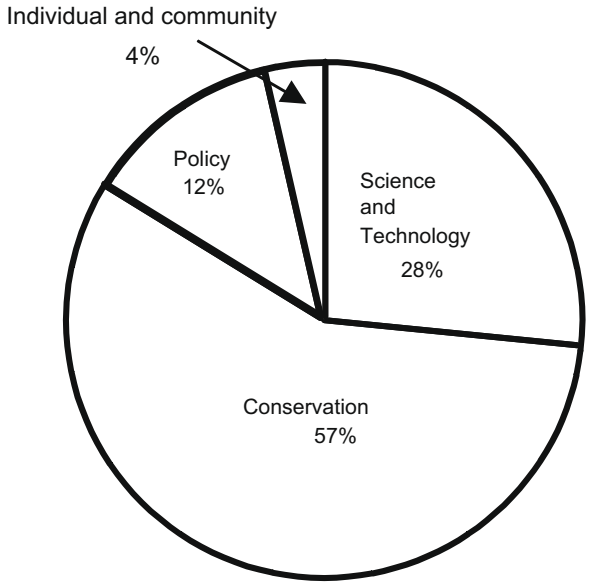


**Fig. 3 – Distribution of recommendations calling for climate change adaptation among different activity sectors: conservation (e.g. reserve purchases, management, restoration and regional coordination), science and technology (e.g. research and modeling), policy (e.g. land-zoning, governance structure and institutional capacity), and individuals and communities (e.g. private landowner practices and grassroots action). Recommendations were counted in all applicable sectors.**

mentary strategies: reserve planning and improving landscape connectivity. We discuss these issues further in the following two sections.

### 4.1. *Reserve planning*

Basing reserve acquisition priorities on predictions of future biome, community or individual species distributions under different climate scenarios is one method for climate change adaptation. The guiding principle is that reserves should be accumulated in areas predicted to be hotspots for biodiversity in the future or to provide habitat for species of high conservation value, warranting increased effort to model species distributions in the future (Rank 12). There are, however, several limitations to the accuracy and precision of simulation and analytical models of future species, biome or community distributions, leading some authors to recommend improved modeling capacity as the first step (Rank 9).

Model prediction error results from variation in model types, emissions, landuse and socio-economic scenarios. There are little-understood, but important, interactions between climate change and other global change drivers that could influence where species and habitats occur in the future (Rank 9). Insufficient data on species distributions (Rank 10) the effects of species interactions on distribution (Ferrier and Guisan, 2006; Kappelle et al., 1999), dispersal (Rank 10) and species, community or ecosystem responses to climate change (Rank 4) are also widely expressed concerns and lead authors to advocate for increased research in these areas before models are accepted. For example, bioclimatic envelope modeling uses current species distributions to predict future distributions as a function of climate. For many species such models can be productive, but in cases where species distributions are limited by factors other than climate, this extrapolation will prove misleading. Willis and Birks (2006) discuss the accuracy of bioclimatic models. Species-envelope model runs were conducted for backward predictions of species distributions and compared to paleo-ecological records. Many species distributions were predicted well, but some were largely inaccurate.

Problems of scaling also raise uncertainty (Rank 6), including scaling-down global climate models (GCMs) to fit management scales, or scaling-up empirical observations typically made at small spatial scales to predict larger scale processes (Root and Schneider, 1995). The scales of global climate models (GCM) and management activities simply do not match. Most reserves are smaller than a single grid cell in a GCM. Climate can vary sharply within this scale, and this variation often drives local patterns of species distribution and abundance – particularly in mountainous or coastal areas. Regional climate models, which are only available for small areas of the globe, are a more appropriate choice for management and planning (Dale and Rauscher, 1994; Guisan and Thuiller, 2005; Kueppers et al., 2005; Mulholland et al., 1997), though they remain limited by key uncertainties, assumptions and costs (Root and Schneider, 1995).

Not surprisingly, these inherent limitations of bioclimatic envelope models generate debate about whether and how to apply them to reserve selection. Some strongly advocate including climate change in reserve selection models and locating new reserves with expected changes in climate (Araujo et al., 2004; Bush, 1996; Dyer, 1994; Pearson and Dawson, 2005). Araujo et al. (2004) compare the ability of six existing reserve selection methods to secure European plant species in the context of climate change. They found species loss from protected reserves on the order of 6–11% of taxa for all models, and they conclude that new reserve-selection models specific to climate change are needed. Hannah et al. (2007)

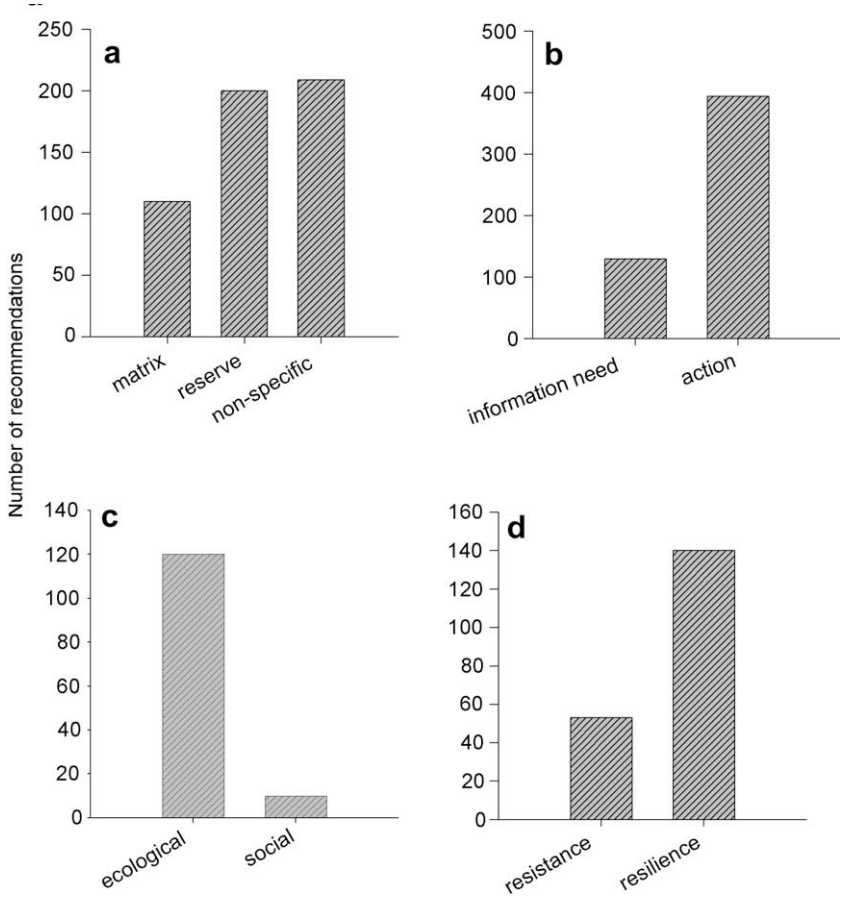


**Fig. 4 – Distribution of recommendations among broad categories referring to (a) type of land targeted, (b) information need or action, (c) type of information need, and (d) management goal. Y-axis ranges vary across graphs because not all recommendations fit into every set of categories.**

make a compelling case for not waiting to incorporate climate change forecasts into reserve selection models despite uncertainty. They use bioclimatic envelope models to explore the need for additional protected areas to achieve representation for thousands of species in three regions (Mexico, South Africa Cape, and Europe) in current and future climate and find that less land is needed in the long-term if planning models are designed to solve for both current and future conditions simultaneously.

Others argue, however, that given tremendous uncertainty, the priority should be to acquire new reserves in locations that minimize the spatial distances among new and existing reserves so that species can migrate (Allison et al., 1998; Collingham and Huntley, 2000; Halpin, 1997; Opdam and Wascher, 2004; Shafer, 1999). Williams et al. (2005) used a simulation model to estimate that 50% more protected land area in particular locations was needed to create reserve corridors to protect *Proteaceae* in the South African Cape region through 2050. Citing a number of sources of potential error in model results, however, they recommend that as much reserve area as possible be set aside. Such strategies do not require extensive modeling capacity and resources and instead focuse on rapid acquisition of land as it becomes available to create porous landscapes. Other authors reason that to facilitate migration and adaptation potential, reserves should be located with reference to focal species or community distributions, such as in their cores (Araujo et al., 2004; Halpin, 1997) or at their northern boundaries (Peters and Darling, 1985; Shafer, 1999). There seems to be little consensus or data to inform this debate. More research is needed about where in a species' range individuals are most likely to survive, migrate or adapt to rapid environmental change (Willis and Birks, 2006).

Debate also arises around the relative advantages of few large versus several small reserves in the context of climate change. The tension is whether large reserves will be large enough to allow species to track changing climate and remain inside reserve boundaries, and whether small preserves along latitudinal, elevational or other climate gradients will be close enough together for species to move between them. Eleven sources recommend protecting large areas (Beatley 1991; Bellwood and Hughes 2001; Burton et al. 1992; Bush 1996; Halpin 1997; Hulme 2005; Morecroft et al. 2002; Peters and Darling 1985; Shafer 1999; Soto 2001; Watson 2005), while two advocate focusing on many small areas (Opdam and Wascher, 2004; Pearson and Dawson, 2005). Eight suggest a compromise strategy of creating ecological networks of small and large reserves embedded within intermediate land uses (Allison et al., 1998; Collingham and Huntley, 2000; de Dios et al., 2007; Gaston et al., 2006; Opdam et al., 2006; Opdam and Wascher, 2004; Shafer, 1999; Welch, 2005).

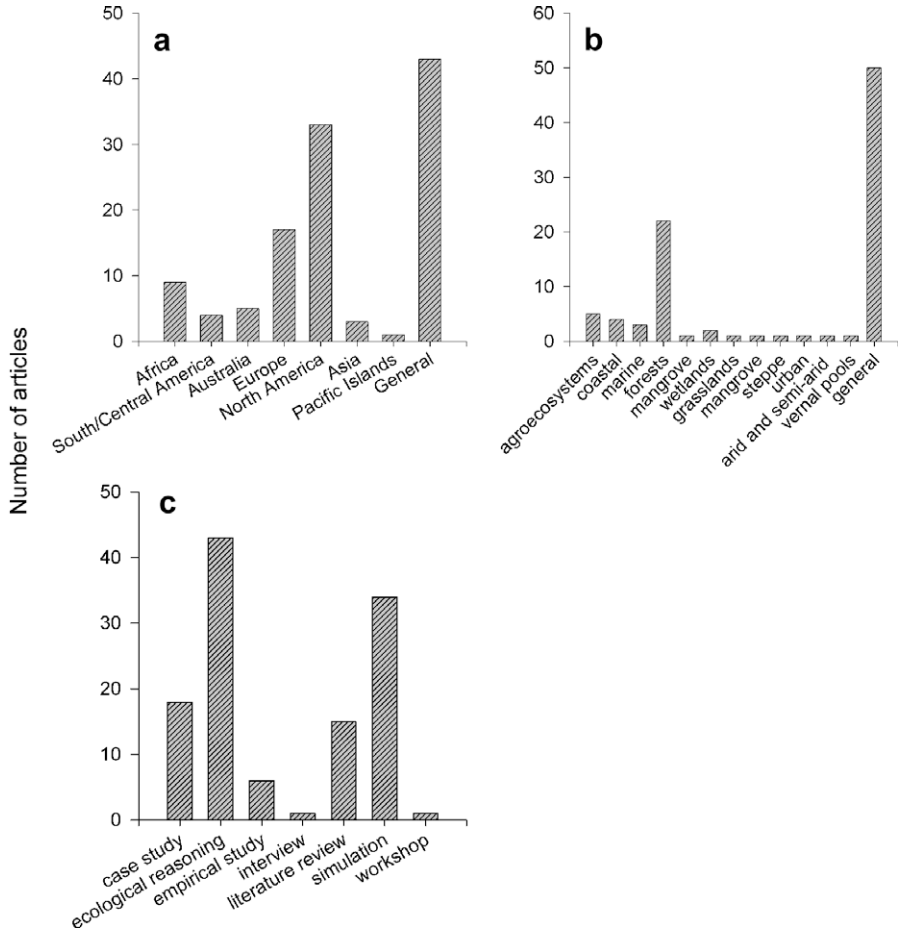


**Fig. 5 – The (a) geographic focus, (b) biome focus, and (c) evidence basis for recommendations addressing climate change adaptation strategies for biodiversity management.**

What all of the recommendations for reserve selection share is an urge to protect more land rapidly (Rank 5). This push will certainly help buffer biodiversity against climate change as well as other threats. However, climate change is likely to exacerbate existing tensions and tradeoffs between protecting areas and meeting basic human needs. Creating more new reserves might be feasible in some settings but must be guided by targeted, well-informed strategies likely to maximize effectiveness in the face of climate change. In most areas, action in lands outside of reserves must also be a part of climate change strategies for biodiversity conservation (Franklin et al., 1992; Lovejoy, 2005).

### 4.2. *Landscape connectivity*

To improve landscape connectivity, so that species can move, is the most frequent recommendation for climate change adaptation in the literature reviewed here (Rank 1). Authors recommend some form of corridor creation via the designation of new parks (de Dios et al., 2007; Halpin, 1997; Scott et al., 2002) oriented longitudinally (Eeley et al., 1999; Noss, 2001; Shafer, 1999), or through actions in non-reserve land, such as protecting riparian habitat and railway lines in cities (Wilby and Perry, 2006), or by planting trees and shrubs to create shelterbelts and hedgerows in farmlands (Donald and Evans, 2006; Guo, 2000; Schwartz et al., 2001). There was little guidance in this literature set for corridor implementation beyond common-sense reasoning, however. Illustrative examples of current corridor projects or elaboration of specific ecological or political tactics for corridor creation might help jump-start this process. For example, case studies of the Dutch Ecological Network and other similar national models to plan and link protected areas may be particularly informative at this stage of adaptation planning (Gaston et al., 2006). Further, despite widespread favor for ecological networks, assessment of their effectiveness remains in its infancy. Similarly, the field of corridor ecology, while recognized as integral to conservation practice in fragmented landscapes for years, is still young (see Hilty et al., 2006). Some authors warn of a significant need for more empirical data to support the effectiveness of corridors, optimize their spatial arrangement, and minimize risks of increased transmission of disease or invasive species before the conservation community embraces corridors uniformly as the tool to combat biodiversity loss in the face of global climate change (Graham, 1988; Halpin, 1997; Scott and Lemieux, 2005; Williams et al., 2005).

A second popular recommendation for improving landscape connectivity is to change how we manage the matrix

(Da Fonseca et al., 2005; Eeley et al., 1999; Lovejoy, 2005). Many authors advocate creating buffer zones around reserves (Rank 8) or flexible landuse zoning at reserve boundaries to allow for land swaps in the future as species distributions shift (Rank 14). Others recommend urban planning and zoning to avoid climate-related risks (Rank 14). In general, enlisting people and human communities to 'soften' landuse through sustainable or less damaging practices (e.g. low intensity forestry or alternatives to building sea walls) (Rank 9) and to restore habitat (Rank 9) will facilitate species movement and persistence in the future.

Despite wide acknowledgement, these connectivity strategies were among the most poorly developed recommendations, limited mainly to very general actions (e.g. "build flexibility", "manage the matrix", "modify landuse practices") without identification of kinds of actors that might need to be involved (e.g. reserve managers, policymakers, individuals) or information gaps. Landuse reform likely needs to bring together local governments, urban planners, community groups and conservation organizations and to involve high degrees of coordination across multiple jurisdictions to provide landscape cohesion (Press et al., 1995). Substantial work to flesh out this process, as well as to guide information acquisition, is needed before new forms of management across landuse types can be implemented.

Even with good landscape connectivity, some species will not be able to migrate. For these species – such as dispersal-limited species, those restricted to rare or confined habitat types, or those with life history traits like low reproductive rates – translocations from within their current range to locations suitable in the future are widely advocated (Rank 4). Translocations are a contentious issue because of the challenges associated with moving populations successfully and predicting suitable future habitats, as well as the potential for unintended consequences from introducing new species into existing communities (Lemieux and Scott, 2005; McLachlan et al., 2007). Empirical evidence suggests that animal translocations tend to be unsuccessful and costly (Fischer and Lindenmayer, 2000). Despite these real problems, we did not find discussion of the feasibility of such programs. Climate change adaptation strategies would likely necessitate moving at least some species outside of their current range, an action that has rarely been pursued thus far. To fully evaluate the feasibility of translocations would require stronger understanding of best available methods, potential risks, and policies for regional coordination to avoid situations in which different conservation objectives are put in conflict (McLachlan et al., 2007).

## 5. Site-scale action

Many land managers feel that there is little they can do about climate change beyond what they are already doing, such as trying to maintain basic ecosystem functioning and mitigate other threats like invasive species and pollution. To a certain extent, recommendations we reviewed validate this perspective. A number of "business as usual" recommendations rank high in their frequency in the literature, e.g. mitigating current threats, such as invasive species and habitat loss (Rank 2), increasing or continuing basic monitoring programs (Rank 7) or managing populations for natural disturbance dynamics (Halpin, 1997; Noss, 2001; Shafer, 1999). Franklin et al. (1992) describe how in forest ecosystems mature trees slow the effects of climate change because they tolerate a wide range of temperatures, while seedling establishment is far more sensitive. Under climate change, removal of long-lived trees will therefore act to intensify and speed-up the rate at which forest ecosystems change compared to intact forests. Restoration and greening efforts function as proactive management to mitigate local-scale warming (Halpin, 1997; Mulholland et al., 1997; Wilby and Perry, 2006). Mulholland et al. (1997) point out that restoration of riparian vegetation, needed to secure wildlife populations and ecosystem services now, will also function to decrease stream temperatures in the future. Wilby and Perry (2006) highlight how green building and landscaping techniques, such as planting green roofs, neighborhood trees, and water structures, will help to counter increasing problems of urban heat-island effects.

Other authors point out that business as usual is probably not enough in many cases. Peters and Darling (1985) suggest that managers consider rescue measures such as adding irrigation or drainage systems to secure sensitive populations. Buckland et al. (2001) anticipate that soil fertility in some grasslands may require manipulation to impede species invasions under warmer conditions. Advice to incorporate a broader range of species and genotypes in restoration and forestry than prescribed based on local provenance was common (Rank 11). This type of strategy would depart significantly from the preference for local genotypes prevailing in restoration and forestry practice to date (Millar and Brubaker, 2006; Millar et al., 2007; Scott and Lemieux, 2007) and warrants increased experimentation to better understand potential costs and benefits (Harris et al., 2006; Rice and Emery, 2003).

### 5.1. *Resilience versus resistance*

A first step for managers will be to wrestle with the question of whether and when they will attempt to resist biotic change, such as by adding irrigation if precipitation declines, rather than try to build resilience to change, such as by facilitating population adaptive capacity through introduction of a wider range of genotypes. In theory resistant strategies attempt to bolster a system's defenses to rapid environmental change, while resilience strategies attempt to bolster a system's ability to absorb rapid environmental change. More recommendations advocate resilience than resistance strategies (Fig. 4d). However, intensive management actions to protect historical species in their current distributions are widely advocated (Rank 4). The latter align best with a fixed-reserve approach focusing on local species precedence, an approach that will be increasingly costly and challenging to maintain as directional global changes accelerate.

For some species and systems, options other than intervention might not exist. Resistance approaches designed to maintain the status quo are nevertheless risky – they may leave systems vulnerable to total collapse if interventions are not maintained or compromise other system components (Harris et al., 2006; Walker et al., 2002). For example, the removal of invasive species has sometimes resulted in unpredicted and negative impacts to ecosystem structure and

function (Zavaleta et al., 2001). Managing for resilience (sensu Holling, 1973) on the other hand explicitly focuses on increasing the flexibility and ability of systems to adapt and self-organize in response to change. To build resilience to climate change into systems, however, may require radical shifts in perspective for many conservation stakeholders and re-evaluation of conservation goals (Rank 10). Land managers might need to view a broader range of ecosystem states as desirable, such as novel or dynamic local assemblages that maintain functioning and trophic complexity but not necessarily species identity (Hulme, 2005), or to re-evaluate operational definitions and guidelines, such as what constitutes an invasive species or when a species can be added to a risk list (Scott and Lemieux, 2005; Scott et al., 2002).

Examples of broad perspective shift are found in the restoration literature. Millar and Brubaker (2006) emphasize the use of paleo-ecological perspectives to guide restoration goals and interventions. They ask that managers and restoration practitioners "make friends with physical and climatic change," arguing for instance that which species are deemed 'natural' or 'invasive' depends on the spatial and temporal resolution of data used to inform perspective. For example, Monterey pines (*Pinus radiata*) are considered native to a small region of California in which they were found at the time of European colonization. The species has since naturalized widely in California from landscaping plantings and is targeted for removal as an unwanted exotic in these regions. Paleo-ecological records of *P. radiata* reveal strong climate-driven dynamics in range, with widespread distribution during favorable periods and retreat during unfavorable periods. Millar and Brubaker (2006) suggest that naturalized populations be restored rather than removed in locations where *P. radiata* thrived when the climate was similar to the present or predicted future. Pearsall (2005) describes an experimental landscape-scale project in North Carolina, USA designed to test a range of restoration options for combating peat-land loss as a result of rising sea level. Options include oyster bed formation, dune formation, native plant establishment, as well as nonnative plant establishment. The experiment is scheduled to run for 25 years with regular evaluation intervals. Bradley and Wilcove (in press) imagine a "transformative restoration" in which the plant species used to repopulate restoration sites are determined by future climate conditions rather than historical presence. For example, based on results of bioclimatic envelope models, areas in the Great Basin ecoregion of the Western US may be restored best with plants introduced from the Mojave Desert, a more arid, neighboring biome. These projects share a broad, long-term and pragmatic perspective on acceptable restoration outcomes, one that may be necessary to tackle climate change.

A key strategy for building the adaptive capacity of systems is to enhance diversity at various scales. Diverse populations tend to be more adaptable, placing a premium on protecting and managing for high genetic diversity (Rank 13). Capturing the full range of bioclimatic variability within preserves and across landscapes and designing high species, structural, and landscape diversity into constructed and managed systems are also recommended (Rank 9). Pockets of outlier vegetation, areas of high endemism, ecotones, and refugia that protected species during climate shifts in the past are anticipated to be important sources for species re-colonization and radiation in the future, as well as provide retreats for migrating or translocated species (Rank 12). Willis and Birks (2006) discuss methods that combine genetic and paleo-ecological evidence to identify sites with distinctive patterns of genetic diversity that resulted from past geological events and refugial isolation.

Resistance and resilience strategies are not mutually exclusive. Very special communities or organisms that are of high conservation value may warrant highly invasive, intense and costly management regimes to maintain them. Regimes for intensive management are likely to be implemented through existing threatened species management frameworks, such as recovery plans. For more widespread populations, communities and ecosystems, which often provide important ecosystem services, a focus on resilience might be most appropriate. At the site-scale, managers need to address a host of practical issues such as the cost and cost-effectiveness of adaptation options, their compatibility with existing regulatory and institutional constraints, and their likely effectiveness in the absence of coordination with adjoining private lands.

## 6. Adapting existing conservation plans

The existing literature does provide an array of actions for managers to build on and consider incorporating into existing conservation plans. A practical first step to climate change adaptation planning is to evaluate the likely outcomes for biodiversity of continuing current management and conservation directions. Most conservation policies and management plans do not yet explicitly consider climate change (Chambers et al., 2005; Groves et al., 2002; Hannah et al., 2002; Scott and Lemieux, 2007). A consistent theme in the literature is at the very least to immediately appraise current conservation and management practice in the context of climate change (Rank 2) with the goal of developing and adopting specific climate change adaptation policies in the near future (Rank 11). The literature here contained some suggestions for how to do this. A few articles emphasized the use of models to guide evaluation and adaptation of existing practices. For example, Christensen et al. (2004) used a simulation model to investigate a coupled system of plants and grazers in the Inner Mongolia Steppe under different climate scenarios. They determined that grasslands were likely to undergo a state-transition to shrublands if existing grazer densities are maintained, and they advocate reducing grazers in this area as well as in other semi-arid managed grassland systems. Hulme (2005) provided a general overview of how mathematical models can integrate long-term demographic and climate data to set climate change-appropriate harvest or stocking schedules or to forecast pest outbreaks.

Some authors highlight existing efforts that are well-suited to tackle climate change and warrant increased funding and research. Donald and Evans (2006) argue that agri-environment incentives and easement programs in the US and the EU, which are growing due to shifts in farm policies, warrant increased funding priority because of their potential to improve habitat availability and landscape connectivity across managed ecosystems. They discuss how these policies

could be modified to tackle climate change directly. Site-specific climate conditions and biotic responses could be mapped on to landscapes and used to prioritize locations for farm diversification. Similar gains could be made by targeting other private landowner biodiversity enrichment programs, like the USDA Forest Legacy Program (http://www.fs.fed.us/spf/coop/programs/loa/flp.shtml) or the National Wildlife Federation's Urban Backyard Wildlife Program (http://www.nwf.org/gardenforwildlife/).

### 6.1. *Holistic strategies*

Issues that currently challenge conservation practice may need to be addressed before the added stress of climate change complicates them further. Communities of local users are often in conflict with conservation objectives (Chan et al., 2007; Suffling and Scott, 2002). Identifying opportunities for reduced conflict and increased synergy between conservation and local communities will become more important as climate changes. A number of authors warn that conservation policies must create positive economic outcomes for local peoples to buffer them against potentially dramatic shifts in livelihoods that will accompany climate shifts (Rank 9). Adaptation requires community buy-in and participation (Chapin et al., 2006). To this end, conservation policies that foster learning and participation (Ramakrishnan, 1998) and provide options that are culturally and economically appropriate, such as those that honor traditional management systems and do not rely on expensive technologies, are more likely to be embraced and implemented (Rank 14). McClanahan et al. (2008) argue that climate-informed conservation planning necessitates site-specific understanding of environmental susceptibility and societal capacity to cope and adapt. They illustrate this process for five western Indian Ocean countries with respect to coral reef conservation. Locations with high environmental susceptibility and low adaptive capacity will be most difficult to secure effectively in the future, while those with low environmental susceptibility and high adaptive capacity will be easiest. Locations with low environmental susceptibility and low adaptive capacity are good candidates for biodiversity investment, but to be effective these locations also require investments in human infrastructure, livelihood diversification and social capital.

Climate change is acting in concert with multiple other drivers of biodiversity loss including habitat degradation, soil loss, nitrogen enrichment, and acidification. Strong policies must simultaneously address more than one issue (Watson, 2005) or risk exacerbating environmental problems in the process of trying to combat them. Emission reduction programs are a significant push for many governments, organizations and individuals. They warrant an important place in any climate change combat strategy (Rank 13). A number of authors in this review urge, however, that emissions reduction programs and the Clean Development Mechanisms (CDMs) in the Kyoto Protocol be implemented in ways that simultaneously address carbon sequestration, biodiversity conservation and human livelihoods, rather than carbon sequestration in isolation (Rank 11).

Finally, climate change provides a much-needed impetus to evaluate how conservation policies respond to change in general. Climate change is only one of several global environmental trends to which biodiversity and its conservation must respond. Uncertainty in the climate change arena and about the future in general should not limit action to strengthen existing conservation strategies, with a focus on enhancing the ability of ecosystems to absorb and recover from rapid and unpredictable change.

## 7. A complete strategy

Climate change challenges conservation practice with the need to respond to both rapid directional change and tremendous uncertainty. Climate change adaptation therefore requires implementation of a range of measures, from short- to long-term and from precautionary and robust to more risky or deterministic, but specifically anticipatory (Fig. 6). To cer-

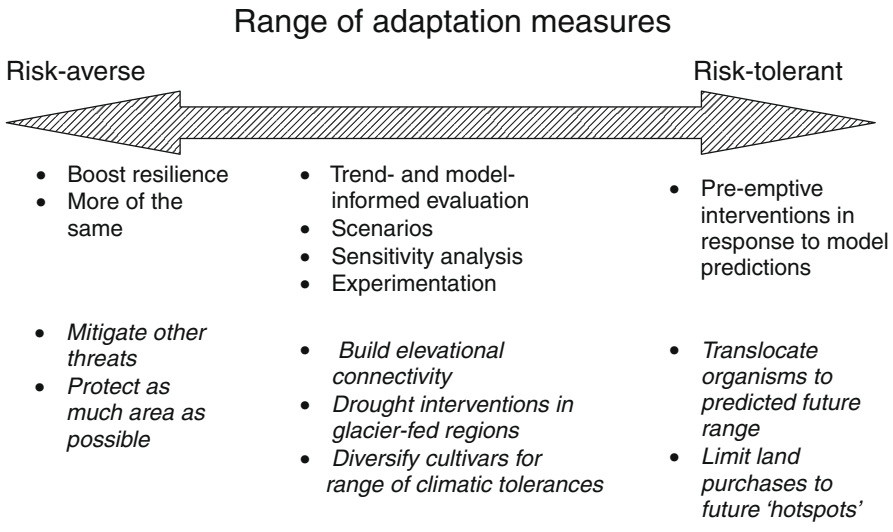


**Fig. 6 – Adaptation measures classified along a risk continuum. Under each risk category are examples of general approaches followed by examples of specific adaptation measures. A complete strategy should span a risk continuum.**

tain degree, risk tolerance of individual actors will guide strategy selection. Millar et al. (2007) discuss how managers must proactively decide whether to adopt deterministic or indeterministic approaches.

Each type of approach has benefits and drawbacks. Precautionary measures such as restoration, increased monitoring of species distribution, and increased investment in reserve protection do not necessarily require highly certain and precise climate change predictions, but such precautionary steps will help managers respond to current biodiversity threats as well as threats that emerge in the future. Precautionary measures alone, however, will not expand our ability to absorb and respond to rapid directional changes in climate, nor do they capitalize on available predictive information and efforts. In worst-case climate scenarios, over-reliance on bet-hedging measures may spread resources too thin or prove insufficient to help biodiversity weather the rapid changes underway. On the other hand, forecast-interventions bear significant risks if they are too deterministic, not robust to alternative futures or have negative unanticipated consequences (Suffling and Scott, 2002). They could also deliver great rewards and should be weighed with sensitivity analyses and scenarios, tested in pilot programs, and implemented initially at small scales (McLachlan et al., 2007). Scenario building – done in ways that are amenable to local data limitations and useable by policymakers and managers – is particularly apt for exploring the range of magnitudes and direction of possible futures and trends without commitment to specific forecasts (Brown, 2006; Millar et al., 2007).

While the range of recommendations in the literature is great, four consistent, broad themes emerge in this review for conservation stakeholders to apply to climate change planning and adaptation: (1) the need for regional institutional coordination for reserve planning and management and to improve landscape connectivity; (2) the need to broaden spatial and temporal perspective in management activities and practice, and to employ actions that build system resilience; (3) the need to incorporate climate change into all conservation planning and actions, which will require increased research and capacity to forecast future conditions and species responses and to deal effectively with unavoidable uncertainty; and (4) the need to address multiple threats and global change drivers simultaneously and in ways that are responsive to and inclusive of diverse human communities and cultures. Action along each of these fronts will involve difficult tradeoffs, barriers to implementation, and collaboration across diverse actors.

Action will also require an adaptation planning process or series of processes appropriate for various scales and applications. Most of the literature to date fails to distinguish adap-

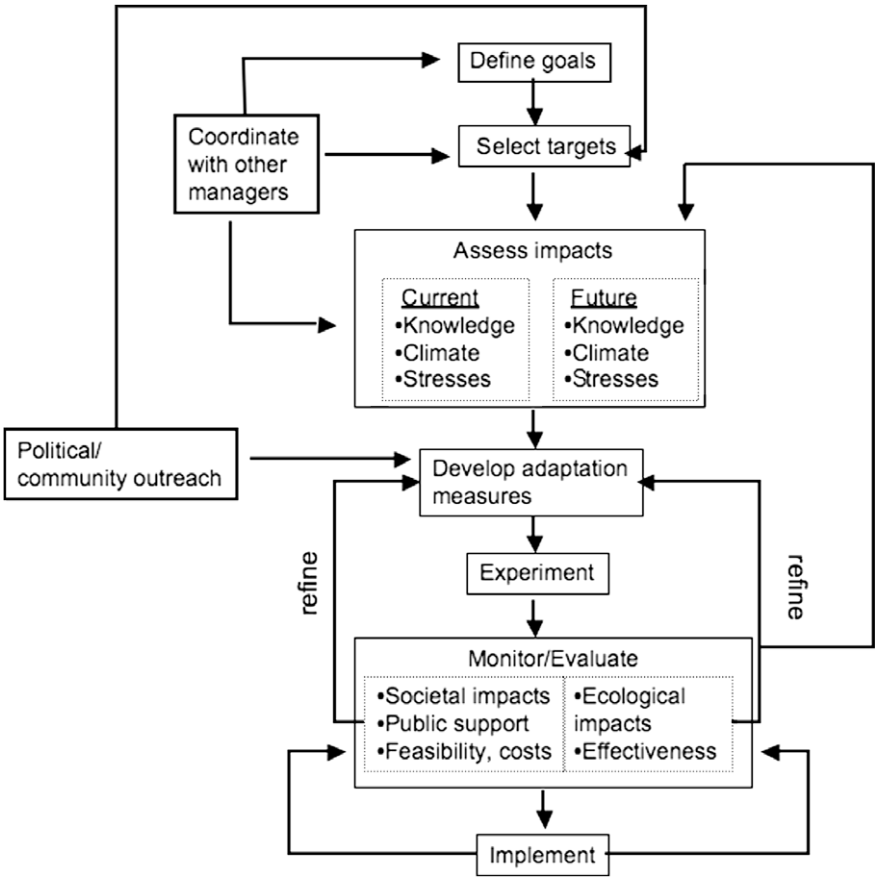


**Fig. 7 – Adaptation planning involves at least a few key steps, each complex and requiring collaboration among actors such as land managers, the public, scientists, funders and lawmakers. Recommendations reviewed here address aspects of these steps, but without specifying where they fit in relation to one another.**

tation from climate change impact assessment, or adaptation planning from implementation. These are distinct steps in an as-yet largely undefined process that the recommendations we survey could inform. We propose a series of general steps that should be modified, elaborated, and tailored to specific needs (Fig. 7). Key to any adaptation planning process will be to follow the principles of adaptive management (Rank 7), in which later steps inform earlier steps in an iterative and on going process.

## 8. Conclusions

Widespread calls exist for immediate action to adapt conservation practice to ongoing climate change in order to ensure the persistence of many species and related ecosystem services. However, the majority of recommendations in the published journal literature lack sufficient specificity to direct this action. Over the last 22 years, general recommendations have been reiterated frequently without the elaboration necessary to operationalize them. Greater effort to increase the availability and applicability of climate change adaptation options for conservation—through concrete strategies and case studies illustrating how and where to link research agendas, conservation programs and institutions—is badly needed.

Recommendations to date also largely neglect social science and are overwhelmingly focused on ecological data (Fig. 4c). This bias is alarming given the obvious importance of human behavior and preferences in determining conservation outcomes (Watson, 2005) and the increasingly important role of multi-use public and private lands in conservation practice. A holistic landscape approach to conservation, driven by a vision of humans and other species co-mingling across reserves and developed lands, has gradually gained prominence over the last 20 years. In their seminal paper, Peters and Darling (1985) provided a number of recommendations that continue to be widely advocated (Table 1), but they did not address the roles of conservation and restoration in human-dominated landscapes. These ideas emerge strongly in more recent literature highlighting a need to integrate ecology with other disciplines and approaches that explicitly address the roles of institutions, policy, politics and people in successful conservation strategies.

Finally, few resources or capacity exist to guide an adaptation planning process at any scale (Hannah et al., 2002; Scott and Lemieux, 2007; Welch, 2005). Such a process would place the sea of adaptation ideas and recommendations in framework and provide practitioners with tools, roles and a structure to evaluate what ideas might be useful and feasible for particular situations. Large-scale adaptation efforts that incorporate many of the recommendations found in this review are currently underway, including governmental efforts such as by Parks Canada or DEFRA in England, and by international non-governmental organizations such as The Nature Conservancy and the Wildlife Conservation Society. Well-documented case studies that focus not only on the outcome but also on the development process of adaptation plans are a promising avenue. These efforts can best enhance and encourage more widespread climate change adaptation, particularly at smaller scales, by capturing what they learn and disseminating it widely.

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# Guidelines for conserving connectivity through ecological networks and corridors

Jodi Hilty, Graeme L. Worboys, Annika Keeley, Stephen Woodley, Barbara Lausche, Harvey Locke, Mark Carr, Ian Pulsford, James Pittock, J. Wilson White, David M. Theobald, Jessica Levine, Melly Reuling, James E.M. Watson, Rob Ament and Gary M. Tabor

Craig Groves, Series Editor

Best Practice Protected Area Guidelines Series No. 30

WCPA WORLD COMMISSION ON PROTECTED AREAS

Convention on Biological Diversity

CONNECTIVITY CONSERVATION Specialist Group

CENTER for LARGE LANDSCAPE CONSERVATION

Yellowstone to Yukon Conservation Initiative

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A full set of guidelines is available at: www.iucn.org/pa_guidelines
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**IUCN PROTECTED AREA DEFINITION, MANAGEMENT CATEGORIES AND GOVERNANCE TYPES**

IUCN defines a protected area as:
**A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.**

The definition is expanded by six management categories (one with a sub-division), summarized below.
**Ia Strict nature reserve:** Strictly protected for biodiversity and also possibly geological/ geomorphological features, where human visitation, use and impacts are controlled and limited to ensure protection of the conservation values.
**Ib Wilderness area:** Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, protected and managed to preserve their natural condition.
**II National park:** Large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems, which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities.
**III Natural monument or feature:** Areas set aside to protect a specific natural monument, which can be a landform, sea mount, marine cavern, geological feature such as a cave, or a living feature such as an ancient grove.
**IV Habitat/species management area:** Areas to protect particular species or habitats, where management reflects this priority. Many will need regular, active interventions to meet the needs of particular species or habitats, but this is not a requirement of the category.
**V Protected landscape or seascape:** Where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and where safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated nature conservation and other values.
**VI Protected areas with sustainable use of natural resources:** Areas which conserve ecosystems, together with associated cultural values and traditional natural resource management systems. Generally large, mainly in a natural condition, with a proportion under sustainable natural resource management and where low-level non-industrial natural resource use compatible with nature conservation is seen as one of the main aims.

The category should be based around the primary management objective(s), which should apply to at least three-quarters of the protected area – the 75 per cent rule.

The management categories are applied with a typology of governance types – a description of who holds authority and responsibility for the protected area. IUCN defines four governance types.
**Type A. Governance by government:** Federal or national ministry/agency in charge; sub-national ministry or agency in charge (e.g. at regional, provincial, municipal level); government-delegated management (e.g. to NGO).
**Type B. Shared governance:** Trans-boundary governance (formal and informal arrangements between two or more countries); collaborative governance (through various ways in which diverse actors and institutions work together); joint governance (pluralist board or other multi-party governing body).
**Type C. Private governance:** Conserved areas established and run by individual landowners; non-profit organisations (e.g. NGOs, universities) and for-profit organisations (e.g. corporate landowners).
**Type D. Governance by Indigenous peoples and local communities:** Indigenous peoples' conserved areas and territories - established and run by Indigenous peoples; community conserved areas – established and run by local communities.

For more information on the IUCN definition, categories and governance types see Dudley (2008). *Guidelines for applyingprotected area management categories*, which can be downloaded at: www.iucn.org/pa_categories

For more on governance types, see Borrini-Feyerabend, et al., (2013). *Governance of Protected Areas: From understanding to action*, which can be downloaded at https://portals.iucn.org/library/node/29138

# Guidelines for conserving connectivity through ecological networks and corridors

**International Union for Conservation of Nature (IUCN)**

IUCN is a membership Union uniquely composed of both government and civil society organisations. It provides public, private and non-governmental organisations with the knowledge and tools that enable human progress, economic development and nature conservation to take place together.

Created in 1948, IUCN is now the world's largest and most diverse environmental network, harnessing the knowledge, resources and reach of more than 1,400 Member organisations and some 15,000 experts. It is a leading provider of conservation data, assessments and analysis. Its broad membership enables IUCN to fill the role of incubator and trusted repository of best practices, tools and international standards.

IUCN provides a neutral space in which diverse stakeholders including governments, NGOs, scientists, businesses, local communities, indigenous peoples organisations and others can work together to forge and implement solutions to environmental challenges and achieve sustainable development.

Working with many partners and supporters, IUCN implements a large and diverse portfolio of conservation projects worldwide. Combining the latest science with the traditional knowledge of local communities, these projects work to reverse habitat loss, restore ecosystems and improve people's well-being.

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**IUCN World Commission on Protected Areas (WCPA)**

IUCN's World Commission on Protected Areas (WCPA) is the world's premier network of protected area expertise. It is administered by IUCN Programme on Protected Areas and has more than 2,500 members, spanning 140 countries. WCPA is one of IUCN's six voluntary Commissions and its mission is to promote the establishment and effective management of a worldwide representative network of terrestrial and marine protected areas, as an integral contribution to the IUCN mission. WCPA works by helping governments and others plan protected areas and integrate them into all sectors, providing strategic advice to policy makers and practitioners to help strengthen capacity and investment in protected areas, and convening the diverse constituency of protected area stakeholders to address challenging issues. For more than 60 years, IUCN and WCPA have been at the forefront of global action on protected areas.

**www.iucn.org/wcpa**

**Convention on Biological Diversity (CBD)**

Opened for signature at the Earth Summit in Rio de Janeiro in 1992, and entered into force in December 1993, the Convention on Biological Diversity is an international treaty for the conservation of biodiversity, the sustainable use of the components of biodiversity and the equitable sharing of the benefits derived from the use of genetic resources. With 196 Parties so far, the Convention has near universal participation among countries.

**www.cbd.int**

**WCPA Connectivity Conservation Specialist Group (CCSG)**

CCSG was established in 2016 under the IUCN World Commission on Protected Areas (WCPA) to support information sharing, active participation, global awareness, and action to maintain, enhance, and restore ecological connectivity conservation around the world. Its objective is to advance the science, policy, and practice at international, national, and subnational levels to meet the growing demand for solutions that advance the identification, recognition, and implementation of consistent connectivity conservation measures.

**www.iucn.org/wcpa-connectivity**
**www.conservationcorridor.org/ccsg**

**Yellowstone to Yukon Conservation Initiative (Y2Y)**

Y2Y connects and protects habitat in North America spanning the Yellowstone to Yukon ecosystems so people and nature can thrive. It highlights and focuses on local issues that have implications for the region as a whole, and works to set the context for regional conservation work by providing the vision for a healthy Yellowstone to Yukon. Working across an area covering over 3,200 square kilometres, Y2Y engages partners across jurisdictions to knit together an interconnected system of wild lands and waters that harmonizes the needs of people and nature.

**www.y2y.net**

**Center for Large Landscape Conservation (CLLC)**

CLLC develops solutions, implements projects and contributes to global efforts that connect and protect crucial habitat across terrestrial, marine and freshwater ecosystems. It provides expertise through four key focus areas: science and research, mentorship and networking, community resilience and policy. By bringing knowledge and experience to bear on connectivity conservation issues worldwide, the Center works with communities, governments and other stakeholders to stop fragmentation and safeguard the legacy of protected and conserved areas by making them part of larger ecological networks for conservation.

**www.largelandscapes.org**

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Craig Groves, Series Editor

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# Foreword

Life on Earth thrives when ecosystems are healthy and ecologically connected. With the vast majority of the world experiencing increasing human impacts, natural ecosystems have been diminished and fragmented into smaller and smaller pieces. The destruction and fragmentation of natural ecosystems are a key cause of the global biodiversity crisis.

The need to both maintain and restore ecological connectivity is critical to the conservation of biological diversity, which provides irreplaceable functions and services, such as the provision of freshwater, food, climate regulation and pollination, just to name a few.

Ensuring that protected and other conserved areas are well-connected across landscapes and seascapes, as part of ecological networks, will both maintain biodiversity and provide an opportunity for species to adapt to climate change as local conditions change. Given the importance of healthy ecosystems to our own health and well-being, we need to urgently address and reverse the current trends of biodiversity loss and fragmentation.

The need for ecological connectivity is essential for the survival of wild species. Internationally, the Convention on the Conservation of Migratory Species of Wild Animals (CMS), a multilateral environment agreement under the United Nations, provides a global platform for States to take necessary collaborative actions to address the conservation and sustainable use of migratory animals and their habitats. At the national level, many countries have passed legislation to foster ecological connectivity, and this number is growing. The thirteenth meeting of the CMS Conference of the Parties (February 2020) affirmed that a commitment to maintaining and restoring ecological connectivity is one of the top priorities for CMS, and invited Parties to make use of these IUCN guidelines.

The World Business Council on Sustainable Development has come out with a call to action stating: “Creating landscapes with healthy, functioning ecosystems is not only key to making progress toward the environmental targets embedded in the Sustainable Development Goals, but also to addressing multiple social and economic targets that depend partly or wholly on the benefits that ecosystems provide to people.”

One of the key roles of the International Union for Conservation of Nature is to develop global guidance toward its vision of “a just world that values and conserves nature.” These guidelines, developed by the Connectivity Conservation Specialist Group of IUCN’s World Commission on Protected Areas, build on this tradition. They bring together the science of connectivity, and a range of case studies from terrestrial, freshwater and marine ecosystems, to provide practical solutions for meeting connectivity challenges. Moreover, they stress the need to connect protected areas and other effective area-based conservation measures into large-scale ecological networks, and are extremely timely, as we embark on a new decade in which better protecting our planet’s biodiversity must be a priority.

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# Executive summary

Ecological connectivity is the unimpeded movement of species and the flow of natural processes that sustain life on Earth. This definition has been endorsed by the Convention on Migratory Species (CMS, 2020) and underlines the urgency of protecting connectivity and its various elements, including dispersal, seasonal migration, fluvial processes and the connectivity that is inherently present in large wild areas. Fragmentation caused by human activities continues to disrupt habitats, threatening biodiversity and impeding climate change adaptation. A large body of science and theory has been developing to address this problem in the context of protected areas.

The purpose of these Guidelines for Conserving Connectivity through Ecological Networks and Corridors is to consolidate this wealth of knowledge and best-available practices to support efforts to combat fragmentation. These Guidelines provide tools and examples (1) for applying ecological connectivity between protected areas and other effective area-based conservation measures, and (2) for developing ecological networks for conservation. In doing so, these Guidelines advance best practices for protecting ecological networks that maintain, enhance and restore connectivity across both intact and human-dominated systems. As demand grows for innovative solutions at international, national and subnational levels, these Guidelines recommend formal recognition of ecological corridors to develop conservation networks and thus ensure effective conservation of biological diversity.

## Key messages

- Science overwhelmingly shows that interconnected protected areas and other areas for biological diversity conservation are much more effective than disconnected areas in human-dominated systems, especially in the face of climate change.
- Although it is well understood that ecological connectivity is critical to the conservation of biodiversity, approaches to identify, retain and enhance ecological connectivity have been scattered and inconsistent. At the same time, countries on every continent, along with regional and local governments, have advanced various forms of corridor legislation and policy to enhance connectivity.
- It is imperative that the world moves toward a coherent global approach for ecological connectivity conservation, and begins to measure and monitor the effectiveness of efforts to protect connectivity and thereby achieve functional ecological networks. To promote these goals, these Guidelines define ecological corridors as ways to identify, maintain, enhance and restore connectivity; summarise a large body of related science; and recommend means to formalise ecological corridors and networks.

# Acronyms

| | |
|---|---|
| ABNJ | Areas Beyond National Jurisdictions |
| CBD | Convention on Biological Diversity |
| CCSG | Connectivity Conservation Specialist Group of WCPA |
| CMS | Convention on Migratory Species of Wild Animals |
| COP | Conference of the Parties |
| EEZ | Exclusive Economic Zone |
| EU | European Union |
| IUCN | International Union for Conservation of Nature |
| OECM | Other Effective Area-based Conservation Measure |
| SSC | IUCN Species Survival Commission |
| UN | United Nations |
| UNEP | United Nations Environment Programme |
| WCPA | IUCN World Commission on Protected Areas |

Migratory species such as the humpback whale (*Megaptera novaeangliae*) demonstrate the need for connectivity conservation. © Adobe Stock

# Introduction: The need for connectivity

1

The annual wildebeest (*Connochaetes* spp.) migration between Tanzania and Kenya is one of the world's great wildlife movement spectacles. © Gary Tabor

The 21st century is a time of crisis in the human relationship with the rest of nature. The climate is changing in dangerous ways, and up to one million species are currently at risk of extinction (IPBES, 2019).

Our planet is not in a uniform condition. For example, about 17% of land has been heavily transformed by cities and agriculture; 56% is characterised by less intense modifications such as mixed rural, urban and suburban development where half or less has been transformed; and about 26% is large wild areas that are largely intact (Locke et al., 2019). Different conservation strategies are needed for these three conditions, but all share the need for ecological connectivity within and across them.

'Ecological connectivity' is the unimpeded movement of species and the flow of natural processes that sustain life on Earth (CMS, 2020). This is not an overstatement. Without connectivity, ecosystems cannot function properly, and without well-functioning ecosystems, biodiversity and other fundamentals of life are at risk. The disruption or absence of ecological connectivity occurs because of human-induced 'fragmentation', the breaking up of a habitat, ecosystem or land-use type into smaller and smaller parcels.

The fundamental problem is that much of the world has been degraded and fragmented already by human activity (Venter et al., 2016). Over 75% of terrestrial ecosystems (excluding Antarctica) have been directly modified by anthropogenic activities (Ellis et al., 2010), and 70% of the world's remaining wilderness is now restricted to just five countries (Watson et al., 2018). The human footprint also extends into the oceans, with 87% of marine biomes impacted by overfishing, nutrient run-off and climate change (Jones et al., 2018).

The goal of conservation must be to retain intact ecosystems, as they provide the best chance to conserve biodiversity in a fast-changing world (Scheffers et al., 2016). Protected areas therefore are the foundation of nature conservation, even in fragmented areas of land, sea or freshwater. However, while protected areas and other effective area-based conservation measures (OECMs) are essential, they are no longer considered sufficient in many places (IUCN WCPA, 2019). It is now understood that active measures must also be taken to maintain, enhance or restore ecological connectivity among and between protected areas and OECMs (Tabor, 2019). Science has clearly demonstrated that in order to achieve long-term biodiversity outcomes, retaining ecological connectivity is essential in a time of climate change (Foden & Young, 2016; Gross et al., 2016). This new understanding is driving a fundamental shift in conservation practice in which actions and goals must vary according to land, freshwater and seascape context. With increasing human alteration of Earth, especially by rapid climate change, it is necessary to think and act at the larger spatial scales at which many species and processes actually operate.

Just one third of the world's rivers remain free-flowing. Dams are the primary barrier to freshwater connectivity. Here, a dam is under construction on the emblematic river Bâsca Mare, Romania, found in the heart of the Carpathian ecoregion of Europe. © Leeway Collective / Balkan River Defence, Courtesy Calin Dejeu

Wildlife crossing signage in Kananaskis Country in Alberta, Canada © Aerin Jacob/Yellowstone to Yukon Conservation Initiative

These Guidelines have been drafted to help clarify and standardise a shift in conservation practice from a narrow focus on individual protected areas to considering them as essential parts of large landscape conservation networks. This is done through creating 'ecological networks for conservation' that are specifically designed, implemented and managed to ensure that ecological connectivity is maintained and enhanced where it is present, or restored where it has been lost (see Bennett, 2003; Bennett & Mulongoy, 2006). Unless systems of protected areas and OECMs retain all essential ecosystem processes, they are not sufficient. A key component of this is ecological connectivity across land, freshwater and marine regions and among and between sites.

Chapter 2 of these Guidelines gives a brief, accessible explanation of the scientific basis for ecological connectivity. With ecological modelling playing an increasing role in connectivity conservation, this chapter also gives an overview of some of the most important methods to identify and model connectivity.

Because conservation at broader scales relies on a common understanding of the concepts involved, Chapter 3 sorts out the terminology that is emerging (both within IUCN and in the wider literature) to describe the ongoing shift in practice. The focus is on two key terms: 'ecological networks for conservation' and 'ecological corridors'. A clear grasp of these terms, and their relationship to established concepts, is essential to creating a common language that promotes better cooperation, sharing of experiences and, ultimately, more effective conservation.

With this foundation in place, Chapter 4 focuses on the concept of 'ecological networks for conservation', explaining what they are and why they are more effective in delivering conservation outcomes than a disconnected collection of individual protected areas.

To address the need for common guidelines regarding connected protected areas, Chapter 5 proposes 'ecological corridors' as a formal conservation designation, thereby recognising them as indispensable parts of ecological networks for conservation of biological diversity. This chapter offers detailed guidelines for establishing, planning, managing, monitoring and evaluating ecological corridors.

Chapter 6 reviews the applications and benefits of ecological corridors in terrestrial, freshwater, marine and mixed environments, as well as emerging considerations of connectivity in Earth's airspaces. Because climate change is affecting all of these environments, a short discussion of climate considerations for ecological corridor management is provided.

Chapter 7 discusses how the scientific understanding of connectivity conservation is increasingly being reflected in global conservation law and policy.

After a brief conclusion (Chapter 8, including a Glossary and References), an Annex provides numerous examples from around the world of efforts to create ecological corridors as part of ecological networks for conservation.

## Box 1
## Definition of key terms

Connectivity

- **Ecological connectivity:** The unimpeded movement of species and the flow of natural processes that sustain life on Earth (CMS, 2020). There are various sub-definitions of ecological connectivity that are useful in the context of these Guidelines:
  - **Ecological connectivity for species (scientific-detailed definition):** The movement of populations, individuals, genes, gametes and propagules between populations, communities and ecosystems, as well as that of non-living material from one location to another.
  - **Functional connectivity for species:** A description of how well genes, gametes, propagules or individuals move through land, freshwater and seascape (Rudnick et al., 2012; Weeks, 2017; see Chapter 2, section on 'Modelling Ecological Corridors').
  - **Structural connectivity for species:** A measure of habitat permeability based on the physical features and arrangements of habitat patches, disturbances and other land, freshwater or seascape elements presumed to be important for organisms to move through their environment. Structural connectivity is used in efforts to restore or estimate functional connectivity where measures of it are lacking (Hilty et al., 2019; see Chapter 2, section on 'Modelling Ecological Corridors').
- **Ecological corridor:** A clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity. The following terms are often used similarly: 'linkages', 'safe passages', 'ecological connectivity areas', 'ecological connectivity zones', and 'permeability areas'.
- **Ecological network (for conservation):** A system of core habitats (protected areas, OECMs and other intact natural areas), connected by ecological corridors, which is established, restored as needed and maintained to conserve biological diversity in systems that have been fragmented. (See Chapter 3, Table 2, for related terms.)
- **OECM (Other Effective Area-Based Conservation Measure):** A geographically defined area, other than a protected area, which is governed and managed in ways that achieve positive and sustained long-term outcomes for the *in situ* conservation of biodiversity with associated ecosystem functions and services and, where applicable, cultural, spiritual, socio-economic and other locally relevant values are also conserved (IUCN WCPA, 2019).
- **Protected area:** A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008; Stolton et al., 2013).]

More than half of the world's wild tigers (*Panthera tigris*) are found in India, and they depend on defined corridors within highly fragmented landscapes to survive. Here, a young tiger traverses Tadoba National Park, Central India. © Grégoire Dubois

# The scientific basis for connectivity

2

Movement ecology is critical for many species. Invertebrates range widely to complete their life cycles. Painted lady butterflies (*Vanessa cardui*) migrate thousands of kilometers each year. © Adobe Stock

Habitat loss and fragmentation are a leading cause of biodiversity loss worldwide, and climate change is exacerbating this problem. Species loss, decreasing population sizes and significant range contractions are caused by human activities that have negative impacts on biodiversity as well as ecosystem functions and services. These changes are happening more rapidly than in previous extinctions (Ceballos et al., 2017).

Historically, establishing individual protected areas, such as national parks, has been the primary focus of *in situ* conservation. The area of land and sea included in protected areas has increased steadily (Figure 1). In addition, protected areas are now supplemented by a range of OECMs – territories currently delivering effective conservation under a range of governance and management regimes even though conservation may not be a primary management objective (IUCN WCPA, 2019). Nevertheless, on a global scale, biodiversity loss continues to accelerate.

## The scientific foundations of connectivity conservation

Protected areas do not always adequately conserve biodiversity, either because they are not well placed or else need stronger management (Venter et al., 2017; Jones et al., 2018). Increasingly, many terrestrial protected areas within human-dominated systems are isolated from one another (Wittemyer et al., 2008). Isolation increases the risk of species extinctions within these areas (Newmark, 1987, 1995, 2008; Brashares et al., 2001; Parks & Harcourt, 2002; Prugh et al., 2008). The relationship between isolation and extinction is founded on island biogeography and metapopulation theory (MacArthur & Wilson, 1963, 1967; McCullough, 1996; Hanski, 1999). The theory of island biogeography states that, on an island, the rates of new species arrival and species extinctions depend on the size and shape of the island and its distance from the mainland. This concept has been transferred from islands to mainland ecosystems, where isolated protected areas are like islands in an ocean of human-dominated systems. In reality, human-dominated systems act as a filter, wherein individuals of some species can pass through freely while others cannot. Metapopulation theory states that many spatially distinct subpopulations can be reconnected by movement of individuals, leading to genetic exchange and the possibility of re-establishing formerly extirpated subpopulations. Together, these theories support the conclusion that larger and more well-connected areas are likely to maintain higher biodiversity over time. They support the need for ecological networks in large-scale land, freshwater and seascape conservation.

It is clear that sufficiently large, well-placed and well-managed protected areas and OECMs can provide connectivity among different habitat patches or resources within their boundaries.

Linear infrastructure development continues to rise unabated in large, previously intact landscapes and in high-biodiversity regions of the world. Deforestation and landscape fragmentation, Cameroon © Grégoire Dubois

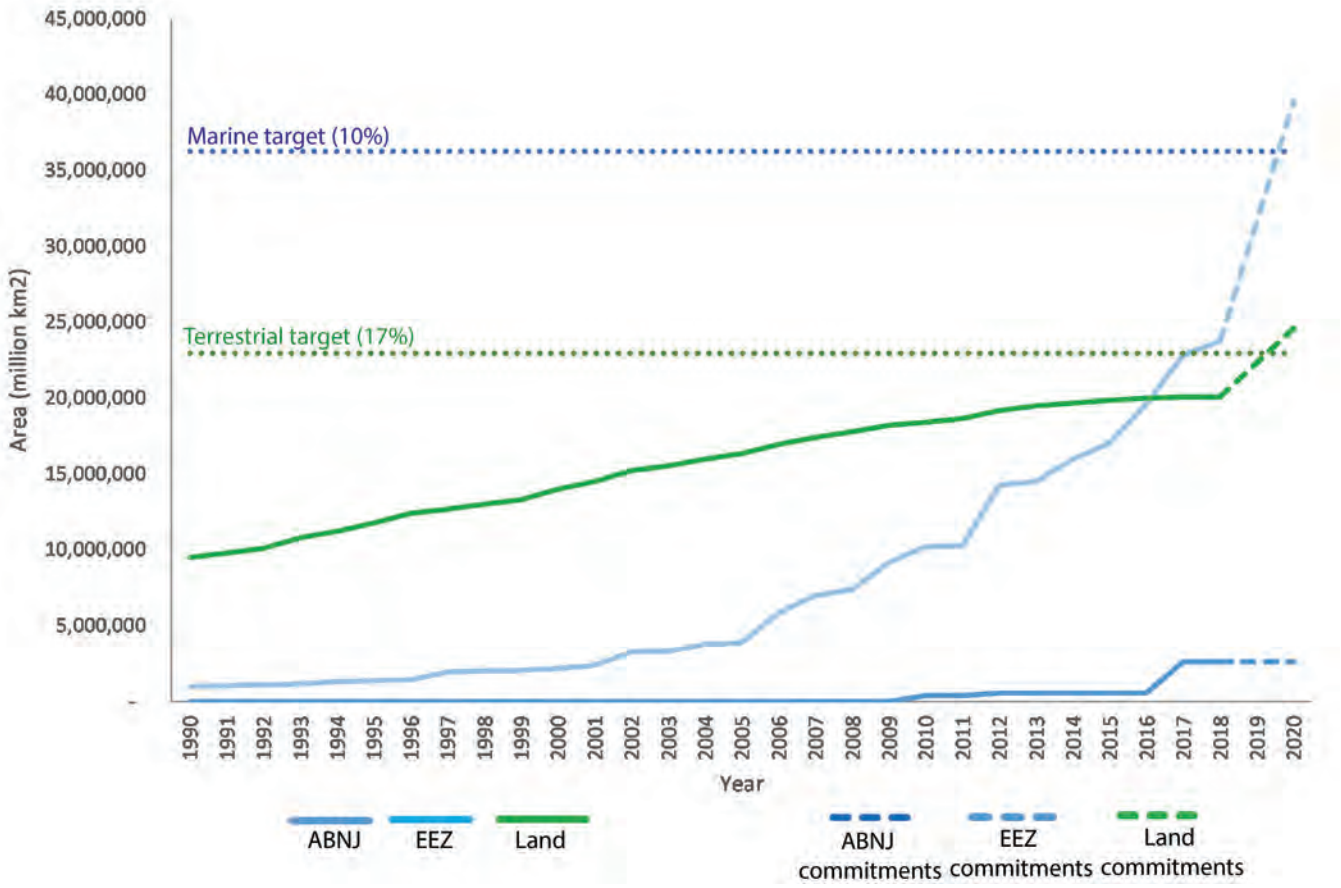


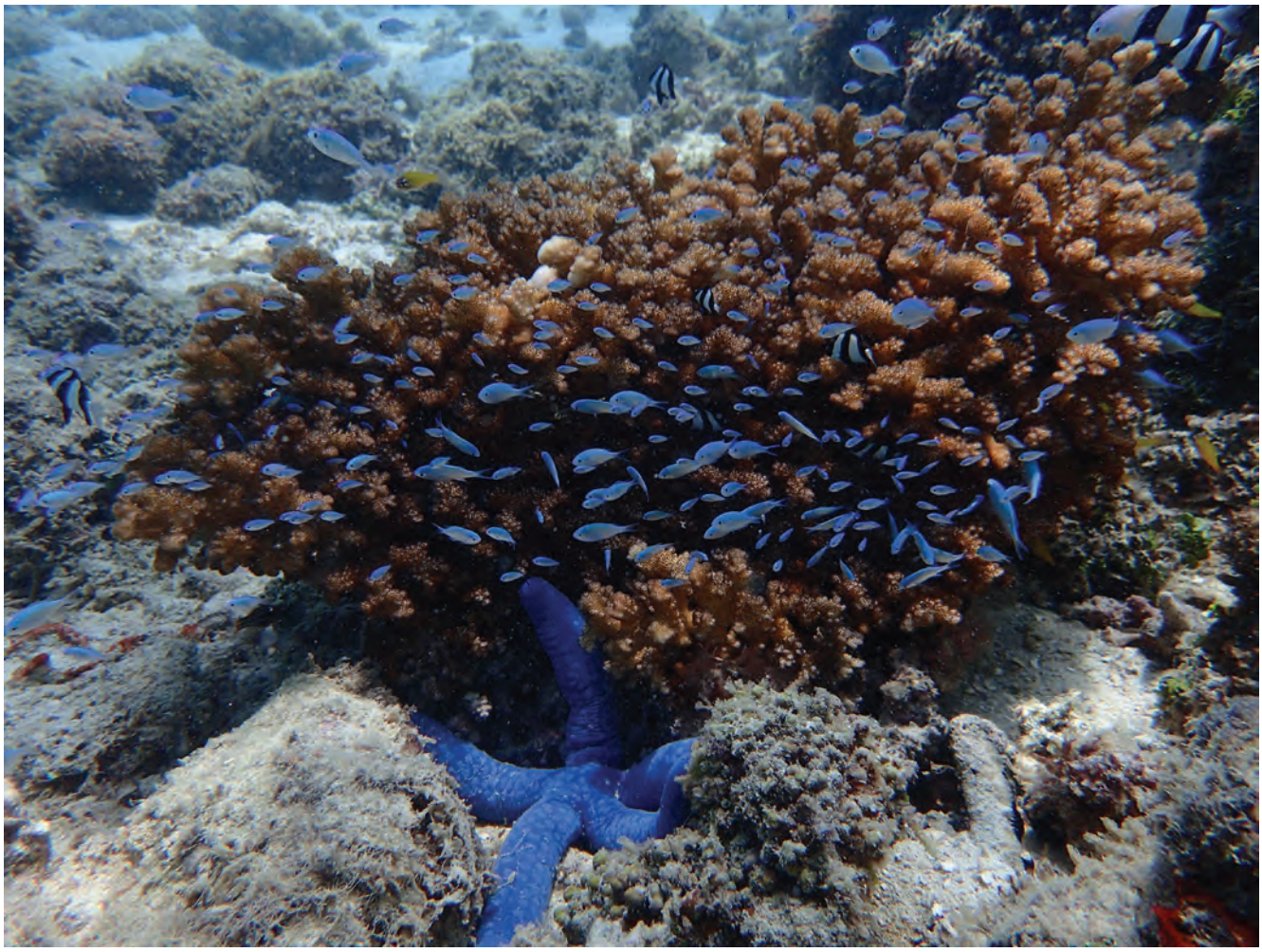

**Figure 1.** Growth in protected area coverage on land and in the ocean between 1990 and 2018, and projected growth to 2020, according to commitments from countries and territories. ABNJs: Areas Beyond National Jurisdiction (i.e. those more than 200 nautical miles from the coast); EEZs: Exclusive Economic Zones (i.e. marine areas under national jurisdiction that are less than 200 nautical miles from the coast). OECMs are new and therefore not incorporated into the figure. (From UNEP-WCMC, IUCN, and NGS, 2018. Reproduced with permission.)

However, because so much of Earth's terrestrial surface is fragmented, improving or sustaining connectivity among and between protected areas and OECMs is key for the effective conservation and management of biodiversity. Where it is not possible or appropriate to create additional protected areas or OECMs, connecting those already in place can serve to enhance biodiversity conservation. Managing for connectivity in ranching or forestry systems can enhance the conservation estate by increasing the total area within the landscape that is effectively connected, thereby reducing extinction risk (Newmark et al., 2017). In the face of climate change, connectivity becomes even more important, allowing some species to respond with range shifts and others to migrate into protected areas offering newly suitable habitat.

Conservation practitioners and scientists have demonstrated that conservation of species, ecosystems and habitats can only be achieved if protected areas are *functionally* connected (Trombulak & Baldwin, 2010; Resasco, 2019). In intact ecosystems, protected areas are *de facto* connected; in fragmented land, freshwater and seascapes, significant attention must be placed on achieving connectivity. Although connecting protected areas and OECMs has not been proven to strengthen conservation in every situation, connectivity has been demonstrated as an important component of many systems (Hilty et al., 2019).

There is some debate in the literature on negative impacts of corridors (Anderson & Jenkins, 2006; Hilty et al., 2019). Most negative effects appear to be related to increased predator activities, the movement of invasive species and diseases or micro-habitat changes (Weldon, 2006). These negative effects might be significant in individual situations. However, the reported benefits of corridors are far greater than any negative impacts (Hilty et al., 2019). Any potential drawbacks should be considered in corridor design, such as minimising potential edge impacts, exotic and invasive species and potential spread of infectious disease, as well as cost trade-offs of investing in corridors versus core habitat areas (Anderson & Jenkins, 2006; Weldon, 2006; Hilty et al., 2019).

Ensuring that protected areas and OECMs in fragmented systems are functionally connected across terrestrial, freshwater and marine realms and associated airspaces is critically important for many species (Marine Protected Areas Federal Advisory Committee, 2017; Hilty et al., 2019). Examples of organisms that move between these realms include anadromous fish that migrate from the sea to rivers to spawn, amphibians that inhabit multiple ecosystems during different life stages and butterflies (e.g. monarch butterflies, *Danaus plexippus*) that use numerous ecosystem types in their continental-scale, trans-generational migration.



Coral reefs need connectivity at a seascape scale to thrive. *Acropora* sp. shelters a *Linckia* starfish and many fish including *Chromis* sp., Piti Chanel, Guam. © Alisha Gill

Maintaining or restoring ecological connectivity may alsohave temporal aspects; migration can occur on a seasonal, annual or multi-year cycle, as evidenced by monarch butterflies (Runge et al., 2015). Usually, such connectivity movement occurs in all directions, but there are instances of unidirectional movement, such as during long-term climate change when species may shift their ranges poleward or upslope.

It is possible to manage for connectivity from small scales (e.g. streams, coral reefs and seagrass beds) to regional and even continental scales (e.g. chains of islands, mountains, major river systems and deep-sea hydrothermal vent ecosystems). Connectivity conservation is needed at local, regional and global levels and across various degrees of human modification. Many large-scale conservation visions seek to connect protected areas on land, in freshwater and in the ocean (Figure 2) (Worboys et al., 2015). Approaches for implementing these visions have been established in several human-dominated systems (Keeley et al., 2019). Notable examples include Baja to Bering (Mexico, US, Canada), Great Eastern Ranges Initiative (Australia), Amazon Freshwater Connectivity (Pan-Amazon, South America), Yellowstone to Yukon Conservation Initiative (US, Canada), and Vatu-i-Ra Seascape (Fiji).

For more information and examples, see the Annex, ‘Approaches to conserving ecological corridors in ecological networks’.

## Modelling ecological corridors

The science of measuring, modelling, and mapping the connectivity of land, freshwater and seascapes has grown steadily over the past two decades. This section is a brief overview of key conceptual issues, available tools for modelling connectivity and useful resources to support the definition and delineation of ecological corridors. Many of the conceptual issues (e.g. Crooks & Sanjayan, 2006; Rudnick et al., 2012; Olds et al., 2016; Hilty et al., 2019) are increasingly well understood and practical implementation and management guidance are available (e.g. Beier et al., 2008, 2011; Hermoso et al., 2011; Olds et al., 2016).

There are a number of ways to categorise connectivity. At the highest level, a key distinction relevant to ecological corridors is that connectivity has both *structural* and *functional* components, which are described further below. Although not addressed in depth here, it is worth noting that connectivity

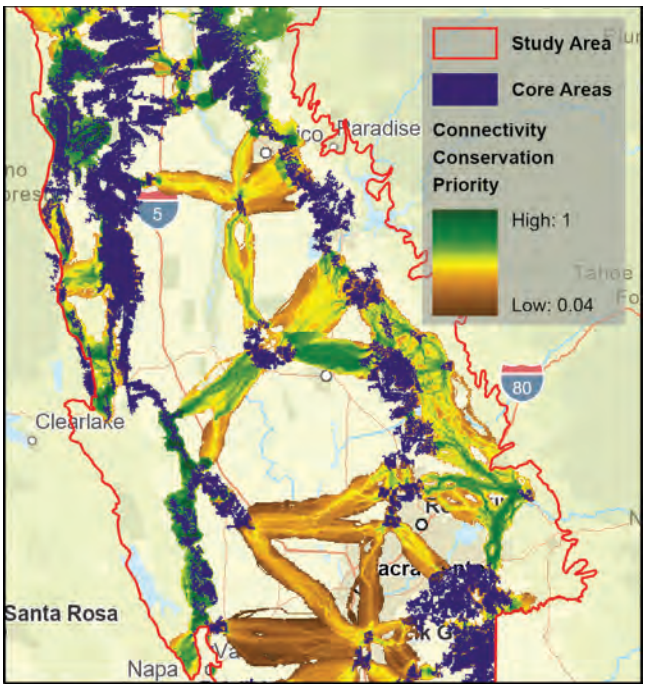
**Figure 2.** A conceptual representation of an ecological network for conservation. Terrestrial protected areas are in dark green and depicted as surrounded by human activities. Marine protected areas are in dark blue. OECMs are represented in orange. Ecological corridors, both those that are continuous and those that function as stepping stones, are outlined with dashed lines. The ecological network for conservation includes protected areas, OECMs and ecological corridors. © Kendra Hoff / CLLC

Experimental corridors provide a controlled environment to study ecological connectivity. The Savannah River Site Corridor Experiment (South Carolina, USA) is the largest corridor experiment in the world. © Ellen Damschen

Avoiding barriers to species movement is the necessary first step in maintaining connectivity; many barriers can be mitigated by, for instance, installing wildlife-permeable fencing. Whitetail deer (*Odocoileus virginianus*) jumping fence © BG Smith/Shutterstock

can be characterised based on the type of habitat (e.g. marine, freshwater and terrestrial, as described in Chapter 6, 'Applications and Benefits of Ecological Corridors'); the degree of human disturbance (e.g. hedgerows to remnant forest corridors; Theobald, 2013); the scale (local, regional, cross-oceanic, continental); or objectives (daily or seasonal movement, dispersal or habitat, long-term persistence, adaptation to climate change; Crooks & Sanjayan, 2006; Rudnick et al., 2012; Olds et al., 2016; Hilty et al., 2019).

'Functional connectivity' describes how well genes, gametes, propagules or individuals move through land- and seascapes (Rudnick et al., 2012; Weeks, 2017). Identifying areas that provide functional connectivity, either now or in the future, based on the known movements of individuals is an effective way to delineate movement corridors (e.g., Sawyer et al., 2009; Seidler et al., 2015; Hilty et al., 2019 (see Annex, Case Study 15 for details). Because it can be difficult to track a sufficient number of individuals over time, a suite of other approaches to define connectivity has been developed (Rudnick et al., 2012). In some cases, indicator or umbrella species are used to identify connectivity areas for a suite of species (e.g. Weeks, 2017). For long-lived species that are difficult to monitor, indirect approaches that can account for changes over time, such as in genetic make-up, can be effective (Proctor et al., 2012). However, genetic approaches




Modelling software, such as Linkage Mapper, is a tool conservation planners can use for decision-making. A synthesis of four Linkage Mapper outputs (Linkage Priority, Pinchpoint Mapper, Linkage Pathways and Centrality Mapper) provides an initial estimate of connectivity conservation priorities for American badger (*Taxidea taxus*), in the Sacramento Valley, California, USA (Gallo et al., 2019). © John Gallo

are generally only a first step to identifying where once-continuous populations are fragmenting. The next step is to delineate potentially important connectivity areas (as per Proctor et al., 2015). Genetic tools can also potentially validate functionality and serve as monitoring tools (Proctor et al., 2018). This approach may be more difficult in marine systems because of data limitations (Balbar & Metaxas, 2019).

'Structural connectivity' is a measure of habitat permeability based on the physical features and arrangements of habitat patches, disturbances, and other land, freshwater or seascape elements presumed to be important for organisms to move through their environment (Hilty et al., 2019). Structural connectivity modelling aims to identify areas through which a variety of species may be able to move. Models often prioritise ecological corridors characterised by a low degree of human modification – areas which are assumed to be permeable to species sensitive to human disturbance (Dickson et al., 2017). In addition, linear areas that provide connectivity, such as river corridors, ocean currents or linear forest fragments, can be identified and prioritised for conservation (e.g. Rouget et al., 2006).

Systematic conservation planning is increasingly incorporating connectivity as a component of planning (e.g., Hodgson et al., 2016; Rayfield et al., 2016; Albert et al., 2017). With a growing number of quantitative approaches, numerous tools are available to map and model connectivity (Table 1). Increasingly, efforts to model connectivity recognise the dynamics of ecological systems, including seasonal or annual dynamics and long-term climate-induced changes (Rouget et al., 2006; McGuire et al., 2016; Simpkins & Perry, 2017).

**Table 1.** Common approaches to connectivity modelling (Urban & Keitt, 2001; McRae, 2006; Theobald, 2006; Rudnick et al., 2012; http://conservationcorridor.org/corridor-toolbox/).

| Model type | Brief explanation |
|---|---|
| **Least-cost** | Estimates the surface area of the least-cost movement path from one location (source patch) to another (destination patch) that an individual or process would likely take, assuming knowledge of the destination location, moving across a surface represented by 'costs' (https://corridordesign.org; McRae et al., 2014). Either the single shortest path from one location to another or the full surface area of least-cost distances can be used. Cost-distance surface areas that were created from single, pairwise, factorial or randomly placed locations can be combined. |
| **Circuit theory** | Adapted from electrical circuits, circuit theory identifies connectivity by modelling random walkers moving from sources across a surface of resistances to destinations (grounds), allowing multiple pathway options (McRae, 2006; https://circuitscape.org). |
| **Graph theory** | Graph theory is the study of graphs that formally represent a network of interconnected objects. Graph theory provides the basis for nearly all connectivity methods, including least-cost and circuit theory. In addition, to prioritise ecological corridors, graph-theoretic metrics can be applied across a 'land- or seascape graph' where patches are nodes and areas of connectivity are edges (Urban and Keitt, 2001; Theobald, 2006; University of Lleida, 2007). |
| **Resistant kernel** | Based on least-cost movement from all locations across a land or seascape, implemented using a kernel (moving window) approach (Compton et al., 2007). This approach calculates a relative density of dispersing individuals around source locations. |
| **Reserve design** | An approach to guide systematic multi-objective planning to support spatial decision-making about the design of terrestrial, freshwater and marine reserves and management areas (e.g. Moilanen et al., 2008; White et al., 2013). |
| **Individual-based modelling** | Simulates movement paths of individuals by following postulated rules. The estimated relative frequency of use is mapped (Horne et al., 2007; Ament et al., 2014; Allen et al., 2016). |

Tracking tiger movement along the Nepal–India border in the Himalayan Terai Arc corridor © Gary Tabor

Connectivity conservation also supports human communities by supporting healthy landscapes. A “superbloom” event paints Carrizo Plain National Monument, California, USA. © Emily Pomeroy / Emily Rose Nature Photography

# Towards a common language of connectivity conservation

3

Connectivity is important for all domains; terrestrial, freshwater, marine, coastal and aerial. Here, a great egret (*Ardea alba*) patiently hunts in Elkhorn Slough State Marine Reserve, California, USA. © Emily Pomeroy / Emily Rose Nature Photography

A high priority for connectivity conservation policy must be to establish a common set of clearly distinguished terms. A central aim of these Guidelines is to define and explain two such terms, both of which are critical to connectivity conservation: 'ecological network for conservation' and 'ecological corridor'. Providing a clear definition of ecological networks for conservation and guidance on how to identify, establish, measure and report on ecological corridors aids many countries in reaching the goal of identifying, establishing, managing and restoring 'well-connected systems', spelled out in Aichi Target 11 of the Convention on Biological Diversity (CBD), and to achieve other commitments (see Chapter 7 for other examples). It is also critical for the post-2020 global biodiversity framework established to advance progress towards achieving the CBD's 2050 Vision of 'Living in harmony with nature'.

## Definition of 'ecological network for conservation'

The idea of an ecological network for conservation is represented by various terms, which are outlined in Table 2. An agreed definition of 'ecological network for conservation' reduces confusion, provides a common standard for global monitoring and database management, and generally improves communication and comparability.

For these purposes, the following definition is used:

> An ecological network for conservation is a system of core habitats (protected areas, OECMs and other intact natural areas), connected by ecological corridors, which is established, restored as needed and maintained to conserve biological diversity in systems that have been fragmented.

Ecological networks are composed of core conservation units – protected areas and OECMs – connected with ecological corridors. The definitions of these areas follow:

- 'Protected areas' are clearly defined geographical spaces, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008; Stolton et al., 2013).
- 'OECMs' ('other effective area-based conservation measures') are geographically defined areas other than protected areas, which are governed and managed in ways that achieve positive and sustained long-term outcomes for the *in situ* conservation of biodiversity with associated ecosystem functions and services, and where applicable, cultural, spiritual, socio-economic and other locally relevant values are also conserved (IUCN WCPA, 2019).

Landscapes are mosaics of interconnected ecological patches which function across spatial scales. The Chignecto Isthmus is the critical landscape gossamer that connects Peninsular Nova Scotia to mainland Canada. © Mike Dembeck

**Table 2.** Other terms (some of which have been translated into English) that have been applied in practice to describe what these Guidelines call 'ecological networks for conservation'. The presentation of terms in this table is meant to illustrate that the central ideas of 'ecological corridor' and 'ecological network' can be similar and expressed in many ways.

| Term | Example |
|---|---|
| **Area of connectivity conservation (ACC)** | Used by the Great Eastern Ranges Initiative of Australia, which is an effort to establish connectivity across a large landscape that may encompass a range of land uses, such as agriculture, forestry and human settlements, in addition to protected areas. |
| **Biological corridor** | Used by the Mesoamerican Biological Corridor, which was initiated in the 1990s to maintain biological diversity, reduce fragmentation and improve the connectivity of the landscape and ecosystems in Central America and southern Mexico (Ankersen, 1994; Ramírez, 2003). |
| **Conservation lands network** | Used in the San Francisco Bay Area of California, USA, as part of a regional prioritisation of connected lands that are important for the protection of biodiversity (Bay Area Open Space Council, 2011). |
| **Conservation management network** | Commonly used in Australia in the context of land-based networks for conservation of threatened ecological communities and remnant vegetation. These networks are supported by landowners/land managers and communities (Context Pty Ltd., 2008). |
| **Conservation mosaic of protected areas** | Commonly used in South America to refer to a network of protected areas and complementary landscapes/seascapes, including combinations of formal protected areas (i.e. core conservation areas) and surrounding areas (e.g., production landscapes, privately owned areas, community areas), where the involved entities cooperatively plan and manage the various pieces (Caballero et al., 2015); similar to a biosphere reserve under the UNESCO Man and the Biosphere programme. A Conservation Mosaic of Protected Areas aims to improve ecological connectivity as well as the conservation and sustainable use of environmental goods and services; for an example, see the Brazil Southern Amazon Mosaic (www.wwf.org.br/?29690/Southern-Amazon-Mosaic-facilitates-Protected-Area-management). |
| **Ecological framework** | In Russia, commonly used to refer to an 'ecologically continuous system of natural communities', not affected by landscape fragmentation, whose natural communities are ensured legal protection due to their large size and high intensity of matter and energy exchange (Sobolev, 1999; 2003). |
| **Ecological network** | Used in nearly all European countries to describe an approach (national and regional) designed to link nature areas more effectively with each other, and with surrounding farmland (Jongman & Bogers, 2008; Miklos et al., 2019). |
| **Flyway sites network** | Used, for example, to describe the East Asia–Australasian Flyway; these networks provide various degrees of connectivity and protection for target bird species (Millington, 2018). |
| **Freshwater systems network** | Used in South America to refer to freshwater aquatic ecosystems that interact hydrologically, biologically and chemically, and in which a key determinant of these interactions is connectivity, requiring integrated management across ecosystems (e.g. streams, rivers, lakes and wetlands) (Abell et al., 2017; Leibowitz et al., 2018); an example is the Project for Sustainable Management of La Plata River Basin of Argentina, Bolivia, Brazil, Paraguay and Uruguay. |
| **Green infrastructure** | Used in the 28 EU Member States and in some regions of the USA. The EU definition: 'Green infrastructure is a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services such as water purification, air quality, space for recreation and climate mitigation and adaptation. This network of green (land) and blue (water) spaces can improve environmental conditions and therefore citizens' health and quality of life. It also supports a green economy, creates job opportunities and enhances biodiversity.' The Natura 2000 network constitutes the backbone of the EU green infrastructure. |
| **Marine protected areas (MPAs) network** | Used in Australia and the USA to refer to networks of formal MPAs that serve in turn as components of even larger ecological networks for conservation (e.g. the California Marine Protected Areas Network) (Almany et al., 2009; Carr et al., 2017). |
| **Territorial system of ecological stability** | In the Czech Republic and Slovakia, used to describe an interconnected complex of both natural and near-natural ecosystems that maintain natural balance (Jongepierová et al., 2012). |
| **Transboundary conservation areas (TBCAs)** | Used to define ecologically connected areas that cross international boundaries and contain protected areas. Research on TBCAs has been ongoing for more than 25 years, and the concept has been recognised by both IUCN and the CBD. |

- An 'ecological corridor' is a clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity (see detailed explanation below).
- 'Ecological networks for conservation' are more effective in achieving biodiversity conservation objectives than a disconnected collection of individual protected areas and OECMs because they connect populations, maintain ecosystem functioning and are more resilient to climate change. In the context of ecological connectivity, 'connect' refers to the enabling of movement by individuals, genes, gametes and/or propagules.

## Definition of 'ecological corridor'

These Guidelines recommend the adoption of a connectivity designation, termed 'ecological corridor', to denote areas within ecological networks that are explicitly devoted to ecological connectivity, and may incidentally also contribute directly to biodiversity conservation. We define the term as follows:

> An ecological corridor is a clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity.

It is worthwhile to elaborate some key phrases and concepts used in this definition to be clear about their intended scope and application in these Guidelines:

- 'Clearly defined geographic space' includes land, inland water, marine and coastal areas or a combination of two or more of these. 'Space' may include the subsurface, the land surface or ocean floor, and the water column and/or airspace including vertical, physical ecosystem structures in three dimensions (adapted from Lausche et al., 2013). 'Clearly defined' means a spatially defined area with agreed and demarcated borders.

## Differences between protected areas, OECMs and ecological corridors

Referring back to the definition of 'ecological network for conservation,' note that it is defined as a system composed of two types of core conservation areas, protected areas and OECMs, with ecological corridors being the third element. They are the 'glue' of conservation networks.

Table 3 clarifies the key differences among the elements of an ecological network. Protected areas and OECMs are the fundamental core elements of conservation and of any ecological network. By definition, they *must* conserve *in situ* biodiversity and *may* also conserve ecological connectivity. On the other hand, ecological corridors *must* conserve connectivity. Depending on their condition and management, ecological corridors *may* also conserve *in situ* biodiversity, but this is not a requirement.

Focal species play a key role in determining connectivity conservation priorities, as the jaguar (*Panthera onca*) does across Central and South America.
© Grégoire Dubois

Seabirds play a critical role in marine, inter-island and coastal connectivity. © Dan Laffoley

**Table 3.** Differences in the role of protected areas, OECMs and ecological corridors. Note that all three terms refer to areas with conservation outcomes. Protected areas and OECMs protect nature as a primary consideration. Ecological corridors play a supporting role for protected areas and OECMs in building ecological networks.

| | Protected areas | OECMs | Ecological corridors |
|---|---|---|---|
| MUST conserve *in situ* biodiversity | ● | ● | |
| MAY conserve *in situ* biodiversity | | | ● |
| MUST conserve connectivity | | | ● |
| MAY conserve connectivity | ● | ● | |

In some cases, ecological corridors can be disjunct patches of habitat, often called 'stepping stones', particularly when supporting long-distance migration of wildlife such as marine mammals, sea turtles and birds. For example, for migratory birds, the distance between sites may not need to be minimised unless they are very far apart or the target species has metabolic constraints (Klaasen, 1996). Rather, the sites need to meet a particular species' natural history requirements (e.g. availability of food, low amounts of disturbance, presence of safe roost sites) at different stages of migration, particularly at staging and stopover sites within the corridors.

Next we turn to an in-depth discussion of ecological networks for conservation.

Tropical forest reserves require connectivity to function as ecological networks for conservation. Sunlight penetrates a shroud of moisture above the cloud forest, Panama. © Marie Read

Corridors can provide the architecture for large-scale conservation in fragmented landscapes. Landholders linking and restoring habitats on rural landscapes with Woomargama National Park, part of the Slopes to Summit alliance, an east–west section of the Great Eastern Ranges ecological corridor in southern New South Wales, Australia. © Ian Pulsford

# Ecological networks for conservation

4

Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Monterey Bay National Marine Sanctuary, California, USA © Emily Pomeroy / Emily Rose Nature Photography

Effective ecological networks for conservation consist of two main elements: 1) areas that protect biodiversity (protected areas and OECMs), and 2) ecological corridors recognised for their contribution to connectivity (refer to Figure 2). Ideally, when designing ecological networks, systematic conservation planning is employed to identify the minimum set of sites needed to protect the most biological diversity in a given region (Margules & Pressey, 2000).

Targets for conservation, which may include focal species, key biodiversity areas, population sizes or habitat areas, are set and the ecological network for conservation is optimised to contain these targets, while also considering their spatial configuration. Socio-economic and political filters may also be considered in systematic conservation planning. Ecological networks are necessary to enhance the integrity, viability and stability of protected areas and OECMs in fragmented systems, making them less vulnerable to all threats, especially in the context of climate change.

In addition to isolation, it is important to consider the size of core habitats (protected areas and OECMs) when meeting the connectivity needs of some species in conservation networks. For large, wide-ranging species, individual protected areas are often not big enough to maintain minimum viable populations. The reality today in many land regions is that creation of new large reserves is not feasible because small habitat fragments are all that remain (Shafer, 1995). Creation of larger reserves is increasingly more common in the ocean. Small protected areas may not be big enough to support populations of even small animals over extended periods (e.g. Henderson et al., 1985; Green et al., 2014). Nevertheless, very small reserves (e.g. those less than 10 ha), even in the most highly fragmented regions, may have critical roles to play in advancing local conservation objectives and community involvement in conservation (Volenec et al., 2020). Moreover, in marine environments, small reserves may in some cases be adequate for specific species and their life-cycle needs. For example, in the sponge reefs off the east coast of Canada, sponge larvae are in the water for just a few days and disperse via currents; they may not go very far, so a marine protected area may readily encompass their dispersal distance. The same is true for invertebrates that are immobile and reproduce by brooding.

Further related to the issue of size, most protected areas and OECMs are not sufficiently large to survive larger-scale ecological disturbances to their biodiversity. For example, natural fires may form part of long-term ecosystem cycles of a protected area, but if it is not large enough the species within will need large tracts of adjacent unburnt habitat to which they can withdraw and recover.

Ideally, protected area and OECM sizes and locations are determined by ecological considerations, but design decisions are often constrained by existing ownership or resource use rights and human activities. To ensure that individuals of species can move between specific core habitats in an ecological network, calculations of appropriate distances between them should be made according to the species' characteristics, such as dispersal range and area required for a minimum viable population. Within these

In many parts of the world, such as East Africa, wildlife populations spend much of their time outside of protected areas, yet utilise protected areas on a seasonal basis. African elephants (*Loxodonta africana*) in Masai Mara, Kenya © Gary Tabor

Free-flowing rivers and their associated riparian corridors link terrestrial and freshwater systems. Aerial view of landscape during flight from Trinidad to Bellavista, Beni Department, Bolivia © World Wildlife Fund (WWF), Photographer Jaime Rojo

parameters, distances ideally should be minimised and the area between core habitats managed so as to maintain ecological connectivity.

Maintaining ecological connectivity, such as through corridors, is important to allow individuals to move among patchy resources and among populations/subpopulations and to facilitate seasonal or periodic migrations. Ecological corridors are also important to facilitate dispersal that ensures genetic diversity and permits recolonisation in areas where populations have gone extinct. These corridors can help increase populations' resilience to large-scale natural disturbances. Ecological corridors also may help extend specific ecosystem services for human use, while serving their main purpose of species movement. Corridors may help maintain ecological processes, such as nutrient cycling, pollination and seed dispersal, across landscapes and seascapes. Finally, even within ecosystems transformed by human activity, ecological corridors provide higher rates of ecosystem recovery in surrounding disturbed areas due to dispersal of seeds and animals from the remaining natural areas (e.g. M'Gonigle et al., 2015; but see also critique from Boitani et al., 2007).

## Ecological networks and climate change

Ecological networks for conservation have been recognised as a means to help many species respond to climate change. When well designed, ecological networks, including corridors, can enable species to shift ranges and colonise newly suitable habitats and adapt to climatic conditions. Conservation strategies that make ecological networks more effective to facilitate adaptation to climate change include increasing the number and size of protected areas and OECMs, managing habitats to increase their resilience, establishing or widening connectivity areas, locating reserves in areas of high heterogeneity, and spanning elevational along with other critical gradients (Heller & Zavaleta, 2009; Anderson et al., 2014; Elsen et al., 2018). Of the different climate adaptation strategies, increasing the amount of conserved habitat is one of the most effective (Synes et al., 2015; Table 4). However, conserving a suitable network of habitats should be a priority, rather than increasing the size of a few isolated protected areas and OECMs (Hodgson et al., 2012).

Much of the world faces unprecedented levels of habitat fragmentation. Corridors of high-quality habitat provide the safety net to save biodiversity. Ranchlands near Punta Burica, Panama © Félix Zumbado Morales / ProDUS Universidad de Costa Rica

**Table 4.** Advantages and disadvantages of strategies to facilitate species range shifts through climate-wise connectivity (adapted from Keeley et al., 2018).

| Strategy | Advantages | Disadvantages |
|---|---|---|
| Increasing the number of protected and conserved areas throughout the land- and seascape | If properly designed, may increase speed of range shifts in fragmented systems; benefits most species; increases persistence for some species | |
| Creating few, large protected or conserved areas | | Slows speed of range shifts; may result in poor representation of the country/region's full ecosystem diversity |
| Adding connectivity areas (ecological corridors or additional protected or conserved areas) between existing protected or conserved areas | Increases speed of range shifts in fragmented systems; benefits most species | In rare cases, restoring connectivity could introduce invasive species and harmful alleles (variant forms of a given gene), particularly in freshwater and marine systems |
| Creating small stepping stones embedded in unsuitable habitat | Increases speed of range shifts in fragmented systems | Only benefits species capable of using stepping stones |
| Increasing the size of existing protected areas | Increases species persistence; improves temporal connectivity for some species; governance and management structure already exist | May not facilitate connectivity with respect to other resources that wildlife needs; may not provide adequate space for species to move in response to climate change |

Ecological networks that collectively encompass temperature gradients can also effectively facilitate species range expansion. This might mean connecting lower- to higher-elevation sites, or inland to coastal areas; sites at different latitudes or ocean depths; or even sites that represent salinity gradients. The Appalachian Mountains in the eastern USA are an example of a mountain range critical for facilitating poleward species movements (Lawler et al., 2013). Likewise, corridor planning in the Albertine Rift region of Africa seeks to ensure elevational and latitudinal connectivity (Ayebare et al., 2013; Plumptre et al., 2016). It should be noted that, in addition to ecological corridors, ecological connectivity can be achieved by expanding existing protected areas and OECMs or adding more of them to a network.

# Planning and implementing ecological corridors

5

Arabian oryx (*Oryx leucoryx*), Dubai, UAE © Peter J Hudson

This chapter provides detailed guidelines on how to plan and implement an ecological corridor, starting with fundamental principles that inform a corridor's ecological objectives. The chapter then describes how to document basic information, select objectives, choose a governance model, delineate boundaries and implement management and monitoring plans that reach the corridor's objectives.

## Fundamental principles

Every ecological corridor should be founded on a set of objectives that concisely explains why the corridor is being designated and what the expected conservation outcomes are. Keeping a few fundamental principles in mind will be helpful.

1. *Ecological corridors are not a substitute for protected areas or OECMs.* They are meant to complement protected areas and OECMs. The purpose of ecological corridors is to maintain connectivity, especially in regions where additional protected areas and OECMs are not possible, and connectivity is required to retain their elements and processes. As noted earlier, ecological corridors provide specific connectivity value complementary to that of protected areas and OECMs (Table 3). Ecological networks for conservation, as understood in these Guidelines, may contain several corridors identified as part of a specific conservation network. The primary purpose of ecological corridors is to facilitate one or more defined types of ecological connectivity between and among protected areas, OECMS or other core habitats.
2. Ecological corridors should be identified and established in areas where connectivity is required with the aim of building ecological networks for conservation.
3. Each corridor should have specific ecological objectives and be governed and managed to achieve connectivity outcomes.
4. Ecological corridors may consist partly or entirely of natural areas managed primarily for connectivity. Corridors can also cross highly managed areas – such as ranches or commercial forests – provided the area within the corridor is explicitly managed for connectivity. In some cases, a corridor can combine a natural area and an area managed for extraction. *So long as their conservation objectives are supported, ecological corridors may include compatible human activities that practise sustainable resource use.* These might include some forms of human habitation, farming, forestry, grazing, hunting, fishing and ecotourism (see Annex, Case Studies 3 and 12).
5. *Ecological corridors should be differentiated from non-designated areas by the specific uses that are allowed or prohibited within them.* Whereas surrounding lands may look similar, and have similar uses, the uses allowed inside a designated ecological corridor cannot harm its specified connectivity purposes.

In many mountainous regions, valley bottoms contain the greatest biodiversity and provide necessary winter habitat. These are also the areas that people tend to inhabit. Connectivity conservation in these areas relies on coexistence strategies for people and wildlife and coherent multi-jurisdictional approaches to land and freshwater management. Pieniny National Park, Poland & Slovakia © Juraj Švajda

**Box 2**

## Ecological corridor objectives — some examples

1. **Movement of individuals:** To allow for the movement of dispersing tigers (*Panthera tigris*) between India's Dudhwa and Jim Corbett national parks (Seidensticker et al., 2010); to allow wildebeest (*Connochaetes taurinus*) to move between the Serengeti Plains in the United Republic of Tanzania and the Masai Mara Reserve in Kenya in a clockwise manner (Serneels & Lambin, 2001); to aid in the recovery of biota after habitat destruction, e.g. due to mining in deep-sea hydrothermal vent ecosystems (Van Dover, 2014).
2. **Genetic exchange:** To allow for the movement of giant pandas (*Ailuropoda melanoleuca*) in China between population segments that have been separated by a highway and associated development (Zhang et al., 2007); to allow for the diadromous migrations of European eel (*Anguilla anguilla*) through rivers and the North Atlantic Ocean (Kettle & Haines, 2006).
3. **Migration:** To facilitate the annual June passage of wood turtles (*Glyptemys insculpta*) from habitat in Canada's La Maurice National Park to breeding beaches outside of the park (Bowen & Gillingham, 2004); to conserve the pathways of fish, such as the dorado catfish (*Brachyplatystoma rousseauxii*) to breeding sites in the Amazon or green sturgeon (*Acipenser medirostris*) in the Pacific Northwest of the USA (Benson et al., 2007); to conserve one or more of the stopover sites that maintain the migration of spoon-billed sandpipers (*Calidris pygmaea*) and other migratory sandpipers that breed in Russia's Siberia and Kamchatka and migrate along the Pacific coast of Asia, wintering from eastern India to southern China (Menxiu et al., 2012).
4. **Multi-generational movement:** To provide habitat for monarch butterflies migrating over several generations along a central flyway in the states of Minnesota, Iowa, Missouri, Kansas, Oklahoma, and Texas, USA (the 'Monarch Highway', www.monarchhighway.org).
5. **Maintenance/restoration processes:** To restore hydrologic function, such as sediment transport or nutrient cycling, by removing dams from small streams in Wisconsin, USA (Doyle et al,. 2000).
6. **Climate change adaptation:** To facilitate range shifts of species to adjacent mountain ranges through restoring riparian corridors in agricultural landscapes in California, USA (Keeley et al., 2018).
7. **Enhancement of recovery:** To serve as a source of conifer seeds for restoring native trees in logged areas of the mixed forest zone of European Russia (Degteva et al., 2015).
8. **Prevention of undesired flows:** To reduce erosion risk by stopping the increasing velocity of surface water flows downslope in rugged terrain of cultivated steppe landscapes in southern Russia, Ukraine, Moldova, Kazakhstan (Ladonina et al., 2001).

6. To achieve their connectivity objectives, *ecological corridors require their own management plans* (terrestrial, freshwater or marine as the case may be). These may be simple or complex depending on the human activities that are permitted and the tenure issues.

In most instances, ecological corridors will connect protected areas and OECMs, and perhaps other intact natural habitats. However, in some regions, an ecological corridor designation may be needed to funnel migrating species through bottleneck zones that do not necessarily connect to protected areas or OECMs. An ecological corridor could, for example, lead from a protected turtle nesting beach out through a set of islands to the open ocean.

It should be noted that protected areas and OECMs that are already effectively conserving connectivity do not need to be overlaid with an ecological corridor designation.

## Objectives

The objectives of an ecological corridor should be clearly stated in its documentation. In addition, it may be useful to show any associated values of the corridor, such as contributions to ecosystem services.

*Ecological connectivity objectives:* The most critical step in documenting an ecological corridor is defining its objectives for ecological connectivity. Connectivity can be established or maintained for any one or a combination of the following purposes, all of which depend on movements between habitat patches: (1) genetic exchange; (2) movement of individuals to meet life-cycle needs, including migration; (3) provision of habitat for daily to multi-generational movement; (4) maintenance of ecological processes; (5) movement and adaptation responses to global change, including climate change; (6) recovery and recolonisation after disturbance; or (7) prevention of undesirable processes, such as the spread of fire. An ecological corridor should have clear and measurable ecological objectives meeting at least one of the above purposes. Examples of the seven ecological connectivity objectives are provided in Box 2.

*Associated ecosystem service values (if applicable):* Ecosystem service objectives can often be achieved along with connectivity conservation, and may also be documented. These can include maintaining or enhancing provisioning

Marine connectivity operates across all dimensions of space, within the water column and over the broad reaches of the seas. Scalloped hammerhead (*Sphyrna lewini*) © Adobe Stock

services such as of food and water; regulating services such as regulation of floods, drought, storm surge, land degradation, disease and carbon sequestration; and supporting services such as soil formation and nutrient cycling. While management for specific ecosystem services may be an important objective, so doing should support the ecological corridor's connectivity objectives. Detailed guidance for documenting ecosystem services can be found in the IUCN publication *Tools for Measuring, Modelling, and Valuing Ecosystem Services* (Neugarten et al., 2018).

*Associated cultural and spiritual objectives (if applicable):* Conservation of important cultural and spiritual values may be associated with an ecological corridor. These values should also be documented in order to maintain support for the corridor.

## Contribution to an ecological network for conservation

The contribution of an ecological corridor to the ecological network for conservation in which it is located should be documented. Such documentation can consider multiple metrics (genetic, demographic, community and ecosystem consequences) depending on the conservation objectives of the network. A diversity of empirical and modelling approaches to measure ecological connectivity exist and are the subject of research to refine and expand them.

At minimum, documenting the existence of successful movement between protected areas is required. Quantitative estimates of the magnitude of connectivity should be provided. If possible, the contribution of connectivity to population and community metrics (e.g. genetic diversity, population size, species diversity) should be calculated. Evaluating the contribution of ecological corridors and connectivity to network performance should, when possible, include the performance of the network relative to a group of unconnected protected areas (Grorud-Colvert et al., 2011, 2014). Bennett & Mulongoy (2006) provide detailed guidance on how to incorporate many of the considerations of ecological networks.

## Social and economic values

While these guidelines are primarily focused on the critical ecological role of ecological corridors, connectivity conservation can have a wide range of social and economic benefits (Hilty et al., 2019, pp. 112–115). Being aware of them can help in corridor design and increase social acceptance, while at the same time maximising their effectiveness. Below are examples of some of the more notable social and economic benefits.

- In some parts of the world, large ecological corridors might be managed for the benefit of mobile peoples, who need connected systems to maintain traditional livelihoods. This is particularly relevant for hunter/

gathering cultures and pastoralist peoples who depend on seasonal movements.

- Ecological corridors can provide a range of co-beneficial recreational values, such as pathways for walking trails (See Annex, Case Studies 10 and 20).
- Corridors established as setbacks, such as forestry or agricultural buffer strips, can protect riparian communities and water quality, and provide flood protection along watercourses.
- Ecological corridors can help define a community's sense of place or distinctiveness, and may help maintain a community's aesthetic preferences or historical grounding.
- Ecological corridors through agricultural areas may serve as a source of pollinators for crops.
- In forest management areas, ecological corridors can provide other benefits, such as acting as wind breaks and sources of seed stock for forest regeneration.

In establishing and managing ecological corridors, it is useful to consider a complete range of social and economic values. If they are to be part of the management plan, the interaction between them and the ecological objectives should be well understood. Any uses of a corridor that support social and economic values should not impair its connectivity (see Annex, Case Studies 16 and 17).

## Delineation

An ecological corridor should be clearly delineated. It should have agreed boundaries demarcated by the entity or entities governing and managing it, whether on land, in inland waters, coastal or marine areas, or any combination of these. These boundaries may sometimes be defined by physical features that move over time, such as river banks, ocean currents or sea ice. Given how rapidly the world is changing, provisions for an ecological corridor to move in time and space may be articulated in its management approach. Although the size of an ecological corridor will vary, it should be large enough to achieve its specific ecological connectivity objectives over the long term.

An ecological corridor can be discontinuous (in which case it is often referred to as a 'stepping stone' corridor) provided that the objectives, governance and management are the same across its segments. In order to provide connectivity, stepping stones must be of an appropriate habitat type, align with mechanisms of dispersal (e.g. ocean currents, flyways), and be of a minimum threshold size (see Annex, Case Studies 24 and 25). In cases where there is more than one governance or management entity, management actions should be harmonised and coordinated.

Semi-domesticated reindeer herding is intertwined with the cultural identity and survival of Sami people of northern Scandinavia. Cultural aspects may be appropriate to consider in designing corridor objectives. Sami reindeer herding area, Finland © Juraj Švajda]

In some cases, the delineation of an ecological corridor may need to include a third, vertical dimension if biodiversity is to be effectively conserved. Some protected areas and OECMs already have vertical limits (e.g. they apply only to a certain depth underground or below the water surface). Vertical limits have become particularly controversial in marine protected areas, where vertical zoning for commercial purposes may undermine conservation objectives (e.g. by disrupting ecological connectivity), as it is extremely challenging to monitor or enforce. Examples of vertical-dimension considerations in terrestrial systems include the placement of wind turbines in flyways that intercept and kill migrating avifauna, and, in marine systems, the deployment of fishing gear (e.g. drift nets) at different levels of the water column that intercept and kill migrating pelagic species. Such considerations may also apply to surface freshwater systems, including deep-water lakes with faunal zonation, but also to subterranean freshwater systems, which require management strategies that recognise these systems might be affected by activities at the surface that are relatively remote from them. The height and depth dimensions of an ecological corridor need to allow for effective management to achieve its connectivity objectives.

Another aspect of vertical dimensionality is subsurface use rights given that accessing underground resources can harm conservation values. For example, subsurface rights to the seafloor vary greatly based on political jurisdictions and types of human activities (e.g. mining, laying pipelines, or constructing offshore oil extraction facilities). Planners should consider how such modifications affect the movement of species targeted for protection.

Gravel bed river systems have riparian corridors that extend well beyond their banks into the subsurface hyporheic zones (see Hauer et al., 2016.) Tusheti, Republic of Georgia © Juraj Švajda

Coral atolls may appear as separated islands but are connected across vast distances to form functional marine ecological networks, New Caledonia. © Dan Laffoley

The annual long-distance movement of certain species such as the wood stork (*Mycteria americana*), pictured here in Mato Grosso, Brazil, led to some of the first global and national policies to conserve migratory species. © Grégoire Dubois

The delineation of an ecological corridor should be based on ecological needs for connectivity rather than on land and sea ownership (cadastral) boundaries. However, where cadastral boundaries approximate ecological needs, it may be useful to use these boundaries for management and governance efficiency. For sites crossing political or jurisdictional boundaries for which it is not feasible to have a common governance mechanism, separate ecological corridors may need to be delineated. Otherwise, a governance mechanism comprising more than one entity coordinated under an umbrella decision-making process will be required. Here, harmonisation and coordination can be major challenges. Governance and management must be adapted to individual sites or sets of sites in multiple countries. This can be done through international frameworks, such as the Eastern Asian-Australasian Flyway Partnership, whose Flyway Site Network coordinates the conservation of migratory waterbirds.

## Governance

Governance arrangements should be clearly articulated in the documentation. As with protected area and OECM governance, ecological corridor governance has three components: how and by whom decisions are made, and who should be held accountable.

The element of 'who' relates to the entities with authority over the ecological corridor. Ecological corridors with complex tenure situations (see next section) may involve many governance authorities (e.g. Indigenous Peoples), along with an agreed mechanism for coordination and oversight (see Annex, Case Studies 6 and 17). The same range of governance types that apply to protected areas and OECMs also apply to ecological corridors (Dudley, 2008; Stolton et al., 2013; Borrini-Feyerabend et al., 2013). These include:

- Governance by government (at various levels);
- Shared governance (sometimes called 'co-management'), including:
    - Transboundary governance (formal arrangements between one or more sovereign States or Territories (see Annex, Case Study 20);
    - Collaborative governance (through various ways in which individuals and institutions work together (see Annex, Case Study 17);
    - Joint governance (e.g. through a pluralist board or other multiparty governing body);
- Governance by private individuals, organisations or companies (see Annex, Case Study 15); and
- Governance by Indigenous Peoples and/or local communities (see Annex, Case Study 3).

The element of 'how' concerns ensuring transparency, accountability, participation and justice in decision-making processes. Governance should strive to be equitable and reflect human rights norms recognised in international and regional instruments and national legislation (see Annex, Case Study 8). Evaluating the ecosystem services associated with proposed ecological corridors helps define the diversity of human benefits associated with them. Any designation of an ecological corridor requires the free, prior

Connectivity conservation provides an avenue to protect biodiversity within the mixed-use landscape matrix. Protected areas are supported by effective conservation outside their boundaries. Homes and agricultural fields in Costa Rica © Félix Zumbado Morales / ProDUS Universidad de Costa Rica

and informed consent of all relevant governance authorities. These principles are applicable to any decision making on allocation, design, establishment, management, redesign, monitoring or evaluation of ecological corridors.

The governance authority may be the same as the landowner or rightsholder of a given portion of an ecological corridor.

There are many mechanisms through which a corridor's ecological objectives might be achieved. An NGO such as a conservancy may do so through a conservation easement, or a written voluntary agreement might be reached in which the landowner/rightsholder agrees to manage a privately owned parcel of land for specific connectivity values (see Annex, Case Studies 13, 14 and 15). Likewise, a group of entities might enter a cooperative agreement, or a local Indigenous or Traditional community may hold legal rights (either by statute or customary law) to certain lands or a defined ocean space within the corridor for sustainable use of a fishery, or conservation and management of an important underwater cultural, historic, sacred or archaeological site.

Effective ecological corridor governance requires building trust, working towards shared values and goals, and developing collaboration across the full range of interests involved (Pullcord et al., 2015).

## Tenure

Tenure is a separate consideration from governance (Lausche, 2011) and may take many forms. It involves the conditions and rights under which land, sea, freshwater or air space, or their associated natural resources, are held, occupied or used. While answers to questions of legal and customary tenure (i.e. who holds those rights) are important in determining governance type, they are not the sole determinant. On the contrary, a mix of tenure, whether legally or customarily defined, can be present under all governance types and be

represented through a variety of instruments such as formal delegation, leasing, contracts or other agreements (Worboys et al., 2015, p. 181).

For a given ecological corridor, the tenure(s) of the area should be clear and articulated. Tenure rights, particularly for large-scale ecological corridors, may be diverse and complex, requiring a much larger scope of social alliances and cooperation to handle (Worboys et al., 2015). This requires identifying statutory and customary ownership and use rights, and negotiating with all rightsholders on their respective connectivity management roles. The fragmentation of tenure without a collaborative plan for connectivity management can be one of the main drivers of land, freshwater and seascape fragmentation.

Special issues may arise with Indigenous and local community tenure rights if there is lack of legal clarity or if they are in dispute. Sometimes this is because such peoples or communities are not recognised as collective legal entities but only as groups of individuals. This is the case in many places in Africa, Asia and Europe (Worboys et al., 2015, p. 193). In these situations, either a constitutional provision or legislative act may be needed to give collective legal recognition to such entities so they can define and defend access to their rights to use, control and transfer land or resources, as well as take on associated responsibilities.

Special problems also may arise with tenure in marine environments because issues there are often different than on land, where rights may be relatively clear (Day et al., 2012). In Exclusive Economic Zones (EEZs; see caption to Figure 1 for definition) under the UN Convention on the Law of the Sea (UNCLOS), for instance, there generally is no individual ownership of either the seabed or water column; rather, this rests with the nation. In many countries, coastal communities may own or have tenure use rights over certain marine areas or resources. These could include customary rights to traditional fishing grounds, access and management rights over sacred sites of cultural or spiritual value, or rights to sustainably use other renewable marine resources generally or on a project basis (Day et al., 2012).

## Documentation of legal or other effective mechanisms

Documentation of the legal or other effective mechanisms that pertain to management of an ecological corridor should describe the governing authority and the legal or customary mechanisms that establish the area's tenure(s). Given the various contexts for the application of ecological corridors around the globe, there will be a diverse array of mechanisms for implementation. These may include:

- Land-use plans and zoning for landscapes;
- Marine spatial plans and zoning for seascapes;
- Covenants and easements;
- Incentives and disincentives;
- Regulatory controls for public health and safety;
- Development controls and building standards; and
- Written voluntary conservation agreements with specific landowners or rightsholders.

In many countries, voluntary conservation agreements are becoming an increasingly popular and effective tool for long-term conservation (see Lausche, 2011 for elaboration of elements and conditions of these agreements). Finally, an emerging area for legal attention is guidance and common rules-of-thumb for design and management of marine ecological corridors (see Lausche et al., 2013).

## Longevity of the ecological corridor

Ecological corridors are expected to endure over significant periods of time, so long as the natural attributes and connectivity values for which they are designated remain. Longevity considerations especially pertain to spatially dynamic corridors, such as migration routes of large marine vertebrates (e.g. cetaceans, pinnipeds, sharks, tuna) that track shifting oceanographic patterns. The documentation needs to demonstrate the longevity and succession of the governance arrangements. In the case of written voluntary agreements, a process or mechanism to transfer implementation activities to subsequent owners should be obligatory. However, some governance mechanisms (e.g. hunting, grazing, soil

The future of the Asian elephant (*Elephas maximus*) depends on coherent conservation strategies that work across land-use tenures © Grégoire Dubois

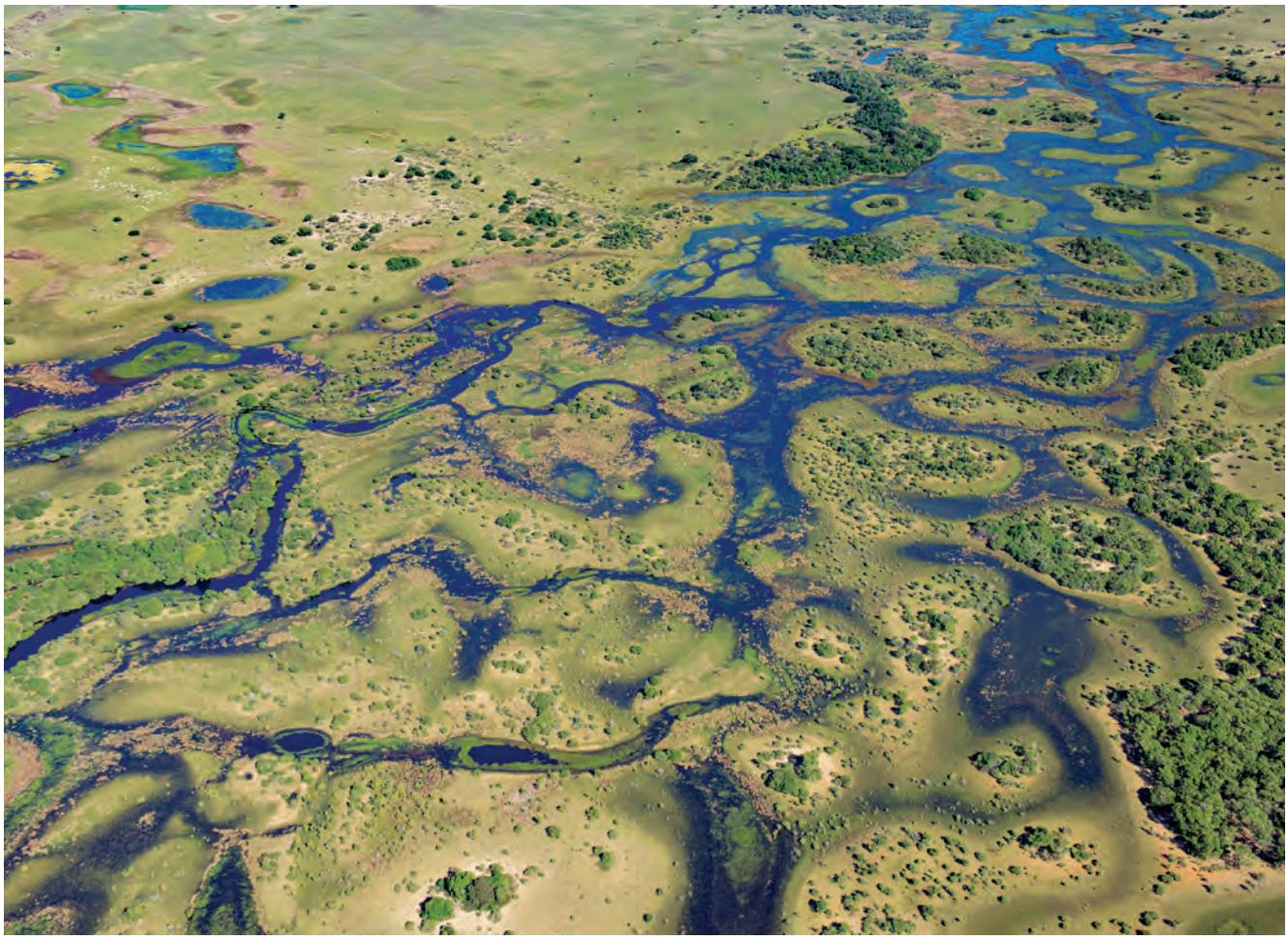
Sea turtle migrations are some of the most wide-ranging in the marine realm, and yet the species are very site specific in their nest habitat fidelity. © Gary Tabor

conservation, fishing regulations, or seasonal use) may be time limited and subject to formal periodic review and renewal. Periodic reviews should include evaluations based on monitoring of ecological, social and economic consequences and performance metrics, when possible.

## Management required to achieve objectives

The plan for an ecological corridor should describe management actions required to retain, restore or enhance ecological connectivity. The allowable activities within a corridor should relate directly to its purpose and therefore will be context specific (see Annex, Case Study 23). A multipurpose ecological corridor that is designed to facilitate the movement of all species due to climate change would likely need many more prohibited uses than one that is focused on facilitating the movement of a single species at a specific time of year. The plan should articulate management actions in terms of:

1. **Structural needs.** Are there structural ecological elements that are important to retain or enhance to ensure the corridor meets its objectives? Examples might include maintenance of a percentage of tree cover, restoration of a coral reef, implementation of riparian setbacks or maintenance of in-stream habitat components such as shaded areas, necessary water volume and velocity (see Chapter 2, section on ‘Modelling Ecological Corridors’ for a discussion of structural and functional connectivity; see also Annex, Case Study 21). Planned management actions should



Ecological communities can be heterogeneous and complex; functional connectivity is a reflection of its ecological context. Capivari River, Pantanal, Mato Grosso do Sul, Brazil © World Wildlife Fund (WWF), Photographer Jaime Rojo

Wildlife crossing structures such as this highway overpass in Croatia, one of 13 in the country, are no substitute for an intact landscape but have value in mitigating the effects of fragmentation for many species. © Djuro Huber

describe practices that achieve sustainable levels of structural ecological elements.

2. **Human activity management.** The management plan should prevent human pressures and threats that would increase fragmentation or undermine restoration efforts undertaken to achieve connectivity (see Annex, Case Study 5). Generally, livelihoods based on compatible activities and incentives that minimise or exclude extractive activities and other modern, industrial-scale activities should be encouraged. Decision makers (e.g. the governance authority) should determine which human activities need to be maintained, and which need to be controlled or prohibited, whether permanently or at specific times, to ensure that the corridor meets its connectivity conservation objectives. These objectives should form the foundation of a corridor's management plan or agreement.

Here are examples of some questions that planners may need to answer. If an ecological corridor includes a river, do human uses include dams, channelisation or other in-stream activities that compromise biodiversity dependent on specific habitats and natural flow regimes? If a corridor includes use by livestock, are there considerations of stocking intensity or fencing? If a corridor allows resource extraction, what management is needed to meet connectivity objectives? Are any human activities occurring that are incompatible with the ecological objectives, such as transportation infrastructure construction or industrial development? Can the design incorporate special wildlife connectivity needs, such as through the creation of wildlife overpasses or tunnels in cases where transportation or other infrastructure may otherwise impede ecological connectivity? Are there any Green Infrastructure plans, projects or methodologies being used or developed?

The management documentation for an ecological corridor should list prohibited or permissible activities and describe any restoration needed to achieve connectivity. For some activities, it may be necessary to specify a level (e.g. 'high', 'medium' or 'low') compatible with the connectivity objectives. One approach could be to create a decision framework for allowable activities (Saarman et al., 2013).

For corridors that traverse areas of poor habitat quality, restoration plans and metrics of success should be encouraged (see Annex, Case Study 11). It will be necessary to determine when an area under restoration is appropriate for inclusion within the corridor.

Corredor Florestal – Pontal do Paranapanema in Brazil demonstrates that large-scale restoration efforts can utilise connectivity conservation strategies. © IPE / Laury Cullen Jr; reproduced under Creative Commons.

Because some ecological corridors also conserve climate gradients in areas impacted by climate change, monitoring efforts can include specific climate variables in periodic assessments. Pinkwood (*Eucryphia moorei*) in higher-rainfall, moist sites on the Great Escarpment, Monga National Park, Great Eastern Ranges ecological corridor, Australia © Ian Pulsford

## Monitoring, evaluation and reporting requirements

The documentation for an ecological corridor should include a monitoring and evaluation plan, along with a strategy for securing resources to implement it. Authorities responsible for an ecological corridor should plan and carry out monitoring to track progress, evaluate effectiveness in achieving stated objectives and adapt management strategies based on results. Monitoring and evaluation should support an adaptive approach to management and take into account climate change impacts. Benefits of a monitoring and evaluation plan include aiding effective resource allocation, promoting accountability and increasing public support (Hockings et al., 2006). The plan should recognise both aspirational and readily feasible components.

'Monitoring' is the collection of information about specific ecological indicators repeatedly over time to discover trends in the ecological status of a corridor and in the effectiveness of management. Monitoring provides data needed to assess the extent to which an ecological corridor is achieving its connectivity objectives (see Annex, Case Studies 6 and 14).

In conjunction with evaluation, monitoring helps assess the adequacy of management and identify necessary adjustments (Hockings et al., 2006). Monitoring and evaluation should be a long-term commitment of an ecological corridor's governance, supported by appropriate resource allocations (see Annex, Case Studies 7 and 10).

Monitoring the effectiveness of an ecological corridor for specific connectivity objectives can take various forms. These range from habitat suitability measures to empirical species movement data to conservation genetics indicators (Bennett, 2003). Where climate mitigation is an anticipated benefit, monitoring variables should include changes in the condition of ecosystems and, when feasible, in the size of carbon stocks and associated stability of storage.

In a growing number of instances, geospatial data technologies such as remote sensing, aerial photographs and satellite imagery may be combined with traditional knowledge and real-time feedback to assist with monitoring. Monitoring approaches may involve time-series collection of information or use of control groups for comparisons. Monitoring methods may be qualitative, quantitative, or both,

and must be reliable, cost-effective, feasible and contextually appropriate. A monitoring plan should identify specific, achievable, relevant, time-bound and measurable indicators.

Monitoring data need to be analysed at an appropriate level to meet information needs. Data analysis should be done regularly so that adjustments to management strategies can be made as part of an adaptive management process (Conservation Measures Partnership, 2013).

Because transparency and accountability are essential components of the governance of ecological corridors, monitoring results and their meaning need to be documented and shared with the public. Documentation should include a communication plan indicating how results will be conveyed to key audiences. It is important to note that these audiences are likely to be quite diverse. They may include affected landowners, rightsholders and other stakeholders, such as local communities, project partners, agency staff, policy makers, scientific and technical advisers, and donors (see Annex, Case Study 7).

## Basic documentation for reporting

Ecological corridors may be documented and tracked at both national and international levels. Appropriate mechanisms will need to be developed to report this information to global databases for area-based conservation measures, such as the Protected Planet Database managed by the UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC). In addition to registering ecological corridors and networks, national and global databases will contribute to monitoring and tracking the status of these areas, as well as progress towards conservation commitments.

The basic documentation for reporting on an ecological corridor should include:

- Name of the site;
- Geographic description
- Map of location using a polygon shapefile;
- Year of establishment; and
- Contact information of reporting organisation.

Chilean flamingos (*Phoenicopterus chilensis*) rely on salt lagoons and soda lakes. These habitats are vulnerable to human disturbance. © Marie Read

Across the world, linear transportation infrastructure threatens wildlife via direct mortality and fragmentation of ecological connectivity. Top: A painted turtle (*Chrysemys picta*) makes a perilous crossing in Valentine National Wildlife Refuge, Nebraska, USA © Marcel Huijser; bottom: Greater rhea (*Rhea americana*) crossing the road near Bonito Mato Grosso do Sul Brazil © Marcel Huijser

# Applications and benefits of ecological corridors in different environments

6

White-lipped tree frog (*Litoria infrafrenata*), a tropical rainforest inhabitant on Cape York, Australia © Ian Pulsford

Connectivity is relevant across a range of environments from terrestrial and marine to freshwater and airspaces. This chapter elaborates upon ecological corridor applications and benefits in different environments.

In ***terrestrial environments,*** ecological corridors may facilitate daily, migratory or dispersal movements. The last ensures gene flow between populations, such as when a young animal looks for a new home range, or wind disperses seeds. Ecological corridors can also serve multi-generational dispersals, such as climate-related range shifts over time and through space. Ecological corridors may vary greatly in size to facilitate migrations, such as those of caribou (*Rangifer tarandus*), which travel hundreds or thousands of kilometres, to those of a population of Jefferson salamanders (*Ambystoma jeffersonianum*) near Burlington, Ontario, Canada, which move a short distance from upland forests to temporary ponds where they lay their eggs.

A terrestrial ecological corridor may be a continuous space, such as that which connects populations of lions (*Panthera leo*) across communal pastoral lands in the Kavango–Zambezi Transfrontier Conservation Area (Angola, Botswana, Namibia, Zambia, Zimbabwe; see Annex, Case Study 2). Alternatively, an ecological corridor can be a series of discontinuous terrestrial spaces that serve as stopover sites for airborne migratory animals, such as monarch butterflies or red knots (*Calidris canutus*), the latter of which migrates between the Northern and Southern hemispheres. However, such discontinuous corridors function only when aligned with migratory pathways (e.g. flyways) to ensure connectivity.

Ecological corridors in ***freshwater systems*** should conserve water flows and riparian communities, along with the movement of sediments and other natural materials. They should also allow for movement by native animals and plants. Freshwater ecological corridors may also facilitate daily, migratory or dispersal movements. These corridors provide pathways for movement between habitat patches within a particular freshwater system or across freshwater habitats (e.g. between the main stems of rivers and floodplains, or between rivers, lakes and estuaries) for species that require access to multiple habitats to complete their life cycles. Freshwater corridors may conserve lateral connectivity, for example between a river channel and an adjacent floodplain, such as in gravel-bed ecosystems that require exchanges of matter and energy to sustain viable populations of certain species (Hauer et al., 2016). Particularly in rivers, natural flows of sediment and gravel are also critical for creating habitats upon which many species rely. The vegetation of riparian

The great monarch butterfly migration serves as the iconic continental-scale migration of all invertebrate species. Migrating across long distances and several life generations, monarch butterflies remind us of how vital movement ecology is for species survival. © Adobe Stock

Wetland systems are essential components of any freshwater connectivity conservation strategy. Kings Plains Lake on Kings Plains–South Endeavour Trust Reserve – a wetland in the wet/dry tropics on Cape York, Australia © Ian Pulsford

Rivers are the lifeblood of terrestrial ecosystems. Terrestrial and freshwater systems are inextricably linked. Gravel-bed stream in Costa Rica © Félix Zumbado Morales / ProDUS Universidad de Costa Rica

areas and floodplains slows down and reduces peaks in the swellings of rivers while retaining sediments, thus decreasing the energy and destructive power of water flows. Freshwater ecological corridors may also help conserve aquifers and protect groundwater-dependent ecosystems such as springs, karst wetlands and certain types of floodplains (Tomlinson & Boulton, 2010). Such corridors often include and require maintenance of riparian vegetation, which influences the quality of freshwater habitat. The corridors may provide habitat and travel routes for terrestrial species, and may act as filters for pollutants and surface flow runoff. Freshwater ecological corridors with riparian vegetation also protect water bodies from undesired inputs of pollutants in highly developed landscapes (Bastian et al. 2015).

Freshwater ecological corridors may be established for water bodies that flow constantly or intermittently. In both cases, riparian zone restoration and prevention of impairments will often be required. As described above, wetlands and other freshwater areas may be part of a discontinuous terrestrial ecological corridor.

Ecological corridors in ***marine environments*** may connect marine protected areas (MPAs) or other key marine, coastal and estuarine habitats (Day et al., 2012). MPAs are unlikely to encompass the full movements of highly mobile marine mammals, fishes or reptiles, or to accommodate the complete larval stages of sessile fishes, invertebrates, plants and algae.

Ecological corridors, as essential elements of marine ecological networks for conservation, can conserve known migration routes and bottleneck zones, such as those between islands that are vulnerable to human activities. Conservation of marine connectivity is also important for juvenile fishes and invertebrate larvae that disperse via ocean currents over periods of days or months before settling on reefs or other substrates (Gotlanders et al., 2003; Cowen & Sponaugle, 2009), as well as for larger animals such as turtles and whales that migrate long distances.

Marine ecological corridors may be especially important for species that use different environments at different stages of their life cycles. For example, marine turtles nest on beaches and may use coastal waters before moving into the high seas, while certain fish may need to migrate to reach a spawning aggregation site. Ecological corridors also facilitate the role of MPAs as sources of species replenishment to populations elsewhere. Marine ecological corridors may need to be quite large given the extent to which oceanic currents, eddies and tides affect processes and the recruitment of organisms. Alternatively, marine ecological corridors could be relatively small to protect migrations of a few kilometres, such as those of red crabs (*Gecardoidea natalis*) on Australia's Christmas Island. Siting of three-dimensional ecological corridors may be affected by water depth; geological features, such as sea mounts; stratification of the water column; or seasonal currents or wind flows (Cowen et al., 2007).

Geophysical processes such as daily tides govern the natural processes that connect and sustain marine and coastal systems. Tropical coral reef on Upolu Island, Samoa © Adobe Stock

Over 50 million red crabs (*Gecarcoidea natalis*) traverse Christmas Island, Australia, to lay their eggs in the ocean. © Adobe Stock

Formal recognition of ecological corridors for marine species such as humpback whales (*Megaptera novaeangliae*) could extend recognised conservation areas from waters under national jurisdiction to the high seas, consistent with the CBD Conference of the Parties decision of 2008 (CBD Guidance on Marine and Coastal Protected Areas and Networks COP 2008 IX/20, Annexes I and II).

***Mixed*** ecological corridors encompass two or all three types of environment (terrestrial, freshwater and/or marine). For example, ecological corridors that span marine and estuarine areas into freshwater reaches may facilitate essential life-cycle movement for anadromous and catadromous fish species (which move from the sea to rivers to spawn and vice versa). Such fish range so widely in marine and freshwater environments that an ecological corridor may not link specific protected or conserved areas but rather conserve critical migration pathways (see Annex, Case Studies 17 and 22).

Likewise, mixed ecological corridors may link MPAs to estuaries to facilitate the movement necessary to sustain species populations and evolutionary processes. These corridors also may connect MPAs with terrestrial protected areas to sustain ecological processes such as migration. There is also an opportunity to maximise the benefits for freshwater and terrestrial species by looking for synergies in migration pathways and habitat needs across realms.

Many birds, insects and other animals move through Earth's ***airspaces.*** The possibility of an air-based or air-column ecological corridor is beginning to be considered due to collisions of birds and bats with wind turbines, high-rise buildings and other human structures (Rydell et al., 2010; Loss et al., 2013). Furthermore, overhead power lines have recently been discovered to produce stroboscopic ultraviolet lights that may act as a barrier to the movement of some bird species (Tyler et al. 2014). Currently, airspace ecological corridors are theoretical, and further work is needed to determine if they are feasible in practice.

In all four of these realms of the biosphere, rapid climate change is increasing the need for ecosystem resilience and for species to adapt to changing conditions. Ecological corridors can contribute to both climate resilience and adaptation. Large, connected terrestrial and aquatic ecosystems are more resilient to climate change because ecological processes important for stability are more likely to be functioning there (Walker & Salt, 2006). Connecting protected areas, OECMs and other important biodiversity areas by means of ecological corridors allows species to adapt to climate change by shifting their ranges to new, suitable habitats and climates. In contrast, habitat loss and fragmentation can prohibit these range shifts. Therefore, protecting and establishing ecological corridors can be an

A toco toucan (*Ramphastos toco*) from Mato Grosso, Brazil, flies across habitat patches in search of food. © Grégoire Dubois

effective strategy to facilitate species persistence (reviewed in Keeley et al., 2018; see Annex, Case Study 8).

Ecological corridors can be designed and managed taking climate considerations into account. Approaches include (see also Gross et al., 2016):

- Ensuring that they contain diverse topography that provides different microclimates for species persistence;
- Establishing them to connect protected areas and conserved areas that can serve as climate refugia;
- Prioritising those that connect protected and conserved areas that together encompass temperature gradients;
- Managing them to account for the rapidity of climate change;
- Managing them to account for animal and plant population dynamics at the leading and trailing edges of ranges;
- Designing them for multiple species redistributions to maintain critical species interactions (e.g. those of mutualists);
- Designing them to facilitate redistribution of genetic diversity in a representative manner;
- Designing them so they can change spatially in sync with climate changes (e.g. those affecting winds, ocean currents, deep-sea chemistry and temperatures, or riparian zones);
- Ensuring that they are sufficiently wide to provide live-in habitat for slow-moving species; and
- Where appropriate, restoring or enhancing vegetation with drought-resistant species to provide resources for wildlife throughout the year.

# The emergence of connectivity conservation law and policy

7

Indian rhinoceros (*Rhinoceros unicornis*), Kaziranga National Park, Assam, India © Grégoire Dubois

Most global and regional legal instruments dealing with biodiversity conservation, climate change and environmental sustainability have objectives that will not be met without addressing connectivity conservation effectively over the long term. As a result, at the international level there is growing recognition of ecological connectivity in law and policy. Maintaining connectivity as a core conservation objective can be found in the Aichi Biodiversity Targets of the CBD, the Call to Action for Landscape Connectivity of the World Business Council for Sustainable Development, *A Global Standard for Identification of Key Biodiversity Areas* (IUCN, 2016) and *Guidelines for Applying Protected Area Management Categories* (Dudley, 2008).

In 2010, the Parties to the CBD adopted a 10-year Strategic Plan for Biodiversity that included the 20 Aichi Biodiversity Targets (CBD, 2011). Aichi Target 11 states that by 2020 the planet's area under protection will be increased to at least 17% of terrestrial and inland waters, and 10% of marine and coastal areas, in "effectively and equitably managed, ecologically representative and well-connected systems of protected areas" (CBD, 2011). A recent review of 746 MPAs found that only 11% identified connectivity as a management consideration (Balbar & Metaxas, 2019). Most countries lag significantly behind in implementing the connectivity element of Aichi Target 11.

A principal recommendation of these Guidelines is that the designation 'ecological corridor' be recognised in law and policy internationally. Ecological corridors provide an important mechanism for countries to advance legal obligations and policy commitments, which notably include the CBD, Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar Convention), Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention) and its ancillary instruments, World Heritage Convention, UNCLOS, UN Framework Convention on Climate Change, and UN Educational, Scientific and Cultural Organization's (UNESCO's) Man and the Biosphere Programme. There are also numerous regional conventions, including the Revised African Convention on the Conservation of Nature and Natural Resources (Maputo Convention) and the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention; promoting the European 'Emerald' Network), the UN Convention on Non-Navigational Uses of International Watercourses, and the Convention on the Protection and Use of Transboundary Watercourses.

At the international level there are also non-treaty conservation networks, such as the European Union's (EU's) Natura 2000, which covers terrestrial, freshwater and marine environments and applies to all EU Member States, and also includes other directives such as the Water, Marine Strategy, and Maritime Spatial Planning Frameworks (Lausche et al., 2013; European Parliament & Council, 2014). In addition, the IUCN WCPA's Transboundary Conservation Specialist Group has developed detailed guidance on transboundary conservation that is highly relevant to connectivity (Vasilijević et al., 2015).

Vicuñas (*Vicugna vicugna*) are found across the high slopes of the Andes. Reserva de Producción de Fauna Chimborazo, Ecuador © Gabriel Oppler

An Assam roofed turtle (*Pangshura sylhetensis*) takes advantage of a connected wetland area within and surrounding Kaziranga National Park, Assam, India.
© Grégoire Dubois

At the national level, a variety of policies, laws, administrative authorities, regulations and plans also require or benefit from connectivity conservation to meet their objectives (Lausche et al., 2013). Government policies and plans such as National Sustainable Development Strategies and National Biodiversity Strategies and Action Plans (NBSAPs) guide overall development. Virtually all national legal systems also have specific laws relevant to ecological corridors that deal with nature, wildlife and biodiversity conservation, and sustainable use (e.g. laws covering forestry, fisheries, grazing lands and water flows) and use direct regulation or voluntary conservation agreements, often with incentives.

Connectivity objectives are increasingly prevalent in national and sub-national planning and policy initiatives. Until recently, connectivity legislation was rare at the national or even sub-national level (Lausche et al. 2013). Now, countries such as Bhutan, Costa Rica and Tanzania, and sub-national jurisdictions such as California and New Mexico (USA), have enacted corridor legislation. Additionally, site-specific legislation has been enacted in some countries. For example, the South Korea Act on the Protection of the Baekdu Daegan Mountain System, 2003 (Act no. 7038), which came into effect in 2005, designates an area of 263,427 ha. Of this, 86% is made up of 183 existing protected areas and 14% consists of new buffer and core areas that create a biodiversity corridor along the main mountain range of the Korean Peninsula (Miller & Hyun, 2011; see also Farrier et al., 2013, and KLRI, 2014, for other case studies of legal actions to protect specific connectivity areas).

For the most part, however, current national and sub-national efforts to conserve connectivity utilise and adapt existing policies and laws. Conservation and sustainable resource use laws are the first tier for this purpose. These include protected areas laws, general biodiversity or nature conservation laws, and resource-specific laws such as those relating to sustainable use of forests, fisheries, soils or water. These instruments normally involve direct regulation and arguably should give attention to connectivity conservation to meet their objectives effectively. Supportive laws may extend to hunting controls, integrated resource management and environmental pollution controls. Major substantive areas of law beyond traditional conservation instruments are also important. These include laws and policies on land-use planning; development controls (e.g. through zoning); marine spatial planning; acquisition of rights by government permits and licences for transportation, infrastructure, mining and energy; conservation easements and voluntary agreements; and strategic and project-focused environmental assessments.

Economic instruments are another suite of available tools that may reinforce direct regulation or serve as an alternative approach to support connectivity conservation. These instruments may encourage certain behaviour that could include actions of landowners and rightsholders to further

Private land incentives are critical in supporting connectivity efforts that span private and public land domains. Intensively managed Naturpark Beverin, Switzerland © Juraj Švajda

Zebras from Masai Mara Reserve, Kenya, range widely into surrounding communal lands. The rise of private conservancies in Africa has potential to support connectivity conservation goals. © Gary Tabor

specific ecological corridor objectives. Such instruments include positive incentives (e.g. technical assistance, subsidies, tax credits, or reduced tax liability); negative incentives (e.g. tax increases or withholding of technical assistance); compensation for conservation actions or loss of economic productivity; payments for environmental services or stewardship (e.g. maintenance of forest cover, restoration of riparian areas, or other green infrastructure); and market-driven tools such as tradeable permits and conservation/bio-banking (see Lausche et al., 2013, for an extensive discussion of such tools for both terrestrial and marine environments).

The formal process of amending or enacting new legal instruments takes significant time and should not delay efforts to protect and secure ecological corridors. While legal approaches will vary, most countries' legal systems – national and sub-national (provincial, state, etc.) – already have a number of tools in place to begin the essential process of recognising and protecting ecological corridors, including through such instruments as NBSAPs and national Climate Change Action Plans (see Annex, Case Studies 1 and 2). These tools should be identified and analysed as soon as possible for key connectivity sites before their conservation is no longer economically or politically feasible, even as the longer-term process of amending or enacting new connectivity-specific legislation is pursued.

The development of ecological corridors contributes to the broader approach known as 'Nature-based Solutions', defined by IUCN as "actions to protect, sustainably manage, and restore natural or modified ecosystems, that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits." Guidance on Nature-based Solutions can be found in Cohen-Shacham et al. (2016).

## Nomination of ecological corridors and ecological networks for conservation to the Protected Planet Database

Governance authorities may voluntarily report ecological corridors and ecological networks for conservation to the Protected Planet Database managed by UNEP-WCMC and IUCN, which encourage the practice. At the time of publication, the reporting structure is under development with partners. Check with www.protectedplanet.net to verify if this database is online.

Generally, a given country's focal point for the Protected Planet Database would report the ecological corridor or an ecological network for conservation using the reporting portal. There is also an opportunity for individual governance authorities to report directly to the Protected Planet Database. Landowners or rightsholders retain the right to object to the external nomination or recognition of their area as an ecological corridor in cases in which their free, prior and informed consent has not been obtained. This applies to all four governance types, as set out in the 'Governance' section of Chapter 5.

Inscribing an area as an ecological corridor or an ecological network for conservation in the Protected Planet Database places a heightened responsibility on the governance authority to continue to manage the area over the long term in ways that achieve its specific connectivity goals. The authority is responsible for reporting any changes in boundaries, governance or objectives. While national circumstances differ, it is hoped that national or regional legislation will provide greater support and recognition to existing governance systems and not supplant or unnecessarily alter any local arrangements.

# Conclusion

8

Red-shouldered hawk (*Buteo lineatus*), Chesapeake & Ohio Canal National Historical Park, Maryland, USA © Nicholas Tait

Ecological corridors in terrestrial, freshwater and marine ecosystems are a critical conservation designation needed to ensure healthy ecosystems. They are a key component of ecological networks for conservation and complement the objectives of protected areas and OECMs by knitting together these core habitats and other intact natural areas. These Guidelines support the growing demand for connectivity conservation, recognised by scientists, policy makers and practitioners. Connectivity conservation requires innovative implementation approaches to conserve lands and water within the conservation matrix – across patterns of resource use, jurisdictions, cultures and geographies. These Guidelines provide direction on how to conserve vital ecological connectivity values in every conservation situation in a consistent and measurable fashion. The toolbox for connectivity conservation includes various types of formal and informal recognition, national legislation, local and regional zoning regulations, conservation easements, conservancy design and transportation planning. Our world needs such a diversity of actions to maintain and restore ecological connectivity, an essential part of halting biodiversity loss and adapting to climate change.

There are many dimensions of ecological connectivity, including gene flow, movement of individuals, metapopulation dynamics, migration, seasonal dispersal and flows of ecological processes. The terms ecological networks and ecological corridors have been defined and operationalised throughout these Guidelines to establish a common set of terms, principles and approaches that can be consistently applied, yet tailored to the specific contexts of ecological connectivity around the world. Connectivity conservation will be enhanced by speaking this common language and working together toward shared successes.

The science underpinning connectivity conservation clearly supports that larger, well-connected areas are more likely to maintain biodiversity and ecological integrity. Given the current biodiversity and climate crises, there is an urgent need to restore and sustain ecological connectivity among and between protected areas, OECMs and other intact natural areas. By connecting these areas with each other, it is possible to arrest and reverse ecosystem fragmentation.

Well-connected ecosystems support a diversity of ecological functions including migration, water and nutrient cycling, pollination, seed dispersal, food security, climate resilience and disease resistance.

The loss of ecological connectivity is most often a consequence of policy and management decisions made by the development, transportation, agriculture and extraction sectors. These Guidelines and Case Studies provide insights into examples and best practices to demonstrate approaches that can ensure ecological connectivity for different ecosystems and species, and at different spatial and temporal scales. An emphasis on human and technical capacity is required for mainstreaming and accelerating uptake of connectivity conservation measures to buffer and better adapt to the impacts of climate change.

Ecological connectivity often transcends national boundaries and can span different ecosystems within a country. The strategies and approaches outlined here take into careful consideration how national and regional transboundary measures can be formed and contribute to aggregated accomplishments internationally. Planning and implementing ecological networks and corridors require specific objectives to be set, and governance and management mechanisms to be aligned with achieving effective conservation outcomes.

Most global, regional and national targets for biodiversity conservation, climate change and environmental sustainability cannot be met unless ecological connectivity conservation is addressed. The importance of connectivity in achieving the objectives of the Convention on Biological Diversity cannot be overstated. As such, it is highly relevant for accomplishing the current and future objectives of many other Multilateral Environmental Agreements. Ecological connectivity – if further recognised in law and policy around the world – can serve as an integrative and cross-cutting mechanism to advance obligations and commitments within and across national borders. Overall, connectivity conservation, by linking together protected areas, OECMs and ecological corridors, offers scalable solutions for environmental, social and economic challenges. The world needs – and it is in our collective interest — to protect, maintain and restore ecological connectivity.

# Glossary

**Biodiversity:** The variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems (CBD Article 2, 1992).

**Connectivity**

- **Ecological connectivity:** The unimpeded movement of species and the flow of natural processes that sustain life on Earth (CMS, 2020).

  There are various sub-definitions of *ecological connectivity* that are useful in the context of these Guidelines:

  - **Ecological connectivity for species (scientific-detailed definition):** The movement of populations, individuals, genes, gametes and propagules between populations, communities and ecosystems, as well as that of non-living material from one location to another.
  - **Functional connectivity for species:** A description of how well genes, gametes, propagules or individuals move through land, freshwater and seascape (Rudnick et al., 2012; Weeks, 2017).
  - **Structural connectivity for species:** A measure of habitat permeability based on the physical features and arrangements of habitat patches, disturbances and other land, freshwater or seascape elements presumed to be important for organisms to move through their environment. Structural connectivity is used in efforts to restore or estimate functional connectivity where measures of it are lacking (Hilty et al., 2019).

**Conservation:** The protection, care, management and maintenance of ecosystems, habitats, wildlife species and populations, within or outside of their natural environments, in order to safeguard the natural conditions for their long-term permanence.

**Dispersal:** The condition of individuals or seeds moving from one site to a breeding or growing site.

**Ecological corridor:** A clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity. The following terms are often used similarly: 'linkages', 'safe passages', 'ecological connectivity areas', 'ecological connectivity zones', and 'permeability areas'.

**Ecological indicator:** A measurable entity related to a specific ecological information need, such as the status of a population, a change in a threat or progress toward an ecological objective (Hilty & Merenlender, 2000).

**Ecological network (for conservation):** A system of core habitats (protected areas, OECMs and other intact natural areas), connected by ecological corridors, which is established, restored as needed and maintained to conserve biological diversity in systems that have been fragmented (see Bennett & Mulongoy, 2006).

**Ecosystem:** A dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit. It is the sum total of all the abiotic and biotic processes going on in an ecosystem that transfer energy and matter within and between ecosystems (e.g. biogeochemical cycles, primary production, etc.) (CBD Article 2, 1992).

- **Ecosystem functioning:** The collective life activities of plants, animals and microbes and the effects these activities – feeding, growing, moving, excreting waste, etc. – have on the physical and chemical conditions of the environment (Naeem et al., 1999).
- **Ecosystem services:** The benefits people obtain from ecosystems. These include provisioning services such as food and water production; regulating services such as flood and disease control; cultural services such as spiritual, recreational and cultural benefits; and supporting services such as nutrient cycling that maintain the conditions for life on Earth (Millennium Ecosystem Assessment, 2005).
- **Ecosystem structure:** The biophysical architecture of an ecosystem; the composition and arrangement of all the living and non-living physical matter at a location (Russi et al., 2013).

**Flyway:** The entire range of a migratory bird species, distinct populations of a species, or groups of related species through which individuals move on an annual, seasonal or multi-year basis from breeding grounds to non-breeding areas. The term also includes intermediate resting and feeding places, as well as the areas within which the birds migrate (Boere & Stroud, 2006).

**Fragmentation:** The breaking up of a habitat, ecosystem or land-use type into smaller and, often, more isolated parcels, thereby reducing the number of species that can be supported.

**Governance authority:** The institution, agency, individual, Indigenous Peoples or community group, or other body acknowledged as having authority and responsibility for decision making over an area, and whose authority may include management of an area (IUCN WCPA, 2019; Borrini-Feyerabend et al., 2013). It is to be recognised that there may be multiple governance authorities, both formal and informal.

**Governed:** The condition in which an area is under the authority of a specified entity or entities conducting the actions, policy and affairs of the area. Ecological corridors can

be governed under the same range of governance types as protected areas.

**Habitat:** The place or type of site where an organism or population naturally occurs (CBD Article 2, 1992).

**Indigenous Peoples:** Tribal peoples whose social, cultural and economic conditions distinguish them from other sections of the national community, and whose status is regulated wholly or partially by their own customs or traditions or by special laws or regulations. The term also includes peoples in independent countries who are regarded as indigenous on account of their descent from the populations that inhabited the country, or a geographical region to which the country belongs, at the time of conquest or colonisation or the establishment of present state boundaries and who, irrespective of their legal status, retain some or all of their own social, economic, cultural and political institutions (Borrini-Feyerabend et al., 2004; following IUCN's use of the International Labour Organization's ILO Convention 169 on Indigenous and Tribal Peoples). Preferred terminology varies around the world, and terms such as 'Aboriginal' or 'Traditional Peoples' are sometimes used instead.

**Landscape:** A heterogeneous space comprising a cluster of interacting ecosystems, geological features and ecological processes, and often including human influences (Forman & Godron, 1986; Wu, 2008). Landscapes are generally large, but can be defined at a range of spatial scales. Interaction of landscape spatial elements can result in emergent effects not inherent to each element separately (e.g. viability of populations, microclimates, runoff regulation, aesthetic quality, etc.).

**Local community:** A human group sharing a territory and involved in different but related aspects of livelihoods such as managing natural resources, producing knowledge and culture, and developing productive technologies and practices. Since this definition can apply to a range of community sizes, it can be further specified that the members of a 'local community' are those who are likely to have face-to-face encounters and/or direct mutual influences in their daily lives. In this sense, a rural village, a clan or the inhabitants of an urban neighbourhood can be considered a 'local community', but not all the inhabitants of a district, a city quarter or even a rural town. A 'local community' could be permanently settled or mobile (Borrini-Feyerabend et al., 2004).

**Managed:** In the context of an ecological corridor, the condition of taking active steps to conserve or restore the natural (and possibly other) values to ensure functionality. Note that 'managed' can include decisions not to intervene in an area.

**Migration:** The regular annual or seasonal movement of individual animals or populations of animals between distinct habitats, each of which is occupied during different parts of the year (Lindenmayer & Burgman, 2005).

**Migratory species:** The entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdiction boundaries (CMS Article 1, 1979).

**Monitoring:** The collecting of information on indicators and/or targets repeatedly over time to evaluate trends in the status of conservation targets, often related to effectiveness of management and/or governance activities (e.g., Hilty & Merenlender, 2000).

**OECM (Other Effective Area-Based Conservation Measure):** A geographically defined area other than a protected area, which is governed and managed in ways that achieve positive and sustained long-term outcomes for the *in situ* conservation of biodiversity with associated ecosystem functions and services and, where applicable, cultural, spiritual, socio-economic and other locally relevant values are also conserved (IUCN WCPA, 2019).

**Populations:** All the organisms of the same species that live in a specific geographic area at the same time and have the capability of interbreeding.

**Protected area:** A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008; Stolton et al., 2013).

**Resilience:** In the context of ecological networks for conservation, the capacity of a part or the whole of an ecological network to withstand changes to the processes that control its structures and functions (Holling & Gunderson 2002).

**Restoration:** In the context of ecological corridors, the recovery of ecological connectivity that has been diminished, impaired or destroyed (modified from Society for Ecological Restoration International Science & Policy Working Group, 2004). Restoration is guided by scientific inputs that help prioritise actions.

**Rightsholders, stakeholders:** In the context of protected areas and conservation, the term 'rightsholders' refers to people (such as but not limited to landowners) socially endowed with legal or customary rights with respect to land, water and natural resources. By contrast, 'stakeholders' possess direct or indirect interests and concerns about these resources but do not necessarily enjoy a legally or socially recognised entitlement to them (Borrini-Feyerabend et al., 2013).

**Seascape:** A spatially heterogeneous marine region that can be delineated at a range of scales and which includes physical, geological and chemical aspects of oceans. It can be a combination of adjacent coastline and sea, such as mangroves, coral reefs, seagrass beds, tidal marshes and deep seas. It includes the features of the geology and

morphology of the sea floor as well as the living communities of the benthos, water column and surface, and often includes the influence of humans (Pittman, 2017; Fuller, 2013). Seascapes are generally large, but can be defined at a range of spatial scales.

**Sustainable use:** The use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining the potential to meet the needs and aspirations of present and future generations (CBD Article 2, 1992).

The Russian River corridor in California, USA, maintains ecological connectivity as the river passes through agricultural, residential and urban landscapes.
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# Annex: Approaches to conserving ecological corridors in ecological networks

## Introduction

This compendium of case studies illustrates initiatives around the world that are working toward protecting or restoring ecological connectivity. The case studies offer insight into the breadth of approaches being used to advance conservation of ecological corridors to benefit ecological networks in terrestrial, freshwater and marine realms (Table 5). Each case study describes the context and challenges to connectivity in the study region, explains the approach to conservation, presents an example of an ecological corridor in the network, and shares some results. The case studies were selected to demonstrate a variety of ecological networks for conservation and ecological corridors within them, as well as a variety of approaches to their conservation. These examples can help us understand both the diversity of current efforts and the need to move toward formalising ecological corridors as elements of ecological networks for conservation

**Table 5.** Schematic overview of the case studies.

| Case study title | Type of study region | Greatest threat to connectivity | Approaches to conserving ecological corridors |
|---|---|---|---|
| 1. Kilimanjaro Landscape: Ensuring the viability of wildlife populations | terrestrial, rural | habitat loss and fragmentation | • conservation lease programme for private landowners |
| 2. Connectivity conservation in the Kavango Zambezi Transfrontier Conservation Area: The Zambezi-Chobe Floodplain Wildlife Dispersal Area | terrestrial, rural | deforestation, uncontrolled settlements, overgrazing, over-exploitation of fish, uncontrolled fires | • establishment of a five-country transfrontier conservation area<br>• development of integrated development plans<br>• creating awareness and engaging local stakeholders<br>• establishment of community conservancies<br>• promotion of conservation agriculture<br>• establishment of wildlife sanctuaries |
| 3. Conserving six landscapes of the Albertine Rift to ensure connectivity | terrestrial, rural | habitat loss and fragmentation | • facilitating cooperation<br>• developing sustainable-use community areas |
| 4. The Kilombero Valley Ramsar site, United Republic of Tanzania | terrestrial, rural | sustained human immigration and growing settlements and agriculture | • designation as a Ramsar site<br>• transitional governance approach from central management of large protected areas to management of a mosaic of smaller protected areas |
| 5. Ecological corridor for the reunion of giant pandas in the Qinling landscape | terrestrial, rural | highway and human land use | • baseline survey and mapping<br>• habitat restoration<br>• community engagement<br>• traffic management<br>• capacity enhancement<br>• wildlife monitoring |
| 6. Thailand's experience in ecologically connecting its protected areas | terrestrial, rural | deforestation and conversion of forests into plantations | • establishment of non-hunting areas and buffer zones<br>• management of lands for connectivity |
| 7. East Coast Conservation Corridor in Tasmania | terrestrial, rural | land-use change | • restoration<br>• land-use planning<br>• management for connectivity |
| 8. The Great Eastern Ranges: Australia's first continental-scale ecological network for conservation | terrestrial, rural | land degradation | • restoration<br>• conservation by private landowners<br>• community education<br>• biological surveys<br>• research programs |

**Table 5 (continued).** Schematic overview of the case studies.

| Case study title | Type of study region | Greatest threat to connectivity | Approaches to conserving ecological corridors |
|---|---|---|---|
| 9. COREHABS to BearConnect: Securing ROAMing in the wilderness corner of Europe | terrestrial, rural | rapid infrastructure development | • identification and assessment of ecological corridors<br>• integration of protected areas and ecological corridors into cadastral plans and land registers |
| 10. Ecological connectivity in an urban context: Utrechtse Heuvelrug, Netherlands | terrestrial, urbanised | pressures from infrastructure, urban expansion, intensive agriculture and recreation | • landscape defragmentation through road crossings and open space preservation |
| 11. The Spanish National Network of Drover's Roads (Vías Pecuarias) | terrestrial, rural and urbanised | loss of extensive livestock farming and transhumance | • legal protection<br>• ecological corridor demarcation<br>• fostering of extensive livestock farming, encouragement of young people to transhumance and cattle farming<br>• restoration<br>• education<br>• exploitation of multifunctionality |
| 12. ECONET: Ecological network in the Kostroma Region, Russia | terrestrial, rural | deforestation | • ecological network consisting of protected areas and ecological corridors<br>• protected areas with different regimes of multifunctional activities |
| 13. Sustaining forested landscape connections in the northern Appalachians: The Staying Connected Initiative | terrestrial, rural and urbanised | fragmentation from roads and human development | • focus work in nine highest-priority linkage areas<br>• strategic land protection<br>• land-use planning<br>• community outreach and engagement<br>• habitat restoration<br>• transportation mitigation |
| 14. Yellowstone to Yukon (Y2Y): Connecting and protecting one of the most intact mountain ecosystems | terrestrial, rural | fragmentation from roads and human development | • protection of areas important for biodiversity<br>• restoration and maintenance of areas for ecological connectivity<br>• direction of development away from areas of biological importance<br>• promotion of people and wildlife living in harmony |
| 15. Conserving long-distance migration: The Red Desert to Hoback Mule Deer Corridor, Wyoming, USA | terrestrial, rural | human development | • detailed mapping of migration routes<br>• assessments of land-use patterns and threats along the routes<br>• land protection<br>• land management<br>• road crossings |
| 16. Corridors for life: Improving livelihoods and connecting forests in Brazil | terrestrial, rural | landscape fragmentation from agriculture and settlements | • vision plan for large-scale reforestation<br>• enlargement and eventual connection of forest fragments through reforestation<br>• adoption of biodiversity-friendly land-use options<br>• promotion of change in land-use practices<br>• adoption of sustainable agriculture and agroforestry<br>• improvement of farmers' livelihoods<br>• carbon offsets |
| 17. Connectivity, ecosystem services and Nature-based Solutions in land-use planning in Costa Rica | terrestrial, rural | human development | • municipal land management plans |

**Table 5 (continued).** Schematic overview of the case studies.

| Case study title | Type of study region | Greatest threat to connectivity | Approaches to conserving ecological corridors |
|---|---|---|---|
| 18. The Jaguar Corridor Initiative: A range-wide species conservation strategy | terrestrial, rural | human land-use changes | • modelled ecological corridors<br>• prioritised populations and ecological corridors<br>• validated modelled corridors using a rapid-assessment interview-based methodology<br>• varied implementation action at local level |
| 19. Grassroots reserves have strong benefit for river ecosystems in the Salween River Basin | freshwater, rural | overfishing | • ecological networks of small riverine reserves |
| 20. The ecological corridor Mura-Drava-Danube and future five-country biosphere reserve | freshwater, rural | human land-use changes | • transboundary cooperation for harmonised conservation, integrated management and restoration<br>• establishment of a transboundary biosphere reserve |
| 21. Pacific salmon watersheds: Restoring lost connections | freshwater, rural | dams hindering fish migrations | • dam removal and mitigation to benefit salmon and other migratory fishes |
| 22. Fragmentation of riparian protections throughout catchments, Oregon, USA | freshwater, rural | human land uses and fragmented land protections along the continuum of the river | • development of an understanding of the mosaic of protective efforts to identify gaps in them |
| 23. Protection of the free-flowing Bita River | freshwater, rural | extractive industries, livestock grazing, large timber plantations, and urbanisation | • formation of an alliance<br>• working with local stakeholders<br>• decision-making framework to choose best conservation actions<br>• protection as a Ramsar site |
| 24. The Great Barrier Reef – Systematically protecting connectivity without connectivity data | marine | recurrent coral reef bleaching, cyclones, invasive species outbreaks, poor water quality, unsustainable fishing, dredging and coastal development | • networks of strategically placed marine reserves<br>• zoning based on systematic planning principles |
| 25. Northern Channel Islands: Connectivity across a network of marine protected areas contributes to positive population and ecosystem consequences | marine | human impacts such as fisheries, invasive species, and climate change | • marine protected area network with resulting ecological corridors |

# Terrestrial connectivity: Africa

## 1. Kilimanjaro Landscape: Ensuring the viability of wildlife populations

Kathleen H. Fitzgerald, *African Wildlife Foundation*

### Context and challenge

The transboundary Kilimanjaro Landscape stretches from Amboseli National Park to Chyulu National Park and Tsavo West National Park in Kenya to Mount Kilimanjaro National Park in Tanzania (Figure 1). Amboseli National Park, 392 km$^2$, forms the core of the ecosystem while six community lands, group ranches, surround the park. Amboseli National Park is world-renowned for its elephants and magnificent views of Mount Kilimanjaro, but the park is too small to support viable populations of wildlife. Wildlife depends on the unprotected areas outside the park. If the ecosystem is to support wildlife in the long term, the areas surrounding the park must be protected.

The greatest threat in the landscape is habitat loss and fragmentation (Figure 2). A majority of the group ranch land surrounding the park was subdivided into 0.8-ha, 4-ha and 24-ha lots allocated to individual Maasai landowners. The subdivision is primarily due to a breakdown in communal systems, failure of the group ranch system to deliver equitable benefits and improve community livelihoods, and a more sedentary way of life. Some Maasai landowners are selling their land for development and agriculture.

### Approach

In 2008, the African Wildlife Foundation (AWF, www.awf.org) launched a conservation lease program to:

**Key lesson**

Conservation lease agreements support the viability of Amboseli National Park wildlife populations, and could move toward being enduring ecological corridor(s) recognised by the world.

- Contribute to the sustainability of Amboseli National Park by protecting strategic ecological corridors;
- Prevent conversion of habitat; and
- Provide incentives directly to landowners to keep their land open and passable to wildlife.

AWF worked with individual landowners to help them understand that collectively their land was more valuable than individually, which resulted in the landowners forming associations. This enabled them to make collective decisions while retaining and benefitting from their individual landownership. These associations range in size from 50 to 90 landowners. Through these associations, AWF engaged the landowners in a discussion about conservation leases and payment for ecosystem services (PES). AWF proposed to lease land from the Maasai via a PES arrangement and pay them to keep their land open for wildlife. Different organisations now manage and pay for the leases in the Amboseli ecological corridors, including AWF, Tawi Lodge

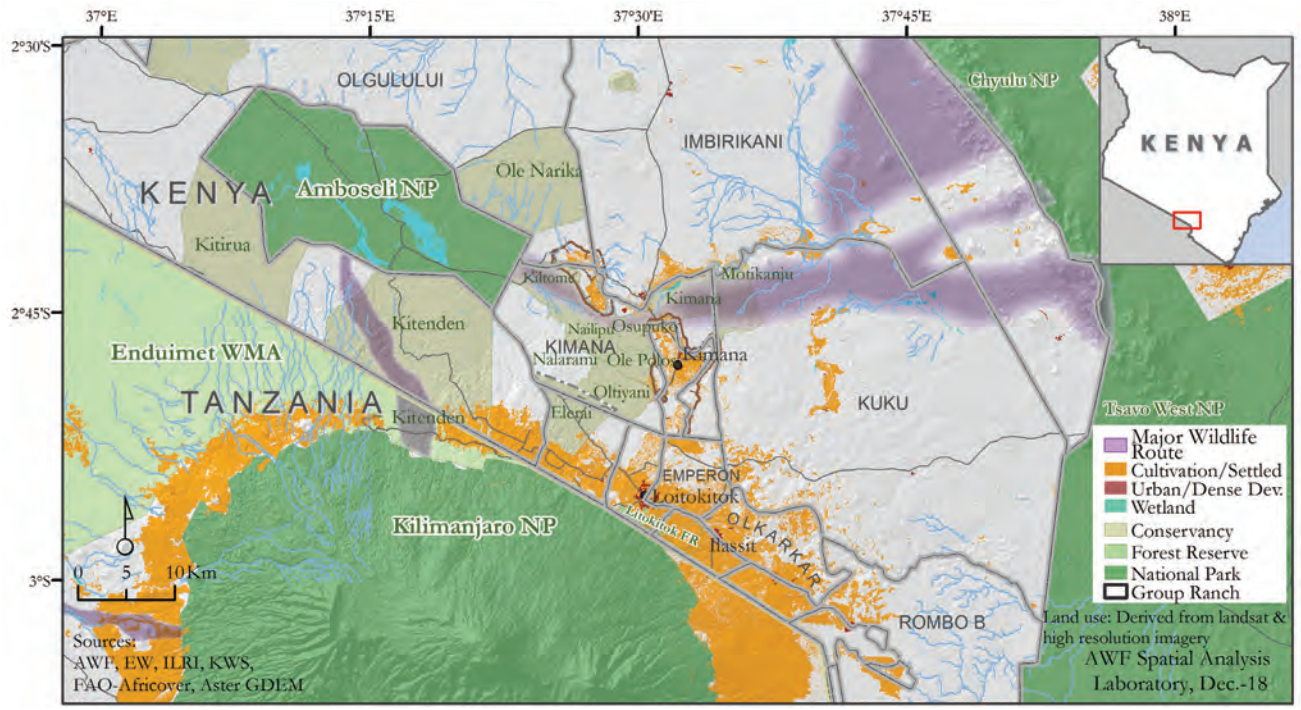


**Figure 1.** The Kilimanjaro landscapes showing community-owned wildlife conservancies established by AWF to protect key ecological corridors
© African Wildlife Foundation

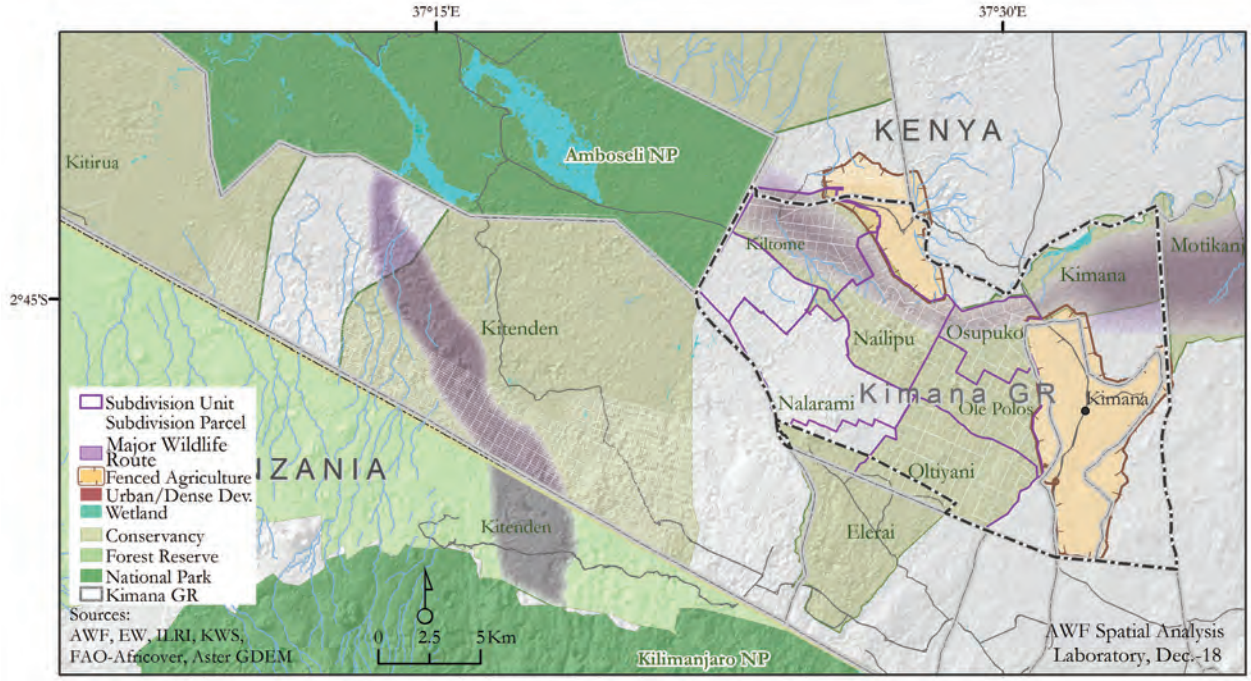


**Figure 2.** Land subdivision in the Kilimanjaro landscape. The Kimana Group Ranch is located east of Amboseli National Park. © African Wildlife Foundation

(www.tawilodge.com), the Big Life Foundation (www.biglife.org), and IFAW, the International Fund for Animal Welfare (www.ifaw.org).

### Example of an ecological corridor

In one specific area, the Kimana Group Ranch, directly east of Amboseli, AWF worked with the landowners and presented a conservation lease agreement in a series of community meetings. Women, youth and men participated in these meetings. They were held in the local language, Kimaasai, with translation as needed into Swahili and English. AWF's community organiser, who was from the Kimana community, was pivotal in organising and facilitating these meetings.

The conservation lease outlines the purpose, terms, land-use restrictions, retained rights, payment requirements, how violations will be addressed, and other relevant issues. The purpose of the conservation lease is to "provide habitat, dispersal and movement areas for wildlife" and to help "connect conservation areas" and "contribute to the survival of wildlife areas in the Amboseli ecosystem as well as the continued existence of ecotourism as a means of poverty reduction and economic development and overall public benefit by ensuring that wildlife species endure for the benefit of future generations."

The conservation lease prohibits building new houses, fencing, logging, mining, dredging, agriculture, resource extraction, non-tourism-related commercial activity, and illegal taking of wildlife. Grazing is permitted in compliance with a management plan. The community selected a Maasai attorney who met with them (in the absence of AWF) to review the lease agreement in its final stage before signing. By having this meeting without AWF, community members were free to voice concerns, and changes were made as a result. AWF paid the fees of the attorney for the community. The extensive community engagement took approximately eight months. AWF determined the value of the lease by doing a market assessment of other leases related to tourism and agriculture in the region. While these leases are not permanent, the hope is that this will be a step toward permanent protection.

### Results

Currently there are five community conservancies involving more than 350 individual landowners that protect approximately 8,000 ha of ecological corridors that connect protected areas. With an average household of seven, the lease program is directly benefitting over 2,450 individuals, and this does not include employment beneficiaries, such as scouts.

One of the challenges with PES programs is sourcing the funds. The protected area authority recognises the importance of the ecological corridors, but is unable to pay; thus, the project relies on donors. Because the land is privately owned and the program entirely voluntary, there are landowners who have chosen not to participate. This has resulted in fragmentation and fencing, putting at risk the long-term viability of the program.

## 2. Connectivity conservation in the Kavango Zambezi Transfrontier Conservation Area: The Zambezi-Chobe Floodplain Wildlife Dispersal Area

Lésa van Rooyen, *Peace Parks Foundation*

### Context and challenge

The Kavango Zambezi (KAZA) Transfrontier Conservation Area (TFCA) is situated in the Kavango and Zambezi river basins where the borders of Angola, Botswana, Namibia, Zambia and Zimbabwe converge (Figure 1). It spans an area of approximately 520,000 km$^2$ and includes 36 proclaimed protected areas. The KAZA TFCA countries support over 200,000 elephants, most of which are found south of the Zambezi River. Due to human activities, the KAZA TFCA faces habitat fragmentation and loss of connectivity. Protected areas could become isolated ecological islands, leading to reduced biodiversity and blocked elephant movement. The major threats to the area are as follows:

- the deforestation of the area to create fields for agriculture and for making charcoal;
- uncontrolled settlements along main roads and watercourses, which cause fragmentation of the landscape;
- overgrazing of the area due to uncontrolled cattle numbers;
- over-exploitation of fish due to unsustainable fishing practices; and
- uncontrolled fires in the Simalaha floodplain wetland ecosystem.

**Key lesson**

Designated wildlife dispersal areas established in collaboration with local communities are a promising step toward legal agreements to maintain connectivity for wildlife.

A key objective of the KAZA TFCA is to form a transboundary ecological network to ensure connectivity between key protected wildlife areas and, where necessary, reconnect isolated wildlife areas.

**Figure 1.** Kavango Zambezi Transfrontier Conservation Area. The major threat to biodiversity in the project area is the over-utilisation of resources in the sensitive wetlands of the Simalaha Floodplain, identified in the centre of the figure. The Kasaya River marks the boundary between the two chiefdoms and flows through the middle of the Simalaha Community Conservancy. © Peace Parks Foundation

**Approach**

The KAZA TFCA commenced in 2006 when a memorandum of understanding was signed by the five partner countries to establish the world's largest transfrontier conservation area. Each of the five countries agreed to create an Integrated Development Plan to indicate how the national development plans will link across borders. The process was also used to create awareness and engage local stakeholders. A Master Integrated Development Plan was created that identifies six transboundary wildlife dispersal areas (WDAs), which are critical to re-establish connectivity and conserve large-scale ecological systems that extend beyond the boundaries of protected areas.

**Example of an ecological corridor**

The Zambezi-Chobe Floodplain WDA contains several sensitive areas, mainly along the rivers and associated floodplains, which are not formally protected. Located centrally in this WDA is the Simalaha floodplain in Zambia, which was identified by the communities as a critically important area that should be secured to ensure connectivity between Chobe National Park in Botswana and Kafue National Park in Zambia. The communities recalled that the area used to be a haven for animals, and mobile species such as elephant and buffalo used to move through the area.

Peace Parks Foundation has worked with the Sesheke and Sekute chiefdoms over the past ten years to establish and develop the Simalaha Community Conservancies (180,000 ha) in collaboration with the local traditional leadership and communities to secure the land for conservation. The Sesheke and Sekute chiefdoms created a steering committee made up of members of the Kutas, the two traditional councils. A working group was established, with representation from the Kutas and Peace Parks Foundation, to coordinate activities such as acting as liaison with communities and developing a land-use plan. Peace Parks was requested to assist with fundraising to implement the project. The first funds received assisted with an awareness and sensitisation programme during which the working group members visited different villages to explain the community conservancy concept. During this time the boundaries of the conservancy were delineated with input from the community. The two chiefs confirmed the boundary by signing a copy of the map, and submitted it to the Ministry of Land for its records.

The Simalaha Community Conservancy is managed on business principles and registered as a legal entity. A local attorney was appointed to assist with the drafting of a constitution and the establishment of an appropriate legal structure. A community trust was created that is the owner of the assets. The trust established a for-profit company that manages the business side of things and also looks after the wildlife management and tourism development. Any profits made by the company are paid to the trust for distribution to the beneficiaries according to a predetermined formula. Seven Village Action Groups were formed to represent the communities. The Simalaha Community Conservancy was officially launched in 2012.

**Results**

From the start, there was general acceptance of the project and great enthusiasm from the traditional leadership. However, because the development of a wildlife product takes time and significant resources, it was important also to create alternative livelihood options. Conservation agriculture was successfully introduced and became the preferred farming method, producing higher yields than traditional methods.

A 24,000-ha wildlife sanctuary was fenced and stocked with plains game species (wildebeest, *Connochaetes* spp.; zebra, *Equus* spp.; defassa waterbuck, *Kobus defassa*; impala, *Aepyceros melampus*; red lechwe, *Kobus leche*; puku, *Kobus vardonii*; giraffe, *Giraffa camelopardalis*; and buffalo, *Syncerus caffer*). Initially, around 780 animals were translocated, a number which increased to over 1,400 animals by the end of 2018.

Twenty village scouts were trained to look after the wildlife. In the five years that wildlife has been in the sanctuary, only one poaching incident was recorded – a person from outside the area set snares. The local community reported the incident, showing that the communities have taken ownership of the wildlife. Although fences initially played an important role in containing the translocated wildlife, the long-term plan is to remove them and allow the wildlife to move freely. Seasonal migration of wildlife is already observed, as wildlife move into the woodlands and higher ground during the flooding period and back to the floodplain along the Zambezi River during the dry winter period.

The story of the Simalaha Community Conservancy spread quickly between traditional leaderships and soon other chiefs visited the area to learn more about the project. Other conservancies are being established as a result. Exchange visits with traditional leaders in Namibia may lead to the expansion of existing conservancies on the Namibian side to ensure a link between Chobe National Park to Simalaha Community Conservancy.

The Zambezi-Chobe Floodplain is, at this stage, not a functional WDA. Once existing community conservancies have been expanded and new ones added, the Zambezi-Chobe Floodplain is expected to start functioning as a WDA. Improved law enforcement capacity in Angola and Zambia along the Kwando river is increasing the numbers of elephants moving into Luengue Luiana National Park in Angola because of the increased safety.

## 3. Conserving six landscapes of the Albertine Rift to ensure connectivity

Andrew J. Plumptre, *Key Biodiversity Areas Secretariat (formerly of Wildlife Conservation Society)*

### Context and challenge

The Albertine Rift region spans six countries (Burundi, Democratic Republic of Congo, Rwanda, Uganda, United Republic of Tanzania, Zambia) and is one of the most biodiverse parts of Africa, with more endemic and threatened species of vertebrates than elsewhere on the continent (Figure 1) (Plumptre et al., 2007). It is also a region with one of the highest human population densities in Africa, and as a result has lost 30% of its natural habitat to agriculture and settlement (Ayebare et al., 2018). While relatively well covered by protected areas, many of them are separated from each other and in danger of becoming isolated islands of natural habitat in a sea of agriculture.

### Approach

In 2000, the MacArthur Foundation financed a collaborative planning approach for the Albertine Rift that brought together the national governments and many conservation organisations to develop a conservation framework plan.

**Key lesson**

Local communities are engaged in connectivity conservation by recognising that designating areas for ecological connectivity will also protect their ancestral lands from new settlers. Recognition of local connectivity areas at the federal and/or global level would help local connectivity conservation.

This overarching framework identified six key landscapes in the Albertine Rift that potentially could be managed at the landscape level to ensure connectivity between protected areas (Figure 1).

Detailed conservation plans were developed for each of the six landscapes. The two transboundary landscapes (the Greater Virunga Landscape and the Congo-Nile Divide) each developed a memorandum of understanding (MOU) for

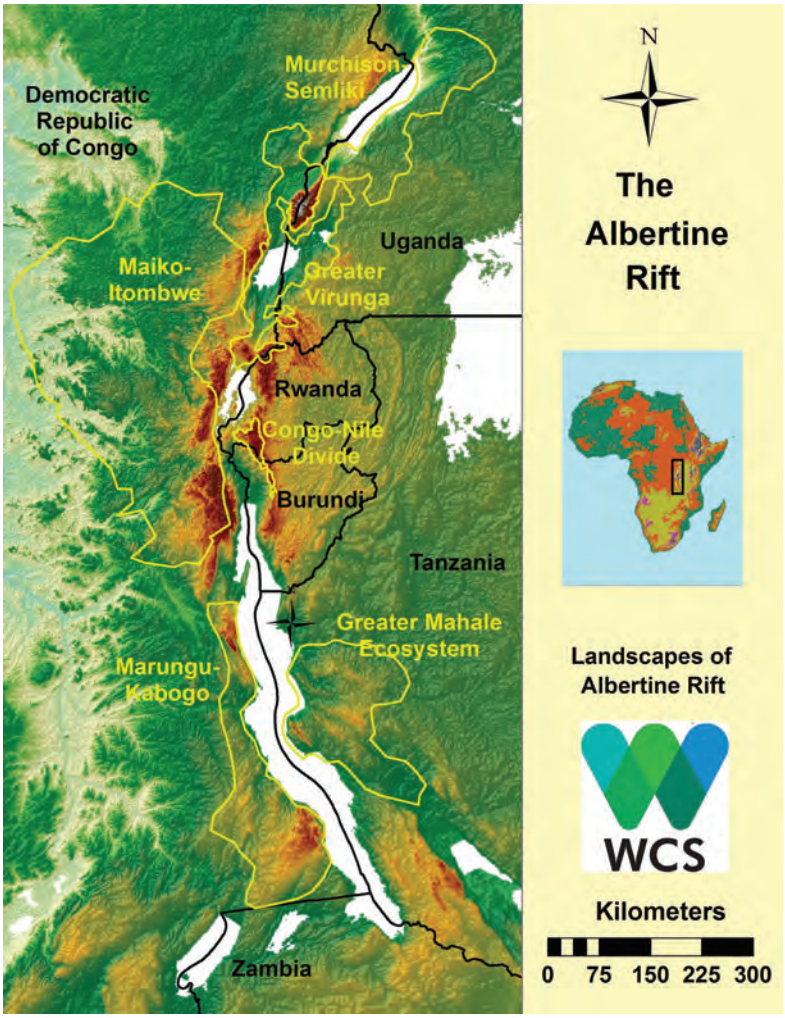


**Figure 1.** The six landscapes of the Albertine Rift © A.J. Plumptre

collaboration. In the Greater Virunga Landscape the MOU evolved into a transboundary treaty for conservation of the landscape. Funds were then raised to implement the plans. In some regions, biodiversity surveys were conducted, and systematic conservation planning was done using distribution models of endemic species in the region. This analysis identified additional critical areas outside the existing ecological networks for conservation in the six landscapes (Plumptre et al., 2017).

**Examples of ecological corridors**

Implementation of connectivity conservation in the Albertine Rift varied greatly. In the Murchison-Semuliki Landscape, a highly populated, fragmented region with many immigrants looking for land, the focus was on conserving remaining ecological corridors (Figure 2). Forest corridors along streams and rivers and a savannah corridor along the escarpment above Lake Albert were protected. In the Maiko-Itombwe Landscape, large areas of contiguous tropical forest still exist. Therefore, the focus was on working with local people to set aside some of the most important areas as protected areas and linking them with ecological corridors in the form of sustainable-use community areas (Figure 3). Local communities were willing to engage in the process because they realised that it would help them protect their ancestral lands from people migrating into the area from outside their culture.

In the two transboundary landscapes the main focus was on the protected areas because most natural habitat outside of them had already been lost. However, landscape-scale conservation and management are still important for species moving long distances, such as lions, elephants, spotted hyenas, leopards, chimpanzees, mountain gorillas and vultures. Ensuring that the existing connectivity between protected areas will not be severed by park developments and tourism infrastructure is important for these species.

**Results**

Since 2000, conservation action plans have been developed for each of the six landscapes and are recognised locally, nationally, and for the transboundary landscapes, internationally. Maintaining or restoring connectivity between existing protected areas has been more successful in some landscapes than others.

Biodiversity surveys in parts of the Democratic Republic of Congo led to the creation of four new protected areas: Itombwe Natural Reserve and Tayna Reserve in the Maiko-Itombwe Landscape, and Kabobo and Ngandja reserves in the Marungu-Kabobo Landscape. They ensure maintenance of connectivity and conservation of endemic and threatened species in these two landscapes. To maintain connectivity, several other community reserves were designated and are

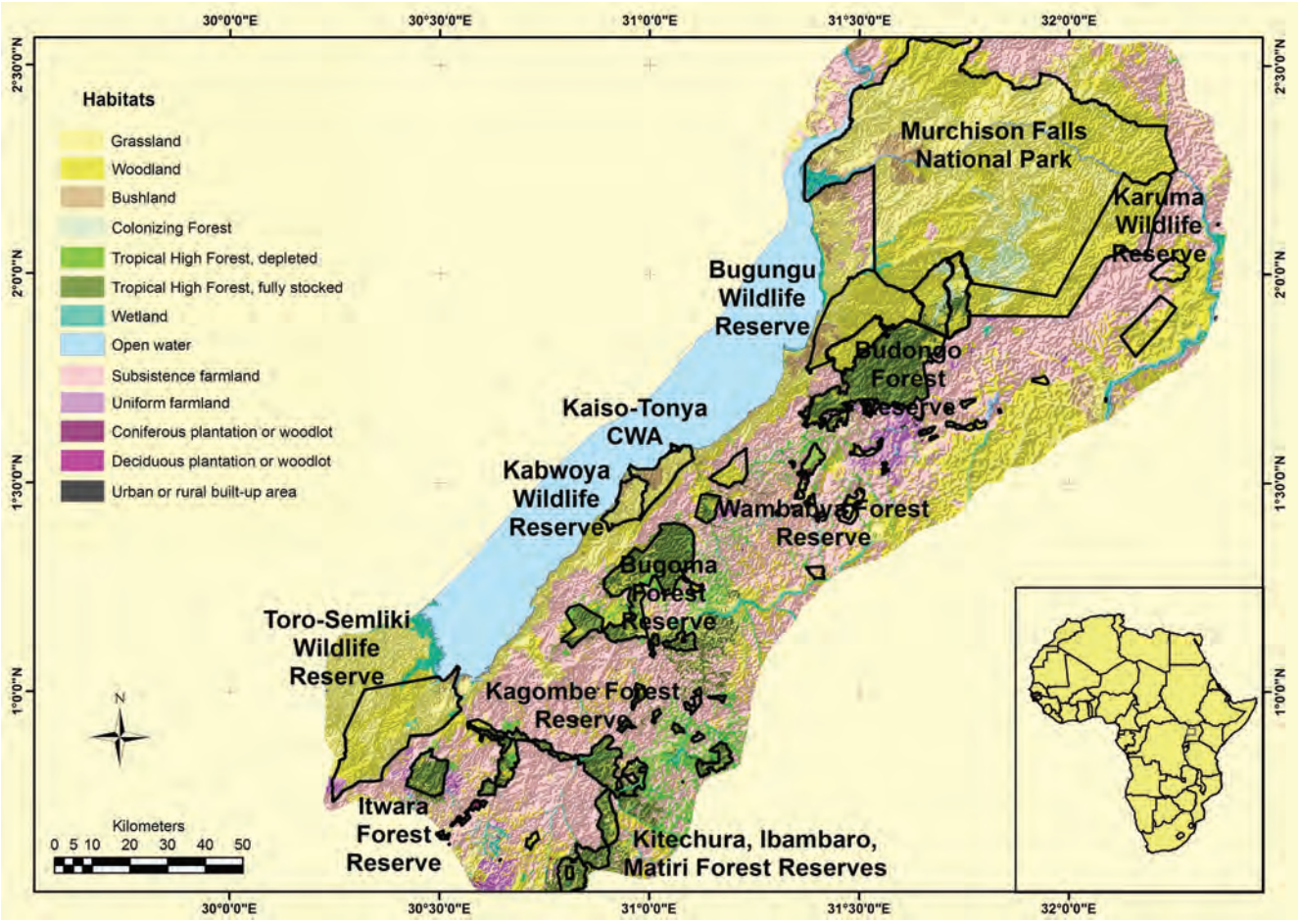


**Figure 2.** The main protected areas and natural habitats in the Murchison-Semuliki Landscape © A.J. Plumptre

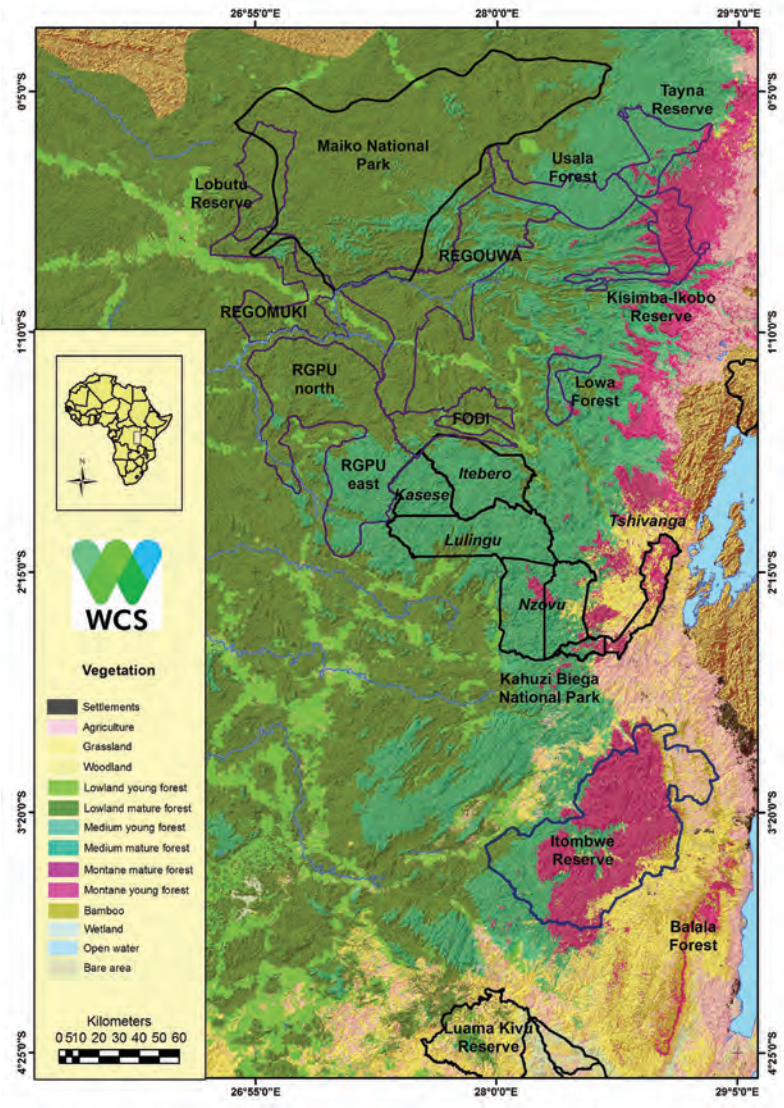


**Figure 3.** The main protected areas (black borders), community reserves (blue borders) and natural habitat in the Maiko-Itombwe Landscape © A.J. Plumptre

locally recognised in the Maiko-Itombwe Landscape, but have not been legally recognised at the national level. In addition, a fifth protected area, Oku Primate Reserve, is being established by local communities in the same landscape to better connect and conserve Grauer's gorilla and elephant populations.

In the Marungo-Kabobo region, efforts were made to establish these two contiguous protected areas, which represent the largest block of forest along Lake Tanganyika.

While connectivity still exists in the Greater Mahale Landscape, a too-narrow focus on chimpanzees is hindering the conservation of several other endemic species, many of which have different habitat and connectivity requirements. There is a need to develop conservation plans that consider the broader biodiversity of this region. However, the recognition of these large landscapes is helping with their longer-term conservation and management. More resources are needed to implement conservation action, but limited resources are being used effectively to maintain connectivity at the landscape scale.

## 4. The Kilombero Valley Ramsar site, United Republic of Tanzania

Giuseppe Daconto, *formerly of the Belgian Development Agency / Tanzanian Ministry of Natural Resources and Tourism*

### Context and challenge

The Kilombero Valley is a floodplain about 220 km long and up to 70 km wide in the Rufiji River catchment in southern Tanzania, sandwiched between the Udzungwa Mountains and the Mahenge Hills (Figure 1). Multiple tributaries converge in the valley, forming the Kilombero River. During the rainy season, water runoff from the steep tributaries rapidly reaches the valley floor and transforms it into a large swamp. The extensive valley used to be a dry-season refuge and offered multiple connectivity routes for wildlife populations moving between the Udzungwa range and the Selous Game Reserve, and thus played a critical role for connectivity at a regional scale in southern Tanzania. The floodplain used to host significant wildlife populations, including elephants and a large number of the near-threatened puku antelope. Starting in the 1990s, the landscape underwent radical change, driven by sustained human immigration and growing settlements, massive expansion of rice farming and livestock grazing, deforestation and development of infrastructure. Rice growing and grazing have drastically reduced the natural wetland habitat. Land-use changes and settlements have almost completely disrupted wildlife connectivity across the valley. Game populations have been decimated (Leemhuis et al., 2017).

**Key lesson**

This Ramsar site requires a framework for conservation that includes ecological corridors to guide efforts by the central government and local stakeholders.

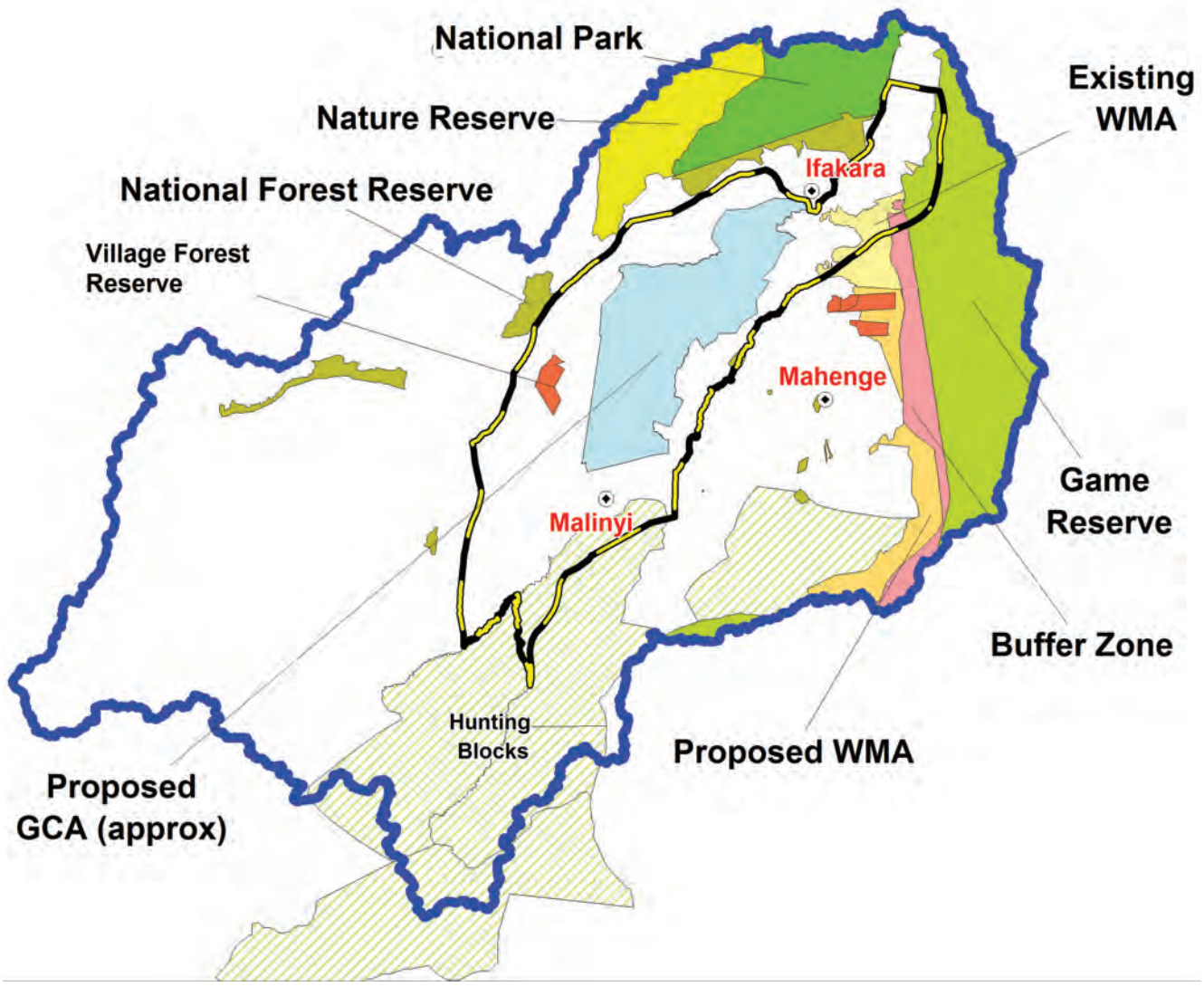


**Figure 1.** Protected areas in the Kilombero catchment (source: plan document). The Ruipa Ecological Corridor connects Udzungwa National Park and Kilombero Nature Reserve to the Selous Game Reserve, crossing the Kilombero Valley south of Ifakara. The black-and-yellow line outlines the Ramsar site.

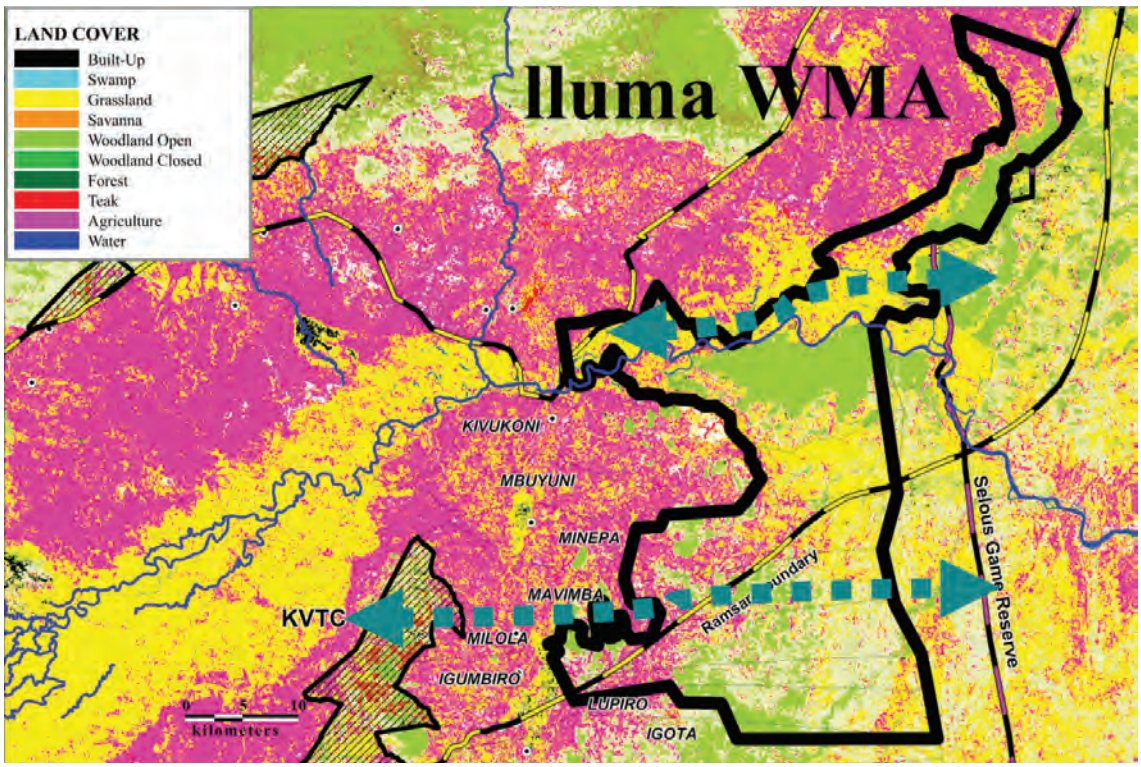


**Figure 2**. Detailed land-use analysis of the Ruipa-East corridor connecting the valley to Selous Game Reserve. Source: Plan documents.

### Approach

The central government has maintained nominal authority over the core area and large tracts of land in the watersheds. The designation of the area as a Ramsar site in 2000 underscored the importance of the landscape. However, social and economic change has been mostly unregulated. Land conflicts abound and are heavily politicised. The management of the landscape, including the conservation of residual wildlife areas, maintenance of connectivity, and the preservation of broader ecological values and functions of the valley requires mediation across several local and national interests. Management of the valley needs to include several sectorial agencies, four district authorities and hundreds of villages, which are the ultimate land management authorities in Tanzania. The governance approach needs to transition from the traditional central management of large protected areas to management of a mosaic of smaller ones embedded in thriving agricultural areas, some under central government, and others under local control. The Integrated Management Plan for the Kilombero Valley Ramsar Site, developed 2016–2018 by the Ministry of Natural Resources and Tourism, is a framework to enable this gradual transition. The preparation of the plan was supported by Belgian Aid and the European Union, through the Kilombero and Lower Rufiji Ecosystem Management Project. Background analysis and planning documents are available from https://kilomberovalley.wordpress.com/.

Maintaining and restoring ecological connectivity will require actions at local, regional and national levels:

1. Consolidation of the core area of the valley (about 2,000 km$^2$) under central government control.
2. Management of development pressure in the agricultural and settlement belt around the core area. The population of this belt is projected to exceed 1 million by about 2040 at the present trend.
3. Consolidation and effective protection of a constellation of small areas across the landscape. Some of these are owned by villages and managed under the devolved statutes of wildlife management areas or village forest reserves; others are hunting concessions, private land leased for forestry and farming, or areas protected by a local government.
4. Protection and rehabilitation of residual natural habitat on farmland along the tributaries to the main river. This requires effective planning and control over village land use and farming practice, which are mostly very weak, and the coordination of land use across multiple villages, which is almost non-existent.
5. Preservation of the hydrological cycle of the river and its seasonal pulse through effective catchment-scale water resource management.

### Example of an ecological corridor

The Ruipa ecological corridor is a link for wildlife moving between Selous Game Reserve in the east and the Udzungwa Mountains in the west (Figure 2). This large-mammal corridor (0.5–6 km wide, 20 km long) crosses a mosaic of habitats, including riverine forest, woodland, scrub, degraded pasture and swamp. Much of the western part of the corridor is degraded but the eastern part still retains limited functionality. Elephants (*Loxodonta* spp.) and buffalo (*Syncerus caffer*) use the corridor annually to migrate between protected areas, although their numbers have declined significantly in recent years. Other animals historically reported

Buffalo (*Syncerus caffer*) © Adobe Stock

from the corridor include the aardvark (*Orycteropus afer*), Angolan black-and-white colobus (*Colobus angolensis*), bushbuck (*Tragelaphus sylvaticus*), crested porcupine (*Hystrix cristata*), Harvey's duiker (*Cephalophus harveyi*), hippopotamus (*Hippopotamus amphibius*), leopard (*Panthera pardus*), lion (*Panthera leo*), puku (*Kobus vardonii*), spotted hyaena (*Crocuta crocuta*), waterbuck (*Kobus ellipsiprymnus*) and the Udzungwa red colobus (*Procolobus gordonorum*), which is endemic to the Udzungwa Mountains. The Ruipa Corridor and several others that cross the Kilombero floodplain have a high conservation significance, as they are perhaps the only viable links remaining between the western and southern Tanzania elephant populations.

**Results**

The plan provides an overall framework for the very complex undertaking of managing this landscape and rehabilitating its ecological connectivity. Extensive appraisals during the plan preparatory process and other works have identified several action priorities. The implementation requires an institutional mechanism able to:

1. Coordinate many local stakeholders and diverging priorities for land and water use;
2. Establish an effective coordination between the government's sectors of land administration, conservation and water resource management;
3. Bridge central government control and effective devolution and decentralisation (mostly through the national framework for community-based natural resource management, but also by ensuring that local authorities receive some minimum budget transfers from the central government); and
4. Negotiate land-use coordination in priority connectivity areas.

A long-term vision anchored in the conservation agencies could in principle underpin a long-term adaptive management process, but a shared vision, financial resources and institutional capacities are not yet available for the implementation of the plan. The plan proposes a key near-term milestone: the mobilisation of financial resources through central and local government budgets to establish an initial mechanism of local coordination. An appraisal showed that this would be financially feasible. This first step would be independent of external support (which eventually will be required), and would therefore promote local ownership and leadership of managing the landscape for ecological connectivity.

Note: Images produced by the KILOREWMP project, funded by the European Union and Belgian Aid and implemented by the Ministry of Natural Resources and Tourism (via the Wildlife Division and the Tanzania Wildlife Management Authority) and the Belgian Development Agency (Enabel) in collaboration with the districts of Ulanga, Kilombero and Malinyi of Morogoro Region and of Rufiji of Coast Region.

# Terrestrial connectivity: Asia

## 5. Ecological corridor for the reunion of giant pandas in the Qinling Landscape

Hui Wan, *formerly of WWF*

### Context and challenge

National Road 108 was built in the 1970s through the Qinling Landscape in central China and over time brought heavy traffic (Figure 1). The road divided an intact forest and caused the fragmentation of previously connected panda habitat. It also gave the local human population access to the forest. Consequent use of wild resources further degraded the habitat. The resident panda population was gradually split in two: the Xinglongling subgroup to the west and the Tianhuashan subgroup to the east.

### Approach

In 2000, a tunnel was built by the government to accommodate a new road. The abandonment of the old road and the re-establishment of habitat on land on top of the tunnel provided the opportunity to reconnect the separated panda groups. In 2003, Shaanxi Guanyinshan Nature Reserve was legally established, and in 2005 the World Wildlife Fund (WWF) together with the reserve launched the G108 Qinling vehicle tunnel corridor restoration project (Figure 2). The main strategic activities in the ecological corridor include:

**Key lesson**

Mitigating fragmentation caused by roads with underground tunnels can be an effective way of restoring connectivity for wildlife; monitoring of the restoration is important to document outcomes.

- Baseline survey and mapping to understand the population status of the panda subgroups, the physical distance between them, the socio-economic condition of local communities, the management capacity of the reserve and the forest tenure in the area.
- Habitat restoration through bamboo plantings in gap plots to improve habitat quality, providing connected habitat and thereby a path for panda movement.
- Local community engagement, including providing support to local households, demonstrations of sustainable forest management and education programs about the significance of habitat conservation.
- Traffic management to enforce the ban on humans and vehicles using the abandoned road.

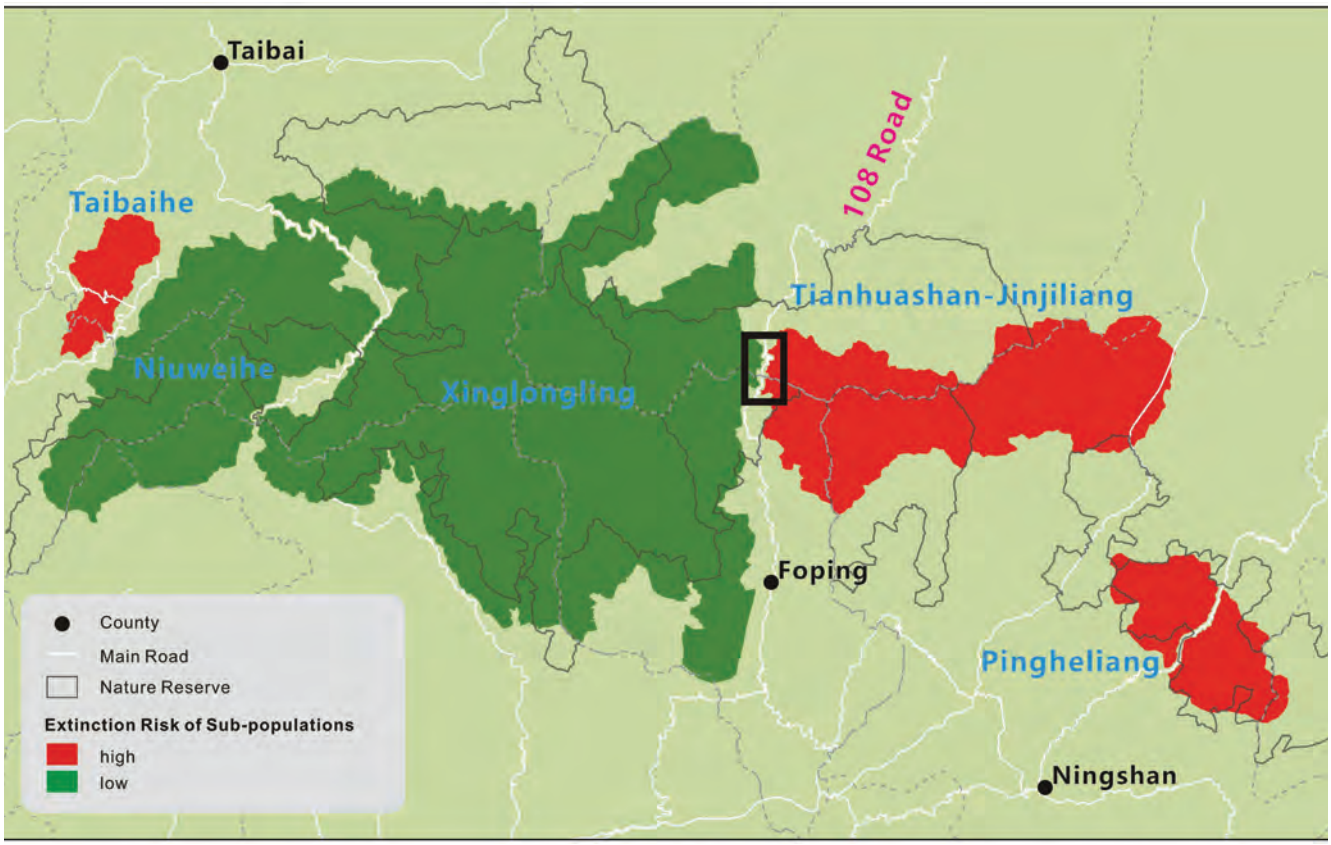


**Figure 1.** Panda subpopulations in the Qinling landscape. National Road 108 is running from north to south. The black rectangle indicates the location of the ecological corridor. © WWF China

- Capacity enhancement to improve the management effectiveness of Guanyinshan Nature Reserve.
- Wildlife monitoring.

**Results**

Giant pandas have been documented in the ecological corridor, which includes land on top of the road tunnel and surrounding lands connecting the core areas. The ecological distance between the subgroups has been reduced and is now shorter than the daily activity range of a panda. The number of mammal and pheasant species found in the corridor area has increased from zero to 15.

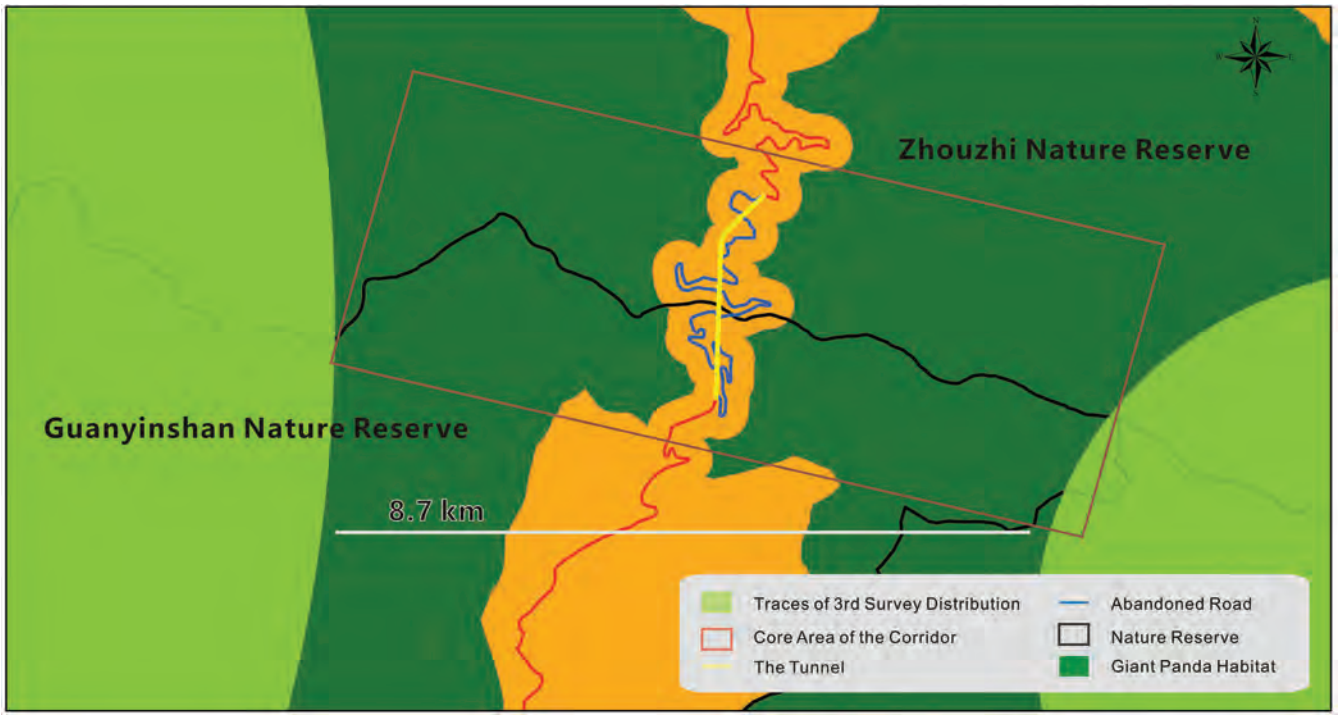


**Figure 2.** The ecological corridor includes the non-protected area on both sides of the road (orange). The corridor is now connecting the habitat of two panda subgroups. © WWF China

Giant panda (*Ailuropoda melanoleuca*) © Adobe Stock

## 6. Thailand's experience in ecologically connecting its protected areas

Songtam Suksawang, *Thailand National Parks Office, Department of National Parks Wildlife and Plant Conservation, Ministry of Natural Resources and Environment*

### Context and challenge

In recent years, Thailand has markedly expanded its protected areas system. The kingdom now has 128 terrestrial national parks, 26 marine national parks, 60 wildlife sanctuaries, and 63 non-hunting areas managed by the Department of National Parks, Wildlife and Plant Conservation (DNP). These protected areas cover about 23% of Thailand's territory, a figure justified by the numerous benefits conservation delivers to the Thai people. Where protected areas are adjacent or close together, they can be managed as ecological networks for conservation, but many of them are smaller areas fragmented by highways, railroads and other infrastructure.

Thailand's protected areas are generally effective at curtailing deforestation within their boundaries (a significant exception being the continued poaching of particularly valuable timber such as rosewood). But continued deforestation and conversion of forests into plantations in areas surrounding many of Thailand's protected areas is making them islands of nature in a sea of agriculture, too small to support all the species that occupied the landscape before it became fragmented.

**Key lesson**

Monitoring and evaluation of identified corridors suggest that some corridors are already working; management of allowable activities in these corridors will be important over the long term.

### Approach

To promote landscape connectivity, DNP has adopted the concept of ecological networks, which are referred to as 'forest complexes'. National parks and wildlife sanctuaries are ecologically linked to form a larger area that will be able to support viable populations of wide-ranging species of plants and animals, as well as contribute to regional social and economic development through provision of ecosystem services. These areas can be connected by ecological

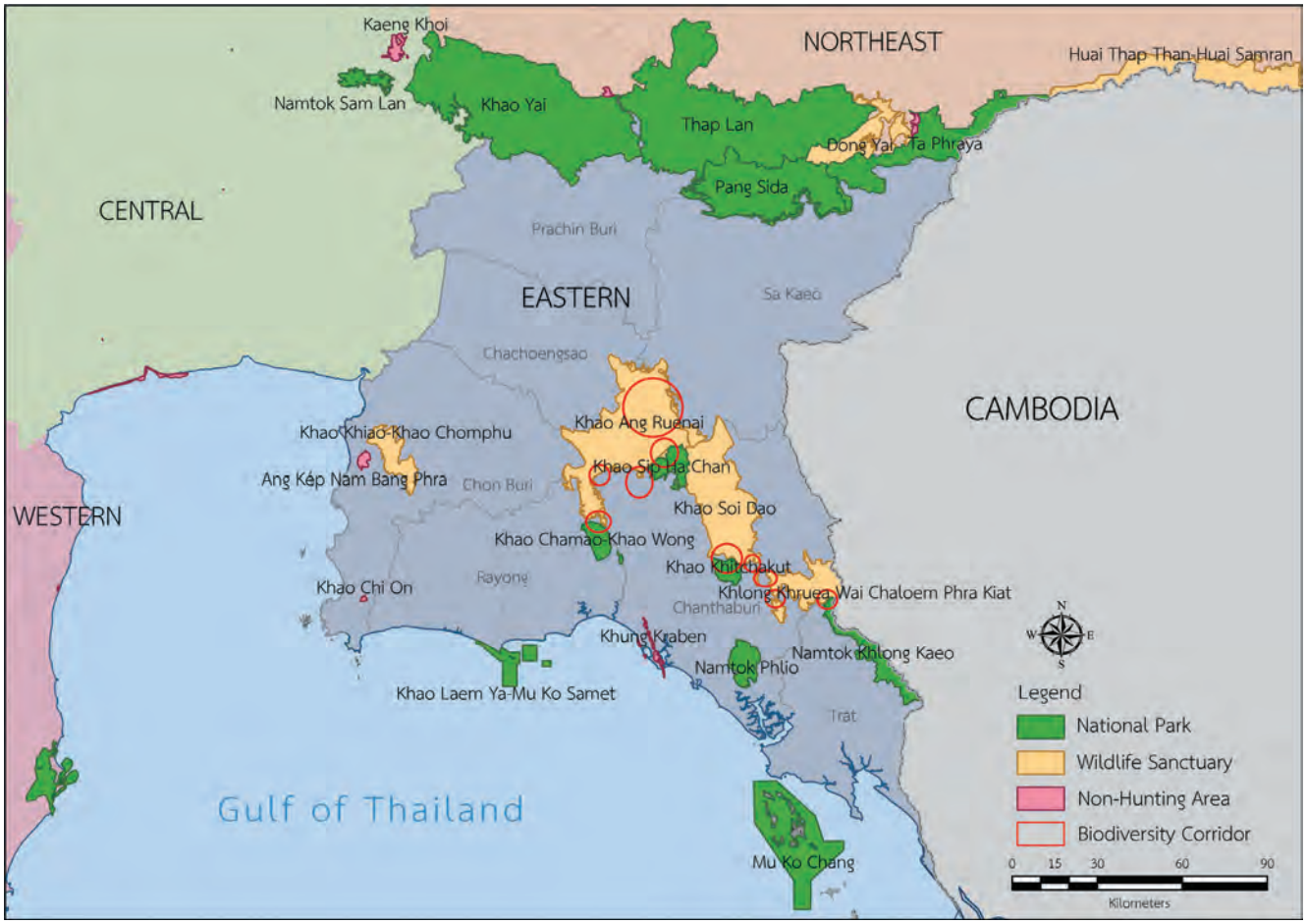


**Figure 1.** Ecological corridors in the Eastern Forest Complex © Songtam Suksawang / Thailand National Parks Office, Department of National Parks Wildlife and Plant Conservation, Ministry of Natural Resources and Environment

corridors that include non-hunting areas, buffer zones, lands managed by government agencies other than DNP and private lands. This approach requires senior protected area staff to consider managing their sites as parts of larger landscapes.

DNP has been learning lessons about ecosystem complexes by establishing pilot activities in selected sites in two complexes: the Eastern Forest Complex (Figure 1, previous page) and the Western Forest Complex (Figure 2). A forum brought together about 50 of Thailand's most experienced protected area managers and other experts on forest

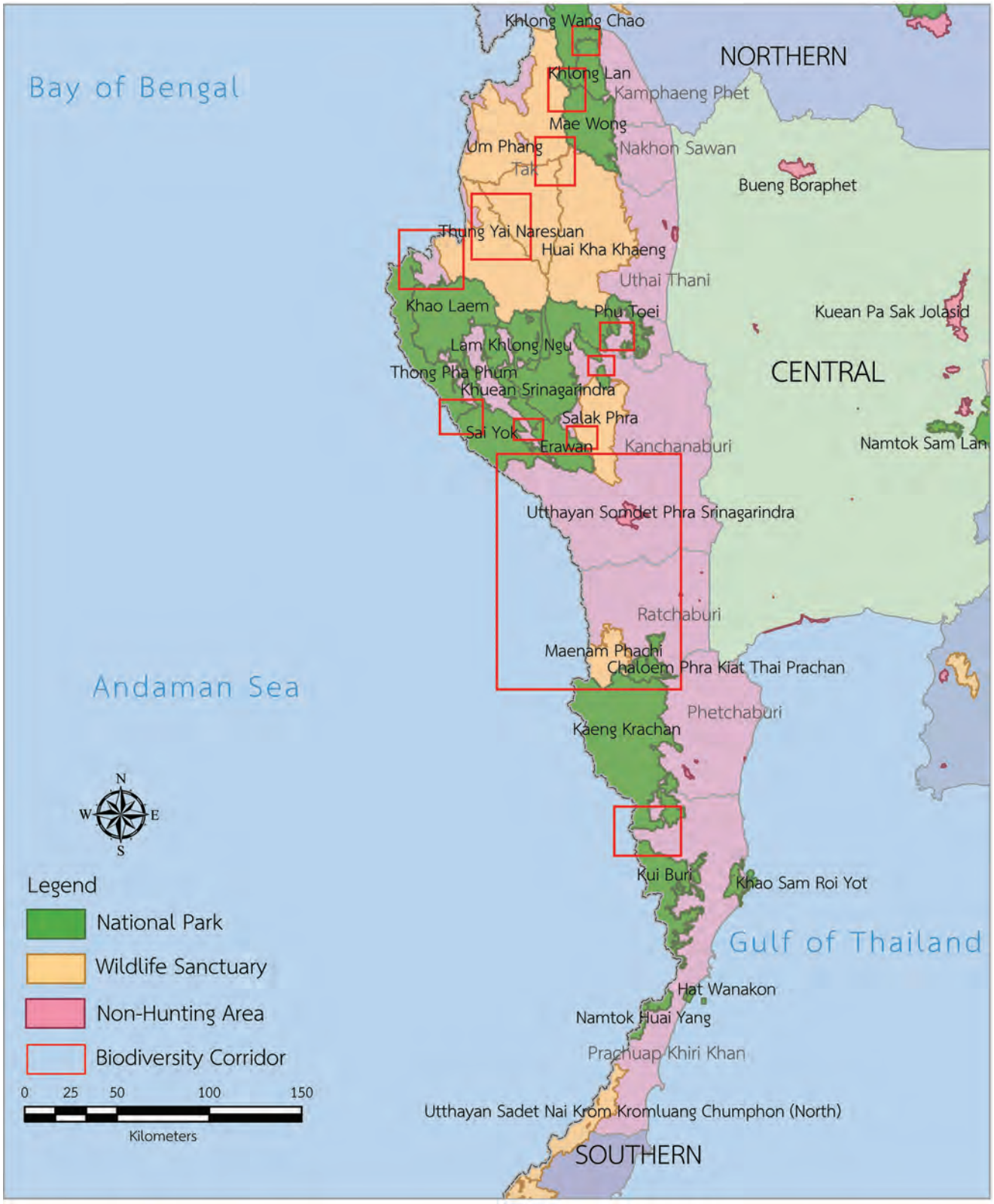


**Figure 2**. Ecological corridors in the Western Forest Complex. © Songtam Suksawang / Thailand National Parks Office, Department of National Parks Wildlife and Plant Conservation, Ministry of Natural Resources and Environment

Khao Ang Rue Nai Wildlife Sanctuary, Thailand © Adobe Stock

complexes to discuss how ecological corridors can connect protected areas, expanding their effective size to enable the movement of plants and animals between them, physically linking habitats and providing an effective means of adapting ecosystems to climate change.

The forest complexes approach is promising but DNP also needs to consider how to manage any potential negative ecological impacts of connectivity. Without proper management, the connecting corridors could facilitate the spread of disease, invasive alien species, forest fires, and other natural hazards. Ecological corridors may also pose some visitor management challenges. For example, it will be important to ensure that visitors who have paid for admission to a national park do not then expect that they necessarily have the right to enter an adjacent, strictly protected wildlife sanctuary that limits visitation (a potential issue in the case of Huay Kha Khaeng Wildlife Sanctuary).

**Examples of ecological corridors**

The Eastern Forest Complex includes eight protected areas (Figure 1). Khao Chamao-Khao Wong National Park (84 km$^2$) is slightly separated from Khao Ang Rue Nai Wildlife Sanctuary (1078 km$^2$), but an ecological corridor has been shown to be feasible; its establishment depends on the owners of the connecting land being convinced to work with the protected areas. Khao Sipha Chan National Park (118 km$^2$) is adjacent to Khao Ang Rue Nai and forms part of a naturally connected ecosystem. Similarly, the relatively small Khao Khitchakut National Park (58 km$^2$) is connected to Khao Soi Dao Wildlife Sanctuary (744 km$^2$), so they also form a natural unit. Klong Krua Wai Wildlife Sanctuary is connected to Namtok Khlong Kaew National Park, making them part of a long and rather narrow natural unit. They share a boundary with Cambodia, and DNP is working on transboundary protected area conservation with Cambodia's Samlout Protected Area (this is being promoted by the Asian Development Bank).

All the protected areas of the Western Forest Complex are ecologically connected and form Thailand's largest contiguous forest ecosystem complex, covering 14,866 km$^2$ (Figure 2). Three national parks (part of Khao Laem National Park, Thong Pha Phum National Park, and Sai Yok National Park) are separated from the other sites in the western complex by a highway and various commercial developments along the highway, posing an ecological barrier that will need mitigations with crossing structures, such as broad overpasses covered with vegetation to enable free movement of large mammals.

**Results**

There is conclusive evidence that tigers, which are well protected in Huay Kha Khaeng Wildlife Sanctuary in the Western Forest Complex, are expanding their population, with "new" tigers dispersing northward to Mae Wong and Klong Lan national parks, where they have become well established. Many other species, including the reintroduced Eld's deer, may also repopulate these national parks from Huay Kha Khaeng, indicating its importance as a source of wildlife for other areas due to the existence of ecological corridors. Local communities have been involved in demarcating boundaries in Mae Wong National Park and have benefitted from multiple-use zones, which can serve as ecological corridors. Communities surrounding Huay Kha Khaeng Wildlife Sanctuary have established community development zones that have been formally recognised as contributing to the objectives of the protected area. More work is clearly needed to develop and implement connectivity conservation in the protected area complexes, but the Eastern and Western forest complexes have shown the practical utility of the approach.

# Terrestrial connectivity: Australia

## 7. East Coast Conservation Corridor in Tasmania

Todd Dudley, *North East Bioregional Network*

**Key lesson**

Finding common interests among many entities and communicating with different types of partners can lead to the ecological restoration of connectivity; long-term efforts, including monitoring, can be ensured through endowments.

### Context and challenge

The East Coast Conservation Corridor (ECCC) is a landscape-scale ecological network for conservation extending 280 km north–south from Cape Portland to Cape Pillar, covering 2½ degrees of latitude on the East Coast and hinterland of Tasmania. The existing protected area system and ongoing conservation projects provide a solid foundation for realising what is known as the 'WildCountry vision' of a protected connected landscape in North East Tasmania (Figure 1). In 2012, noted natural heritage expert Peter Hitchcock stated that "the East Coast connectivity corridors have been assessed collectively to have National Heritage significance – one of the more important latitudinally connected tracts of native habitat in Australia."

While the ECCC still has a high level of landscape connectivity, it is under threat from a variety of impacts, including expansion of intensive agriculture and associated dams, forestry (plantations and native forest), coastal development, invasive plants and feral animals. The challenge is to extend the existing protected area system to limit the extent and impact of threats and to strategically restore areas important for connectivity.

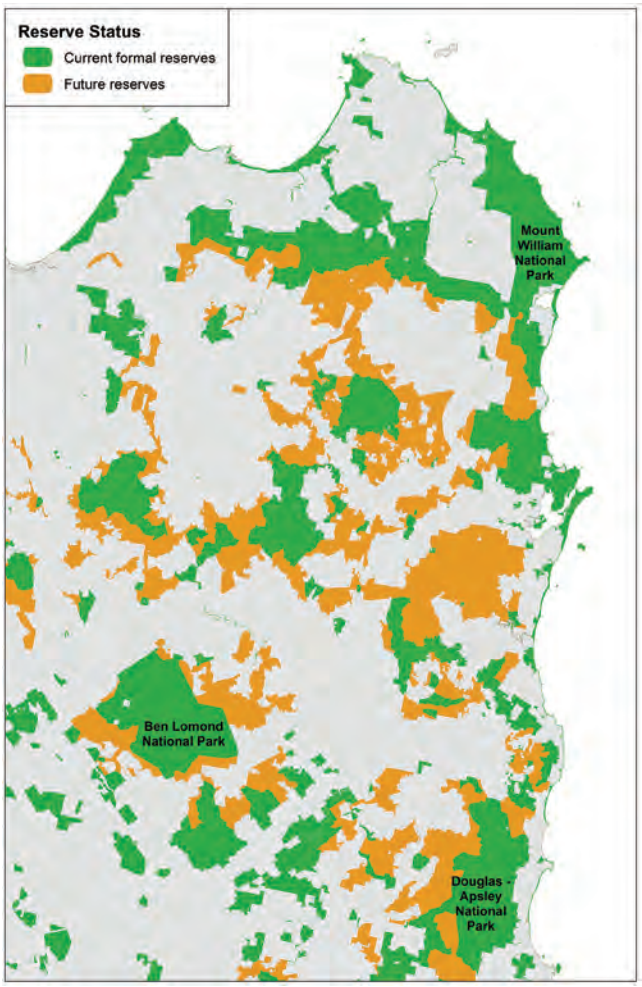


**Figure 1**. Reserves to improve landscape connectivity in North-East Tasmania
© North East Bioregional Network

### Approach

The approach is focused on holistic cross-tenure conservation land management with an emphasis on increasing the extent and improving the condition and landscape connectivity of native vegetation and habitat. Identifying and addressing the physical and ethical causes of ecological decline, such as human population growth, consumption and the ideological support of growth economics in a finite world, is part of the strategy.

The North East Bioregional Network is an entirely voluntary organisation that works with about 45 government entities, communities, companies, private organisations and private landholders on issues where common ground can be found. They are in the process of establishing an endowment fund that will enable a long-term commitment to protect and restore the unique flora, fauna and landscapes of eastern Tasmania.

### Example of an ecological corridor

The Skyline Tier restoration project is returning 2,000 ha of non-native radiata pine plantation back to biodiverse native forest (Figure 2). By re-establishing the native ecosystem, this ecological corridor will reconnect protected coastal and hinterland areas. The land is owned by the government but leased to a private company, and now co-managed by the company and the North East Bioregional Network.

### Results

Activities that have contributed to improved landscape connectivity in the ECCC area since 2005 include:

- Creation of 30 permanent conservation covenants and 60 registrations under the Land-for-Wildlife program on private land.
- Facilitation of the employment and training of over 80 people over the last five years through ecological restoration projects of the North East Bioregional Network, which has had significant ecological, social and

economic benefits and helped consolidate conservation as a highly beneficial activity in remote rural communities.

- Prohibition of new subdivisions within 1 km from the coast in the Break O'Day municipality, thus maintaining an ecological corridor between the coast and hinterland.
- Establishment of a North East Tasmania Land Trust as a non-government organisation to purchase and receive tax-deductible donations of private land for nature conservation.
- Transfer of management of over 100,000 ha of public native forest from the department of Forestry to that of National Parks and Wildlife in North East Tasmania (Figure 1).
- Release of a conservation action plan for the Break O'Day municipality.
- Consideration of connectivity conservation plans in municipal land planning.
- Production of connectivity conservation plans that explicitly seek to protect wildlife corridors and landscape linkages from inappropriate development and are legally binding in municipal planning schemes.

Learn more: www.northeastbioregionalnetwork.org.au

**Figure 2.** Skyline Tier Ecological Restoration Project. (top) A mature radiata pine plantation was harvested, followed by a hot ecological burn. (bottom) Six years later, intensive restoration work helped regenerate native forest. © North East Bioregional Network

## 8. The Great Eastern Ranges: Australia's first continental-scale ecological network for conservation

Ian Pulsford, *Connectivity Conservation and Protected Area Consultant*
Gary Howling, *Great Eastern Ranges Initiative*

### Challenge

Australia is one of 17 mega-diverse nations globally, with 6,794 vertebrate fauna species – including 1,350 endemic terrestrial vertebrate species, the highest number for any nation – as well as 22,000 species of flora. The greatest concentration of this outstanding biodiversity is found along the rugged eastern mountains and coast. This area comprises a substantial part of Conservation International's "Forests of East Australia" global high-biodiversity hotspot. Substantial sections are conserved in an archipelago of embedded protected areas, including three World Heritage areas, as well as lands used for agriculture, mining, urban development, infrastructure and forestry. Clearing and fragmentation of habitat; land degradation; introduced exotic species of plants, animals and pathogens; and climate change are major threats that degrade and fragment this ecological network for conservation.

### Approach

The Great Eastern Ranges (GER) Initiative was established in 2007 with a bold mission to protect, restore and relink habitat to allow nature and people to continue to thrive. The initiative comprises natural lands that extend along the mountainous ranges on the eastern seaboard of Australia for more than 3,600 km from the Grampian Mountains in Victoria, through eastern New South Wales (NSW) and the Australian Capital Territory (ACT), to Cape York in the far north of Queensland (Figure 1). Countless species rely on the Great Eastern Ranges to move and adapt to a climate of extremes. The GER Initiative is an ecological network for conservation that helps people to work together to restore and reconnect nature in areas of high biological importance such as gaps and areas that are fragmented. This work is guided by a vision for the ecosystems of Australia's Great Eastern Ranges to be healthy and connected, which will contribute to the long-term economic, social, cultural and spiritual well-being of the community, and of native plants and animals.

The GER Initiative is one of a very few connectivity conservation initiatives worldwide that have been initiated by government. The initiative began in 2007 with funding from the state of NSW, enabling its Department of Environment, Climate Change and Water to demonstrate a new approach to conservation based on collaborative partnerships. Five 'regional partnerships' were established in five priority connectivity areas. Partners included non-governmental conservation organisations, land care groups, Aboriginal groups, academic institutions, local governments and other government agencies. In 2010, governance devolved to a public–private partnership group of five non-governmental lead partners. Regional groups expanded to ten by 2016. In 2017, governance was transferred to Great Eastern Ranges Ltd. with a board of eight independent directors.

**Key lesson**

A bold mission to protect, restore and relink habitat to allow nature and people to continue to thrive despite changing climatic conditions can lead to engagement of many parts of society and on-ground conservation activities.

**Figure 1.** The Great Eastern Ranges ecological network for conservation forms a 3,600-km arc of mostly interconnected natural lands that extends from the Grampians in Victoria to Cape York in far north Queensland. © Great Eastern Ranges Ltd.

Great Eastern Ranges Ltd. is now a not-for-profit entity that operates as an equal partner in a national network of regional partners in 10 partnership areas in Victoria, NSW, the ACT and Queensland.

**Examples of ecological corridors**

Regional partnership groups consist of public and private organisations and individuals involved in on-ground voluntary conservation activities that come together to collaborate and share resources and capacity (Figure 2). A number of the connectivity partnership areas link north–south along the central mountainous spine and several areas extend east to the coast and west onto the slopes connecting the mountains to the inland. For example, the Slopes to Summit and Kanangra to Wyangala are ecological networks linking alpine and montane forest to the inland. The Kosciuszko2Coast ecological network links the Alps to the east coast. The Victorian Biolinks Alliance works to connect tall-forest landscapes in the central Victorian highlands and the transboundary Border Ranges Alliance works to maintain and improve connectivity of World Heritage-listed rainforests and tall eucalypt forest on the border between NSW and Queensland.

**Results**

From funding provided by the NSW and Australian governments over 10 years, the GER Initiative and partners coordinated voluntary conservation activities through a suite of instruments. These included whole-of-paddock restoration agreements, voluntary conservation agreements, land for wildlife agreements, grants to fence stream banks, tree planting, habitat restoration, feral animal and weed control, community education through community field days, development of a range of communication products including videos and a web site, biological surveys, and research programs.

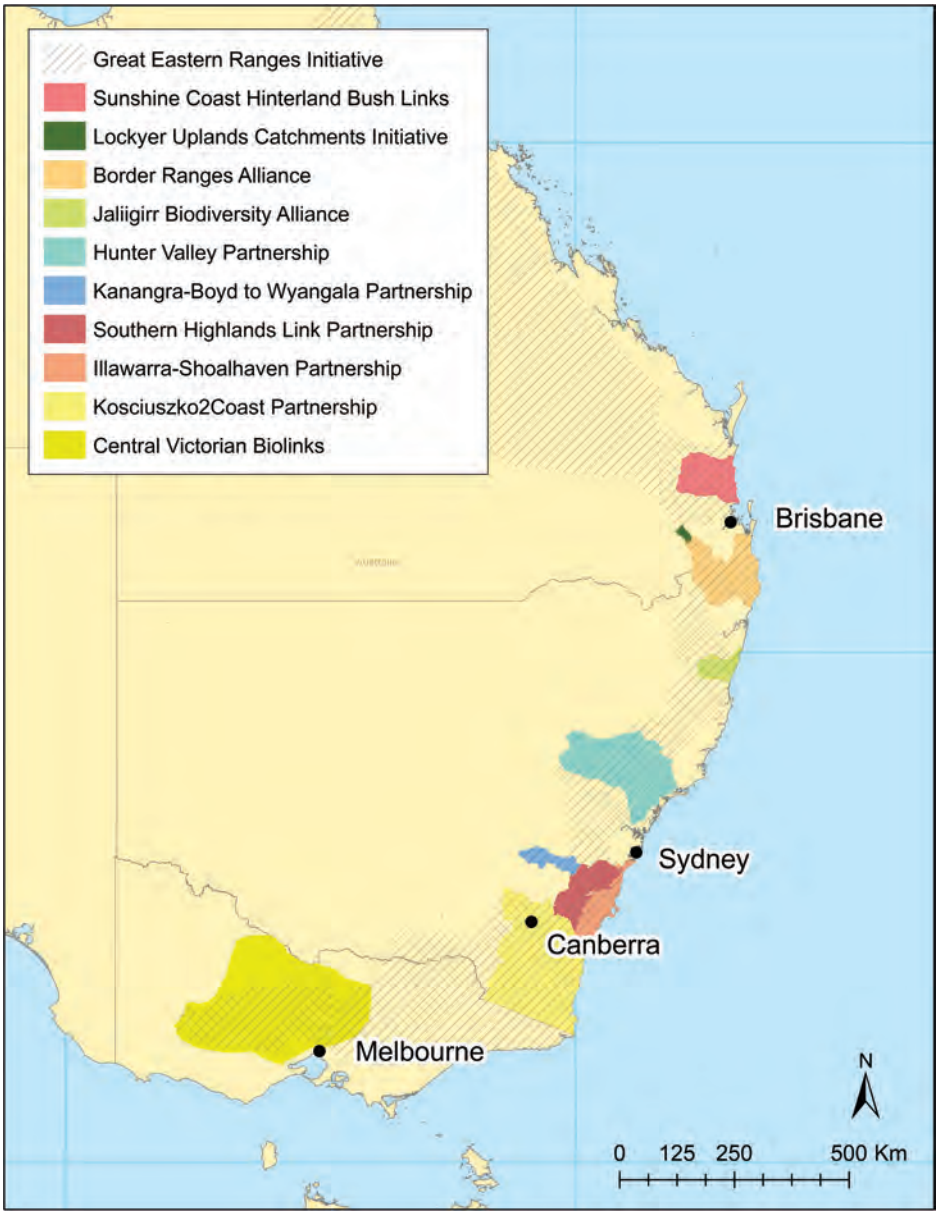


**Figure 2.** Great Eastern Ranges network of regional partnership areas of connectivity conservation © Great Eastern Ranges Ltd.

# Terrestrial connectivity: Europe

## 9. COREHABS to BearConnect: Securing ROAMing in the wilderness corner of Europe

Ancuta Fedorca, *Transilvania University*

### Context and challenge

The Romanian portion of the Carpathian Mountains holds the biggest continuous forest ecosystems in Europe, harbours many well-preserved natural habitats, and is home to large herbivores and carnivores, including brown bear (*Ursus arctos arctos*), wolf (*Canis lupus lupus*) and lynx (*Lynx lynx*) (Figure 1). The mountain range is a biodiversity hotspot situated at the crossroads of several important biogeographic regions. Recent changes in land ownership and rapid infrastructure development (highways, industrial and human settlements, tourist facilities) are threatening the largely intact nature of the Romanian Carpathians. A total of 30.2% of the national territory is covered by forest, including virgin forests and ancient beech forests. While some of the forest is in public ownership, a large proportion is privately owned due to restitution that took place in recent decades. A large number of sites, adding up to 24.46% of the terrestrial national territory, are included in the Natura 2000 network; however, these sites are spatially disconnected.

**Key lesson**

Romanian legislation requires modelling to identify ecological corridors that can help maintain genetic diversity of wildlife and facilitate adaptation to climate change.

### Approach

In 2015, an initiative called COREHABS (Ecological corridors for habitats and species in Romania) brought together six entities (two public universities, one national research institute and three NGOs) to design a national ecological network for ensuring habitat connectivity in tandem with sustainable development. COREHABS is providing corridor modelling as a decision support tool for stakeholders, giving them the opportunity to develop infrastructure while considering the ecological measures necessary to ensure the long-term viability of species and habitats. In 2017, COREHABS combined forces with BearConnect (Functional connectivity

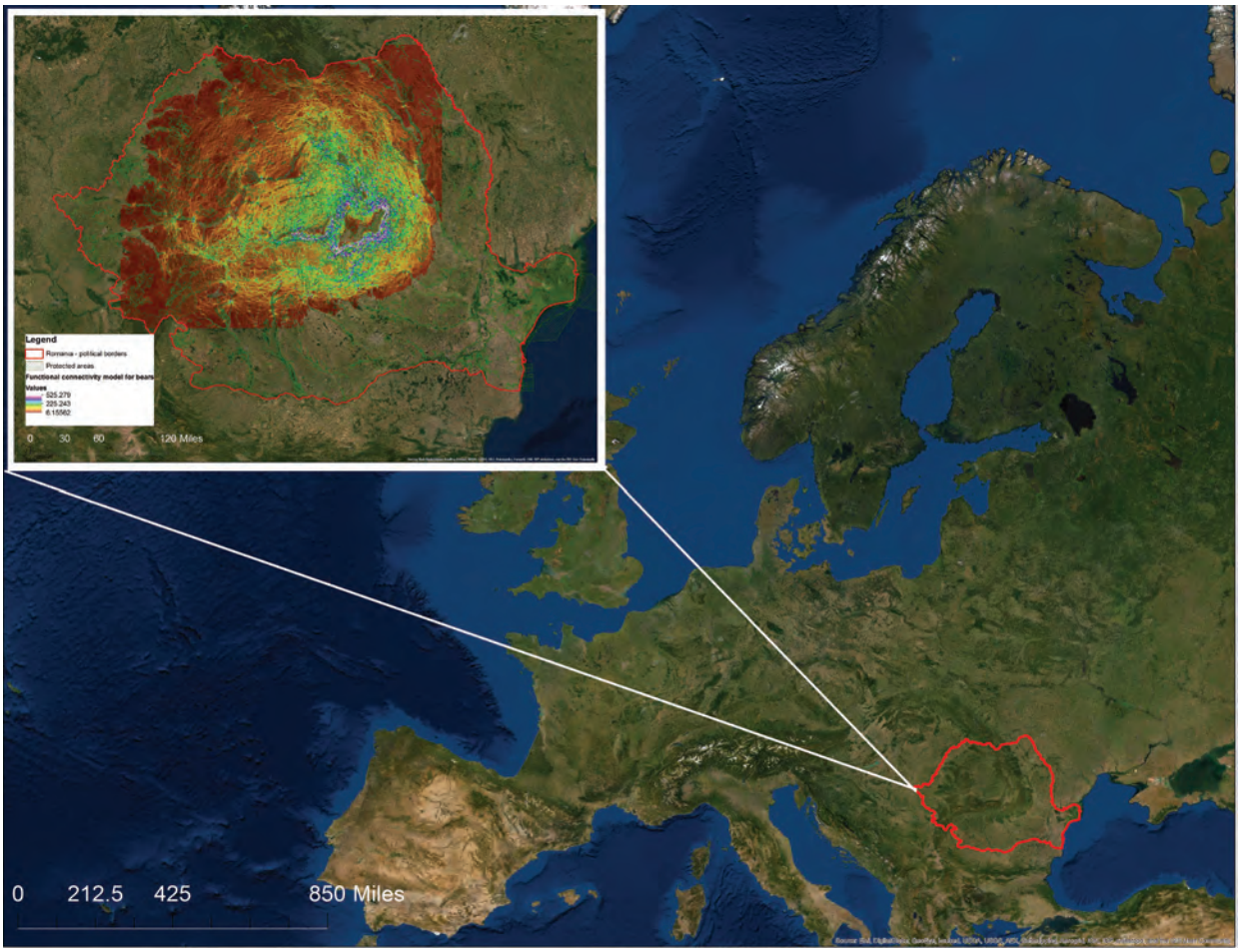


**Figure 1.** The Carpathian mountain range runs in an arc through the centre of Romania. This map shows modelled values for predicted functional connectivity across brown bear habitat, overlaid with protected areas in Romania. © Ancuta Fedorca

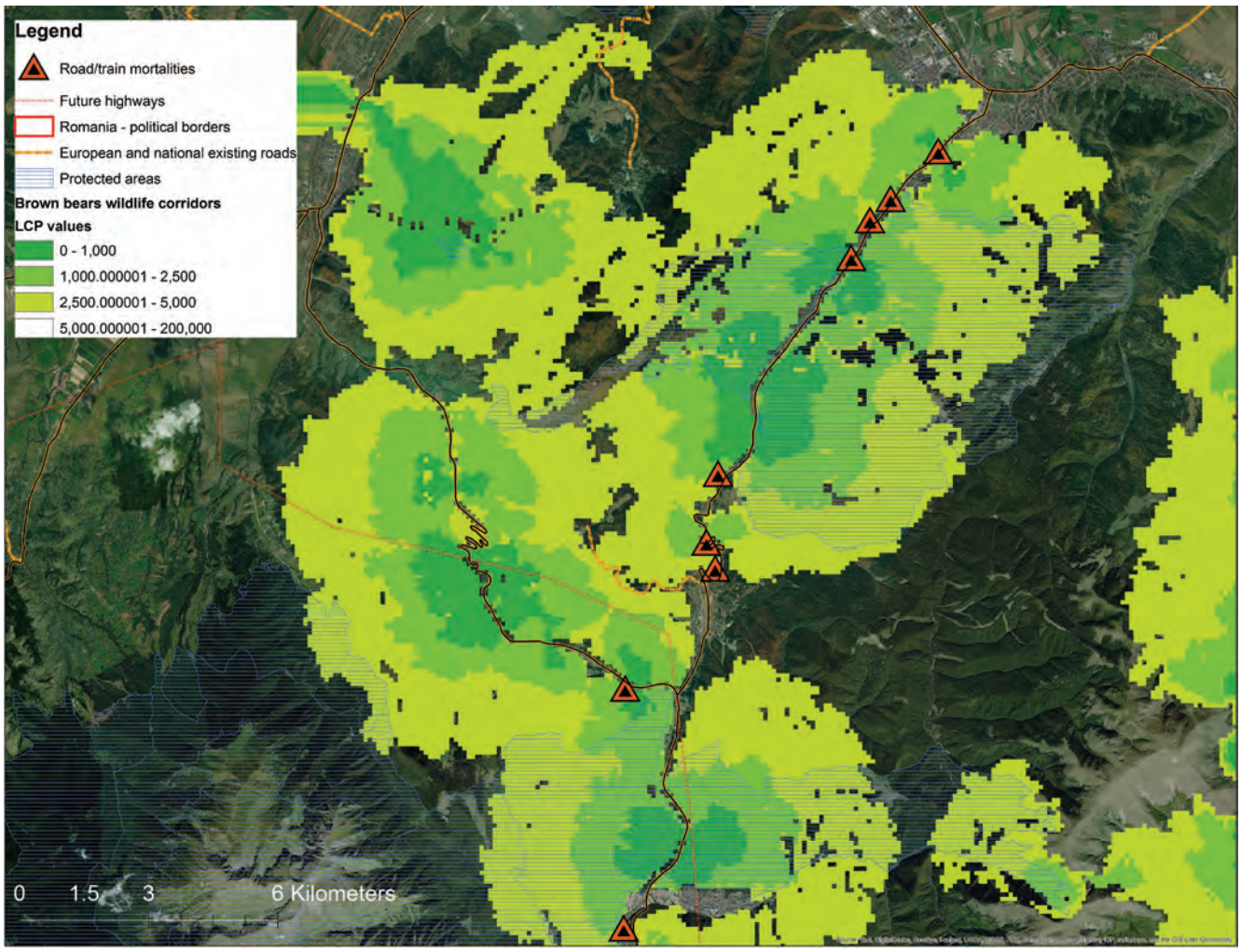


**Figure 2.** The protected areas in blue need to be connected (Bucegi Nature Reserve, Bucegi Natural Park, and Bucegi Protected Area in the north and Piatra Mare Protected Area and Postavaru Protected Area in the south). The shades of green show highest (darkest green) to lowest (lightest green) areas of predicted connectivity to help prioritise where conservation activities should occur. © Ancuta Fedorca

and ecological sustainability of European ecological networks), an organisation focusing on the brown bear. To achieve ecological corridor conservation and facilitate specific ecosystem processes, the organisations are investigating the degree to which existing ecological networks, which include national protected areas and the Natura 2000 network, ensure landscape functional connectivity and ecological sustainability at different scales, and provide practical recommendations for connectivity conservation.

Romanian legislation on ecological corridor designation (GO 57/2007) mandates the protection of connectivity by designating spatially explicit ecological corridors based on field-informed modelling and empirical validation. Ecological corridors are established on the basis of scientific studies and are designated by an order of the head of the Authority for Forest and the Environment after receiving the acceptance of the Romanian Academy of Science. Protected areas and ecological corridors are integrated into national, regional and local rural and urban planning, cadastral plans and land registers by the National Agency for Cadastre and Real Estate Advertising, and noted in the parcel identification system. Partners for implementation include ministries and agencies responsible for natural resources and infrastructure, Transilvania University of Brasov, and the National Institute for Research and Development, local and regional councils, private forest owners and NGOs.

### Examples of ecological corridors

An area of about 10x10 km has been identified as important to connectivity for brown bears between the Bucegi protected areas in the south and the Piatra Mare and Postavaru protected areas in the north (Figure 2). The majority of the land is owned by the state, with small areas being held by the community and private owners.

### Results

COREHABS developed an efficient mechanism for identification and assessment of ecological corridors, and is providing specialists in local planning and implementation of a national ecological network for conservation. Romania is on track to protecting a coherent ecological network of protected areas and ecological corridors, which will allow wildlife populations to interbreed, improving long-term genetic viability and climate change resilience.

## 10. Ecological connectivity in an urban context: Utrechtse Heuvelrug, Netherlands

Rob H.G. Jongman, *Independent Scientist*
Chris Klemann, *Province of Utrecht*

### Context and challenge

Netherlands is a largely urbanised country and nature faces pressures from urban expansion, infrastructure, intensive agriculture and recreation. The Utrecht Hills (Utrechtse Heuvelrug) stretch from north-west to south-east and comprise several important nature reserves and a national park. This area is dissected by several motorways and railroad lines, which were making it nearly impossible for fauna to move through the landscape. However, the area is part of the Netherlands Nature Network. Therefore the province of Utrecht and the responsible nature management agencies, Utrechts Landschap (https://www.utrechtslandschap.nl/) and Goois Natuurreservaat (https://gnr.nl/), were mandated to restore connectivity for wildlife.

'The polluter pays' is a basic principle in environmental policy in Netherlands. Therefore, the owner and manager of transportation infrastructure is responsible for financing and implementing all ecopassages (green bridges and culverts); the funds do not come out of the nature conservation budget. This is the main reason why ecopassages were not implemented in the 1990s. The district's mandate to restore connectivity and lack of actions by the national road authorities (which have an implementation budget) created tensions. Coordination between national and provincial authorities was needed for realising necessary connecting measures for provincial roads for an optimal return on investments.

**Key lesson**

Netherlands offers a model of 'the polluter pays' that helps finance connectivity, such as safe passage across roads, and allows activities compatible with connectivity goals (e.g. recreation) to occur in the corridors.

### Approach

A renewed effort was made to speed up the process of landscape defragmentation through the Netherlands Nature Network, which consists of protected areas and the linkages between them, and a national defragmentation plan that came with extra funds. Both programs were scheduled for implementation from 2004 to 2018.

### Examples of ecological corridors

For the province of Utrecht, priority measures were planned for the Utrecht Hills to improve wildlife movement across national motorways and railroad lines, which is a national responsibility. The province was expected to contribute to the plan by implementing defragmentation measures for the roads under their responsibility.

Accordingly, the province of Utrecht has elaborated plans and actions for the Utrecht Hills (http://www.hartvandeheuvelrug.nl/projecten/ecologische-verbindingen/). The project 'Hart van

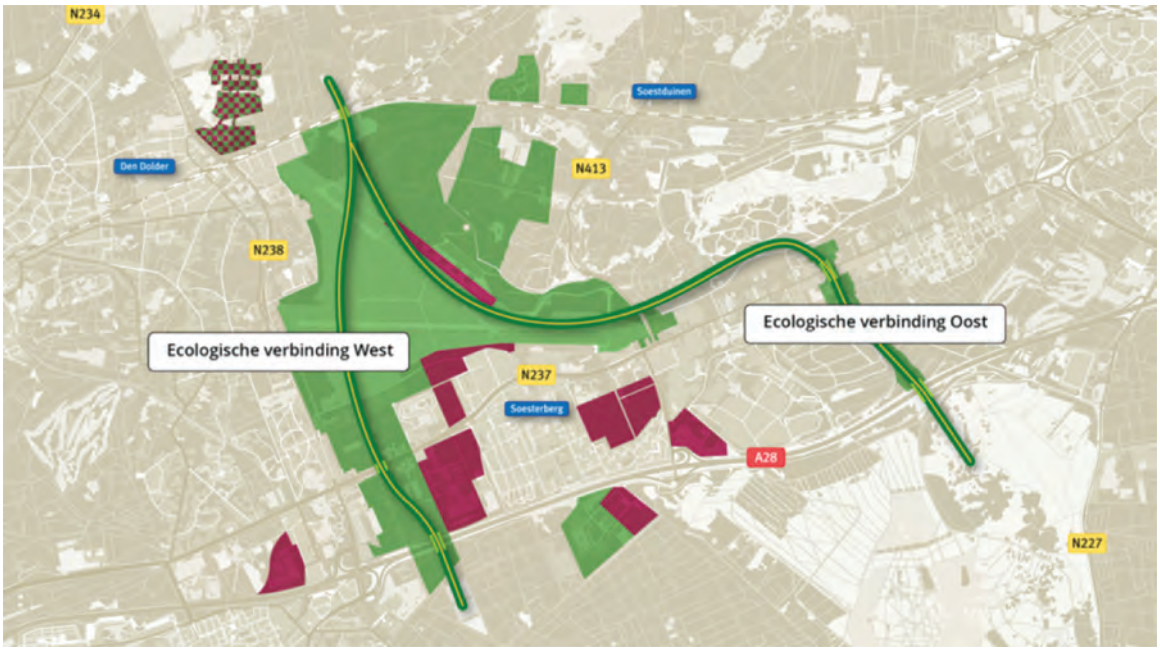


**Figure 1.** The West and East ecological corridors in the Utrecht hills. The numbers indicate motorways (red) and link roads (yellow). The blue names indicate built-up areas; purple: heathland; green: forest. © Provincie Utrecht

**Figure 2.** Ecoduct Op Hees, crossing the Utrecht–Amersfoort rail line. The recreation cycle path is situated at the foreground side of the bridge © ProRail

de Heuvelrug' consists of two main ecological corridors that merge in the north (Figure 1).

The western part of the project area is a forest corridor, with the eastern part a heathland corridor. Both corridors contain many small tunnels that cross under roads (such as a tunnel in the south-east of the province under road N225; https://www.youtube.com/watch?v=hHAn-Clwy8Q&feature=youtu.be). To realise connectivity, an additional five ecoducts have been built in these two ecological corridors, including the Ecoduct Op Hees (Figure 2), which was completed in 2013 and crosses a busy railroad line between the cities of Amersfoort and Utrecht. In addition to facilitating wildlife movements, it also serves as a recreation corridor. For this purpose, the ecoduct has been made wider to accommodate cyclists and pedestrians.

**Results**

The two ecological corridors act as movement routes for mammals (such as roe deer, *Capreolus capreolus*; badger, *Meles meles*; and tree marten, *Martes martes*) and as a temporary living and breeding area for smaller mammal species. Through these ecological corridors, plants and animals can spread and move from Gooimeer (Gooi Lake) in the north-west to the Veluwe National Park in the south-east.

## 11. The Spanish National Network of Drover's Roads (Vías Pecuarias)

Marcos Pradas, *Independent Forest Engineer*

### Context and challenge

The Spanish National Network of Vías Pecuarias is a network of drover's roads (routes traditionally used to drive livestock on foot from one place to another, e.g. to market or to summer pastures) and additional elements used for transhumance and smaller cattle movements (Figure 1). They criss-cross Spain some 125,000 km in length and covering an area of 400,000 ha, linking a wide variety of protected, unprotected and urban areas. They hark back to prehistory, having been first documented in Roman times and legally protected by decrees issued in AD 654, 1273 and 1995. The Mediterranean region is a biodiversity hotspot where humans are such an integral part of the environment that rural exodus and disappearance of traditional uses are regarded as two of the major ecological threats to the Iberian Peninsula.

Droves are not just trodden and dusty ways, but are open or wooded pastures with a trail in the middle. They often contain trees, hedgerows, dry-stone walls, ponds, wells and watering holes. They can be very biodiverse, many times more so than their surroundings. In addition, they are important for the protection of many ancient breeds of farm animals, many of which are in danger of extinction. They serve as ecological corridors in different ways. Cattle and sheep spread organisms along them. It is estimated that herds of 1,000 sheep or 100 cows spread 3 to 5 million seeds and some 3 tons of dung on a daily basis, thus contributing to species range shifts, a useful adaptation to climate change (Manzano & Malo, 2006). Drover's roads cross protected, conserved and unprotected areas, including urban areas, and

**Key lesson**

A transportation network originally established for moving livestock can provide ecological connectivity among protected areas, especially when restored for that function.

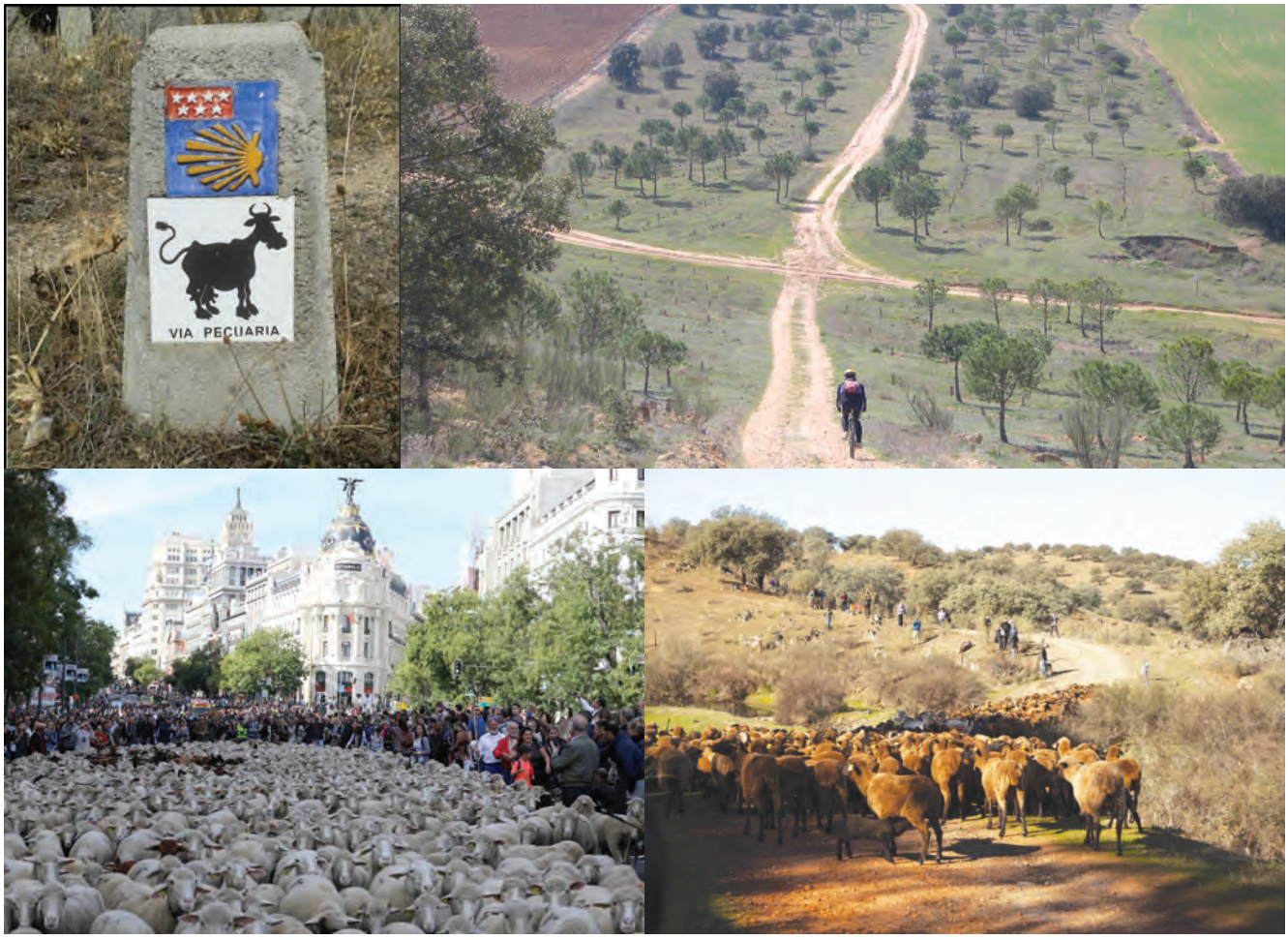


**Figure 1**. Scenes from drover's roads in Spain.
(upper left) A standard marker (courtesy of Juan Díaz Hidalgo)
(upper right) The Droveway of Salamanca, illustrating its multifunctionality and value as an ecological corridor © Federico Sanz
(lower left) The Fiesta de la Transhumancia in Madrid (courtesy of Diario de Madrid)
(lower right) A road important for four local domestic animal races: the white and black Merina sheep, Verata goat, and Andalusian donkey, which is the oldest donkey breed of Europe and now classified as being in critical danger of extinction © Agustín Pérez, la Siberia Extremeña Biosphere Reserve

are vital for connecting the Natura 2000 network of protected areas. They are particularly important for promoting functional connectivity between isolated grasslands. Because they are linear structures in the landscape, migrating species, including birds, follow them and also use them to rest, drink and feed.

The ecological significance of drover's roads, including their role as ecological corridors, is now being fully acknowledged, and the necessity to protect them has been recognised under Article 8 of the Convention for Biological Diversity, the Sustainable Development Goals, and covenants such as the United Nations Convention to Combat Desertification and the United Nations Framework Convention on Climate Change, among others. The main threat to drover's roads is the decline of extensive livestock farming and transhumance. Other threats include the lack of a true strategy for conservation, reluctance of the government to protect the Vías, illegal settlements, dumping, fencing, resource extraction, pesticides and capping of wells. Many drove ways are now irretrievably occupied and their status as public domain has been or is in the process of being revoked.

### Approach

State law 'Ley 3/1995, de 23 de marzo, de Vías Pecuarias' specifies that drover's roads are in the public domain, are unseizable, inalienable and imprescriptible. The law protects an important ecological corridor, and obliges governments to demarcate them. Numerous individuals, agencies, associations, universities, NGOs and working groups are exploring different ways to protect, recover, and foster the droves and bring them to the attention of a wider sector of society. They work toward restoring and fostering extensive livestock farming, attracting young people to transhumance and cattle farming, and rapidly finishing the demarcation of all drove ways. Other actions include pressing governments to enforce the laws; fully exploiting the multifunctionality (livestock transport, ecosystem services, biodiversity conservation, recreation, etc.) of the Vías Pecuarias; and reaching out to a wider sector of society.

### Example of an ecological corridor

In Spain, the network of drover's roads is densest in the Autonomous Community of Madrid (Figure 2). Many actions are being taken to protect them. For instance, ecological functionality of the Real Cañada Segoviana (Royal Segovian Droveway) is being improved by the Repsol Foundation and Reforesta through reforestation with native species, fencing of endangered plants, restoration of ponds and creation of new ones, establishment and fencing of refugia for different animal species, habitat improvement for insects, environmental education and monitoring.

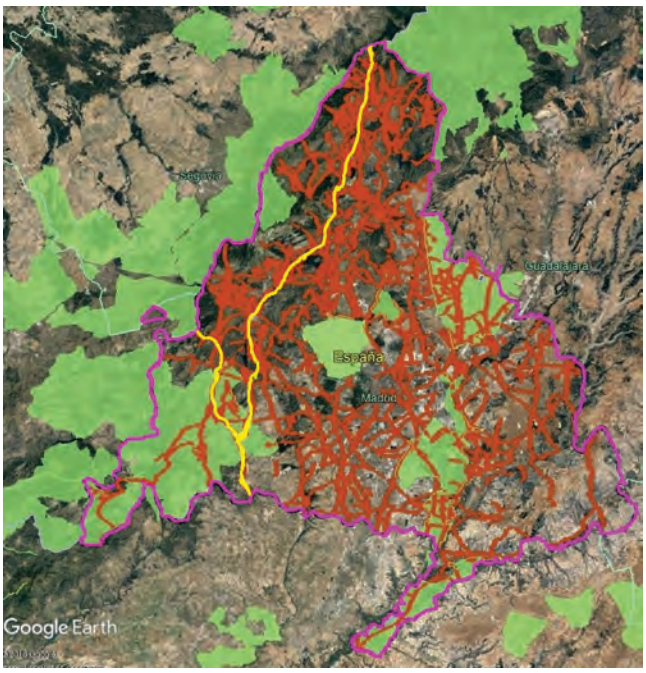


**Figure 2.** Vías pecuarias of the Autonomous Community of Madrid superimposed on protected areas. Note how they link rural, urban, protected and unprotected areas. In yellow, the Cañada Real Segoviana. Droves outside the Autonomous Community are not depicted. © Marcos Pradas, Spanish Instituto Geográfico Nacional and the Community of Madrid; Base data courtesy of Google Earth

### Results

Governments tend to be ambivalent about the issue. On the one hand, of 125,000 km of droves, 40,000 km may already be lost. Governments often permit a change of use of these roads. When their utility for cattle is lost, they decree by law the land-use change and take them out of the public domain. The Autonomous Community of Madrid is no exception and may have lost around 38% of its drover's roads over the past 20 years. One example is the Cañada de Madrid: a linear city was built illegally along 14.2 km of the Galiana's Royal Droveway. On the other hand, many governments are demarcating drover's roads, educating the public, and taking action in the field to protect them and maximise their ecosystem services. In a world that urgently presses to reduce the environmental impacts of meat consumption, a new generation of transhumance practitioners offers the responsible consumer the opportunity to eat animal products that have a positive ecological footprint. Protecting Spain's drover's roads will support this market and, in addition, allow these ecological corridors to continue to deliver their much-needed ecosystem services.

Learn more:
http://www.pastos.es/
https://www.viaspecuariasdemadrid.org/
http://transhumancia.cat/es/inicio/
http://trashumanciadehoy.emiweb.es/paginas/cartografia-y-conocimiento-de-los-caminos.html

## 12. ECONET: Ecological network in the Kostroma Region, Russia

Alexander V. Khoroshev, *Lomonosov Moscow State University*

### Context and challenge

Recent undesirable changes to the landscape of the Kostroma region in central European Russia revealed the need for a strong ecological network for conservation. The region is located in the watershed divide between the Caspian and the White seas. Here, Siberian species transition to European species, and taiga is replaced by broad-leaved forest. Landscape diversity is highest where depressions among morainic hills are combined with post-glacial lakes, fens, bogs, and old-growth and secondary forests that control water runoff and ensure valuable wetland habitats. In recent decades, vast forest areas decreased considerably due to timber harvesting. This harvesting expanded to remote catchment areas, which caused a decrease of runoff volume, loss of opportunities for navigation on rivers, and the degradation of fish resources, all with obvious negative economic consequences for local people. This resulted in the need to preserve the remnants of virgin southern taiga stands within an ecological network.

**Key lesson**

Ecological corridors that encompass riparian and forested corridors can have multiple benefits such as decreasing erosion and improving water quality.

### Approach

The mission of the Kostroma ECONET project, launched in 2003 with strong support of the regional government, was to ensure the protection and connectivity of the most ecologically valuable landscapes as well as to facilitate restoration of lost traditional economic opportunities for local people. The Kostroma ECONET project is based on the idea of critical significance of a connected landscape.

The core areas of the ecological network for conservation are composed of four types of landscapes: (1) intact landscapes representative of the European southern taiga, such as moraine plains with spruce and fir forests (e.g. Kologriv Forest Nature Reserve); (2) fluvioglacial terraces with pine forests, and mires; (3) rare and unique landscapes (e.g. larch forests on sandy terraces); and (4) landscapes with key habitats for migratory birds and mammals (e.g. floodplains used by geese on their spring migration from western Europe to northern Siberia). The full range of typical interfluvial and river valley landscapes is represented in the network (Figure 1), with a higher concentration of protected areas in the upper parts of the river basins that have a higher proportion of mires close to watershed divides. The legal regime of the ECONET prohibits clearcutting in key locations to ensure runoff formation in the interfluves and safeguards the necessary proportion of forests

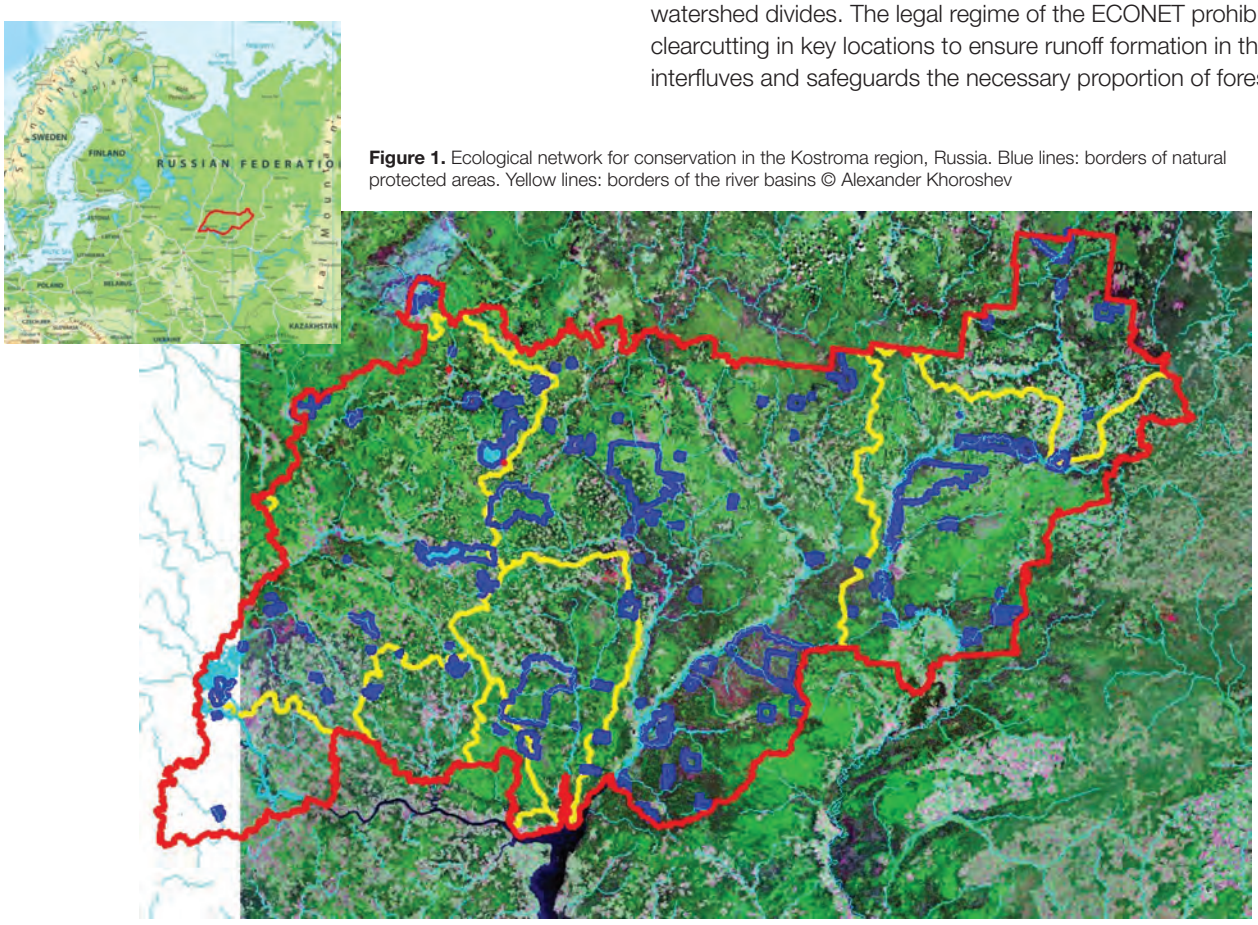


**Figure 1.** Ecological network for conservation in the Kostroma region, Russia. Blue lines: borders of natural protected areas. Yellow lines: borders of the river basins © Alexander Khoroshev

Kostroma Taiga, Russia © Adobe Stock

in a given basin. The process of planning protected areas included intensive consultations with local stakeholders.

**Example of an ecological corridor**

The protected areas are connected by ecological corridors consisting either of riparian forests or of zonal coniferous forests embedded in a matrix of timber harvesting areas. The ecological network recognises the crucial contribution of the regional landscapes to the functioning of the larger watershed, the Volga River basin, because the three largest tributaries in its upper reaches come from the Kostroma region. The ecological corridors comprise hydrologically important zones along the slopes of river valleys, terraces and floodplains. Thus, in addition to connecting core protected areas, the ecological corridors decrease erosion, water eutrophication and undesirable surface runoff.

**Results**

A scheme to develop an ecological network for conservation was adopted by the regional authorities in 2008. Fifty-nine protected areas are being established, with reasonable limitations on timber harvesting, human development, and, if necessary, hunting and fishing embedded in land-use plans. The scheme is now an obligatory part of territorial planning at both the regional and municipal levels.

The experience of the Kologriv Forest Nature Reserve provided evidence that prohibiting hunting in rather small areas can result in an increase of game species populations, their expansion to the adjacent non-protected landscapes and, therefore, an increase in game resources. Some of the established protected areas successfully combine nature protection, recreation and ecological tourism. This is of particular importance to communities in Kostroma's remote districts who struggle with insufficient sources of income. The most serious current challenge to the ECONET project is the delayed designation of protected area borders by state authorities, which results in conflicts with the timber industry and agricultural producers.

# Terrestrial connectivity: North and South America

## 13. Sustaining forested landscape connections in the northern Appalachians: The Staying Connected Initiative

Jessica Levine, *The Nature Conservancy*

### Context and challenge

The 32 million-ha Northern Appalachian–Acadian ecoregion – which includes parts of five US states and three Canadian provinces – contains the largest expanse of temperate broadleaf forest remaining in the world. Protected areas within the region include a national forest, state and provincial parks, national parks and conservation easements. Yet these tracts are nested within a matrix of rural development and human uses. The region is only a half-day's drive from several major urban centres, including New York, Boston and Montreal, and is increasingly in danger of fragmentation from roads and other human development. In 2009, public agencies and private organisations from across the bi-national region formed the Staying Connected Initiative (SCI) to address this challenge.

**Key lesson**

In the United States, conservation easements are an important tool to permanently secure connectivity.

### Approach

The SCI is a partnership of over 55 organisations, including natural resource and transportation departments from the US states and Canadian provinces of the region, conservation organisations and universities. Partners actively collaborate to maintain, enhance and restore landscape connectivity across this large region. On-the-ground efforts are focused on ensuring landscape permeability, today and into the future as the climate changes, in nine highest-priority linkage areas (Figure 1). In these, partners apply a combination of strategies to conserve connectivity, recognising that no single strategy is sufficient and that partners have different areas of influence and expertise. Primary strategies include:

- Strategic land protection of priority parcels for connectivity such as forested pathways and riparian corridors;

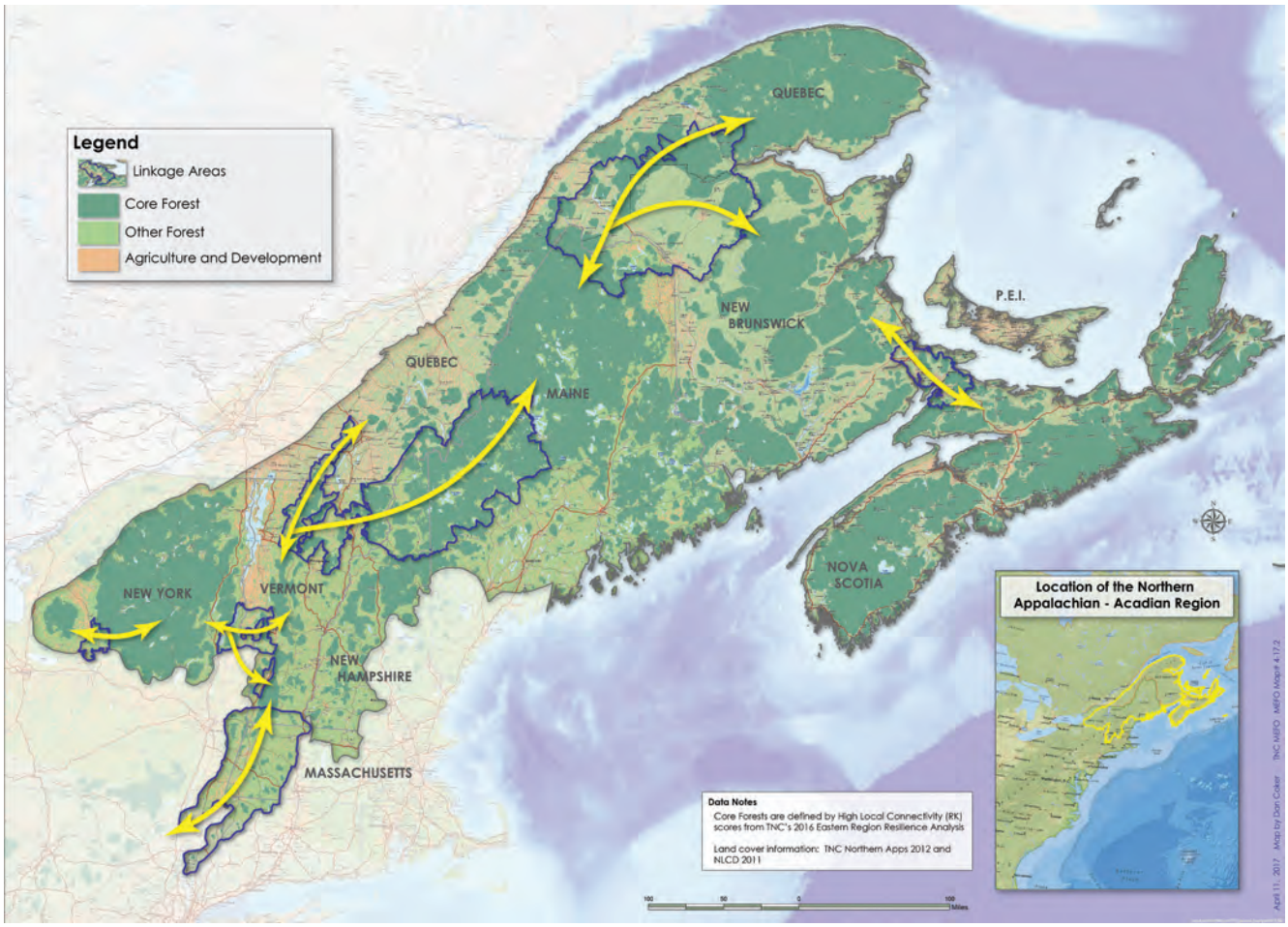


**Figure 1.** Staying Connected Initiative region and linkage areas © The Nature Conservancy

- Land-use planning to steer development away from critical connectivity areas;
- Community outreach and engagement to build awareness and appreciation among private landowners and encourage private land management to maintain landscape permeability;
- Habitat restoration in key locations such as wetlands and roadside parcels; and
- Facilitation of the movement of wildlife under roads by means of improved bridges and culverts, signage and fencing.

At the regional scale, partners share best practices and lessons learnt through webinars, meetings and written communications.

**Example of an ecological corridor**

The Northern Green Mountain linkage area encompasses 2,923 km$^2$ and is centred on the spine of the Green Mountains. The linkage area stretches from Mt. Mansfield State Forest, which contains Vermont's highest peak, north to Mont Orford National Park in Quebec. Most of the area is forested, with agriculture and small towns and villages in the many valleys that bisect the mountain spine. Within this linkage area, Jackson Valley is an important ecological corridor along the US–Canada border (Figure 2). A 2010 study of the 379-ha parcel found that it served as a key trans-border ecological corridor for a range of animals. Jackson Valley links conserved Atlas Timberlands to the south, Jay State Forest to the east, and a 652-ha preserve in Quebec, protected by Nature Conservancy of Canada, to the north. In 2012, with funding from the US Forest Legacy Program, The Trust for Public Land completed years of work to conserve Jackson Valley. A conservation easement, held by the state of Vermont, prevents development and subdivision in the ecological corridor and requires sustainable management for wildlife, timber, public recreation and soil conservation. The corridor is open to hikers and skiers, and for other forms of non-motorised recreation.

Conservation of this parcel as an ecological corridor is leveraged by the work of many SCI partners on both sides of the border. This work includes land protection in other parts of the linkage (over 12,140 ha to date), technical assistance to municipalities on land-use planning to steer development away from critical ecological corridors, scientific studies along major roadways to identify potential sites for wildlife mitigation measures, and outreach to private landowners on sustainable forest management.

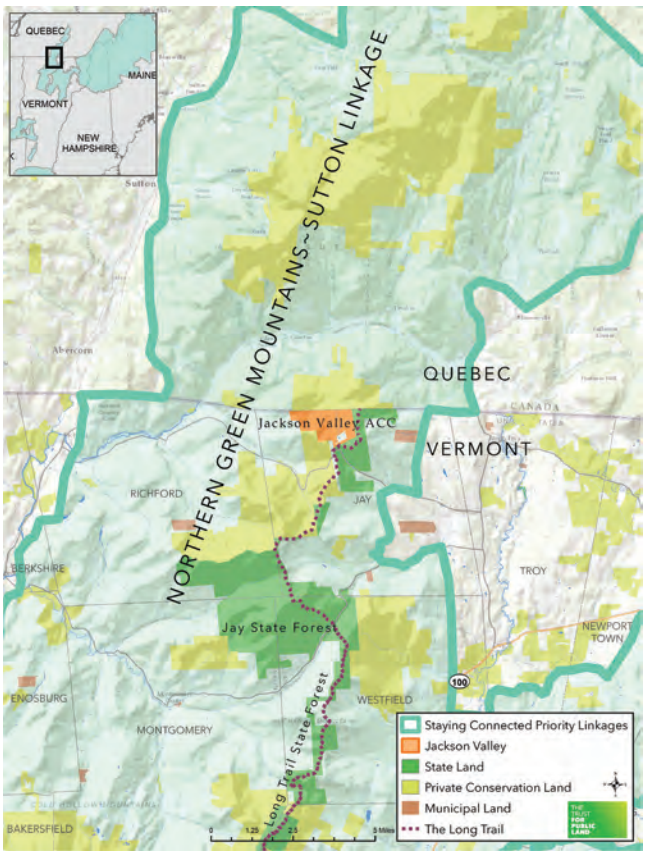


**Figure 2.** Jackson Valley Ecological Corridor in the Northern Green Mountains linkage area © The Trust for Public Land

**Results**

Since 2009, SCI government and land trust partners have secured permanent protection of over 222,500 ha in the nine linkage areas. At least 30 land-use plans in the linkage areas, and all five state Wildlife Action Plans in the region, explicitly incorporate wildlife connectivity. Partners from SCI helped to develop and advance the 2016 Resolution on Ecological Connectivity passed by the Conference of New England Governors and Eastern Canadian Premiers, and SCI government agency partners are leading its implementation. The resolution acknowledges the importance of ecological connectivity from a climate adaptation perspective and calls on relevant agencies within the 11 jurisdictions to work together for improved connectivity through transportation improvements, land protection, forest management and other efforts.

Learn more about SCI and the resolution at http://stayingconnectedinitiative.org/ and https://www.coneg.org/wp-content/uploads/2019/01/40-3-Ecological-Connectivity-EN.pdf.

## 14. Yellowstone to Yukon (Y2Y): Connecting and protecting one the of the most intact mountain ecosystems

Jodi Hilty, *Yellowstone to Yukon Conservation Initiative*

### Context and challenge

Increasing human activities threaten to fragment the 3,200-km-long Yellowstone to Yukon (Y2Y) mountain region in western North America (Figure 1), thus impacting natural processes, wild areas and wildlife, ranging from grizzly bears (*Ursus arctos horribilis*) and mountain caribou (*Rangifer tarandus caribou*) to

**Key lesson**

Realisation of a larger ecological network vision requires science, on-the-ground action, and monitoring the impact of the collaborative conservation efforts in order to assess whether connectivity goals are ultimately met.

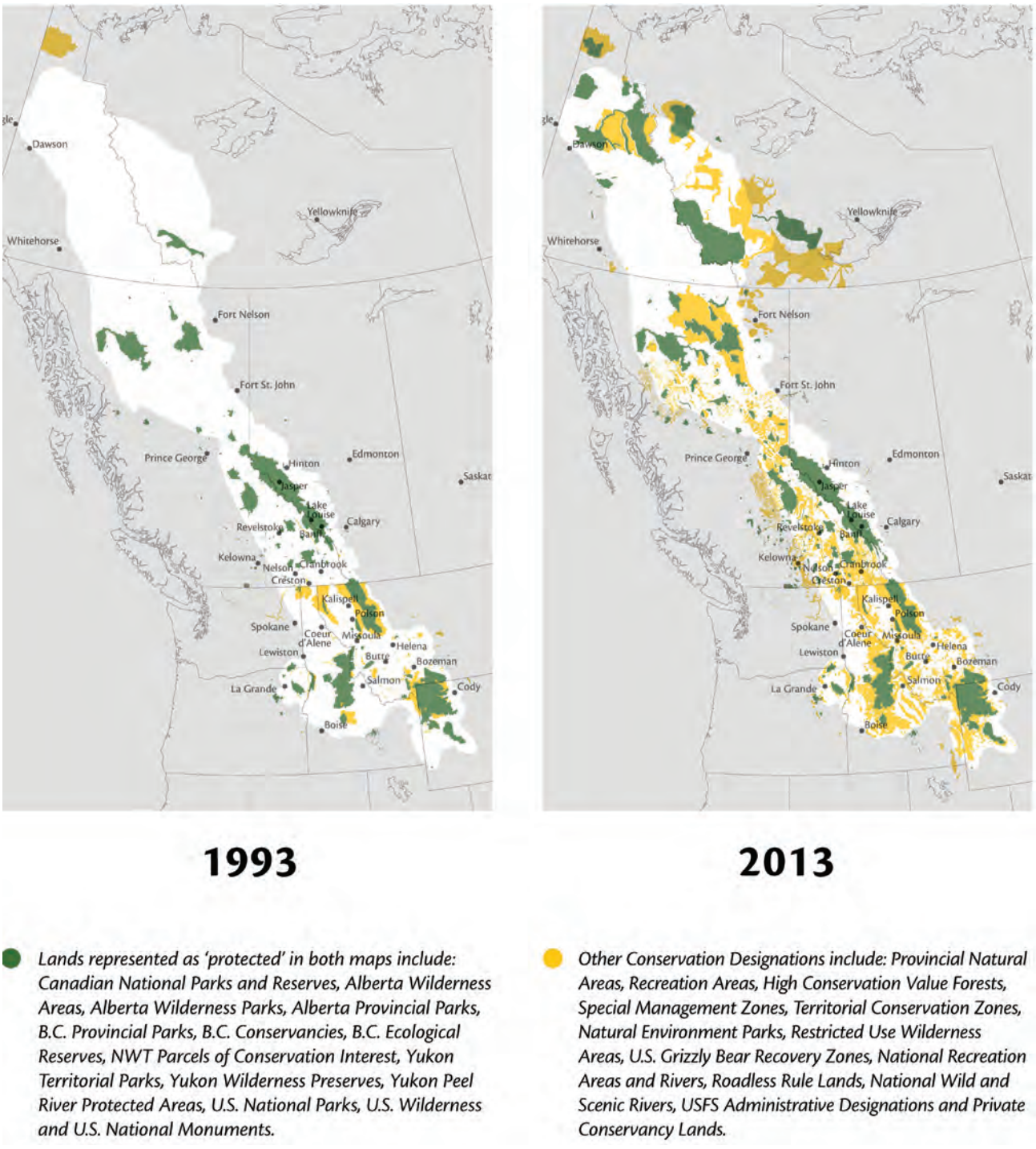


**Figure 1.** Increase in protected areas over two decades in the Y2Y region of North America © Y2Y

jumping slugs (*Hemphillia dromedarius*) and migratory birds. The region has a myriad of jurisdictions, including many Indigenous territories. The US and Canadian governments have classified approximately 80% of Y2Y lands as public and 20% as private or tribal reservation lands.

### Approach

Since 1993, a joint Canada–US not-for-profit organisation, the Yellowstone to Yukon Conservation Initiative, has brought partners together to achieve the vision of connecting and protecting the region so that people and nature can thrive within an ecological network for conservation. More than 400 different entities have been or currently are engaged in collaborative conservation that advances the vision across this ecological network. These include conservation groups, local landowners, Indigenous entities, businesses, government agencies, funders and donors, and scientists. The conservation progress across the Y2Y region is due to the collective work of these different groups. Conservation priorities range from protecting areas important for biodiversity and restoring and maintaining areas between protected areas for ecological connectivity, to directing development away from areas of biological importance and promoting people and wildlife to live in harmony across the region. Protected areas include designations such as national, state and provincial parks, and wilderness areas. In the Y2Y region, increased connectivity may be achieved through large and well-placed protected areas, privately conserved lands, or other lands designated for long-term management that allows for connectivity.

### Examples of ecological corridors

Within the Y2Y landscape, a variety of groups has been working in the British Columbia, Montana and Idaho trans-border region to identify and reconnect small, isolated grizzly bear populations along the Canada–US border in southeast British Columbia. Using genetics, scientists identified that once-continuous grizzly bear populations had begun to fragment; the scientists then identified the best remnant corridors (Figure 2). Many different groups worked to implement connectivity-friendly management (such as securing private lands and providing tools for coexistence). Ultimately, a decade later, it was possible to demonstrate movements of grizzly bears between previously fragmented ecosystems, accompanied by reproduction (Proctor et al., 2018).

### Results

Progress toward protecting a regional ecological network is being made. Protected areas increased more than 50% across the Y2Y region, and a number of ecological corridors and other areas conserving connectivity have been identified, restored and/or maintained between protected areas. Likewise, conservation projects have multiplied across the region to significantly decrease human–wildlife conflicts. Some animals, such as grizzly bears and wolves (*Canis lupus*) in the lower 48 US states, have increased in number and range, but significant conservation remains to be done, as other animals such as mountain caribou have continued to decline in numbers across the region.

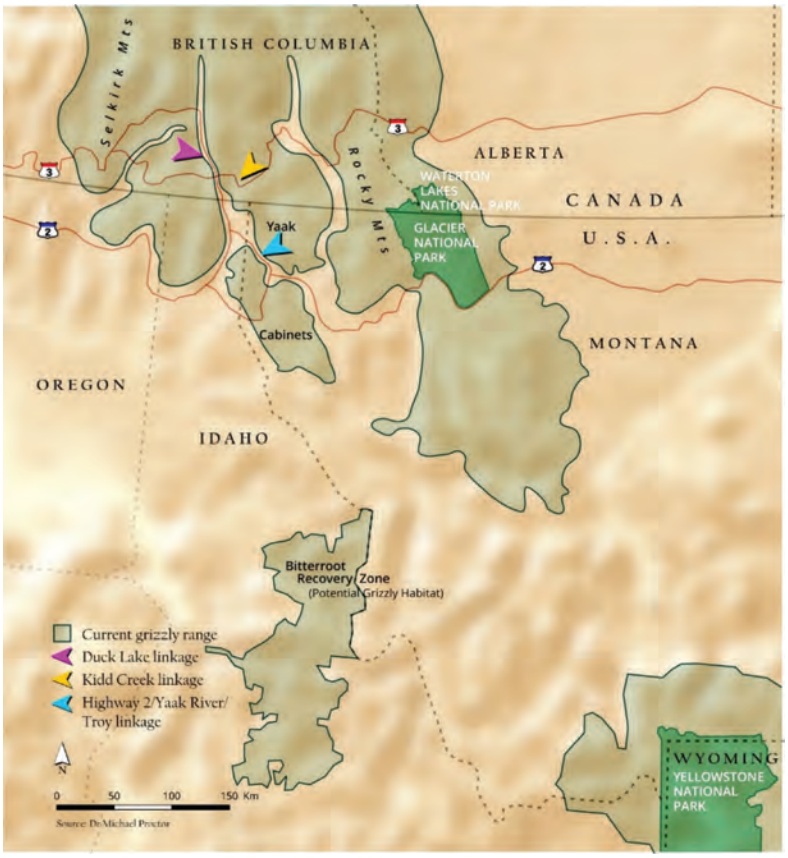


**Figure 2.** The Y2Y transboundary region including key grizzly bear distribution and linkages. The three arrows point to three different linkages – Duck Lake, Kidd Creek and Yaak River – where private land acquisitions have secured ecological corridors for grizzly bears. © Y2Y

## 15. Conserving long-distance migration: The Red Desert to Hoback Mule Deer Corridor, Wyoming, USA

Matthew J. Kauffman, *Wyoming Cooperative Fish and Wildlife Research Unit*
Holly Copeland, *Wyoming Cooperative Fish and Wildlife Research Unit; Hall Sawyer, Western EcoSystems Technology, Inc.*

### Context and challenge

Effective protection of landscapes for migratory species is recognised as a global conservation challenge in the face of ever-increasing anthropogenic land-use changes. Ungulates that migrate long distances must move across a variety

**Key lesson**

This work demonstrates how scientific studies documented migratory corridors for wildlife, resulting in the purchase of private lands that otherwise would have been developed.

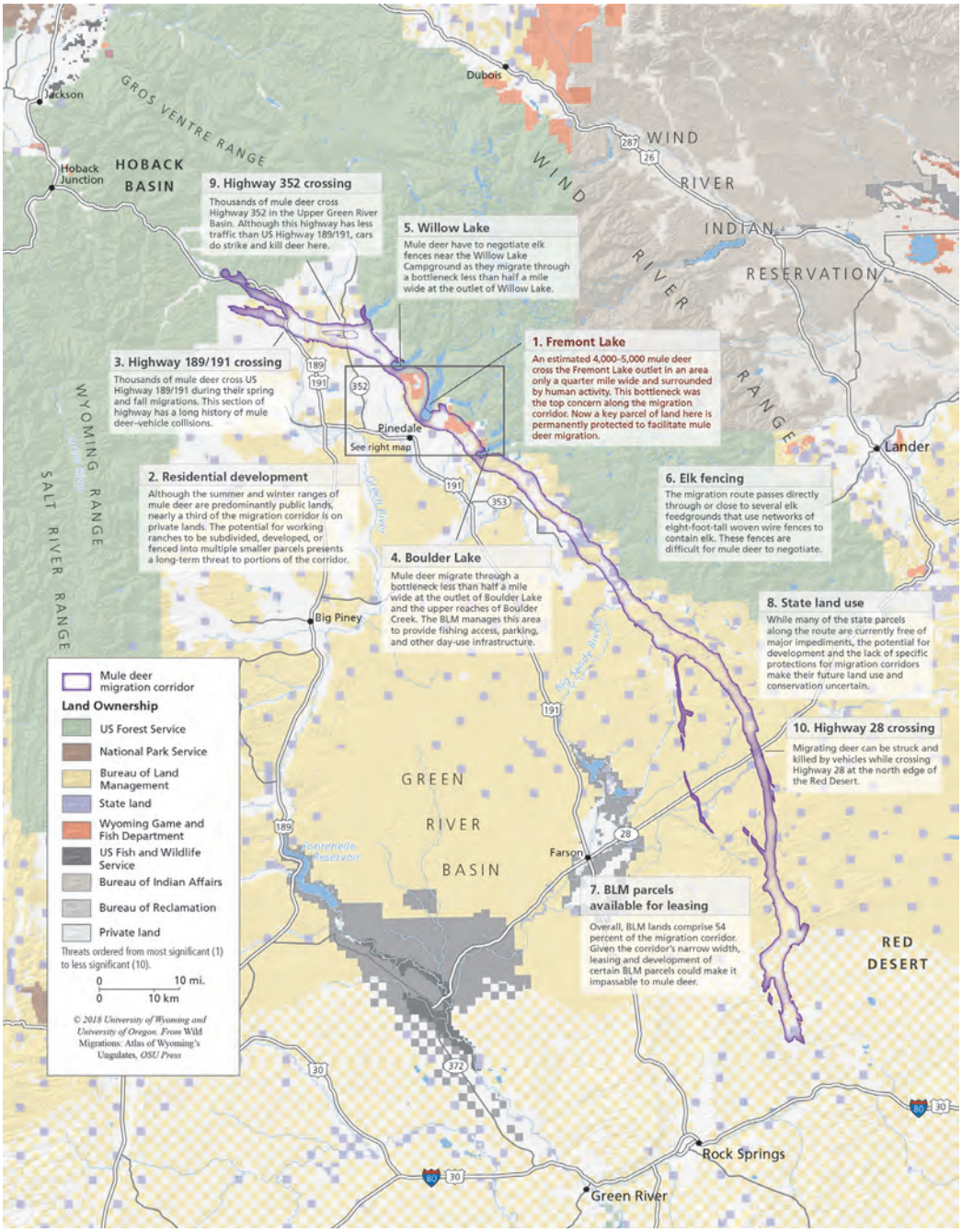


**Figure 1.** The Red Desert to Hoback mule deer migration corridor spans 240 km in southwest Wyoming, USA, crossing a multiple-use landscape. The top ten potential obstacles to the continuity of the corridor are noted. Map from *Wild Migrations: Atlas of Wyoming's Ungulates,* Oregon State University Press. © 2018 University of Wyoming and University of Oregon. Image courtesy of Wyoming Migration Initiative (migrationinitiative.org).

of jurisdictional boundaries, altered or degraded habitats, and human obstacles such as roads, fences, housing and energy development. Globally, long-distance terrestrial migrants continue to decline as a result of these challenges, and ungulates in the American West are no exception. Mule deer (*Odocoileus hemionus*) are an iconic migratory species of the western US, and Wyoming has some of the longest, most intact mule deer migrations in the lower 48 states. In western Wyoming, the Upper Green River Basin is a region known to contain some of the largest mule deer populations in North America. Dozens of long-distance migration routes traveled by mule deer, elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*) have now been mapped across Wyoming's mountains and plains. As anthropogenic influences increase and migratory ungulates continue to decline worldwide, a focus on landscape connectivity is needed to broaden conservation efforts beyond winter and summer ranges to include migration routes as critical habitat.

### Approach

Detailed mapping of migration routes has emerged as a first step towards identifying threats and implementing long-term conservation, aided by new data on ungulate movements from global positioning system (GPS) telemetry studies. The new maps allow assessments of land-use patterns and threats along the routes, which can directly inform conservation action.

### Example of an ecological corridor

In 2014, scientists discovered a 240-km-long mule deer migration route, stretching from the desert basins in southwest Wyoming to surrounding mountain ranges. It is known as the Red Desert to Hoback corridor (Figure 1). An estimated 1,000 mule deer travel a one-way distance of 240 km from the Red Desert to the Hoback Basin and surrounding mountain ranges, where they merge with 4,000 to 5,000 other deer that winter in the foothills of the Wind River Range. They all then travel a narrow corridor along the base of the mountains for 96 km before crossing the upper Green River Basin.

Researchers mapped the ecological corridor in detail and then published an assessment analysing land-use patterns and threats for each section (Sawyer et al., 2014). This assessment identified the top ten threats along the length of the corridor and provided conservation organisations with information needed to direct scarce funds to sites where they are most needed, such as specific bottlenecks, road crossings or unprotected segments of private land. At the top of the threats list was the Fremont Lake 'bottleneck', a 400-m-wide constriction created by the lake and the expanding town of Pinedale, where 4,000 to 5,000 deer squeezed through twice a year. The deer were required to either swim (or, when frozen, walk across) the lake, or ford its outlet, which put them on the wrong side of a 2.5-m-high woven wire fence.

### Results

The Fremont Lake bottleneck consisted largely of a 145-ha parcel of private lands that was slated for subdivision and conversion to lakeside cottages which, if developed, would have blocked deer migration. Guided by information within the assessment, The Conservation Fund, a national non-profit conservation organisation, identified and purchased the parcel. The land was given to the Wyoming Game and Fish Department, which subsequently protected it through designation as the Luke Lynch Wildlife Habitat Management Area, thereby maintaining in perpetuity the connectivity of the ecological corridor at this key pinch point (Figure 2).

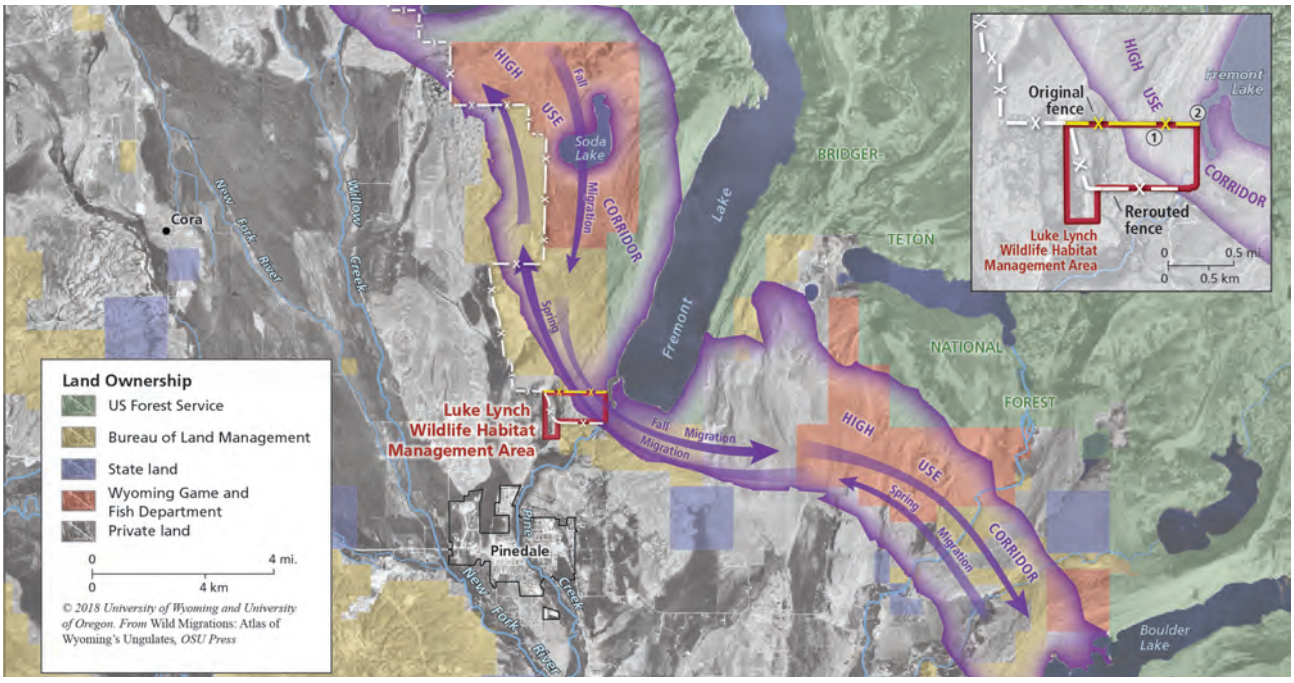


**Figure 2.** Location of the Fremont Lake bottleneck, now conserved as the Luke Lynch Wildlife Habitat Management Area. Map from *Wild Migrations: Atlas of Wyoming's Ungulates,* Oregon State University Press. © 2018 University of Wyoming and University of Oregon. Image courtesy of Wyoming Migration Initiative (migrationinitiative.org)

## 16. Corridors for life: Improving livelihoods and connecting forests in Brazil

Laury Cullen, *Instituto de Pesquisas Ecológicas, Brazil*

### Context and challenge

In Brazil, the largest Atlantic Forest remnants in the interior lie in the Pontal do Paranapanema area of western São Paulo state. Originally a 124,000-ha public forest reserve was designated, but it was progressively encroached upon during 1960–1990 by large-scale ranching and sugarcane establishments. In the mid-1990s, with pressure for land redistribution from the Landless Rural Workers' Movement (MST) and other groups, many such forests were first occupied by families of MST affiliates and later expropriated for public land reform settlements, dramatically increasing the density of human occupation. After the settlement of many landless households, the pace of land redistribution slowed, and national policies now seek to consolidate existing settlements. Promoting income generation for settlers is urgently needed, as is protecting the remaining fragmented forests within this productive landscape before further pressures ensue. Although agrarian reform settlements and large landowners pose a series of barriers to biodiversity conservation, they also offer important and replicable opportunities for large-scale landscape forest restoration.

**Key lesson**

When working with agricultural communities, focusing on multiple benefits of restoring ecological corridors, such as improving livelihoods and obtaining carbon sequestration funding, is vital.

### Approach

The Corridors for Life project focuses on (1) encouraging the adoption of 'biodiversity-friendly' land-use options; (2) promoting changes in land-use practices of small- and large-scale farmers in rural fragmented landscapes, and enhancing the adoption of sustainable agriculture and agroforestry on their lands; (3) improving the farmers' livelihoods; and (4) providing investors a return in the form of high-quality carbon offsets. Strategically selected areas for agroforestry and restoration will increase habitat viability by means of ecological corridors to increase connectivity between 'core' forest fragments, ensuring genetic exchange. Where corridors are not feasible, this exchange will be achieved through

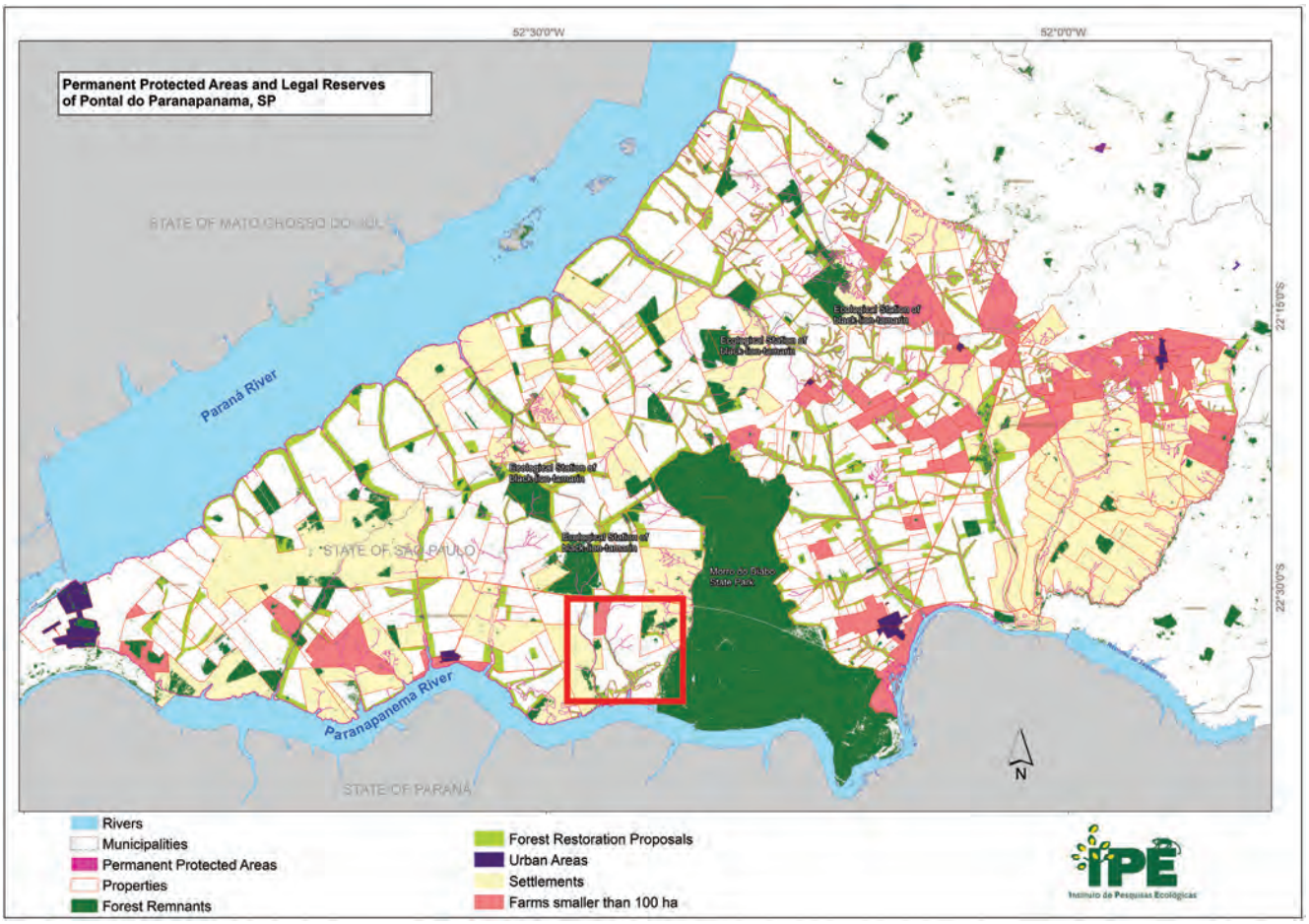


**Figure 1.** IPÊ's 'dream map' for Pontal de Paranapanema uses ecological and property data in order to create the best approach for reforestation efforts. The red polygon contains the largest ecological corridor (1,200 ha) restored in the Atlantic Forest, linking Morro do Diabo State Park and Black Lion Tamarin Ecological Station. © Instituto de Pesquisas Ecológicas

developing stepping stones. Agroforestry and restoration will also minimise degradation around biologically important landmarks, including Morro do Diabo State Park, as the main reservoir of populations of key and endangered species. Enlarging and eventually connecting forest fragments are two main goals of reforestation projects. From an ecological perspective, this is essential to maintaining viable populations of flora and fauna and mitigating harmful edge effects, such as exposure to light and wind, diseases and invasive species. The Instituto de Pesquisas Ecológicas (IPÊ) developed a 'dream map' for Pontal de Paranapanema, the extreme western municipality of São Paulo, where the institute was founded. This plan for wide-scale reforestation of the Atlantic Forest takes into consideration information on local properties as well as proximity to public protected areas and existing forest fragments to calculate where reforestation efforts would be most effective (Figure 1, previous page). Among the main project partners are state and federal rural extension agencies, private companies interested in the carbon neutralisation market, companies that produce and commercialise ethanol and sugar, and other national and international electric power holding companies.

**Example of an ecological corridor**

A conceptual map was used to guide the creation of Brazil's largest reforestation corridor (Figure 2), which, after ten years of effort, links two main remnants of Atlantic Forest in the Pontal de Paranapanema region. This ecological corridor is approximately 7 km long with average width of 400 m. It was restored entirely on privately owned lands. It is protected by the Law for Protection of Native Vegetation, passed in 2012, with which the Brazilian National Congress revised the 'old forest code', as the previous version of the law was known. The 2012 law reaffirms the obligation of private landowners to conserve or restore permanent preservation areas and legal reserves on their properties.

**Results**

To date, approximately 1,800 ha of forest have been restored in Pontal do Paranapanema. This includes the 1,200 ha of the main ecological corridor, another 600 ha in five smaller corridors and 90 agroforestry stepping stones on rural properties. This project consolidates strategies that represent sustainable livelihood alternatives for communities of the land reform movement in Brazil, replicating good practices and policies in income generation and biodiversity conservation. At the policy level, IPÊ, together with other civil organisations in the region, are influencing policies that affect land use and conservation. By using scientific evidence, cooperating with new settlers and large landowners, and collaborating with state and federal agencies, the program is implementing a land-use framework that promotes sustainable agriculture and biodiversity conservation over the long term.

**Figure 2**. Some 2.4 million trees make up IPÊ's 1,200-ha ecological corridor connecting two main Atlantic Forest fragments, the largest in Brazil.
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## 17. Connectivity, ecosystem services and Nature-based Solutions in land-use planning in Costa Rica

Félix Zumbado Morales and Jonathan Agüero Valverde, *Research Program in Sustainable Urban Development, University of Costa Rica*

### Context and challenge

Costa Rica is a small nation of 51,000 km$^2$ that contains about 5% of global biodiversity. The sustainable management of biodiversity is one of the pillars of the work carried out by the country. Protected areas are the country's primary conservation strategy, playing a crucial role in the protection of ecosystems. Costa Rica's second most important conservation strategy is the ecological corridor program, managed by the Costa Rican government, but working hand in hand with communities through local ecological corridor committees. Municipal land management plans have emerged as a third tool complementing protected areas and ecological corridors. These management plans generate the guidelines necessary to allow human development activities to be carried out while maintaining sustainable landscapes, taking into consideration the comprehensive use of the regions. Protected areas and ecological corridors are incorporated into the land management plans; the same is true for the principles of ecosystem services and Nature-based Solutions as decision-making tools.

**Key lesson**

Costa Rica has a three-pronged approach to land conservation: protected areas, ecological corridors and sustainable management of the matrix; different levels of human use are allowed depending on the protection level.

### Approach

Land management plans are a tool that local governments can use to generate regulations that complement protected areas and ecological corridors. These three land management tools are complementary and must be developed in an integrated fashion to achieve a systematic approach to planning. Management plans implement ecological corridors through tools such as the establishment of specific areas for focal species; the preservation of agricultural areas that function as biological, conservation and sustainable tourism corridors; the creation of buffer zones around protected

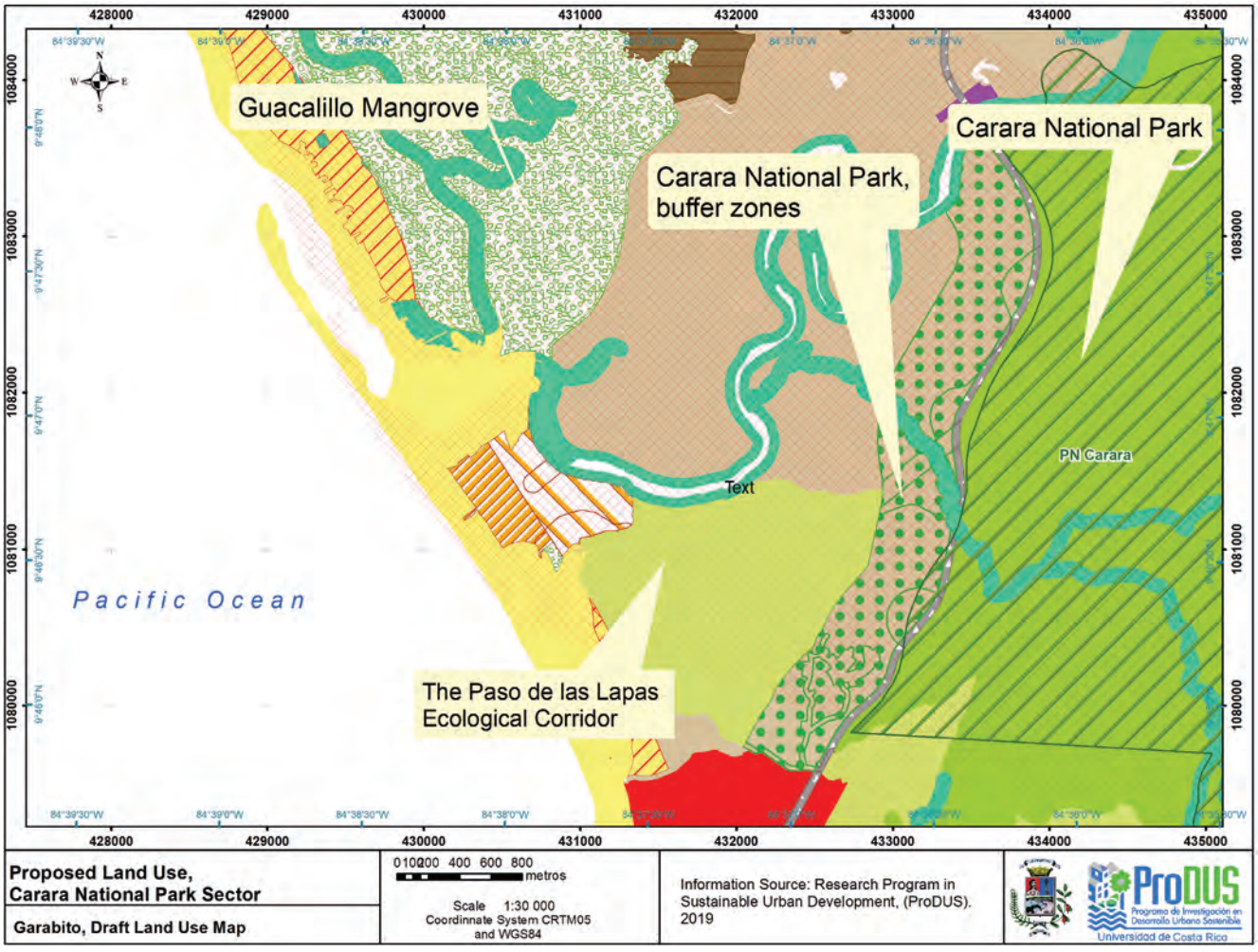


**Figure 1.** Proposed land uses in the region of Canton of Garabito containing the Paso de las Lapas Ecological Corridor © Research Program in Sustainable Urban Development (ProDUS) Universidad de Costa Rica

Carara National Park, Costa Rica © Adobe Stock

areas; and the zoning of aquifer recharge zones for the protection of water sources for local and regional populations. Through the University of Costa Rica's Sustainable Urban Development Research Program (UCR-ProDUS is the Spanish acronym), land management plans for more than a dozen municipalities have been developed, including the protected areas Corcovado National Park, Piedras Blancas National Park, Ballena Marine National Park, Juan Castro Blanco Water National Park and Carara National Park.

**Example of an ecological corridor**

UCR-ProDUS developed a land management plan for the Canton of Garabito, which contains the Paso de las Lapas Ecological Corridor (Figure 1). This ecological corridor encompasses 56,200 ha and connects protected areas in the mountains (La Cangraja National Park, Cerros de Turrubares protected area and Carara National Park) with coastal areas. The Paso de las Lapas Ecological Corridor was established in 2007 through an executive order. In Costa Rica, ecological corridors are not state conservation areas, but are a different conservation strategy promoted by the National System of Conservation Areas through the national program of ecological corridors. The ecological corridors connect protected areas, preserve water resources and protect biodiversity. The land plan establishes regulations that ensure the sustainable management of the region. Planning took into account the location of protected areas; the benefit of ecosystem services such as carbon capture, aquifer recharge zones protection and flood regulation; and the value of Nature-based Solutions such as national park buffer zones, river basin management and agricultural land protection. The land management plan strengthens the functionality of the ecological corridors and gives greater control over their management through the input of local governments. Buffer zones and proposed wildlife crossings are important elements of corridor management and implementation. In the land management plan for the Canton of Garabito, measures to protect the Paso de las Lapas Ecological Corridor include zoning of protected areas, low-intensity agriculture and ecotourism areas.

**Results**

Land management can be an ally of conservation and sustainable development. It can promote ecological connectivity by strengthening ecological corridors that link protected areas. Currently, the Paso de las Lapas land management plan is in the final phase of the approval process. The regulations of the land management plan can help to:

- Reduce conflicts between owners and the municipality;
- Protect ecological connectivity;
- Promote ecotourism and other low-intensity activities;
- Support the ecological corridor's conservation objectives;
- Restrict intensive uses such as residential and industrial development, and other incompatible land uses; and
- Protect fragile ecosystems such as wetlands and mountains.

## 18. The Jaguar Corridor Initiative: A range-wide species conservation strategy

Kathy Zeller, *Massachusetts Cooperative Fish & Wildlife Research Unit*

### Context and challenge

Species conservation efforts are often conducted on discrete populations and are usually envisioned at small scales. Thinking about conservation throughout the entire range of a species allows us to broaden our perspective and identify species' needs across political and jurisdictional boundaries. This perspective also allows for the identification of large-scale patterns of threats and anthropogenic development.

**Key lesson**

Some large-scale visions for multi-country ecological networks focus on wide-ranging umbrella species such as the jaguar. Ecological corridors in these networks can encompass multiple land uses and different land ownership, from federal entities to individual landowners.

In 1999, the Wildlife Conservation Society and the Universidad Nacional Autonóma de México brought together jaguar (*Panthera onca*) experts to develop a range-wide research and conservation plan for the species. This effort identified 51 jaguar population centres from Mexico to Argentina (Sanderson et al., 2002). Shortly after this plan was developed, a genetic study provided evidence of widespread gene flow across jaguar range (Eizirik et al., 2001), indicating that these populations were still connected and that there was little evidence of geographic barriers to gene flow. These results inspired the Jaguar Corridor Initiative, an approach conceived by the late Dr. Alan Rabinowitz, to maintain connectivity and gene flow across jaguar range.

### Approach

To model connectivity, we first updated the 1999 range-wide population data with new information and identified 90 important jaguar populations throughout the species' range,

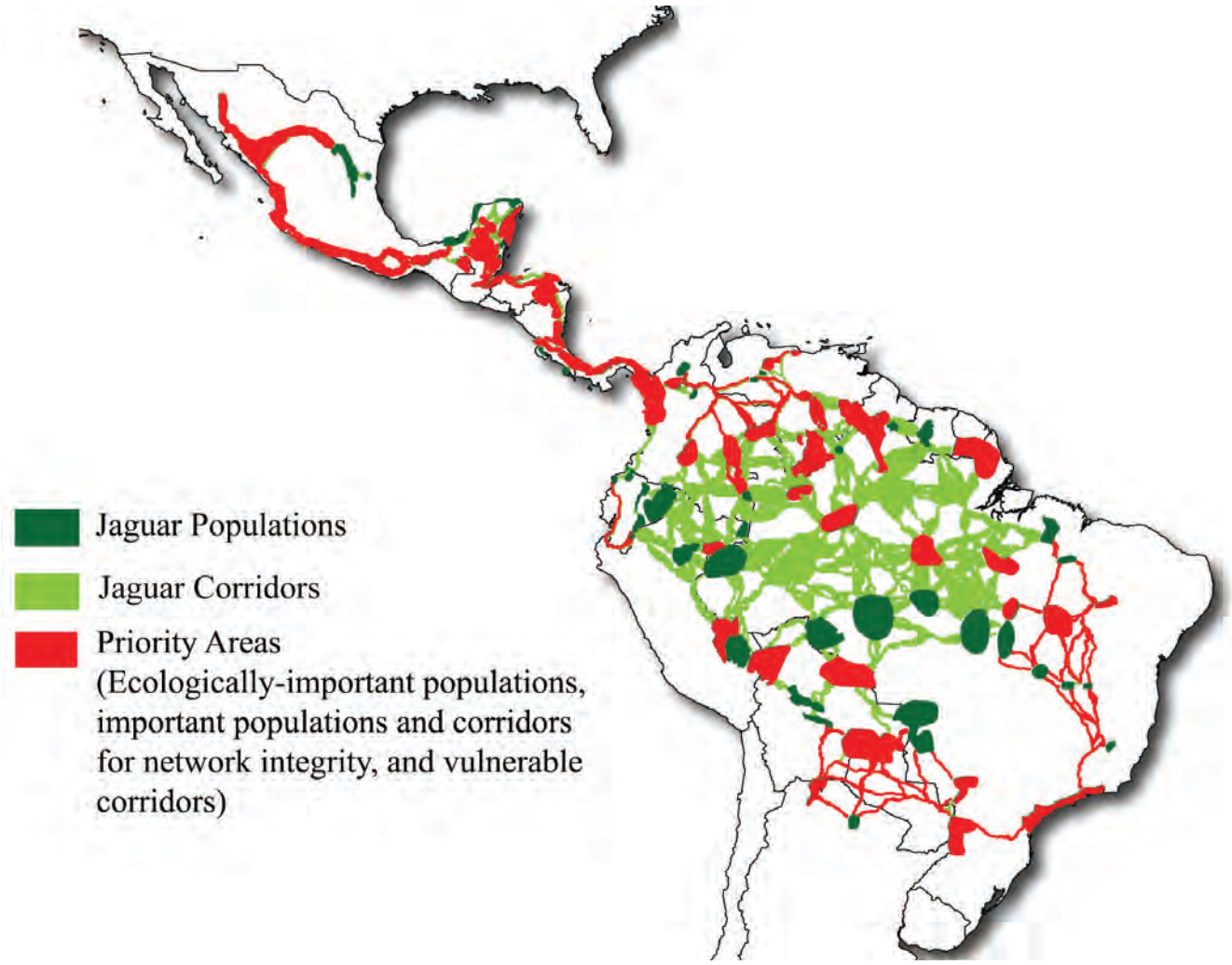


**Figure 1.** Jaguar populations and corridors across its range. Populations and ecological corridors were prioritised according to ecological importance, network integrity and vulnerability. They were combined to identify all priority areas across jaguar range. © Kathy Zeller

Jaguar (*Panthera onca*) © Adobe Stock

which measured 1.9 million km$^2$. We then invited 15 jaguar experts to assign cost or resistance values to six GIS layers known to affect jaguar movement. We combined these scored layers into a single resistance surface and modelled least-cost corridors between the 90 populations (Rabinowitz & Zeller, 2010). The resulting 182 corridors measured 2.6 million km$^2$ for a total conservation network of 4.5 million km$^2$ (Figure 1, previous page). When compared with the World Database on Protected Areas, 67% of the jaguar populations and 46% of the ecological corridors were under some form of protection.

In order to focus research and conservation efforts across this vast network, we prioritised jaguar populations and ecological corridors using three criteria: ecological importance, network importance and corridor vulnerability (Figure 1) (Zeller et al., 2013). We directed our field-based conservation efforts towards these prioritised areas.

Because the ecological corridors were identified with coarse-scaled GIS data and expert-derived resistance values, we wanted to validate the corridors before conducting site-based conservation activities. This was a challenge, however, because the corridors were often large and comprised numerous landowners. So we developed a rapid assessment, interview-based methodology that allowed us to estimate occupancy for jaguars and their main prey species in the corridors (Zeller et al., 2011; Petracca et al., 2017). All the corridors in Central America have now been validated and adjusted, and validation is currently being conducted in South America. Conservation work across the Jaguar Corridor Initiative is mostly led by the non-profit organisation Panthera (www.panthera.org).

**Example of an ecological corridor**

The Barbilla-Destierro Jaguar Corridor is located in Costa Rica and links the Talamanca Mountains in the south with the Central Volcanic Range in the north. The corridor, which contains myriad land uses, comprises private, municipal and federal lands. Conservation strategies from the federal to the individual landowner level have been implemented. Examples include:

- Incorporating the corridor into Costa Rica's National Program of Biological Corridors;
- Developing a local corridor council, which brings together landowners once a month to discuss and address threats and opportunities;
- Working with a hydroelectric company to direct its environmental mitigation and restoration projects toward areas that will enhance connectivity across the corridor;
- Training and establishing a Wild Cat Conflict Response Unit to investigate depredations on livestock and implement anti-predator strategies; and
- Providing science-based recommendations to development projects for maintaining connectivity across the corridor.

**Results**

The Jaguar Corridor Initiative has provided a conservation blueprint across the species' entire geographic range. Panthera is currently leading conservation efforts similar to those described for the Barbilla-Destierro Jaguar Corridor in 11 of the 18 countries where jaguars reside. Jaguar research is ongoing across the ecological network and corridor monitoring plans are being established. Support for the initiative has been steadily growing across jaguar range with the backing of numerous governments, landowners, corporations and scientists. With growing support, the vision of a connected and protected ecological network for jaguars from Mexico to Argentina hopefully will become reality.

# Freshwater connectivity: Asia

## 19. Grassroots reserves have strong benefit for river ecosystems in the Salween River Basin

Aaron A. Koning, *Cornell University*

**Key lesson**

Recognition and enforcement of river reserves by the local communities, which benefit local fisheries and enhance the health of the river system, is a significant first step to increasing in-stream connectivity in the Mae Ngao River in Thailand.

### Context and challenge

In many low-income countries, people depend highly on inland fisheries for daily nutrition, creating strong incentives to access the resource regardless of regulations. Even in protected areas that contain human populations, hunting bans rarely extend in practice to fish. While national fishery regulations and guidelines exist in Thailand, in remote areas such as the Mae Ngao River, enforcement is difficult and rare. Due to their linear nature and the dependence of many sectors upon rivers and their waters, it is a challenge to create ecological corridors covering entire river basins or even individual rivers.

### Approach

Throughout Southeast Asia, in response to perceived declines in fish populations, concerns for continued resource security, and encroachment from outsiders using illegal fishing gear (e.g. electric shocking), small no-take reserves on rivers have been created by local communities, established by non-governmental organisations or imposed by national governments. These small reserves are effectively the only management action for these intensive-harvest fisheries. In tributaries of the Salween River in north-western Thailand, ecological networks of small riverine reserves continue to grow, particularly among fishery-dependent communities where overharvest is common.

### Example of an ecological corridor

One such ecological network is located in the Mae Ngao River Basin of north-western Thailand, which encompasses 1,000 km$^2$ and over 8,000 people among more than 70 villages (Figure 1). Over 25 years ago, the first community-created reserve was established following a meeting with a local NGO, which suggested creating small areas closed to fishing as a conservation measure. Initially, only one community took this action, but the practice has slowly spread since to include more than 50 others, which largely act independently and are unsupported by government or other outside entities. Communities individually determine reserve locations, sizes and penalties for non-compliance, which range from the equivalent of 15 USD to over 300 USD. Inside reserves, all harvest activities are prohibited, including harvest of snails and other aquatic invertebrates, which otherwise are commonly eaten, particularly during the extended dry season (November–May). Outside of reserves, harvest effort is high, using a variety of methods (e.g. gill nets, lines, traps, hand spears). Fishing effort often extends from the borders of the reserve for hundreds of meters both upstream and downstream, creating a gauntlet of nets and hooks for fish moving outside of protected areas. Several neighbouring communities have added additional regulations outside reserves, notably banning the use of diving masks in collecting snails and spearfishing. Spearfishing, particularly in the dry season when water temperatures are warm, the water is clear, and local schools are on break, is thought to have a large impact on populations of fish of all sizes.

### Results

There is no broader strategic planning among communities regarding the creation of reserves. In fact, there is a general lack of recognition even among community members of the number of reserves in existence throughout the Mae Ngao River Basin. Nevertheless, there are now 52 reserves that, basin-wide, cover 2% of all perennially flowing water, and form a network of protected areas within the larger river network. This network has been entirely created and enforced by individual communities.

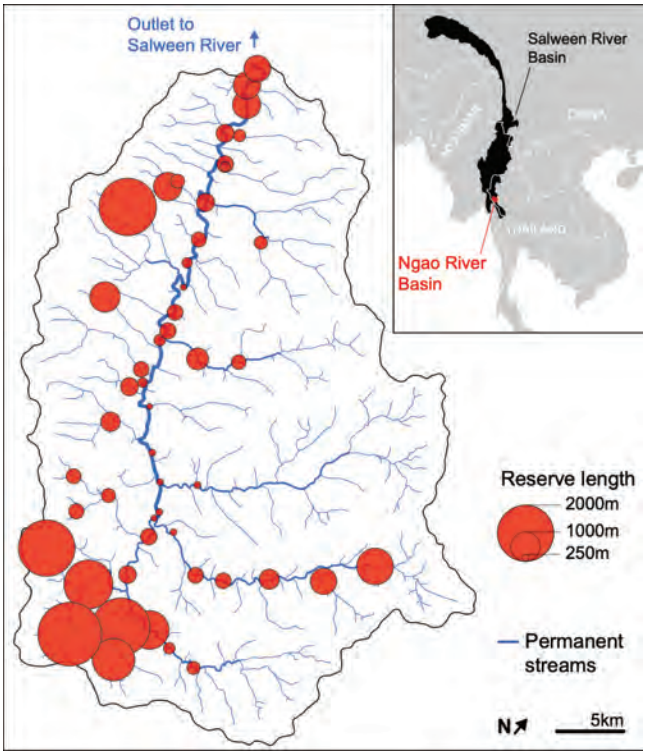


**Figure 1**. Ecological network of no-take reserves on the rivers in the Mae Ngao River Basin in north-western Thailand © Aaron A. Koning

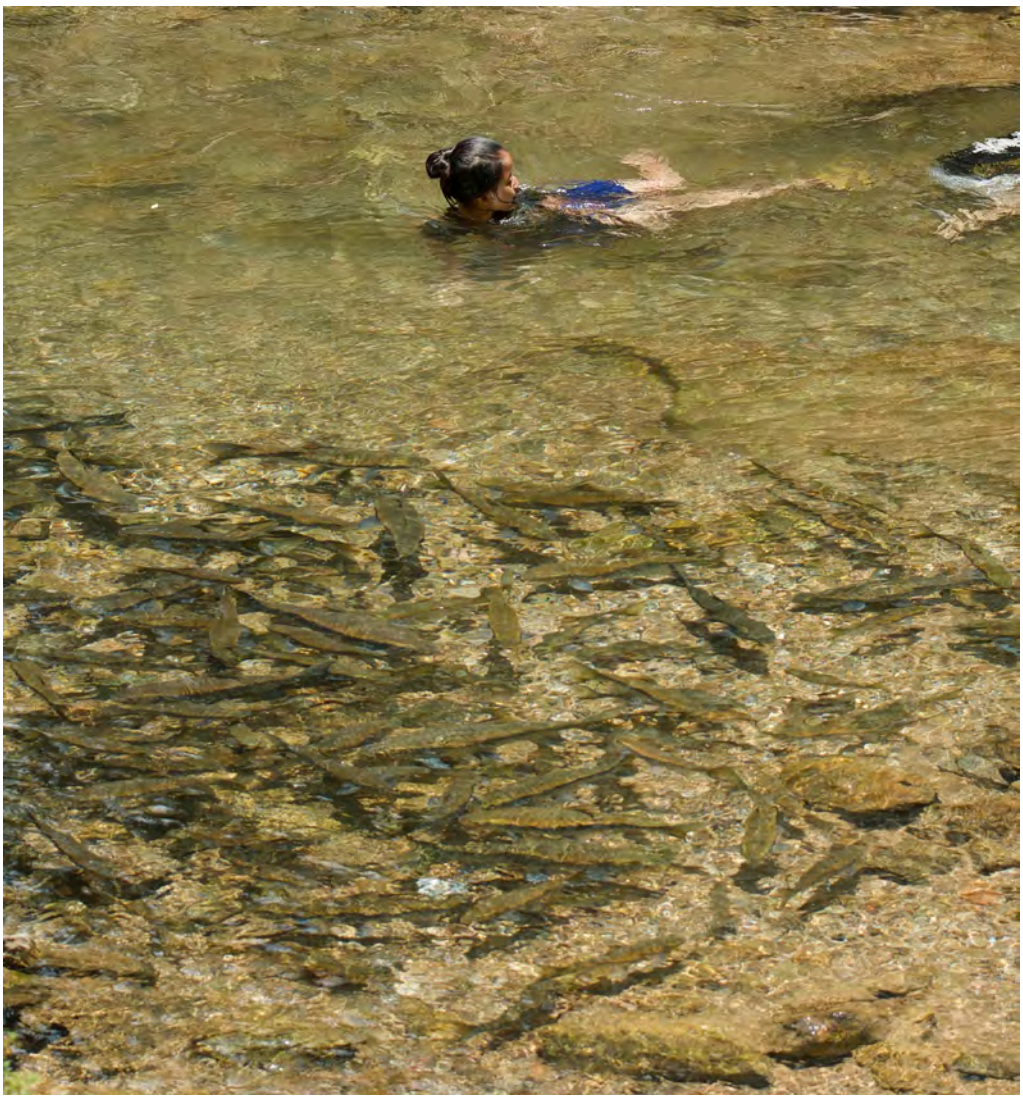

**Figure 2.** In no-take reserves, large schools of fish can be seen from the riverbank. © Aaron A. Koning

However, intense fishing effort forms a large barrier to connectivity between and among reserves. Viewed at more local scales, though, individual reserves are typically long enough to connect habitats within the river network, including pools that are critical refugia for many species during dry season. In the rainy season, when river levels increase by up to 5 m from dry-season lows, fishing effort goes down and systemwide connectivity goes up, giving fish the opportunity to move for breeding.

Because of the disparity in harvest effort between reserves and other areas, the effects of the conservation action can be seen even from the river bank, where large schools of fish become points of interest for tourists and travellers in the area (Figure 2).

A comparison of 23 of these small reserves with adjacent fished areas showed gains in fish species richness, density and biomass commensurate with reported gains from marine reserves (Koning, 2018; 2019). Specifically, richness increased in reserves relative to fished areas by 27% and density by 124%, and biomass was 23 times higher on average. Although benefits were often observed only three to five years after a reserve was established, gains were sustained through time.

Community members regularly harvest large fish outside of reserves and credit fish movement out of reserves for such catches. It remains unclear whether reserves are sufficiently large to maintain populations over the long term and whether there is regular movement among reserves that would transfer critical genetic diversity among potentially isolated sub-populations. Given the seasonal fluctuations in the river, though, it seems likely that fish movement occurs during the rainy season.

The extent to which these small reserves are able to benefit local fish populations is all the more remarkable given that communities have largely acted independently without a broader coordination of effort. Next steps for this reserve network would be to work with communities, informed by the surveys conducted previously and the body of reserve design theory that has been developed for marine systems, to attempt to optimise reserves individually and collectively for maximum conservation and fishery benefits.

# Freshwater connectivity: Europe

## 20. The ecological corridor Mura-Drava-Danube and future five-country biosphere reserve

Arno Mohl, *WWF Austria*
Ivana Korn Varga, *WWF Adria*
Emöke Györfi, *WWF Austria*

### Context and challenge

For a long time, large parts of the river landscapes along the former Iron Curtain between the Baltic Sea and the Black Sea in Europe remained largely unaffected by serious encroachments. With the end of Communism in Europe in the late 1980s and the subsequent enlargement of the EU eastward, these forgotten river paradises were catapulted into another age. Suddenly, they were in areas of human economic interest. On the one hand, this pressure has threatened to irreversibly destroy the last intact areas. On the other hand, new opportunities for cooperation in nature conservation and sustainable development have emerged. Transboundary Biosphere Reserves (TBRs) are an appropriate tool to tackle this major need for large-scale cross-border river protection, management and restoration. Current examples can be found on the lower reaches of Drava and Mura rivers and in the adjacent floodplains of the middle Danube River between Austria, Slovenia, Croatia, Hungary and Serbia (Mohl et al., 2009).

**Key lesson**

Conserving river connectivity can be achieved through a series of protected areas and a vision that prohibits dams and other developments that would impair the long-term connectivity of river systems, but promotes benefits that are compatible with connectivity.

### Approach

As borders between states are political rather than ecological, ecosystems often stretch across national boundaries, and may be subject to different, or even conflicting, management and land-use practices. TBRs provide a tool for common management. A TBR is an official recognition at the international level and by a UN institution, UNESCO, with the political will to cooperate in conservation and sustainable use through common management of a shared ecosystem (UNESCO, 2017). The initiative for the five-country Biosphere Reserve Mura-Drava-Danube between Austria, Croatia, Serbia, Slovenia and Hungary goes back to 1993. It has been developed as a counterproposal to emerging threats of new hydropower dam projects after the fall of the Iron Curtain and as a tool to connect and better protect all national river areas of the corridor under one international management framework (Schneider-Jacoby & Mohl, 2012).

Campaigning against large-scale water management and hydropower dam projects which were threatening the riverine area has been an important approach to achieve protection of this valuable ecosystem. The campaign has increased public and political awareness, created pressure on governments and triggered the establishment of 13 major protected areas, including the 88,000-ha regional park Drava-Mura in Croatia. Mostly part of the Natura 2000 network, these protected areas fall under several categories. Setting up an ecological network for conservation has laid the foundation for transboundary cooperation for harmonised conservation, integrated management and restoration within the future Biosphere Reserve Mura-Drava-Danube.

Since 1993, WWF, EuroNatur and local NGOs have been campaigning to protect the unique landscape of the three rivers in a five-country TBR (Figure 1). Increasingly, governments and NGOs cooperate to jointly achieve, stepwise, the TBR. They are establishing Europe's largest protected river corridor (700 km, 1,000,000 ha) through innovative cross-sector cooperation and harmonised sustainable regional development that also supports cross-border reconciliation (WWF, 2013). Once fully established, the biosphere reserve will form an ecological network for conservation that consists of core zones embedded in buffer zones and transitional zones.

### Example of an ecological corridor

Spanning Austria, Croatia, Hungary, Serbia, and Slovenia, the lower courses of the Drava and Mura Rivers and related sections of the Danube are among Europe's most ecologically important riverine areas – the so-called Amazon of Europe. Despite numerous human-made changes in the past, this region hosts amazing biological diversity and is a hotspot of rare natural habitats, such as large softwood forests, wet meadows, river islands, gravel and sand banks, steep banks, side branches and oxbows (Figure 2).

The area is home to the highest density of breeding pairs of white-tailed eagles (*Haliaeetus albicilla*) in Continental Europe, and other endangered species such as the black stork (*Ciconia nigra*), beaver (*Castor fiber*), otter (*Lutra lutra*) and the nearly extinct ship sturgeon (*Acipenser nudiventris*). Many of the species are indicators of a natural river corridor, including the little tern (*Sternula albifrons*). Every year, more than 250,000 migratory waterfowl use the rivers to rest and feed. The largest and best-preserved floodplains and forests can be found around the confluence of the Danube and Drava, shared between Croatia, Hungary and Serbia. Most parts of this transboundary area are assigned to the core zone of the TBR. In addition to high levels of biodiversity, the river and floodplain areas are vital

to the local communities. Local fishers rely upon the fish populations for their livelihoods. The extensive floodplains lower the risks from floods, secure favourable groundwater conditions and provide self-purification of water, which is essential for drinking water, forests and agriculture. People also enjoy recreational activities along the rivers by walking, swimming, fishing and canoeing (WWF Austria, 2014).

### Results

Driven by the vision of establishment of the five-country TBR, major progress has been made over the past 30 years toward better protection and management of the river corridor:

- Thirteen major protected areas along the Mura, Drava and Danube, which are forming the TBR's backbone, have been established by the governments of the five countries.
- So far 270 km of natural river stretches have been successfully defended from being destroyed by large-scale water management and hydropower dam projects.
- In 2009, Croatia and Hungary signed a joint declaration to establish the TBR, followed in 2011 by a five-country ministerial declaration. In 2012, the riverine areas in Croatia and Hungary were granted biosphere reserve status, soon followed by those in Serbia (2017), Slovenia

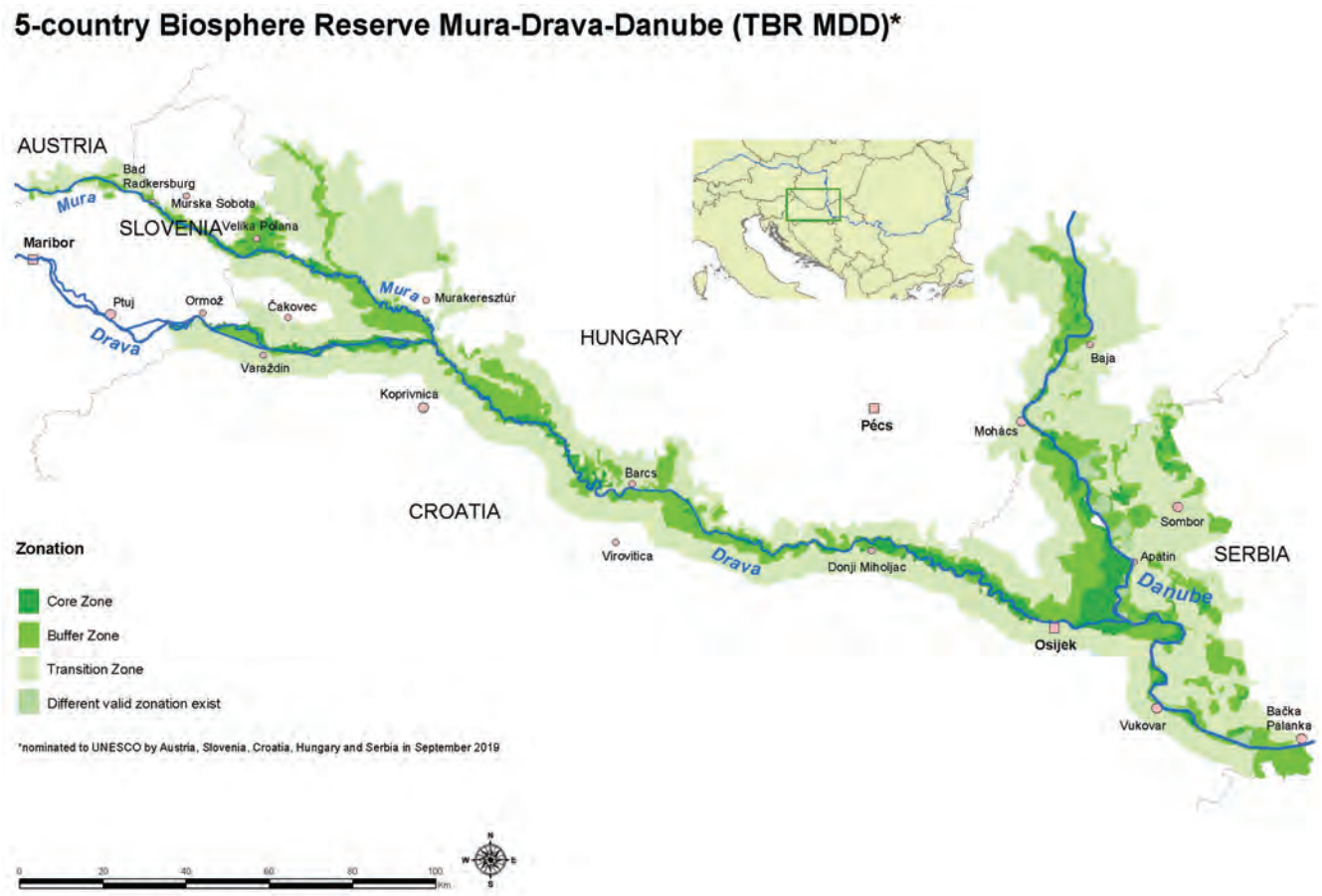


**Figure 1.** The future five-country UNESCO Biosphere Reserve Mura-Drava-Danube © World Wildlife Fund (WWF)

**Figure 2.** (left) Floodplains of the Danube in Croatia © Mario Romulic. (right) The Drava River in Croatia © Arno Mohl

Black stork (*Ciconia nigra*) © Adobe Stock

(2018) and Austria (2019). The strictly protected core and buffer zone, which consists of those 13 major protected areas, amounts to 280,000 ha. It is surrounded by 650,000 ha of transitional zone.

- Triggered by the TBR, several projects co-funded by the EU are already being implemented across the five countries in the area, aiming to achieve better protection and sustainable development. Within the 'coop MDD' project, the protected area administrations of the Mura-Drava-Danube region have been cooperating since 2017 to jointly focus on common goals and trans-border nature protection measures. The 'Resilient riparian forests as ecological corridors in the Mura-Drava-Danube Biosphere Reserve' project started in June 2019, aiming at preservation and sustainable management of floodplain forests in the TBR. At the same time, the 'Amazon of Europe Bike Trail' ecotourism project started. Furthermore, river restoration is being implemented to create new natural habitats and recreational areas for people to truly experience the stunning landscape along the rivers.

Also in 2019, the dossier was prepared for the five-country TBR nomination, which will harmonise all existing biosphere reserves in the region under one international designation. The next step is for UNESCO to finalise and approve the nomination. Once officially designated, the five-country TBR should take steps to achieve a fully functional biosphere reserve in line with UNESCO requirements. This includes establishing a joint management structure and implementing a joint action plan and projects.

Further information: http://www.amazon-of-europe.com/
http://www.interreg-danube.eu/approved-projects/coop-mdd
http://www.interreg-danube.eu/approved-projects/refocus
http://www.interreg-danube.eu/approved-projects/amazon-of-europe-bike-trail

# Freshwater connectivity: North and South America

## 21. Pacific salmon watersheds: Restoring lost connections

Lauren Law and Jonathan Moore, *Simon Fraser University*

**Key lesson**

Even in an otherwise protected watershed, dams impair connectivity of the headwaters to the ocean; dam removal can restore biotic and abiotic processes, as demonstrated in the Elwa River in the USA.

### Context and challenge

Coastal watersheds that drain into the northern Pacific Ocean support populations of culturally and economically important migratory salmon. Pacific salmon are born and initially develop in freshwater environments and then migrate to the open ocean, where they forage and grow before returning to natal freshwaters to spawn. Across North America and Asia, 8% of high-value catchments that drain into the northern Pacific Ocean are at least partially protected, predominantly in areas that are higher in elevation and distant from the ocean (Pinsky et al., 2009). However, even if portions of catchments are protected, dams have fragmented many salmon systems. Dams, such as for hydroelectric production, may block or hinder salmon migration, alter hydrological regimes and modify downstream river habitat. As a result of the imperilled or extirpated status of many salmon populations (Gustafson et al., 2007), there have been substantial investments in conservation and recovery.

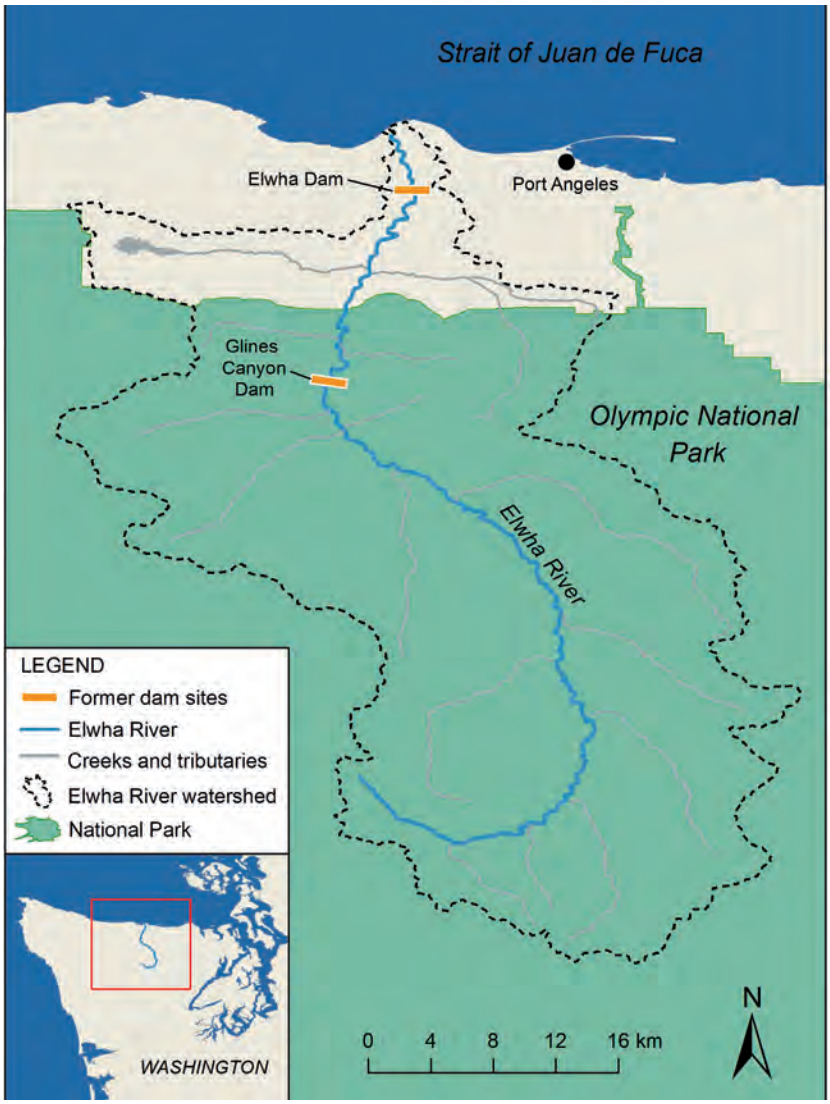


**Figure 1.** Elwha River watershed within Olympic National Park, Washington, USA. The removal of the Elwha Dam and Glines Canyon Dam restored connectivity between the upper and lower portions of the watershed. © Jonathan Moore

Chinook salmon (*Oncorhynchus tshawytscha*) © Adobe Stock

**Approach**

Over the last several decades, there has been increasing dam removal and mitigation to benefit salmon and other migratory fishes. Across the USA, more than 1,200 dams had been removed by 2017 (Bellmore et al., 2017). Dam removal generally occurs through a decentralised decision-making process involving numerous stakeholder groups, including federal agencies, state agencies, and private dam owners. Although some dam removals have been voluntary, many have been the result of legal proceedings that fall under the regulatory powers of the Federal Energy Regulatory Commission. Initial removal efforts were focused on older dam structures, which were too costly to maintain and no longer in compliance with modern safety standards. However, in recent years there has been a greater focus on dam removal for environmental protection and habitat restoration. In the USA, the Wild and Scenic River Act (1968) is a legal mandate to preserve rivers having exceptional natural, cultural and recreational values in a free-flowing state.

**Example of an ecological corridor**

In the USA, one of the largest dam removals that has restored connectivity in a protected salmon watershed was on the Elwha River. The vast majority of the 72-km-long river is within Olympic National Park in the state of Washington. Historically one of the most productive salmon rivers in the Pacific Northwest, the Elwha was disturbed in the early 1900s when two dams were constructed on it, disconnecting the protected upper portion of the watershed from the seascape that migratory salmon rely on. Migration of salmon was blocked, and the movement of sediment and woody debris was disrupted. The building of these large-scale dams led to a 90% reduction in fish populations, a loss of habitat connectivity and decline in habitat complexity (Pess et al., 2008).

In 1992, the Elwha River Ecosystem and Fisheries Restoration Act authorised the removal of the dams to restore the river ecosystem. The US National Park Service removed the dams in phases, starting with the removal of the smaller dam beginning in 2011 and eventually completing the removal of the larger dam in 2014.

**Results**

The removal of the Elwha River dams led to renewed riverine fluxes of sediments and large woody debris downstream that had been trapped in the dam reservoirs for nearly a century. Approximately 30 million tons of sediment were released, causing some 60 ha of river delta growth (Ritchie et al., 2018). The supply of sediment and large wood to the fluvial system restored channel morphology to its former complexity and resulted in increased river braiding, sediment-bar growth and pool filling.

Renewed connectivity of upstream protected habitat with the seascape in the Elwha River watershed is fostering the return of several salmon species (Chinook, *Oncorhynchus tshawytscha*; coho, *Oncorhynchus kisutch*; chum, *Oncorhynchus keta*; sockeye, *Oncorhynchus nerka*; and pink, *Oncorhynchus gorbuscha*) as well as anadromous trout (e.g. steelhead, *Oncorhynchus mykiss*; and bull, *Salvelinus confluentus*). Scientists have already observed record numbers of Chinook salmon returning to the Elwha, with high returns anticipated to follow for other species. About 30,000 Chinook and coho salmon and 270,000 pink salmon are expected to return annually. Salmon returns will eventually sustain local and regional fisheries.

The Elwha is one of many coastal catchments that has protected salmon habitat in its headwaters but whose connectivity to the seascape was severed. As illustrated by the Elwha project, dam removal and restoration of the free-flowing status of rivers can effectively connect protected headwaters with the seascapes on which migratory fishes such as salmon depend.

## 22. Fragmentation of riparian protections throughout catchments, Oregon, USA

Rebecca Flitcroft, *USDA Forest Service*
Brett Boisjolie, *Massachusetts Department of Conservation and Recreation*
Mary Santelmann, *College of Earth, Ocean and Atmospheric Sciences, Oregon State University*

**Key lesson**
Maintaining functional habitat can require policy protections and voluntary restoration efforts, both guided by science; monitoring and evaluation are critical to ensure that the actions will indeed result in the desired outcome.

### Context and challenge

Lotic and lentic environments provide lateral connectivity to floodplain and riparian ecosystems. They can be passages for movement of aquatic organisms to and from headwater areas and marine environments, and are important components of global biogeochemical cycles (Butman & Raymond, 2011). Riparian environments also provide critical buffers between human land uses adjacent to the water's edge by filtering nutrients, retaining sediment and contributing biotic material that constitutes significant food inputs into freshwater food webs.

In many places, protection for freshwater taxa and their habitats is linked to the ribbon of riparian areas that flank rivers and lakes. Riparian protections, in turn, are often linked to land ownership, which changes along the length of a river, from its headwaters to the sea. However, this approach to conservation results in fragmented protections along the continuum of the river.

In coastal Oregon, USA, high-gradient headwater streams tend to be located within dense Douglas fir forest where the primary land use is timber harvesting. Downstream of these areas are low-gradient lowland areas that have been converted to agriculture, residential and urban development (Figure 1). Historically, these streams supported thriving

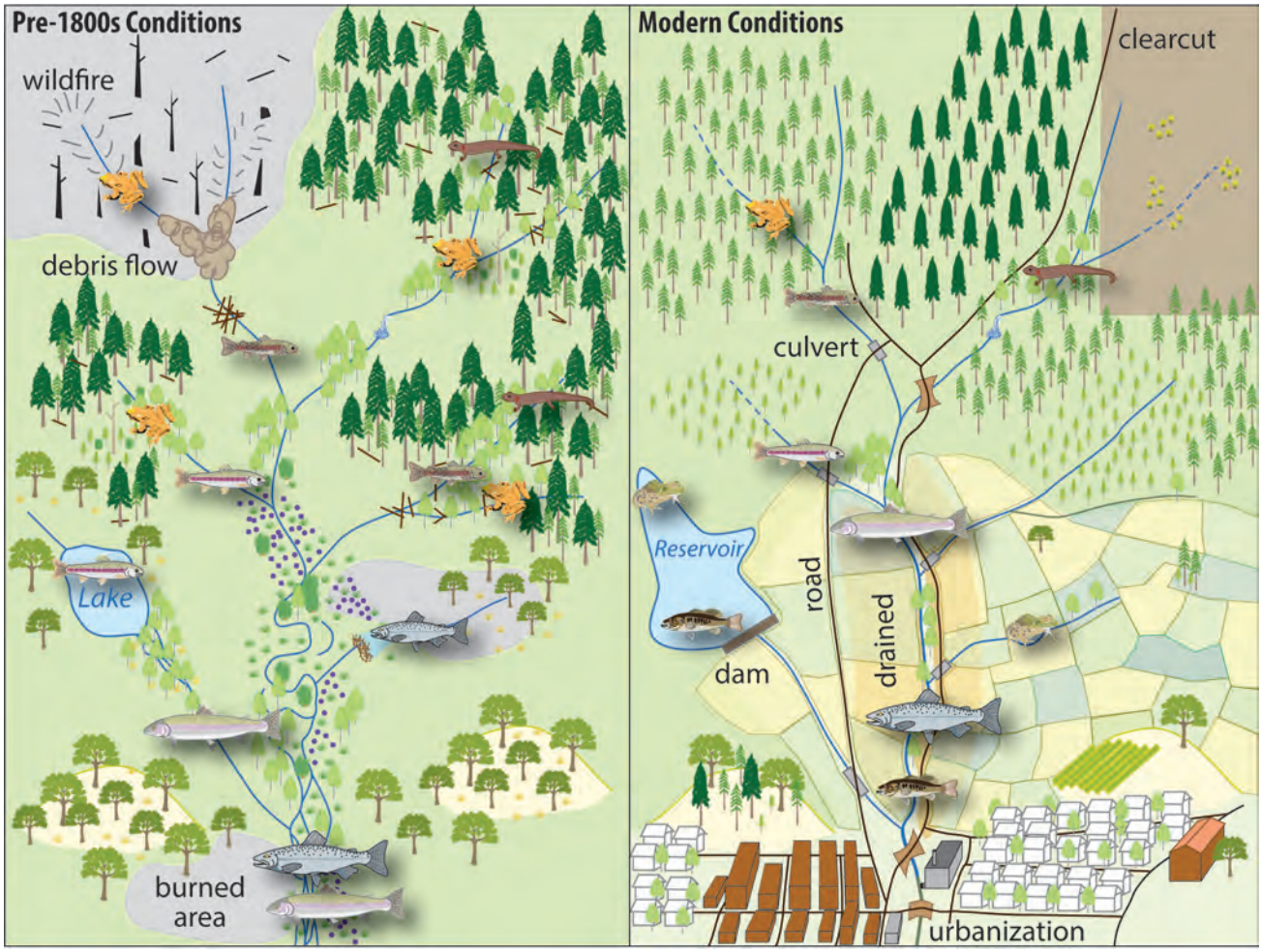


**Figure 1.** Historically, river systems of the Pacific Northwest connected a diverse array of freshwater and wetland habitats. Over time, development has reduced stream complexity and fragmented landscapes coincident with anthropogenic land uses such as agriculture, timber harvesting or residential development. Figure from Penaluna et al., 2017.

populations of anadromous salmonids that found spawning and rearing habitats throughout the connected corridors of the river network. The extensive floodplain of the Coquille River was a highly productive area for coho salmon (*Oncorhynchus kisutch*). However, this and other flat floodplains were colonised quickly by European settlers and continue to be used for agriculture.

In recent decades, migratory anadromous salmonids, including coho salmon, have been listed as 'threatened' or 'endangered' under the US Endangered Species Act, making them critical drivers of restoration and habitat protection. Millions of dollars of public funds have been spent on restoration intended to enhance the habitat and population-scale survival of this species. However, fish abundance continues to be lower than historical levels.

**Approach**

In coastal Oregon, riparian protection measures include a variety of approaches, from voluntary best management practices to legislated prescriptions (Boisjolie et al., 2017). The most rigorous protections are generally associated with extractive natural resource uses such as timber harvest or mining, while the least rigorous are linked with agricultural land uses. Policy approaches include prescriptive policies intended to eliminate pollution to waterways by specifying requirements for riparian areas and explicitly limiting certain management actions. For agricultural lands, outcome-based policy approaches are intended to minimise water pollution, allowing landowners discretion in land management so long as it does not negatively impact water quality standards. The efficacy of these approaches can be difficult to assess at a catchment scale. Prescriptive approaches may constrict

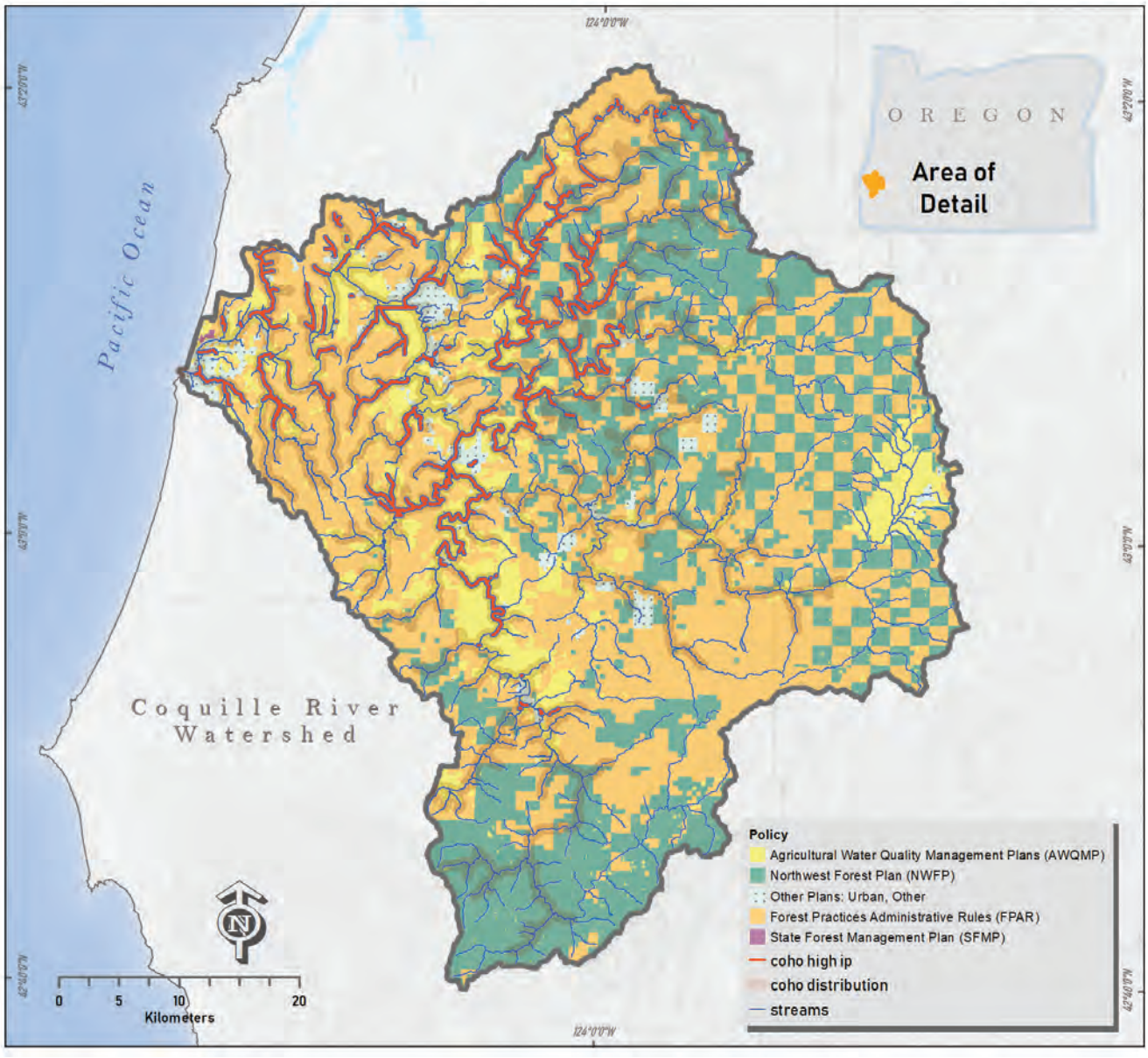


**Figure 2.** Coho salmon in the Coquille River Basin have historically utilised low-gradient floodplain areas. On the modern landscape, these areas are often associated with agricultural land uses. © Rebecca L. Flitcroft

Juvenile coho salmon (*Oncorhynchus kisutch*) © Adobe Stock

dynamic ecosystems to meet an ideal target condition, while outcome-based policies and a reliance on voluntary efforts can create gaps in protective efforts.

Protective efforts influence habitat conditions in time and space. Consequently, the variability in protective efforts has strong implications for the conservation of riparian ecological corridors. Overcoming fragmented riparian protections can be aided by:

- Legislative efforts;
- Restoration incentives;
- Collaborative restoration projects;
- Conservation designations;
- Technical assistance; and
- The formulation of collaborative governance bodies to address habitat and/or ecosystem degradation.

Understanding the extent of variable protective efforts can inform multi-agency policy responses for species recovery or conservation priorities. Developing an understanding of the mosaic of protective efforts can help identify and quantify gaps in them.

**Example of an ecological corridor**

For the Coquille River system, maps of riparian policy protections were overlaid with the distribution of coho salmon and areas of high intrinsic potential to support them (Figure 2). The maps show that the majority of riparian areas within the distribution of this fish are managed for agriculture, followed by timber harvesting. Further, areas with high intrinsic potential to support coho salmon are mostly located in agricultural areas. This shows a mismatch between riparian protection of coho salmon streams (which is determined by land ownership) and the location of habitats appropriate for different life stages of these highly migratory fish (which is determined by the hydro-geomorphic context of the river).

**Results**

Policies intended to protect riparian areas and coho salmon are more specific and enforceable in areas these fishes are less likely to occupy (Boisjolie et al., 2019). This gap in protections has led to the development of voluntary incentives for stream restoration actions and the management of working lands in the Coquille Basin. By mapping protections, their fragmentation along the continuum of the river network can be identified, allowing for targeted restoration or additional protection work. Tracking the effects of voluntary riparian protections, prescribed protections, voluntary approaches to stream restoration and collaborative landscape management are critical in evaluating the success of freshwater recovery throughout the river network. A broader perspective on identifying and quantifying fragmentation, as well as connectivity, is necessary if protections are to be effective for highly migratory fishes that must access habitats throughout a river system.

## 23. Protection of the free-flowing Bita River

Jose Saulo Usma and Cesar Suarez, *WWF Colombia*
Fernando Trujillo, *Omacha Foundation*
Michele Thieme, *WWF-US*

### Context and challenge

The Bita River in Colombia is 520 km long and its basin covers about 822,000 ha (Figures 1, 2). The river begins as a small, spring-fed stream in the middle of the llanos, a network of grasslands and seasonally flooded plains. The river meanders freely through this important and unique ecosystem, creating deep lagoons and beautiful beaches, until it reaches the Orinoco River. Along its path, the still-free-flowing Bita River supports rich biodiversity: freshwater fish, turtles (*Podonecmis* spp.) and crocodiles (*Crocodylus* spp.), river dolphins (*Inia geoffrensis*), jaguars (*Panthera onca*), tapirs (*Tapirus terrestris*), otters, and many other mammals, reptiles and birds.

Despite Colombia's wealth in natural assets, research has revealed that the llanos are one of the most under-protected ecosystems in the country. The country's ecosystems are increasingly under pressure from extractive industries, livestock grazing, large timber plantations and urbanisation. Additionally, the connectivity afforded by the Bita River allows migration of freshwater fish and seasonal movements of dolphins, both of which are critical for local livelihoods, including sustainable tourism, birdwatching and sport fishing.

**Key lesson**

Management agreements within this Ramsar site are important to maintain connectivity for both freshwater and terrestrial species by managing activities in the watershed such as sport-fishing and agriculture.

### Approach

The Alliance for the Bita River was created in 2014 and is composed of the Omacha Foundation, the Alexander von Humboldt Research Institute for Biological Resources, Corporinoquia, the Vichada Government, the Colombian Navy, Colombia's National Parks, the Palmarito Foundation, the Orinoco Foundation, La Pedregoza Corporation, and WWF. Since then, the alliance, fishers, tourism

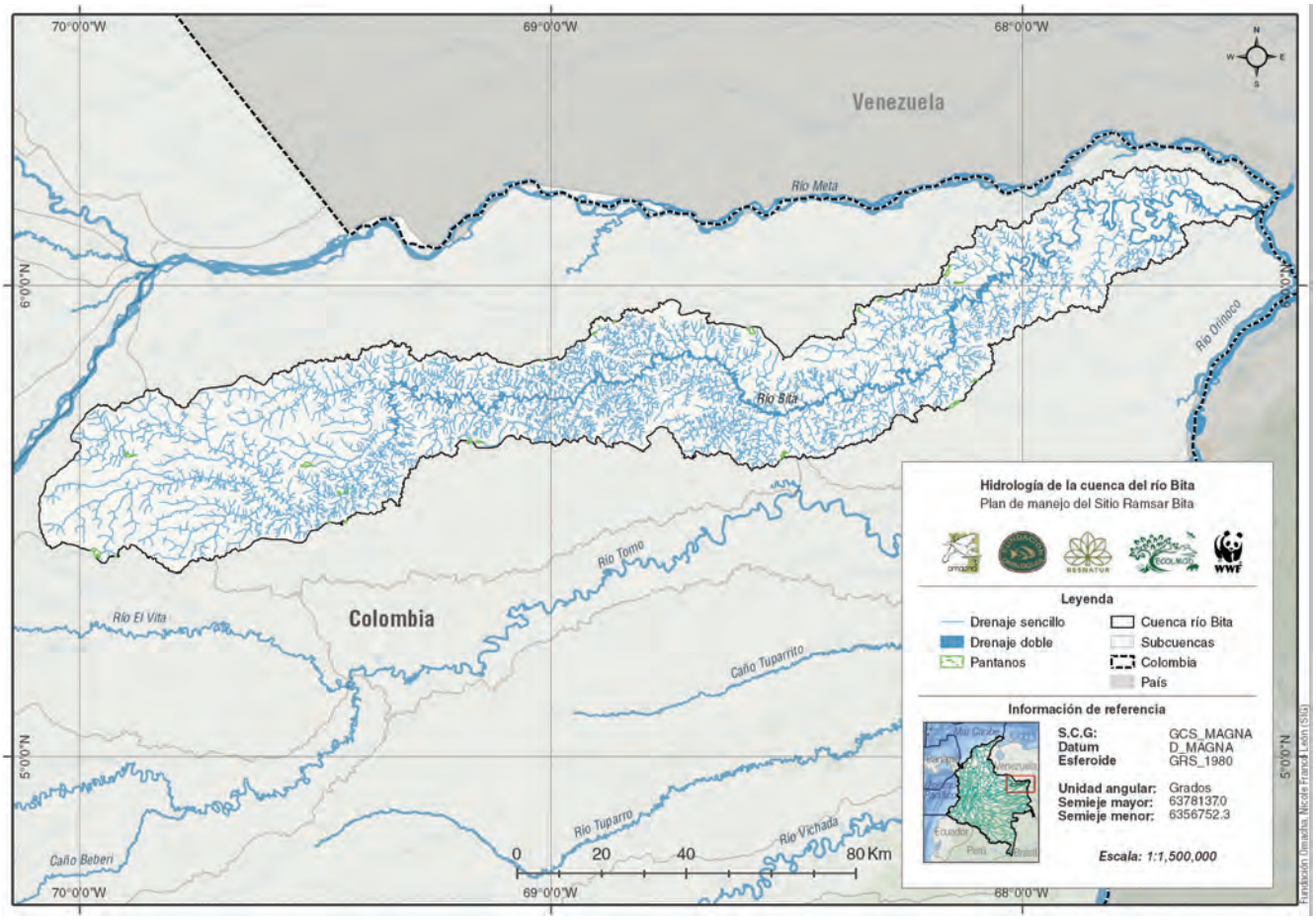


**Figure 1.** The Bita River Ramsar site in Colombia © Omacha Foundation, Courtesy Fernando Trujillo

**Figure 2.** Aerial view of the Bita River landscape © Omacha Foundation, Courtesy Fernando Trujillo

representatives, social and environmental organisations, scientists and local people have all been working together to protect the Bita.

To advance conversations about legally protecting the Bita, the alliance hosted a series of workshops with local stakeholders to understand the connections among various activities (such as agriculture and sustainable tourism) and protection. After better understanding the cause-and-effect relationships of these multi-sector activities, the group developed a decision-making framework that uses quantitative data to demonstrate the impacts of certain actions. This framework helped the government, the alliance and other partners choose the best actions to take to conserve the Bita River while meeting the needs of stakeholders.

### Example of an ecological corridor

The free-flowing Bita River supports movement and migration of many species, including the following:

- River dolphins: The Bita has one of the best populations of river dolphins thanks to its proximity to the Meta and Orinoco rivers, which supply food (fish) for the dolphins and key habitats for their reproduction.
- Migratory fish: The different types of water and the longitudinal and lateral connectivity between the Bita (black waters), Meta (white waters), and Orinoco (mixed waters) and their wetlands favour the reproduction of many migratory species.
- Tapirs, jaguars, and pumas: It is estimated that 600–700 tapirs, 60–70 jaguars and 100–120 pumas (*Puma concolor*) live in the Bita River Basin thanks to the ecological integrity of its forests and wetlands.
- Other species: The river corridor will support the conservation of other species such as peacock bass (*Cichla* spp.), freshwater stingrays (*Potamotrygon* spp.), giant otters (*Pteronura brasiliensis*), and river turtles.

### Results

On June 23, 2018, the Bita River was added to the List of Wetlands of International Importance of the Ramsar Convention. It is the largest Ramsar site in Colombia and one of the first anywhere to protect an entire free-flowing river and its basin (822,600 ha). Since the declaration, a management plan has been developed for the Ramsar site by the Omacha Foundation, Orinoquia Foundation, National University of Colombia, and RESNATUR (a private nature reserve network).

The management plan details actions to conserve and sustainably use the Bita's fisheries because the river is the epicentre for sport fishing in Colombia and important for the ornamental fish trade. Additionally, an agreement has been made to create within the Ramsar site an ecological corridor (228,000 ha) that connects the Upper and Middle Bita rivers and allows movement of 34 species of medium- and large-sized mammals including tapir, jaguar, puma, river dolphins, otters and migratory fishes. Among others, the agreement was signed between the Ministry of Environment, the Omacha Foundation, the Project Design Developers-Folgers Inc., the Tapirs Specialist Group of IUCN SCC, the forestry sector, and the farmers who are located within the ecological corridor in the Ramsar site. These parties committed to undertake sustainable agricultural practices and livestock production, forestry and responsible fruit production within the corridor and support the monitoring of flagship wildlife populations.

# Marine connectivity: Australia

## 24. The Great Barrier Reef: Systematically protecting connectivity without connectivity data

Michael Bode, *School of Mathematical Sciences, Queensland University of Technology, Australia*
Jon C. Day, *ARC Centre of Excellence for Coral Reef Studies, James Cook University, Australia*

**Key lesson**
In barrier reef systems, placement of protected areas and management of activities in buffer zones can promote stepping-stone connectivity, thus maintaining larval movements, migrations from inshore to offshore habitats, and movements of adult benthic and pelagic organisms.

### Context and challenge

Australia's Great Barrier Reef (GBR) is the world's largest coral reef ecosystem, and one of the country's most important ecological and economic assets. Most of the GBR is enclosed within the Great Barrier Reef Marine Park (GBRMP), a multiple-use marine park comprising eight different usage zones (Figure 1), with one-third zoned no-take. The Australian government, acting primarily through the GBRMP Authority, is responsible for management, undertaken in conjunction with other federal and Queensland agencies, Indigenous Traditional owners and various other stakeholders.

Although the GBRMP was originally created to protect the reef from mining exploration, its coral reefs are now mainly threatened by recurrent bleaching, cyclones and outbreaks of crown-of-thorns starfish. Large areas, particularly the inshore and northern reefs, have lost large proportions of their live coral cover in recent years. Secondary threats include adverse water quality, unsustainable fishing, dredging and coastal development. Despite these pressures, the condition of the GBR is good compared with that of many other reef systems globally.

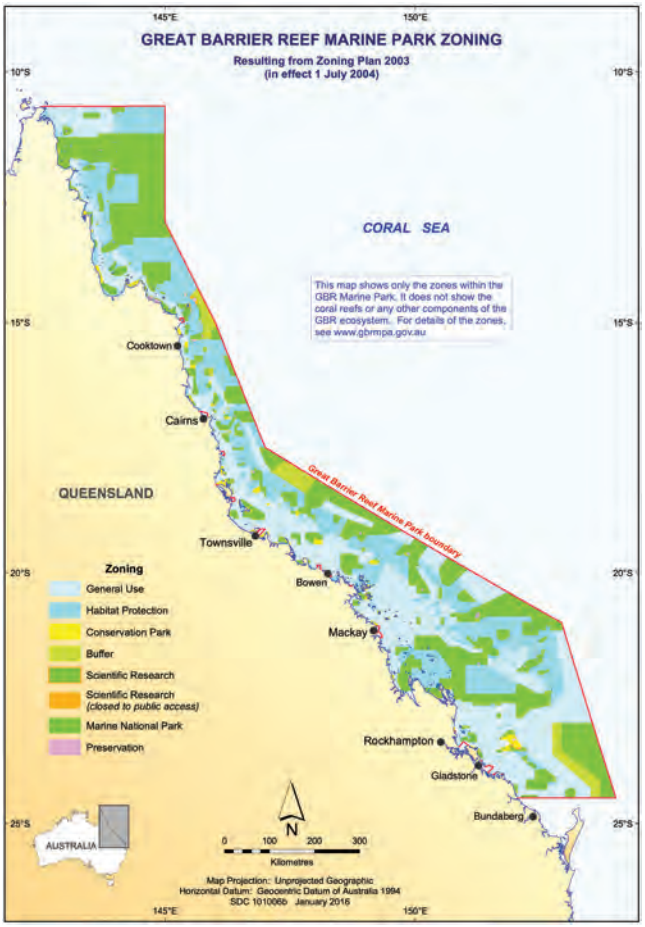


**Figure 1.** Current zoning for Great Barrier Reef Marine Park (resulting from the 2003 Zoning Plan, in effect since 1 July 2004). Map supplied by Spatial Data Centre, Great Barrier Reef Marine Park Authority, © Commonwealth of Australia (GBRMPA).

### Approach

Conservation of the GBR's coral habitat requires three types of connectivity to be protected. The first, and most important, is larval connectivity: most organisms on reefs have an obligate pelagic larval dispersive phase making connectivity a constant demographic necessity. Oceanic currents create spatiotemporally complex larval connectivity patterns that drive population dynamics on the GBR. These connectivity patterns are similar to terrestrial ecological corridors, but the dispersing organisms are not exposed to threats during dispersal, and so marine ecological corridors do not require protection. Instead, conservation outcomes are enhanced by networks of marine reserves that exchange large amounts of larvae, while fishery outcomes are improved when no-take zones are connected to fished areas. The second form of connectivity is ontogenetic migration, typically where species spend their early life-stages in estuarine/inshore habitats, before migrating offshore as adults; Figure 2 shows one example. The third is small-scale movement of adults for foraging or reproducing. Most coral reef species are benthic-associated, and so these movements occur at within-reef scales. However, pelagic species can undertake longer-distance adult movements between reefs.

The GBRMP was substantially rezoned and expanded in 2003, based on systematic planning principles. Eleven biophysical operating principles (BOPs) (GBRMPA, 2002) were devised to protect representative examples of each of the GBR's 70 bioregions (30 reef habitat; 40 non-reef) (Fernandes et al., 2005). The maintenance of connectivity was also an explicit goal of the marine park – both the total size of the no-take marine reserves and their individual locations were taken into account. As an overarching goal, BOP 9 recommended that no-take zones be chosen to maintain connectivity across the GBR. However, minimal data about connectivity were available at the time of the rezoning, and so several of the

BOPs were designed to prioritise potential proxies for each form of connectivity. BOPs 1 and 2 aimed to protect larval connectivity, particularly self-recruitment. For example, BOP 2 recommended that no-take zones be as large as possible, motivated by models indicating self-recruitment increased with reserve dimensions. BOP 4 recommended that no-take zones include whole reefs where possible, to protect connectivity for foraging and migrating adults.

**Results**

Little information on connectivity was available for the 2003 rezoning, so proxies were used to design networks of no-take zones that would ensure the exchange of larvae between them, as well as the export of larvae to fished areas. Recent empirical studies and biophysical modelling demonstrate that this approach was successful to some extent, with larval dispersal connecting no-take zones at a range of scales, from local self-recruitment (Harrison et al., 2012) to consistent bi-directional exchanges of over 250 km (Williamson et al., 2016; Bode et al., 2019).

There are three possible reasons why a network of no-take zones that was not designed with explicit connectivity data was nevertheless able to achieve connectivity outcomes. First, the GBRMP contains a very large proportion of effective no-take zones (33% of the entire area). We would generally expect that higher levels of protection will achieve superior connectivity outcomes. Second, explicit connectivity proxies form the basis of several BOPs, and these likely improved connectivity outcomes beyond the simple null expectation.

The final reason is less obvious. The GBRMP is a global exemplar of a systematically planned network. Several BOPs (specifically 5 and 7) aimed to create a 'representative' network, with no-take zones distributed across bioregions, latitudes and cross-shelf position. While these goals do not mention connectivity, evidence suggests that representiveness allows no-take networks to effectively protect previously unknown biodiversity features (e.g. mesophotic reefs, as in Bridge et al., 2016). It is entirely possible that representativeness principles are also responsible for the protection of connectivity in the GBR.

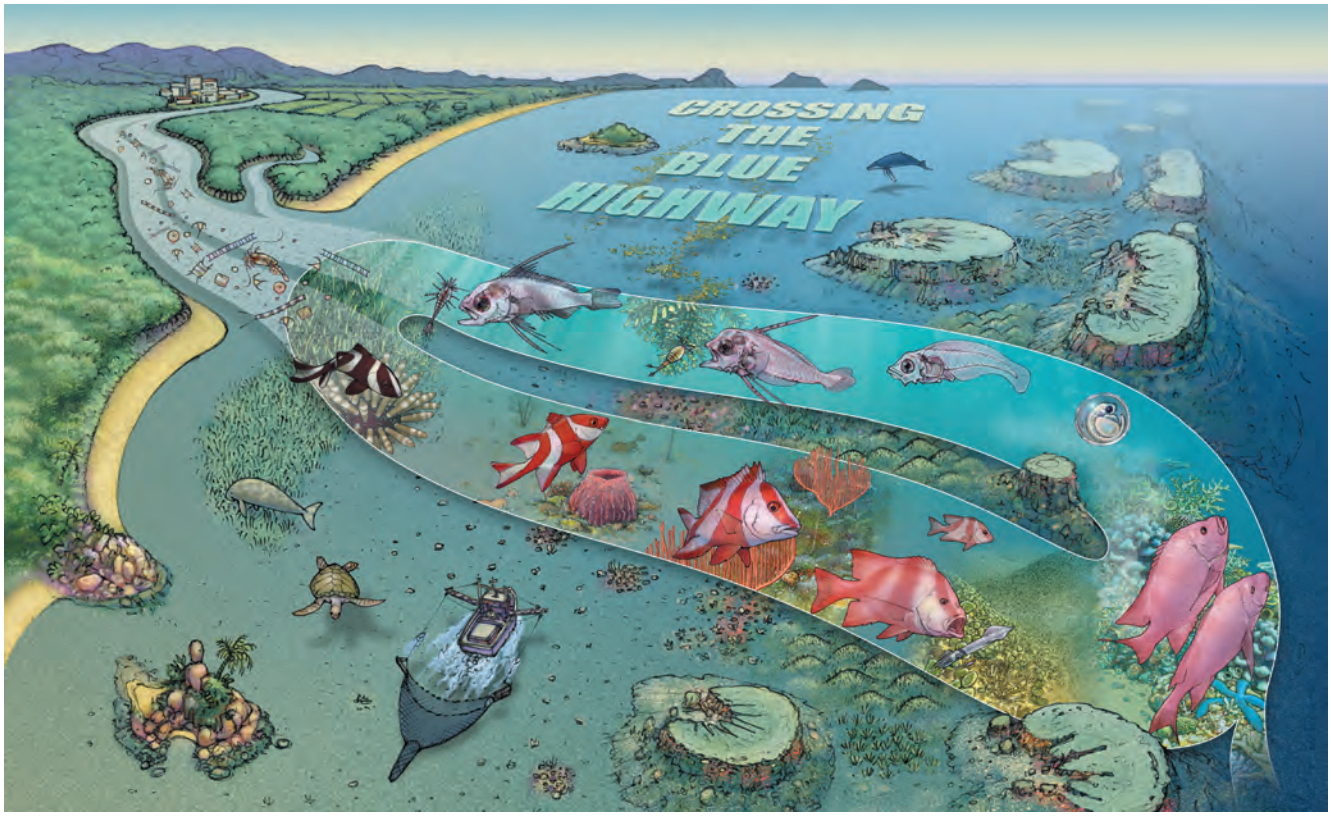


**Figure 2.** 'Crossing the Blue Highway': The red emperor (*Lutjanus sebae*) spends different stages of its life cycle utilising different habitats across the GBR.
© Russell Kelley/Australian Coral Reef Society, http://www.russellkelley.info/print/the-blue-highway/

# Marine connectivity: North America

## 25. Northern Channel Islands: Connectivity across a network of marine protected areas contributes to positive population and ecosystem consequences

Jennifer Caselle, *Marine Science Institute, University of California Santa Barbara*
Mark Carr, *Department of Ecology and Evolutionary Biology, University of California Santa Cruz*
J. Wilson White, *Coastal Oregon Marine Experiment Station, Oregon State University*

### Context and challenge

Temperate coastal marine ecosystems produce a diversity of ecosystem services, including the support of recreationally and commercially important fisheries, economically important ecotourism and other cultural values. One temperate marine ecosystem of particular importance is kelp forests, which support some of the most species-rich and productive ecosystems on Earth. They are subjected to a host of human impacts, particularly from fisheries, invasive species, and various manifestations of global climate change.

**Key lesson**

The creation of an ecological network of marine protected areas has helped to restore species, increased connectivity and made the network more robust to invasive species.

### Approach

In 1998, a group of fishers, managers and other citizens in southern California, USA, was concerned about declining resources such as abalone, lobsters and rockfishes in nearshore ecosystems, including kelp forests. This group approached the California Fish and Game Commission with a proposal to set aside areas for protection in the northern Channel Islands, a chain of four islands north-west of Los Angeles and separated from the mainland by the Santa Barbara Channel. In 2003, following a multi-year public process, the state of California, in collaboration with Channel Islands National Park (CINP), created 13 marine protected areas (MPAs) within state and national park waters. In 2007, the National Oceanic and Atmospheric Administration extended eight of these MPAs into Channel Islands National Marine Sanctuary (CINMS) waters (Figure 1). Thus, the MPAs encompass both state and federally managed waters. The objectives of the MPAs were to help restore biodiversity, ecosystem health and fisheries species by protecting marine life and habitats. Extending from the intertidal zone to depths of 1,400 m, the MPAs encompass a diversity of ecosystems, distinguished by seafloor type (rock versus sand) and depth.

Today's Channel Islands MPA network has a large number of overlapping agency jurisdictions. Eleven federal, state and local agencies have some jurisdiction in the planning region. While both CINMS and CINP overlap around the northern Channel Islands, neither agency regulates commercial or recreational fishing. The California Department of Fish and

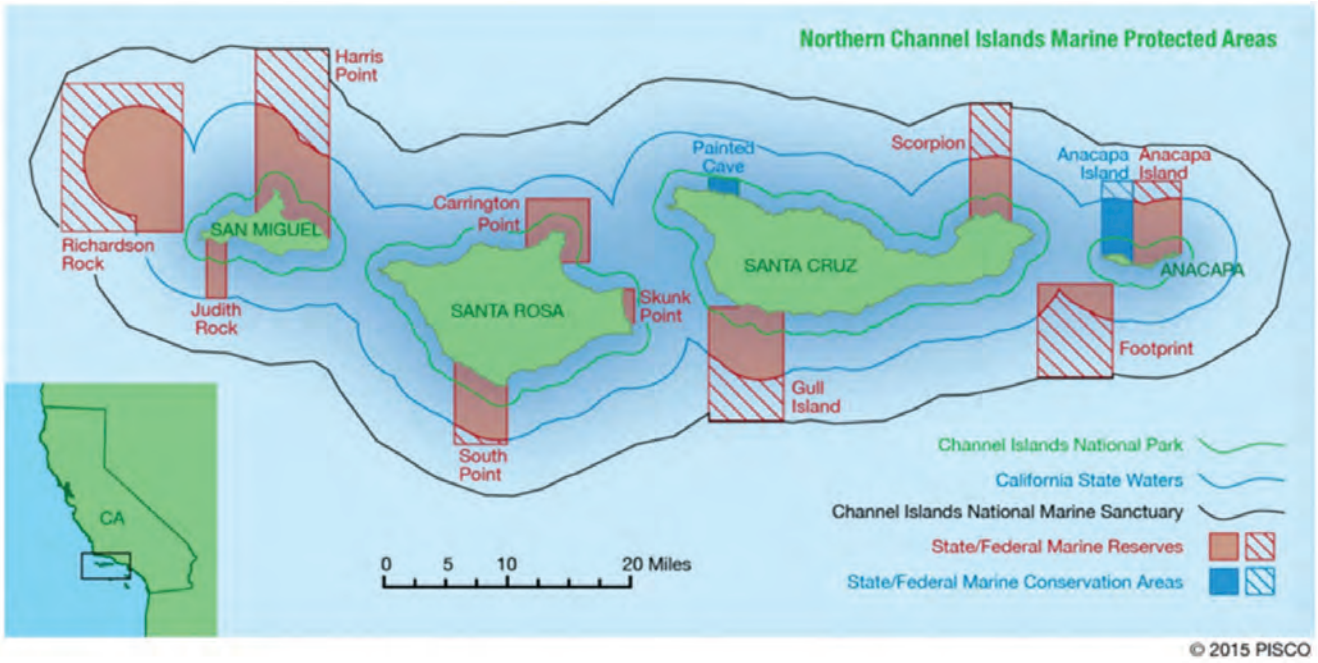


**Figure 1.** Map of the distribution of marine protected areas across the Northern Channel Islands archipelago off the coast of southern California, USA (see inset). Map indicates the jurisdictional ranges of state and federal institutions and the two types of protected areas (marine reserves and marine conservation areas)
© The Partnership for Interdisciplinary Studies of Coastal Oceans

Kelp forest © Adobe Stock

Wildlife manages all fisheries in state waters (within 5.6 km of the shore), while the California Fish and Game Commission (an appointed body) has authority to set all state fishery regulations, including the creation of MPAs.

### Examples of ecological corridors

Though not originally designed as a network of MPAs connected to one another by the dispersal of young (i.e., fish and invertebrate larvae), subsequent analyses of oceanographic currents and larval dispersal patterns indicated that young generated in the MPAs very likely are transported to and contribute to the replenishment of populations and communities in other MPAs, thus forming a *de facto* network. The primary way ecological corridors have been analysed is by simulating the movement of larvae using numerical ocean circulation models that describe currents in the region. For example, Watson et al. (2010) simulated the movement of larvae of two important fishery species – kelp bass (*Paralabrax clathratus*) and kelp rockfish (*Sebastes atrovirens*) – to and from sites throughout southern California, including the Channel Islands MPAs. The simulations calculated the probability of larvae travelling from one location to another; the authors then multiplied those probabilities by estimates of the spawning biomass at each location to predict how many larvae travelled along each potential ecological corridor. The analysis showed that kelp bass larvae produced inside MPAs on Santa Cruz and Anacapa islands likely disperse to other MPAs in the network and to fished areas; the same was true of kelp rockfish larvae produced in MPAs on San Miguel Island (Figure 2). Thus, the MPAs are linked by ecological corridors, but different corridors are used by different species, depending on habitat. In this case, kelp bass prefer the warmer water of the eastern islands while kelp rockfish prefer the cooler western waters.

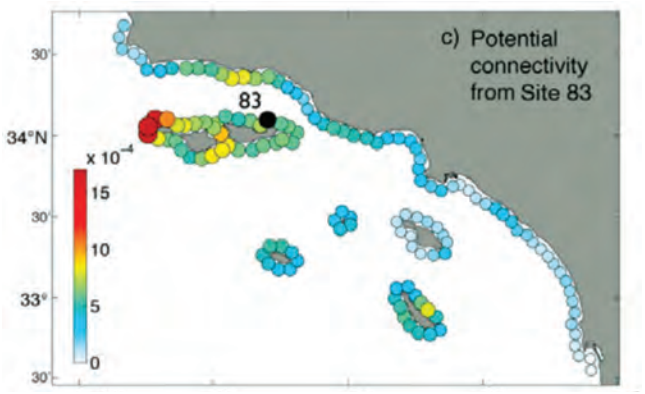


**Figure 2.** Predicted dispersal of larval kelp bass using an ocean circulation model of the Southern California Bight (Watson et al., 2010). Each coloured circle corresponds to a spatial node (site) in the model from which simulated larvae could be released and to which they can settle. In this example, the connectivity from Site 83 (which overlaps with the Scorpion State Marine Reserve on Santa Cruz Island) is shown. The colour of each dot represents the relative number of larvae that travel along the ocean corridor from Scorpion to the other sites (the numerical values are expressed as a proportion of the total number of larvae released from all sites in the simulation). Thus, there are strong connections to the other MPAs in the Channel Islands, as well as to non-MPA sites.

### Results

The ecological network of MPAs implemented in the Channel Islands region contains 21% of the CINMS waters in 11 state marine reserves (no commercial or recreational fishing allowed) and two conservation areas (where some types of fishing are allowed). Following a decade of protection, monitoring of nearshore kelp forests in the Channel Islands MPAs showed increases in the biomass of targeted fish species inside the MPAs relative to fished areas. While the biomass did not increase spectacularly, the dramatic declines that were predicted by some models as a result of potential displacement and compaction of fishing effort did not take place either. More recently, protection of higher-level predators within older, fully protected areas has been shown to prevent invasion of a non-native macroalgae.

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# PLANNING FOR CONNECTIVITY UNDER CLIMATE CHANGE:

## USING BOBCAT MOVEMENT TO ASSESS LANDSCAPE CONNECTIVITY ACROSS SAN DIEGO COUNTY'S OPEN SPACES

*Photo Credit: Shouqin Huo*

SAN DIEGO STATE UNIVERSITY

**FINAL REPORT**

**JUNE 2013**

PREPARED FOR THE SAN DIEGO FOUNDATION

GRANT NUMBER C-2011-00177

BY:

MEGAN JENNINGS

REBECCA LEWISON

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## EXECUTIVE SUMMARY

Our assessment of connectivity using bobcat movement and habitat use through camera, mortality, telemetry, and genetic data indicate that while functional connectivity is intact in some areas of the San Diego MSCP preserve network, data revealed that connectivity is impaired in other areas. Our connectivity assessment suggests:

- Overall, there is evidence of connectivity in the inland and coastal areas of the MSCP network that we sampled.
- Genetic analysis showed some degree of genetic differentiation between coastal bobcats west of I-15 and inland animals to the east, but did not indicate subpopulation differentiation has occurred. This supports the assertion that the coastal and inland areas have some level of connectivity.
- Movement analyses (camera and telemetry) showed direct use of five of seven linkages that were monitored. Detected movement was highest in Linkage 6-7, Linkage 8-10, and Linkage 5-6.
- For linkages not directly monitored, results from landscape models suggest that at least five other areas identified as putative linkages may have limited to no current connectivity, and another nine may only function partially. These limitations will likely increase under projected land use.
- Habitat alteration and recreation, in addition to other ecological variables, are currently affecting wildlife occupancy. These effects may increase under projected land use shifts.
- Heavily traveled secondary roads with traffic moving at high rates of speed may pose the largest threat to medium-wide ranging wildlife species attempting to move between core conserved areas, especially from coastal to inland areas. Roadkill mortality appears to increase with seasonal increases in animal movement.
- Projected habitat shifts resulting from climate change did not lead to substantial changes in habitat suitability or effective distance between preserves. However, future land use plans that lead to increased areas of altered use categories are likely to reduce habitat suitability in and around inland preserves.

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## INTRODUCTION

Current land management plans throughout the U.S. and Europe are designed to protect biodiversity by establishing a network of core habitat areas that are connected via linkages (Nelson *et al.* 2003). The central principle of this large-scale conservation planning is that viable populations and natural communities can be supported by a connected landscape network (Beier *et al.* 2006, Crooks and Sanjayan 2006, Boitani *et al.* 2007, Barrows *et al.* 2011), particularly as the landscape becomes altered by anthropogenic features like roads and housing developments. Landscape connectivity allows for movement among patches of suitable habitat, reduces the chance of extinction and effects of demographic stochasticity on small populations (Brown and Kodric-Brown 1977), and maintains gene flow between populations in patchy landscapes (Simberloff *et al.* 1992). Over longer time scales, and in the face of changing abiotic conditions, connectivity may also prove critical for range shifts in response to landscape changes caused by changing climate and altered disturbance regimes (Hannah *et al.* 2002, Heller and Zavaleta 2009).

In southern California, this landscape-scale network approach has been adopted in response to the widespread habitat conversion and fragmentation that has resulted from intense development (Riverside County 2003, Ogden 1996). Although the direct effects of anthropogenic landscape alteration, namely habitat loss and fragmentation, are paramount in this region (Crooks 2002, Beier *et al.* 2006, Soulé 1991), the potential for large scale shifts in vegetation and habitat types as a result of climate change may present an equally large risk to ecological networks.

General predictions from numerous climate models for the western United States suggest that temperatures will increase, there may be an increase in aridity (Westerling *et al.* 2003), and an overall reduction in rainfall (Hannah *et al.* 2002). These conditions are likely to extend fire seasons and increase fire frequency (Swetnam and Betancourt 1998, Brown *et al.* 2004). These predicted shifts in vegetation distribution and more frequent and/or severe wildfires driven by drier summers and earlier Santa Ana seasons (Miller and Schlegel 2006) may result in large-scale vegetation type conversion to non-native annual grasslands (Bachelet *et al.* 2001, Lenihan *et al.* 2003) and reductions in standing water availability.

All of these projected changes may have direct and indirect (*i.e.* food web) effects on wildlife. Temperature shifts may drive migration upslope to cooler climates (Hughes 2000) or westward to areas with greater marine influence and lower temperatures. Some species or individuals, such as females rearing young, may need improved access to water sources in the form of dense riparian areas and perennial streams, which are found in western portions of San Diego County. Whatever the response, shifts in distribution and habitat use can present a fundamental challenge to the currently designated landscape conservation network.

One of the central sources of uncertainty regarding how wildlife will respond to climate change is the lack of baseline data on current connectivity. In this study, we use bobcats as a model species to establish a foundation of knowledge on the present status of connectivity. Among wildlife species in southern California, bobcats respond negatively to habitat fragmentation, particularly when it results in smaller or more isolated habitat patches (Crooks 2002, Lyren *et al.* 2006, 2008, 2009). As a result, bobcats have been identified as a priority focal species for connectivity monitoring in southern California (Ogden 1996, Crooks 2002, County of San Diego 2004, South Coast Wildlands 2008). Bobcats also have the potential to function as an umbrella species, whereby conservation of viable populations and suitable habitat would confer

protection to other species using similar habitats and movement corridors. Because bobcats are medium-ranging habitat generalists, studying their movement ecology and genetic diversity allows insight into landscape connectivity on a sub-regional scale. Because of their sensitivity to anthropogenic impacts to their habitat, bobcats also present an ideal system to study the effects of human recreation activities on wildlife. Understanding how this species responds to the complex interaction between human development and shifting habitats resulting from climate change is essential to preserve long-term connectivity and efficacy of the ecological network in this landscape.

Quantifying or assessing landscape connectivity, however, is non-trivial (Fagan and Calabrese 2006) given the context-dependent nature of connectivity (Crooks and Sanjayan 2006). Spatial and temporal scales may be different for wide-ranging species with a home range of tens of kilometers that responds to large-scale ecosystem processes versus a non-vagile species with a limited home range. Crooks and Sanjayan (2006) suggest connectivity assessments consider both physical and structural connectivity of an area, *i.e.* the physical arrangement of habitat on the landscape, as well as the response to that arrangement by individuals or species (Taylor *et al.* 1993, Tischendorf and Fahrig 2000a, 2000b). While conceptually this is intuitive, measuring both physical and functional connectivity is logistically difficult. There is a general lack of knowledge of how animals are currently using the landscape, and how landscape use changes in response to dynamic landscape processes over time. Most recent efforts in connectivity assessment and planning utilize the concepts of resistance and cost (*sensu* Adriaensen *et al.* 2003) in evaluating functional connectivity. The former refers to the friction, or difficulty, in moving through each individual cell in the landscape and the latter represents the cumulative resistance encountered traveling through a linkage.

To assess the status of connectivity in a landscape-scale conservation network in southern California like the San Diego MSCP, this study was designed to collect robust, multi-faceted data to evaluate habitat use, response to human recreation, use of landscape linkages, and gene flow using bobcats as a focal species. The goal of the project was to establish the current state of landscape connectivity as well as connectivity under projected future conditions resulting from land use and climate shifts. Using bobcats as an indicator, we compared the use of urbanized and more natural habitats and determined how landscape features influenced home range size and distribution. Using these multiple, complementary datasets we asked the research questions: ***1) What is the current state of physical and functional connectivity in the MSCP? 2) Are there barriers to movement through linkages? If so, what and where are those barriers? 3) Does human recreational activity affect wildlife use in habitat cores? 4) How is movement across the landscape likely to change under climate change and land use projections?***

## METHODS

### Data Collection

*Study Area*

This study was conducted within the San Diego Multiple Species Conservation Plan Area in southern California across three sites, the Peñasquitos /SR56 area representing fragmented, coastal habitats, the SR67 Corridor between Lakeside and Poway, and the Ramona/SR78 area (Figure 1). The natural habitats and protected open space in the area are primarily publicly-owned, and include Los Peñasquitos Canyon Preserve, Black Mountain Open Space, Sycamore Canyon and Goodan Ranch Preserves, Boulder Oaks Preserve, San Vicente Highlands Preserve,

Iron Mountain, San Dieguito River Park lands, and a portion of the Cleveland National Forest in Pamo Valley, north of the town of Ramona. These areas are also centered on major transportation corridors that cross the preserve networks, specifically SR56 near the coast, SR67 inland, and SR78 to the north.

Elevation across the three study sites ranged from sea level at the coast to 1000 m in the inland foothills. Habitat type in the study area varied with both elevation and distance from the coast, but was predominantly a shrubland ecosystem. Habitats across these areas included coastal sage scrub dominated by California sagebrush (*Artemesia californica*), chaparral habitat types generally dominated by scrub oak (*Quercus berberidifolia*) or chamise (*Adenostoma fasciculatum*), oak woodland with coast live oak (*Quercus agrifolia*), grasslands dominated by non-native annual grasses, riparian zones with an oak (*Quercus agrifolia*) or sycamore (*Platanus racemosa*) overstory and herbaceous understory, as well as urban and altered areas. The Mediterranean-climate of the study region is characterized by hot, dry summers and mild, wet winters with precipitation often less than 300 mm.

*Remote Cameras*

To measure animal distribution, quantify occupancy across the MSCP, and consider the effect of recreation on animal distribution, remote camera stations were established across the study area in locations ranging from internal preserve cores to linkage areas and road crossings (Figure 2). Placement of the 36 camera stations was established on a 2 km grid, based on the minimum expected home range for a bobcat in urbanized landscapes in southern California. Locations for 12 cameras in each of the three study areas were selected to represent an equal sampling of the landscape features listed above, as well as a range of recreational use intensity (Table 1). We primarily utilized two types of cameras, the Cuddeback Expert white-flash camera (Cuddeback, Green Bay, WI, USA) and the LTL Acorn 5210A940 infrared camera (Old Boys Outdoors, Stone Mountain, GA, USA). As a result of theft, vandalism, and equipment failure, some of the older model Cuddeback Expert cameras were eventually replaced with Cuddeback Attack cameras. Cameras were deployed between November 30, 2011 and March 16, 2012 and were run for periods ranging from nine to 12 months. Cameras were set to capture images 24 hours per day, logging over 300,000 images from the 36 stations. Images were manually processed to identify species in each photo and entered into the program Camera Base 1.6 (Tobler 2012), an Access-based database for camera data and photo management.

*Mortality Assessment*

During the project, we identified and mapped any roadkilled bobcats reported by the public, cooperators, or project staff. Roadkill locations identified prior to the project period were also incorporated into our mapping. If possible, the carcass was collected and stored for necropsy where we collected a variety of samples to be stored for genetic analysis and for possible future use (*e.g.* anticoagulant screening of blood samples). We also collected a number of bobcat carcasses provided by the wildlife rehabilitation center, Fund for Animals Wildlife Center in Ramona, CA. Any patients that arrived and did not survive were stored for us, which included a number of animals that succumbed to notoedric mange. For all carcasses, we recorded cause of death (if known or identifiable), date of collection, sex, weight, body condition, and size. These data are now incorporated into the long-term bobcat mortality database managed by collaborators Lisa Lyren and Erin Boydston, United States Geological Survey – Western Ecological Research Center.

*Animal Capture and Telemetry*

Bobcats (n = 17) were trapped in baited cage traps (61cm x 43cm x 109cm) and sedated with a combination of ketamine HCl and xylazine HCL. All trapping, collaring, and tracking efforts were conducted by San Diego State University project staff (California Department of Fish and Game Scientific Collecting Permit #SCP-009632, SDSU Animal Protocol # 10-09-027L) between 2009 and 2012. Animals were weighed, measured, ear tagged, and fitted with one of two GPS collar brands (TCG181 or TCG271, Sirtrack Ltd., Havelock North, New Zealand; Quantum 4000, Telemetry Solutions, Concord, California, USA). During animal processing, we opportunistically collected all samples with the potential for future beneficial use. Blood, tissue, and buccal swab samples were taken from captured individuals for genetic testing to examine genetic connectivity across the project area.

Collars were set to collect fine-scale movement, gathering locational fixes eight times per day 5 days/week and 48 times per day 2 days/week, to track individual movement in relation to cores, linkages, potential barriers, human development over the course of six to nine months. Data were retrieved from collars with remote download, or stored-on-board until retrieval through recapture or a timed remote drop-off component in the collar. Data were checked and filtered for inaccurate and erroneous locations prior to analysis, and all locations with poor quality, undefined location (1-dimension or 1d) fixes were removed.

*Genetic Sampling*

To evaluate the functional connectivity (*i.e.* gene flow) across the sampled area of the MSCP, we collected tissue samples from a total of 62 bobcats gathered from a combination of live trapping, roadkill, and from assembling samples collected opportunistically by collaborators from areas in San Diego County. Genetic samples collected in the field were stored frozen at -20°C until they could be processed in the laboratory. All genetic lab work was conducted in the lab of Dr. Holly Ernest at UC Davis using microsatellite markers that had previously been tested on bobcat samples by Dr. Jennings in 2007 and 2008. Genomic DNA was extracted from blood and tissue using the QIAamp DNeasy blood and tissue kit, and from buccal swabs using the QIAamp DNA Mini and Blood Mini Kit (Qiagen Inc., Valencia, CA, USA), all following the manufacturer's protocols. We amplified 22 microsatellite loci (Table 2) for polymerase chain reaction (PCR). After initial optimization and testing, primers were grouped into multiplexes and prepared for PCR using the Qiagen Multiplex PCR Kit (Qiagen Inc., Valencia, CA, USA). PCR protocols followed the manufacturer's recommendations for the Multiplex PCR Kit. Thermal cycling parameters included an initial denaturing step at 95° C for 15 minutes, followed by 35 cycles of 94° C for 30 seconds; 54-60° C for 90 seconds; 72° C for 90 seconds, and then a final extension step at 72° C for 10 minutes. PCR product was analyzed using an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) and STRand software (Toonen and Hughes 2001). All PCR and genotyping was duplicated until two consistent results were obtained to reduce genotyping errors that can result in false alleles or allelic dropout.

**Data Analysis**

*Remote Cameras and Occupancy Modeling*

We analyzed all camera data using an occupancy modeling approach to identify the occupied rates within the monitored area. An occupancy approach does not monitor abundance;

rather it is used to establish the covariates that affect detection rates as well as the likelihood of species presence at each station. To analyze the camera data using this occupancy framework, we identified all photos of bobcats at all camera stations and created a capture history based on two week time intervals. If a bobcat was detected at a station within the selected two week period, it was recorded as a presence (1), and if not, as a non-detection (0). If the camera was not functioning or not present for a given time frame, a no-data value was recorded. Due a high level of missing values at four camera stations (78-BV, PV-SYC, 56-BV, and PQ-805) resulting from malfunctioning equipment, only 32 camera stations were included in the occupancy modeling. The time period analyzed included 18 two week periods between January and September 2012. These data were input in program PRESENCE 3.1 (Hines 2010) along with covariates for each camera station, including site type (core, bridge, culvert, or any linkage), recreation level (low or high), elevation, distance to major and local roads, and distance to water. We also recorded the proportional area in a 30m buffer around each camera station of each land use type and habitat type described in the habitat modeling section above. Survey covariates, or factors that may influence detection, included camera model at each station and whether the time period was during the wet or dry season. Models were run as single-season, assuming a closed population with no colonization or extinction. Model selection was based on the information theoretic approach using AIC, ΔAIC, and model weights (Burnham and Anderson 1998).

*Mortality Assessment*

We evaluated our mortality database to determine common causes of mortalities from the carcasses we salvaged during the study period. To visualize vehicle-caused mortalities for bobcats, we mapped all sites where mortalities occurred and identified common features of roadkill sites. With increasing numbers of mange mortalities during the project, we also established a database of incidences of mange reported to us by colleagues in the County, identified on remote cameras, or diagnosed during necropsy.

*Home Range*

Bobcat habitat use and range was calculated with a 95% adaptive local convex hull method (LoCoH, Getz and Wilmers 2004), using a=18,000 for bobcats. The LoCoH method is well-suited for constructing home ranges in landscapes with features that result in a distribution of point locations exhibiting sharp boundaries, corners, or holes, as is the case for the study area in southern California. The open spaces that make up the bobcat habitat in the study area are intersected by freeways, highways, and secondary roads, and abutted by housing developments and business parks, features generally avoided by bobcats. In addition to calculating the overall home range area with the LoCoH methods, we also calculated the proportion of home range area overlapping urban areas for an estimation of the degree to which animals may be constrained by unsuitable habitat adjacent to open space preserves.

*Habitat Models*

One component of our connectivity assessment was developed using habitat models. To model bobcat habitat suitability relative to the human landscape and other environmental factors, we used the telemetry data from bobcat GPS collars and evaluated the areas used relative to four different habitat categories: habitat features (habitat type and distance to water), anthropogenic landscape features (land-use type, distance to major roads, and distance to local roads), shifting fire-frequency (fire-return interval departure) and topographic variables (elevation). Habitat

covariates were developed from the San Diego Association of Government's (SANDAG) vegetation data which were reformatted into seven groupings, water and wetlands (WAT), altered habitat (ALT), grasslands (GRS), shrublands (SHB), riparian areas (RIP), forested areas (FOR), and other (OTH), which included small areas of desert scrub. Additional information on methods employed can be found in Appendix A.

Based on the results of the habitat selection models, we evaluated the current state of landscape connectivity and the predicted state under projections of future climate and land use changes. There were three components to this assessment: habitat suitability, landscape resistance, and effective distance (*i.e.* cost-weighted distance). We followed established methods (Singleton *et al.* 2004, Beier *et al.* 2007, Spencer *et al.* 2010, Beier *et al.* 2011), and first identified landscape permeability by assigning habitat suitability values, based on empirical values from generalized linear mixed models (GLMMs), between ten (least suitable) and 100 (most suitable) to categories in the GIS raster layers based on the results of univariate modeling and the multivariate model for each species. The biological interpretation of these values, as suggested by Beier *et al.* (2007) is that 100 is equivalent to the best habitat with highest survival and reproductive success, 80 is the lowest value with successful breeding, 60 is associated with consistent use and breeding, 30 represents occasional use for non-breeding activities and anything below 30 is avoided (see Appendix B for more information on methods).

We calculated these surfaces both under current and future conditions, incorporating habitat shifts and land use changes to provide a comparison. Planned land use data from SANDAG's Series 12 Regional Growth Forecast (2050) provided input for projected shifts in land use. We also employed current and future habitat data developed from models established by Stralberg *et al.* (2009). The projected future vegetation classification models used Random Forest algorithms and were based on projections from two different climate models: NCAR CCSM3.0 (National Center for Atmospheric Research Community Climate System Model) averaged from 2038-2069 (478-610 ppm $CO_2$), and the GFDL CM2.1 (Geophysical Fluid Dynamics Laboratory Coupled Climate Model) averaged from 2038-2070 (478-615 ppm $CO_2$). When analyzed in our connectivity assessment, the difference between the two climate models was negligible, thus only results from the GFDL CM2.1 model are presented in comparison to the current vegetation condition. The vegetation projection models, like all climate models, are not perfect; the highest spatial resolution is 800 m grid cells and there is inherent uncertainty in modeling future scenarios. However, these vegetation classification models are a published and peer-reviewed product and represent the best available data at the present time.

*Genetic Assessment*

Data were initially assessed in the Excel Microsatellite Toolkit (Park 2001). Based on published findings of restricted gene flow in southern California (Riley *et al.* 2006, Lee *et al.* 2012), data were split into two putative subpopulations, coastal and inland, for analysis. The data were evaluated in Microchecker 2.2.3 (Van Oosterhout *et al.* 2004) to test for issues of stuttering, null alleles and allelic drop-out. GENEPOP on the Web (Raymond and Rousset 1995, Rousset 2008) was used to test populations for Hardy-Weinberg equilibrium and linkage disequilibrium. $F_{ST}$ and population differentiation was calculated in GENEPOP, and followed by tests to estimate subpopulation differentiation ($D_{est}$) using Software for Measurement of Genetic Diversity (Crawford 2010) given recent criticisms of $F_{ST}$ (Jost 2008). To evaluate the putative subpopulation structure we defined, we ran program STRUCTURE 2.3.3 2 (Prichard *et al.* 2000, Falush *et al.* 2003) to identify genetically distinct subpopulations (K). We ran a burn in of 10,000

and ran 1,000,000 Markov Chain Monte Carlo iterations. We tested K from 1 to 5 populations, and repeated the analysis 100 times for each K to verify the consistency of likelihood values between runs. In order to choose which value of K best fits our population we analyzed ln P(X|K) as suggested by the STRUCTURE manual (Prichard *et al.* 2000) as well as the ΔK method (Evanno *et al.* 2005).

## RESULTS

During the course of the project, we handled 19 bobcats and collared 17, collected over 300,000 photos from camera stations, identified 24 roadkill locations, and processed 62 genetic samples.

*Remote Cameras and Occupancy Modeling*

Photos processed from the remote camera stations identified bobcats at all but two camera stations during 28 two-week sampling periods. An additional four stations only detected bobcats once during the camera monitoring. Stations with the lowest detection of bobcats included Iron Mountain, Mount Woodson, San Vicente Highlands, Upper Beelor Canyon, three crossings under SR78, Carmel Valley Road at Black Mountain, and Santa Luz at Camino del Sur. Stations with the greatest detections of bobcats (22-26 detections out of 28 sampling periods) included Goodan Ranch, McGonigle Canyon, and Boulder Oaks (see Appendix C for more information on model selection and results). Models suggested that bobcat detection was lower with the older model Cuddeback cameras, and occupancy was negatively associated with bridges, altered habitat, and camera stations within putative linkage zones compared to those in core conserved areas. Although not significant, we also found that bobcat occupancy rates were lower at stations with high recreation and at lower elevation (*i.e.* coastal) stations. Occupancy rates ranged from 0.66 at the Black Mountain Road bridge over Los Peñasquitos Creek to 0.91 at Boulder Oaks Open Space Preserve with higher occupancy rates overall in the inland study areas (Figure 3).

Although we have not yet quantitatively analyzed the patterns of species co-occurrence at remote camera stations, through our image processing, we observed a number of other species that were often detected at stations with frequent detection of bobcats, suggesting bobcats may serve as an indicator of connectivity for these species. Not surprisingly, species known to be tolerant of or associated with urbanized habitats and human activity, *e.g.* coyotes (*Canis latrans*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*), were detected at most stations, including those where bobcat detections were high. In addition, less common species like greater roadrunner (*Geococcyx californianus*), Western spotted skunk (*Spilogale gracilis*), long-tailed weasel (*Mustela frenata*), gray fox (*Urocyon cinereoargenteus*), mule deer (*Odocoileus hemionus*), and Cooper's hawk (*Accipiter cooperii*) were all observed at many of the stations with frequent bobcat detections. Of these, images of mule deer were repeatedly captured at many of the stations except for the culvert crossings under SR67 where there were only occasional images of mule deer. Beyond these commonly co-occurring species, we also obtained a number of puma images at several of our camera stations in the inland portions of our study area east of SR67.

*Mortality Assessment*

The primary sources of mortality we identified were vehicle collisions, followed by mange, caused by the felid-specific mange mite, *Notoedris cati*. We identified 24 roadkill

locations (Figure 4) across San Diego County. Upon review of the data collected for each roadkill, we determined that the majority of these occurred on undivided, secondary roadways. Vehicles on these roadways often travel at high speeds but through terrain that may make detecting oncoming traffic difficult for animals attempting to cross over the roadway, as opposed to an underpass or culvert. In fact, a number of the roadkilled animals we collected were found near crossing structures, which they may have used rather than going over the road, if the structures had been better placed, not blocked with vegetation, or had appropriate wildlife fencing to direct animals into the crossing structure. Our data also suggest that many of the vehicle-caused mortalities occurred between late September and early March, during the bobcat breeding season. Increased movement activity and exploration out of home ranges in an attempt to find a mate may result in a greater number of crossing attempts resulting in the increased mortalities during this time period.

During the course of this study, we also identified mortality caused by what appeared to be a mange epizootic in the greater Ramona/SR67 area. From detection on cameras, reports from the public, and calls for assistance into the Fund for Animals Wildlife Center rehabilitation center, we counted approximately 21 unique individuals affected by moderate to severe mange between 2010 and 2012 between SR67, the San Diego Country Estates, and SR78 in San Pasqual Valley. Without intervention, all of these animals would eventually die from emaciation or secondary infection resulting from the mange. We provided these data to collaborators focused on studying the prevalence and impact of mange in southern California at University of California - Los Angeles, University of California – Davis, and the Santa Monica Mountains National Recreation Area (Foley *et al.*, in review).

*Telemetry and Home Range Analysis*

We handled a total of 19 bobcats (14 males, 5 females; Table 3), collared 17, and have retrieved data from eight of the collars. The duration of tracking lasted between 11 and 465 days. Over 12,000 point locations were gathered from seven male and one female bobcat (Figure 5). Radio collar loss or malfunction limited the data we were able to retrieve, although there are still three animals we will attempt to recapture in June 2013 after the kitten season has ended. Additional locations collected through manual triangulation of the VHF signal from each collar are still being processed to incorporate data from the individuals that experienced collar failure.

We calculated the Local Convex Hull (LoCoH) home ranges for each individual (Table 4, Figure 6) utilizing all points available for each animal, and found that the mean home range size was 5.15km$^2$. Home range size varied greatly between individuals with some animals traveling long distances between core areas. Overall, we found that the majority of landscape used by bobcats was classified as natural habitat. However, animals were found to move relative to the constraints of their surroundings, *e.g.*, bobcats in Los Peñasquitos Canyon had smaller home ranges than in other areas. Similarly, animals in this and other developed areas were found to use more urban habitat than average. In comparison, the animals tracked in Pamo Valley had almost no urban association, showing a link between habitat use and environmental constraints.

*Habitat Models*

We created 15 different *a priori* models of bobcat presence incorporating combinations of habitat, land use, human development, and topography to identify which variables were most influential in explaining bobcat presence (Table 5). Models including elevation, all habitat variables, and all land use variables outperformed all other models (AIC$w_i$ > 0.999; Table 6).

The model output indicates that bobcat presence was most closely associated with water/wetland habitats, low elevation, and distance from major and local roads, as well as avoidance of shrublands and urban habitat (Table 7). Although our fire-return interval departure variable did not provide significant explanatory power in our models to predict bobcat presence, our previous research has found this to be a critical variable in analysis of movement data from Orange County that is often overlooked, resulting in overestimations of connectivity (Jennings 2013). Although we did not carry this variable forward in our analyses, it would be useful to continue monitoring fire-return intervals and the potential for vegetation type conversion across the preserve network.

*Connectivity Assessment*

To assess connectivity, we created three different raster layers based on the empirical data from our modeling efforts: suitable habitat, landscape resistance, and cost-weighted distance. Initially, habitat suitability values for each variable category that was determined to be significant predictor of bobcat presence (land cover, elevation, distance to roads, distance to water, and habitat) were established based on our modeling results (Table 8). Under current climate and land use conditions, our analyses suggest that habitat suitability is relatively high in and around core areas, more so in inland areas than the more fragmented coastal portions of the preserve network. Through our cost-weighted distance connectivity analysis, we found that connectivity among core areas is likely limited in a number of locations, *e.g.* Linkage 1-2b, Linkage 2-3a, Linkage 4-5, Linkage 6-7, Linkage 12-13, and Linkage 5-13 (all linkage designations are those identified in the Connectivity Monitoring Strategic Plan for the San Diego Preserve System 2011). Through our camera and GPS telemetry, we also found that some linkages, or segments of designated linkages do appear to serve as true conduits of animal movement among core areas. This includes Linkage 8-10, the eastern segment of Linkage 11-12, the western segment of Linkage 5-8, and to some degree, Linkage 5-6 under SR67.

In response to projected climate change (GFDL model between 2038 and 2070) and planned land use changes projected by SANDAG (Figure 7), we found little evidence of significant changes in the amount or distribution of suitable habitat resulting from climate conditions. However, the shifts in projected land use, particularly to altered categories of use in inland backcountry areas caused declines in suitable habitat, both within preserve cores, as well as in the areas between protected lands identified as putative landscape linkages.

When we calculated the effective distance between protected lands, the average effective distance for bobcats to travel between protected lands did not appear to change significantly in geographic position or overall value (Figure 8). However, current choke points that are already locations of concern necessary for connecting core preserve lands are likely to become more impacted in the future, further limiting connectivity through these linkages. In particular, several linkage zones identified by the MSCP Connectivity Strategic Plan (2011), *e.g.* Linkage 10-11, Linkage 12-13, Linkage 6-7, Linkage 5-13, Linkage 4-5, Linkage 1-2b, and Linkage 2-3a, may become impassable under future land use development. These linkages represent important connections both north to south and east to west and likely represent highly restricted movement from core preserves in more fragmented urban areas to larger blocks of intact habitat.

*Genetic analysis*

A total of 62 genetic samples were processed and genotyped and then separated into two putative bobcat subpopulations, a coastal and an inland unit, for analysis (Figure 9).

Microchecker analysis identified that there was no evidence of null alleles in the coastal population, but potential evidence for four loci in the inland population (FCA45, FCA90, Lc110, FCA35). Tests for linkage disequilibrium identified 22 potentially linked loci pairs. FCA35, FCA8, FCA90, and Lc111 were found to be in linkage disequilibrium in both subpopulations, so were eliminated from further analyses. Tests to determine whether each population was in Hardy-Weinberg equilibrium revealed that the coastal population was in equilibrium ($p = 0.0654$) and that the inland populations may be out of equilibrium ($p < 0.001$). This finding may be a result of skewed data, with a larger number of related individuals in inland areas sampled during live captures within a small geographic area. Analysis of relatedness is necessary to test this hypothesis. Tests of genotypic variation suggested that the coastal and inland populations are genetically distinct ($X^2 = 70.20$, $df = 36$, $p < 0.001$), and that distribution of alleles at all 18 loci differed significantly between coastal and inland populations. We also observed lower allelic richness in coastal bobcat populations, suggesting isolation in fragmented coastal preserves may be limiting gene flow. However, further analyses indicate that the samples tested were not from two distinct subpopulations. Both analyses of subpopulation differentiation ($D_{est} = 0.003$, $F_{ST} = 0.006$) indicate low genetic differentiation between the putative subpopulations. The analysis of the results from our STRUCTURE runs from K= 1 to K=5 also reveal that the samples tested were from a single panmictic population (Figure 10).

## DISCUSSION

Our assessment of connectivity using bobcat movement and habitat use through camera, mortality, telemetry, and genetic data indicate that while functional connectivity is intact in some areas of the San Diego MSCP preserve network, data revealed that connectivity is impaired in other areas. Our connectivity assessment suggests:

- Overall, there is evidence of connectivity in the inland and coastal areas of the MSCP network that we sampled.
- Genetic analysis showed some degree of genetic differentiation between coastal bobcats west of I-15 and inland animals to the east, but did not indicate subpopulation differentiation has occurred. This supports the assertion that the coastal and inland areas have some level of connectivity.
- Movement analyses (camera and telemetry) showed direct use of five of seven linkages that were monitored. Detected movement was highest in Linkage 6-7, Linkage 8-10, and Linkage 5-6.
- For linkages not directly monitored, results from landscape models suggest that at least five other areas identified as putative linkages may have limited to no current connectivity, and another nine may only function partially. These limitations will likely increase under projected land use.
- Habitat alteration and recreation, in addition to other ecological variables, are currently affecting wildlife occupancy. These effects may increase under projected land use shifts.
- Heavily traveled secondary roads with traffic moving at high rates of speed may pose the largest threat to medium-wide ranging wildlife species attempting to move between core

conserved areas, especially from coastal to inland areas. Roadkill mortality appears to increase with seasonal increases in animal movement.

- Projected habitat shifts resulting from climate change did not lead to substantial changes in habitat suitability or effective distance between preserves. However, future land use plans that lead to increased areas of altered use categories are likely to reduce habitat suitability in and around inland preserves.

**Current levels of connectivity**

Genetics and movement data (camera and telemetry) suggest that there is some level of connectivity between the inland and coastal areas of the MSCP we studied, and varying levels of connectivity between core conserved areas within both the east and west (Figure 11, Table 9).

*Genetics*

Our analysis of genetic samples revealed some level of genetic differentiation between coastal and inland bobcats (Figure 9) at the loci we analyzed, but this level of differentiation has not led to subpopulation structure. This disparity could be the result of two factors, one related to our sample size and distribution, the other associated with population size and genetic drift. We sampled approximately 30 individuals in coastal (closest to coast) and inland (animals east of Interstate 15), however, it is possible that we did not have sufficient sample sizes to detect subpopulation structuring between these areas. It is also possible that the preserves closest to the coast (and farther from I-15) are smaller and more isolated and may in fact, have limited gene flow with outside areas.

The disparity in our results for genetic differentiation may also be the result of limited genetic drift in San Diego County's coastal preserves. Smaller populations are likely to experience higher rates of genetic drift and may show differentiation in fewer generations. In San Diego's coastal areas where we collected genetic samples, the preserves are larger blocks of land and are slightly less isolated than the sampling locations from the previous research in the Santa Monica Mountains (Riley *et al.* 2006) or Orange County (Lee *et al.* 2012). Previous research (Riley *et al.* 2006, Lee *et al.* 2012) has found bobcat subpopulation structuring and limited gene flow across major freeways in southern California. In both these studies, the preserves on at least one side of the freeway are small and relatively isolated from other preserves, differing from the slightly larger and more connected preserves in San Diego's coastal preserves.

*Movement data*

We have direct camera and telemetry evidence that some movement is occurring between coastal and inland preserves. We documented bobcats moving under I-15 (Figure 5), which may be enough to allow for gene flow between preserves to the east and west of this potential barrier. However, the flow from that point to areas farther inland, such as Sycamore Canyon, appear to be limited by development and altered habitat between I-15 and preserves just west of SR67, with only one bobcat detection at Upper Beelor Canyon, one of the few corridors of open space between coastal and inland zones. We observed a number of animals crossing SR67 through culverts (Figure 3), but also collected roadkilled animals in the area (Figure 4), which represent a barrier to connectivity if the crossings are not fenced and improved, especially as traffic is likely to increase along this transportation corridor in the future. Along the northern east-west linkage, some movement was documented through our Pamo Valley/SR78 study area (Figure 5). In this

case, we observed individuals moving along the eastern part of the linkage within San Pasqual Valley, but were not able to monitor the zone to the west through Lake Hodges that is necessary to link eastern to western preserves in this area. Numerous crossings of SR78 were documented in at least one of the four underpasses monitored (Figure 3), but poor placement of culverts, agricultural habitat, and high levels of human movement appeared to restrict movement through the other three crossings.

Within the coastal study area, our data indicate that there is functional movement, at least between preserves on either side of SR56. We observed not only numerous crossings under the three bridges we monitoring along SR56, but movement and behavior (*e.g.* adults with kittens, foraging individuals) suggesting bobcats are utilizing the natural habitat under these bridges as part of their home ranges rather than just as movement corridors. VHF telemetry documented the movement of one individual from Los Peñasquitos Canyon to the Black Mountain Open Space region, but until we retrieve GPS collar data, we will not know which of the bridges he used and whether it was through the putative linkage identified through McGonigle Canyon.

Connectivity between the north and south inland areas appears to be the most problematic for wildlife movement. We were only able to monitor one culvert along SR67 in the region of Mount Woodson, because there is only one available for crossing. This camera station had almost no bobcat activity documented (Figure 3), and we detected at least one roadkill along this section of roadway. While movement to the south through the Scripps-Poway Parkway wildlife tunnel was regularly documented, there is still a large amount of unprotected and developed habitat for animals to move through to get to northern conserved lands. In particular, the crossing of Poway Road appears to be a challenge with multiple roadkills (Figure 4) observed along the winding stretch of road just west of SR67. One animal was tracked as he moved from the northern preserves in San Pasqual Valley up to the Ramona Grasslands, but he did not proceed south to Mount Woodson or to cross SR67 toward Iron Mountain (Figure 5).

*Habitat models*

Our habitat suitability models, as well as the cost-weighted distance connectivity assessment provide a means of comparing the likelihood of connectivity across the landscape. We found evidence of lower quality habitat both within core areas of the MSCP and in associated putative linkages, namely, Linkage 8-10, 5-8, 2-3a, and 1-2b (Figure 7). While some animals may be willing to use and traverse these unsuitable areas, there are still questions of whether enough animals will do so, whether those that attempt the crossing will be successful, and whether they will find suitable and unoccupied habitat at the other end of the linkage. The cost-weighted distance analysis similarly identified a number of areas where additional linkages are needed as the resistance/cost between one preserve to the next likely limits connectivity (see notations on Figure 8).

**Potential impediments to connectivity**

Our analyses reinforce the idea that development (current and projected), human use, and road crossings may limit movement in certain areas of the San Diego MSCP preserve network.

*Recreation*

The occupancy modeling of the remote camera stations across the study area revealed that bobcat occupancy was lowest in areas outside of core conserved areas, in altered habitats, and in the coastal area of our study. While the effect of recreation was not identified as a primary

factor, this may have been the result of limited power to detect these effects. We did find overall fewer total detections of bobcats at the camera stations with the highest recreation like Iron Mountain, Los Peñasquitos Canyon, and at the San Dieguito River trailhead at Bandy Canyon Road and SR78 (Figure 3). In fact, only three photos of bobcats were taken at the Iron Mountain station, where tens to hundreds of people passed daily, over the course of the year-long sampling. In contrast, 32 bobcat detections were gathered at camera 67-C4 at the culvert along SR67 just below the hiking trail at Iron Mountain. It is likely that our coarse categorization of recreation into high and low levels to assess its impact on species occupancy oversimplified a more complex interaction between wildlife and human recreation, which has been documented in other studies of the effects of recreation on mammalian carnivore species (George and Crooks 2006, Reed and Merenlender 2008). A more detailed analysis of the recreation data we gathered, including rates, types, and temporal patterns of both recreation and animal detections, could yield results that provide more guidance on the effect of recreation in and around linkages.

*Road mortality*

Our mortality assessment determined that a high number of mortalities occurred on highly traveled secondary roads where vehicle speeds are often > 50 mph (Figure 4). A number of roadkilled bobcats we collected were found along guardrails near culverts or tunnels suggesting that the animal elected to attempt to cross over the road, rather than go through the crossing. This may be related to crossing type, placement, or simply a result of inadequate or inappropriate wildlife fencing to direct the animal into the crossing. We observed poorly placed (*e.g.* not connected to the crossing structure) and broken fencing, barbed wire fences, and no fencing at a number of the camera stations along SR67. In fact, the SR67 study area faces the greatest challenges for road crossings with high roadkill numbers along secondary roads in an area bounded by highways, virtually on all sides.

*Other mortality sources*

In addition to limitations on movement across or under roads, there appear to be additional stressors to animals in this area as evidenced by the mange epizootic observed during the study. Our assessment indicated that, as in other areas of southern California (Riley *et al.* 2007), mange is a concern for San Diego bobcat populations. While we were not primarily focused on assessing this disease in our bobcat populations, there is a need for continued cooperation and collaboration with other researchers to provide information about ongoing issues related to mange in San Diego County. It is worth noting that this and other disease outbreaks may be related to connectivity as disease may spread more readily in constrained, highly developed areas, *e.g.* Los Peñasquitos Canyon, as has been observed in other areas of southern California (Riley *et al.* 2007, Foley *et al.*, in review). Research on the prevalence of mange in southern California has detected a correlation between incidences of mange and bobcat exposure to anticoagulant rodenticides which may occur both in highly urbanized areas as well as areas of exurban development where housing and wildlands are intermixed to a greater degree. The apparent mange epizootic we observed during our study supports this relationship. The large projected increase in altered land use categories from the SANDAG models may have indirect effects on the health of wildlife populations beyond the immediate impacts of habitat fragmentation and a decline in habitat suitability.

*Development*

Bobcat movement and activity in more heavily impacted and fragmented areas of the MSCP network (Los Peñasquitos Canyon into Carmel Valley/Rancho Santa Fe) indicate that connectivity may be particularly constrained in these areas (Table 4, Figure 6). No tracked bobcats traveled beyond the bounds of open space into urban neighborhoods on the edges of Los Peñasquitos Canyon. Indeed, the large number of males captured in this area suggests that urban animals may be experiencing home range pile-ups (*sensu* Riley *et al.* 2006) and occur at higher densities when alternatives for dispersing are limited. Although many bobcats appeared to be tolerant of or adapted to the high level of human activity and urbanized landscape in the coastal cores, this response may be a result of limited options to avoid these areas. Certainly, dispersal remains a concern for bobcats and for the viability of protecting populations of a variety of species in this highly fragmented area. In comparison, bobcats in the north inland area around Pamo Valley, San Pasqual Valley, and SR78 have ample habitat to move through, and as a result, these animals successfully avoided development and areas with increased levels of human activity.

**Connectivity under climate change and land use projections**

When we evaluated connectivity under potential future climate conditions, we did not see a substantial change in habitat suitability. This may be a result of the coarse scale at which the habitat models were developed, similar to most current climate change models. More notably, when we incorporated data on planned land use for 2050, we saw a marked decline in suitable habitat, particularly in the inland areas surrounding the SR67 study area. There were six linkages identified that displayed the most obvious changes in suitability, which also happened to be areas already experiencing limited movement, *e.g.* Linkages 6-13, 5-13, 6-7, 2-3a, 2-3b, and 1-2b (see notations on Figure 7).

The assessment of connectivity using cost-weighted distance revealed a slight increase in the effective distance required to traverse certain areas under future conditions. The areas of greatest concern with regard to connectivity appear to be Linkages 10-11, 12-13, 6-13, 5-8, 5-13, 4-5, 1-2b, and 2-3a (see notations on Figure 8). Identifying site-specific corridors in these areas with potential alternatives is the first step to re-establishing connectivity at these locations. Then, on a case-by-case basis, steps to improve each linkage can be developed. As higher resolution climate models are released for the MSCP region, these analyses should be repeated. By continuing to monitor both the change in habitat and in land use, local land management agencies will have a greater ability to successfully create and protect connectivity.

**Future Directions**

The first steps to begin addressing current issues with connectivity include early corridor identification based on empirical data, rather than mapping exercises or expert opinion. We have taken this important first step in analyzing connectivity for San Diego County's ecological network with this synoptic assessment. However, further investigation prior to developing concrete management recommendations is warranted. There are many methods available and in use to assess connectivity, and there is no scientific consensus as to the ideal method (Beier *et al.* 2011). Instead, many experts recommend an ensemble approach, whereby several methods are applied, *e.g.* CircuitScape, MaxEnt, and Zonation programs. Results from these analyses can then be compared to identify areas of agreement that require management action to protect or re-establish connectivity. Integrating data from other ongoing connectivity studies in the region that use both empirical and analytical approaches, it would be possible to evaluate connectivity for a

wider range of organisms. While bobcats serve as an indicator for connectivity, a synthetic analysis that incorporates connectivity from other organisms into a comprehensive assessment is an important next step. Utilizing a robust and diverse data set to identify site-specific corridors will also allow us to assess the remainder of MSCP and MSHCP (planned and in-progress) where site-specific data are not currently available.

Once these thorough assessments have been completed, planning efforts can identify and prioritize action for each given corridor. These actions may be to acquire land, restore habitat, protect habitat, and even create corridor redundancy to allow for a changing landscape given uncertainty of future conditions. Considering the potential impact of recreation on bobcat activity patterns, as well as what has been encountered by other studies (George and Crooks 2006, Reed and Merenlender 2008), limiting recreation either temporally or spatially in critical crossing and linkage areas may be another step to consider in re-establishing and protecting connectivity. As this work is being conducted in an ever-changing environment with new and improved information and ways of assessing information constantly evolving, it is important that connectivity assessments be seen as an iterative process. We recommend that monitoring and direct management action be taken in locations that were identified as areas where connectivity was impaired. These areas should continue to be re-evaluated based on projected future change, as well as continued monitoring data, as more information becomes available. Taking a proactive and empirically-based approach to assessing connectivity at this sub-regional scale will allow San Diego's preserve network to continue moving forward as a functioning land, habitat, and species conservation plan, while allowing for future change in a planning environment challenged by the nature of fixed spatial extents and a dynamic landscape.

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# FIGURES AND TABLES

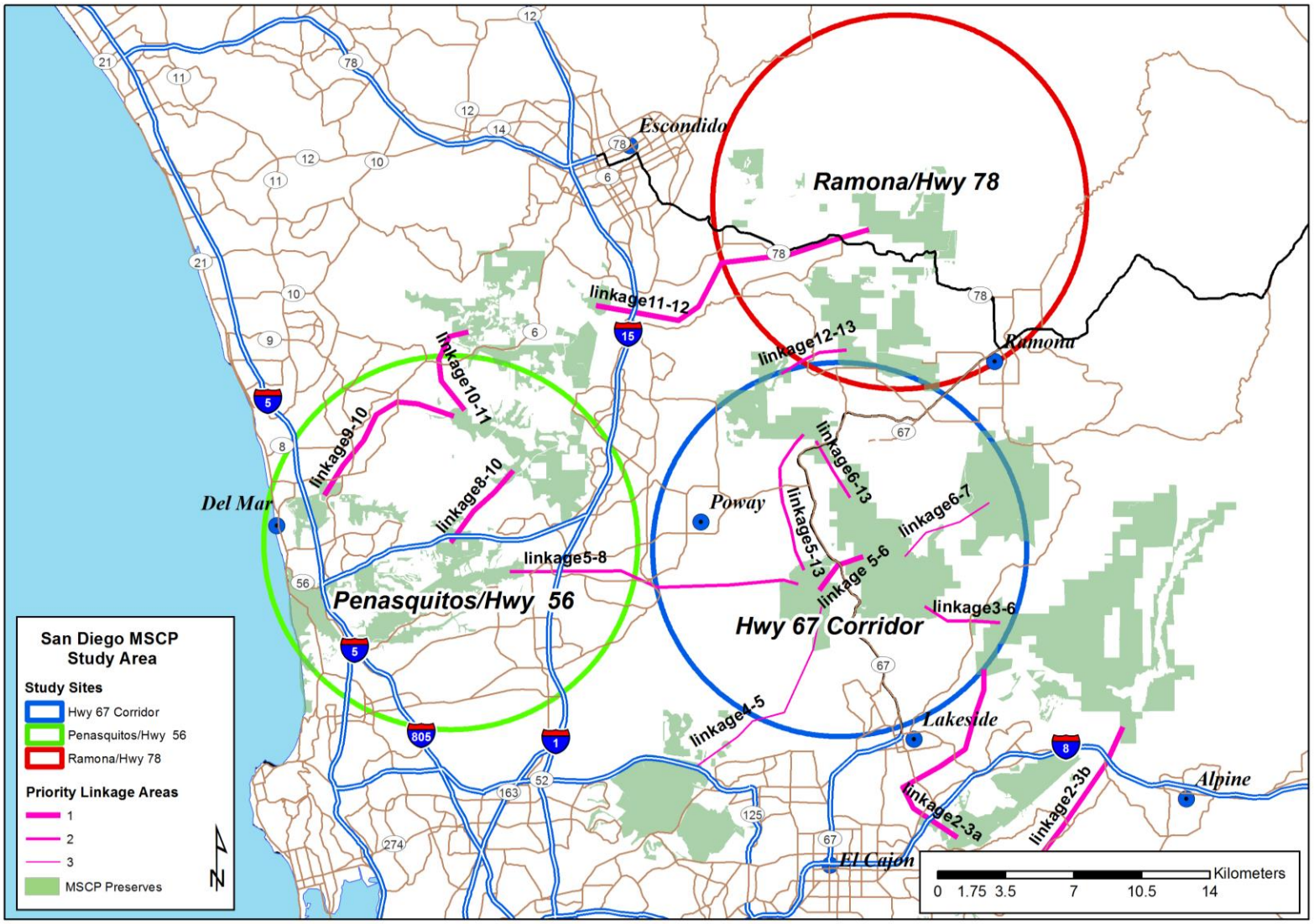


Figure 1. Map of study areas monitoring San Diego County MSCP open space network with core preserves in green. Pink lines represent putative linkage areas previously identified by the MSCP Connectivity Monitoring Strategic Plan. Large circles identify three primary study areas in coastal and inland sites along three major transportation corridors.

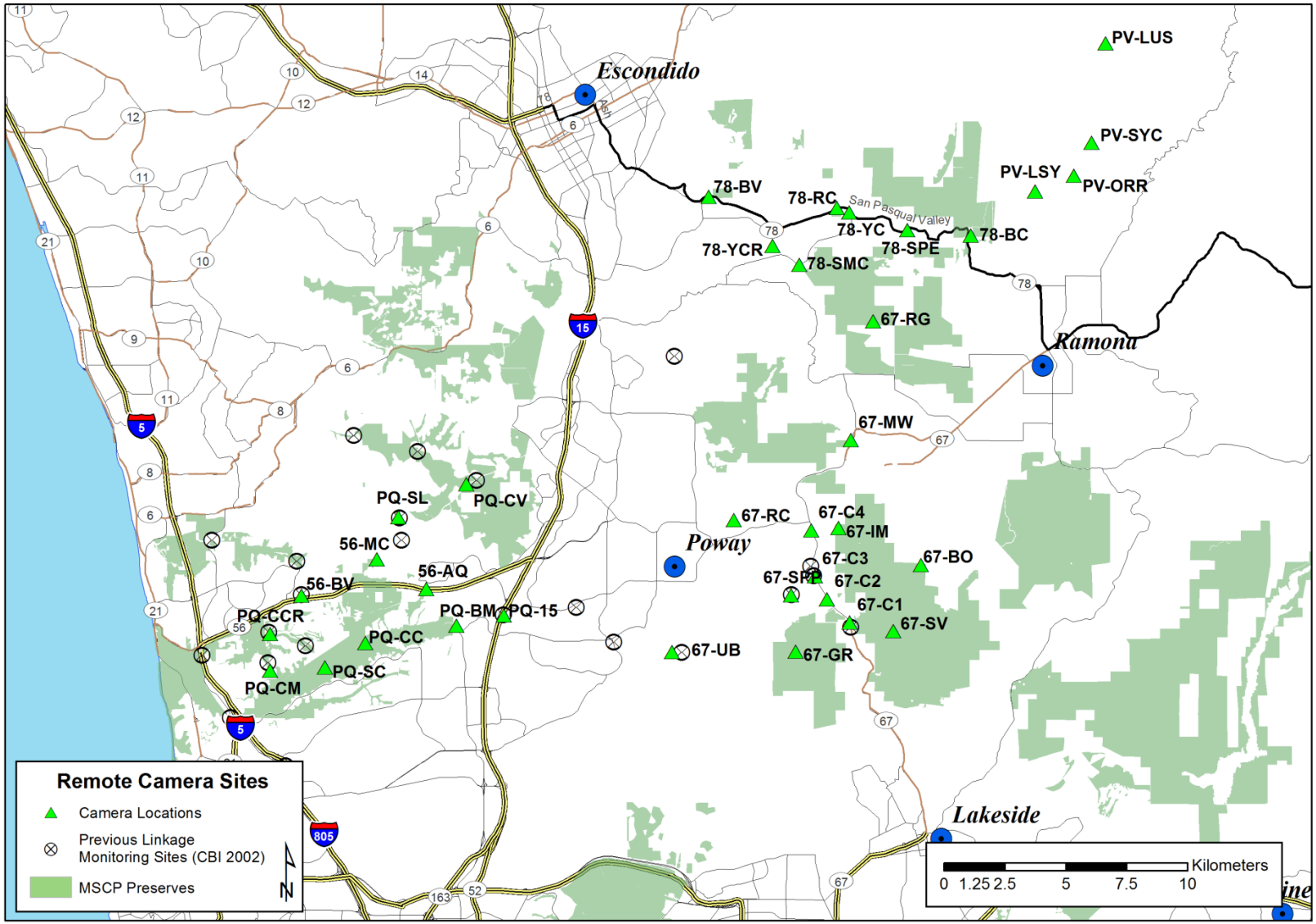


Figure 2. Map of study area with remote camera station monitoring locations (green triangular symbols) with respect to preserve lands. Recommended linkage monitoring sites previously identified (CBI 2002) are represented by circles with an X.

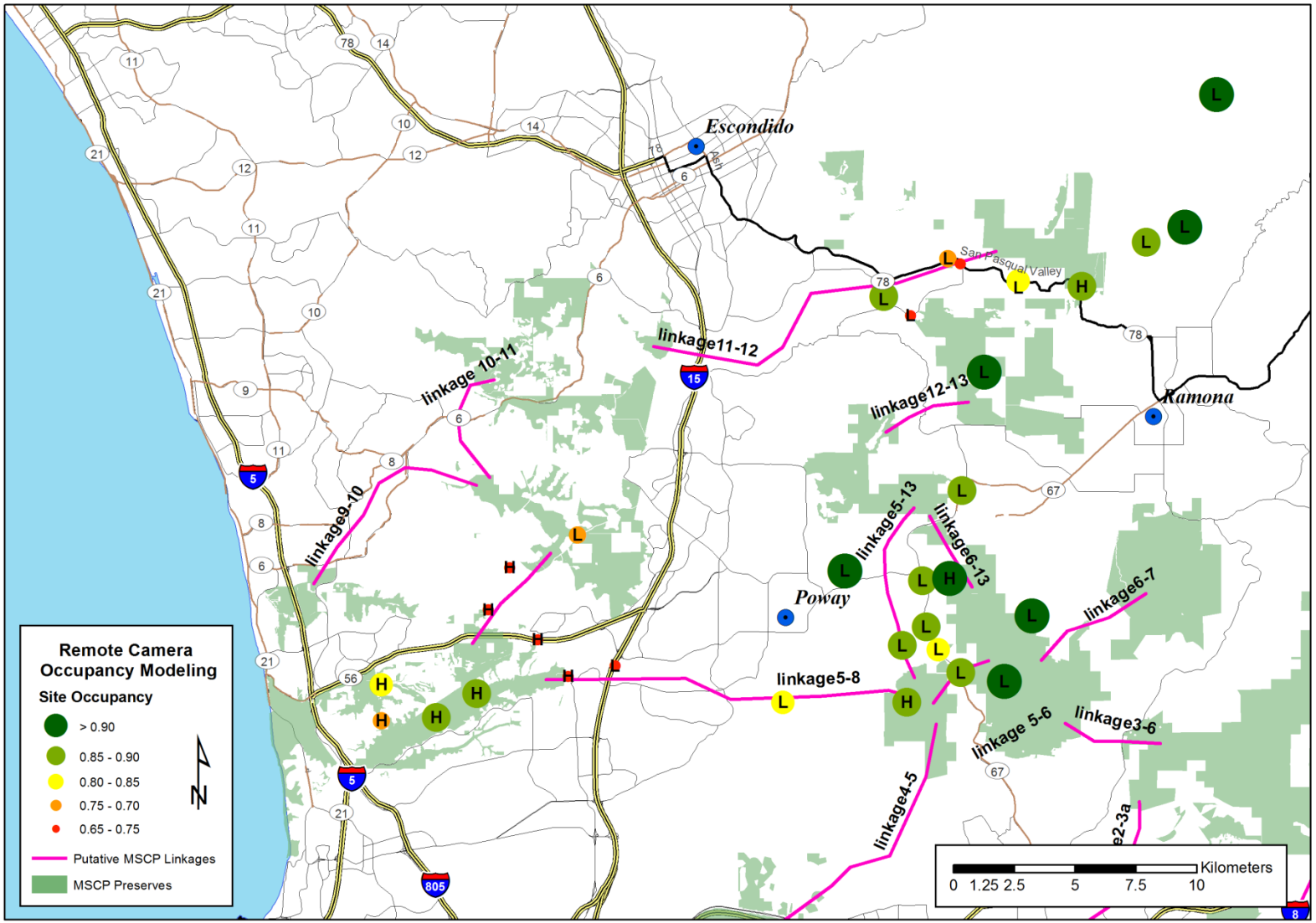


Figure 3. Map of bobcat occupancy rates at remote camera stations (n = 32) determined by occupancy modeling. Rates range from 0.66 to 0.907, represented by smaller red shades at lower occupancies to larger, green shades at the highest occupancy rates. Recreation level at each station is denoted as high (H) or low (L).

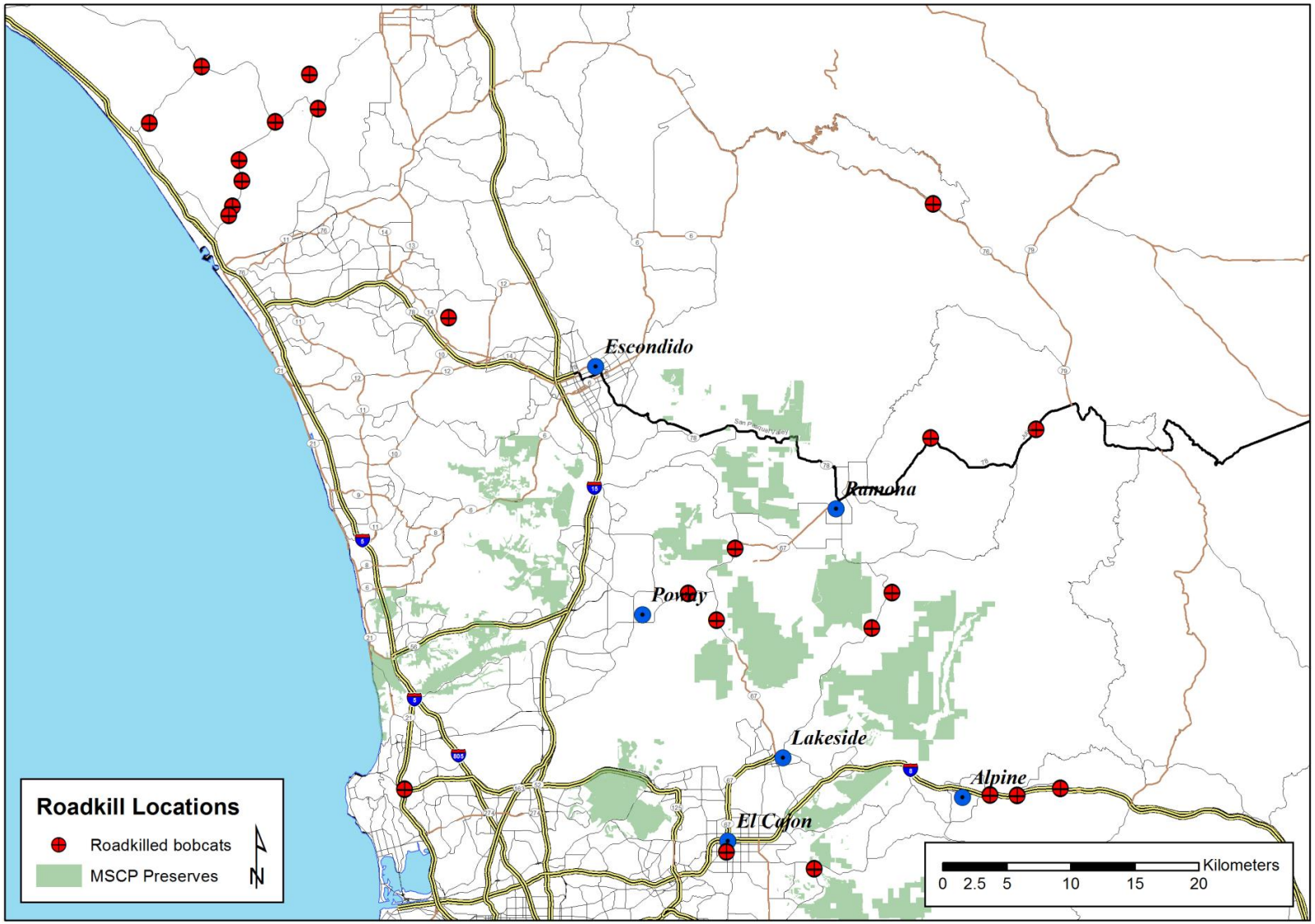


Figure 4. Locations of roadkill bobcats (n = 24) collected or recorded in San Diego County between 2010 and 2013, with the exception of one roadkill location at Marine Corps Base Camp Pendleton collected in 2007.

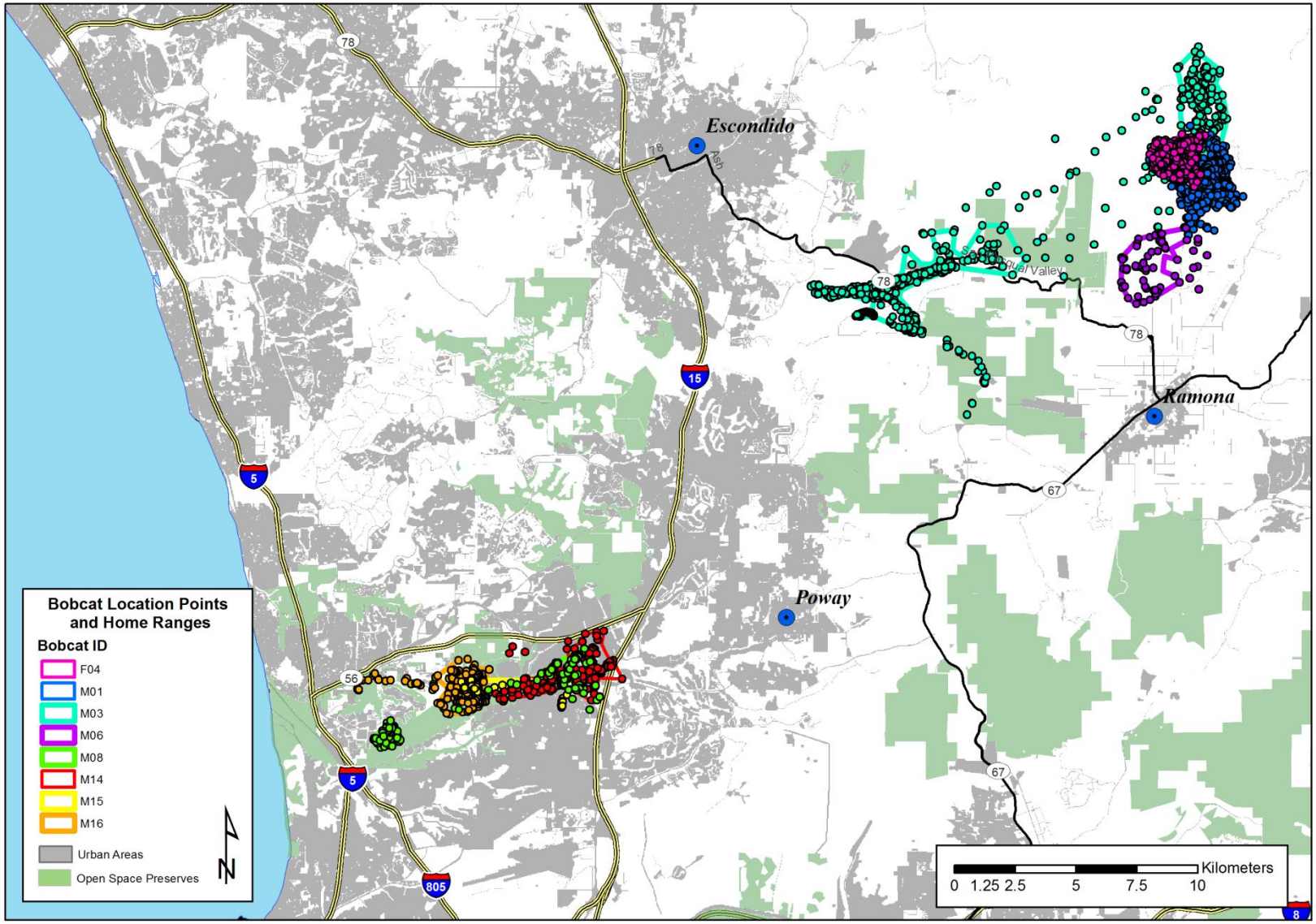


Figure 5. GPS point locations and LoCoH home range estimates for tracked bobcats. Each individual (n = 8) is represented by a different color. Locations are depicted with respect to urban areas, shaded in gray.

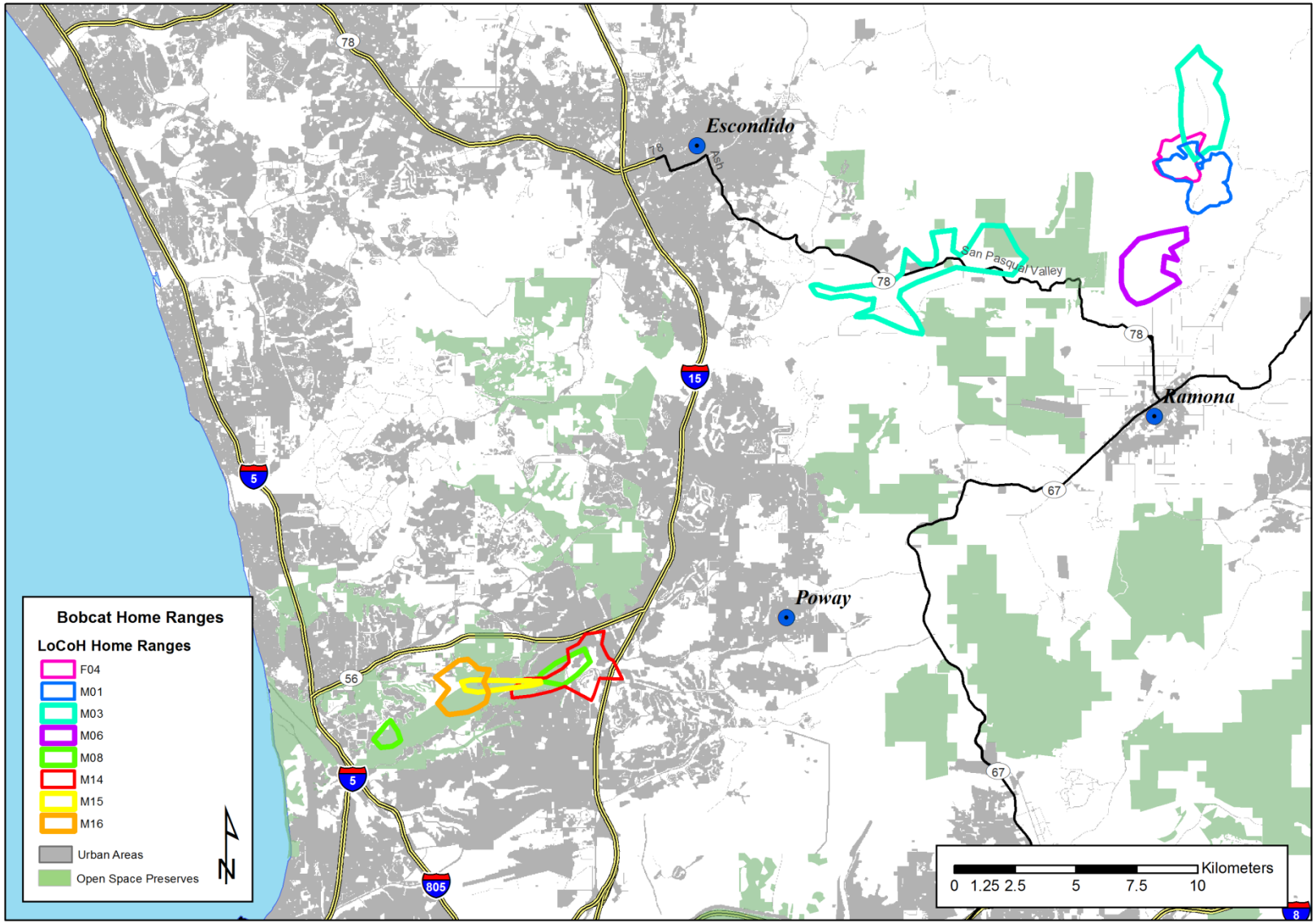


Figure 6. Local Convex Hull (LoCoH) home ranges for all bobcats with GPS collar data retrieved (n = 8). Home ranges are shown with respect to open space preserve boundaries (in green), and areas of urban development (in gray).

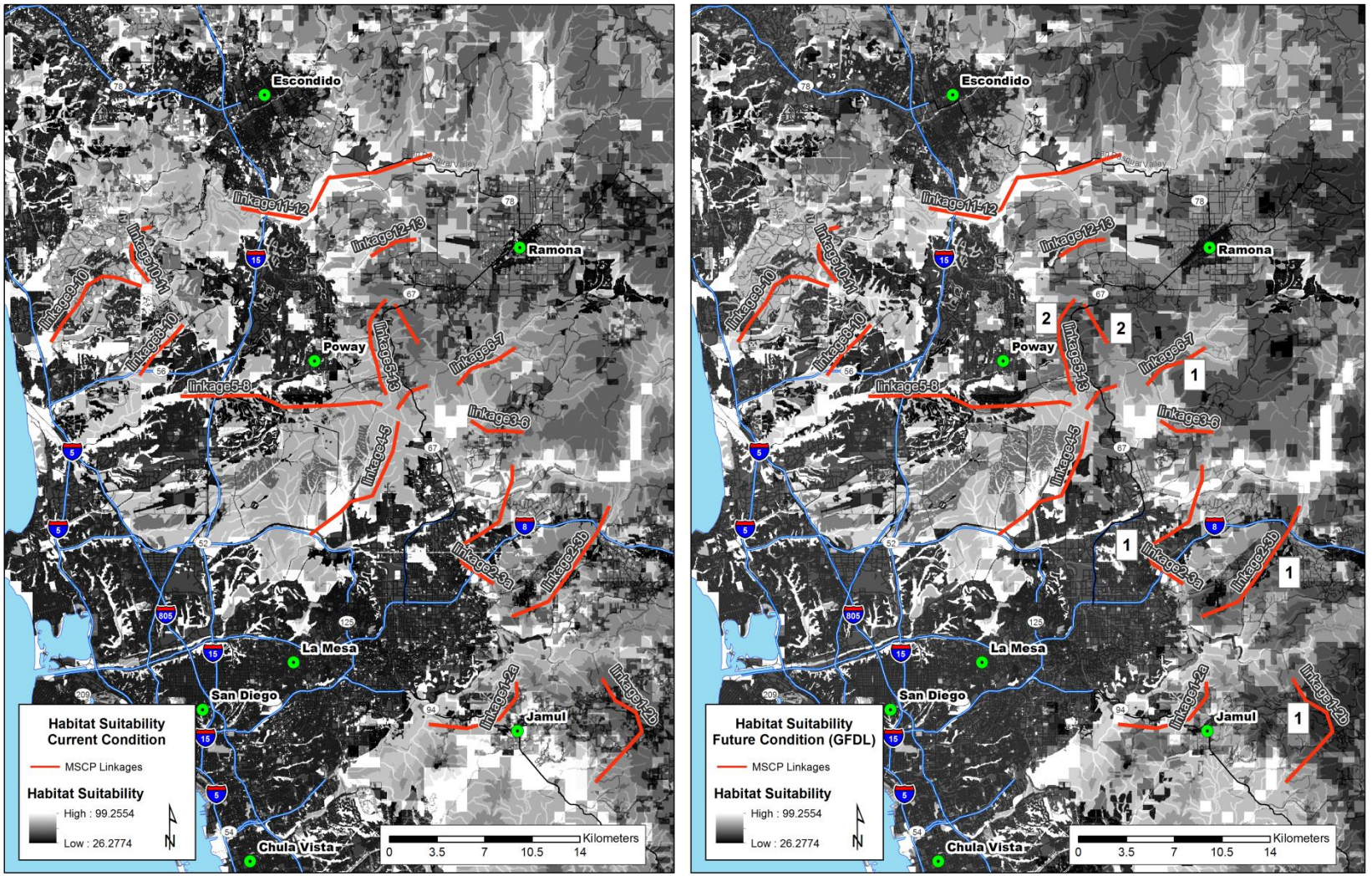


Figure 7. Habitat suitability for the MSCP area under current climate and land use conditions (left panel), and under future climate scenario GFDL and 2050 planned land use conditions (right panel). Lighter areas indicate high habitat suitability. Putative linkage areas are identified by red lines. Numbered squares in right hand panel indicate locations with decreased habitat suitability: 1) due to habitat alteration; 2) due to habitat alteration and roads.

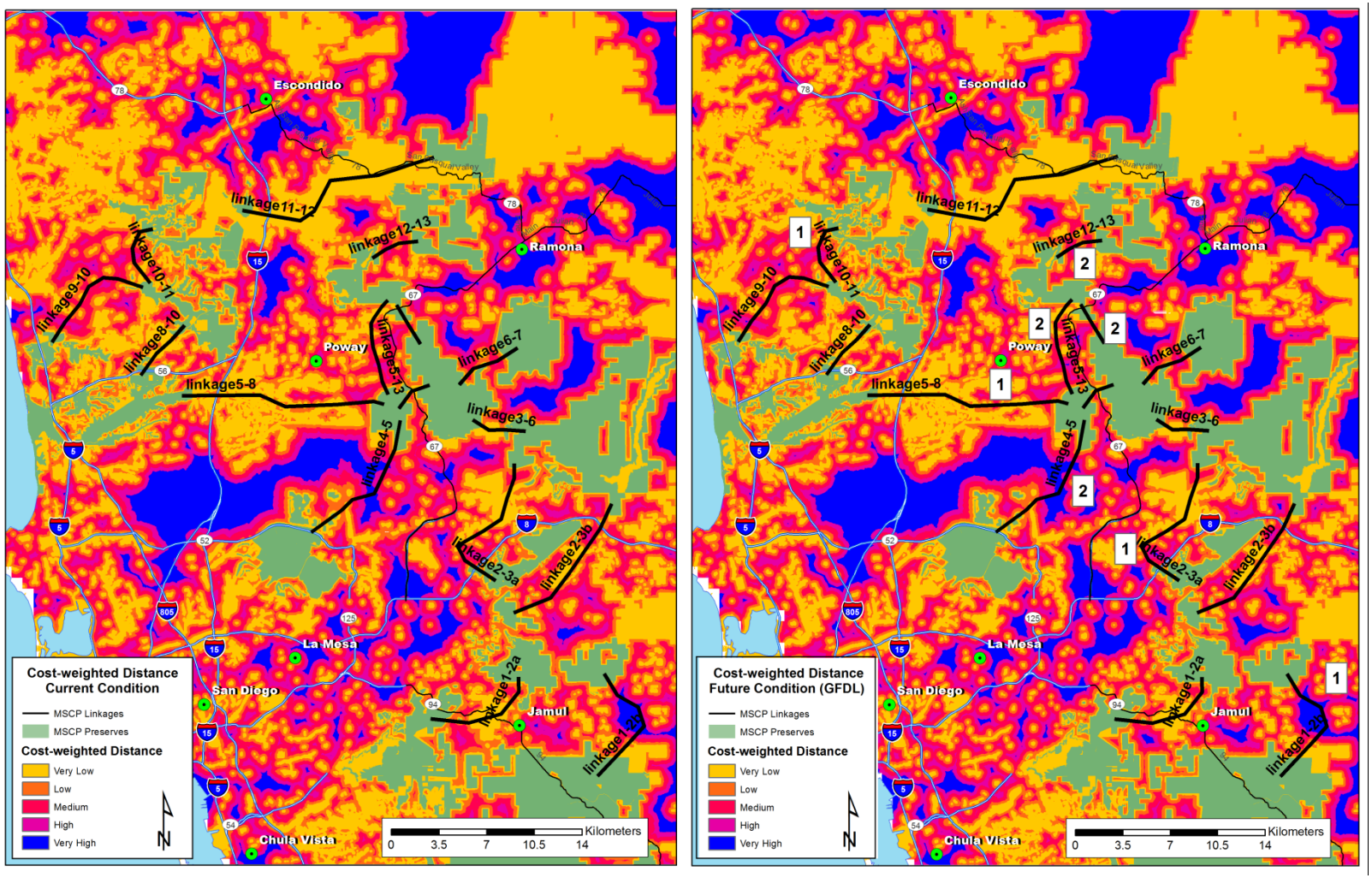


Figure 8. Landscape connectivity assessed by cost-weighted distance for the MSCP area under current climate and land use conditions (left panel), and under future climate scenario GFDL and 2050 planned land use conditions (right panel). Warmer colors indicate areas of lowest effective distance, increasing to highest distances in cooler colors. Putative linkages are identified by black lines. Numbered squares in right hand panel indicate locations with decreased connectivity: 1) due to habitat alteration/development; 2) due to habitat alteration and roads.

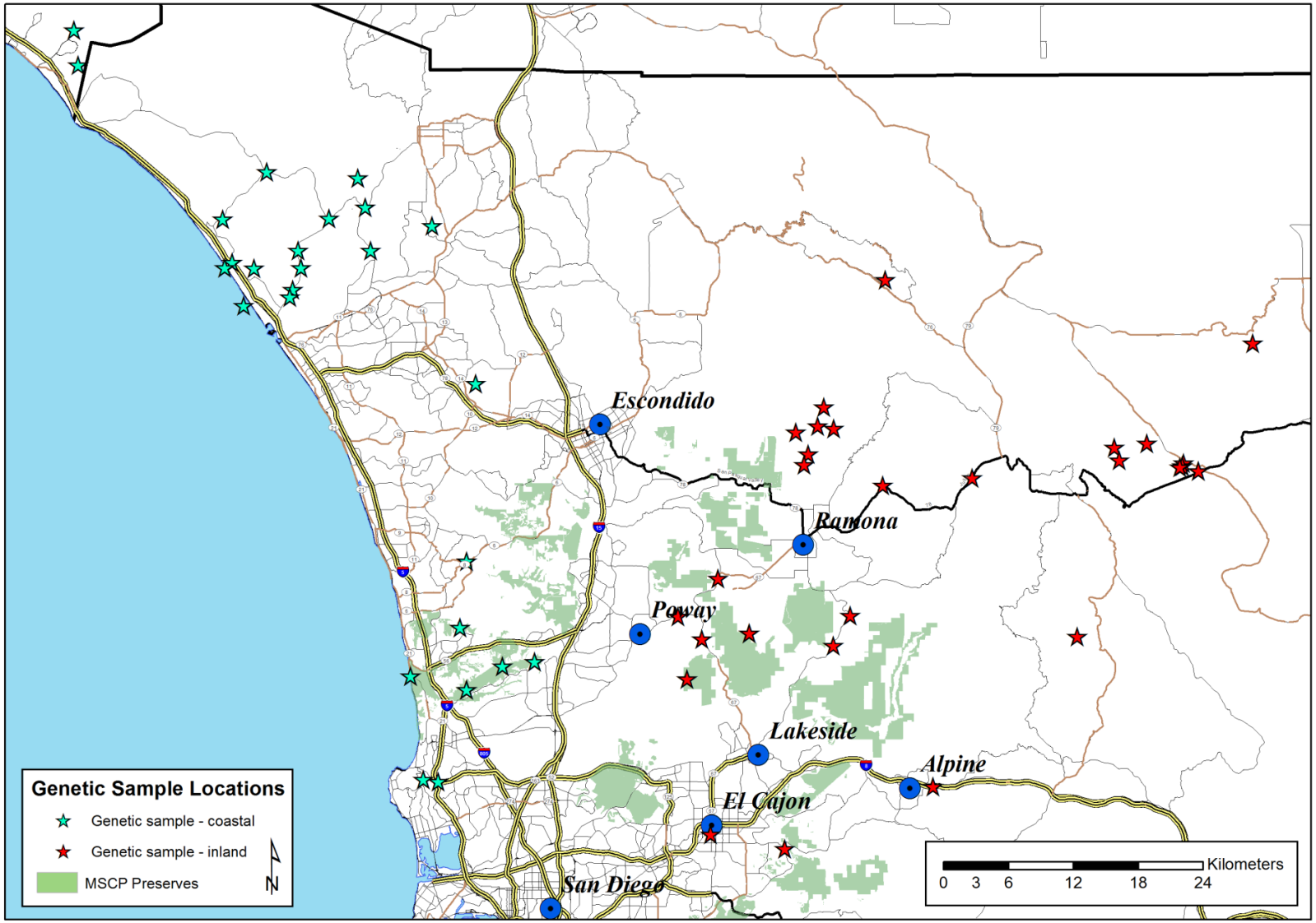


Figure 9. Map of sampling locations for genetic data analyzed (n = 62) and putative subpopulation assignment. Individuals assigned to the coastal population (west of I-15 freeway) are in turquoise, and those in the inland population (east of I-15) are in red.

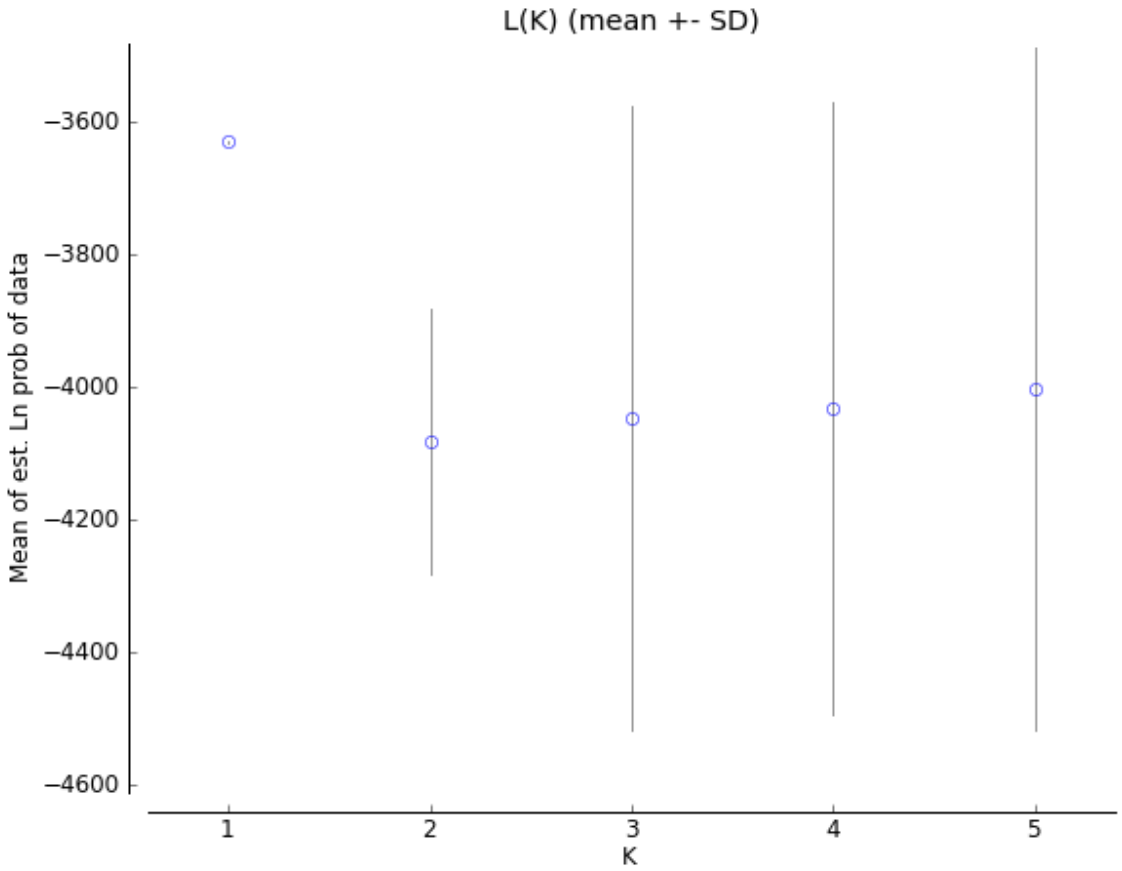


Figure 10. Mean estimated (± SE) probability of the number (K = 1 to 5) of subpopulations of bobcats supported by STRUCTURE analysis. Results support identification of one, panmictic population.

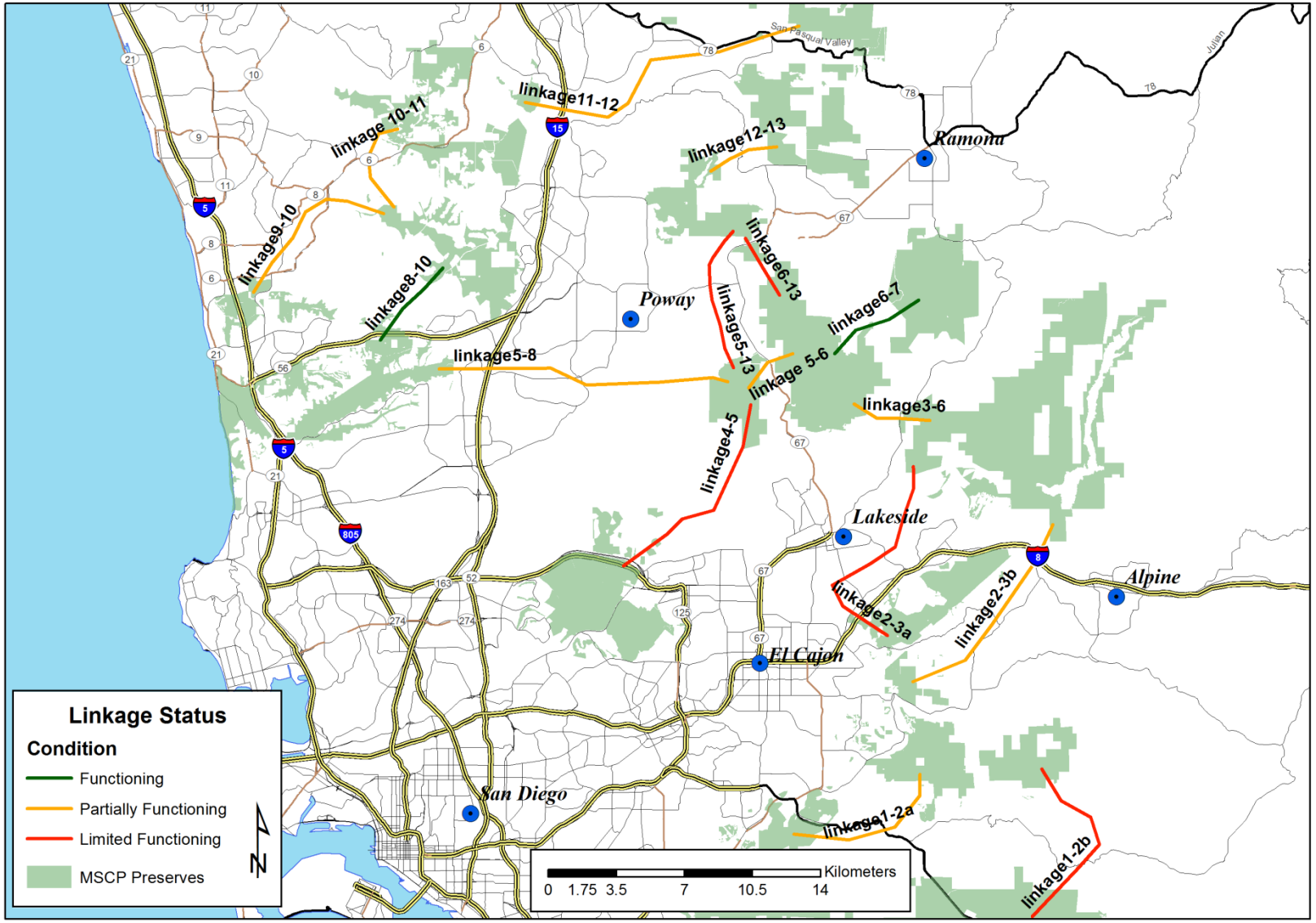


Figure 11. Linkage status map. Status was assessed based on empirical data and modeling results. Red indicates only limited linkage functioning, orange - partial functioning, and green represents functioning linkages.

| *Station ID* | *Study Area* | *Site Type* | *Recreation* | *Camera* |
|---|---|---|---|---|
| 56-AQ | Los Peñasquitos/SR56 | Bridge | M | Cuddeback |
| 56-BV | Los Peñasquitos/SR56 | Bridge | L | Cuddeback |
| 56-MC | Los Peñasquitos/SR56 | Bridge | M | LTL Acorn |
| 67-BO | SR67 | Core | L | LTL Acorn |
| 67-C1 | SR67 | Culvert | L | Cuddeback |
| 67-C2 | SR67 | Culvert | L | LTL Acorn |
| 67-C3 | SR67 | Culvert | L | LTL Acorn |
| 67-C4 | SR67 | Culvert | L | Cuddeback |
| 67-GR | SR67 | Core | M | LTL Acorn |
| 67-IM | SR67 | Core | H | LTL Acorn |
| 67-MW | SR67 | Culvert | L | LTL Acorn |
| 67-RC | SR67 | Core | M | LTL Acorn |
| 67-RG | SR67 | Core | L | LTL Acorn |
| 67-SPP | SR67 | Tunnel | M | LTL Acorn |
| 67-SV | SR67 | Core | L | Cuddeback |
| 67-UB | SR67 | Linkage | L | LTL Acorn |
| 78-BC | Pamo Valley/SR78 | Core | M | LTL Acorn |
| 78-BV | Pamo Valley/SR78 | Bridge | L | Cuddeback |
| 78-RC | Pamo Valley/SR78 | Bridge | L | LTL Acorn |
| 78-SMC | Pamo Valley/SR78 | Bridge | L | Cuddeback |
| 78-SPE | Pamo Valley/SR78 | Tunnel | L | LTL Acorn |
| 78-YC | Pamo Valley/SR78 | Bridge | H | Cuddeback |
| 78-YCR | Pamo Valley/SR78 | Linkage | L | LTL Acorn |
| PQ-15 | Los Peñasquitos/SR56 | Bridge | M | Cuddeback |
| PQ-805 | Los Peñasquitos/SR56 | Bridge | M | Cuddeback |
| PQ-BM | Los Peñasquitos/SR56 | Bridge | H | LTL Acorn |
| PQ-CC | Los Peñasquitos/SR56 | Core | H | Cuddeback |
| PQ-CCR | Los Peñasquitos/SR56 | Tunnel | H | LTL Acorn |
| PQ-CM | Los Peñasquitos/SR56 | Bridge | M | LTL Acorn |
| PQ-CV | Los Peñasquitos/SR56 | Bridge | L | LTL Acorn |
| PQ-SC | Los Peñasquitos/SR56 | Core | H | Cuddeback |
| PQ-SL | Los Peñasquitos/SR56 | Bridge | H | Cuddeback |
| PV-LSY | Pamo Valley/SR78 | Core | M | LTL Acorn |
| PV-LUS | Pamo Valley/SR78 | Core | L | LTL Acorn |
| PV-ORR | Pamo Valley/SR78 | Core | L | Cuddeback |
| PV-SYC | Pamo Valley/SR78 | Core | L | Cuddeback |

Table 1. Remote camera location identifiers and designation by study area, site type, recreation level, and camera type.

| *Primer* | *Species* | *Repeat* | *Size range* | *Number of alleles* | *Ho* | *He* | *PIC* | *Reference* |
|---|---|---|---|---|---|---|---|---|
| BCD8T | Bobcat | tetra | 156-180 | 5 | 0.26 | 0.35 | 0.33 | 1 |
| BCE5T | Bobcat | tetra | 256-280 | 6 | 0.77 | 0.71 | 0.66 | 1 |
| BCG8T | Bobcat | di | 275-299 | 12 | 0.89 | 0.85 | 0.83 | 1 |
| FCA126 | Domestic cat | di | 132-154 | 7 | 0.70 | 0.80 | 0.76 | 2 |
| FCA132 | Domestic cat | di | 182-194 | 7 | 0.79 | 0.83 | 0.80 | 2 |
| FCA149 | Domestic cat | di | 133-149 | 8 | 0.74 | 0.77 | 0.73 | 2 |
| FCA23 | Domestic cat | di | 144-158 | 6 | 0.79 | 0.73 | 0.69 | 2 |
| FCA26 | Domestic cat | di | 138-166 | 13 | 0.82 | 0.87 | 0.84 | 2 |
| FCA31 | Domestic cat | di | 237-255 | 9 | 0.79 | 0.87 | 0.84 | 2 |
| FCA35 | Domestic cat | di | 120-150 | 16 | 0.80 | 0.91 | 0.89 | 2 |
| FCA391 | Domestic cat | tetra | 210-236 | 5 | 0.55 | 0.67 | 0.61 | 2 |
| FCA43 | Domestic cat | di | 131-139 | 5 | 0.74 | 0.74 | 0.69 | 2 |
| FCA45 | Domestic cat | di | 147-173 | 7 | 0.65 | 0.83 | 0.79 | 2 |
| FCA559 | Domestic cat | tetra | 115-135 | 5 | 0.70 | 0.64 | 0.57 | 2 |
| FCA742 | Domestic cat | tetra | 104-134 | 5 | 0.62 | 0.71 | 0.65 | 3 |
| FCA77 | Domestic cat | di | 130-140 | 8 | 0.63 | 0.73 | 0.69 | 2 |
| FCA8 | Domestic cat | di | 140-156 | 9 | 0.81 | 0.74 | 0.71 | 2 |
| FCA82 | Domestic cat | di | 246-266 | 10 | 0.90 | 0.85 | 0.83 | 2 |
| FCA90 | Domestic cat | di | 108-126 | 7 | 0.66 | 0.77 | 0.73 | 2 |
| FCA96 | Domestic cat | di | 189-209 | 10 | 0.71 | 0.84 | 0.82 | 2 |
| Lc110 | Lynx | di | 92-104 | 7 | 0.51 | 0.60 | 0.55 | 4 |
| Lc111 | Lynx | di | 157-217 | 7 | 0.79 | 0.76 | 0.72 | 4 |

Table 2. Locus name, species developed from, repeat motif of microsatellite markers used in genetic analysis. Size range, number of alleles, expected and observed heterozygosity and PIC were based on analysis of 62 bobcat samples. Reference indicates initial publication of markers by: 1. Faircloth *et al.* 2005; 2. Menotti-Raymond *et al.* 1999; 3. Menotti-Raymond *et al.* 2005; Carmichael *et al.* 2000.

| *Individual* | *Capture Date* | *Status* | *Location* | *Comments* |
|---|---|---|---|---|
| M01 | 5/13/2009 | Collared | Pamo Valley | |
| M02 | 1/2/2010 | Collared | Pamo Valley | Collar not retrieved |
| M03 | 8/22/2010 | Collared | Pamo Valley | |
| F04 | 9/23/2010 | Collared | Pamo Valley | Mortality – suspected puma |
| F05 | 10/13/2010 | Collared | Pamo Valley | Collar failure |
| M06 | 11/9/2010 | Collared | Pamo Valley | |
| M07 | 10/15/2011 | Collared | Los Peñasquitos | Collar not retrieved |
| M08 | 10/27/2011 | Collared | Los Peñasquitos | Mortality – suspected coyote or domestic dog |
| M09 | 10/29/2011 | Collared | Los Peñasquitos | Collar not retrieved |
| M10* | 11/29/2011 | Collared | FFAWC rehab release – Black Mtn. | Animal missing |
| F11* | 11/22/2011 | Ear tagged | FFAWC rehab release - Tenaja | |
| M12* | 11/29/2011 | Collared | FFAWC rehab release – Los Peñasquitos | Attempting to recapture |
| F13* | 11/22/2011 | Ear tagged | FFAWC rehab release – Torrey Pines | |
| M14 | 1/1/2012 | Collared | Los Peñasquitos | |
| M15 | 1/7/2012 | Collared | Los Peñasquitos | |
| M16 | 1/8/2012 | Collared | Los Peñasquitos | |
| M17 | 2/4/2012 | Collared | Goodan Ranch | Collar being inspected for data retrieval |
| F18 | 2/12/2012 | Collared | Boulder Oaks Preserve | Animal missing |
| M20 | 3/3/2012 | Collared | Boulder Oaks Preserve | Rehabbed for mange first; Attempting recapture |

Table 3. Data for all bobcats sampled (n = 19), including individual identifier, date of capture or processing*, tracking status (collar or ear tag only), location of capture, and notes on animal or collar fate. *Four animals were rehabilitated animals from the Fund for Animals Wildlife Center in Ramona. Only two of those animals were collared prior to release back into the wild.

| Animal | Urban | Altered | Natural | HR Area ($km^2$) |
|---|---|---|---|---|
| M01 | 1% | 8% | 92% | 4.79 |
| M03a | 5% | 42% | 54% | 10.12 |
| M03b | 1% | 31% | 68% | 6.37 |
| F04 | 1% | 1% | 98% | 2.79 |
| M06 | 0% | 9% | 91% | 5.13 |
| M08a | 3% | 0% | 97% | 0.72 |
| M08b | 31% | 7% | 61% | 1.55 |
| M14 | 40% | 5% | 55% | 5.26 |
| M15 | 14% | 0% | 86% | 1.05 |
| M16 | 8% | 0% | 92% | 3.43 |

Table 4. LoCoH home range information for each bobcat with GPS collar data available. Data include total home range area ($km^2$) and percentage of home range in land use categories urban, altered, and natural.

| *Variable* | *Coefficient* | *SE* | *p-value* |
|---|---|---|---|
| ***Fire*** | | | |
| Fire return interval departure (6 classes) | | | |
| -999 | 1.323 | 0.837 | 0.114 |
| -3 | 0.518 | 0.838 | 0.537 |
| -2 | 0.529 | 0.837 | 0.528 |
| -1 | 1.598 | 0.84 | 0.057 |
| 1 | 0.987 | 0.841 | 0.241 |
| 2 | 1.608 | 0.84 | 0.056 |
| ***Habitat*** | | | |
| Herbaceous | 0.492 | 0.057 | 0 |
| Shrubland | -0.521 | 0.039 | 0 |
| Hardwood | 0.656 | 0.067 | 0 |
| Agricultural | 0.089 | 0.087 | 0.307 |
| Urban | -0.205 | 0.077 | 0.008 |
| Water/Wetland | 3.188 | 0.397 | 0 |
| Distance to water/100 | -0.237 | 0.013 | 0 |
| ***Land Use*** | | | |
| Urban (LU URB) | -1.179 | 0.119 | 0 |
| Altered | 0.137 | 0.062 | 0.027 |
| Natural | 0.186 | 0.055 | 0.001 |
| Distance to local road/100 | -0.042 | 0.005 | 0 |
| Distance to major road/100 | 0.004 | 0.001 | 0 |
| ***Topography*** | | | |
| Elevation/100 | -0.322 | 0.015 | 0 |

Table 5. Univariate logistic regression results for each model variable from bobcat telemetry point modeling.

| *Model* | $AIC_c$ | *ΔAIC* | $AICw_i$ |
|---|---|---|---|
| **All Habitat, All Land Use, and Topography (HERB + HDW + WAT + SHB + URB + DIST WAT + LU URB + MAJRD + LOCRD + ELEV)** | **15520.22** | **0** | **>0.999** |
| Avoided Land Use and Topography (LU URB + ELEV) | 15672.69 | 152 | <0.001 |
| All Habitat, Avoided Land Use and Topography (HERB + HDW + WAT + SHB + URB + DIST WAT + LU URB + ELEV) | 15995.97 | 476 | <0.001 |
| All Habitat and Topography (HERB + HDW + WAT + SHB + URB + DIST WAT + ELEV) | 16114.3 | 594 | <0.001 |
| Topography (ELEV) | 16316 | 796 | <0.001 |
| All Habitat and All Land Use (HERB + HDW + WAT + SHB + URB + DIST WAT + LU URB + NAT + MAJRD + LOCRD) | 16517.46 | 997 | <0.001 |
| All Vegetation and Water (HERB + HDW + WAT + SHB + URB + DIST WAT) | 16621.26 | 1101 | <0.001 |
| All Vegetation (HERB + HDW + WAT + SHB + URB) | 16863.75 | 1344 | <0.001 |
| Avoided Vegetation (SHB + URB) | 17013.01 | 1493 | <0.001 |
| Selected Vegetation (HERB + HDW + WAT) | 17044.07 | 1524 | <0.001 |
| Avoided Land Use and Roads (URB + MAJRD + LOCRD) | 17127.4 | 1607 | <0.001 |
| All Land Use and Roads (LU URB + NAT + MAJRD + LOCRD) | 17128.84 | 1609 | <0.001 |
| All Land Use (URB + NAT) | 17263.78 | 1744 | <0.001 |
| Avoided Land Use (LU URB) | 17265.31 | 1745 | <0.001 |
| Selected Land Use (NAT) | 17370.26 | 1850 | <0.001 |

Table 6. Models of bobcat presence with regard to landscape variables, ranked by Akaike's information criteria for small samples ($AIC_c$) with ΔAIC, and model weights $AICw_i$. Variables for each model can be found in Table 5. Bold indicates model with greatest support.

| *Effect* | *Coefficient* | *Odds ratio* | *95% confidence limit odds ratio* | |
|---|---|---|---|---|
| Intercept | 1.391 | | | |
| HERB | -0.334 | 0.716 | 0.503 | 1.018 |
| HDW | -0.001 | 0.999 | 0.850 | 1.174 |
| **WAT** | **2.031** | **7.624** | **2.947** | **19.719** |
| **SHB** | **-0.566** | **0.568** | **0.335** | **0.963** |
| URB | 0.064 | 1.066 | 0.385 | 2.951 |
| DISTWAT | -0.062 | 0.940 | 0.788 | 1.120 |
| **LU_URB** | **-1.323** | **0.266** | **0.160** | **0.444** |
| **LOCRD** | **0.073** | **1.076** | **1.013** | **1.144** |
| **MAJRD** | **0.034** | **1.035** | **1.018** | **1.051** |
| **ELEV** | **-0.921** | **0.398** | **0.281** | **0.565** |

Table 7. Beta coefficients, odds ratios, and 95% confidence limits for odds ratios for variables in the final selected GLMM. Bold indicates variables with the greatest influence on predictions of bobcat presence.

| ***Land Cover*** | | ***Elevation*** | | ***Distance to Road*** | | ***Distance to Water*** | | ***Habitat*** | |
|---|---|---|---|---|---|---|---|---|---|
| *Class* | *Score* | *Class* | *Score* | *Class* | *Score* | *Class* | *Score* | *Class* | *Score* |
| Urban | 20 | <200 m | 100 | 20 m | 20 | 20 m | 100 | Wetland | 100 |
| Altered | 50 | 200 - 400 m | 80 | 40 m | 40 | 40 m | 80 | Altered | 50 |
| Natural | 100 | 400 - 600 m | 50 | > 40 m | 100 | 60 m | 60 | Grassland | 60 |
| Water | 80 | > 600 m | 30 | | | >60m | 40 | Riparian | 60 |
| | | | | | | | | Shrub | 30 |
| | | | | | | | | Forest | 50 |
| | | | | | | | | Other | 40 |
| Weight | 0.3 | | 0.2 | | 0.1 | | 0.1 | | 0.3 |

Table 8. Assigned habitat suitability values based on empirical results from univariate and GLMM modeling of bobcat habitat selection. Bottom row indicates weight assigned to each variable type, based on strength of response in models.

| Name | Condition | Primary Concerns | Data Used for Assessment |
|---|---|---|---|
| Linkage 6-7 | Functioning | Future habitat alteration | Cameras, Habitat suitability and connectivity modeling |
| Linkage 8-10 | Functioning | | Cameras, Telemetry, Habitat suitability and connectivity modeling |
| Linkage 1-2a | Partially Functioning | Road crossing and altered habitat | Habitat suitability and connectivity modeling |
| Linkage 2-3b | Partially Functioning | Road crossing and altered habitat | Habitat suitability and connectivity modeling |
| Linkage 5-6 | Partially Functioning | Road crossing and altered habitat | Cameras, Roadkill, Habitat suitability and connectivity models |
| Linkage 5-8 | Partially Functioning | Development/altered habitat, secondary roads, total distance | Cameras, Telemetry, Habitat suitability and connectivity modeling |
| Linkage 9-10 | Partially Functioning | Development/altered habitat, secondary roads | Habitat suitability and connectivity modeling |
| Linkage 10-11 | Partially Functioning | Development/altered habitat, secondary roads | Habitat suitability and connectivity modeling |
| Linkage 11-12 | Partially Functioning | Road crossing and altered habitat | Cameras, Telemetry, Habitat suitability and connectivity modeling |
| Linkage 12-13 | Partially Functioning | Development/altered habitat, secondary roads | Habitat suitability and connectivity modeling |
| Linkage 3-6 | Partially Functioning | Secondary roads | Roadkill, Habitat suitability and connectivity modeling |
| Linkage 1-2b | Limited Functioning | Road crossing and altered habitat | Habitat suitability and connectivity modeling |
| Linkage 2-3a | Limited Functioning | Road crossing and altered habitat | Habitat suitability and connectivity modeling |
| Linkage 4-5 | Limited Functioning | Development/altered habitat, secondary roads, total distance | Habitat suitability and connectivity modeling |
| Linkage 6-13 | Limited Functioning | Road crossing and altered habitat | Cameras, Habitat suitability and connectivity modeling |
| Linkage 5-13 | Limited Functioning | Development/altered habitat, secondary roads | Cameras, Roadkill, Habitat suitability and connectivity modeling |

Table 9. Assessment of linkage status across the MSCP preserve network, with primary concerns for connectivity.

## APPENDIX A: HABITAT MODELING METHODOLOGY

For the habitat models developed from bobcat GPS collar data, we identified the proportional area of each of these types within a 30 meter buffer around each location point. We also calculated a distance to water variable (DIST WAT), measuring the Euclidian distance to blue line streams from the USGS National Hydrology Dataset stream layer. Land-use variables were developed from the Southern California Association of Government's (SCAG) land-use data layers, which were categorized into four groups of urban (URB), altered (LU ALT), natural (NAT) and water (LU WAT) and calculated as the proportional area within 30 meters of each point. Euclidian distances from major (DIST MAJRD) and local roads (DIST LOCRD) were also incorporated into the models, and were developed from the CalTrans TIGER data. Topographic data consisted of elevation data (ELEV) from digital elevation models. To assist in interpretation of model results, the distances to water, major and minor roads, and elevation were scaled by dividing each value by 100 m. The fire-return interval departure data is a measure of the shifting fire regime (meanCC FRI), which is a categorical variable with seven classes representing the condition class, or the degree of departure from the natural fire regime with respect to the fire-return interval (Hann and Bunnell 2001, Safford *et al.* 2011). For this last variable, increasingly negative values (-1 to -3) equate to areas that have burned more frequently than the natural fire-return interval (FRI) and are at increasing risk of type conversion. Increasing positive values (1 to 3) reflect areas that have not burned as often as expected when compared to historic FRI. The remaining category represents urban or altered areas that do not have the vegetative structure to carry fire and therefore, do not have a condition class or FRI.

We ran binary generalized-linear-mixed models (GLMM) of bobcat presences and pseudoabsences (Pearce and Boyce 2006, Aarts *et al.* 2012) using the PROC GLIMMIX function in SAS. GLMMs are a robust tool to analyze habitat-selection with telemetry data because the random effects resulting from serial correlation in location data from each individual can be estimated to allow for more accurate and appropriate analysis of population-level effects (Gillies *et al.* 2006, Bolker *et al.* 2009, Burdett 2010). To create binary data, we generated pseudoabsences in proportion to the number of presences for each individual within the 100% MCP using the Geospatial Modelling Environment command to generate stratified random points (Beyer 2012). All variables were first tested using binary logistic regression to determine which were significant on their own and whether the response to each indicated selection or avoidance, which was then factored into GLMM development. Models calculated random effects with the random intercept method with an autoregressive covariance structure and the Huber-White Sandwich variance estimator to calculate empirical standard errors that are robust to the lack of independence in the telemetry data due to both the spatial autocorrelation of locations and correlation of points from each bobcat (Clark and Stevens 2008). GLMMs were fit using the random intercept method and Laplace likelihood approximation, which is a less biased method for fitting GLMMs than pseudo-likelihoods (Bolker *et al.* 2009). We created a correlation matrix of predictor variables with Spearman rank coefficients to determine which variables were correlated at $r > |0.6|$ and these variables were run separately to avoid multicollinearity.

We took a stepwise approach to determine which variables in the GLMM model best explained bobcat response to landscape features. In this stepwise approach, all significant, uncorrelated variables were entered into the model according to the variable categories described above (vegetation, land-use, terrain, and fire). We based model selection on an information theoretic approach using the small sample correction of Akaike's Information Criteria ($AIC_c$)

and compared overall differences between models with ΔAIC to determine which model best fit the data. We also calculated model weights, AIC$w_i$, or the likelihood of a model, according to Burnham and Anderson (2002). To better understand which variables in the best models were influencing patterns of bobcat presence, we recorded the odds ratios for each variable, as well as the 95% confidence limits for those odds ratios. Odds ratios with confidence limits that bound one are considered less influential in the model.

## APPENDIX B: HABITAT SUITABILITY AND CONNECTIVITY MODELING METHODOLOGY

The development of bobcat habitat suitability models and the cost-weighted connectivity assessment were based on the empirical data from our habitat use modeling and developed using raster datasets in GIS. To ensure model comparability, we determined which environmental rasters to use based on whether it included one or more variables that contributed to a significant improvement in predicting bobcat presence in the selected GLMM. For bobcats, habitat suitability was based on values assigned to rasters of habitat type, land-use, Euclidian distance from roads and water, and elevation. After assigning habitat suitability values within each category, we then needed to combine all rasters into a single landscape permeability raster by using the weighted geometric mean, which is recommended over the arithmetic mean (Beier *et al.* 2011). We weighted each raster type according to the relative influence in the models, so that the total of the weights for all rasters would equal 1.0. Habitat suitability was assessed at a 30-m pixel scale and clipped to the region where we had collected telemetry locations for bobcats.

After calculating habitat suitability, which is assumed to represent permeability of the landscape, we then used the inverse of this value to reflect landscape resistance (Singleton *et al.* 2002). Given that 100 was the maximum habitat suitability value, we subtracted the calculated habitat suitability value of each pixel from this maximum to get the complement, resistance. This resistance layer was then used as the cost value to assess the effective distance for each species to move between protected lands using the cost-weighted distance tool from the GIS Spatial Analyst toolbox. Because bobcat movement in this region is likely concentrated between areas of protected, natural lands, we used a state-wide database of conserved lands, California Protected Areas Database (CPAD 1.8, 2012) as the source features between which we calculated the cost-weighted distance. The output of this analysis represents the effective distance, or lowest cost of traveling between source locations, or in this case, protected lands.

## APPENDIX C: OCCUPANCY MODEL SELECTION AND RESULTS

To eliminate modeling issues associated with missing data values, the camera sampling period analyzed in Program PRESENCE (Hines 2010) included 18 of the sampling periods, ranging from January 11, 2012 to September 19, 2012. To determine the effects of survey covariates on detection of bobcats, we first ran models with no covariates and tested for the effect of camera type and wet/dry season on probability of detection and determined that only cameras (estimate ± SE; 1.308 ± 0.229) appeared to be an important covariate for detection probability, with a lower detection probability resulting from the use of the older Cuddeback Expert model cameras, which reduced detection rates by approximately half (0.3509 compared to 0.6667). For all subsequent occupancy models, we used this detection model. We ran numerous models of occupancy testing for the effects of site type (core, bridge, culvert, or any linkage), recreation (low and high), land use, habitat type, elevation, distance to major and local roads, and distance to water on bobcat occupancy across all stations. No single model outperformed the others, and therefore, the top seven ranked models were averaged (Table C1). From our modeling efforts, several important covariates emerged for predicting bobcat occupancy at camera stations: lower occupancy rates at stations placed at bridge crossings (-2.193 ± 1.240), lower rates at stations with a greater proportion of altered habitat (-1.759 ± 1.150), and lower occupancy at stations within putative linkage zones (-1.38 ± 1.220), compared with core conserved lands. Although two other variables were identified in the top-ranked occupancy models, neither was significant. These covariates were high recreation (-0.576 ± 1.08) with lower occupancy at high recreation stations, and elevation (0.005 ± 0.010) with higher occupancy rates at the higher elevation stations in the inland study area.

| *Model* | *AIC* | *ΔAIC* | *AICw$_i$* | *Model likelihood* | *Parameters* |
|---|---|---|---|---|---|
| Psi (bridge) , p (camera) | 538.04 | 0.00 | 0.3203 | 1.0000 | 4 |
| Psi (altered habitat ), p (camera) | 539.55 | 1.51 | 0.1505 | 0.4700 | 4 |
| Psi (bridge+altered habitat), p (camera) | 539.71 | 1.67 | 0.1390 | 0.4339 | 5 |
| Psi (.), p (camera) | 539.77 | 1.73 | 0.1348 | 0.4211 | 3 |
| Psi (linkage area), p (camera) | 540.29 | 2.25 | 0.1040 | 0.3247 | 4 |
| Psi (elevation), p (camera) | 540.49 | 2.45 | 0.0941 | 0.2938 | 4 |
| Psi (high recreation), p (camera) | 541.48 | 3.44 | 0.0573 | 0.1791 | 4 |
| Psi (.), p (.) | 572.51 | 34.47 | 0.0000 | 0.0000 | 2 |

Table C1. Top occupancy models ranked by Akaike's information criteria with ΔAIC, and model weights AIC$w_i$. As no model clearly outperformed the others, all models were included in model averaging of occupancy rates for each camera station. Covariates included were used to model detection rates (p), and occupancy rates (Psi).

# Appendix M-2

Center for Biological Diversity References (Comment Letter O-9)

# COMPREHENSIVE MULTI-SPECIES CONNECTIVITY ASSESSMENT AND PLANNING FOR THE HIGHWAY 67 REGION OF SAN DIEGO COUNTY, CALIFORNIA

SAN DIEGO STATE UNIVERSITY

**Final Report**
**June 2017**

*Prepared for*

SANDAG No. 5004388
Task Order 3

*Prepared by*

Megan Jennings and Katherine Zeller

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## LIST OF ACRONYMS AND ABBREVIATIONS

AWDT – Average Weekday Daily Traffic

BISON – Biodiversity Information Serving Our Nation

Caltrans – California Department of Transportation

CDFW – California Department of Fish and Wildlife

CEHC – California Essential Habitats Connectivity Plan

CFWO – Carlsbad Fish and Wildlife Office

CMSP – Connectivity Management Strategic Plan

CNLM – Center for Natural Lands Management

EHL – Endangered Habitats League

FLCP – Factorial Least Cost Path

GBIF – Global Biodiversity Information Facility

IEMM – Institute for Ecological Monitoring and Management

MCB – Marine Corps Base

MHCP – Multiple Habitats Conservation Plan

MOM – Master Occurrence Matrix Database

MSCP – Multiple Species Conservation Plan

MSPA – Management Strategic Plan Area

MSP – Management Strategic Plan

NCCP – Natural Community Conservation Plan

SANDAG – San Diego Association of Governments

SDMMP – San Diego Management and Monitoring Program

SDSU – San Diego State University

SR – State Route

TNC – The Nature Conservancy

USFWS – United States Fish and Wildlife Service

## ACKNOWLEDGMENTS

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**Disclaimer: The use of firm, trade, or brand names in this report is for identification purposes only and does not constitute endorsement by state or federal government.**

## EXECUTIVE SUMMARY

Through a comprehensive, multi-species connectivity analysis using robust analytical approaches, we created a connectivity plan, tools to facilitate the implementation of this plan, and a wildlife crossing infrastructure plan for key roadways in our study area. Through this data-driven approach, we:

- Assembled a multi-species connectivity analysis using a suite of data types and species complemented by a landscape-focused land facet analysis
- Analyzed a suite of data types using cutting-edge analytical techniques appropriate to each data type
- Leveraged survey and monitoring data from our study region, producing a data-informed connectivity plan without the collection of any new field data
- Identified and mapped 12 spatially-explicit focal species corridor segments and one land facet corridor to facilitate wildlife movement within the SR-67 region of San Diego's Multiple Species Conservation Plan area
- Assessed the potential functionality of those corridors for additional species including five federally listed species and 13 other species of interest
- Attributed those spatially-explicit corridors with data on land conservation status, biological variables, and threats and stressors to inform decision-making
- Created a decision support tool for scoring potential acquisitions, habitat restoration projects, or other land management and planning decisions
- Used our connectivity models, species data, site specific information, and previously collected data on crossing use and roadkill to inform wildlife crossing infrastructure recommendations for SR-67 as well as other roadways within our analysis area
- Worked with a variety of stakeholders throughout this process to gather information, feedback, and key input to generate a connectivity plan and conservation tool that could readily be implemented by the diverse range of land management and planning entities working in this region of San Diego County

# INTRODUCTION

### *Importance of Connectivity*

Habitat fragmentation and degradation are two of the greatest threats to habitat availability and quality, posing a direct risk to species' persistence and consequently, to biodiversity. As anthropogenic features such as roads and housing developments alter the landscape, landscape connectivity for wildlife may be reduced. Current land management plans throughout North America and Europe are designed to protect biodiversity by establishing a network of core habitat areas that are connected via corridors or linkages. The central tenet of this large-scale conservation planning is that viable populations and natural communities can be supported by a connected landscape network (Beier *et al.* 2006, Crooks and Sanjayan 2006, Boitani *et al.* 2007, Barrows *et al.* 2011), particularly as the landscape becomes altered by anthropogenic features. Landscape connectivity allows for movement among patches of suitable habitat, reduces the chance of extinction and the effects of environmental variability on small populations (Brown and Kodric-Brown 1977), and maintains gene flow between populations in patchy landscapes (Noss 1987). Connectivity also allows for more rapid recovery of populations after events such as fire and disease outbreaks. Over longer time scales, and in the face of changing abiotic conditions, connectivity may also prove critical for range shifts in response to landscape changes caused by a changing climate and altered disturbance regimes (Hannah *et al.* 2002, Heller and Zavaleta 2009).

Roadways in particular pose a significant challenge to landscape functioning (Laurence and Balmford 2013). Though roads can have many negative indirect effects on wildlife, two mechanisms directly impact habitat suitability and continuity (Fahrig and Rytwinski 2009): the *barrier effect* whereby the road blocks species' movement across the landscape, and *direct mortality* through wildlife-vehicle collisions (Bissonette 2002). The degree of impact of a road may depend on several factors such as the location of the road relative to open space and protected habitats, traffic volume and traffic speed (Fahrig *et al.* 1995), and the sensitivity of species affected by the road. Although many conservation network plans acknowledge the negative effects roads can have on connectivity, few have thoroughly assessed and developed approaches to mitigate barrier and mortality effects of roads that fall within ecological networks.

### *San Diego County Preserve Network and State Route 67*

In southern California, the landscape-scale network approach has been adopted in response to the widespread habitat conversion and fragmentation that has resulted from development in the region (Riverside County 2003, County of San Diego 1998). Specifically, in San Diego County, there are a number of public and private conservations plans and ecological networks, including the San Diego Multiple Species Conservation Program (MSCP) and Multiple Habitats Conservation Program (MHCP), that were designed to create an interconnected preserve system. The overarching goal of these plans is to preserve the biological diversity of San Diego County through the conservation and management of functional habitats and linkages[1,2,3]. In January

[1] Management Goals and Objectives (Section 1.51, p.49-50) under the Framework Management section of the San Diego MSCP Plan identify viability of ecosystem function and processes, long-term persistence of populations, functional habitats and linkages, as well as ability to adapt to changing circumstances as key goals of the plan.
[2] Poway Sub-Area Plan (SAP) p. 2-10 identifies two regional wildlife corridors through Poway and into adjoining jurisdictions, one of which is bisected by SR-67 study area.

2011, the Connectivity Monitoring Strategic Plan (CMSP) for the San Diego Preserve System was drafted. One of the primary objectives for connectivity management identified in the CMSP was to "inform adaptive management and other conservation actions by identifying important movement areas/chokepoints between cores for various species."[4] Based on the findings from previous research, as well as the initial studies conducted to meet the Priority Objectives in the CMSP, State Route (SR)-67 was named as one of the primary barriers to wildlife movement and connectivity in the MSCP and MHCP areas. The identification of SR-67 as a major threat/stressor was reiterated in the 2013 Management Strategic Plan (MSP)[5] for the MSCP area, which prioritized further connectivity research in the vicinity of SR-67 and the development of a wildlife crossing infrastructure plan as a management and mitigation goal[6]. This area has also been characterized as a priority area by the California Essential Habitat Connectivity Project (CEHC, Spencer *et al.* 2010) where local-scale analyses and road crossing improvement plans were recommended prior to the development of site-specific connectivity management and enhancement goals.

Further discussions about subregional connectivity in the area were prompted by a California Department of Transportation (Caltrans) proposal for a median barrier safety project as the major widening and highway improvement project that is expected to occur within the next 20 to 30 years. These projects may further challenge wildlife movement, but they also provide opportunities to make significant improvements to wildlife connectivity. Although the widening of SR-67 may not be initiated until 2040, a comprehensive, data-driven assessment is necessary to facilitate conservation planning in the interim. This planning will ensure acquisitions, habitat restoration, and management actions to establish a functionally connected landscape can progress towards a strategy that will support viable wildlife populations in perpetuity.

***Multi-species Connectivity Planning for SR-67***

In response to this need for data on wildlife movement along SR-67, The Institute for Ecological Monitoring and Management at San Diego State University (SDSU) has conducted a multi-faceted research project to examine connectivity across SR-67 and to preserve or improve existing crossings through identifying functioning crossing features along the highway. This assessment leverages previously collected telemetry, occurrence, camera, and road-kill data to conduct a multi-species comprehensive connectivity assessment for the SR-67 region. The goal of this project was to provide a data-driven analysis that would inform connectivity planning for the area. Our ultimate objective with this research was to improve functional connectivity of the SR-67 area and increase permeability of the roadway through installation of larger and appropriately-sited crossing structures. The analysis and data products produced during this project are intended to promote proactive conservation efforts within an area of the MSCP that has frequently been cited as a major threat to wildlife movement. One of the main objectives was to develop recommendations for improving connectivity across SR-67 and to preserve habitat and wildlife corridors adjacent to SR-67 prior to the initiation of any road development or improvement. This synthesis of data will facilitate the management of healthy wildlife

[3] Poway SAP p. 3-2 highlights the needs to maintain functional connectivity within Poway as well as between Poway and adjoining jurisdictions.
[4] CMSP, p.5
[5] MSP, Volume 1, p. 2-2
[6] MSP, Volume 2, p. 4-31

populations within the MSPA by providing data-driven recommendations that can be used to take immediate action to improve landscape connectivity in the SR-67 area, and can serve as a template in other regions of San Diego's NCCP plans faced with limited connectivity caused by roadways.

Connectivity is often considered from two different perspectives, physical and functional connectivity. *Physical connectivity* indicates whether there is structure connecting two patches of habitat, whereas *functional connectivity* accounts for how wildlife respond to that structure and the implications of those considerations for the species of concern (Taylor *et al.* 1993, Tischendorf and Fahrig 2000a, 2000b). The distinction between physical connectivity and functional connectivity in fragmented landscapes is critical when implementing conservation and mitigation measures to prevent irreversible habitat fragmentation. There are a variety of factors that can affect this response, including but not limited to, life history traits of the affected species, habitat configuration, degree of habitat fragmentation, and type of fragmenting features (*e.g.*, roads, houses). Furthermore, this response will differ among species with some demonstrating a greater sensitivity to these factors than others. Quantifying or assessing landscape connectivity, however, is non-trivial (Fagan and Calabrese 2006) given the context-dependent nature of connectivity (Crooks and Sanjayan 2006) and the expense and effort of acquiring movement data for species of interest. Currently, one of the primary barriers to conducting data-driven connectivity analyses is the general lack of knowledge of how animals are currently using the landscape, and how landscape use changes in response to dynamic landscape processes over time. For this reason, one of the other main objectives of this research was to identify approaches for data synthesis that would allow us to leverage the existing data that had been collected during monitoring and management activities in San Diego's preserve network. We investigated a range of analytical techniques that would support a robust, comprehensive, data-driven study using cutting-edge methodologies to assess and map connectivity that were appropriate for the species-specific types of data that were available.

To fully assess connectivity throughout the portion of the preserve network surrounding SR-67 and provide clear, implementable actions to achieve the desired status of landscape connectivity, we carried out a two-phased project. Phase I focused on the collection, organization, and analysis of available data for a suite of focal species as well as comprehensive mapping of corridors. In Phase II, we utilized the data and resulting maps generated in Phase I to develop spatially-explicit corridors attributed with relevant management data that was linked to the Management Strategic Plan for the preserve network (Figure 1) as well as a wildlife infrastructure improvement plan for improving permeability of SR-67 and other roadways in the study area. This detailed infrastructure plan for the roadway identifies recommendations for improvements that can be made prior to the anticipated widening as well as the major wildlife infrastructure repairs and replacement that would take place during widening. Phase II products were developed in cooperation with land managers, conservation planners, Caltrans, and other stakeholders in the region.

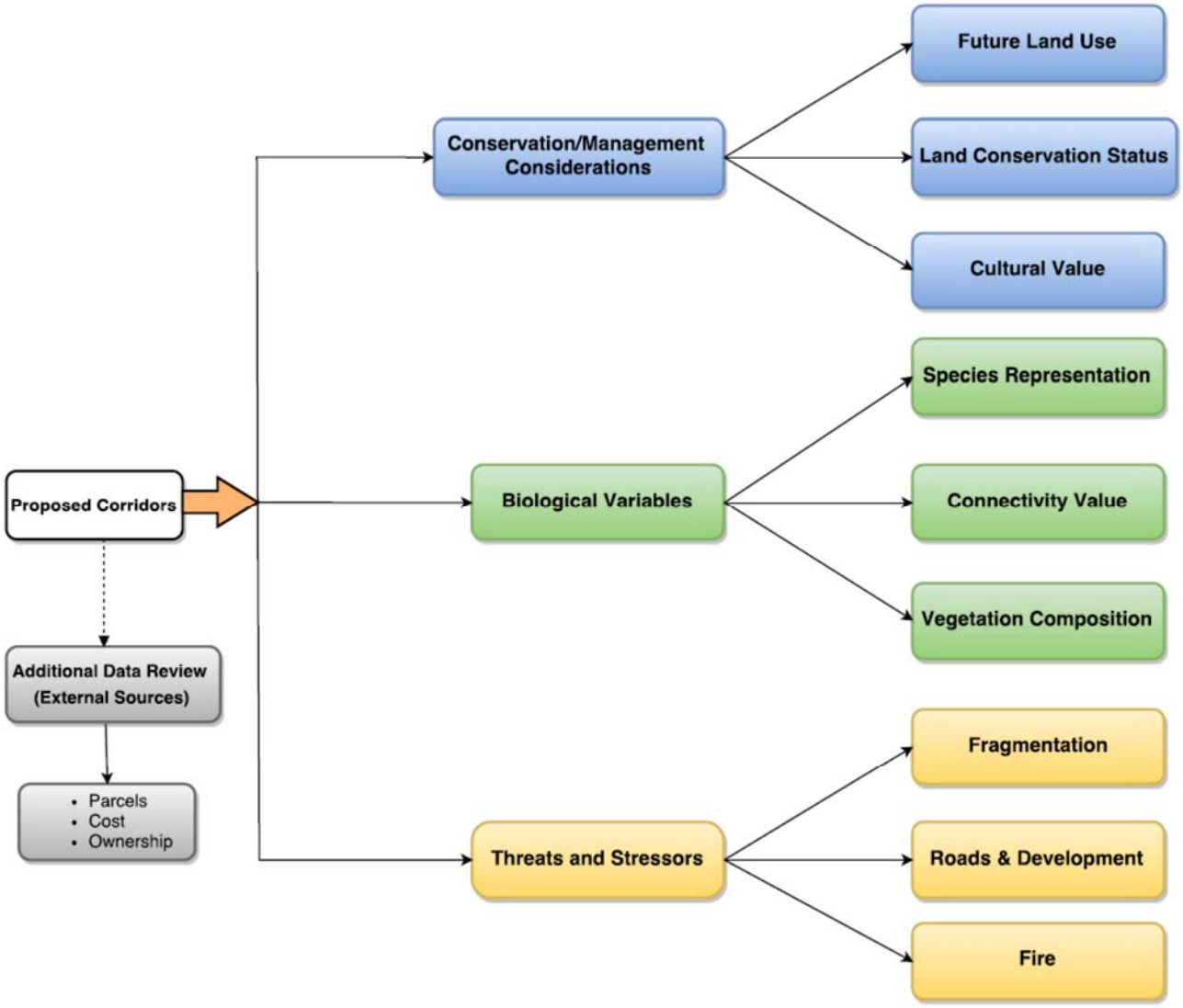


**Figure 1.** The corridor attribution guide developed for this project illustrates the three main categories of attributes as well as example data types for each.

The data integration, compilation, and analysis were used to inform the development of specific data products for this project:

Phase I – Data synthesis, analysis, and corridor mapping

- Habitat suitability surfaces for all focal species
- Probability of movement and landscape genetic surfaces for selected focal species
- Resistance surfaces for all focal species
- Connectivity flow for all focal species

Phase II – Identification and prioritization of management actions

- Spatially-explicit corridors and corridor attributes
- Decision support guide for using corridor criteria in decision making
- Infrastructure placement and design for wildlife road crossings

***Stakeholder Coordination***

A key component to the development of the geospatial and data products we produced for this project was stakeholder engagement. Since the inception of this project, we have coordinated with stakeholders to ensure we had as much information as possible on prior and current research that could inform our assessment. Based on this input, we have worked to identify any opportunities to leverage existing data and efforts of other projects. We also worked to share our findings during the course of this project with other researchers, planners, and land managers to facilitate wildlife and connectivity management in this region of San Diego County. Through these engagement sessions, we gathered information that allowed us to create actionable science and decision support tools that would allow end users to integrate the SR-67 connectivity implementation plan into ongoing efforts.

The process of stakeholder engagement began before this project started, in September 2014. That initial meeting, which served as a platform for information-sharing and coordination of research and planning activities involving SR-67, allowed us to fully form the research proposal for this project. Once we officially kicked off the SR-67 Multi-species Connectivity Planning Project in March 2016, we broadened our stakeholder outreach, eventually contacting 55 stakeholders from 19 organizations (Table F1). Our outreach and engagement sessions included three types of meeting formats: 1) full stakeholder meetings for all interested parties, 2) focused engagement sessions with small groups of experts in planning and management, and 3) one-on-one sessions with individual researchers or species experts. During the project period, we convened three stakeholder meetings of our full group, three focused engagement sessions with small groups, and numerous feedback sessions with experts at several stages of the project. Details on each of the engagement sessions as well as agendas, notes, and attendee lists from these meetings are included in Appendix F.

Through this engagement process, we have been able to hone and refine our analyses and data products in ways that will best serve the end users of our products. The requests and suggestions we received during our feedback sessions not only improved our data products and recommendations, but also have allowed our stakeholders to envision using these data products and influence their design and delivery.

## METHODS

### *Study Area*

The study was conducted within the San Diego Multiple Species Conservation Plan Area and a portion of the Draft North County Multiple Species Conservation Plan Area in southern California. This project was focused on areas surrounding SR-67 in central San Diego County between Mapleview Rd. in Lakeside and Etcheverry Street in Ramona, CA. The natural habitats and protected open space in the area are primarily publicly owned, and include Sycamore Canyon and Goodan Ranch Preserves, Boulder Oaks Preserve, San Vicente Highlands Preserve, Iron Mountain, Ramona Grasslands Preserve, San Dieguito River Park lands, and a portion of the Cleveland National Forest in the eastern portion of the study area. The analysis area included ~54,000 hectares (~133,500 acres) within the region identified as Management Unit 4 in the MSP area. Beyond the roadway, we evaluated connectivity based on previous data collected in MSCP core preserves 5, 6, 12, and 13 (Figure 2).

Elevation across the study site ranged from 58 meters (m) in the western section of the San Diego River and 1,110 m at the highest point of the study area, El Cajon Mountain. Vegetation types in the study area varied with elevation and proximity to the roadway. Habitat types in the study area varied with both elevation and distance from the coast, but was predominantly a shrubland ecosystem. Habitats across these areas included coastal sage scrub dominated by California sagebrush (*Artemesia californica*), chaparral habitat types generally dominated by scrub oak (*Quercus berberidifolia*), ceanothus (*Ceanothus* sp.), or chamise (*Adenostoma fasciculatum*), oak woodland with coast live oak (*Quercus agrifolia*), grasslands dominated by non-native annual grasses, riparian zones with an oak *(Quercus agrifolia*) or sycamore (*Platanus racemosa*) overstory and herbaceous understory, as well as urban and altered areas. Sections of the study area within the highway right-of-way and near industrial and urbanized areas near both Ramona and Lakeside were dominated by a mix of non-native plants (*e.g.*, *Bromus* spp., *Avena*, spp., *Centaurea melitensis*, and *Ricinus communis*), and barren or sparse areas, interspersed with coastal sage scrub and chaparral. The Mediterranean-climate of the study region is characterized by hot, dry summers and mild, wet winters with precipitation often less than 300 millimeters (mm).

State Route 67 is a highway that runs north and south for a distance of 24.38 miles from its southern terminus at Interstate 8 in El Cajon, CA to its northern end at the intersection of SR-78 in Ramona, CA. The highway is a four-lane divided freeway from El Cajon to Lakeside, CA, where it becomes an undivided highway ranging from two to four lanes. In 2008, traffic volumes on this section of highway ranged from 23,400 Average Weekday Daily Traffic (AWDT) to 26,600 AWDT. Expanding development in the backcountry of San Diego County has led to increasing traffic volumes on the road, which has in turn, added to traffic congestion. In addition, the speed at which vehicles are traveling on the highway has increased over the last decade, resulting in a number of severe and/or fatal collisions creating concerns for human. The convergence of a heavily traveled roadway bisecting the natural habitats along SR-67 has also led to a concurrent concern about safe road crossings for wildlife and wildlife-vehicle collisions, which we examined in this assessment.

### *Data Synthesis*

To identify road crossings and assess landscape-level corridors across the study area, we (1) identified focal species and available data for those species, (2) ran spatially-explicit models to estimate habitat use and resistance to movement across the study area for each species, (3) modeled connectivity and road crossing locations for each species, and (4) combined results across species. San Diego County was the study area extent used to develop species habitat use, movement, and landscape genetic models. The connectivity and road crossing analyses were conducted in the SR-67 study area, described above and included a buffer to account for possible edge effects produced by the models (Figure 2). We used corridor attributes as the basis for a conservation decision-support tool and the road crossing attributes to prioritize crossing locations and provide wildlife-specific recommendations for the wildlife infrastructure plan. Methodological approaches are summarized below and detailed methods are provided in Appendix B.

### *Focal Species and Environmental Variables*

Through stakeholder input and discussions with local biologists, we identified a number of focal species for this analysis. This initial list was narrowed to nine species that had adequate data for analysis and represented a wide range of movement abilities and habitat requirements. Species and data sources are listed in Table 1.

We used environmental variables thought to affect habitat use and movement for the focal species. These included topographic, land cover, water, and human development variables (Table 2). These environmental variables were used for all species except for puma. The puma models were mostly developed during previous research in collaboration with Drs. Winston Vickers and Walter Boyce at the University of California – Davis, Karen C. Drayer Wildlife Health Center Southern California Mountain Lion Project.

Before running the models, we smoothed each environmental variable using various smoothing factors to capture the appropriate scale, or zone of influence for each variable for each species. We ran all our models for each variable at each scale and selected the scale for each variable that resulted in the best model performance for each species.

### *Habitat use and resistance modeling*

For species with occurrence points, we combined occurrence points with the environmental variables to develop ensemble Species Distribution Models (SDMs, Araujo and New 2007, Grenouillet *et al.* 2011). These SDMs were used to predict habitat suitability across San Diego County. We assumed areas with a high habitat suitability would have a low resistance to movement and areas with a low habitat suitability would have a high resistance to movement. Therefore we used a non-linear inverse transformation to convert habitat suitability to resistance for each species.

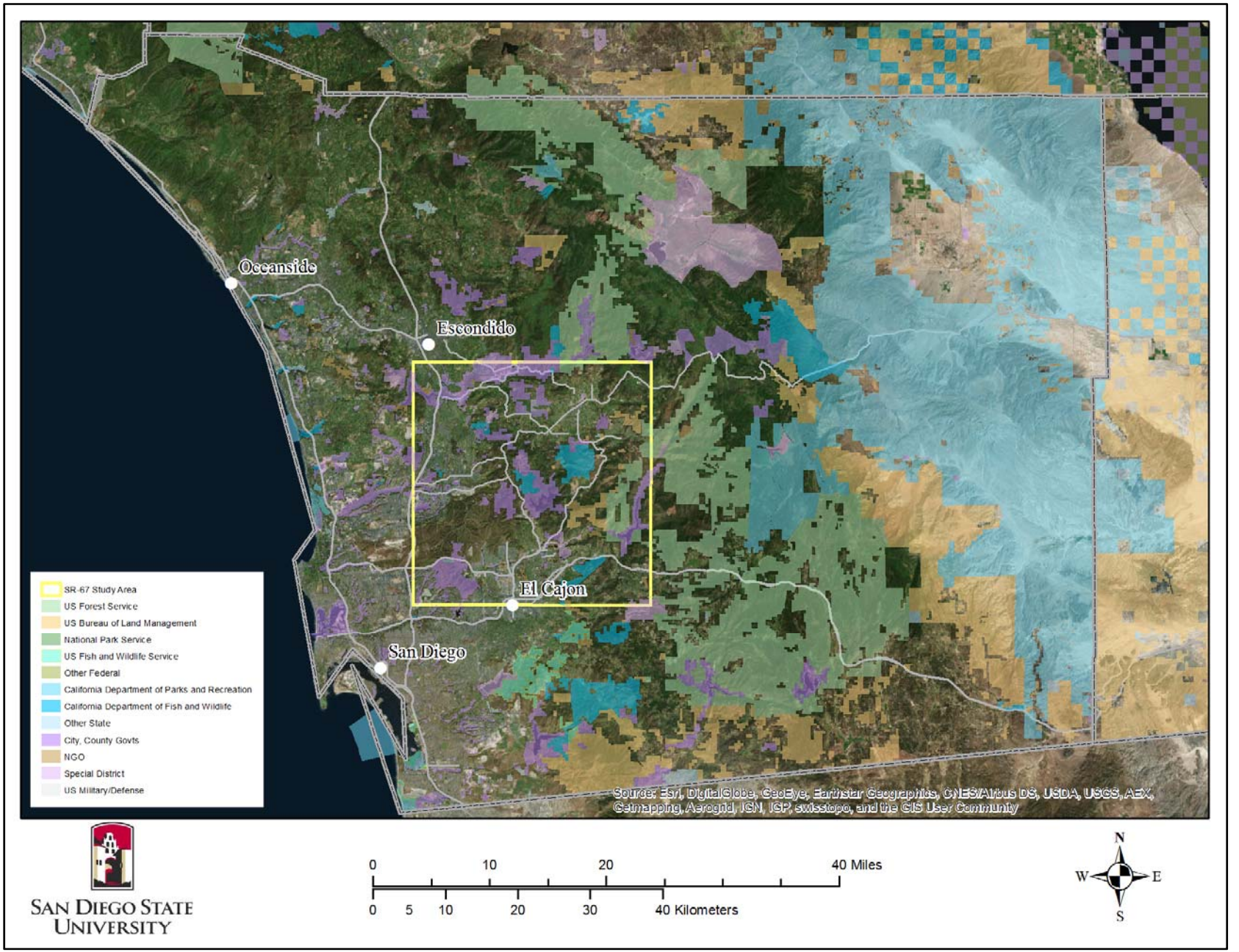


**Figure 2.** Map of SR-67 study area, depicted in yellow box within the context of San Diego County's network of conserved lands.

**Table 1.** Focal species, available data types, data sources, and analytical models used in the analysis. Data sources are as follows: 1) San Diego Natural History Museum, *In Prep*; 2) County of San Diego 2016; 3) eBird 2016; 4) Jennings and Lewison 2013; 5) Marine Corps Base Camp Pendleton, *Unpublished Data*; 6) Center for Natural Lands Management, *Unpublished Data*; 7) San Diego Management and Monitoring Program 2016; 8) Mitelberg and Vandergast 2016; 9) Ernest *et al.* 2014 and Zeller *et al.* 2016; 10) Franklin *et al.* 2009.

| **Focal species** ***(scientific name)*** | **Data type(s)** | **Data source(s)** | **Analytical method(s)** |
|---|---|---|---|
| **California mouse** *(Peromyscus californicus)* | Occurrence points | SDNHM Mammal Atlas[1], SanBIOS[2] | Species Distribution Model |
| **Big-eared woodrat** *(Neotoma macrotis)* | Occurrence points | SDNHM Mammal Atlas[1], SanBIOS[2] | Species Distribution Model |
| **Wrentit** *(Chamaea fasciata)* | Occurrence points | eBIRD[3] | Species Distribution Model |
| **Mule deer** *(Odocoileus hemionus californicus*) | Occurrence points & Genetic data | SDNHM Mammal Atlas[1], SanBIOS[2], SDSU[4], MCB Camp Pendleton[5], CNLM[6], SDMMP MOM[7], USGS[8] | Species Distribution Model & Landscape genetics analysis |
| **Bobcat** *(Lynx rufus)* | GPS telemetry & genetic data | SDSU[4] | Resource and Movement Selection Functions & Landscape genetics analysis |
| **Puma** *(Puma concolor)* | GPS telemetry & genetic data | University of California, Davis[9] | Resource and Movement Selection Functions & Landscape genetics analysis |
| **Coachwhip** *(Coluber flagellum)* | Species Distribution Model | USGS[10] | Species Distribution Model |
| **Western whiptail** *(Aspidoscelis tigris)* | Species Distribution Model | USGS[10] | Species Distribution Model |
| **Western toad** *(Anaxyrus boreas)* | Species Distribution Model | USGS[10] | Species Distribution Model |

For species with GPS telemetry data (puma and bobcat) we performed two analyses. First, we estimated resource use using a point selection function, which we used for estimating the relative probability of habitat use across San Diego County. Second, we estimated resource use during movement events with a path selection function (PathSF, Cushman *et al.* 2010, Zeller *et al.* 2016), which we used to estimate the relative probability of movement across San Diego County. We used the inverse of the probability of movement surfaces to estimate resistance for puma and bobcat.

For species with genetic data (puma, bobcat, and mule deer), we performed a landscape genetic analysis, which correlates the genetic distance between individuals across the landscape with the resistance distance between individuals across the landscape (Manel *et al.* 2013). This analysis estimates resistance directly so no transformation to resistance was needed. To develop the final resistance surface for species with genetic data, we multiplied the resistance surface derived from

the SDM or PathSF analyses with that derived from the landscape genetic analysis and rescaled this surface from 1 – 100 (1 = low resistance and 100 = high resistance; Zeller *et al.* 2017).

**Table 2.** Environmental variables used in developing habitat use and resistance surfaces for each focal species.

| | Variable | Source/Derivation | Year | Citation |
|---|---|---|---|---|
| Roads and Development | All Roads | Open Street Map | 2014 | Open Street Map 2014 |
| | Primary roads | Open Street Map; Motorways | 2014 | |
| | Secondary roads | Open Street Map; primary road, secondary road, and trunk road | 2014 | |
| | Tertiary roads | Open Street Map; living street, residential, rest area, road, service, tertiary, and unclassified | 2014 | |
| | Unpaved roads/trails | Open Street Map; bridleway, cycleway, footway, path, and track, | 2014 | |
| | Percent Imperviousness | Derived from a hybrid of the National Land Cover Database percent impervious surface and updated data from the San Diego Association of Governments land use surface | 2011/ 2012 | NLCD 2011 SANDAG 2012 |
| Topography | Elevation | National Elevation Dataset | 2009 | USGS 2009 |
| | Percent Slope | Derived from National Elevation Dataset | - | - |
| | Terrain Ruggedness | Total curvature derived from National Elevation Dataset with DEM Surface Tools (Jenness 2013) | - | - |
| | Topographic Position Index | Derived from National Elevation Dataset | - | - |
| | Ridges | Derived from Topographic Position Index values >= 8 | | |
| | Canyons | Derived from Topographic Position Index values <=- 8 | | |
| | Steep Slope | Derived from Topographic Position Index values -8 – 8, slope >=6° | | |
| | Gentle Slope | Derived from Topographic Position Index values -8 – 8, slope <=6° | | |
| Water | Streams | National Hydrography Dataset streams layer | 2011 | USGS 2011 |
| | Distance to Water | Derived from National Hydrography Dataset calculated as Euclidean distance to blue line streams | | |
| Vegetation Type | Agriculture | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Chaparral | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Coastal Scrub | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Coniferous Forest | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Desert Scrub | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Hardwood Forest | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Herbaceous Grassland | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Riparian | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Sparse/Disturbed | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |
| | Water and Wetlands | Vegetation Data of San Diego County | 2014 | SANDAG 2014 |

A depiction of the data types and analytical methods used to estimate resistance for each species is provided in Figure 3.

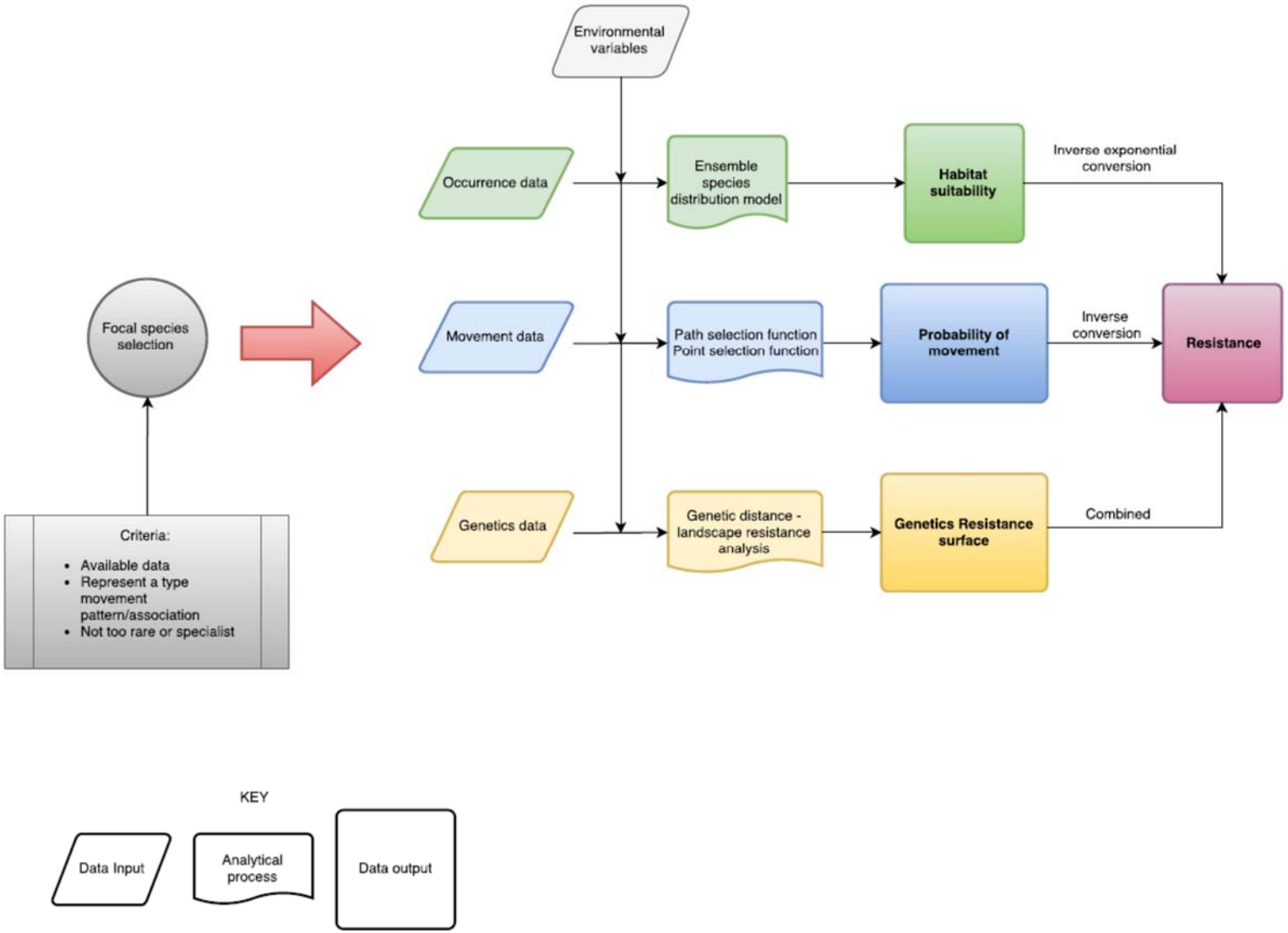


**Figure 3.** Analytical approaches used to develop resistance from each of the data types we had available for the multi-species connectivity planning project

We assessed the SDMs for coachwhip, western whiptail, and western toad that had been developed by Franklin *et al.* (2008) and provided by USGS. These SDMs were developed at a regional scale and at a coarse spatial resolution. Because of this, the predictive ability of these models was poor in the SR-67 study area. The input we obtained from the stakeholders confirmed that these layers were inadequate for connectivity modeling for this project. Therefore, we decided not to use these data or these species in the connectivity analysis. We did, however, use these data in the corridor attribution process.

### *Connectivity Modeling and Identification of Multi-species Corridors and Road Crossing Locations*

Across the final resistance surface developed for each species, we identified landscape corridors using two connectivity modeling approaches; Resistant kernels (Compton *et al.* 2007) and OmniScape (McRae *et al.* 2016). Resistant kernels require the identification of source points in the study area from which connectivity is modeled. We identified 1,000 source points for each species. These points were distributed probabilistically on each habitat suitability surface so that areas with higher habitat suitability had more source points than areas with lower habitat suitability. OmniScape sources were identified as any pixel that had a resistance less than 20. To create a multi-species connectivity model, we averaged the connectivity surfaces derived from the resistant kernel analysis across all species. Discrete corridors were identified on this multi-species connectivity surface by clipping this surface to the top 30% of connectivity values (70-100% of connectivity values). These corridors were expanded slightly by including areas identified from the OmniScape analysis that enforced east-west and north-south connectivity across the study area. We divided the final corridor into 12 different sub-corridors based upon the location of protected areas and other important features on the landscape.

From this connectivity surface we also produced three additional layers that may be helpful in land management and planning; corridor isopleths, a normalized flow surface, and a corridor resiliency map. The corridor isopleths depict the top 10% of the multi-species connectivity surface (areas with the highest average connectivity across all six focal species), the top 10-20% of the connectivity surface, and the top 20-30% of the connectivity surface. The normalized flow surface shows the connectivity surface in terms of how concentrated or diffuse connectivity is across the study area. Areas of concentrated flow indicate naturally restricted flow, such as steep canyons, restricted flow due to human development, or a combination of these factors. Where flow is concentrated due to human development might be areas facing more imminent fragmentation threats. Normalized flow was derived by running the resistant kernel connectivity model across a uniform resistance surface (where there is no restriction of movement), and then dividing the multi-species connectivity surface by this unrestricted connectivity surface. The corridor resiliency map used a layer developed by The Nature Conservancy that depicts resiliency of areas to climate change. We multiplied this map by the multi-species connectivity surface to derive a map where high values indicate areas that are both good for connectivity and resilient to climate change.

We also conducted a Land Facet corridor analysis (Appendix E). Land Facets identify areas of similar topographic and climactic makeup. Corridors based on these land facets have been promoted as a way to ‘preserve nature’s stage’ in the face of climate change and allow for flow amongst similar topographic and climatic features (Anderson and Ferree 2010, Beier and Brost

2010). We identified 15 land facets across the study area, created resistance surfaces for each land facet, and derived corridors for each land facet using a least cost corridor analysis. Our multi-species corridor generally overlapped these land facet corridors, with the exception of one land facet composed of gentle slopes at mid-elevation with high solar insulation. This land facet encompassed grassland features across the study area, specifically, the Ramona grasslands. Because none of our focal species were associated with grasslands, we added this single land facet corridor to our final corridor layer so that grassland species were represented, bringing the total number of corridors to 13.

To identify road crossing locations, we ran Factorial Least Cost Paths (FLCPs) across our study area for each species (Cushman *et al.* 2014). FLCPs create pairwise least-cost paths between all source points on the landscape. Due to computational limitations, we reduced the number of source points to 300. We identified probable road crossing locations for each species at the intersection of FLCPs and major roadways in the study area (Cushman *et al.* 2014). These roads included SR-67 as well as SR-52, Interstate 8, Wildcat Canyon Road, Poway Road, and Scripps Poway Parkway. We conducted a point density analysis using the *Point Density Tool* in ArcGIS to determine a distance at which we could aggregate crossing locations into a single crossing zone. We determined that we had greater clustering at a distance of 300 m and created crossing zones around the largest clusters of FLCP points. We then reviewed the crossing zone locations, determined if the zone included an existing structure that could be retrofitted, and made slight placement adjustments to incorporate preexisting structures that had some level of functionality for wildlife movement.

A flow chart depicting the methodological approach for identifying corridors and road crossing locations is provided in Figure 4.

### *Development of Connectivity Decision Support Tool and Road Crossing Structure Recommendations*

We attributed each of the 13 corridors with over 100 variables which we categorized into conservation and management variables, biological variables, and threats and stressors. Conservation and management variables included the conservation status of each corridor, future land use predictions, and cultural sites. Biological variables included attributes such as the multi-species connectivity value as well as connectivity values for each focal species, the presence of threatened and endangered species and other species of interest, and variables describing the composition and configuration of vegetation types. Threats and stressors included levels of development and fragmentation for each corridor, as well as the potential for fire.

We developed a Connectivity Decision Support Tool that incorporates parcel-level data as well as the corridor attributes described above to help managers and planners prioritize areas for acquisition and management. This tool requires planners and land managers to develop a scoring rubric that meets their mandates and can be applied consistently across decision points.

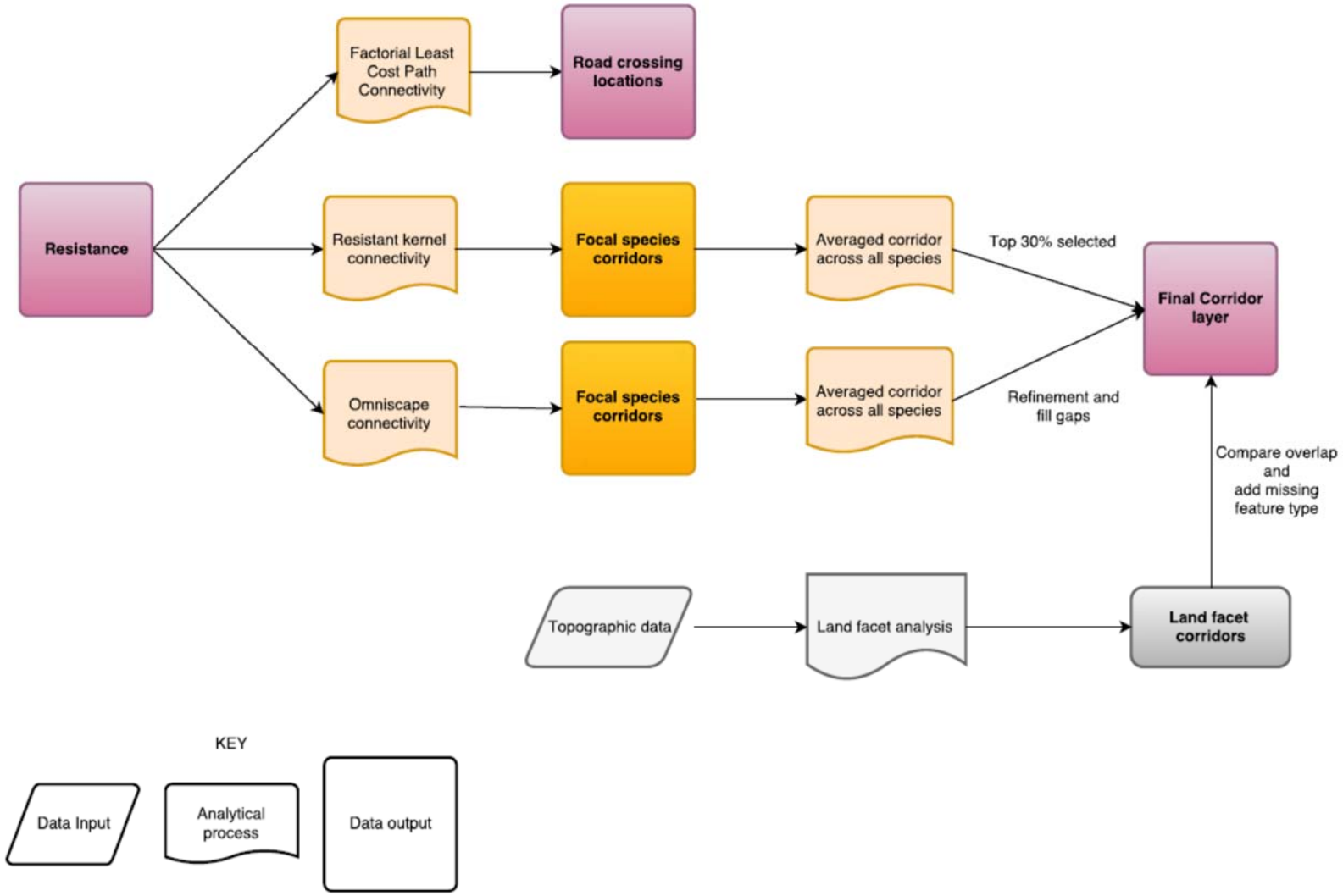


**Figure 4.** Flowchart of the methodological approach used to develop corridors and identify road crossing locations for the SR-67 area

***Road Crossing Recommendation Process***

The process we took for identifying road crossing locations and specifications was intended to generate recommendations that were optimal for supporting wildlife movement. This is the first step in the process for developing a fully scoped wildlife crossing infrastructure plan. The recommendations we present here are not cost-constrained and, although we did solicit feedback from Caltrans on our initial recommendations, further refinement will be necessary through collaboration and cooperation with a full team of Caltrans planners including engineers, hydrologists, and biologists. Once site-specific details and tradeoffs have been discussed, the final step will be to estimate costs and further refine the wildlife infrastructure plan based on the available budget.

To ensure our recommendations were appropriate and site-specific we reviewed site characteristics using terrain data, street-view in Google Earth, information from prior data collection, and location knowledge. During this process, we selected one site within each crossing zone (if there was no existing structure within the crossing zone), which we focused on for our design specifications. To identify the need for species-specific design specifications, we reviewed point location data for additional species of interest and identified which species we would want to accommodate at each structure to further inform our crossing structure design recommendations. We completed this by creating buffers around point data for our species of interest based on their dispersal abilities (Table 3). We categorized the size and type of species to be considered in the design of each structure and used a comprehensive literature review on wildlife crossing structure evaluations and guides (Appendix G) to make initial recommendations on crossing structure sizing and type. For each site, we provided recommendations on both the optimal design specifications as well as the minimum with respect to structure type and size. During our literature review, we also identified best management practices to complement the species-specific design recommendations for each crossing structure. We validated our structure recommendations with another site-specific review and added on species-specific design features to provide cover for smaller animals and to enhance connectivity for flying species. We then estimated the minimum length of fencing necessary based on the literature and site conditions to direct species towards structures and away from the roadway.

After completing a draft of these initial recommendations, we solicited input from biologists and a planner at Caltrans. Based on the input we received, we made further refinements and developed a prioritization criterion. To aid decision-making regarding wildlife crossing structure improvement, we added two prioritizations to our crossing structure recommendations. The first was focused on the importance of each site to the suite of wildlife we considered in our analyses. This includes not only the focal species we modeled, but the suite of species stakeholders requested we consider in our multi-species validation. The second prioritization was designed to allow transportation agencies to identify opportunities for near-term improvements based on whether existing crossings could be enhanced through minor alterations. These minor improvements include clearing of sediment and debris in existing crossing structures, enhancing line of sight through the structure, controlling invasive plants in areas surrounding the crossings, restoring native vegetation.

**Table 3.** Species considered for potential to use proposed road crossings and wildlife corridors. Data sources are as follows: 1) County of San Diego 2016; 2) San Diego Management and Monitoring Program 2016; 3) U.S. Fish and Wildlife Service 2017; 4) Marschalek; 5) BISON 2017 6) GBIF 2017; 7) San Diego Natural History Museum, *In Prep*

| Species Common Name | Data source | Movement distance (m) | Movement distance reference |
|---|---|---|---|
| **Quino checkerspot butterfly** (*Euphydryas editha quino)* | SanBIOS[1], SDMMP[2], CFWO[3] | 1,000 | USFWS 2003 |
| **Arroyo toad** (*Anaxyrus californicus)* | SanBIOS[1], SDMMP[2], CFWO[3] | 1,082 | Brehme and Fisher 2017 |
| **Cactus wren** (*Campylorhynchus brunneicapillus)* | SanBIOS[1], SDMMP[2], CFWO[3] | 1,590 | Atwood 1997 |
| **California gnatcatcher** (*Polioptila californica)* | SanBIOS[1], SDMMP[2], CFWO[3] | 3,000 | Mock 2004 |
| **Stephens' kangaroo rat** (*Dipodomys stephensi)* | SanBIOS[1], SDMMP[2], CFWO[3] | 400 | Price *et al.* 1994 |
| **Hermes copper butterfly** (*Lycaena hermes)* | SDSU[4], SDMMP[2] | 100 | Deutschman et al. 2010 |
| **Coachwhip** (*Coluber flagellum)* | SanBIOS[1], BISON[5], GBIF[6] | 1,618 | Brehme et al., *Unpublished data* |
| **Granite spiny lizard** (*Sceloporus orcutti)* | BISON[5], GBIF[6] | 91 | Brehme et al., *Unpublished data* |
| **Two-striped garter snake** (*Thamnophis hammondii* ) | SDMMP[2], BISON[5], GBIF[6] | 239 | Brehme et al., *Unpublished data* |
| **Western toad** (*Anaxyrus boreas)* | SanBIOS[1], BISON[5], GBIF[6] | 1,552 | Brehme et al., *Unpublished data* |
| **Western whiptail** (*Aspidoscelis tigris)* | BISON[5], GBIF[6] | 300 | Brehme et al., *Unpublished data* |
| **Pallid bat** (*Antrozous pallidus)* | SanBIOS[1], SDMMP[2] | 2,000 | Baker *et al.* 2008 |
| **Townsend's big eared bat** (*Corynorhinus townsendii)* | SanBIOS[1], SDMMP[2] | 10,500 | Fellers and Pierson 2002 |
| **American badger** (*Taxidea taxus)* | SDNHM[7] | 1,450 | Lindzey 2003 |
| **Ringtail** (*Bassariscus astutus)* | SDNHM[7] | 1,000 | Lonsinger *et al.* 2015 |

## RESULTS

### *Species-specific habitat suitability, resistance, and connectivity*

Species-specific habitat suitability and movement models, resistance surfaces, and connectivity outputs are depicted for each of the six focal species in Appendix C. These data products and modeling outputs are available for individual species upon request.

### *Multi-species Connectivity and Corridor Products*

The final corridor connects lands from east to west and north to south across the study area and has an area of 103,838 acres. Figure 5 displays the final multi-species connectivity surface across the study area and Figure 6 displays the final corridor product, which consists of 12 multi-species corridors and one land facet corridor. Currently 35% of the final corridor is comprised of protected lands, 9% is comprised of PAMA land, and 5% is comprised of draft PAMA lands

from the Northern San Diego County MSCP. From a modeling study conducted by Butsic *et al.* (2017), we estimate that approximately 10% of the corridor is comprised of developable land (land that has not yet been developed, but has the potential to be developed in the future). Each of the 13 sub-corridors is described in detail in Appendix A.

To aid in the planning and management process, we provided additional spatial products derived from the multi-species connectivity surface: corridor isopleths (Figure 7), a normalized flow surface (Figure 8), and a corridor resiliency map (Figure 9). The normalized flow surface highlights areas of concentrated flow in the outer regions of the study area. In the northeastern part of the study area, this concentrated flow is due to natural features, however, in the northwest and the south, this concentrated flow is due to human development. Areas where flow is impeded mostly coincide with more heavily developed lands. The corridor resiliency map suggests that much of the center of the study area and corridors therein have high resilience to climate change, while corridors in the northeast and southeast of the study area have less resilience.

The conservation and management, biological, and threats and stressor attributes for each of the 13 corridors is provided in Table A1. We describe how each attribute was calculated along with the source of the data used and the minimum and maximum values across corridors. For cross-referencing purposes with the corridor GIS shape file product, we also provide the names of the shape file table that correspond with each attribute.

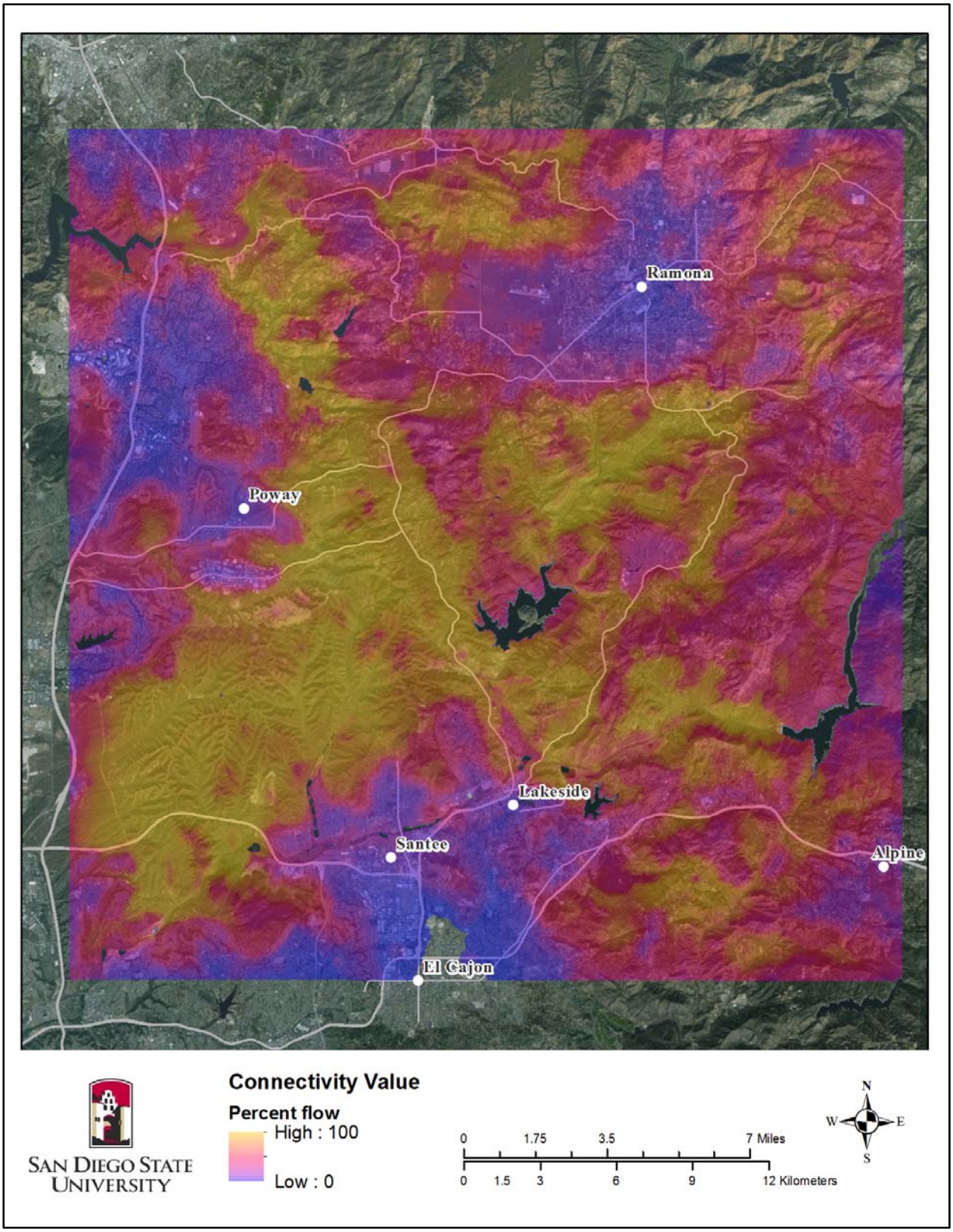


**Figure 5.** Multi-species connectivity value map depicts percent flow across the study area.

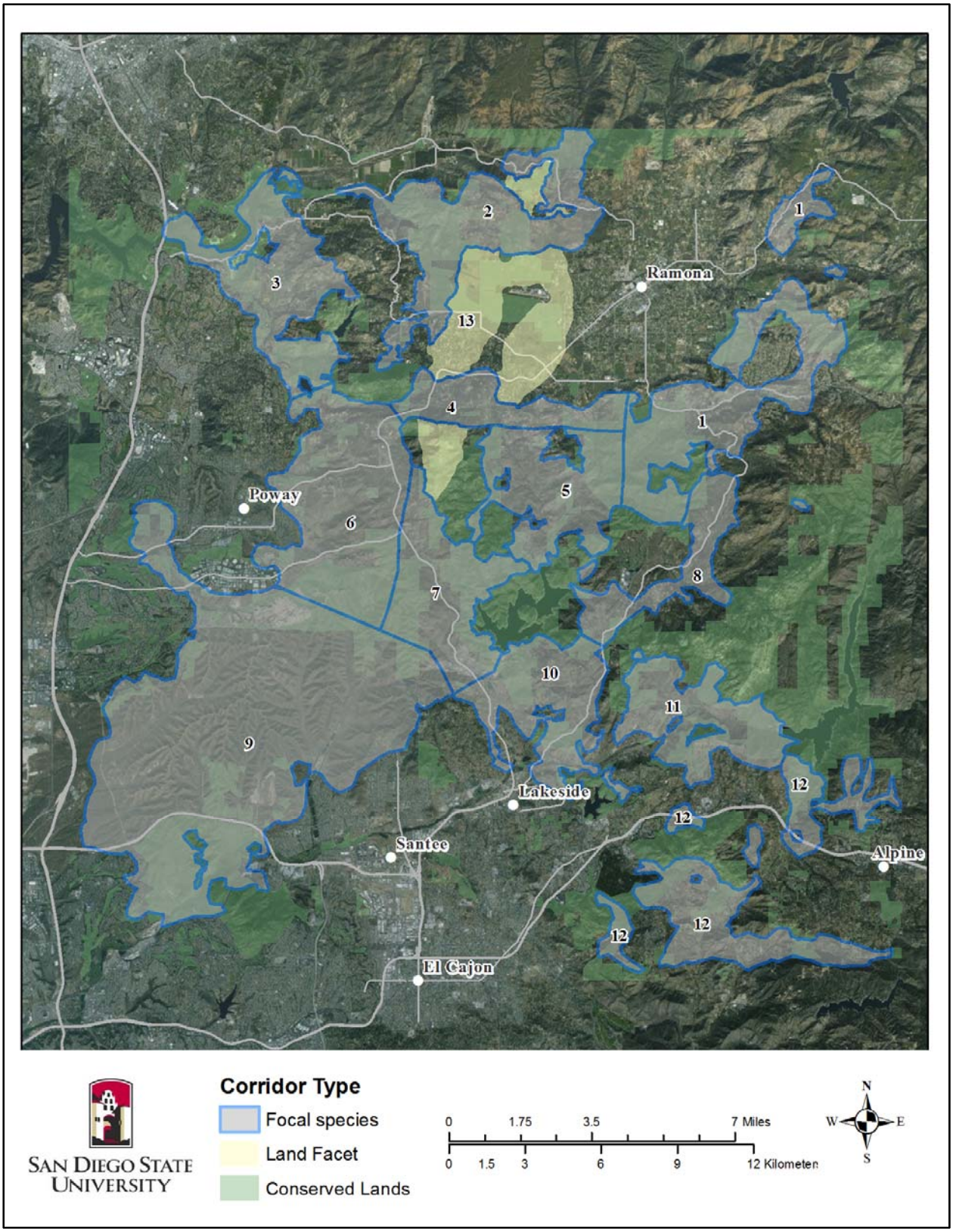


**Figure 6.** Final combined focal species and land facet corridor map with corridor segments labeled and conserved lands depicted.

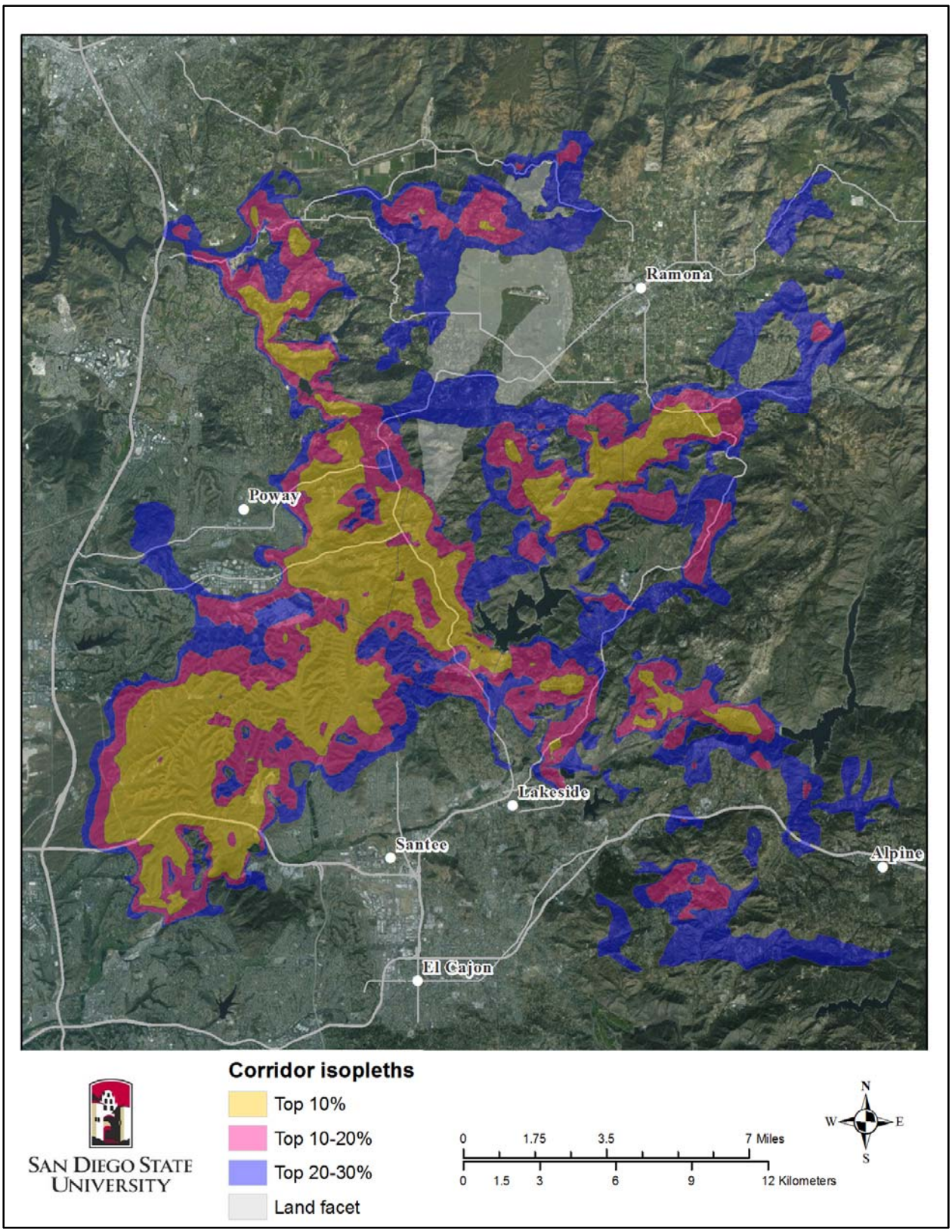


**Figure 7.** Map of corridor isopleths depicting each corridor broken down into the top 10%, top 10-20%, or top 20-30% of connectivity flow

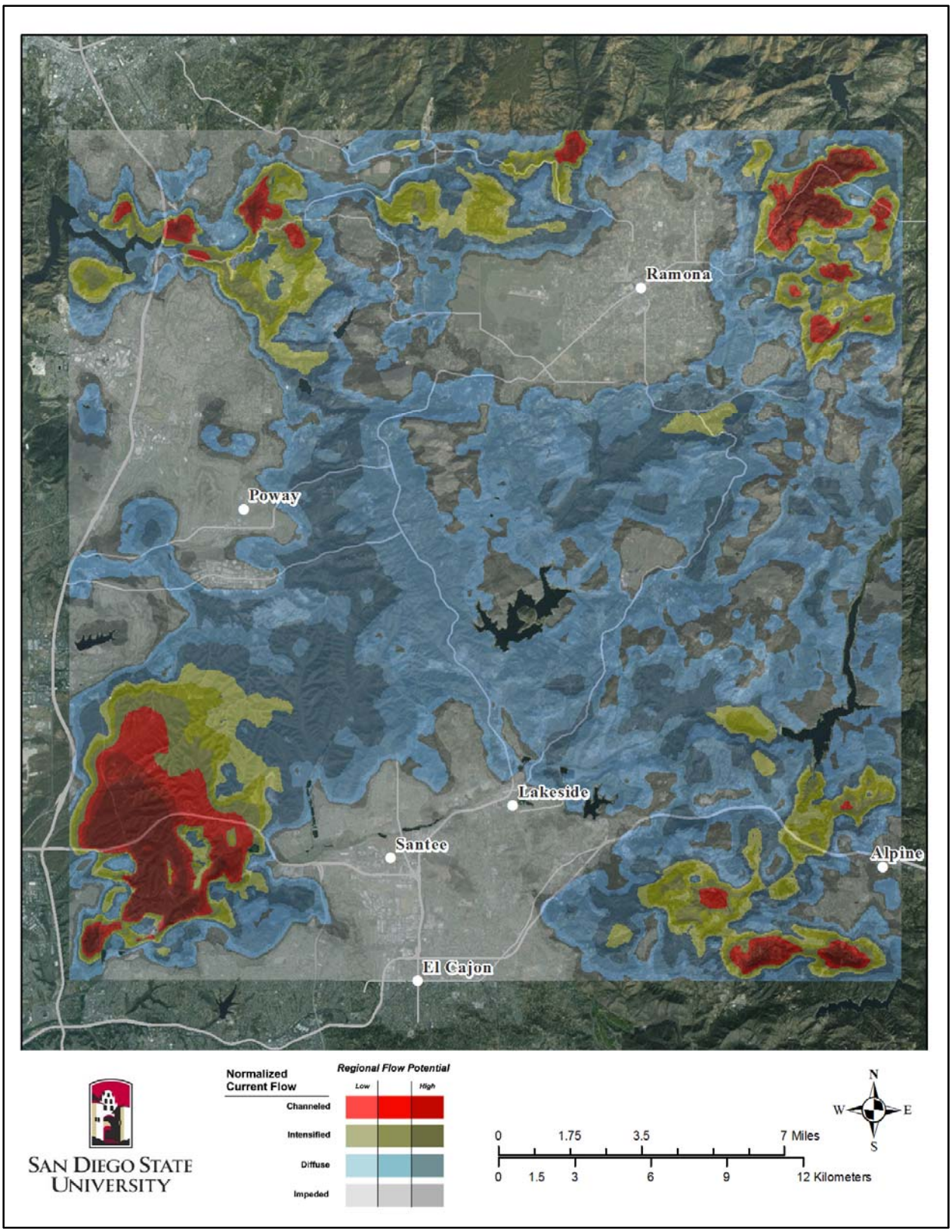


**Figure 8.** Normalized current flow map that depicts areas where connectivity flow is either channeled, intensified, diffuse, or impeded

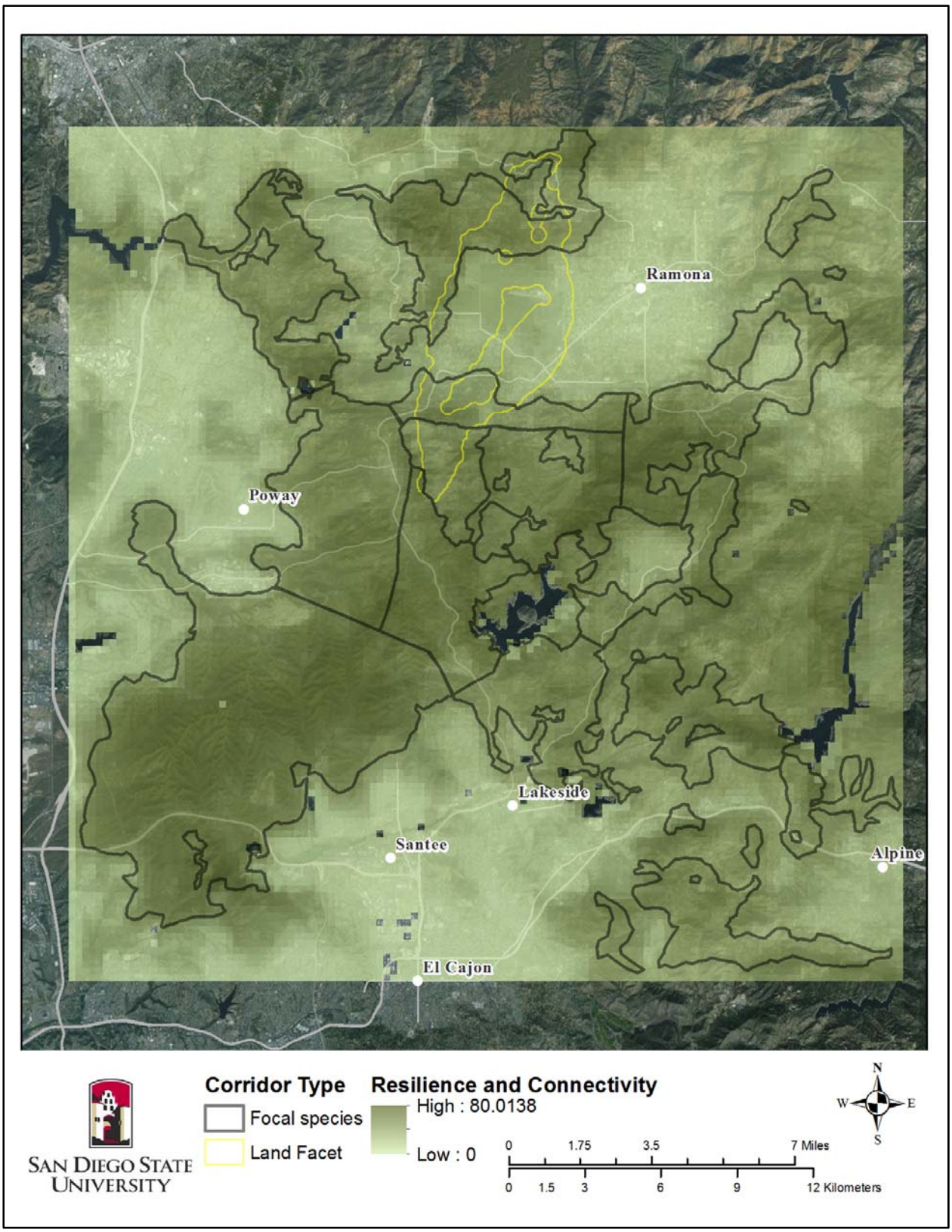


**Figure 9.** Map of the combined connectivity and resilience to climate change of the study area. Areas of darker green are both more resilient and provide for a greater degree of connectivity

***Connectivity Decision Support Tool***

The Connectivity Decision Support Tool was designed so that end users can apply a score to a parcel or management site of interest so that parcels and sites can be prioritized across a project. Figure 10 depicts decision points, assessment criteria, and where attributes of the parcel or site of interest might be assigned a score. We developed the support tool so that each land manager / planner could develop a unique scoring system that applies to their management objectives. We reiterate the importance of developing a single scoring rubric that is applied consistently across all decisions.

After identifying a parcel or site of interest, the first decision point is reached. If the site is within a corridor one may decide to move on in the scoring process. If the site is not within a corridor one may decide to examine another site. Then, one might assign a score to the site depending on which corridor isopleth that site falls within. Then, it might be helpful to look at site-specific data. For example, would acquisition be cost-prohibitive or not, what is the area of the parcel, does it fall within PAMA or draft PAMA lands, and by protecting that parcel, how much would that increase the proportion of conserved land in a corridor? Once assessing the parcel specific data, another decision point is reached and one must choose whether to proceed or not. Assuming the parcel still meets management criteria, corridor-specific scores can be applied to the conservation and management variables, biological variables, and threats and stressors of interest. The sum of all the scores results in a final compiled score for the site of interest, which can be compared with other sites for prioritization, acquisition, and management needs.

We have provided a brief example of a scoring rubric and will walk through the application of this rubric using two parcels selected in the study area (Table 4). Our example scoring criteria assigns a score from 1-5 for each variable assessed, with 5 being the best. Both example parcels are in a corridor area. Example parcel #1 is in Corridor 9 and is relatively small in size, whereas parcel #2 is in Corridor 10 and is relatively large. Following along with the Connectivity Decision Support Tool, once we deemed these parcels were in a corridor, we reached the first decision point and decided to move forward. We then noted that parcel #1 is in the middle isopleth (10-20% of the top connectivity values) while parcel #2 is in the top isopleth (the top 10% of connectivity values). We then applied scores to these parcels using our pre-determined scoring criteria. Then we assessed parcel-specific criteria and decided to move on to the corridor attributes. Once we reach this point in the Decision Support Tool, we pulled information directly from the corridor attributes table. We scored two conservation and management attributes, two Biological attributes, and two Threat and Stressors attributes. We then added up the scores for each parcel to obtain a final score. It is worth noting that there are dozens of attributes to select from in developing a scoring criteria and that this is a just a simplified example for illustrative purposes.

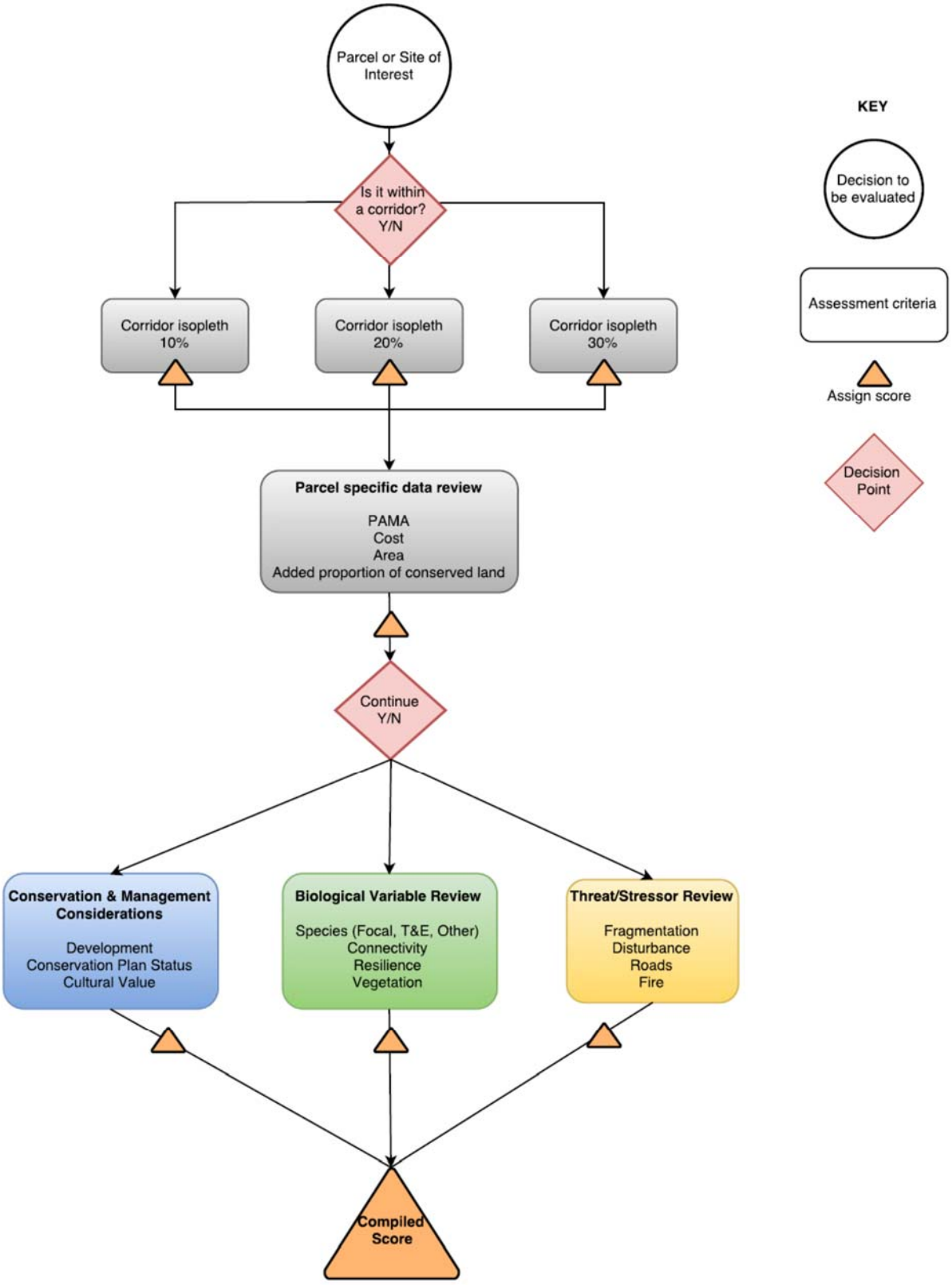


**Figure 10.** Diagram of the connectivity decision support tool created that depicts decision points, assessment criteria, and scoring guidance

**Table 4.** Example application of decision support tool to two parcels in the study area. The table provides a simplified version of how one would walk through the process of applying a scoring rubric to compare parcels. Our example scoring criteria assigns a score from 1-5 for each variable assessed, with 5 being the best.

| Variable | Scoring criteria | Parcel #1 value | Parcel #1 score | Parcel #2 value | Parcel #2 score |
|---|---|---|---|---|---|
| Is it in a corridor? | Y / N | Y, Corridor 10 | - | Y, Corridor 9 | - |
| What isopleth is it in? | 1 = 20 – 30 %<br>3 = 10 – 20%<br>5 = 1 – 10% | 10 – 20% | 3 | 1 – 10% | 5 |
| Parcel size | 1 = small<br>3 = medium<br>5 = large | 14 acres | 3 | 240 acres | 5 |
| Proportion of corridor currently conserved | 1 = 15 – 23%<br>2 = 23 – 31%<br>3 = 31 – 39%<br>4 = 39 – 47%<br>5 = 47 – 56% | 30% | 2 | 25% | 2 |
| Number of cultural sites | 1 = 31 - 105<br>2 = 106 - 180<br>3 = 181 - 255<br>4 = 256 - 330<br>5 = 331 – 402 | 126 | 2 | 402 | 5 |
| Whether Arroyo Toad has been detected in that corridor | 0 = N<br>5 = Y | N | 0 | Y | 5 |
| Average multi-species connectivity value in corridor | 1 = 68 - 72<br>2 = 73 – 77<br>3 = 77 – 81<br>4 = 81 - 85<br>5 = 86 – 90 | 86 | 5 | 81 | 4 |
| Percent of corridor comprised of natural land cover types | 1 = 80 - 83<br>2 = 83 - 86<br>3 = 86 - 89<br>4 = 89 - 92<br>5 = 92 – 96 | 80 | 1 | 89 | 3 |
| Road density | 1 = 6.3 - 5.5<br>2 = 5.5 - 4.7<br>3 = 4.7 – 4.0<br>4 = 4.0 - 3.3<br>5 = 3.3 - 2.6 | 6.29 | 1 | 5.4 | 2 |
| **Total Score** | | | **17** | | **31** |

***Wildlife Crossing Infrastructure Recommendations***

Based on our initial FLCP corridors from our focal species analyses, we identified 176 potential crossing locations (Figure 11). After examining clusters of crossing points within a 300 m buffer distance, we narrowed those 176 locations down to 33 proposed road crossing zones. Of these 33 zones, 12 were along SR-67, three were on SR-52, four were on I-8, seven on Wildcat Canyon Road, one on San Vicente Road, two on Poway Road, and five on Scripps Poway Parkway. After determining whether there was already an existing structure at or near the crossing zones and attributing these with data on topography, vegetation composition, and our 17 validation species as well as our original six focal species, we performed a site-specific review and identified a proposed crossing site. If there was an existing structure at the site, we targeted it for a retrofit at the present site, otherwise we recommended new siting. At two of the locations on Scripps Poway Parkway, the topography and road cut was deemed to be prohibitive for placement of a wildlife crossing structure in the recommended zone or adjacent to it. We therefore eliminated those two locations from our final site recommendations bringing our site recommendations down to 31 locations. However, based on prior culvert monitoring data collected during an earlier study for Caltrans (Jennings and Lewison 2016), we noted that there were two existing culverts on SR-67 that were functioning for some species that were not incorporated into our initial 33 zones. We incorporated those two existing culvert locations into our proposed crossing site recommendations for a total of 33 sites (Figure 12).

On SR-67, the primary focus of our wildlife crossing infrastructure recommendations, we identified and prioritized 14 crossing sites (Table 5). All but one of these locations has an existing structure that could be retrofitted. Of those sites, six could be improved with minor effort whereas the remaining eight would require major redesign to facilitate wildlife movement. We identified four sites along the highway that were of extremely high importance to wildlife movement, six that were of high importance, and four that were of moderate importance. Sites targeted for minor improvements only fell within our high and moderate importance categories for wildlife movement. Site specific details for each of the recommendations for wildlife crossing structures on SR-67 as well as the recommendations on the other major roads in our study area can be found in Appendix B.

Based on a thorough review of the literature and input from Caltrans as well as our stakeholder group, we identified 25 best management practices to be incorporated into the wildlife infrastructure planning for SR-67 (Table 6). We classified these by the type of recommendation into seven categories related to conservation planning, design of structures, barriers, fencing, and material selection, and construction and maintenance considerations.

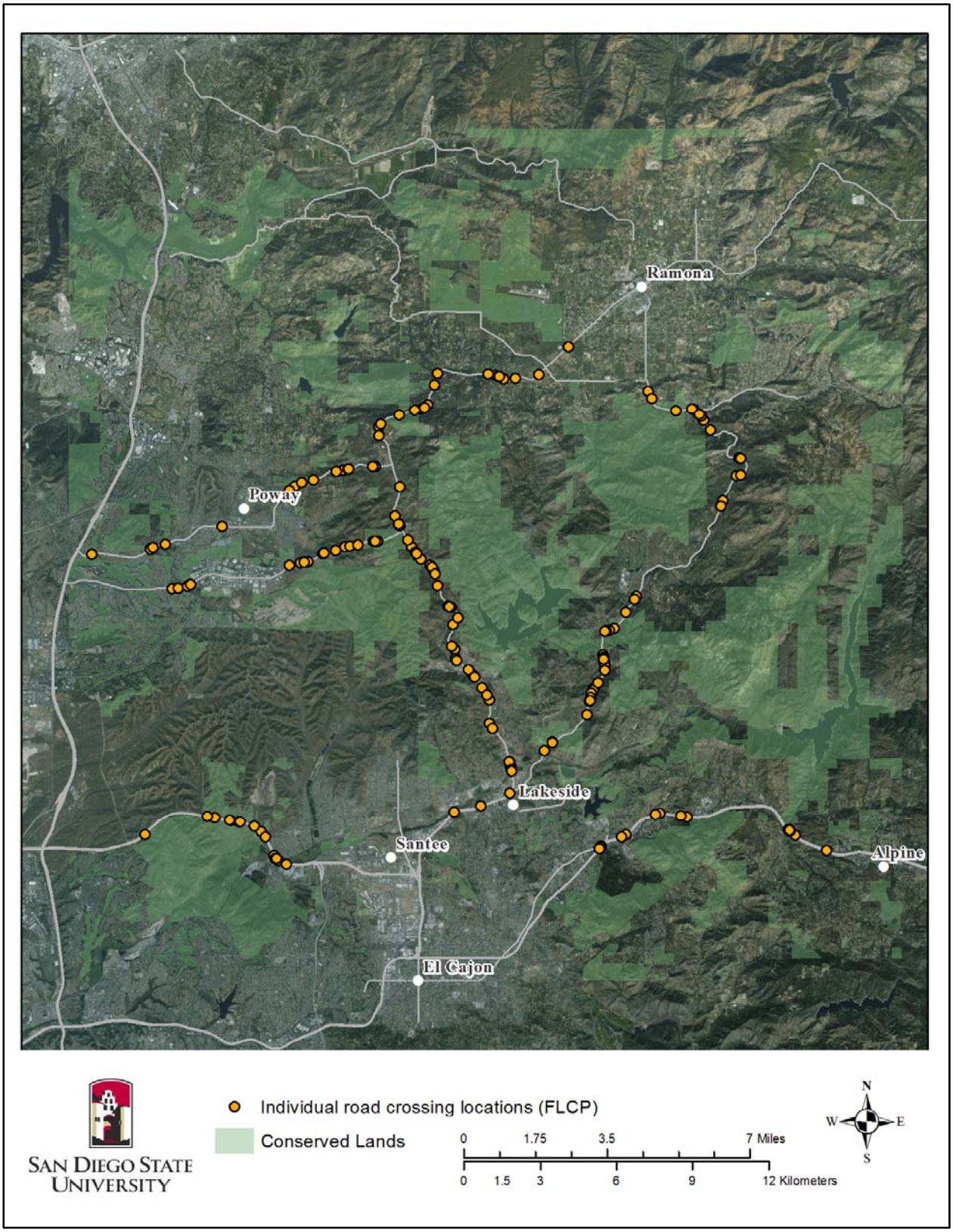


**Figure 11.** Map of potential road crossing locations identified from the factorial least cost path connectivity modeling (FLCP).

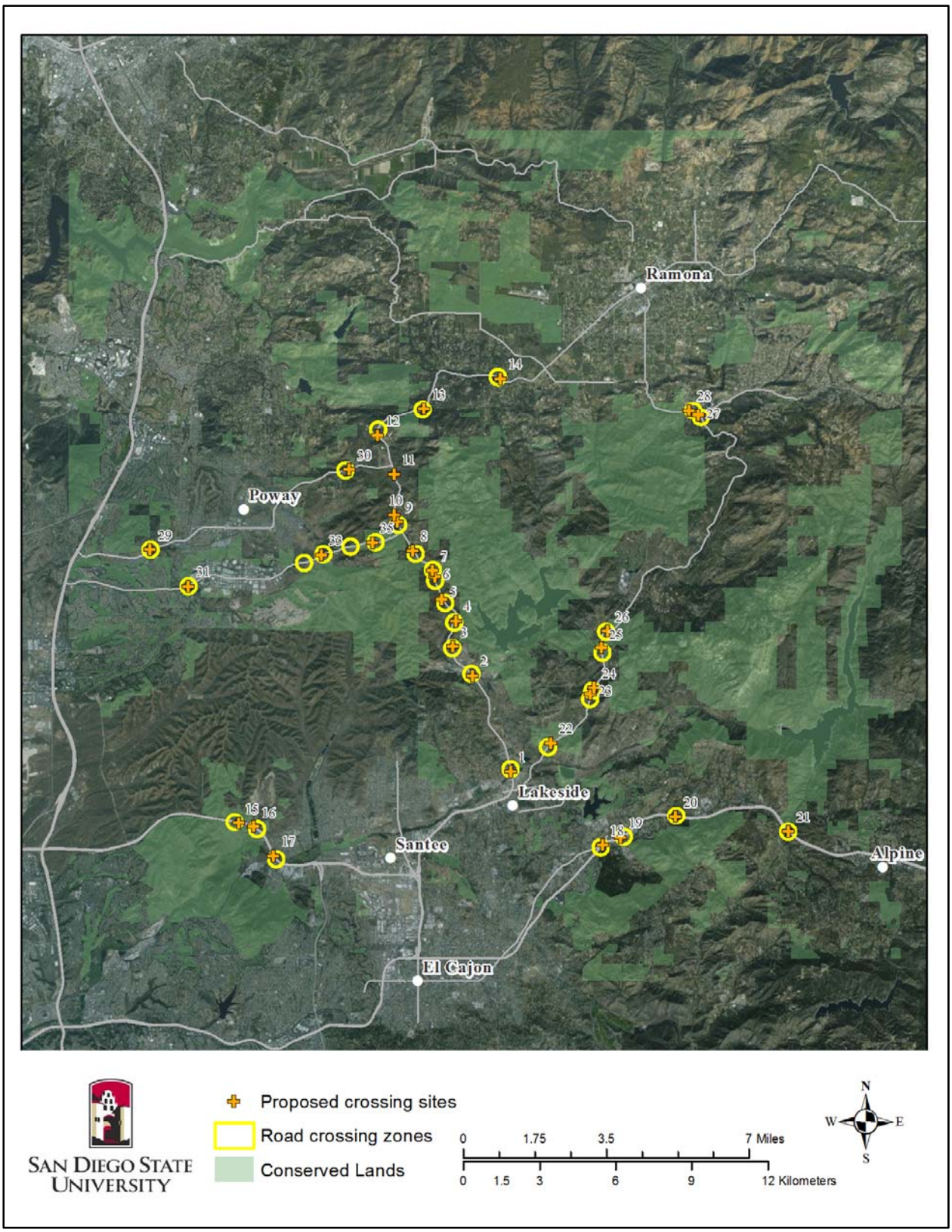


**Figure 12.** Map of potential road crossing locations identified from the factorial least cost path connectivity modeling (FLCP)

**Table 5.** Wildlife crossing infrastructure recommendations for SR-67

| Site ID | Wild-life Priority | Improve-ment Type | Rd width (ft) | Right -of-way (ft) | Optimal Crossing Type | Minimum Crossing Type | New, Retro, or Exists | Optimal width (ft) | Optimal height (ft) | Min width (ft) | Min height (ft) | Existing diameter (ft) | Min fence length E or S (ft) | Min fence length N or W (ft) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **1** | 2 | Minor | 45.9 | 164.0 | Bridge | | Exists | – | 13.1 | – | 9.8 | NA | – | – |
| **2** | 3 | Minor | 114.8 | 141.1 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 7.0 | – | 7.0 | 590 | 656 |
| **3** | 1 | Major | 164.0 | 502.0 | Arched or box culvert | | Retrofit | 26.2 | 14.8 | 19.7 | 13.1 | 4.0 | 1,312 | 1,476 |
| **4** | 2 | Major | 101.7 | 150.9 | Arched or box culvert | | Retrofit | 16.4 | 9.8 | 13.1 | 6.6 | 1.5 | 1,640 | 2,460 |
| **5** | 3 | Major | 144.4 | 150.9 | Pipe culvert | | Retrofit | 6.6 | – | 3.3 | – | 3.0 | 820 | 328 |
| **6** | 1 | Major | 131.2 | 150.9 | Arched or box culvert | | Retrofit | 26.2 | 14.8 | 19.7 | 13.1 | 7.5 | 984 | 1,312 |
| **7** | 2 | Minor | 85.3 | 157.5 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 7.5 | – | 7.5 | 1,312 | 2,624 |
| **8** | 3 | Minor | 88.6 | 141.1 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 6.6 | 6.6 | – | 3.0 | 771 | 1,082 |
| **9** | 1 | Major | 170.6 | 160.8 | Arched or box culvert | | Retrofit | 26.2 | 14.8 | 16.4 | 9.8 | 5.5 | 1,148 | 820 |
| **10** | 2 | Minor | 55.8 | 150.9 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 7.0 | – | 7.0 | 1394.4 | 820.2 |
| **11** | 2 | Minor | 55.8 | 150.9 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 8.5 | – | 8.5 | 1378.0 | 2296.6 |
| **12** | 2 | Major | 82.0 | 150.9 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 6.6 | 6.6 | | 3.0 | 1804.5 | 1804.5 |
| **17.61** | 1 | Major | 114.8 | 311.7 | Wildlife overpass | | New | 229.7 | | 164.0 | | | | |
| **20.17** | 3 | Major | 82.0 | 114.8 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 6.6 | 6.6 | | 3.0 | | |

**Table 6.** Wildlife crossing infrastructure best management practices recommendations

| Type | Best Management Practices Recommendations |
|---|---|
| Barriers | If median barriers are installed or the k-rails along the section of SR-67 just north of Vigilante Road remain, stagger placement and installing scuppers to allow wildlife to pass through if they become trapped in the roadway |
| Conservation | Work to acquire parcels on either side of the road at all crossing locations |
| Conservation | Work to acquire parcels to connect conserved lands on either side of crossing locations |
| Construction | Implement mitigation measures to protect wildlife from wildlife-vehicle collisions and impacts during construction |
| Construction | Implement a BACI study to monitor efficacy of structures beginning prior to construction |
| Crossings | Maintain small culvert structures for small animal use at intervals of ~90m (300 feet). Structures should have diameter of 0.5 - 1.5m |
| Crossings | Target an average of 1 crossing per 2 km (1.2 mi) of roadway for medium to large animals |
| Crossings | Ensure structures have a straight alignment with no bends or curves; there should be a continuous line of sight |
| Crossings | If hydrological issues preclude optimal structure design for wildlife, consider dual siting of structures for drainage and wildlife movement |
| Fencing | Bury fencing several inches to prevent digging underneath |
| Fencing | Construct fence lip to prevent climbing/jumping over |
| Fencing | Ensure fence ends are tied into existing barriers (topographic or anthropogenic) wherever possible. If none exist, consider adding boulders or a berm to block access and line of sight |
| Fencing | Construct longer fences for funneling wildlife to crossing structures where possible (especially for large mammals) |
| Fencing | Construct walls or fencing high enough to encourage flight up and over traffic to avoid bird-vehicle collisions, possibly with flagging added for visibility |
| Fencing | Install jump outs at regular intervals based on length of fencing segments |
| Fencing | Conduct roadkill monitoring after crossing construction to determine if extended fencing or jump outs are necessary |
| Fencing | Once final fencing lengths have been determined, identify locations for jump outs to allow wildlife to exit the roadway if they become trapped. Recommend jump outs at 1/2 mile spacing if there in uninterrupted fencing |
| Fencing | Consider working with home owners to install gates or cattle guards at driveways to improve the functionality of fencing |
| Fencing | If gates and cattle guards on driveways are not possible, consider fence turn arounds to redirect animals. Recommend revisiting literature for new driveway fencing guidelines prior to the finalizing fencing plan. |
| Fencing | Place fencing as close to roadway as possible (rather than at the ROW) to limit wildlife crossing fencing to reach attractive habitat on the other side |
| Maintenance | Maintain structures free of sediment and debris build up; remove invasive and native vegetation that block access or line of sight through structure |
| Material | Native surface bottoms when possible |
| Material | Use noise dampening structure materials |
| Material | Avoid zinc coating if crossing is to be made of metal |
| Material | Consider limiting the use of rip rap at structure entrances where possible to facilitate use by small animals |

## DISCUSSION

Through a comprehensive, multi-species connectivity analysis using robust analytical approaches, we created a connectivity plan, implementation guidance through a decision support tool, and a wildlife crossing infrastructure plan for key roadways in our study area. Through this data-driven approach, we:

- Assembled a multi-species connectivity analysis using a suite of data types and species complemented by a landscape-focused land facet analysis
- Analyzed a suite of data types using cutting-edge analytical techniques appropriate to each data type
- Leveraged survey and monitoring data from our study region, producing a data-informed connectivity plan without the collection of any new field data
- Identified and mapped 12 spatially-explicit focal species corridors and one land facet corridor to facilitate wildlife movement within the SR-67 region of San Diego's Multiple Species Conservation Plan area
- Assessed the potential functionality of those corridors for additional species including five federally listed species and 13 other species of interest
- Attributed those spatially-explicit corridors with data on land conservation status, biological variables, and threats and stressors to inform decision-making
- Created a decision support tool for scoring potential acquisitions, habitat restoration projects, or other land management and planning decisions
- Used our connectivity models, species data, site specific information, and past data collection on crossing use and roadkill to inform wildlife crossing infrastructure recommendations for SR-67 as well as other roadways within our analysis area
- Worked with a variety of stakeholders throughout this process to gather information, feedback, and key input to generate a connectivity plan and conservation tool that could readily be implemented by the diverse range of land management and planning entities working in this region of San Diego County

### *Application of the Connectivity Plan*

The data products we developed during this project are intended to be used in planning for subregional connectivity between core complexes of the preserve network of the MSCP and the draft NCMSCP. This information can be applied to connectivity planning and implementation decision-making, particularly when considering connectivity as a key component of reserve design. The focal species approach as well as the species we selected was intended to identify corridors to provide connectivity for preserving biodiversity for the most species. By linking additional quantitative metrics to our corridors, we strived to facilitate acquisition decision-making, the identification of restoration targets to improve connectivity, and to aid in end-users in the evaluation of the potential impacts of development projects on wildlife connectivity in this region.

Although our focal species approach provides specific information about connectivity for the six species we used throughout our modeling process, the data we present here is not appropriate for use in single-species conservation planning or decision-making, particularly those species that are narrow habitat specialists such as those species reliant on native grasslands or vernal pools.

Our analyses and results are also not suitable for assessing connectivity for extreme dispersal-limited species that may move within a core, but not among core preserve areas. Finally, although we did model connectivity irrespective of the delineation of conserved lands, our final products are not appropriate for use in making determinations about core habitat, *e.g.*, habitats important for foraging or breeding, other than the importance of those areas to wildlife movement on a landscape scale.

***Decision Support and Implementation***

We have provided a suite of data products to support the use of this information in many different management and planning scenarios. By generating geospatial data on our corridor extents to represent the entire corridor area as well as isopleths of the top 10%, 20%, and 30% of connectivity flow for our focal species, we have considered the need for management options in different decision-making circumstances. To highlight the areas of greatest conservation need with the most channelized flow, we have generated a normalized flow surface to pinpoint locations where natural or anthropogenic features constrict connectivity. We have also provided options for end users to consider conserving resilience to climate change both through the land facet corridor analysis we performed, and by combining a resilience surface (The Nature Conservancy, San Francisco, CA, unpublished) with our multi-species connectivity surface.

Through our engagement with stakeholders, we identified an array of variables to facilitate use in planning and decision-making at many levels. We considered factors related to land conservation and management such as the conservation status within each corridor and targets under the NCCP plan. We also incorporated projections of future land use and development potential in our corridor attribution. To explore the potential co-benefits of the conservation of lands for connectivity and engage potential tribal stakeholders, we assessed a measure of cultural value by accounting for the number of archaeological sites, isolated artifacts, and historic structures within each corridor. To account for the range of biological variables relevant to our corridors, we calculated the modeled connectivity value of each segment for our focal species as well as the connectivity potential for five species listed under the Endangered Species Act and an additional 13 species of interest identified by the stakeholder group. We also evaluated the connectivity of different vegetation types within each corridor. Finally, we considered several threats and stressors in our corridor review. We accounted for fragmentation by calculating metrics such as the edge-to-interior ratio and intactness values as well as road density and the proportion of the corridor that had been developed. Metrics related to fire risk and increasing fire frequency were also incorporated into our corridor assessment.

In addition to providing relevant data for implementation of this connectivity plan, we also created a decision support tool to demonstrate how end users might apply the information provided about these corridors to their decision-making processes. Our worked example demonstrates how an organization might go about assigning their scoring criteria prior to decision making and continue through the process to determine whether land acquisition, habitat restoration, or conversely, development may or may not meet management goals and objectives related to connectivity. The example provided is not prescriptive, and we recommend that each organization carefully consider how to assign scoring prior to initiating use and then proceed to use that scoring process consistently. This type of decision support tool allows for transparency

in the decision-making process and can lend quantitative backing to justify decisions that may require external support.

The wildlife crossing infrastructure plan we designed through this project is just the first phase in the process of designing a full infrastructure plan for SR-67 or other roadways in the study area. Implementation of a wildlife crossing plan will require further engagement with the full complement of Caltrans staff (including engineers, hydrologist, biologists, and planning) for review and planning. What we have established is a starting point informed by the data and our models that targets an optimal design for wildlife movement given the species, topography, and habitat. Although we did get initial feedback and guidance from Caltrans on our preliminary recommendations, the structure specifications we have provided are not cost-constrained and have not undergone full review by a transportation planning team. However, to facilitate that next step, we have added our two levels of prioritization, wildlife importance and improvement type, to the crossing structure recommendations we have made in this report. We believe these prioritizations should help guide discussions to improve the permeability of SR-67 for wildlife.

***Future Applications***

The science and statistical approaches for evaluating wildlife space-use, movement, and connectivity is constantly evolving and improving. Our ability to use a wider range of data to assess and plan for landscape connectivity has grown in recent years and now presents opportunities to expand on prior regional connectivity plans to address wildlife movement and barriers to that movement at different spatial and temporal scales. The products we have created for the SR-67 region illustrate how spatially-explicit corridors can be linked to the organization and guidance of management plans so they are directly connected with management actions and decision-making rather than standing out as a separate management task to be executed. Through this project, we have developed a model for utilizing commonly available biological data to design and implement a comprehensive multi-species connectivity plan. The analysis and implementation plan we have assembled here can readily be adapted to different regions, scenarios, species, and habitats to facilitate planning at many levels and should be applied more broadly to advance data-informed planning and management actions.

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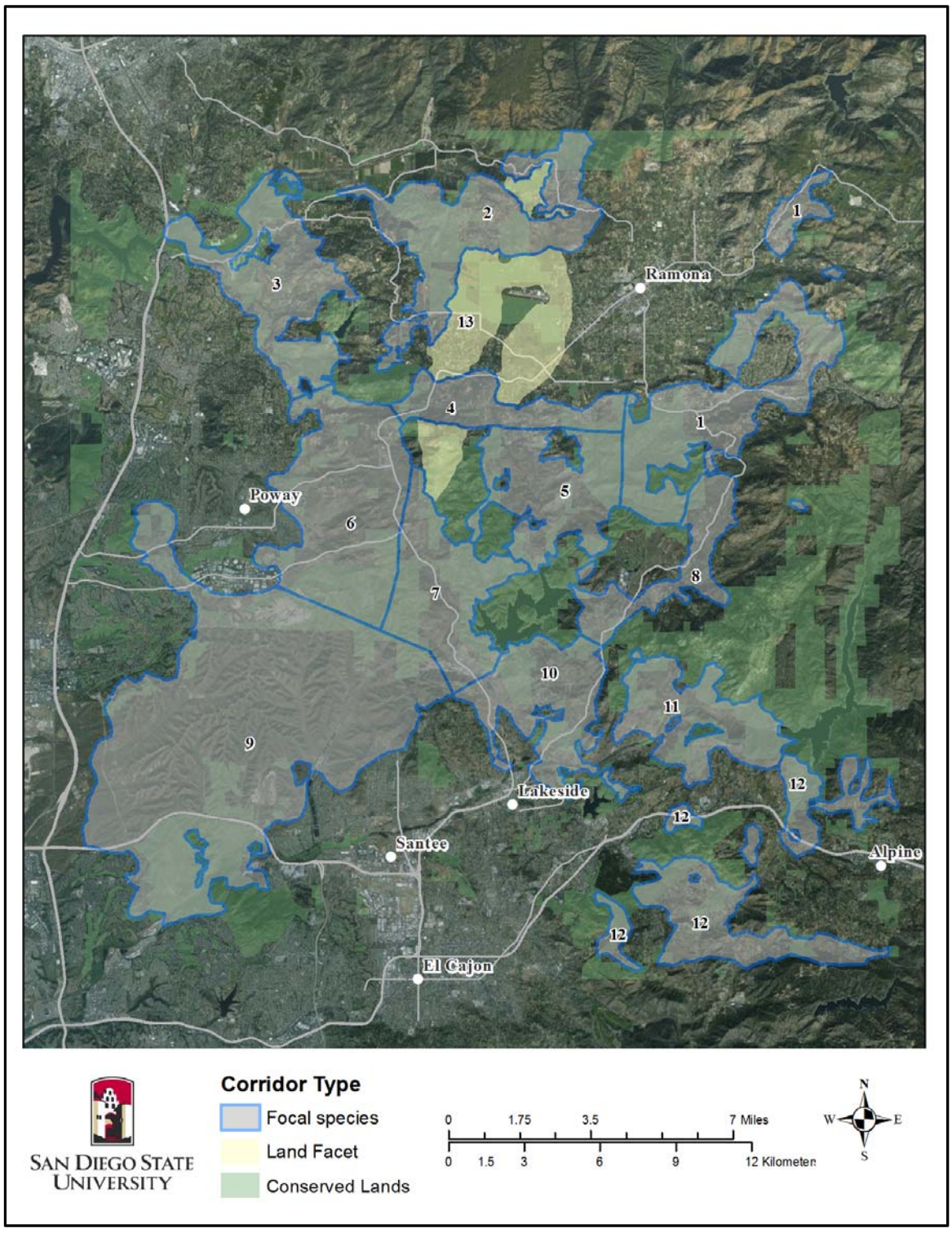
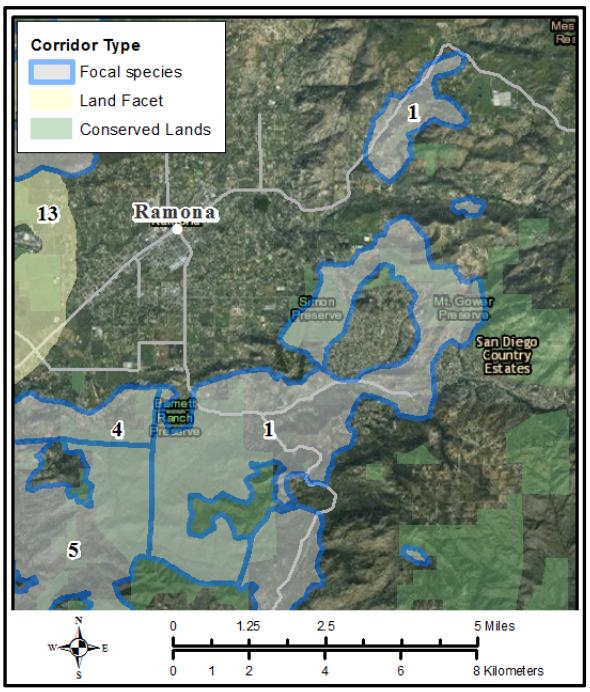
# APPENDIX A. CORRIDOR SEGMENT MAPS AND DESCRIPTIONS AND CORRIDOR METADATA TABLE



## Corridor 1




8,233 acres

46% conserved

1% PAMA

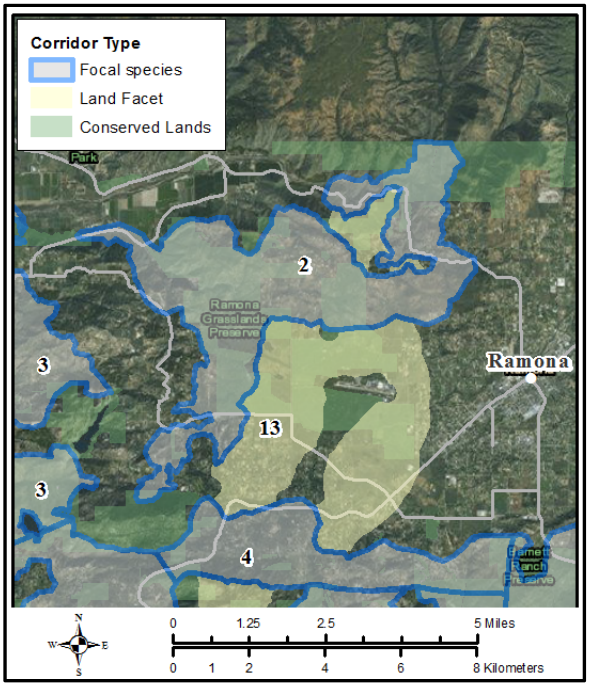
32% Draft PAMA

Average connectivity value: 76

Corridor 1 is on the east side of the study area and runs just south of the developed lands of the city of Ramona. It provides connectivity from the Mesa Grande Reservation to the Barnett Ranch Preserve and is the only connection to the northeastern corner of the study area. This corridor also contains two important road crossing zones on Wildcat Canyon Road. The northernmost section of this corridor is in the outer isopleth (top 20-30% of connectivity values) and has highly channelized flow, indicating connectivity is restricted.

Eighty-five percent of this corridor is comprised of natural land cover types and two out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, hardwood forest and riparian. Developable parcels make up 10% of this corridor.

## Corridor 2




7,579 acres

43% conserved

6% PAMA

13% Draft PAMA

Average connectivity value: 72

Corridor 2 is in the north-central part of the study area and encompasses much of the Ramona Grasslands preserve. It connects Cleveland National Forest lands in the northern part of the study area with Mt. Woodson in the south. Flow through this corridor is channelized in the very

north, at its connection with the Cleveland National Forest, and then becomes more diffuse further south at Mt. Woodson. One of the critical connections of this corridor, from the Ramona Grassland Preserve to Mt. Woodson, is in the outer isopleth (top 20-30% of connectivity values).

Eighty-eight percent of this corridor is comprised of natural land cover types and four out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and riparian. Developable parcels make up 14% of this corridor.

## Corridor 3

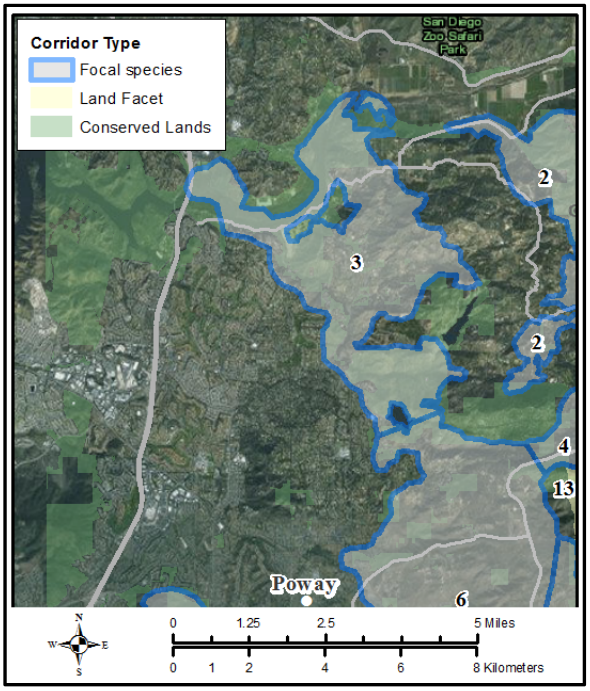
6,141 acres

50% conserved

4% PAMA

3% Draft PAMA

Average connectivity value: 84




Corridor 3 connects the San Dieguito River in the north with Lake Poway Recreation Area and the Blue Sky Ecological Reserve in the south. Though this corridor is mostly comprised of the inner two isopleths (top 1-20% of connectivity values), it has areas of highly channelized flow leading up to and along the San Dieguito River. Corridor 3 also has a narrow section (3,300 feet wide or less) south of the Maderas Golf Club along Old Coach Road that is vulnerable to fragmentation.

Eighty-three percent of this corridor is comprised of natural land cover types and three out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include coastal sage scrub and riparian. Developable parcels make up 19% of this corridor.

## Corridor 4

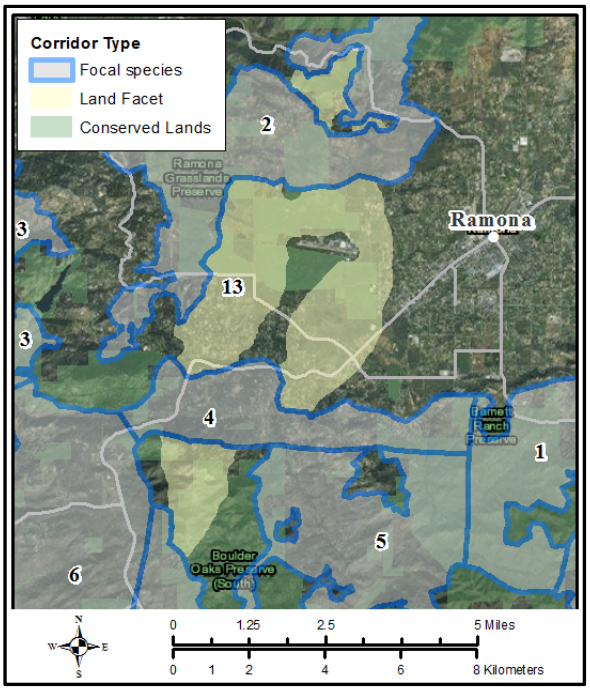
3,205 acres

18% conserved

1% PAMA

5% Draft PAMA

Average connectivity value: 70




Corridor 4 provides east-west connectivity from Mt. Woodson, across SR-67 to the Barnett Ranch Preserve. This corridor is mostly comprised of the outer isopleth of connectivity values (top 20-30% of connectivity values). Corridor 4 contains two important wildlife road crossing zones along SR-67.

Eighty-four percent of this corridor is comprised of natural land cover types and one out of the five threatened and endangered species assessed is present here. Land cover types with good connectivity across this corridor include chaparral and hardwood forest. Developable parcels make up 39% of this corridor.

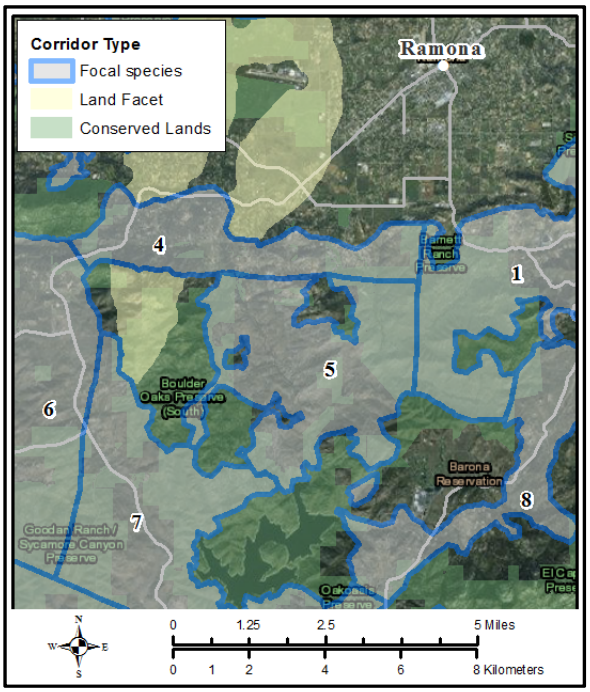
## Corridor 5

5,518 acres

46% conserved

25% PAMA

Average connectivity value: 86




Corridor 5 is in the center of the study area between Boulder Oaks Preserve to the west and Barnett Ranch Preserve and Cañada de San Vicente to the east. Developable parcels make up 41% of this corridor. Corridor 5 is comprised of areas with diffuse flow, but has one pinchpoint between the north and south segments of the Boulder Oaks Preserve that measures only 750 feet across. This arm of the corridor is in the outer isopleth (top 20-30% of connectivity values).

Ninety-six percent of this corridor is comprised of natural land cover types and two out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, hardwood forest, and riparian.

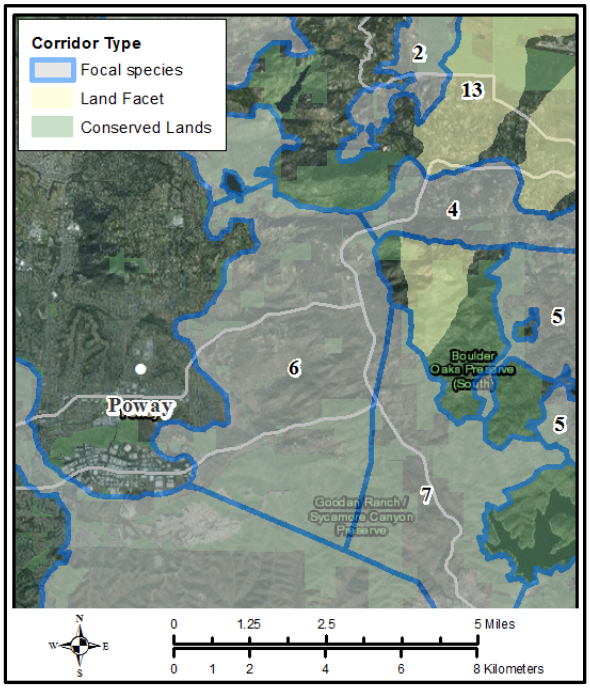
## Corridor 6

9,422 acres

33% conserved

10% PAMA

Average connectivity value: 90




Corridor 6 is a fairly wide and intact north-south corridor connecting Mt. Woodson in the north with Sycamore Canyon. This corridor has diffuse flow and is mostly comprised of the top two connectivity isopleths (top 1-20% of connectivity values. Corridor 6 contains two important wildlife road crossing zones on SR-67, one on Poway Road, and three on Scripps-Poway Road.

Eighty-eight percent of this corridor is comprised of natural land cover types and one out of the five threatened and endangered species assessed is present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 41% of this corridor.

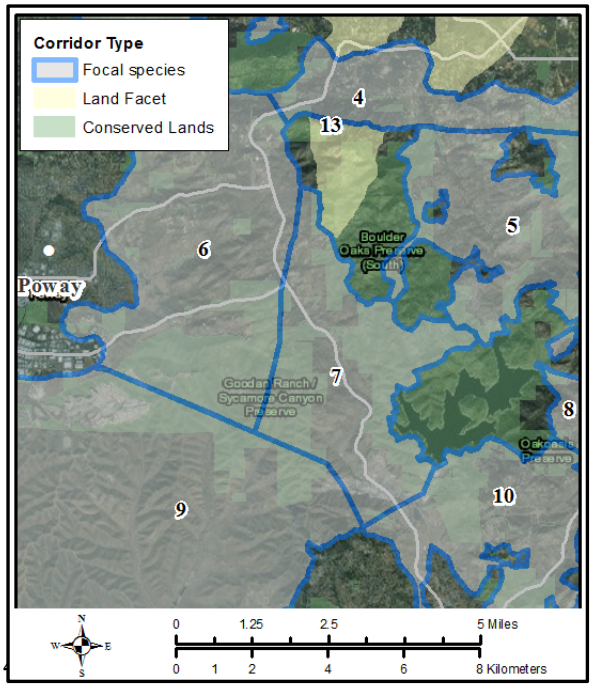
## Corridor 7

5,599 acres

56% conserved

10% PAMA

Average connectivity value: 86




Corridor 7 provides connectivity from the San Vicente Highlands and Boulder Oaks preserves on the east side of SR-67 to Sycamore Canyon and Goodan Ranch Preserves on the west side. This corridor contains seven important wildlife road crossing locations on SR-67. Corridor 7

is mostly made up the top two corridor isopleths (top 1-20% of connectivity values), however there is one important arm of east-west connectivity north of the San Vicente Reservoir that is in the outer corridor isopleth (top 20-30% of connectivity values).

Ninety percent of this corridor is comprised of natural land cover types and two out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 34% of this corridor.

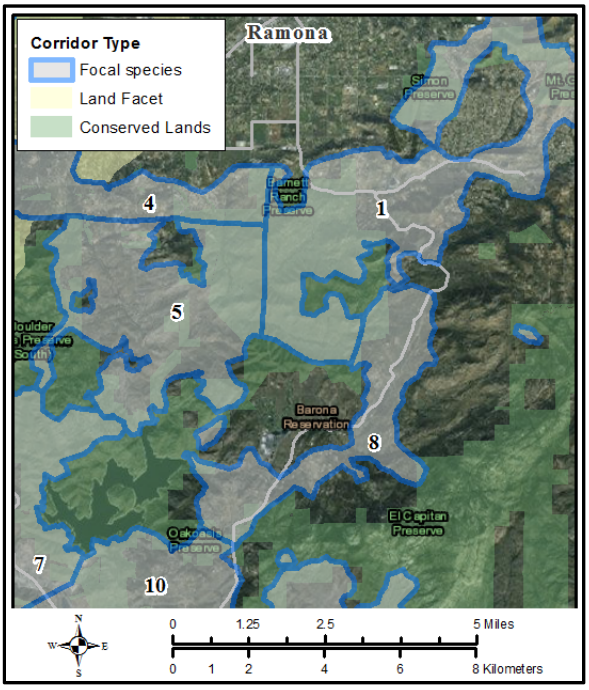
## Corridor 8

3,143 acres

15% conserved

4% Draft PAMA

Average connectivity value: 78




Corridor 8 connects the Barona Reservation and Cañada de San Vicente Preserve in the northeast with the Oakoasis Preserve in the southwest. It is comprised of diffuse flow and the out two corridor isopleths (top 10-30% of connectivity values). Compared with other corridors in the study area corridor 8 is narrow and has a pinch point that measures only ~2,600 feet wide. Corridor 8 also contains one important wildlife road crossing location on Wildcat Canyon Road.

Ninety-four percent of this corridor is comprised of natural land cover types. None of the endangered species assessed are present in this corridor. Land cover types with good connectivity across this corridor include chaparral and hardwood forest. Developable parcels make up 8% of this corridor.

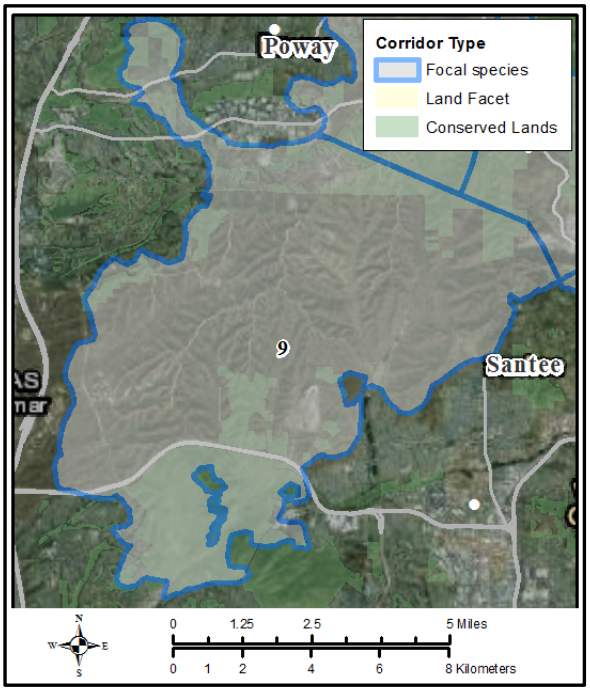
## Corridor 9

27,849 acres

25% conserved

2% PAMA

Average connectivity value: 87




Corridor 9 is the largest corridor and connects Sycamore Canyon and Goodan Ranch Preserves in the north with Mission Trails Regional Park in the south. Marine Corps Air Station Miramar is a major land owner in this corridor. Corridor 9 contains diffuse flow in the north, but transitions to highly channelized flow in the south. It is mostly comprised of the top two corridor isopleths (top 1-20% of connectivity values). Corridor 9 has one important wildlife road crossing location on Poway Road, one on Scripps-Poway Parkway, and two on SR-52.

Eighty-nine percent of this corridor is comprised of natural land cover types and three of the five endangered species are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 9% of this corridor.

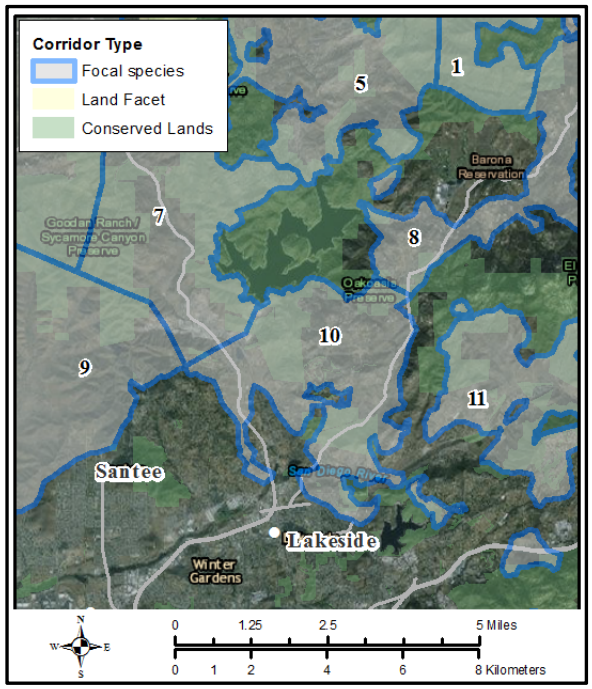
## Corridor 10

5,211 acres

30% conserved

24% PAMA

Average connectivity value: 81




Corridor 10 connects the San Vicente Reservoir and the Oakoasis Reserve in the north with the San Diego River and Lake Jennings in the south. It contains diffuse flow and is comprised mostly of the outer two corridor isopleths (top 10-30% of connectivity values). It contains one important wildlife road crossing location on SR-67 and one on Wildcat Canyon Road.

Eighty percent of this corridor is comprised of natural land cover types, and two of the five endangered species assessed are present. Land cover types with good connectivity across Corridor 8 include chaparral, coastal sage scrub, and riparian. Developable parcels make up 37% of this corridor.

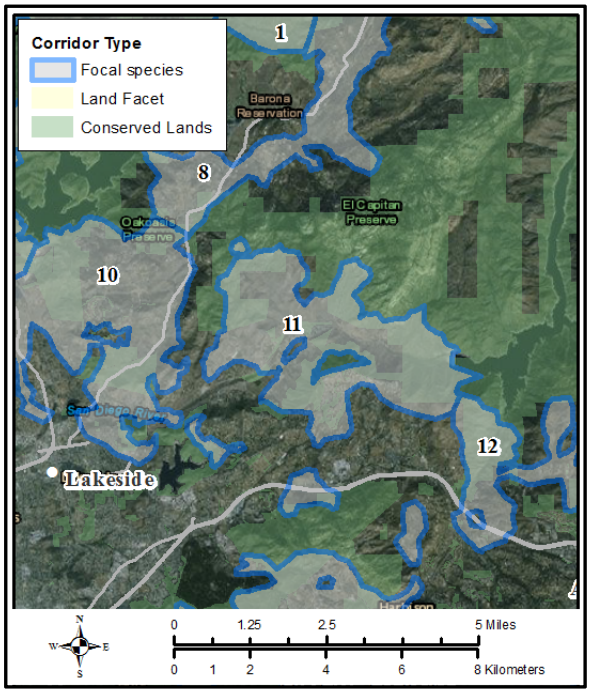
## Corridor 11

4,648 acres

50% conserved

36% PAMA

Average connectivity value: 81




Corridor 11 is in the southeastern section of the study area and provides connections from the El Capitan Reservoir with El Capitan County Preserve and the Cleveland National Forest to the northwest. This corridor has mostly diffuse flow, though flow does begin to get more concentrated in the southeast near the reservoir.

Ninety-one percent of this corridor is comprised of natural land cover types and three of the five endangered species assessed are present here. Land cover types with good connectivity across Corridor 11 include chaparral, coastal sage scrub, and riparian. Developable parcels make up 21% of this corridor.

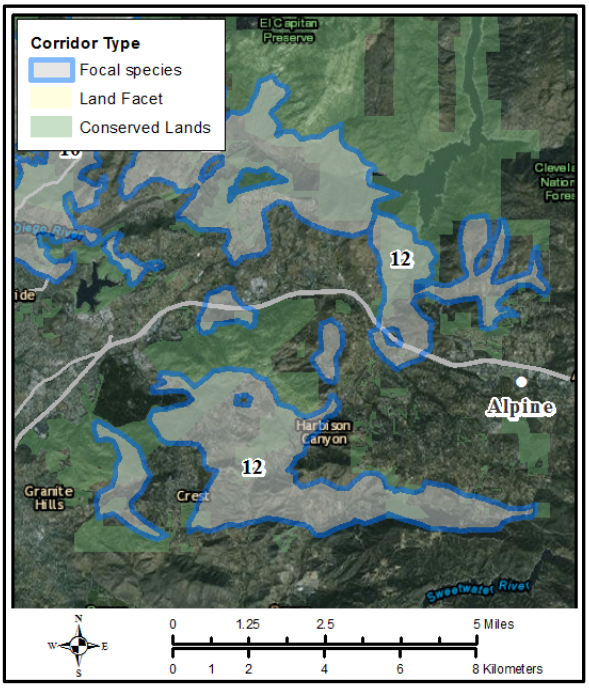
## Corridor 12

7,332 acres

32% conserved

14% PAMA

Average connectivity value: 69




Corridor 12 is a collection of smaller connections in the very southeastern part of the study area. It contains and connects the Cleveland National Forest and El Capitan County Preserve to the north of Interstate 8 with Crestridge Ecological Reserve, Crest, and Crest-

Worley Preserves south of the interstate. Flow is restricted or highly channelized through most of this corridor and it is primarily comprised of the outer connectivity isopleth (top 20-30% of connectivity values). Corridor 12 has two important wildlife road crossing locations on I-8, one of which is the Chocolate Creek crossing.

Eighty-two percent of this corridor is comprised of natural land cover types and two of the five endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and riparian. Developable parcels make up 4% of this corridor.

## Corridor 13

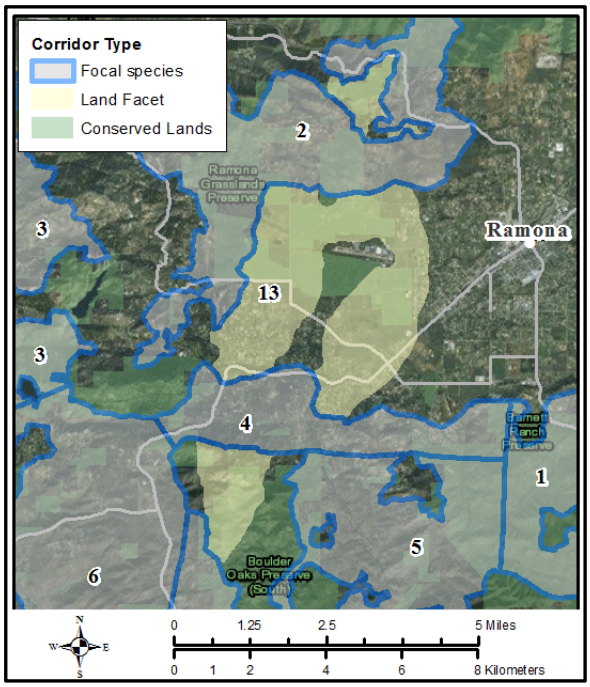
9,958 acres

34% conserved

3% PAMA

31% Draft PAMA

Average connectivity value: 42




Corridor 13, the land facet corridor, connects Cleveland National Forest lands in the north with Iron Mountain in the south through much of the Ramona Grasslands Preserve. This corridor contains one important wildlife road crossing on SR-67.

Seventy-five percent of this corridor is comprised of natural land cover types and three of the five endangered species are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 31% of this corridor.

**Table A1.** Corridor metadata table. This table displays the metric calculated for various attributes for each of the 13 corridors as well as the minimum and maximum value for each metric and the corresponding field abbreviation for the corridor shapefile product.

| Category | Type | Variable / Metric | Shapefile field abbreviation | Min Value | Max Value |
|---|---|---|---|---|---|
| | | Corridor ID number | Id | 1 | 13 |
| | | Corridor Type, species–specific or land facet | C_Type | | |
| | | Corridor area in acres | Area_Ac | 3,142 | 27,849 |
| Conservation/Management | Conservation Status | Percent of corridor area with conserved status | Pct_Cnsvd | 15 | 56 |
| Conservation/Management | Conservation Status | Acres of corridor conserved | Ac_Cnsvd | 479 | 6,874 |
| Conservation/Management | Conservation Status | Acres of corridor unconserved | Ac_UNCnsvd | 2,320 | 20,974 |
| Conservation/Management | Conservation Status | Acres of corridor in PAMA | Ac_PAMA | 0 | 1670 |
| Conservation/Management | Conservation Status | Percent of corridor area in PAMA | Pct_PAMA | 0 | 36 |
| Conservation/Management | Conservation Status | Acres of corridor in with draft PAMA status | Ac_D_PAMA | 0 | 2,597 |
| Conservation/Management | Conservation Status | Percent of corridor area with draft PAMA status | Pct_DPAMA | 0 | 32 |
| Conservation/Management | Future Land Use | developable parcels | No_Dev_Pcl | 10 | 330 |
| Conservation/Management | Future Land Use | Number of parcels with developable land | Ac_Dev_Pcl | 267 | 3,904 |
| Conservation/Management | Future Land Use | Percent of corridor area with developable land | Pct_Dev_Pc | 4 | 41 |
| Conservation/Management | Future Land Use | Average probability of development | ProbDev_Av | 0.001 | 0.043 |
| Conservation/Management | Future Land Use | Minimum probability of development | ProbDev_Mn | 0 | 0.002 |
| Conservation/Management | Future Land Use | Maximum probability of development | ProbDev_Mx | 0.004 | 0.327 |
| Conservation/Management | Future Land Use | Area weighted mean average cost of developable land | priceAWM | $51,081 | $984,126 |
| Conservation/Management | Future Land Use | Area weighted sum of cost of developable land | priceAWS | $595,710 | $113,979,498 |
| Conservation/Management | Cultural | Number of recorded cultural sites in corridor | Csites | 31 | 402 |
| Biological Variables | Connectivity | Average value in corridor of the multi-species connectivity surface | All_spp_Val | 68.6 | 89.9 |
| Biological Variables | Resilience | Mean climate change resiliency value | Resilience | 0.103 | 0.287 |
| Biological Variables | Resilience | Proportion of corridor covered by Land Facet 1 | Prop_LF1 | 0 | 71 |
| Biological Variables | Resilience | Proportion of corridor covered by Land Facet 2 | Prop_LF2 | 4 | 100 |
| Biological Variables | Resilience | Proportion of corridor covered by Land Facet 3 | Prop_LF3 | 0 | 91 |

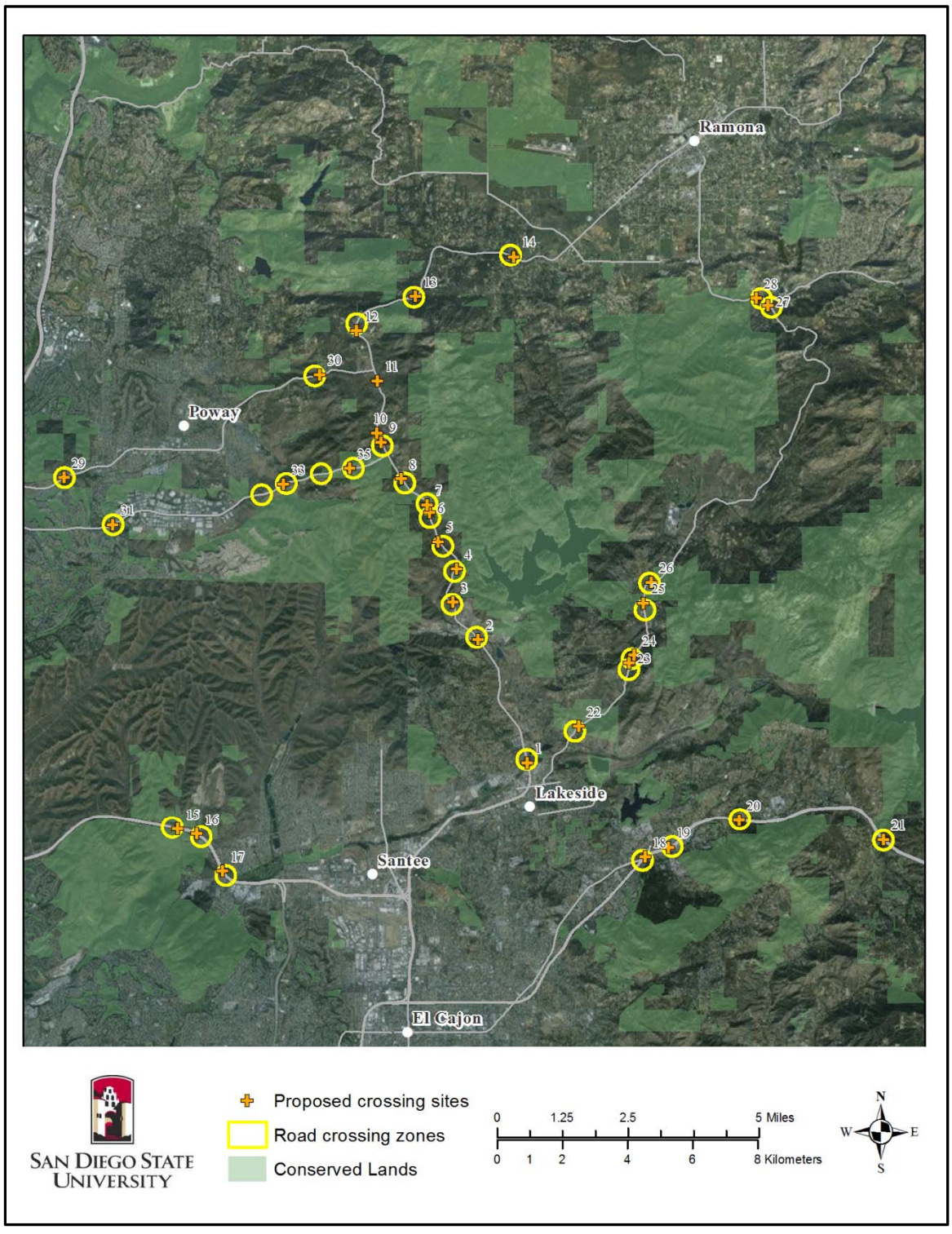
| Category | Type | Variable / Metric | Shapefile field abbreviation | Min Value | Max Value |
|---|---|---|---|---|---|
| Biological Variables | Resilience | Proportion of corridor covered by Land Facet 4 | Prop_LF4 | 0 | 95 |
| Biological Variables | Focal Species Corridor | Proportion of the corridor covered by the puma-only corridor | Puma_Corr | 2 | 100 |
| Biological Variables | Focal Species Connectivity | Average value in corridor of the connectivity surface for puma | Puma_Val | 33.4 | 95.3 |
| Biological Variables | Focal Species Corridor | Proportion of the corridor covered by the bobcat-only corridor | Bcat_Corr | 43 | 100 |
| Biological Variables | Focal Species Connectivity | Average value in corridor of the connectivity surface for bobcat | Bobcat_Val | 44.6 | 89.2 |
| Biological Variables | Focal Species Corridor | Proportion of the corridor covered by the deer-only corridor | Deer_Corr | 33 | 100 |
| Biological Variables | Focal Species Connectivity | Average value in corridor of the connectivity surface for deer | Deer_Val | 42 | 91.2 |
| Biological Variables | Focal Species Corridor | Proportion of the corridor covered by the woodrat-only corridor | Wrat_Corr | 73 | 97 |
| Biological Variables | Focal Species Connectivity | Average value in corridor of the connectivity surface for woodrat | Wrat_Val | 53.3 | 84.6 |
| Biological Variables | Focal Species Corridor | Proportion of the corridor covered by the wrentit-only corridor | Wrtit_Corr | 26 | 100 |
| Biological Variables | Focal Species Connectivity | Average value in corridor of the connectivity surface for wrentit | Wrtit_Val | 47.5 | 84 |
| Biological Variables | Focal Species Corridor | Proportion of the corridor covered by the CA mouse-only corridor | Mouse_Corr | 67 | 91 |
| Biological Variables | Focal Species Connectivity | Average value in corridor of the connectivity surface for CA mouse | Mouse_Val | 56.8 | 79.5 |
| Biological Variables | T&E Species | Number of Arroyo toad occurrence points in corridor | ARTO_pts | 0 | 149 |
| Biological Variables | T&E Species | Proportion of Arroyo toad points in corridor out of total in study area | ARTOpropts | 0 | 0.47 |
| Biological Variables | T&E Species | Number of Cactus wren occurrence points in corridor | CACW_pts | 0 | 7 |
| Biological Variables | T&E Species | Proportion of cactus wren points in corridor out of total in study area | CACWpropts | 0 | 0.048 |
| Biological Variables | T&E Species | Mean habitat suitability value in corridor for Cactus wren | CACWMN | 0.028 | 0.435 |
| Biological Variables | T&E Species | Number of CA gnatcatcher occurrence points in corridor | CAGN_pts | 0 | 181 |
| Biological Variables | T&E Species | Proportion of California gnatcatcher points in corridor out of total in study area | CAGNpropts | 0 | 0.17 |
| Biological Variables | T&E Species | Mean habitat suitability value in corridor for California gnatcatcher | CAGNMN | 0.017 | 0.463 |

| Category | Type | Variable / Metric | Shapefile field abbreviation | Min Value | Max Value |
|---|---|---|---|---|---|
| Biological Variables | T&E Species | Number of Quino checkerspot butterfly occurrence points in corridor | QUCH_pts | 0 | 6 |
| Biological Variables | T&E Species | Proportion of Quino checkerspot butterfly points in corridor out of total in study area | QUCHpropts | 0 | 0.286 |
| Biological Variables | T&E Species | Mean habitat suitability value in corridor for Quino checkerspot butterfly | QUCHMN | 0.088 | 0.362 |
| Biological Variables | T&E Species | Number of Stephens' kangaroo rat occurrence points in corridor | SKR_pts | 0 | 10 |
| Biological Variables | T&E Species | Proportion of Stephens' kangaroo rat points in corridor out of total number | SKRpropts | 0 | 0.059 |
| Biological Variables | Species Representation | Number of Hermes copper butterfly occurrence points in corridor | HECO_pts | 0 | 343 |
| Biological Variables | Species Representation | Proportion of Hermes copper butterfly points in corridor out of total in study area | HECOpropts | 0 | 0.762 |
| Biological Variables | Species Representation | Number of coachwhip occurrence points in corridor | MAFL_pts | 0 | 5 |
| Biological Variables | Species Representation | Proportion of coachwhip points in corridor out of total in study area | MAFLpropts | 0 | 0.091 |
| Biological Variables | Species Representation | Number of granite spiny lizard occurrence points in corridor | SCOR_pts | 0 | 10 |
| Biological Variables | Species Representation | Proportion of granite spiny lizard points in corridor out of total number | SCORpropts | 0 | 0.097 |
| Biological Variables | Species Representation | Number of two-striped garter snake occurrence points in corridor | THHA_pts | 0 | 6 |
| Biological Variables | Species Representation | Proportion of two-striped garter snake points in corridor out of total | THHApropts | 0 | 0.075 |
| Biological Variables | Species Representation | Number of W. whiptail occurrence points in corridor | ASTI_pts | 0 | 16 |
| Biological Variables | Species Representation | Proportion of W. whiptail points in corridor out of total in study area | ASTIpropts | 0 | 0.246 |
| Biological Variables | Species Representation | Number of western toad occurrence points in corridor | ANBO_pts | 0 | 151 |
| Biological Variables | Species Representation | Proportion of western toad points in corridor out of total in study area | ANBOpropts | 0 | 0.351 |
| Biological Variables | Species Representation | Mean habitat suitability value in corridor for Bell's sparrow | SASPMN | 0.61 | 0.738 |
| Biological Variables | Species Representation | Mean habitat suitability value in corridor for California thrasher | CATHMN | 0.425 | 0.631 |
| Biological Variables | Species Representation | Mean habitat suitability value in corridor for Costa's hummingbird | COHUMN | 0.471 | 0.688 |
| Biological Variables | Species Representation | Number of pallid bat occurrence points in corridor | ANPA_pts | 0 | 4 |

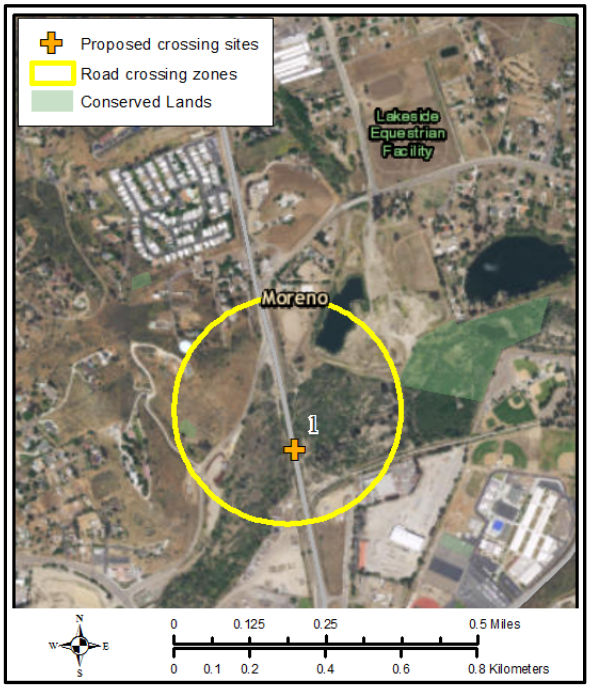
| Category | Type | Variable / Metric | Shapefile field abbreviation | Min Value | Max Value |
|---|---|---|---|---|---|
| Biological Variables | Species Representation | Proportion of pallid bat points in corridor out of total in study area | ANPApropts | 0.02 | 0.11 |
| Biological Variables | Species Representation | Number of Townsend's big-eared bat occurrence points in corridor | COTO_pts | 0 | 4 |
| Biological Variables | Species Representation | Proportion of Townsend's big-eared bat points in corridor out of total | COTOpropts | 0 | 0.308 |
| Biological Variables | Species Representation | Number of American badger occurrence points in corridor | TATA_pts | 0 | 2 |
| Biological Variables | Species Representation | Proportion of American badger points in corridor out of total in study area | TATApropts | 0 | 0.2 |
| Biological Variables | Species Representation | Number of ringtail occurrence points in corridor | BAAS_pts | 0 | 4 |
| Biological Variables | Species Representation | Proportion of ringtail points in corridor out of total in study area | BAASpropts | 0 | 0.364 |
| Biological Variables | Vegetation | Vegetation types connected in corridor | Veg_connec | qualitative | |
| Biological Variables | Vegetation | Percent of corridor comprised of chaparral | PLAND_CHP | 10.491 | 71.621 |
| Biological Variables | Vegetation | Degree to which chaparral is aggregated in the corridor | CLUMPY_CHP | 0.752 | 0.893 |
| Biological Variables | Vegetation | Index of travel distance through chaparral in the corridor | GYRATE_CHP | 322.921 | 2,850.39 |
| Biological Variables | Vegetation | Percent of corridor comprised of coastal scrub | PLAND_CSC | 1.694 | 49.27 |
| Biological Variables | Vegetation | Degree to which coastal scrub is aggregated in the corridor | CLUMPY_CSC | 0.717 | 0.89 |
| Biological Variables | Vegetation | Index of travel distance through coastal scrub in the corridor | GYRATE_CSC | 90.654 | 1,652.09 |
| Biological Variables | Vegetation | Percent of corridor comprised of grassland | PLAND_GRS | 1.052 | 7.803 |
| Biological Variables | Vegetation | Degree to which grassland is aggregated in the corridor | CLUMPY_GRS | 0.672 | 0.835 |
| Biological Variables | Vegetation | Index of travel distance through grassland in the corridor | GYRATE_GRS | 92.23 | 277.159 |
| Biological Variables | Vegetation | Percent of corridor comprised of riparian | PLAND_RIP | 0.648 | 7.223 |
| Biological Variables | Vegetation | Degree to which riparian is aggregated in the corridor | CLUMPY_RIP | 0.502 | 0.742 |
| Biological Variables | Vegetation | Index of travel distance through riparian in the corridor | GYRATE_RIP | 129.12 | 777.73 |
| Biological Variables | Vegetation | Percent of corridor comprised of woodland | PLAND_WDL | 0.754 | 16.61 |
| Biological Variables | Vegetation | Degree to which woodland is aggregated in the corridor | CLUMPY_WDL | 0.617 | 0.773 |
| Biological Variables | Vegetation | Index of travel distance through woodland in the corridor | GYRATE_WDL | 59.69 | 408.75 |
| Threats and Stressors | Development | Percent of the corridor that has been developed | PCT_DEV | 4.54 | 19.59 |

| Category | Type | Variable / Metric | Shapefile field abbreviation | Min Value | Max Value |
|---|---|---|---|---|---|
| Threats and Stressors | Fragmentation | Mean intactness value in the corridor | Intactness | -0.277 | 0.408 |
| Threats and Stressors | Fragmentation | Amount of corridor that is comprised of core area | EI_Ratio | 18 | 73 |
| Threats and Stressors | Roads | Average road density in the corridor | Road_Dens | 2.597 | 6.285 |
| Threats and Stressors | Fragmentation | Percent of corridor comprised of natural cover types | PLND_NAT | 80 | 96 |
| Threats and Stressors | Fragmentation | Degree to which natural areas are aggregated in the corridor | CLUMPY_NAT | 0.5 | 0.77 |
| Threats and Stressors | Fragmentation | Index of travel distance through natural areas in the corridor | GYRATE_NAT | 1,572 | 4,046 |
| Threats and Stressors | Disturbance | Percent of corridor comprised of sparse vegetation | PLAND_SPS | 4.54 | 19.59 |
| Threats and Stressors | Disturbance | Degree to which sparse vegetation is aggregated in the corridor | CLUMPY_SPS | 0.712 | 0.828 |
| Threats and Stressors | Disturbance | Index of travel distance through sparse vegetation in the corridor | GYRATE_SPS | 127.38 | 1,013.83 |
| Threats and Stressors | Fire | Frequency of departure from the mean fire return interval | FRIDMN | -54.94 | -33.56 |
| Threats and Stressors | Fire | Frequency of departure from the minimum fire return interval | FRIDMIN | -84.2 | -67.1 |
| Threats and Stressors | Fire | Frequency of departure from the maximum fire return interval | FRIDMAX | 43.1 | 71.8 |
| Threats and Stressors | Fire | Proportion of corridor in a low fire threat category | ThreatV0 | 0.021 | 0.209 |
| Threats and Stressors | Fire | Proportion of corridor in a moderate fire threat category | ThreatV1 | 0.011 | 0.166 |
| Threats and Stressors | Fire | Proportion of corridor in a high fire threat category | ThreatV2 | 0.012 | 0.537 |
| Threats and Stressors | Fire | Proportion of corridor in a very high fire threat category | ThreatV3 | 0.096 | 0.879 |
| Threats and Stressors | Fire | Proportion of corridor in an extreme fire threat category | ThreatV4 | | 0.347 |

# APPENDIX B: SR-67 WILDLIFE CROSSING STRUCTURE MAPS, DESCRIPTIONS, AND INFRASTRUCTURE RECOMMENDATIONS



## Crossing Site 1

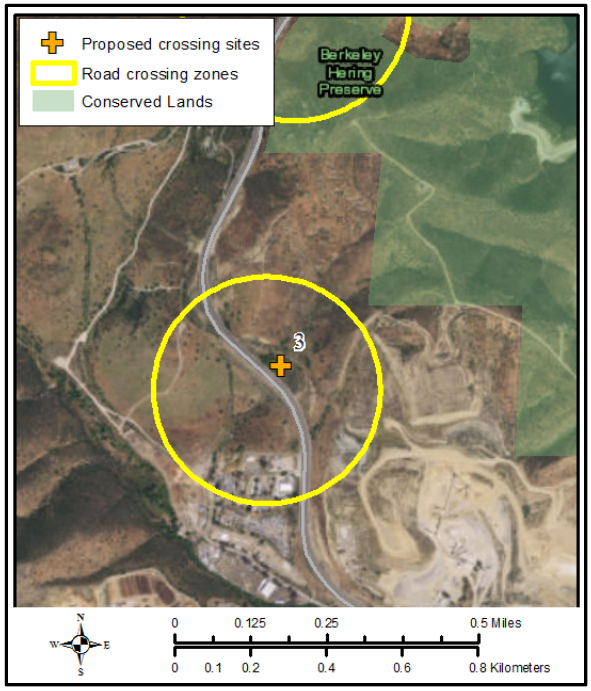



Crossing site 1 is located at the bridge over the San Diego River at Post Mile R5.95. The land on either side of the road in this location is in private ownership. The site is of high importance to wildlife and would only require minor improvements for enhancing wildlife movement. The overall size of the structure is appropriate but fencing is recommended on either side of the road running perpendicular to the bridge to prevent wildlife from accessing the industrial development in the surrounding area. Removal of the non-native vegetation in the San Diego River channel will also enhance wildlife movement through this structure.

## Crossing Site 2

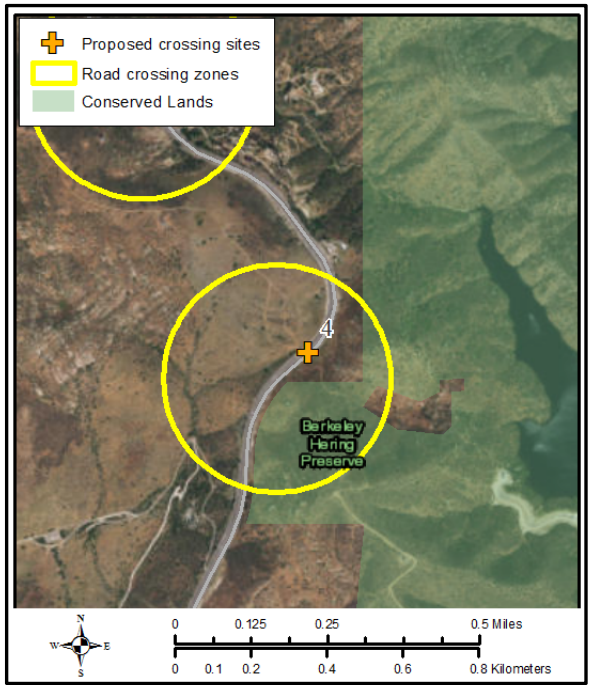
Crossing site 2 is located just south of Vigilante Road in Lakeside at Post Mile 9.05. It is of moderate importance to wildlife because there is limited suitable habitat for wildlife movement in the surrounding industrial development despite the proximity to conserved lands. The existing culvert is 7 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Removal of the non-native vegetation and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. Revegetation of the dirt span leading to the culvert on the east side of the road to connect to existing vegetation should also be prioritized. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

## Crossing Site 3



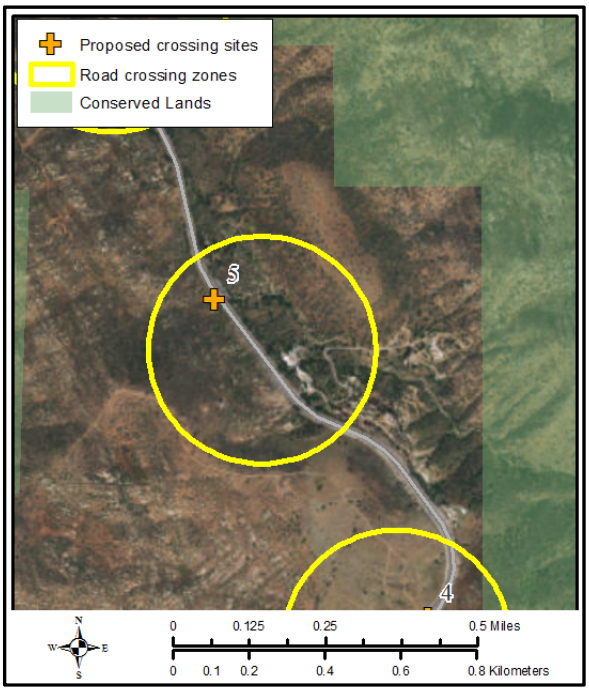

Crossing site 3 is located mid-slope on the grade leading out of Lakeside north of Vigilante Road at Post Mile 9.96. It is of extremely high importance to wildlife as it connects areas of suitable habitat and is adjacent to a large area of conserved land to the east. However, this section of road has experienced moderate levels of wildlife vehicle collisions. The existing culvert is long, narrow and set far back from the road, so will either need a major redesign or dual siting of a wildlife structure to accommodate wildlife movement. The optimal design for this site would be an arched or box culvert 26.2 feet wide by 14.8 feet high. However, the minimum recommendation for this site is 19.7 feet wide by 13.1 feet high. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

## Crossing Site 4




Crossing site 4 is near the top of the grade north of Lakeside at Post Mile 10.76. It is of high importance to wildlife to connect nearby preserved lands to the east. The existing culvert at this location is only 1.5 feet in diameter, so a major redesign is necessary to facilitate wildlife movement. The optimal design for this site would be an arched or box culvert 16.5 feet wide by 9.8 feet high. However, the minimum recommendation for this site is 13.1 feet wide by 6.6 feet high. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

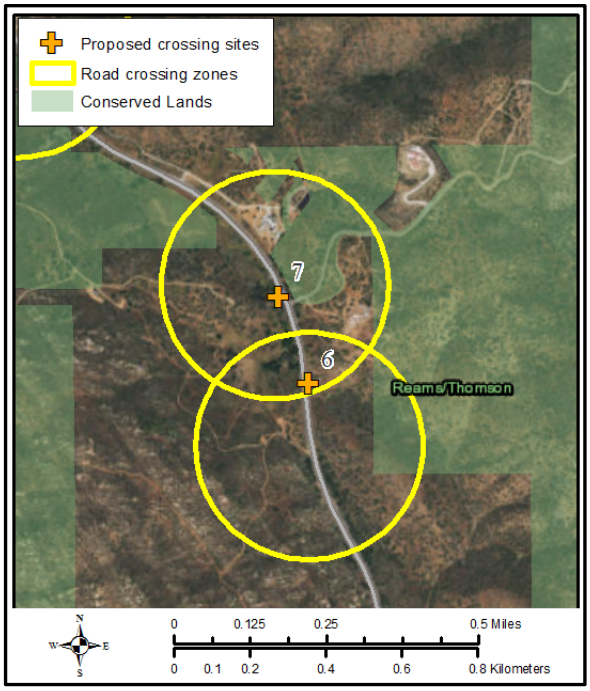
## Crossing Site 5




Crossing site 5 is at the top of the grade north of Lakeside at Post Mile 11.46. It is of moderate importance to wildlife to connect nearby preserved lands. The existing culvert at this location is 3.0 feet in diameter, and will require a major redesign to facilitate wildlife movement. Because this crossing will primarily serve small animals, the optimal design is a pipe culvert 6.6 feet in diameter. However, the minimum recommendation for this site is a 3.3 foot diameter culvert. On both sides of the road, 3.5 foot high fencing with an impenetrable bottom should also be used to reinforce wildlife movement through the existing culvert.

## Crossing Site 6

Crossing site 6 is located immediately south of Foster's Truck Trail at Post Mile 12.05. It is of extremely high importance to wildlife as it connects areas of suitable habitat and is one of the few locations on the road where there are conserved lands on either side of the road. Although the existing culvert is large, with a diameter of 7.5 feet, it should be larger and more open to accommodate movement, particularly of larger species. The optimal design for this site would be an arched or box culvert 26.2 feet wide by 14.8 feet high. However, the minimum recommendation for this site is 19.7 feet wide by 13.1 feet high. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

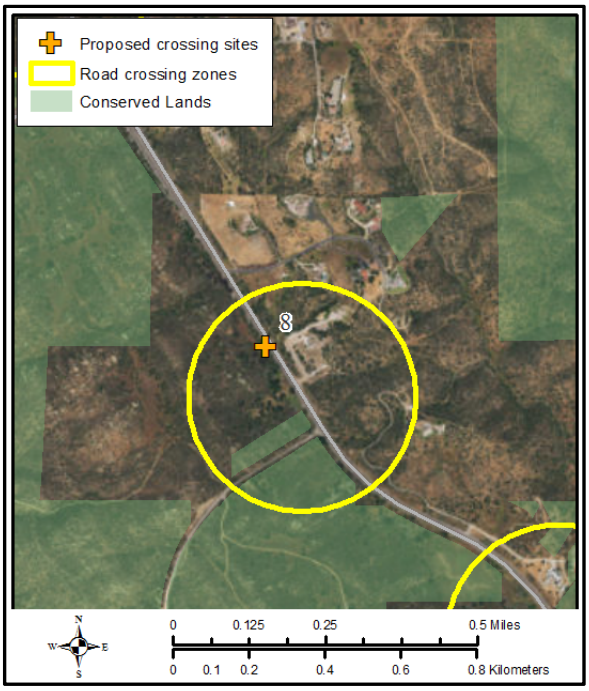



## Crossing Site 7

Crossing site 7 is located just north of Foster's Truck Trail at Post Mile 12.25. It is of high importance to wildlife as it connects areas of suitable habitat and is one of the few locations on the road where there are conserved lands on either side of

the road. However, the siting and approach to this culvert make it less attractive for wildlife movement than the site for Crossing 6. The existing culvert is 7.5 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Removal of the non-native vegetation and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

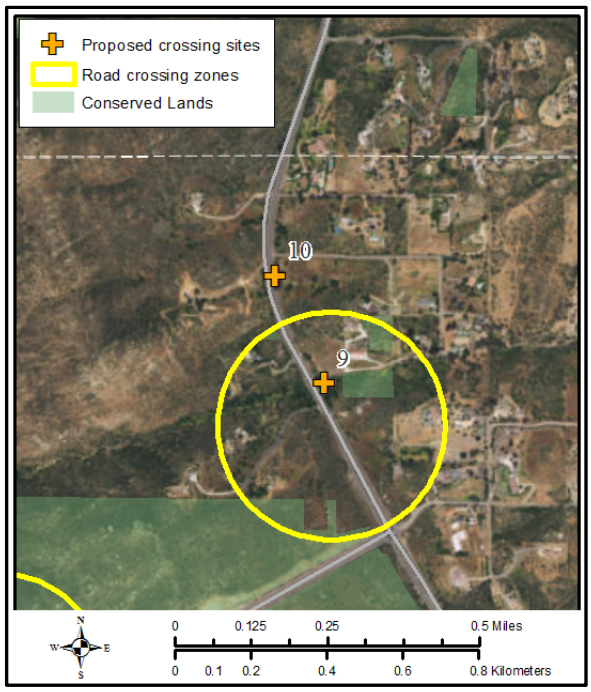
## Crossing Site 8




Crossing site 8 is located just north of Lazy Acres Drive at Post Mile 12.95. It is of moderate importance to wildlife as there is scattered housing through the area, which is dominated by non-native vegetation. There are adjacent conserved lands nearby, but they are not contiguous across the roadway. The existing culvert on site is 3.0 feet in diameter, and although the optimal crossing design would be an arched or box culvert 13.1 feet wide by 6.6 feet high, a pipe culvert 6.6 feet in diameter would still provide for adequate wildlife movement. Although this is a change in size from the current structure, we have identified it as a minor improvement because this retrofit could occur during normal culvert replacement. Removal of the non-native vegetation and addressing erosion and gullying leading to the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the structure.

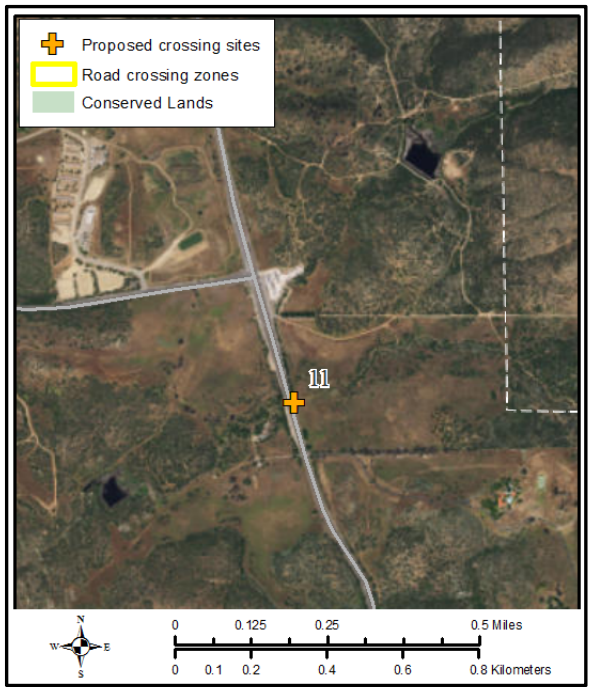
## Crossing Site 9

Crossing site 9 is located in the riparian zone that crosses SR-67 north of Scripps Poway Parkway at Post Mile 13.75. It is of extremely high importance to wildlife as it connects areas of suitable habitat and experiences moderate levels of wildlife vehicle collisions. The existing culvert is large at 5.5 feet in diameter, but major improvements are necessary to enhance wildlife movement across the road in this location. The optimal design for this site would be an arched or box culvert 26.2 feet wide by 14.8 feet high. However, the minimum recommendation for this site is 16.4 feet wide by 9.8 feet high. If hydrologic issues preclude optimal wildlife design, dual siting of structures for drainage and wildlife are recommended. On both sides of the road, 6-8 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.




## Crossing Site 10

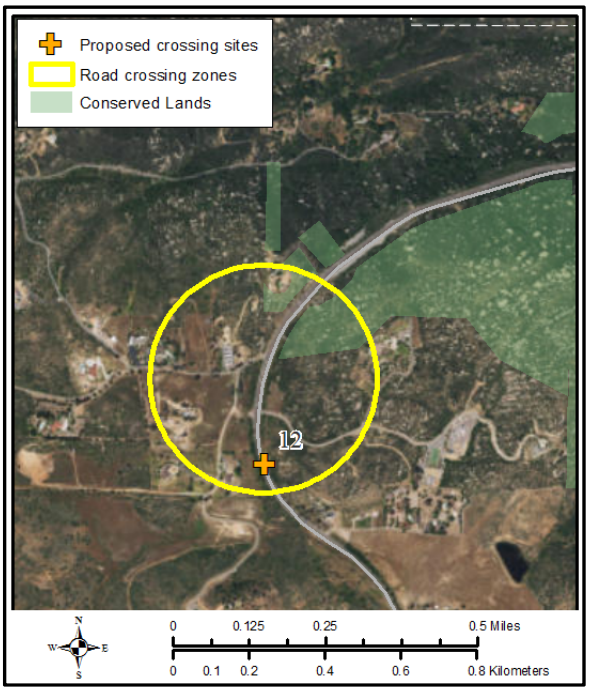
Crossing site 10 is located north of Scripps Poway Parkway at Post Mile 13.9. Although it was not identified by our modeling approach, it is of high importance to wildlife as it connects areas of suitable habitat and past monitoring has documented multiple species crossing the road at this location (Jennings and Lewison 2015). The existing culvert is 7.0 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Removal of the non-native vegetation and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.




## Crossing Site 11

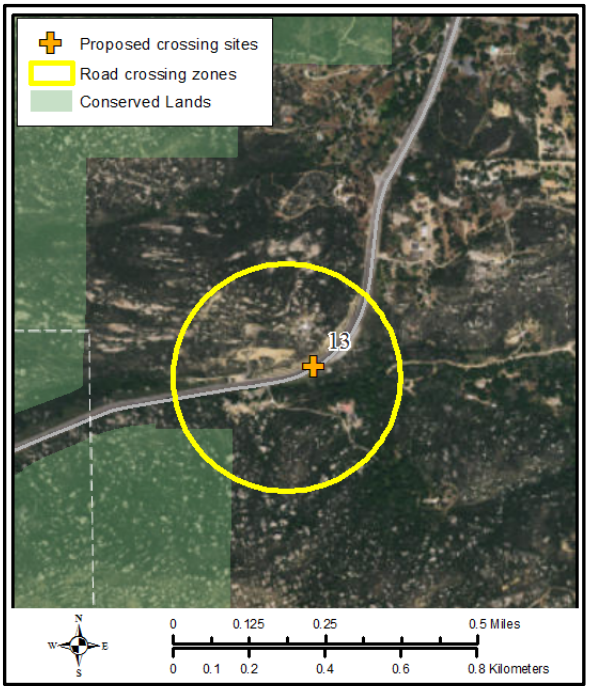
Crossing site 11 is located south of Poway Road at Post Mile 14.98. Although it was not identified by our modeling approach, it is of high importance to wildlife as it connects areas of suitable habitat and has been documented in past monitoring (Jennings and Lewison 2015) as accommodating multiple species crossing the road. The existing culvert is 8.5 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Enhancing native vegetation leading to the structure on the east side and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

## Crossing Site 12




Crossing site 12 is south of Chaparral Way on a curve leading toward Mount Woodson at Post Mile 16.05. It is of high importance to wildlife as it connects areas of suitable habitat and is adjacent to conserved lands. The existing culvert at this location is only 3.0 feet in diameter, so a major redesign is necessary to facilitate wildlife movement. The limited grade relief at this site will require additional work to accommodate a larger structure. The optimal design for this site would be an arched or box culvert 13.1 feet wide by 6.6 feet high. However, the minimum recommendation for this site is a 6.6-foot diameter culvert. On both sides of the road, 6-8 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

## Crossing Site 13



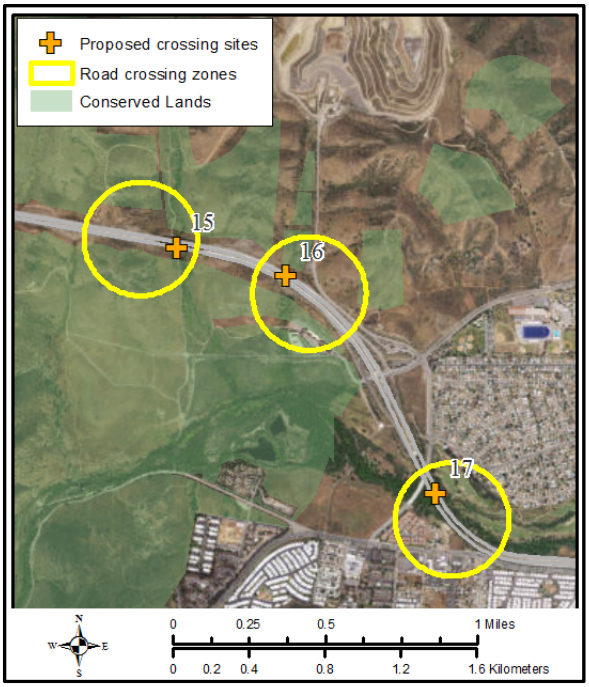

Crossing site 13 is located at the top of the Mount Woodson grade at Post Mile 17.61. It is of extremely high importance to wildlife as it connects areas of unique suitable habitat, conserved lands, and has experienced high levels of wildlife vehicle collisions. There is no existing structure providing for wildlife movement in this area, so it will require a major improvement to construct a suitable wildlife crossing structure. Based on topography and movement patterns of focal species for this crossing structure, a wildlife overpass is the optimal design for this site. The overpass should be between 164 and 230 feet wide and will need to connect in an area where wildlife will be likely to approach the overpass. The structure should also be appropriately vegetated to encourage wildlife to approach and use the structure for crossing the highway. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

## Crossing Site 14

Crossing site 14 is between Via Penasco and Rancho de Oro Drive at Post Mile 20.17. It is of moderate importance to wildlife as it connects areas of suitable habitat but there are no conserved lands in the vicinity. The existing culvert at this location is only 3.0 feet in diameter, so a major redesign is necessary to facilitate wildlife movement. The limited grade relief at this site will require additional work to accommodate a larger structure. The optimal design for this site would be an arched or box culvert 13.1 feet wide by 6.6 feet high. However, the minimum recommendation for this site is a 6.6-foot diameter culvert. Fencing should be considered for this site, but there are few places to anchor fence ends and there are a number of driveways in the area that could limit fence functionality.

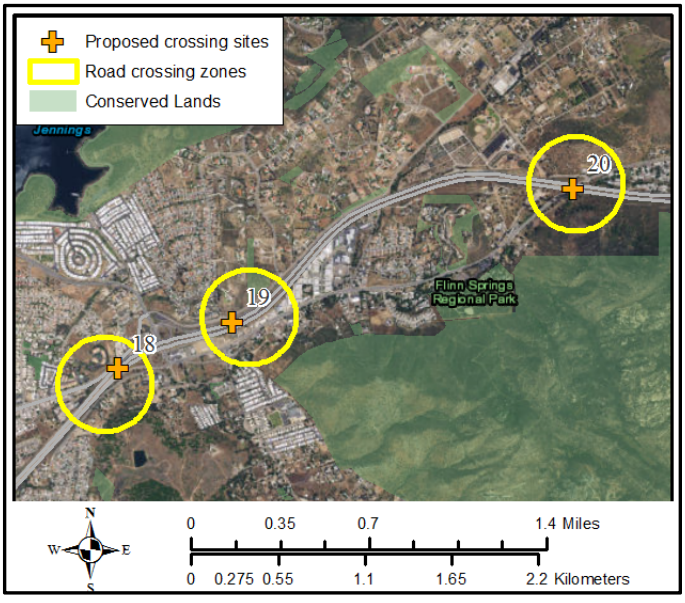
### *Additional Crossing Structures*

#### SR-52 Crossings

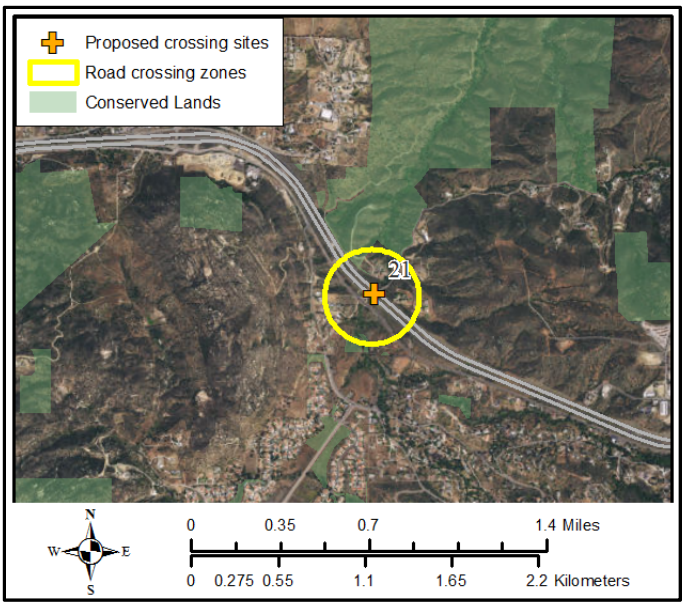


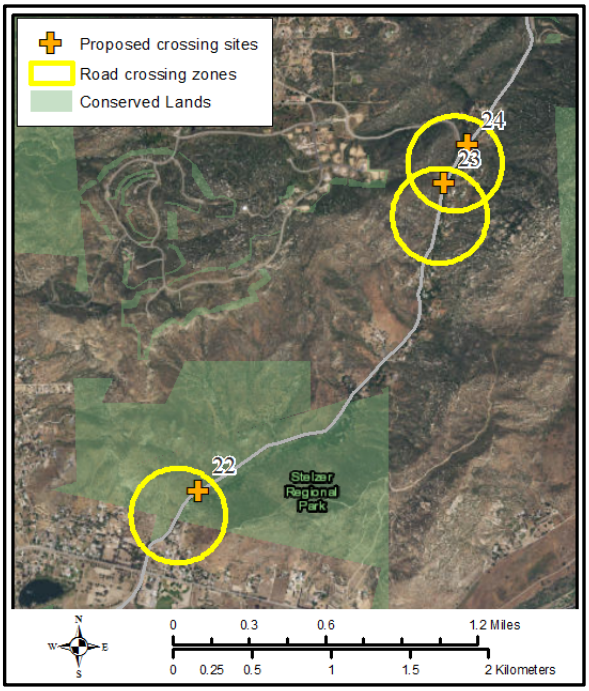

There are three sites along SR-52 that are important wildlife crossing areas: Post Miles 12.44, 12.64, and 13.72. This area is one of the primary connections for wildlife moving in and out of Mission Trails Regional Park. All three only require minor improvements as they likely facilitate wildlife movement in their current design. The installation of fencing to reinforce wildlife use of the structures, as well as some clearing of non-native vegetation under one of the bridges, is likely to improve the condition of the structures for wildlife movement.

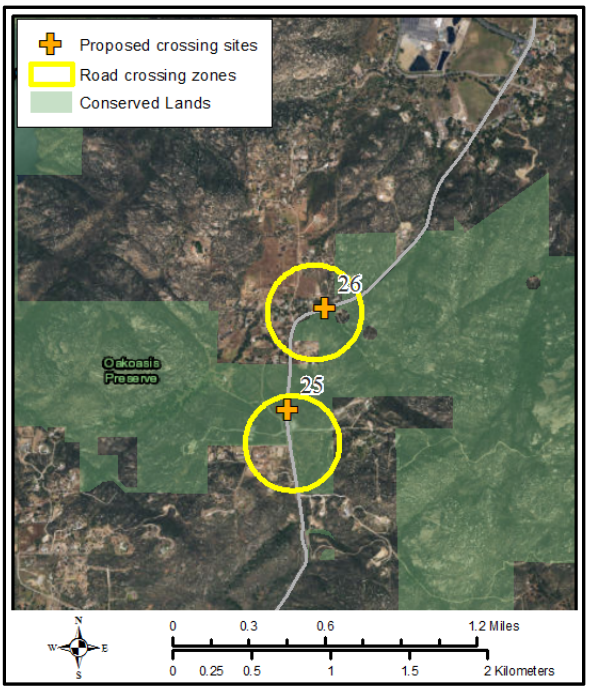
#### I-8 Crossings




There are four sites along I-8 that are important wildlife crossing areas: Post Miles 21.66, 22.13, 23.67, and 26.75. The first two are of moderate importance for wildlife movement, but the other two are of high and very high importance. As no structures exist at these sites that can accommodate wildlife movement, major improvements are necessary at all four sites. Once redesigned, the installation of fencing to reinforce wildlife use of the structures is likely to improve the condition of the structures for wildlife movement.

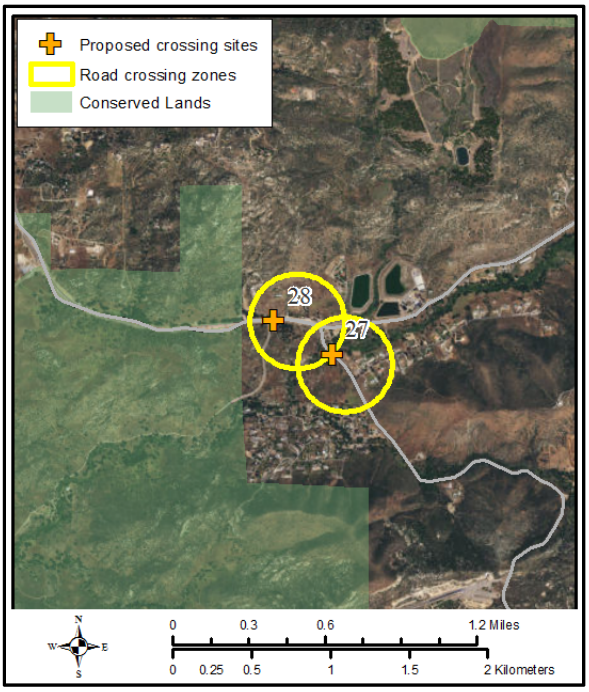


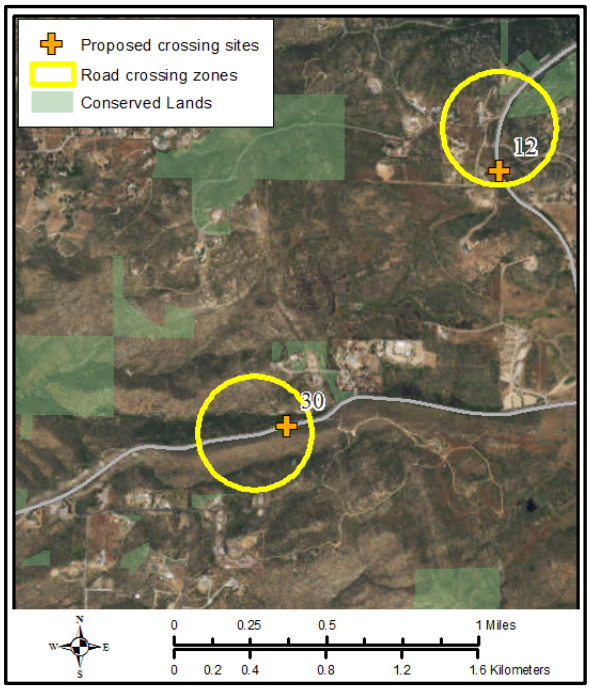




## Wildcat Canyon Road Crossings

There are seven sites along Wildcat Canyon Road (with one of those being adjacent to Wildcat Canyon Road on San Vicente Road) that are important to wildlife movement. Most are of moderate or high importance to wildlife, but many require major improvements because there are not existing structures adequate to support wildlife movement. In total, four out of seven site will need major improvements. Only minor improvements are needed at the existing wildlife tunnel site. Some sediment flow and




erosion control may be necessary here as well as revegetation with native species, but otherwise, this site appears functional. The installation of fencing to reinforce wildlife use of the structures, as well as some clearing of non-native vegetation under one of the bridges, is likely to improve the condition of the structures for wildlife movement.

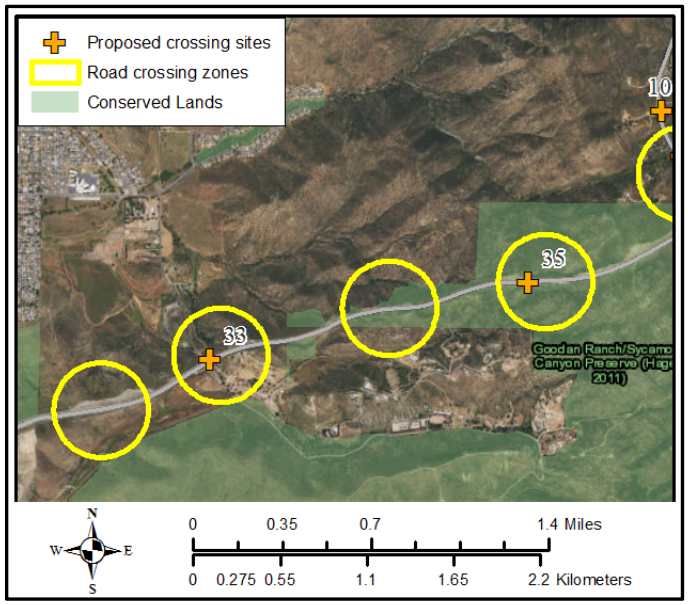


## Poway Road Crossings

There were two sites identified as having a high importance to wildlife movement on Poway Road. At one site, there is no existing structure, and a major improvement is

necessary. At the other, there is an existing culvert that can accommodate the movement by small animals at that location. The installation of fencing to reinforce wildlife use of the structures is also likely to improve the condition of the structures for wildlife movement.

## Scripps Poway Parkway Crossings




Although there were originally five crossing zones identified along Scripps Poway Parkway through our modeling results, there are final recommendations for only three of those sites. The remaining two had few options for siting and placement given the topography, road cut, and proximity of other proposed wildlife crossings. Two of these three sites were of high importance for wildlife movement and require major improvements to accommodate an adequate degree of wildlife movement. The third site is the location of the Scripps Poway Parkway wildlife tunnel that is functional but could benefit from fence extension and improvement.

**Table B1.** Detailed wildlife crossing recommendations for SR-67

| Id | Post Mile | Wildlife Priority | Improve-ment Type | Nearest Crossing (mi) | Rd width (ft) | Right-of-way (ft) | Optimal Crossing Type | Minimum Crossing Type | New, Retro, or Exists | Optimal width (ft) | Optimal height (ft) | Min width (ft) | Min height (ft) | Existing diameter (ft) | In corridor | Conserved | Min fence length E or S (ft) | Min fence length N or W (ft) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **1** | R5.95 | 2 | Minor | 1.209 | 45.9 | 164.0 | Bridge | | Exists | - | 13.1 | - | 9.8 | Unknown | Y | N | - | - |
| **2** | 9.05 | 3 | Minor | 0.896 | 114.8 | 141.1 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 7.0 | - | 7.0 | Y | N | 590.6 | 656.2 |
| **3** | 9.96 | 1 | Major | 0.636 | 164.0 | 502.0 | Arched or box culvert | | Retrofit | 26.2 | 14.8 | 19.7 | 13.1 | 4.0 | Y | N | 1312.3 | 1476.4 |
| **4** | 10.76 | 2 | Major | 0.629 | 101.7 | 150.9 | Arched or box culvert | | Retrofit | 16.4 | 9.8 | 13.1 | 6.6 | 1.5 | Y | N | 1640.4 | 2460.6 |
| **5** | 11.46 | 3 | Major | 0.588 | 144.4 | 150.9 | Pipe culvert | | Retrofit | 6.6 | - | 3.3 | - | 3.0 | Y | N | 820.2 | 328.1 |
| **6** | 12.05 | 1 | Major | 0.151 | 131.2 | 150.9 | Arched or box culvert | | Retrofit | 26.2 | 14.8 | 19.7 | 13.1 | 7.5 | Y | N | 984.3 | 1312.3 |
| **7** | 12.25 | 2 | Minor | 0.151 | 85.3 | 157.5 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 7.5 | - | 7.5 | Y | N | 1312.3 | 2624.7 |
| **8** | 12.95 | 3 | Minor | 0.696 | 88.6 | 141.1 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 6.6 | 6.6 | - | 3.0 | Y | N | 771.0 | 1082.7 |
| **9** | 13.75 | 1 | Major | 0.194 | 170.6 | 160.8 | Arched or box culvert | | Retrofit | 26.2 | 14.8 | 16.4 | 9.8 | 5.5 | Y | N | 1148.3 | 820.2 |
| **10** | 13.9 | 2 | Minor | 0.194 | 55.8 | 150.9 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 7.0 | - | 7.0 | Y | N | 1394.4 | 820.2 |
| **11** | 14.98 | 2 | Minor | 0.996 | 55.8 | 150.9 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 8.5 | - | 8.5 | Y | N | 1378.0 | 2296.6 |
| **12** | 16.05 | 2 | Major | 1.034 | 82.0 | 150.9 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 6.6 | 6.6 | - | 3.0 | Y | N | 1804.5 | 1804.5 |
| **13** | 17.61 | 1 | Major | 1.311 | 114.8 | 311.7 | Wildlife overpass | | New | 229.7 | - | 164.0 | - | - | Y | N | - | - |
| **14** | 20.17 | 3 | Major | 2.016 | 82.0 | 114.8 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 6.6 | 6.6 | | 3.0 | Y | N | - | - |

| Id | Post Mile | Fence specifics | Design features | Near-term Recommendation | Aerial connectivity considerations | Notes |
|---|---|---|---|---|---|---|
| **1** | R5.95 | Site visit needed to determine if fencing to direct wildlife under bridge is necessary | Clear some vegetation to ensure clear path and line of sight. Remove invasives | Clear some vegetation to ensure clear path and line of sight. Remove invasives | Directional structure to encourage flight behavior higher than traffic | Fencing perpendicular to road may be possible within Caltrans right-of-way but would need adjacent land owners to agree |
| **2** | 9.05 | 8-10 ft high, impenetrable bottom, fine mesh | Enhance vegetative strip on east side of road - expand to crossing structure. Improve water drainage in low area of crossing. Control erosion off of industrial development areas on the E side of highway | Clear sediment and debris in southern-most structure to increase height on east side (currently partially obstructed). Control invasives surrounding crossings, especially on west side. Restore native vegetation on both sides of highway | Directional structure to encourage flight behavior higher than traffic. Need to improve vegetative structure/height on east side to support aerial crossings | |
| **3** | 9.96 | 8-10 ft high, impenetrable bottom, fine mesh | Lighting inside structure, contour entrance to structure on E side to enhance line of sight through structure. This should also happen on slope on W side | Install seasonal signage and flashing lights to increase awareness about this area as a wildlife-vehicle collision hot spot and slow traffic during fall evening rush hour | Directional structure to encourage flight behavior higher than traffic - topography and natural veg support aerial crossings just north of underpass location. Need additional vegetative structure on E and W slopes to support crossings | Lighting could come from skylight/tube in median, addition of reflective paint inside structure at either end, or a light powered via a wired solar panel outside the structure. |
| **4** | 10.76 | 8-10 ft high, impenetrable bottom, fine mesh | | | Directional structure to encourage flight behavior higher than traffic; Could also plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides | |
| **5** | 11.46 | 3.5 ft high, impenetrable bottom, fine mesh | Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species | Clear sediment and debris | Directional structure to encourage flight behavior higher than traffic; Could plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides | New structure will need to emerge at a higher elevation closer to road on east side than current structure |
| **6** | 12.05 | 8-10 ft high, impenetrable bottom, fine mesh | Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species | Straighten structure to improve line of sight. Install minor lighting inside. Clear vegetation, especially on east side to allow easier access and line of sight | Directional structure to encourage flight behavior higher than traffic | Best existing structure for deer. Potential project in the future; flagged for future repair |
| **7** | 12.25 | 8-10 ft high, impenetrable bottom, fine mesh | | Clear some vegetation from W side to enhance visibility; remove some | Directional structure to encourage flight behavior higher than traffic; Could also | |

| Id | Post Mile | Fence specifics | Design features | Near-term Recommendation | Aerial connectivity considerations | Notes |
|---|---|---|---|---|---|---|
| | | | | sediment to increase structure height; clean up debris on both sides to enhance habitat at structure; remove invasives (e.g., pepper tree) | plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides | |
| **8** | 12.95 | 8-10 ft high, impenetrable bottom, fine mesh | | Remove invasives near structure. Address erosion and gullying in drainage to structure | Directional structure to encourage flight behavior higher than traffic; Could also plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides | |
| **9** | 13.75 | 6-8 ft high; fine mesh and impenetrable bottom | Rocks and logs on inside and outside of structure for small-scale habitat | | | Only true riparian culvert on SR-67. Culvert in good condition and likely won't need replacement for drainage |
| **10** | 13.9 | 8-10 ft high, impenetrable bottom, fine mesh | | | | Metal pipe in poor shape; Caltrans will likely line |
| **11** | 14.98 | 8-10 ft high, impenetrable bottom, fine mesh | | | | Metal pipe in poor shape; Caltrans will likely line |
| **12** | 16.05 | 6-8 ft high; fine mesh and impenetrable bottom | Restore native vegetation, control erosion/gullying in area | | Topography may not support aerial connectivity here | |
| **13** | 17.61 | ~800 ft on either side of roadway, 8-10 ft high | | | May be some connectivity for flying species if overpass is adequately vegetated | Recreational path on bridge should be physically and visually isolated from remainder of overpass |
| **14** | 20.17 | No good tie in. Any fencing should be fine mesh and have impenetrable bottom to funnel small animals | low cover on outside and inside of structure (rocks, logs) | | Topography may not support aerial connectivity here | Location is a minor draw but topography is generally flat in this area |

**Table B2.** Detailed wildlife crossing recommendations for other roads in the SR-67 regional study area

| Id | Road | Wildlife Priority | Improve-ment Type | Nearest Crossing (mi) | Rd width (ft) | Right-of-way (ft) | Optimal Crossing Type | Minimum Crossing Type | New, Retro, or Exists | Optimal width (ft) | Optimal height (ft) | Min width (ft) | Min height (ft) | In corridor | Conserved | Min fence length E or S (ft) | Min fence length N or W (ft) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **15** | SR-52 | 1 | Minor | 0.371 | 820.2 | 508.5 | Bridge | | Exists | | 13.1 | | 9.8 | Y | Y | | |
| **16** | SR-52 | 2 | Major | 0.371 | 180.4 | 511.8 | Arched or box culvert | Pipe culvert | Exists | 16.4 | 9.8 | 13.1 | 6.6 | Y | Y | 2460.6 | 984.3 |
| **17** | SR-52 | 2 | Minor | 0.865 | 492.1 | 187.0 | Bridge | | Exists | | 13.1 | | 9.8 | N | N | | |
| **18** | I-8 | 3 | Major | 0.487 | 426.5 | 475.7 | Arched or box culvert | | New | 23.0 | 11.5 | 16.4 | 8.2 | N | N | 1148.3 | 721.8 |
| **19** | I-8 | 3 | Major | 0.487 | 574.1 | 393.7 | Arched or box culvert | | New | 23.0 | 11.5 | 16.4 | 8.2 | N | N | 2624.7 | 1443.6 |
| **20** | I-8 | 2 | Major | 1.443 | 246.1 | 262.5 | Bridge | | Retrofit | | 13.1 | | 9.8 | Y | N | | |
| **21** | I-8 | 1 | Major | 2.786 | 426.5 | 656.2 | Bridge | Arched culvert | Retrofit or new addition | 23.0 | 11.5 | 16.4 | 8.2 | Y | N | | |
| **22** | Wildcat Canyon | 3 | Major | 1.209 | 65.6 | 62.3 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 6.6 | | Y | Y | 1410.8 | 754.6 |
| **23** | Wildcat Canyon | 3 | Major | 0.176 | 65.6 | 62.3 | Arched or box culvert | Pipe culvert | Retrofit | 13.1 | 9.8 | 6.6 | | Y | N | 820.2 | 246.1 |
| **24** | Wildcat Canyon | 2 | Major | 0.176 | 72.2 | 52.5 | Arched or box culvert | Pipe culvert | New | 13.1 | 9.8 | 6.6 | | Y | N | 1017.1 | 754.6 |
| **25** | Wildcat Canyon | 2 | Minor | 0.426 | 78.7 | 59.1 | Box culvert/tunnel | | Exists | 16.4 | 13.1 | 13.1 | 9.8 | Y | Y | | |
| **26** | Wildcat Canyon | 2 | Major | 0.426 | 39.4 | 65.6 | Arched or box culvert | Pipe culvert | New | 13.1 | 9.8 | 6.6 | | Y | Y | 1066.3 | 984.3 |
| **27** | Wildcat Canyon | 1 | Minor | 0.265 | 44.3 | 147.6 | Bridge | | Exists | | 13.1 | | 9.8 | Y | N | | |
| **28** | San Vicente Rd | 2 | Minor | 0.265 | 59.1 | 105.0 | Multiple arched culvert | | Exists | 16.4 | 9.8 | 13.1 | 6.6 | Y | N | 1378.0 | 1640.4 |
| **29** | Poway Rd | 3 | Major | 1.293 | 105.0 | 105.0 | Arched or box culvert | Pipe culvert | New | 13.1 | 6.6 | 6.6 | | Y | N | 459.3 | 1082.7 |
| **30** | Poway Rd | 3 | Minor | 1.090 | 39.4 | 131.2 | Pipe culvert | | Retrofit | 6.6 | | 3.3 | | Y | N | | |

| Id | Road | Wildlife Priority | Improve-ment Type | Nearest Crossing (mi) | Rd width (ft) | Right-of-way (ft) | Optimal Crossing Type | Minimum Crossing Type | New, Retro, or Exists | Optimal width (ft) | Optimal height (ft) | Min width (ft) | Min height (ft) | In corridor | Conserved | Min fence length E or S (ft) | Min fence length N or W (ft) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **31** | Scripps Poway Pkwy | 2 | Major | 1.293 | 121.4 | 108.3 | Arched or box culvert | Pipe culvert | New and retrofit | 13.1 | 6.6 | 6.6 | | Y | Y | 918.6 | 820.2 |
| **33** | Scripps Poway Pkwy | 2 | Major | 1.292 | 105.0 | 124.7 | Arched or box culvert | Pipe culvert | New | 16.4 | 9.8 | 13.1 | 8.2 | Y | N | 1574.8 | 1066.3 |
| **35** | Scripps Poway Pkwy | 1 | Minor | 0.788 | 105.0 | 534.8 | Box culvert/tunnel | | Exists | 16.4 | 13.1 | 13.1 | 9.8 | Y | Y | | |

| Id | Fence specifics | Design features | Near-term Recommendation | Aerial connectivity considerations | Notes |
|---|---|---|---|---|---|
| **15** | | | | May be some connectivity for flying species under bridge | Check height and condition; May need invasive control or some native habitat restoration |
| **16** | 8-10 ft high, impenetrable bottom, fine mesh | Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species; provide adequate native cover leading to either end of culvert | | May be some connectivity for flying species | Major improvement needed because culvert outlets on south side and only extends north to median; must be extended full length of road to allow for wildlife crossings |
| **17** | | | Clear some vegetation to ensure clear path and line of sight. Remove invasives | May be some connectivity for flying species under bridge | Must cross both 52 and West Hills Parkway. Check height and condition under both |
| **18** | 8-10 ft high, impenetrable bottom, fine mesh | Some vegetation restoration (as compatible with transmission line zone) | | Ensure transmission lines have visual markers and low electrocution potential | At transmission line right-of-way |
| **19** | 8-10 ft high, impenetrable bottom, fine mesh | Light tubes at intervals through median sections or install lighting in structure | | Topography may not support aerial connectivity here | N side elevated above S side. May require deeper structure and site prep on N side or different structure type or angle |
| **20** | Increase fence height to 8-10 m. Current placement OK. | | | May be some connectivity for flying species under bridge | Crossing should be moved E to Flinn Springs bridge on Old Highway 80. Bridge length should be expanded and aprons moved back to allow for vegetated strip under bridge for wildlife movement parallel to traffic on either side. Good vegetative cover already |
| **21** | 8-10 ft high, impenetrable bottom, fine mesh | | | May be some connectivity for flying species under bridge | Improve intersection of Peutz Valley Rd and Alpine Boulevard. Need N-S connection of canyon. On Peutz Valley Rd, native vegetation and slope parallel to road should be improved to allow for wildlife movement |
| **22** | 8-10 ft high, impenetrable bottom, | low cover on outside and inside of structure (rocks, logs) | | Topography and vegetation should support this naturally. May need directional structure to encourage | |

| Id | Fence specifics | Design features | Near-term Recommendation | Aerial connectivity considerations | Notes |
|---|---|---|---|---|---|
| | fine mesh | | | flight behavior higher than traffic. | |
| **23** | 8-10 ft high, impenetrable bottom, fine mesh | | Remove invasives | Directional structure to encourage flight behavior higher than traffic - topography and natural veg support aerial crossings here. | Perhaps a single structure just N of driveway for 12050 Wildcat Cyn Rd. |
| **24** | 8-10 ft high, impenetrable bottom, fine mesh | | | | Suggested placement - just north of Muth Valley Road |
| **25** | | Potentially add internal structure elements (rocks, logs) to facilitate movement by smaller species. Consider creating a wildlife-only section of the crossing shielded from the human use area | Control erosion in surrounding area to enhance cover in vicinity of tunnel | May be some connectivity for flying species through tunnel | |
| **26** | 8-10 ft high, impenetrable bottom, fine mesh | Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species | | Directional structure to encourage flight behavior higher than traffic - topography and natural veg support aerial crossings here. | Suggested placement - just south of Cienga Road |
| **27** | | | | May be some connectivity for flying species under bridge | Check height and condition; May need vegetation clearing to allow line of sight for crossings of species like deer |
| **28** | Need extended fencing, 8-10 ft high; fine mesh with impenetrable bottom | | Ensure revegetation with some lower cover and native shrubs is part of restoration of site after widening of San Vicente Road | Topography may not support aerial connectivity here | Double arched culvert under San Vicente Road? Current dimensions may not be suitable for deer crossings |
| **29** | 8-10 ft high, impenetrable bottom, | | Install seasonal signage and flashing lights to increase awareness about this area as a | | Area is a narrow pinchpoint but crossing is important for connecting open spaces to allow for movement into and out of Penasquitos Creek and |

| Id | Fence specifics | Design features | Near-term Recommendation | Aerial connectivity considerations | Notes |
|---|---|---|---|---|---|
| | fine mesh | | wildlife-vehicle collision hot spot and slow traffic during fall evening rush hour | | under I-15. |
| **30** | | | Ensure existing culverts in this stretch are cleared of debris and have adequate energy dissipators to avoid gullying and erosion | Topography will challenge aerial connectivity here | Difficult structure placement due to elevated S side of the road and canyon on N side of the road |
| **31** | 8-10 ft high, impenetrable bottom, fine mesh | Need to restore native vegetation; need dry crossing in structure that runs NW-SE to cross both Pomerado and Scripps Poway Pkwy | Clear sediment and debris in existing crossing. Create dry crossing in existing culvert, restore native vegetation, and rocks, logs, and low veg near entrance and inside structure to provide low cover for small species | | Area is a narrow pinchpoint but crossing is important for connecting open spaces to allow for movement to/from Sycamore Cyn, Beeler Cyn, and Penasquitos Cyn. Need to cross both Scripps Poway Pkwy and Pomerado here |
| **33** | 6-8 ft high; fine mesh and impenetrable bottom | Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species | | | Target crossing for east side of Sycamore Canyon Road |
| **35** | Possible need to extend fencing or increase fence height. Perhaps add wing top to fence to prevent climbing | Potentially add internal structure elements (rocks, logs) to facilitate movement by smaller species. Consider creating a wildlife-only section of the crossing shielded from the human use area | | May be some connectivity for flying species through tunnel | Scripps Poway Parkway Wildlife Tunnel |

**Effects of Wildfire on Wildlife and Connectivity**

*Prepared by: Megan K. Jennings, Ph.D.*

January 23, 2018

## Introduction

In southern California, where human impacts from development are limiting habitat connectivity for wide-ranging vertebrate species, fire is a disturbance regime that may also fragment habitats, further impacting those species. Although fire is a natural process in the southwestern U.S., increasing human development near open spaces has led to unnatural fire regimes with increased fire starts and an increased potential for vegetation-type conversion as a result. In the biodiversity hotspot of southern California, many studies have focused on the effects of urbanization and landscape fragmentation on wildlife. However, there has been relatively little attention to how human-mediated landscape fragmentation may influence natural disturbance processes, like wildfire, and how these synergistic disturbances impact wildlife populations.

Both fire frequency and size are increasing in southern California and are correlated with increasing anthropogenic development and human population growth in the region (Syphard et al. 2007, 2009). These studies suggest that at high human population densities, fire is eliminated from the ecosystem when contiguous vegetation necessary to carry fire is broken up by asphalt, concrete, and buildings. However, at intermediate human densities, housing developments and roadways are a source of increased fire ignitions which then spread into wildlands (Syphard et al. 2007, 2009). Both scenarios (too little fire, too frequent fire) present potential threats for species and community dynamics in southern California as shifts in the natural fire regime, coupled with increasing habitat fragmentation, have the potential to impact wildlife populations, communities, and entire ecosystems. In the highly urbanized landscape of southern California, long-term impacts such as habitat fragmentation and loss and shifts in disturbance regimes like the natural fire cycles, have resulted in persistent landscape changes (Syphard et al. 2009).

This report focuses on the impacts to wildlife connectivity posed by the proposed Newland Sierra project in the context of wildfires and the need for corridor redundancy. The Newland Sierra project proposes to build more than 2,100 homes on the I-15 corridor in the unincorporated portion of San Diego County between Escondido and Temecula. The project would be located in the area proposed for the North County Multiple Species Conservation Program (NCMSCP) on a site that has been identified as pre-approved mitigation area (PAMA).

As described in my previous reports (Jennings 2017a, 2017b), this project poses risks to wildlife connectivity in the area and could compromise overall design objectives of the NCMSCP. The proposed Newland Sierra project will significantly affect high quality core habitat and wildlife movement for both more common and sensitive and protected species to a degree that is not mitigated by the project design. The proposed project will have long-term direct and indirect impacts on wildlife from roadways, increased human activity, edge effects, human activity, and increasing fire frequency on wildlife movement. Due to the risks of wildfire and the numerous cumulative projects proposed along the I-15 corridor in northern San Diego County and southern Riverside County, it is particularly important to account for corridor redundancy in considering the Newland Sierra project. Regional connectivity plans must provide corridor redundancy to serve the range of species that may need to move between patches of habitat (Pinto and Keitt

2009, McRae et al. 2012), and to buffer against landscape disturbances, such as wildfires (Mcrae et al. 2008, McRae et al. 2012, Cushman et al. 2013, Olson and Burnett 2013). The biological analysis in the project's draft environmental impact report lacked sufficient consideration of these issues.

**Impacts of Wildfires and Shifting Fire Frequencies on Wildlife**

Disturbances that occur at large spatial scales, such as Santa Ana wind-driven fires in southern California, like the recent Lilac Fire in San Diego County, are most likely to change landscape configuration, or pattern, which can lead to change in resource availability, environmental features, and corresponding responses in the structure of populations and communities, all key metrics to landscape integrity (Sousa 1984, Pickett and White 1985, Fraterrigo and Rusak 2008, Turner 2010). Large-scale landscape changes, particularly fragmentation (Gardner et al. 1993), have been shown to alter biotic interactions, and lead to a loss of connectivity evidenced by a decline in dispersal, reduced survival rates (Riley et al. 2003), and limited gene flow (Riley et al. 2006). In southern California, the two disturbances that overlap and interact, fire and human development, are the predominant drivers of the landscape. In this region, empirical evidence suggests a shift is underway in the disturbance regime (Keeley and Fotheringham 2003, Safford and Van de Water 2014).

Shifts in fire regime typically involve changes to fire intensity, size, frequency, type, seasonality, and severity (Flannigan et al. 2000). Fire-return intervals, the average time between two fire events, in the shrubland habitats like the areas where the Lilac Fire occurred and the Newland-Sierra development is proposed were historically 30 to 100 years. In similar areas of the County, fires are 33% more frequent now than pre-settlement, due in large part to increased development and roadways (Figure 1; Keeley et al. 1999, Safford and Van de Water 2014). This shifting disturbance regime with shortened intervals between fires interrupts the successional cycle, reduces plant diversity, and results in vegetation and habitat type change to non-native and grass dominated landscapes (Keeley 2005), reducing habitat suitability and connectivity for species dependent on intact shrubland landscape. Shifting weather patterns resulting from climate change may also contribute to the alteration of fire regimes in southern California. Climate models predict that temperatures will increase and humidity will decrease (Miller and Schlegel 2006). Under these conditions, Santa Ana winds, the hot, dry winds from the deserts in the east, may occur more often and later in the season when fuels loads are highest (Miller and Schlegel 2006, Guzman-Morales et al. 2016). The concurrent disturbances of expanding human development and a shifting climate may alter how fire structures the landscape. Extensive development, particularly in exurban areas, results in increases in human-caused ignitions and fires of large spatial extents (Syphard and Keeley 2015), as well as an overall increase in fire threat (Figure 2), which can have long-lasting impacts on the landscape and wildlife habitat.

Many wildlife species that occur in the Mediterranean-type ecosystems of southern California have adapted to wildfires. Wildlife exhibit differential responses to wildfires depending on the availability of refugia and species' mobility, which determine their susceptibility to impacts from the direct effects of the fire. Habitat and diet breadth, population size and growth rates, as well as landscape connectivity can affect post-fire colonization and overall resilience to these types of stochastic events. While some research efforts in southern California have taken advantage of the

natural experiment presented by San Diego's 2003 and 2007 wildfires to gather information about bird (Mendelsohn et al. 2008), small mammal (Brehme et al. 2011, Diffendorfer et al. 2012), large mammal (Schuette et al. 2014), and herpetofauna (Rochester et al. 2010) responses to wildfire, there is much to learn about individual- and population-level responses, in particular as it relates to increasing fire frequency. Linking the effects of shifting fire regimes on wildlife where frequent fire may result in vegetation type conversion from shrublands to grass-dominated habitats (Keeley 2005, Keeley and Brennan 2012) is a significant challenge. There is evidence of the effect of increasing fire frequency on some species, such as the iconic coastal sage scrub species, the threatened California gnatcatcher (*Polioptila californica californica*). Already challenged by habitat loss and fragmentation in the coastal regions of southern California, frequent fires have degraded habitat for the gnatcatcher (Winchell and Doherty 2014) as California sagebrush (*Artemesia californica*), laurel sumac (*Malosma laurina*), and white sage (*Salvia apiana*), key habitat elements for the bird, have been replaced by non-native annual grasses in areas that have experienced repeated fires. Habitat specialists and small species are not the only ones subject to the impacts of increasing fire frequency. Despite the fact that mountain lions (*Puma concolor*) are highly mobile and able to move away from fires, the species is potentially at risk from vegetation-type conversion to non-native annual grasslands (Jennings et al. 2016). Although this species may tolerate grasslands when moving between habitats (Zeller et al. 2014), habitat fragmentation between San Diego County and the Santa Ana Mountains to the north has limited gene flow and resulted in inbreeding for the southern California population (Ernest et al. 2014), a situation which further habitat degradation, particularly as a result of increasing fire frequency, could worsen.

**Wildfire and Connectivity**

Habitat connectivity is essential to climate-smart landscape strategies (Heller and Zavaleta 2009) and strengthens ecosystem resilience to additional stressors such as habitat fragmentation (Beier and Gregory 2012), and other disturbances, e.g., fire and disease (Noss 1991, Hilty et al. 2006). Across much of southern California, the state's Natural Community Conservation Planning (NCCP) program and the federal Habitat Conservation Plan (HCP) have been used to establish conservation networks to protect natural communities and prevent further habitat fragmentation (Ogden Environmental and Energy Services 1996, Riverside County 2003). Although the direct effects of anthropogenic landscape alteration, namely habitat loss and fragmentation, are paramount in this region (Soulé 1991, Crooks 2002, Beier et al. 2006), the indirect effects of intense human development such as changing patterns of natural disturbance regimes, *e.g.* wildfire, may present an equally large risk to landscape integrity. As human populations in southern California have grown dramatically over the last century, particularly in coastal areas, short fire-return intervals paired with habitat fragmentation, may have synergistic and long-term impacts on landscape connectivity that present a formidable conservation challenge. Given that these disturbances exert measurable impacts individually (Lindenmayer et al. 2008, Turner 2010), it is likely that the synergistic effects of shifting disturbance regimes and fragmentation present a serious threat to landscape connectivity (Turner 2010).

Given the importance of landscape connectivity to ensuring population viability and persistence, accurate assessments of physical and functional connectivity are critical. Dynamic landscape processes, like wildfires, may impede movement for many species in the short-term, but an altered fire regime may permanently alter landscape linkages. In particular, shifting disturbance

regimes, like the increase in fire frequency and size reported in southern California, may have synergistic impacts that erode landscape connectivity if efforts are not made to buffer the number or impacts of fire on landscape linkages. New approaches to identifying factors that impair physical and functional connectivity are needed to develop mitigation strategies to maintain landscape connectivity if urbanization is considered on fire-frequent landscapes, with a particular focus on the coastal areas that are most impacted by development, and foothills and valleys where the wildland-urban interface is most at risk for increases in fire frequencies and consequential type conversion.

Building resilience into these networks of conserved lands can be approached from two perspectives: 1) reducing ignitions in fire-prone areas, and 2) account for these altered disturbance dynamics in conservation planning efforts like the Draft NCMSCP. Robust measures to reduce ignitions should be employed. However, reducing ignitions alone is unlikely to protect San Diego County's open spaces from fire and must be paired with complementary approaches to provide for habitat and connectivity when fires do occur. This includes planning for redundancy in linkages connecting habitat patches (Pinto and Keitt 2009). Because a single path is unlikely to equally serve all individuals of a species, let alone all potential species that may need to move between patches of habitat, multiple corridors between landscape blocks are often necessary (Pinto and Keitt 2009, McRae et al. 2012). Furthermore, this redundancy can also buffer against uncertainty and dynamic processes, particularly disturbances, on the landscape (Mcrae et al. 2008, McRae et al. 2012, Cushman et al. 2013, Olson and Burnett 2013). As discussed in my previous comments on the Newland Sierra draft environmental impact report, the project's biological analysis is deficient in its consideration of corridor redundancy. Threats to wildlife connectivity from wildfire emphasize the need to consider corridor redundancy with respect to Newland Sierra and the NCMSCP.

Furthermore, the assessment of connectivity and redundancy to provide for wildlife movement under a variety of conditions must be conducted at a regional scale. For San Diego County, this means consideration of conservation planning efforts and acquisitions as well as development projects in Orange and Riverside Counties. In particular, the Santa Ana-Palomar landscape linkage that has been identified as a critical movement corridor for many species (South Coast Wildlands 2008), most notably the mountain lion (Vickers et al. 2015), spans both San Diego and Riverside Counties and could be affected by several development projects that could limit functional connectivity in northern San Diego County.

Together with the cumulative projects proposed in this region, Newland Sierra could restrict wildlife movement in northern San Diego County as well as any opportunities to build resilience into a regional connectivity plan by providing for corridor redundancy. The Merriam Mountains area is currently one of the few shrub-dominated open spaces in San Diego County that has not experienced overly frequent wildfires which lead to increased risk of vegetation-type conversion from shrublands to non-native annual grasslands (Figure 1). Preserving a relatively intact landscape, such as the Merriam Mountains, is critical to developing a functional preserve system for the NCMSCP. However, the proposed Newland-Sierra Project's new roadways, increased traffic, homes, and increased wildland-urban edge are all known sources of fire ignitions in southern California (Syphard and Keeley 2015) that will threaten to increase the fire frequency in this area, which is already at high risk of fire due to the site's vegetation and terrain features

(Figure 2), as well as the risk of vegetation-type conversion. These same project elements will also further restrict wildlife movement in an area where movement is already constrained. The synergistic effects of restricted movement and habitat degradation caused by increasing fire frequency could greatly reduce connectivity in this region and threaten the functionality of the proposed preserve network under the NCMSCP. Figure 1 illustrates that few linkages remain in San Diego County that are not challenged by crossing urban development or areas that have burned repeatedly and are at risk for weed incursion, habitat degradation, and vegetation-type conversion. When dynamic landscape processes are considered, effective planning for landscape connectivity will require consideration of all potential projects that may affect wildlife movement as well as the synergistic disturbances that also affect landscape connectivity. The NCMSCP provides an opportunity for this type of regional wildlife connectivity planning, but individual development proposals considered in isolation and without adequately accounting for regional corridor redundancy could threaten the overall effectiveness of the planning process.

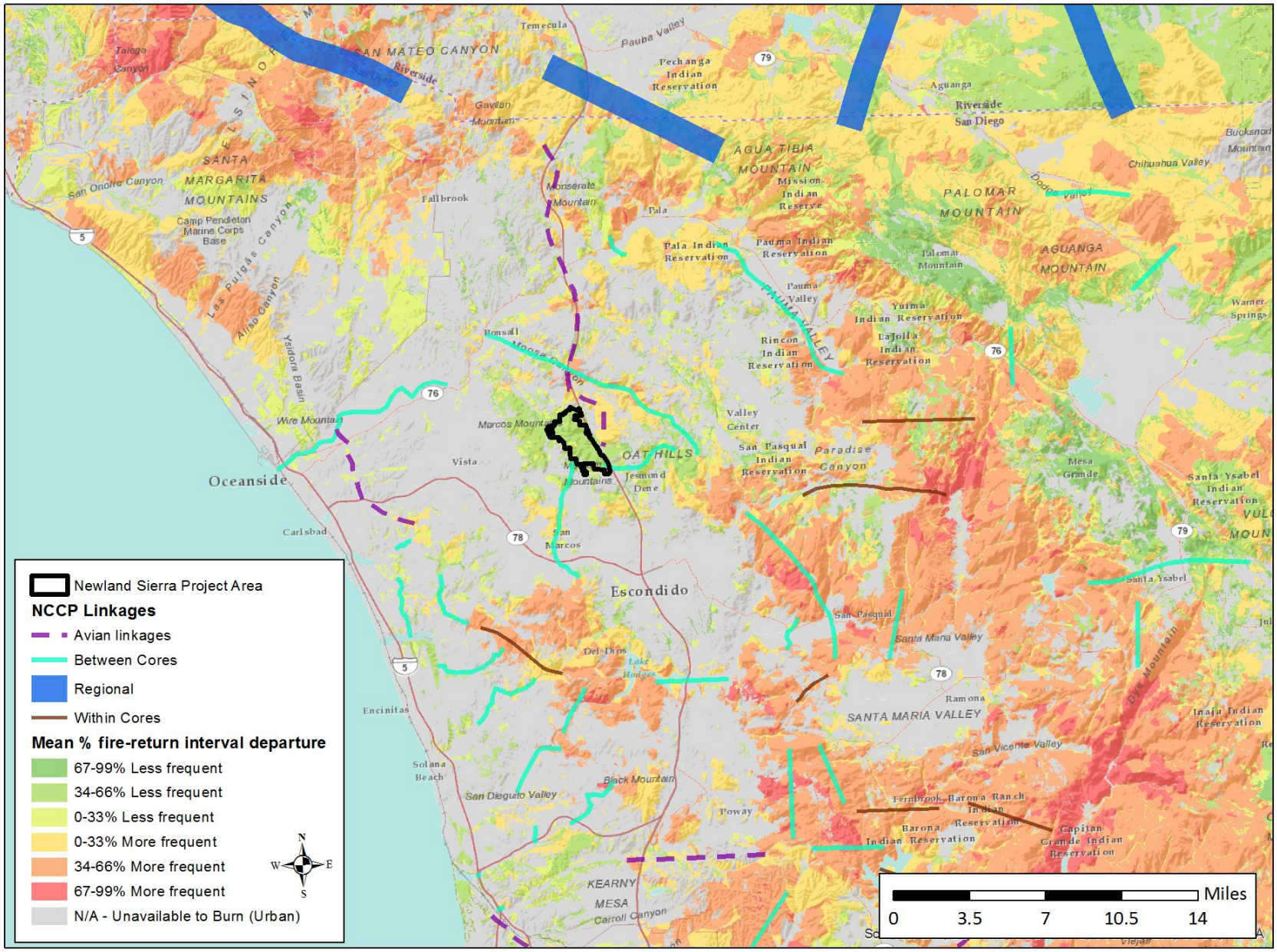



**Figure 1.** Map of fire-return interval departure (Safford and Van de Water 2014) for northern San Diego County and linkages identified in the Management Strategic Plan Connectivity documents for San Diego's NCCP areas.

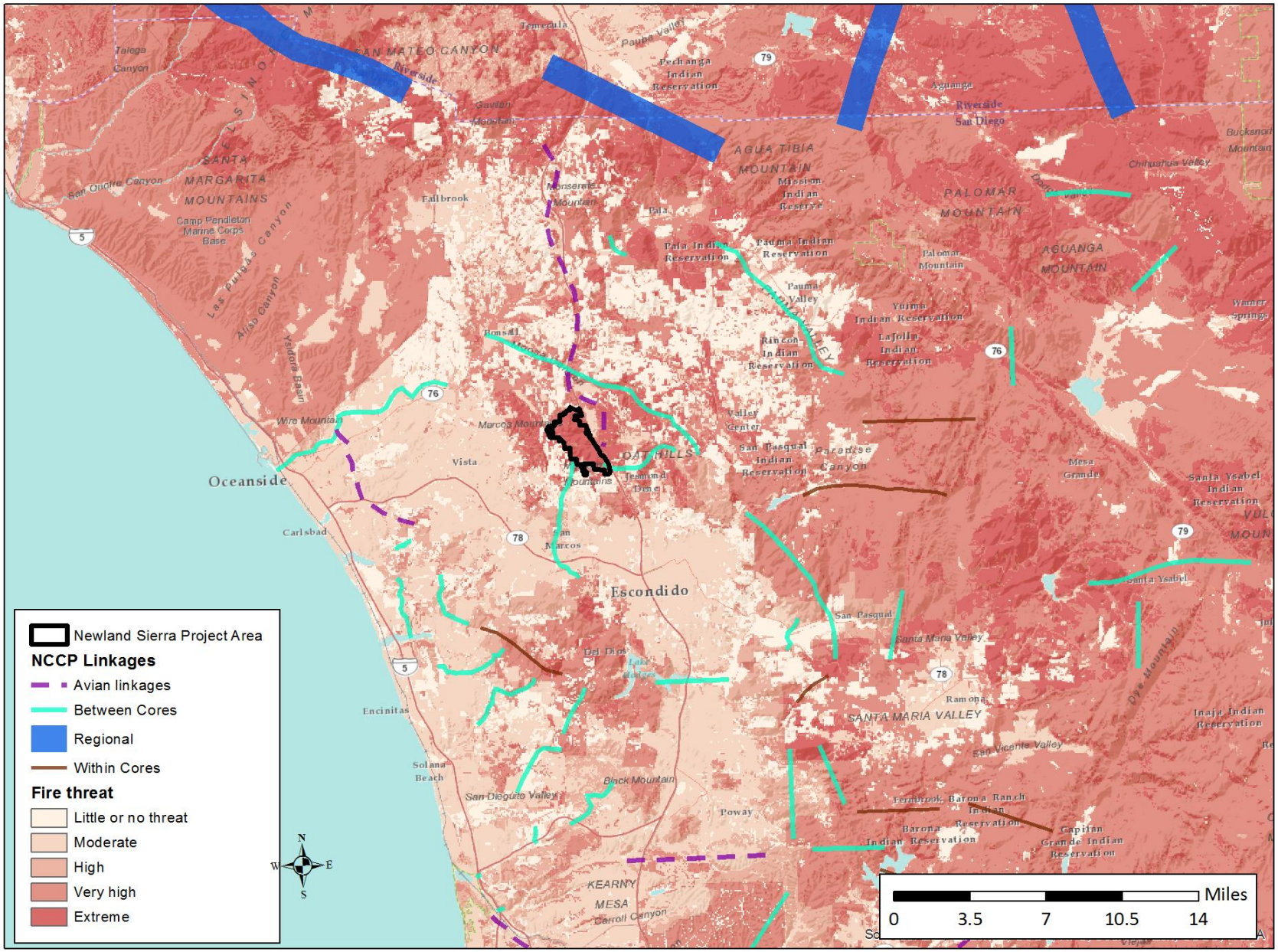



**Figure 2.** Map of fire threat for northern San Diego County as classified by California's Fire and Resource Assessment Program and linkages identified in the Management Strategic Plan Connectivity documents for San Diego's NCCP areas.

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# Spatial risk assessment of eastern monarch butterfly road mortality during autumn migration within the southern corridor

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ABSTRACT

Road mortality may contribute to the population decline of eastern monarch butterflies (*Danaus plexippus* L.). We estimated autumn monarch roadkill rates within the primary Oklahoma to Mexico southern migration corridor (i.e., Central Funnel). Dead monarchs were surveyed along Texas roadsides during four weeks of autumn migration in 2016 and 2017. Roadkill averaged 3.4 monarchs per 100 m transect, reaching 66 per 100 m in a roadkill hotspot in southwestern Texas. Extrapolations of Central Funnel roadkill based on survey data and road types were 3.6 and 1.1 million in 2016 and 2017, respectively. Spatial distribution of roadkill across the Central Funnel was projected from Texas survey data using 30 m resolution MaxEnt niche models. Highest roadkill probability was linked to arid climate and low human population density. The latter variables may not be directly related to roadkill, but instead represent indirect correlates of increased densities of monarchs where the migration corridor narrows southwards. The higher roadkill projected in southwest Texas and Mexico by MaxEnt models agrees with previously reported monarch roadkill hotspots. MaxEnt-based 2016–2017 projections for annual roadkill rates throughout the Central Funnel averaged 2.1 million. This figure is similar to the result by simple extrapolation, and represents about 3% of the overwintering monarch population for these years. Mitigation at roadkill hotspots in the Central Funnel could reduce monarch roadkill mortality during migration and contribute towards conservation efforts for the monarch butterfly.

## 1. Introduction

Wildlife-vehicle collision is the most widely acknowledged impact of roads on wildlife, and can contribute to the decline of species of conservation concern (Tok et al., 2011; Visintin et al., 2016; Bennett, 2017), including globally declining pollinator insect species (Baxter-Gilbert et al., 2015). Roadkill can result in high mortality and lower abundance for species with large area requirements, pronounced migratory movements, small population sizes, and slow reproduction rates (Seiler and Helldin, 2006; Fahrig and Rytwinski, 2009). Wildlife-vehicle collisions are often spatially and temporally aggregated and substantial annual and inter-annual variation has been associated with environmental factors and traffic volume (Seiler and Helldin, 2006; Shilling and Waetjen, 2015). This tendency for high spatio-temporal variability in roadkill can be difficult to interpret based solely on the mapping of field survey data. Accordingly, there is a trend to use predictive spatial models to account for the variability in investigating the impacts of roads on wildlife mortality (Bennett, 2017). Typical roadkill niche models use a combination of environmental and anthropogenic variables and are often restricted to small areas (Visintin et al., 2016). Species distribution modeling has previously been used to project roadkill risk of mammals (Grilo et al., 2009; Roger and Ramp, 2009; Visintin et al., 2016, 2017) and owls (Gomes et al., 2009). Spatial models for insect roadkill have not yet been developed.

Only five out of 215 roadkill studies (2%) between 2011 and 2015 were specifically focused on invertebrates (Bennett, 2017). Despite this taxonomic bias in the literature, roadkill may be a substantial threat to certain insect populations. Baxter-Gilbert et al. (2015) projected that hundreds of billions of pollinating insects are lost annually to roadkill across North America. Although relatively few studies exist on butterfly road mortality, researchers have suggested that butterflies are one of the most common insect orders killed by vehicles (McKenna et al., 2001; Rao and Girish, 2007). Despite the high numbers of road-killed butterflies, the risk of Lepidopteran roadkill has been estimated as low to moderate (Baxter-Gilbert et al., 2015; Muñoz et al., 2015). Several studies have estimated butterfly roadkill numbers and examined

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contributing factors (Munguira and Thomas, 1992; McKenna et al., 2001; Ries et al., 2001; Rao and Girish, 2007; Skórka et al., 2013), but most of these studies concentrate on local, relatively sedentary butterfly populations and their utilization of roadside habitats rather than migratory butterflies. Migratory danaine butterflies (Nymphalidae: Danainae) may be especially susceptible to roadkill during migration (Her, 2008; Taiwan Environmental Protection Administration [EPA], 2010; Santhosh and Basavarajappa, 2014), including the monarch butterfly (*Danaus plexippus* L.) in the United States (McKenna et al., 2001) and Mexico (Correo Real, 2015).

Significant population decline of the eastern migratory monarch butterfly has been observed at the overwintering sites in Central Mexico during the past two decades (Vidal and Rendón-Salinas, 2014; Thogmartin et al., 2017). Consequently, the persistence of the migratory phenomenon of the eastern population may be endangered (Brower et al., 2012). The long-distance migration of monarchs is unique among butterflies. Mortality during the autumn migration (often referred to as fall migration) has been suggested as a contributing factor to the decline (Badgett and Davis, 2015; Ries et al., 2015a; Inamine et al., 2016; Agrawal and Inamine, 2018). Road mortality may significantly affect monarch survival during migration, especially where monarchs become highly concentrated as the migration narrows in Texas and northern Mexico (Badgett and Davis, 2015). Only McKenna et al. (2001) have previously evaluated monarch butterfly roadkill. They reported monarchs as the second-most killed butterfly species during six weeks of autumn in Illinois. They estimated that > 500,000 monarchs were killed statewide along interstate highways during one week in early September 1999 (McKenna et al., 2001). There are several unpublished citizen-science reports of locally high monarch roadkill occurrence in West Texas and northern Mexico during the autumn migration, with observed roadkill reaching 5.7 monarchs per meter near Monterrey, Mexico (Correo Real, 2015; Journey North, 2017). Incidences of high monarch road mortality in northern Mexico have led to the placement of road signs along portions of highways in to reduce speed in the presence of monarchs (Vangaurdia, 2016).

Monarch roadkill has yet to be quantified in relation to an overall population estimate. Seiler and Helldin (2006) point out that any sustained mortality factor, such as roadkill, can be especially damaging for species that are either approaching or are in an annual population decline, such as the monarch. The extent of monarch roadkill needs to be assessed to estimate its potential contribution to the population decline and support conservation planning. Our goal was to develop MaxEnt niche models for monarch road mortality during the autumn migration within the main migration pathway in Texas. The MaxEnt algorithm has been employed before to spatially investigate vehicle-animal collisions of birds and mammals (Ha and Shilling, 2017). The roadkill models were also projected throughout the Central Funnel, which is the identified main southern autumn migratory pathway within the Central Flyway for monarchs from Oklahoma to Mexico (Tracy, 2018; Tracy et al., 2018a). This study includes the first analysis of monarch roadkill data outside of Illinois, and the first development of a spatial roadkill model for an insect. Our specific objectives were to (1) conduct monarch roadkill field surveys within the Central Funnel in Texas, (2) develop MaxEnt niche models for roadkill within the Texas survey area, and project these models throughout the Central Funnel, (3) estimate monarch roadkill numbers within the survey area and the Central Funnel using both simple field survey-based and model-based extrapolation techniques, and (4) discuss the results in the context of monarch conservation and potential applications to other species of conservation concern.

## 2. Methods

### 2.1. Study species

The monarch autumn migration is uniquely accomplished by one generation. Adults begin migrating in late August to September from the summer breeding grounds, traveling to overwintering grounds in Central Mexico (Brower, 1995; Calvert and Wagner, 1999). Most migrants usually reach Oklahoma and North Texas in late September or early October (Calvert and Wagner, 1999; Monarch Watch, 2018a) and arrive at the overwintering grounds in November (Brower et al., 2006). There are two main migration routes, the Central Flyway and the Eastern or Coastal Flyway (Calvert and Wagner, 1999; Howard and Davis, 2009). The Central Flyway through the Great Plains is the most heavily traveled route (Howard and Davis, 2009), which narrows into the Central Funnel from Oklahoma southwards (Tracy, 2018; Tracy et al., 2018a).

Autumn migrants fly during the day and stop at night and during inclement weather to nectar and roost in trees and shrubs (Brower, 1996). These roosts may comprise a few individuals to several thousand individuals and may last one to several days (Davis and Garland, 2004; Howard and Davis, 2009). In the morning, roosting monarchs either resume migration or search for nectar. These behaviors are influenced by wind patterns or lipid levels (Brower, 1996; Davis and Garland, 2004). During unfavorable southerly winds, monarchs may roost for several days (Schmidt-Koenig, 1985). Migrating monarchs are observed to nectar in a variety of locations, including in right-of-ways (Brower et al., 2006), where they may be vulnerable to vehicle collisions. Brower et al. (2006) suggested that monarchs shift their behavior upon reaching Texas and spend more time nectaring to accumulate lipids for the winter and re-migration in the spring. Migrating monarchs regularly fly at high altitudes, around 300–500 m (Gibo and Pallett, 1979; Gibo, 1981, 1986), but may fly close to the ground, especially when facing headwinds or during overcast weather (Gibo, 1986; Brower, 1996), exposing them to road mortality. Citizen science observations also include reports of low flying fall migrating monarchs over roadways (Correo Real, 2015).

### 2.2. Monarch roadkill surveys and simple roadkill extrapolation

Monarch roadkill field surveys were conducted during the main autumn migration through the Central Funnel in Texas (Fig. 1). Four four-day surveys were conducted in each of the autumns of 2016 and 2017, between 10th October to 4th November and 3–27 October, respectively. The survey area was divided into four north to south sections, with surveys timed to generally occur after the dates of average peak migration (Journey North, 2017; Monarch Watch, 2018a) to allow time for the accumulation of road-killed monarchs. Observed monarch roadkill densities most likely represent accumulations of dead migrating monarchs over a period of one or two days to a few weeks during the main migration pulse through an area (Munguira and Thomas, 1992). Surveyed road types included (1) highways, (2) primary roads, and (3) secondary roads. Each survey location comprised at least a single 100 m by 1 m transect along the grassy edge of one side of the roadway. To assess if the side of the road surveyed influenced the number of dead monarchs, additional transects were surveyed across multiple edges of single and divided-lane highways at some sites. Transects were located using a handheld GPS device (accuracy up to ± 3 m). Roadkill transects were spaced according to travel and survey time constraints at about 30 to 100 km intervals along the primarily east to west pre-planned survey routes, with additional surveys in 2016 in the southwestern portion of the study area where high monarch roadkill was found (Fig. 1).

All dead monarchs or parts of monarchs were collected to estimate the total number and sex ratio of dead monarchs along transects. A similar spring monarch roadkill survey was conducted in Texas during April to May of 2017 (Fig. A.1; for details, see Appendix A, section 1.1). The boundary of the background evaluation extent for our roadkill study was defined by a 10 km buffer around a convex hull polygon formed using un-thinned 2016 to 2017 monarch roadkill survey data (Fig. 1). We extrapolated the mean roadkill counts for the three road

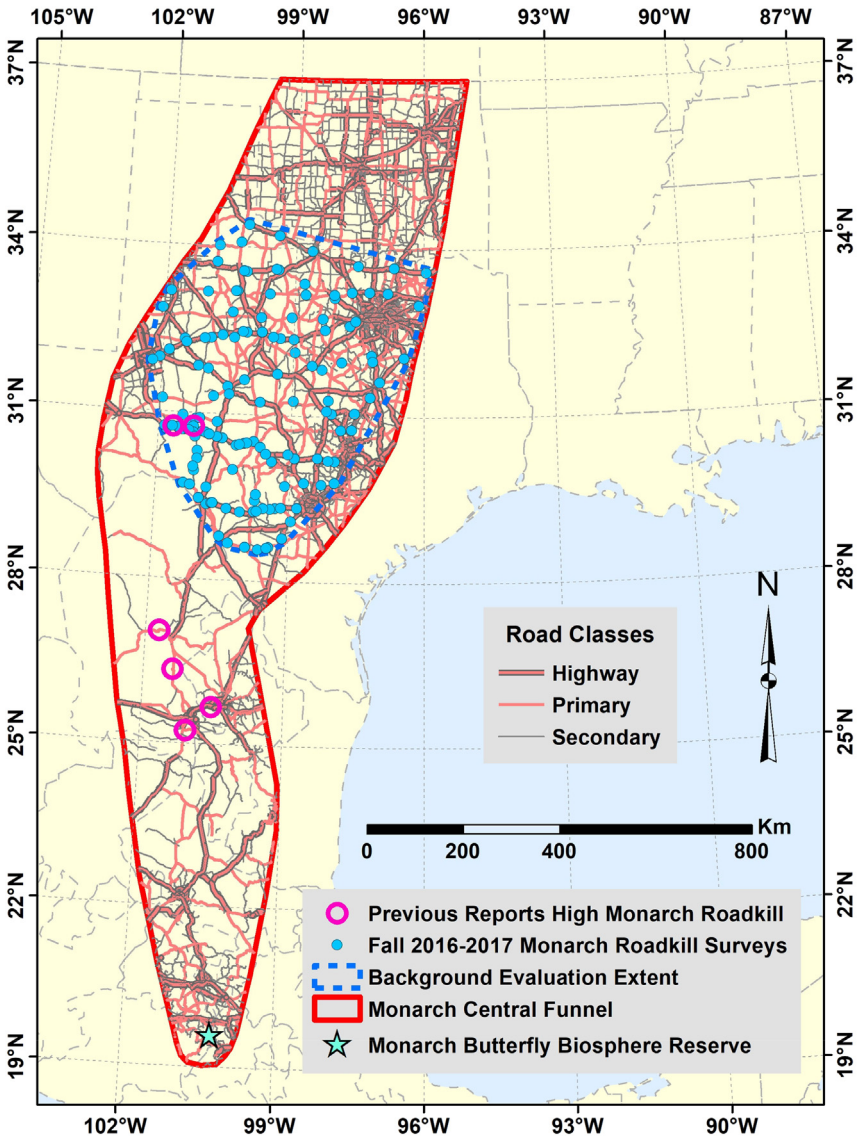


**Fig. 1.** Monarch roadkill survey 100 m transects for autumn 2016 and 2017 along three major road classes within the monarch Central Funnel in Texas.

types over the background evaluation extent and Central Funnel in a manner similar to that of McKenna et al. (2001). Roadkill rates in areas of locally high monarch roadkill (hotspots) can vary greatly between years and highly differ from other areas. Consequently, roadkill rates in hotspots can bias roadkill rates in larger areas if they are disproportionally represented in the sampling. Therefore, in some extrapolations, hotspot roadkill rates were considered separately for each year from non-hotspot locations. This separation allowed us to understand the importance of the roadkill hotspots within a year, and compare the hotspot differences between years. We also made roadkill extrapolations including hotspot roadkill rates with non-hotspot data and thinning the hotspot data in 2016 to be in proportion to the sample effort in non-hotpot locations (for details, see Appendix A, section 2.1).

### 2.3. Environmental variables

Thirty environmental variables were initially screened for use in the roadkill modeling (Table A.1, Fig. A.2). These variables were selected for their value in previous roadkill niche models and for their use in characterizing the environment of the study area. The variables consisted of nine topographic indices (including four stream indices), eight land cover indices, six road indices, three human population indices, and four climatic indices. All indices were either calculated at 30.8 m spatial resolution or resampled with bilinear interpolation to the 30.8 m resolution, to match the resolution of the base layer of 1 arc sec Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) data obtained from USGS Earth Explorer (https://earthexplorer.usgs.gov/). The high spatial resolution of 30.8 m facilitated modeling of roadkill along individual surveyed roadways over a broad area (see more details in Appendix A, section 7).

### 2.4. Monarch roadkill models

Preliminary MaxEnt model runs indicated that there was not enough data from 2017 to obtain good accuracy statistics for both single year models. Consequently, we combined 2016 and 2017 roadkill presence data, which were randomly spatially thinned to 2 km to reduce spatial autocorrelation. Ten thousand background points were randomly generated within the road mask evaluation area. We calculated background/presence versions of the area under the curve statistic ($AUC_{bgp}$) and true skill statistic ($TSS_{bgp}$) using R software (R Core Team, 2018) and the PresenceAbsence package (Freeman and Moisen, 2008). In the same manner, we calculated a presence/absence version of AUC ($AUC_{pa}$) and TSS ($TSS_{pa}$) using transects with no observed monarch

roadkill as absence data, although we acknowledge roadkill may have occurred in these absence locations as well. We adjusted the MaxEnt beta regularization value to two and used only quadratic and hinge features to reduce model complexity and overfitting for improving model generalization (Jiménez-Valverde et al., 2008; Warren and Seifert, 2011; Tracy et al., 2018b).

Roadway rasters served as a mask for analysis of environmental variables. The original set of 30 environmental variables was decreased to 20 variables. We dropped nine variables exhibiting zero or negative testing gain of $AUC_{bgp}$ from a MaxEnt threefold jackknife run (Table A.1, Fig. A.3). We also dropped traffic volume because data were not readily available for Mexico. Traffic volume was utilized in preliminary niche models for the Texas background evaluation extent. Preliminary runs indicated that no substantial gain in model performance was achieved with > 10 of the 20 variables, and that employing fewer variables (three) substantially increased undesired high spatial variability in roadkill among models. Consequently, final MaxEnt roadkill models were developed from ten random sets of ten of the 20 variables to represent model variability due to variable selection. The absolute Spearman rank correlation of variables within random variable sets was limited to < 0.7 using the multiple randomized sequential forward selection procedure within the random subset feature selection algorithm (RSFSA) of Tracy et al. (2018b). The final MaxEnt models were calibrated to binary presence/absence format using a threshold of maximum $TSS_{pa}$ (Liu et al., 2013) and combined using frequency consensus to form a feature subset ensemble. We also created presence/absence niche models for monarch roadkill using linear and quadratic binomial logistic regression with the R Glmnet package (Friedman et al., 2010) for the same ten random sets of ten of 20 variables. These presence/absence models produced lower $AUC_{bgp}$ values and similar $AUC_{pa}$ values compared to MaxEnt models, and these models were not investigated further (results not shown).

## 3. Results

### 3.1. Monarch roadkill survey and simple roadkill extrapolation

We surveyed 16.1 km of roadsides (161,100 m transects), 8.8 km in 2016 and 7.3 km in 2017. We found 581 dead monarchs in 59 locations (102 absence locations) for an average of 3.4 monarchs per transect. We found 546 dead monarchs in 2016 and 35 in 2017 (for raw survey count data, see Appendix A, section 3.1). Of the 546 monarchs in 2016, 499 (91%) were located along or near IH-10 between Sonora and Sheffield (23 of 95 transects) (Fig. 2). This area was defined as a single large 2016 hotspot area extending 95 km along Interstate Highway (IH) 10 from Sonora to 24 km east of the Pecos River. This hotspot included a portion of Texas state highway (SH) 163 extending from 7.6 km south of Ozona to 5 km north of Ozona and a 2 km section of SH-137 extending west from the junction with SH-163. The hotspot was bounded along IH-10 in the west and east by counts of 15 and 10 roadkill per 100 m, and included counts of 21 and 6 roadkill per 100 m on SH-137 and SH-163, respectively. About 93% (466/499) of the dead monarchs in the 2016 hotspot occurred in 14 transects ranging from 10 to 66 per 100 m (Fig. A.4). A total of 257 monarchs were sexed in 2016–2017, of which ca. 38% were female (n = 98). The portion of females was 41% in 2016 (132 males, 91 females) and 21% in 2017 (27 males, 7 females). After the 2 km spatial thinning for spatial modeling, the field survey data consisted of 151 transects (53 presence and 98 absence) and 249 individual dead monarchs. Only two road-killed male monarchs were found among 54 transects in our spring 2017 roadkill survey (Fig. A.1).

Southern edges of roadsides contained 43.8% ( ± 36% SD, n = 13) of the roadkill found in the northernmost edge for both single and divided-lane roads. This relationship was used to estimate roadkill across all two to four edges per roadway when extrapolating roadkill per km per year (for details, see Appendix A, section 5). Estimated roadkill per km ranged from 6.15 to 645 monarchs per km depending on year, road type, and location in relation to the hotspot area (Table 1). In 2016, mean estimated roadkill per km along highways was significantly higher within the Sonora-Sheffield hotspot (645.38; SD = 446.92; n = 15) compared to outside the hotspot (12.64; SD = 22.30; n = 22) (P = 0.00008; Welch *t*-test). Between years, the estimated roadkill per km generally varied widely among road types, and there was no evidence of any hotspot in 2017 (Table 1). Estimates of roadkill within the hotspot area in 2016 and 2017 ranged from about 74,000 to 5000, representing about 10% and 1% of the entire mortality within the Texas background evaluation extent. Using the field survey data from the whole area, including the randomly thinned hotspot data, the estimated roadkill for the Central Funnel in 2016 rose to over 3.5 million monarch butterflies (Table 1). The estimate for 2017 was 1.1 million road-killed monarchs. Combining the data from both of the years yielded an annual estimate of 2.1 million road-killed monarchs. When the hotspot data were separated from the survey data, total estimated annual roadkill rates in 2016 and 2017 were about 1.6 million and 1.0 million monarchs, respectively. In 2016, about 47%–49% of the roadkill within the Central Funnel was projected to occur within the Texas background evaluation extent, of which 5% was projected to occur in the Sonora-Sheffield hotspot area. In 2017, only about 0.3% of the roadkill within the Central Funnel was projected within the hotspot area, and the percent roadkill in the background area ranged from 31% when hotspot data were analyzed separately to 48% when data from the hotspot area were included (Table 1, Appendix A, section 2).

### 3.2. Monarch roadkill model

The feature subset ensemble of ten MaxEnt roadkill niche models provided excellent discrimination of roadkill presence locations from background locations within the background evaluation extent, with $AUC_{bgp}$ values ranging from 0.82 to 0.88 (0.86 ± 0.02, mean ± SD). The models provided marginally poor discrimination of roadkill presences from absences observed in the field, with $AUC_{pa}$ values ranging from 0.60 to 0.67 (0.64 ± 0.02, mean ± SD). Among the top eight variables with the highest permutation importance in the MaxEnt models (Table 2) were three human population density indices and two climatic indices. Other top ranked variables included elevation (m), road density over a 3 km radius (km/~28 $km^2$), and percent cover of artificial surfaces within a 500 m radius. Traffic volume (annual average daily traffic, AADT) ranked third in permutation importance in preliminary models but was not available for Mexico, precluding its use in our final models.

The MaxEnt response curves for population density indices all indicated that lower human population densities had higher association with monarch roadkill (Fig. 3A, E). The climatic indices indicated that roadkill was associated with more arid climates (Fig. 3B, C). Lower road densities and lower percent cover of artificial surface were also associated with higher monarch roadkill (Fig. 4F, G). The response curve for traffic volume, which was not used in the final models, indicated that the highest roadkill was associated with lower traffic volume. The traffic volume response curve was very similar to that of percent cover of artificial surface (Fig. 3G, H), with which it was moderately correlated ($r_s$ = 0.58).

The proportion of MaxEnt models projecting monarch roadkill generally increased from northeast to southwest within both the background evaluation extent and Central Funnel (Fig. 4; see Appendix Section 5 for embedded zipped shapefile of MaxEnt consensus model). The highest number of models projected roadkill within much of southwest Texas and Mexico in the Central Funnel. None of the MaxEnt models projected monarch roadkill over most of the northeastern Central Funnel, including the Dallas/Fort Worth metroplex and most of eastern Oklahoma.

Roadkill extrapolations for each of the ten individual MaxEnt models were made across each year and both years combined.

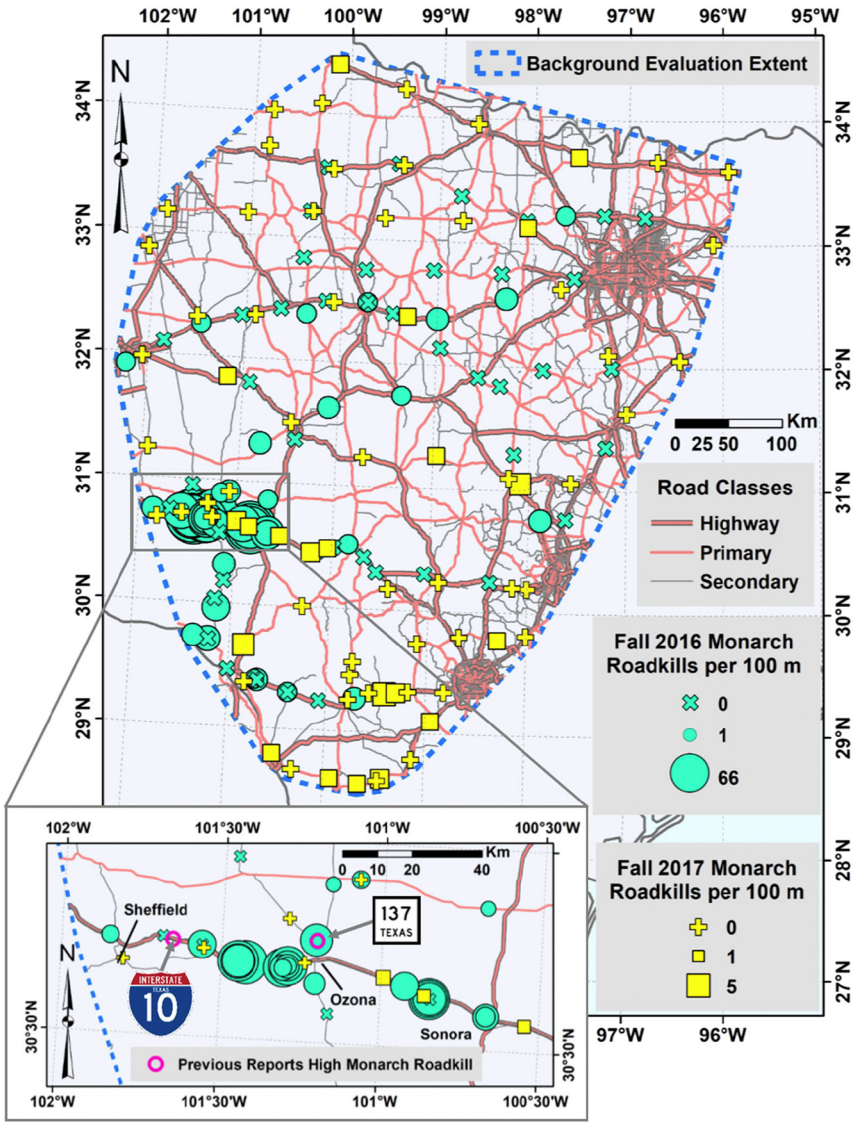


**Fig. 2.** Monarch roadkill autumn 2016 and 2017 survey results for 100 m transects along major road classes within the background evaluation extent in the monarch Central Funnel in Texas, including previously reported locations of high monarch roadkill.

Extrapolations were based upon roadkill rates per km for presence-only transects (no zero roadkill data) of each road type that were multiplied by the MaxEnt model predicted lengths of roadkill presence for the road type. Roadkill rate calculations for extrapolations included data from hotspot transects that were thinned for 2016 as done for simple extrapolations (for details, see Appendix A, sections 2.1, 5). Extrapolating roadkill rates across the Central Funnel, we estimated averages of 3.0 ± 0.7 and 1.1 ± 0.3 million (mean ± SD) road-killed monarchs for 2016 and 2017, respectively (Tables 1, A.2). Combining roadkill data across both years for the Central Funnel yielded annual roadkill rates of 2.1 ± 0.5 million. The mean projected percentage of road-killed monarchs in the Central Funnel that occurred within the Texas background evaluation extent ranged from 67% to 68% in 2016 and 2017 (Tables 1, A.4).

## 4. Discussion

### 4.1. Monarch roadkill survey

In our 2016 roadkill survey (but not 2017), we found a Sonora-Sheffield, Texas, monarch roadkill hotspot that corresponds to the only two previous citizen-science reports of monarch roadkill hotspots in the US (Fig. 2). It is unclear why hotspots have repeatedly occurred in this area. The hotspot location may be partly related to higher densities of migrating monarchs in more southern areas of the Central Funnel. In addition, local stochastic weather events probably influence the occurrence of roadkill hotspots, such as unfavorable winds that may induce lower monarch flight patterns or extended roosting and nectaring behavior close to the ground in the vicinity of roadways. More research is needed to evaluate how frequently roadkill hotspots occur in this region. It is possible that one or both years represent an outlier, and that hotspots may occur in additional areas.

The variation in roadkill rates observed between the two years of our survey was consistent with other roadkill studies (Seiler and Helldin, 2006). Our overall roadkill rates varied from 6 to 646 dead monarchs per km depending on year, road type, and location (Table 1). This range falls within previous reports for monarchs of from 1.3 to 11.9 butterflies per km per week in Illinois (McKenna et al., 2001) to a very high number of 115 road-killed monarchs within a 20 m stretch along toll highway 40D southwest of Monterrey, Mexico in October 2015 (Correo Real, 2015; see Appendix A, section 8 for data). Reported roadkill rates for other butterflies have ranged from 0.45 to 80 per km per day in North America, Asia, and Europe (Rao and Girish, 2007, De la Puente et al., 2008, Yamada et al., 2010, Skórka et al., 2013, Baxter-

**Table 1**
Monarch roadkill estimates per year for 2016 to 2017 over the Sonora-Sheffield roadkill hotspot, Texas background evaluation extent (BEE) and the Central Funnel (Figs. 1–2) from the field data by road type using simple extrapolation or MaxEnt model projections.

| Year | Millions of monarch roadkill[a] | | | | | | |
|---|---|---|---|---|---|---|---|
| | Simple extrapolation | | | | | MaxEnt model extrapolations $\bar{X} \pm$ SD (n = 10)[b] | |
| | Hotspot data separated | | | Hotspot data included | | Hotspot data included | |
| | Sonora-Sheffield hotspot | Texas BEE | Central Funnel | Texas BEE | Central Funnel | Texas BEE | Central Funnel |
| 2016 | | | | | | | |
| Millions of dead | 0.074 | 0.768 | 1.570 | 1.663 | 3.554 | 2.050 ± 0.760 | 3.041 ± 0.743 |
| % Overwintering population[c] | 0.09% | 0.90% | 1.82% | 1.93% | 4.03% | 2.36 ± 0.86% | 3.46 ± 0.82% |
| % Texas BEE mortality | 9.58% | | | | | | |
| % Central Funnel mortality | 4.69% | 48.95% | | 46.78% | | 66.48 ± 14.79% | |
| 2017 | | | | | | | |
| Millions of dead | 0.005 | 0.492 | 1.042 | 0.533 | 1.131 | 0.738 ± 0.272 | 1.084 ± 0.258 |
| % Overwintering population[c] | 0.01% | 0.79% | 1.67% | 0.86% | 1.81% | 1.19 ± 0.43% | 1.73 ± 0.41% |
| % Texas BEE mortality | 1.02% | | | | | | |
| % Central Funnel mortality | 0.32% | 31.34% | | 47.16% | | 68.86 ± 14.18% | |
| 2016–2017 | | | | | | | |
| Millions of dead | 0.058 | 0.561 | 1.138 | 0.995 | 2.118 | 1.460 ± 0.540 | 2.119 ± 0.510 |
| % Overwintering population[c] | 0.09% | 0.91% | 1.82% | 1.59% | 3.33% | 1.96 ± 0.71% | 2.82 ± 0.66% |
| % Texas BEE mortality | 10.25% | | | | | | |
| % Central Funnel mortality | 3.66% | 35.75% | | 27.99% | | 67.90 ± 15.08% | |

[a] Mean roadkill rates (roadkill/km/year) (Table A.2) by road type for extrapolations are calculated from transects in the Texas BEE and incorporate estimates for all road edges. Roadkill rates are multiplied by length of road in various areas to obtain extrapolations (see Table A.3 for road lengths used in simple road type extrapolation) (for all calculations, see Appendix A, section 5).
[b] See Table A.4 for individual MaxEnt model estimates.
[c] Based on 84.61 (2016) and 61.4 (2017) million overwintering monarchs (Monarch Watch, 2018b). Estimated from 21 million monarchs per hectares overwintering (Thogmartin et al., 2017).

Gilbert et al., 2015).

The observed sex ratios of roadkill monarchs were also consistent with previous studies. About 38% of the dead monarchs in our autumn field surveys were females, ranging from 21% in 2017 to 41% in 2016. These figures generally match two separate citizen science observations on the percentage of female monarch roadkill in Mexico of 27% and 36% in October 2015 (Correo Real, 2015). They also are within the range reported from the other roadkill study (McKenna et al., 2001), as well as studies of sex ratios during migration (Borland et al., 2004) or on the overwintering grounds (Steffy, 2015). Davis and Rendón-Salinas (2010) found a decreasing trend (~10%) in percent female monarchs at the Mexican overwintering sites from 1976 to 2008, which they suggested could reflect female biased mortality due to the protozoan parasite *Ophryocystis elektroscirrha*.

While our estimates of monarch roadkill are likely conservative, carcass persistence is not likely to be a major source of bias. However, we did not evaluate persistence in our study, which could vary based on various factors, such as region, time of year, and weather conditions.

Munguira and Thomas (1992) placed butterfly specimens on roadsides and found that only one of their 50 specimens disappeared during

**Table 2**
MaxEnt model variable permutation importance for 19 variables used in ten random sets of ten of the 20 variables in monarch roadkill models.

| Variable[a] | Abbreviation | Permutation importance[b], mean ± SD |
|---|---|---|
| Human population density per km$^2$ in 9 km radius (population/254.47 km$^2$) | *popden9kr* | 44.2 ± 3.8 (3) |
| Autumn quarterly mean monthly actual evapotranspiration/potential evapotranspiration × 1000 | *etrt_autq* | 41.7 ± 23.3 (2) |
| Annual mean monthly rainfall (mm) | *prec_ann* | 36.4 ± 15.6 (4) |
| Human population density per km$^2$ in 3 km radius (population/28.27 km$^2$) | *popden3kr* | 30.1 ± 0.0 (1) |
| Elevation (m) | *elev* | 27.9 ± 5.5 (4) |
| Distance to urban areas (areas with ≥300 humans per km$^2$) (km) | *urbdist* | 27.1 ± 10.8 (4) |
| Road density, km road in 3 km radius (km/28.27 km$^2$) | *roadden3kr* | 19.6 ± 2.4 (2) |
| Artificial surfaces % cover in 500 m radius | *artsur_500mr* | 13.4 ± 3.2 (3) |
| Autumn quarterly mean monthly maximum temperature (°Celsius) | *tmax_autq* | 10.5 ± 9.8 (3) |
| Distance to highways (m) | *hwydist* | 10.4 ± 2.5 (7) |
| Latitude (decimal degrees) | *latitude* | 6.4 ± 4.3 (3) |
| Grasslands % cover in 500 m radius | *grslnd_500mr* | 5.6 ± 3.4 (9) |
| Autumn mean quarterly wind speed (m/s) | *wndsp_autq* | 5.6 ± 5.4 (4) |
| Distance to secondary roads (m) | *secrddist* | 5.1 ± 2.9 (8) |
| Shrublands % cover in 500 m radius | *shrub_500mr* | 4.5 ± 3.4 (9) |
| Distance to primary roads (m) | *primrddist* | 2.3 ± 3.0 (4) |
| Road density, km road in 500 m radius (km/0.79 km$^2$) | *roadden500mr* | 2.2 ± 3.8 (5) |
| Distance to high flow accumulation areas (> 60,000 ~km$^2$ upslope grid cells) (m) | *strmhiflodist* | 1.2 ± 1.0 (5) |
| Topographic Position Index (TPI), 3 km radius | *tpi3kr* | 1.0 ± 0.2 (5) |
| Cultivated land % cover in 500 m radius[c] | *cult_500mr* | 0.0 ± 0.0 (0) |

[a] See Table S1 for sources of variables. Variables ordered from highest to lowest mean permutation importance.
[b] Permutation importance of the variable in the MaxEnt models, number of models in which the variable was used out of the 10 random models in parentheses.
[c] Cultivated land layer was initially included in all 10 random models, but it was not included by MaxEnt in calculating any of the models.

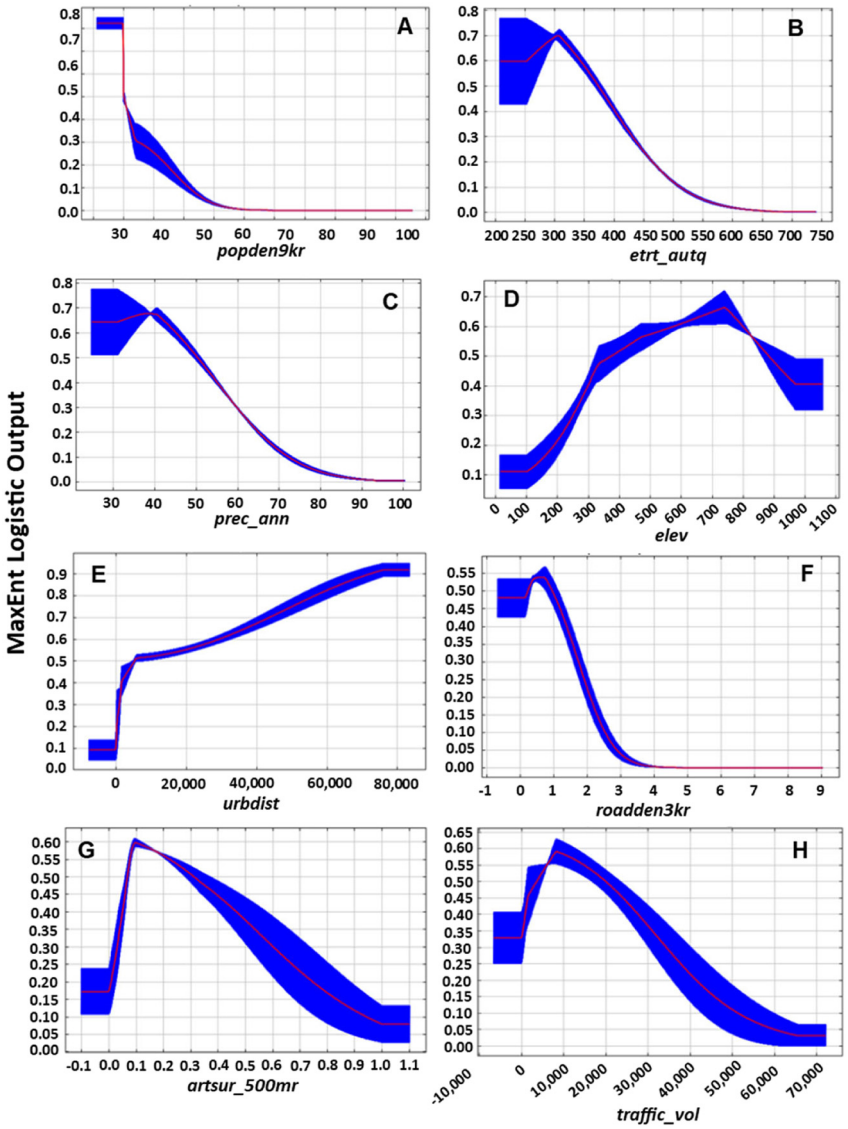


**Fig. 3.** MaxEnt variable response curves (logistic output probability of presence vs. variable) representative of the final ten models (A–G) and for a 30-variable model (H): (A) popden9kr, (B) etrt_autq, (C) prec_ann, (D) elev, (E) urbdist, (F) roadden3kr, (G) artsur_500mr, (H) traffic_vol (traffic volume for 2015) (see Table 2 for abbreviations and permutation importance).

two weeks (daily loss rate of 0.15%). Several factors contribute to the conservative nature of our estimates, including the difficulty in detection of dead monarchs, especially in taller vegetation, shredding of dead monarchs by roadside mowing, and a portion of the monarchs remaining attached to the colliding vehicles (McKenna et al., 2001; Seiler and Helldin, 2006). However, several studies indicate that road killed butterflies are mostly blown to the roadside edge, with individuals rarely trapped in car grills (Munguira and Thomas, 1992; Ries et al., 2001). The overall agreement of our roadkill results with previous studies in terms of the range of roadkill rate variability and sex ratios supports the reliability of the data for extrapolating monarch road mortality according to road types and spatial modeling.

### 4.2. Monarch roadkill models

#### 4.2.1. Roadkill projections

Most of the MaxEnt models projected monarch roadkill from the southwestern portion of the Central Funnel from West Texas to Mexico (Fig. 4). Our MaxEnt consensus projection agrees with all seven of the previously known citizen science reports of monarch roadkill hotspots in North America (Fig. 4), including two hotspots in West Texas (Journey North, 2017) and five hotspots in northern Mexico (Correo Real, 2015; Rogelio Carrerra, Universidad Autonoma de Nuevo Leon, Nuevo Leon, Mexico, personal communication).

Our annual MaxEnt based roadkill estimates for monarch mortality throughout the Central Funnel was 3.0 to 1.1 million for 2016 and 2017, respectively. These MaxEnt roadkill estimates were similar to those based on simple roadkill extrapolation by road type when hotspot data were included (3.6 and 1.1 million, respectively). Most of the roadkill projected by MaxEnt models outside of the study area occurred in Mexico, indicating that more MaxEnt models are projecting roadkill along the sparser road network within the Central Funnel over northern and central Mexico than in the northern parts of the funnel (Fig. 4). As the autumn migration pathway narrows in the South, migrating monarchs become more concentrated in the Central Funnel. This higher concentration may contribute to higher roadkill densities in the southern parts of the Central Funnel in Mexico, where most previous reports of monarch roadkill hotspots originate (Fig. 4). Although our models project some increased southward mortality risk, additional data are needed to assess the extent of this risk in Mexico. The extrapolations including the hotspot data with other roadkill data and projecting higher annual roadkill of up to 3.6 million in the Central Funnel

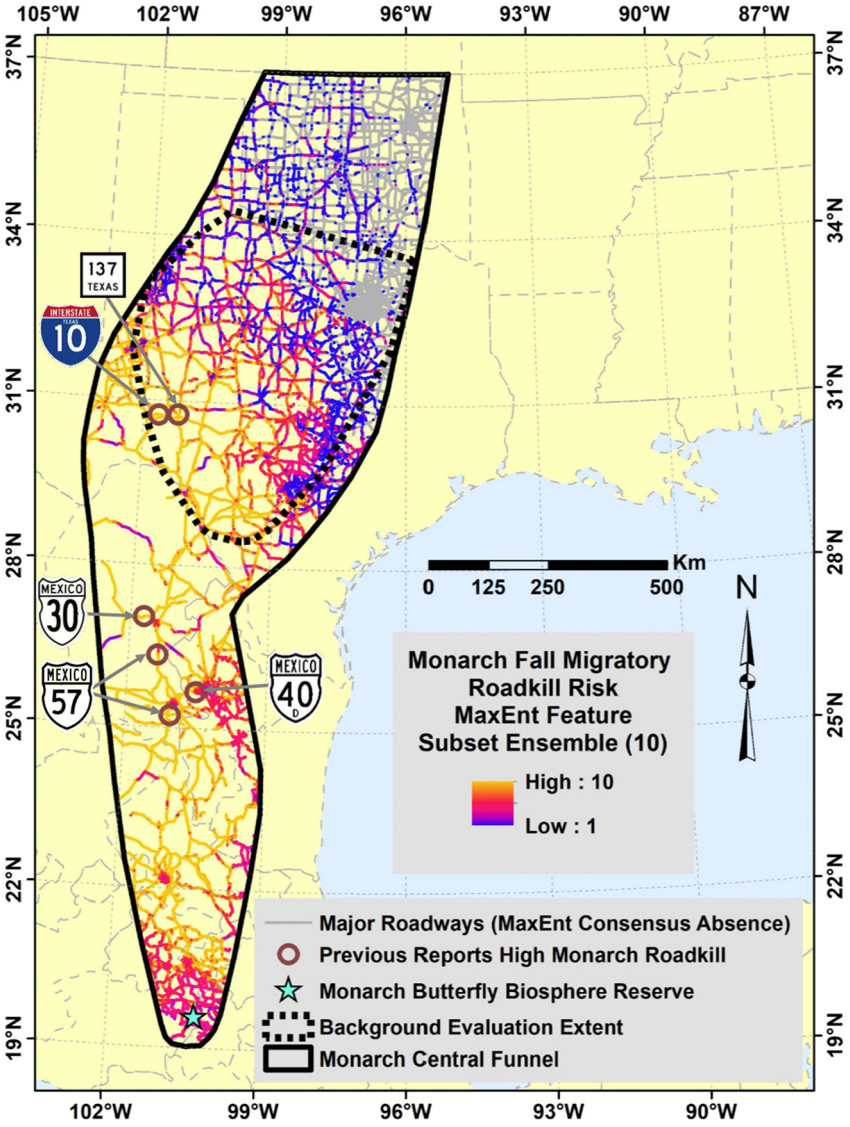


**Fig. 4.** MaxEnt frequency consensus for feature subset ensemble of ten models developed from random subsets of ten of 20 variables correlated < 0.7 (see Appendix Section 5 for embedded zipped shapefile of MaxEnt consensus model).

should be more realistic considering the occurrence of multiple roadkill hotspots in Mexico of higher density than seen in Texas. The MaxEnt models project little to no roadkill in the northeastern part of the funnel area, including the Dallas/Fort Worth area and eastern Oklahoma. However, some roadkill likely does occur in this area, but possibly at a lower rate than in the more southern areas of the Central Funnel. Further research and field surveys are needed to verify roadkill rates outside of our survey area in the southern and northern parts of the Central Funnel. Additional data may allow effective use of roadkill density models, rather than presence only MaxEnt models used in this study. Roadkill density models can better reveal regional roadkill patterns useful in refining projections, especially for northern Mexico where roadkill could be much higher than in Texas. Roadkill field surveys from other parts of the autumn migration pathways could improve estimates for the total impact of roadkill on the monarch population.

#### 4.2.2. Factors affecting roadkill

MaxEnt projections of monarch roadkill within the Central Funnel were generally associated with more arid climate and less densely populated areas (Fig. 3). These conditions generally describe those for the seven previous monarch roadkill hotspots reported from Texas and Mexico, with the possible exception of the roadkill hotspot in the vicinity of Monterrey, Mexico (Fig. 4). This could be related to a variety of factors. For example, autumn migrating monarchs have been observed to spend additional time flying lower to the ground during the afternoon in desert areas, perhaps to seek shelter from the heat or find nectar (Journey North, 2018). Monarchs may need to spend more time searching for nectar in arid environments, although this has not been evaluated. Finally, the increased roadkill rates may simply reflect the increased number of monarchs in more southern areas of the Central Funnel. This southern locality factor cannot be associated with most of the predictors, with the exception of latitude, but it may have the highest influence. Local climate, weather patterns, and geography affect monarch movement and behavior, and they all are likely important contributors to road mortality. Wind patterns (direction, duration, and speed) may especially be more important than anthropogenic factors, but short-term weather events could not be incorporated in the models. Occurrence of these weather events is also highly variable and difficult to predict.

Traffic volume has been noted as one of the most important variables in previous roadkill studies (Bennett, 2017). Traffic volume ranked high in importance in our preliminary roadkill models, but we found that model accuracy (AUC) was not significantly affected by its

removal. Other variables that were correlated with traffic volume likely compensated for its absence, including human population density, artificial surface cover, distance to urban areas (km to population ≥ 300/km$^2$), and road density. In our models including traffic volume, the highest roadkill was associated with fairly low AADT values, similar to the study by McKenna et al. (2001). In general, higher roadkill has been associated with higher traffic volume due to increased probability of vehicle collisions (Seiler and Helldin, 2006; Skórka et al., 2013). Samways (1994) suggested that roads with high traffic volume serve as corridors for high butterfly mortality. In our study, low traffic volume, along with related anthropogenic variables, is correlated with locations of monarch roadkill hotspots, but may not be directly related to the roadkill mortality. As the human population grows, traffic volume should increase, including in the lower traffic volume monarch roadkill hotspot areas, likely leading to higher roadkill rates (Bennett, 2017).

#### 4.2.3. Spatial and temporal variation

Over 70,000 monarch roadkill were estimated in the Sonora to Sheffield, Texas hotspot in 2016, compared to about 5000 in 2017. This illustrates the high spatio-temporal variability of roadkill and the potential contribution of hotspots to the monarch road mortality. The timing of our field surveys relative to the peak migration in those years may have varied among transect locations and years, which could have influenced our results. If peak migration occurred after our field surveys in one or both years, we may have underestimated roadkill numbers. For example, the autumn migration in 2017 was later than usual due to unusually hot summer (Agrawal and Inamine, 2018). Few other studies have identified roadkill hotspots for butterflies (but see Samways, 1994, Her, 2008). Monarch roadkill hotspots may vary from year to year and may be difficult to locate or may not occur in some years.

We observed much higher monarch road mortality during autumn migration than in the spring (Fig. A.1), indicating that seasonality is a factor contributing to monarch roadkill rates. However, the monarch spring migration is more spatio-temporally dispersed making comparisons difficult. Temporal variability can occur between years, within the migration phase, or even within a day. For example, monarch behavior, such as flying low in the mornings (McKenna et al., 2001), probably affects the risk of roadkill at different times of day. Temporal patterns affecting monarch roadkill should be investigated further. Other sampling methods may be effective in detecting additional roadkill hotspots, such as adaptive cluster sampling, which was developed for inventorying scattered and clustered phenomena (Thompson, 1990). More frequent samples in a given location can also be critical for detecting roadkill hotspots (Santos et al., 2015).

### 4.3. Implications and impacts in relation to monarch conservation

#### 4.3.1. Autumn migration mortality

Butterfly roadkill is a density independent mortality factor (Rodewald and Gehrt, 2014) with the incidence of roadkill being subject to high variability. Consequently, roadkill percentage of the migrating population is very unpredictable in any given year. We estimated a conservative annual percentage of migrating monarchs subject to road mortality in the Central Funnel by dividing a roadkill estimate by the sum of overwintering populations and roadkill estimate (overwintering cohort). The size of the overwintering populations is calculated by multiplying the hectares of roosting monarchs at the Mexican overwintering sites from Rendón-Salinas et al. (2018) by the value of 21.1 million monarchs per ha suggested by Thogmartin et al. (2017). Based on these amounts, the estimated annual roadkill rates from our combined years of 2016–2017 MaxEnt models in the Central Funnel represent an average of 2.8% (2.1 million) of the overwintering cohort. In 2016, roadkill within the Central Funnel may have represented about 4.0% of the overwintering cohort (Table 1). The corresponding roadkill for 2017 ranges from 1.5% to 1.8% of the overwintering cohort. In contrast, the projection of 500,000 road-killed monarchs by McKenna et al. (2001) in Illinois during one week in 1999 represents only 0.26% of the overwintering cohort that year (191 million, 9.05 ha), indicating potentially lower roadkill rates for areas north of the Central Funnel in some years.

The actual monarch population decline within a given year can be much higher than the differences in overwintering cohort sizes from year to year, since it includes the unknown quantities of butterflies recruited, or not recruited due to habitat loss, during spring and summer breeding. Mortality at the Mexican overwintering sites due to occasional winter storms can produce very high mortality, estimated at around 75% in 2002 (Brower et al., 2004) and > 40% in 2016 (Brower et al., 2017). Average monarch overwintering mortality is around 36% ± 21% (n = 7; range 4–55%) based on data from Ries et al. (2015b; see their Fig. 24.7). Lowered recruitment due to loss of milkweed habitat has been identified as the primary factor in monarch population declines (Pleasants, 2017; Thogmartin et al., 2017), with losses of milkweed resources in Iowa estimated at 76% from 1999 to 2014 (Pleasants et al., 2017). Other studies place more importance on mortality during the autumn migration in the decline of monarchs (Badgett and Davis, 2015; Inamine et al., 2016; Agrawal and Inamine, 2018). Consequently, it is complex to evaluate the relative importance of roadkill to other factors in the monarch population decline, but it is probably lower compared to the factors of milkweed habitat loss and overwintering mortality. Northward expansion of the monarch summer breeding range is anticipated with climate change (Batalden et al., 2007; Lemoine, 2015), making the southward autumn migration route even longer, increasing both exposure to traffic and associated road mortality (Badgett and Davis, 2015). Monarch roadkill during autumn migration should be further evaluated in the context of other mortality factors along the migration path (Baxter-Gilbert et al., 2015).

Brower et al. (2012) fitted an exponential decline curve to the estimated monarch overwintering populations (ha) in Mexico from 1995 (winter 1994–1995) to 2011 (P = 0.015, $R^2$ = 0.336). Inclusion of seven additional years of data through 2018 (Vidal and Rendón-Salinas, 2014; Monarch Watch, 2018b) strengthens fit of an exponential curve ($y = ae^{bx}$ Fig. 5) (P = 0.0009; adjusted $R^2$ = 0.486; ZunZun.com, 2018). A concave exponential curve represents the most serious form of species population decline, indicating constant proportional negative pressure on the population (Di Fonzo et al., 2013). A standard geometric population growth curve, fit to the modeled exponential curve,

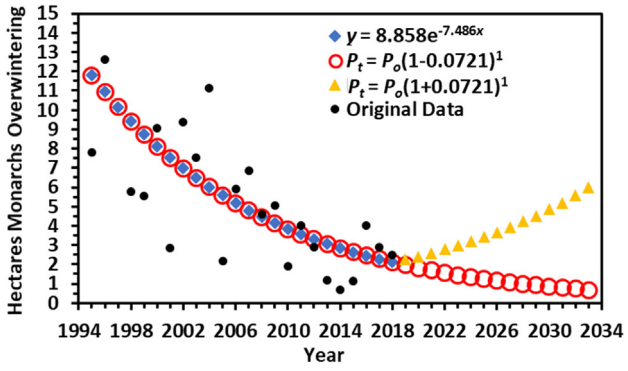


**Fig. 5.** Annual monarch population in hectares in Mexican overwintering sites from 1995 to 2018 (original data, black circles; Vidal and Rendón-Salinas, 2014; Monarch Watch, 2018b) with fitted exponential curve, $y = ae^{bx}$ (adjusted $R^2$ = 0.49; P = 0.00009; blue diamonds), and corresponding geometric population growth equation curve, $P_t = P_o(1 + r/n)^{nt}$, where $P_t$ is the final hectares (2.11), $P_o$ is the initial hectares (11.79), $t$ is the number of years (23), $n$ is the number of sub-periods (1), and $r$ is the population growth (or declination) rate (derived population declination of 7.21% per year; open red circles). Fifteen years to restore 6 ha of overwintering monarchs based on totally reversing the current decline to 7.21% growth per year (gold triangles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reveals an average − 7.21% annual population decline over the last 23 years associated with an overall 82% population reduction (for details, see Appendix A, section 8). In comparison, a fitted exponential curve until 2011, as used by Brower et al. (2012), yielded a slightly lower annual decline rate of 6.46%. The updated results indicate that the decline rate may have increased or at least has not slowed down. Continuance of the 7.21% rate of decline would result in an average of 0.24 ha of overwintering monarchs occurring in 29 years (by 2046–2047), greatly increasing the chance of extirpation of eastern migrating monarchs by an extreme winter storm mortality event as the overwintering population crosses below the 0.25 ha quasi-extinction threshold (Semmens et al., 2016). A total reversal of the 7.21% annual monarch decline, coupled with an annual 7.21% population increase (net change 14.4%), would be needed to restore the size of the overwintering population to current conservations goal of six hectares (Thogmartin et al., 2017) over the next 15 years. A 0.5% annual reduction in migrating monarch mortality through roadkill mitigation could significantly contribute to a reversal in the long-term 7.2% annual exponential decline in monarch populations (Fig. 5).

#### 4.3.2. Roadkill mitigation

While some major factors in the monarch decline are difficult to reduce, such as overwintering mortality, the opportunity for reducing road mortality is possible through roadkill mitigation (see Rytwinski et al. (2016) for a review on mammal roadkill mitigation). The potential ability to locate re-occurring monarch roadkill hotspots could facilitate more effective mitigation. Scattered and unpredictable monarch roadkill would be more difficult to mitigate. A variety of roadkill mitigation measures have been implemented for danaine migratory butterflies. In Taiwan, a four-meter high net was placed along a 400 m section of bridge on National Freeway 3 to successfully induce spring migrating purple crow butterflies (*Euploea* spp.) to fly over and above the traffic, reducing on site roadkill from around 2.5% to 0.5%. In addition, an outer traffic lane was closed when > 500 butterflies per minute were crossing (Her, 2008; Taiwan EPA, 2010). In response to heavy autumn migratory monarch roadkill observed in Coahuila state of Mexico, traffic signs were posted in 2015 limiting the maximum speed to 60 km per hour (37 mph) in the presence of monarchs (Miranda, 2015). Police have been observed slowing traffic in Nuevo Leon state in Mexico to reduce monarch mortality along a highway south of Monterrey (Dr. Orley R. Taylor, personal communication). Additional research is needed to test and assess the effectiveness of these types of butterfly roadkill mitigation strategies for monarch roadkill hotspots in west Texas and Mexico.

## 5. Conclusions

Our study represents a novel approach for projecting roadkill of a migratory insect through ecological niche modeling. Annual monarch roadkill rates during autumn migration varied substantially. We found close agreement between two methods of estimating monarch roadkill rates, simple extrapolation by road type and MaxEnt roadkill model projections. We project about 1.0 to 3.6 million road-killed monarchs per year during autumn migration over the Central Funnel, which could represent 2–4% of the Mexican monarch overwintering population. MaxEnt model roadkill projections also aligned with several previously known monarch roadkill hotspots, which suggests MaxEnt models could be used to identify additional monarch roadkill within the Central Funnel. Roadkill rates may differ throughout the Central Funnel compared to those observed in the Texas survey area, and should be further investigated. Monarch road mortality should also be investigated along the Coastal Funnel, especially from Texas to Mexico. We recommend more detailed investigation into the spatial and temporal variability in monarch road mortality in the Central Funnel, including how local and short-term weather events, especially related to wind, influence monarch roadkill hotspots. With the new information on monarch road mortality in the Central Funnel, conservation efforts could be implemented to mitigate mortality at monarch roadkill hotspots. Reducing roadkill rate over the Central Funnel for the eastern monarch population is as an important step towards reversing the continuing decline of this iconic butterfly.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.01.008.

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# Reexamining Fire Suppression Impacts on Brushland Fire Regimes

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**California shrubland wildfires are increasingly destructive, and it is widely held that the problem has been intensified by fire suppression, leading to larger, more intense wildfires. However, analysis of the California Statewide Fire History Database shows that, since 1910, fire frequency and area burned have not declined, and fire size has not increased. Fire rotation intervals have declined, and fire season has not changed, implying that fire intensity has not increased. Fire frequency and population density were correlated, and it is suggested that fire suppression plays a critical role in offsetting potential impacts of increased ignitions. Large fires were not dependent on old age classes of fuels, and it is thus unlikely that age class manipulation of fuels can prevent large fires. Expansion of the urban-wildland interface is a key factor in wildland fire destruction.**

California shrublands frequently fuel massive high-intensity wildfires that are of increasing concern to resource managers and the public. Despite increased expenditures on fire suppression, each new decade experiences increased loss of property and lives from brushland wildfires (*1*). By the middle of this century, it was suggested that the problem stemmed in large part from the burgeoning population and poor zoning regulations attendant with urban sprawl into the foothills (*2*).

Accepting expanded urbanization as the source of the wildfire problem has profound economic and political implications. An alternative view to emerge in the early 1970s was that the primary problem was tied to the overly successful state and federal fire suppression programs. As a consequence of eliminating fires from the wildland ecosystem, it has been widely held that we have exacerbated the situation by allowing unnatural fuel accumulation (*3*). Thus, when the inevitable fire does come, it is larger and more destructive. A computer model relating fire size to chaparral fuel loading predicted that the prevailing management strategy of fire suppression in California brushlands leads to fewer, but larger and more intense fires (*4*).

A 9-year Landsat imagery record that showed that fires between 5000 and 10,000 ha were slightly more abundant in southern California than in adjacent Baja California (*5*) has been widely cited as support for a link between fire suppression and fire size. On the basis of this study, it has been hypothesized that large wildfires in California shrublands are a modern artifact, due to fire suppression, and that they can be prevented by creation of a mosaic landscape of patches of different ages (*6*). The model is predicated on assertions that, because of fire suppression, (i) the number of fires has declined over time, (ii) fires are substantially larger today than in the past, (iii) contemporary fires burn with greater intensity than in the past, (iv) large fires result from extensive stands of very old age classes, and (v) there has been a decline in area burned, as suggested by some (*3*), but not all (*5*), studies. None of these assertions have been documented.

To investigate historical changes in fire regimes, we used the recently available California Statewide Fire History Database, which includes all records from the California Department of Forestry and U.S. Forest Service and other county records (*7*). We limited our analysis to counties dominated by shrublands with a stand-replacing fire regime: from north to south, Monterey, San Luis Obispo, Santa Barbara, Ventura, Los Angeles, San Bernardino, Riverside, Orange, and San Diego. Records date from the late 19th century for some counties and from at least 1910 for others (*8*).

Collectively, since 1910, there has been a highly significant increase ($r^2 = 0.61$, $P < 0.01$, $n = 9$) in the number of fires per decade. This increase is due largely to southern California counties, which also had significant increases in area burned (Fig. 1) (*9*). In no county was there a significant decline in number of fires or area burned. All counties exhibited significant interdecadal differences in area burned [$P < 0.01$, one-way analysis of variance (ANOVA)]. For most counties, the 1920s and 1970s were high and the 1930s and 1960s low. Collectively, area burned was significantly correlated ($r^2 = 0.71$, $P < 0.01$, $n = 9$) with number of fires, which was also correlated ($r^2 = 0.51$, $P < 0.05$, $n = 9$) with population density (*10*).

All counties reported very large fires from the beginning of record keeping; indeed, one of the largest fires in Los Angeles County was a 24,076-ha fire in 1878 (Fig. 2). During the 20th century, there has been no increase in mean fire size for any county, but four exhibited significant declines (Fig. 2). One contributor to this decline could be a purported inclination by agencies early in the century to not record very small fires (*8*). However, if fires less than 100 ha in size are removed from the data set, there is still a slight downward trend in fire size this century (all counties combined, $r^2 = 0.02$, $P < 0.001$, $n = 2766$). Another factor that could explain a trend toward smaller mean fire size is the increase in human-caused (*11*) ignitions (Fig. 1), coupled with the fact that many are ignited under moderate weather conditions and along roadways, factors contributing to their suppression at a small size (*12*). If we focus just on large fires, greater than 1000 ha, the trend toward smaller fires disappears, but still no county had a significant increase in fire size (ranges: $r^2 = 0.00$ to $0.02$, $P > 0.10$ to $0.99$, $n = 82$ to $159$). The assertion that large wildfires are an artifact of modern fire suppression is not supported.

Contrasting fires after 1950, when fire suppression impacts would be greatest (*13*), with those in and before 1950, we see no significant change in pattern of burning (Fig. 3A); a small percentage of fires account for the bulk of area burned, now and in the past [10% of the fires accounted for 75% (in and before 1950) to 79% (after 1950) of the area burned]. The primary change has been in the proliferation of fires between 10 and 100 ha (Fig. 3B), reflecting both increased ignitions under moderate conditions—that favor suppression—and increased reporting of small fires. In these brushland ecosystems, the frequency of small to medium size fires cannot be used to quantify the risk of large fires (*14*).

Contrasting fire regimes between the first and second halves of this century, we found that fire frequency increased in all but one county (Table 1). The majority of counties exhibited no significant change in mean or median fire size; however, three southern California counties had highly significant declines in mean fire size. Fire rotation intervals, the time required to burn the equivalent

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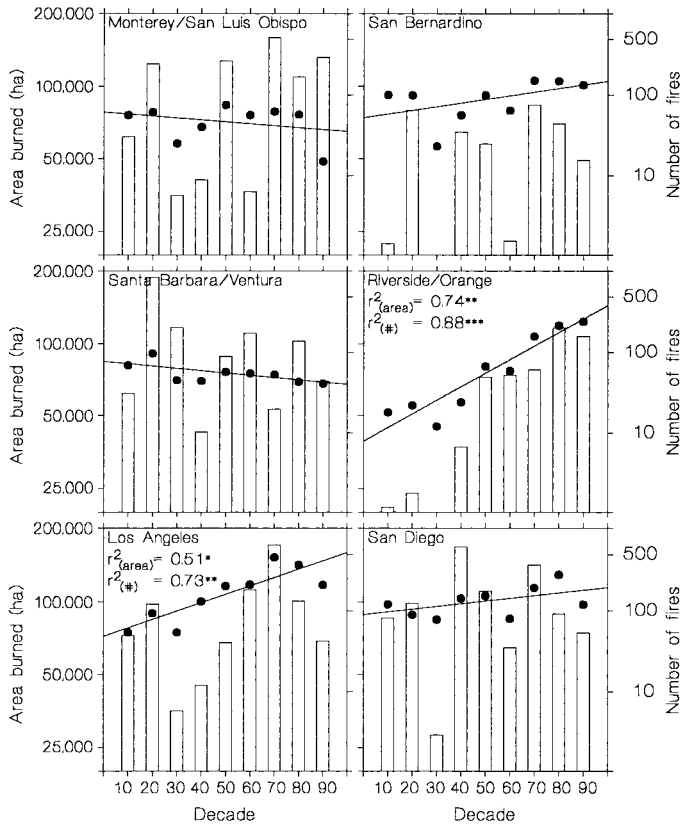


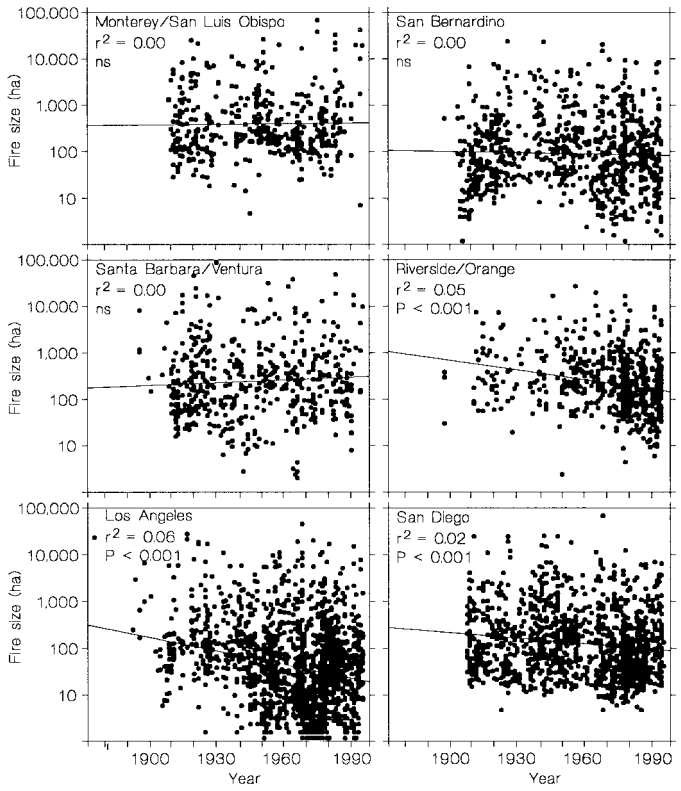


**Fig. 1 (left).** Area burned (bars) and fire frequency (circles) by decade (1910–1990) for brush-dominated counties in central-coastal and southern California. $r^2$ is included only when significant: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. **Fig. 2 (right).** Magnitude of individual fire size for all records for brush-dominated counties.

**Table 1.** Brush-covered area as of 1985 and fire statistics for 1910–1950 and 1951–1997 with estimated fire rotation interval (area of brush (*22*)/average area burned) for California counties. Trends with medians are the same for each county.

| County | Brush ($10^3$ ha) | Number of fires | | Mean fire size (ha) | | | Fire rotation interval (years) | |
|---|---|---|---|---|---|---|---|---|
| | | Before 1951 | After 1950 | Before 1951 | After 1950 | *P* | Before 1951 | After 1950 |
| Monterey | 358 | 102 | 129 | 1220 | 1998 | >0.32 | 115 | 64 |
| San Luis Obispo | 250 | 93 | 119 | 1760 | 2068 | >0.68 | 60 | 48 |
| Santa Barbara | 250 | 125 | 61 | 1622 | 2341 | >0.45 | 47 | 81 |
| Ventura | 189 | 143 | 172 | 1568 | 1508 | >0.93 | 121 | 34 |
| Los Angeles | 320 | 357 | 1392 | 827 | 360 | <0.001 | 44 | 30 |
| San Bernardino | 209 | 311 | 544 | 609 | 480 | >0.33 | 46 | 37 |
| Riverside | 290 | 57 | 613 | 871 | 565 | <0.01 | 225 | 38 |
| Orange | 42 | 25 | 48 | 1721 | 1317 | >0.68 | 36 | 29 |
| San Diego | 365 | 456 | 770 | 939 | 544 | <0.001 | 35 | 41 |

of the total brush area in the county (Table 1), declined in all but two counties (*15*).

These fire rotation intervals do not support the assertion that large fires derive from ancient stands of brush. To investigate the true fire return interval, we used digitized fire maps for the Santa Monica Mountains in Los Angeles and Ventura counties (*16*). Fires in this brush-dominated range have included numerous large catastrophic and costly fires, such as the 1961 Bel Aire Fire or the recent 1993 Green Meadow Fire. Age classes of fuels consumed by all fires exceeding 5000 ha in the past 30 years demonstrate that large fires are not dependent on old classes (Fig. 4). Collectively, there was a significant ($P < 0.05$ with one-way ANOVA, $n = 8$) difference across age classes, with fuels 11 to 20 years old representing 38%, which was more than double the consumption of older age class fuels. Because of the proximity of this range to urban centers, the age classes consumed may not be representative of more remote sites; however, these data demonstrate that large catastrophic wildfires are not dependent on ancient stands of brush and contradict the assertion that young stands less than 20 years of age prevent fire spread (*5*, *6*).

Inferences that fires today are of greater intensity are based on the assertions that fire rotation intervals have increased and there has been a seasonal shift toward autumn burning (*6*). However, rotation intervals have generally declined (Table 1) and September has remained the peak month of burning throughout this century (Fig. 5).

Humans directly affect fire regimes in two ways: They ignite fires and they suppress fires. In brush-covered landscapes of southern and central-coastal California, there is no evidence that fire suppression has altered the natural stand-replacing fire regime in the manner suggested by others (*3*, *5*). This is

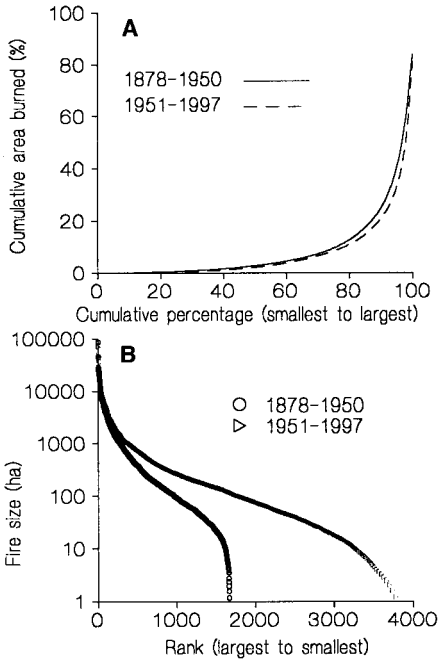


**Fig. 3.** (**A**) Cumulative area burned and (**B**) fire size distribution, for all counties before and including 1950 and after 1950.

in striking contrast to coniferous forests throughout much of the western United States, where the stand-thinning fire regime has proven amenable to near total fire exclusion, resulting in demonstrably hazardous fuel accumulation and increased potential for catastrophic wildfires (*17*). The primary hazard in brushland ecosystems is the marked increase in fire frequency during the latter half of this century that often results in type conversion to nonnative exotic grasslands (*18*), and fire suppression plays a crucial role in offsetting this impact.

Large catastrophic wildfires in brush-covered regions of California are often driven by high winds, and under these conditions even modern fire suppression techniques are ineffective (*19*). Today, people ignite most of these fires; however, in their absence, lightning storms that typically occur just weeks before the autumn foëhn winds (*11*) would have provided a natural source of ignition. Although fuel structure is an important determining factor in fire behavior, the role of structure diminishes markedly under foëhn winds that can blow at speeds exceeding 100 km/hour and are responsible for the majority of area burned in California brushlands (*19*). Under these conditions, fires readily burn through all age classes of fuels (Fig. 4), and thus, rotational burning programs that attempt to modify vast stretches of chaparral landscape through age class modification are not likely to be effective in stopping these catastrophic fires.

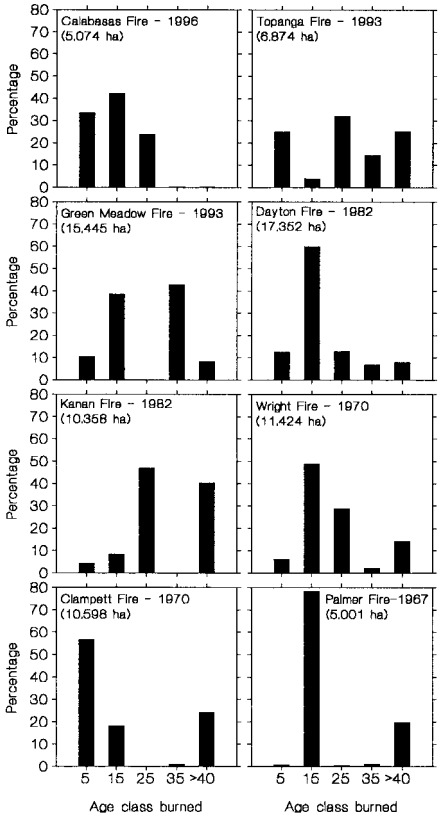


**Fig. 4.** Age classes burned by all fires over 5000 ha from 1967 to 1996 in the Santa Monica Mountains. Indicated on the abscissa are midpoints of age classes 1 to 10, 11 to 20, 21 to 30, 31 to 40, and over 40 years.

This may come as welcome news to resource managers because the combination of legal restrictions and financial constraints makes large-scale prescribed burning of brushland landscapes unobtainable. Our results support the conclusion that the most effective strategy (*20*) for reducing catastrophic losses from wildfires is to minimize the management effort spent on the bulk of the chaparral landscape and focus on strategic locations. The worst fires predictably follow landscape features, and these patterns can be used to select buffer zones at the urban-wildland interface for more intensive fuel management. However, the urban-wildland interface is so extensive now that even strategically focused intensive management could have enormous ecological impacts. Preference for a rural life-style and the skyrocketing cost of suburban housing in large metropolitan areas continue to expand the urban-wildland interface, and of particular concern is the prediction that rural population will soon exceed urban growth (*21*).

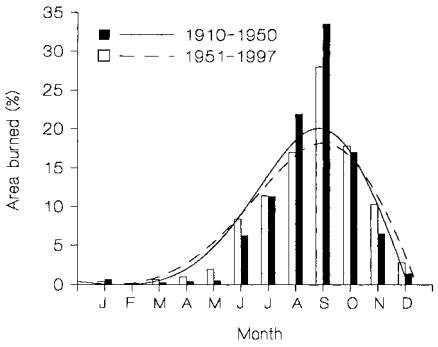


**Fig. 5.** Area burned by month for 1910–1950 and 1951–1997, for all counties except Riverside and San Bernardino, which were excluded because of incomplete data.

### References and Notes


1. T. M. Bonnicksen and R. G. Lee, *J. Environ. Manag.* **8**, 277 (1979). Since 1990, two brushland fires have each exceeded $1 billion in losses (http://frap.cdf.ca.gov/projects/fire_mgmt/fm_main.html).
2. J. A. Zivnuska and K. Arnold [*Calif. Agric.* **4**, 8 (1950)] warned "it is known that one of the significant trends in recent population changes has been the increase in number of residences in the flash-fuel types adjacent to primary watersheds."
3. M. Dodge, *Science* **177**, 139 (1972); T. M. Bonnicksen, *Environ. Manag.* **4**, 35 (1980); H. H. Biswell, *Prescribed Burning in California Wildland Vegetation Management* (Univ. of California Press, Berkeley, 1989); S. J. Pyne, *World Fire* (Holt, New York, 1995).
4. R. C. Rothermel and C. W. Philpot, *J. For.* **71**, 640 (1973); C. W. Philpot, *U.S. Forest Serv. Gen. Tech. Rep. WO-3* (1977), pp. 12–16.
5. R. A. Minnich, *Science* **219**, 1287 (1983). This study did not demonstrate any statistical differences, and the mapped comparison (Fig. 1 of that study) was biased by presentation of two massive fires (1932 and 1970) that were outside the Landsat comparison (1972–1980) period and were based on records available only for southern California. More importantly, the conclusion that fire suppression policy is the only difference between southern California and Baja California has never been rigorously demonstrated and ignores landscape, climate, and land-use differences.
6. R. A. Minnich and R. J. Dezzani, in *California Watersheds at the Urban Interface,* J. J. DeVries and S. G. Conard, Eds. (Water Resources Center Report 75, University of California, Davis, 1991), pp. 67–83; R. A. Minnich, in *Brushfires in California Wildlands: Ecology and Resource Management*, J. E. Keeley and T. Scott, Eds. (International Association of Wildlife Fire, Fairfield, WA, 1995), pp. 133–158.
7. California Department of Forestry, Fire and Resource Assessment Program (FRAP), Sacramento, CA. Small fires are not recorded; for example, the U.S. Forest Service records only fires over 16 ha. However, the threshold limit varies with the agency.
8. Fires recorded here burned predominantly in chaparral, which sometimes forms a mosaic with coastal sage scrub, grassland, oak woodland, and coniferous forests. Early in the century, there may be a deficit of small fires because of incomplete reporting, but total area burned is not likely to be affected because small fires are a minor portion and large fires are less likely to have been missed.
9. Adjacent counties were combined for presentation purposes; statistical tests discussed in the text were performed on counties both separate and combined. Data for the 1990 decade were standardized by dividing the average for the first 8 years by 0.8.
10. For population density statistics, see www.census.gov/population/cencounts/ca190090.txt
11. For these counties, natural lightning-ignited fires typically make up less than 5% of all fires [J. E. Keeley, *U.S. Forest Serv. Gen. Tech. Rep. PSW-58* (1982), pp. 431–437].
12. M. A. Moritz, *Ecol. Appl.* **7**, 1252 (1997); P. J. Gee, thesis, University of California, Berkeley (1974).
13. Techniques introduced in the 1950s increased fire suppression potential [S. J. Pyne *et al.*, *Introduction to*

*Wildland Fire* (Wiley, New York, ed. 2, 1996)]. Additionally, because of low rates of decomposition in these ecosystems, if fire suppression were to result in fuel accumulation, the magnitude of this impact would be cumulative with time and be greatest in the latter half of the century.
14. Compare B. D. Malamud, G. Morein, D. L. Turcotte, *Science* **281**, 1840 (1998).
15. F. W. Davis and D. A. Burrows [in *Patch Dynamics*, S. A. Levin *et al*., Eds. (Springer-Verlag, New York, 1993), pp. 247–259] predicted that anthropogenically driven landscape fragmentation would increase the fire return interval; their model is sensitive to ignition frequency and most applicable to central-coastal counties, which have not experienced marked increases in fire frequency.
16. Fires over 40 ha from 1925 to 1996; Santa Monica Mountains National Recreation Area, U.S. National Park Service.
17. *Sierra Nevada Ecosystem Project Final Report to Congress* (Centers for Water and Wildlife Resources, University of California, Davis, 1996), vol. II, pp. 1033–1202.
18. J. E. Keeley, in *North American Terrestrial Vegetation*, M. G. Barbour and W. D. Billings, Eds. (Cambridge Univ. Press, Cambridge, 1999), pp. 201–251.
19. C. M. Countryman, *U.S. Forest Serv. Gen. Tech. Rep. PSW-7* (1974).
20. S. G. Conard and D. R. Weise [*Tall Timb. Fire Ecol. Conf. Proc.* **20**, 342 (1998)] found no evidence that fire suppression affected fire size in the San Bernardino National Forest and recommended strategically placed fuel management zones in the wildland areas (that is, fuel breaks) coupled with intensive fire risk management zones to protect the wildland-urban interface.
21. T. D. Bradshaw, *U.S. Forest Serv. Gen. Tech. Rep. PSW-101* (1977), pp. 15–25; J. B. Davis, *Fire Manag. Notes* **50**, 22 (1989).
22. R. Z. Callaham, *California's Shrublands* (Wildlife Resource Center Report 5, University of California, Davis, 1985).
23. We thank C. Gray, M. Moritz, and J. Woods for assistance and J. Agee, M. Borchert, F. Davis, J. Greenlee, C. Skinner, and N. Stephenson for comments.

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# Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests

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**The incidence and importance of fire in the Amazon have increased substantially during the past decade, but the effects of this disturbance force are still poorly understood. The forest fire dynamics in two regions of the eastern Amazon were studied. Accidental fires have affected nearly 50 percent of the remaining forests and have caused more deforestation than has intentional clearing in recent years. Forest fires create positive feedbacks in future fire susceptibility, fuel loading, and fire intensity. Unless current land use and fire use practices are changed, fire has the potential to transform large areas of tropical forest into scrub or savanna.**

Fire is recognized as a historic but infrequent element of the Amazonian disturbance regime (*1*, *2*). Currently, however, fires in Amazonian forests are frequent because of the accidental spread from nearby pastures and the increased susceptibility of partially logged or damaged forests (*3*–*6*). Here, positive feedbacks associated with accidental forest fires are reported; these constitute a threat to the integrity of a large part of the Amazonian forest.

Field studies were concentrated in the Tailândia region (Fig. 1). Ten 0.5-ha plots (eight fire-affected and two control), spread over 100 km$^2$, were established in 1996 to study fire impacts on forest structure, biomass, and species composition (*3*). These plots were recensused after the dry season of 1997, during which eight of the plots burned to varying degrees. Fire recurrence, tree mortality, and biomass combustion levels within forests of different burn histories were quantified. In addition, combustible fuel mass was assessed with the planar intersect method (*7*) as adapted by Uhl and Kauffman (*8*, *9*).

We also examined characteristics of fires while they were occurring in four forest types (previously unburned, once-burned, twice-burned, and more than two previous burns) in December 1997. Direct observations of fires were made at widely scattered locations within a 150-km$^2$ area south of Tailândia. For each observed fire, flame heights and depths (the width of the flaming front) were measured or estimated (*10*). The time the fireline took to move across a known distance was used to calculate the rate of spread and was combined with flame depth data to calculate the average range of flame residence times at a point. Flame height was used as a conservative estimate of total flame length for the calculation of fireline intensity (*11*) because wind and slope were minimal (*12*).

The first fire to enter a forest usually moves slowly along the ground (Table 1) and is similar to a prescribed burn ($<$50 kW m$^{-1}$) in intensity (*13*). These fires consume little besides the dry leaf litter, but because of the characteristically thin tree bark [7.3 $\pm$ 3.7 mm for $>$20 cm diameter at breast height (dbh) (*8*)] protecting the cambium tissues, they still kill roughly 95% of the contacted stems $>$1 cm dbh. Large, thicker barked trees survive. After the fire, a rain of combustible fuels of all sizes falls from the standing dead trees (Table 1) (*14*). Fire damage and windthrow in these thinned forests continue to cause mortality for at least 2 years after the fire (*4*, *15*). Fuel levels rise substantially and the open canopy (50 to 70% cover) allows greater solar heating and air movement to dry out the forest fuels. Previously burned forests thus become susceptible to fire during common dry season weather conditions (*3*).

Previously burned forests were much more likely to burn than were unburned forests in 1997 (Table 1). Burned forests are often adjacent to fire-maintained pasture and agricultural plots and are therefore frequently exposed to sources of ignition. Second fires are faster moving and much more intense. We estimate heat release (*12*) of $<$7500 kW m$^{-2}$ in first burns but of 75,000 kW m$^{-2}$ or more in subsequent burns. Because of the increased flame depth, the residence time increases despite faster rates of spread, resulting in greater tree mortality. Large trees have little survival advantage during these more intense fires. Fire-induced tree mortality can be modeled as a function of bark thickness and fire residence time (*16*). For the observed fire characteristics and bark thickness distribution (*8*), no more than 45% of trees over 20 cm dbh are susceptible to fire-induced mortality in the initial fires. However, in recurrent fires, up to 98% of the trees become susceptible to fire-induced mortality.

The impacts of recurrent fires are much worse than those of initial fires. Higher mortality results in a very open canopy (10 to 40% cover), large inputs of combustible fuels, and faster drying. During the 1997 fires, substantial amounts of carbon were released to the atmosphere, with combustion reducing onsite biomass by approximately 15, 90, and 140 Mg ha$^{-1}$ in first, second, and recurrent burns, respectively. Invading grasses and weedy vines add highly combustible live fuels to the already

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# Historic Fire Regime in Southern California Shrublands

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**Abstract:** *Historical variability in fire regime is a conservative indicator of ecosystem sustainability, and thus understanding the natural role of fire in chaparral ecosystems is necessary for proper fire management. It has been suggested that the "natural" fire regime was one of frequent small fires that fragmented the landscape into a fine-grained mixture of age classes that precluded large, catastrophic fires. Some researchers claim that this regime was lost because of highly effective fire suppression and conclude that if fire managers could "restore" a regime of frequent fires with widespread prescription burning, they could eliminate the hazard of catastrophic fires. The primary evidence in support of this model is a study that compared contemporary burning patterns in southern California, U.S.A., a region subject to fire suppression, with patterns in northern Baja California, Mexico, where there is less effective fire suppression. We found that differences in fire regime between these two regions are inconclusive and could not be ascribed conclusively to differences in fire suppression. Historical records suggest that the natural fire regime in southern California shrublands was rather coarse-grained and not substantively different from the contemporary regime. There is no evidence that fire-management policies have created the contemporary fire regime dominated by massive Santa Ana wind-driven fires. Increased expenditures on fire suppression and increased loss of property and lives are the result of human demographic patterns that place increasing demand on fire-suppression forces.*

Régimen Histórico de Incendios en Zonas Arbustivas del Sur de California

**Resumen:** *La variabilidad histórica del régimen de incendios es un indicador conservador de la sostenibilidad del ecosistema y por lo tanto se necesita conocer el papel natural del fuego en ecosistemas de chaparral para un manejo adecuado. Se ha sugerido que el régimen 'natural' de incendios estuvo compuesto por pequeños incendios que fragmentaron el paisaje en una mezcla de grano fino de clases de edades que previno incendios grandes catastróficos. Algunos investigadores aseguran que este régimen se perdió debido a la alta efectividad en la suspensión de incendios y concluyen que si los manejadores de incendios pudieran 'restaurar' un régimen de incendios frecuentes mediante la prescripción de quemas dispersas se podrían eliminar los peligros de los incendios catastróficos. La evidencia primaria en apoyo a este modelo es un estudio que comparó los patrones contemporáneos de incendios en el sur de California, USA (sujeto a supresión de incendios) con patrones del norte de Baja California, México (con menor supresión efectiva de incendios). Encontramos que las diferencias en el régimen de incendios entre estas dos regiones son inciertas y que estas diferencias no se pueden atribuir conclusivamente a las diferencias en supresión de incendios. Los registros históricos sugieren que el régimen natural de incendios en las zonas arbustivas del sur de California fue mas bien de un grano grueso y no fue sustancialmente diferente al régimen contemporáneo. No existe evidencia de que las políticas de manejo de incendios han creado el régimen contemporáneo de incendios dominado por fuegos masivos conducidos por vientos de Santa Ana. El incremento en gastos para la supresión de incendios y el incremento en la pérdida de propiedades y vidas son el resultado de patrones demográficos que colocan una demanda creciente en la supresión de incendios.*

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## Introduction

The types of inferences drawn from observations differ among disciplines and often contribute to scientific disputes, such as the controversy over the natural fire regime in southern California and Baja California shrublands (Minnich 1983; Keeley et al. 1989; Moritz 1997; Conard & Weise 1998; Zedler & Oberbauer 1998; Minnich & Franco-Vizcaino 1999). We examined the evidence from past fire regimes, the inferences drawn from those observations, and the implications for contemporary fire management of southern California shrubland ecosystems.

Understanding the natural role of fire in any ecosystem has value beyond merely satisfying curiosity. Modern land managers are increasingly concerned with sustainable, ecosystem-level management, and the historical variability in fire regime is considered a conservative indicator of sustainability (Millar 1997). We know from empirical studies that diversity in chaparral is threatened by fire frequencies that are too high (Keeley 1995), and theoretical studies suggest that very low frequencies may also be a threat (Zedler 1995). Thus, an understanding of natural fire regimes may provide useful guidelines for future management.

## Reconstructing the Natural Fire Regime in California Shrublands

Some ecosystems, such as the ponderosa pine–dominated forests in the western United States, have a well-documented fire history (Skinner 1997). Fire scarred trees indicate that low-intensity surface fires were common prior to European colonization, and fires have largely been suppressed during the twentieth century. In contrast, California shrublands burn in stand-replacing crown fires that kill all aboveground biomass; thus, we lack a precise historical record of fires. Consequently, conclusions about the historical role of fire in chaparral will always be more controversial than those for many other forested ecosystems.

One attempt to fill this void of historical information was a Landsat remote imagery study (Minnich 1983) comparing a 9-year record (1972–1980) of burning in chaparral and coastal sage shrublands between southern California and Baja California and demonstrating differences in burning patterns north and south of the U.S.–Mexico border (Fig. 1a). It was posited by Minnich (1983, 1989, 1995, 1998) that because fire suppression was not practiced in Mexico, the burning patterns observed south of the border reflected the "natural" condition for southern California. This regime was hypothesized to be one of frequent, small fires that fragmented the landscape into a fine-grained mixture of age classes that precluded large, catastrophic fires. Minnich claimed that the primary reason this natural regime had been lost in southern California was the practice of highly effective fire suppression. Further, he proposed that if fire managers could "restore" a natural fire regime of frequent, small fires through prescription burning, they could eliminate the hazard of catastrophic fires in southern California. This philosophy is currently reflected in fire-management plans for all southern California national forests (Conard & Weise 1998). Because of the social, economic, and political implications of these ideas, they deserve critical examination.

## Evaluating the Baja California Model

Minnich's (1983) study, represented in Fig. 1a, has an inherent bias that has not been widely appreciated. Although the figure legend in the original paper purported to show only the difference in burning patterns as observed from Landsat remote imagery over a 9-year period (1972–1980) in both Baja and southern California, the figure was biased by the inclusion of two massive fires (1932 and 1970) in southern California that were outside the comparison period. These two fires were the largest in California's history and were mapped from U.S. Forest Service records not available for Baja California. With these two fires removed (Fig. 1b), the differences are far less striking and the conclusion that large fires are restricted to north of the border is called into question. Strauss et al. (1989) examined only the legitimate Landsat imagery comparison (Fig. 1b) and found no evidence of differences between the regions north and south of the border (cf. Chou et al. 1993).

Later studies (Freedman 1984; Minnich 1989, 1995, 1998; Minnich & Dezzani 1991) used historical aerial photographs of Baja California to compensate for the detailed records available north of the border. These studies concluded that, in contrast to the situation in southern California, large fires were absent from Baja California as far back as 1920.

Techniques used to achieve a long-term absence of large fires in Baja California make it difficult to embrace this finding. Studies by Minnich were based on three aerial photographic records, 1938, 1956, and 1972, representing a 16- to 18-year gap between photographs. Minnich contended he was able to detect all fire boundaries that had occurred during the gap between photographs; fire perimeters were even drawn back to 1920, despite a lack of photographs before 1938. The support for this procedure was the author's testimony that he could detect known fire perimeters many years after a fire. A more rigorous and acceptable scientific procedure is the use of a "blind control," in which an observer is asked to detect patterns without prior knowledge of fire perimeters. Although we do not doubt that localized fires known to the observer may remain detectable from aerial photographs for a decade or more, large fires not known to the observer, particularly ones with borders that extend beyond the scale of the photograph, may not be recogniz-

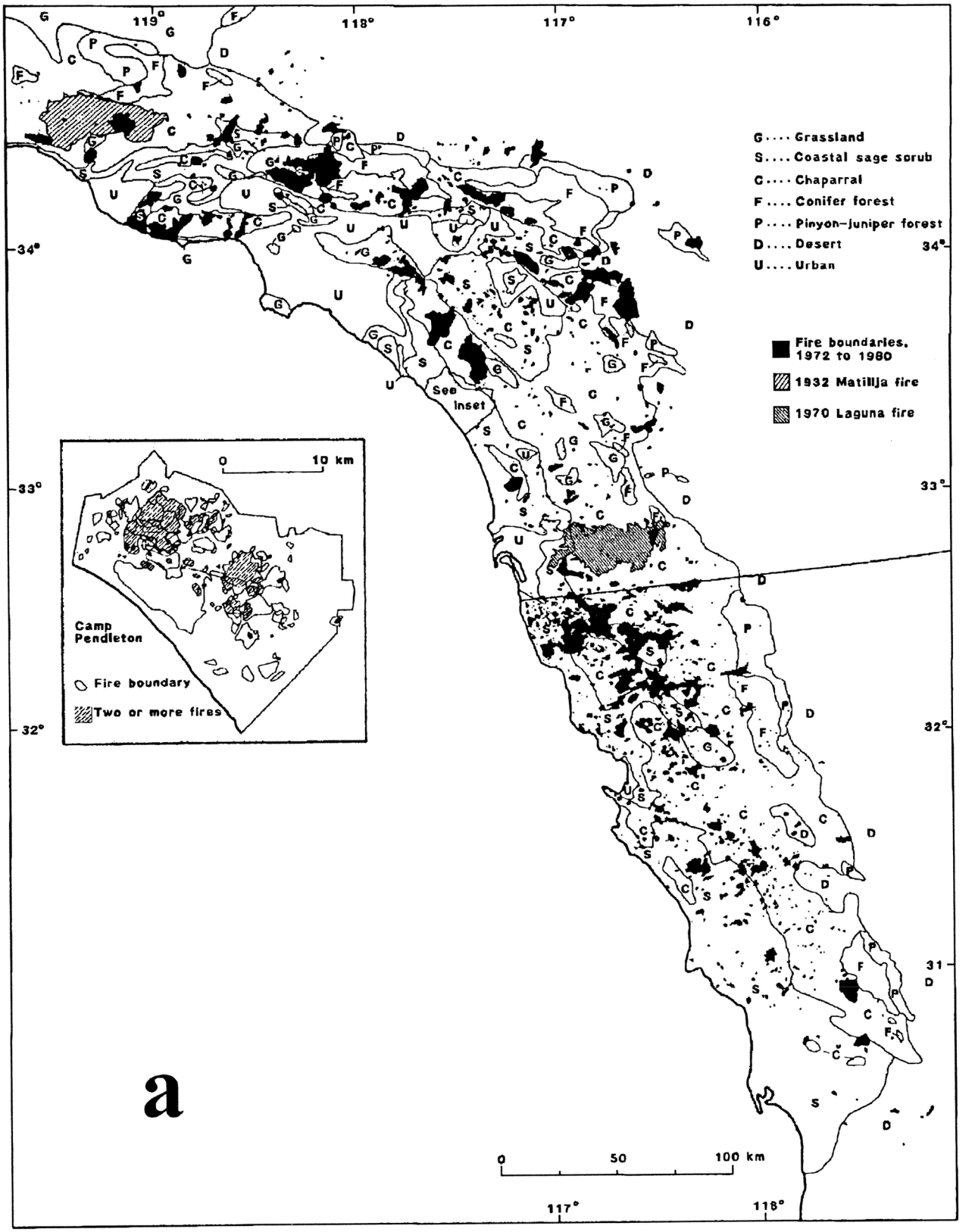


*Figure 1. Figure 1 from Minnich (1983) showing (a) "Wild-land fires in southern California and northern Baja California, 1972 to 1980. . .[D]ata were mapped from Landsat imagery." Although not stated in the original figure legend, (a) includes the two largest fires in California history, which occurred outside the Landsat imagery period. (b) Wildland fires in southern California, and northern Baja California, with large fires that fell outside the Landsat imagery study removed. We acknowledge permission of the American Association for the Advancement of Science to reprint Fig. 1 from Minnich (1983, Science* ***219:****1288).*

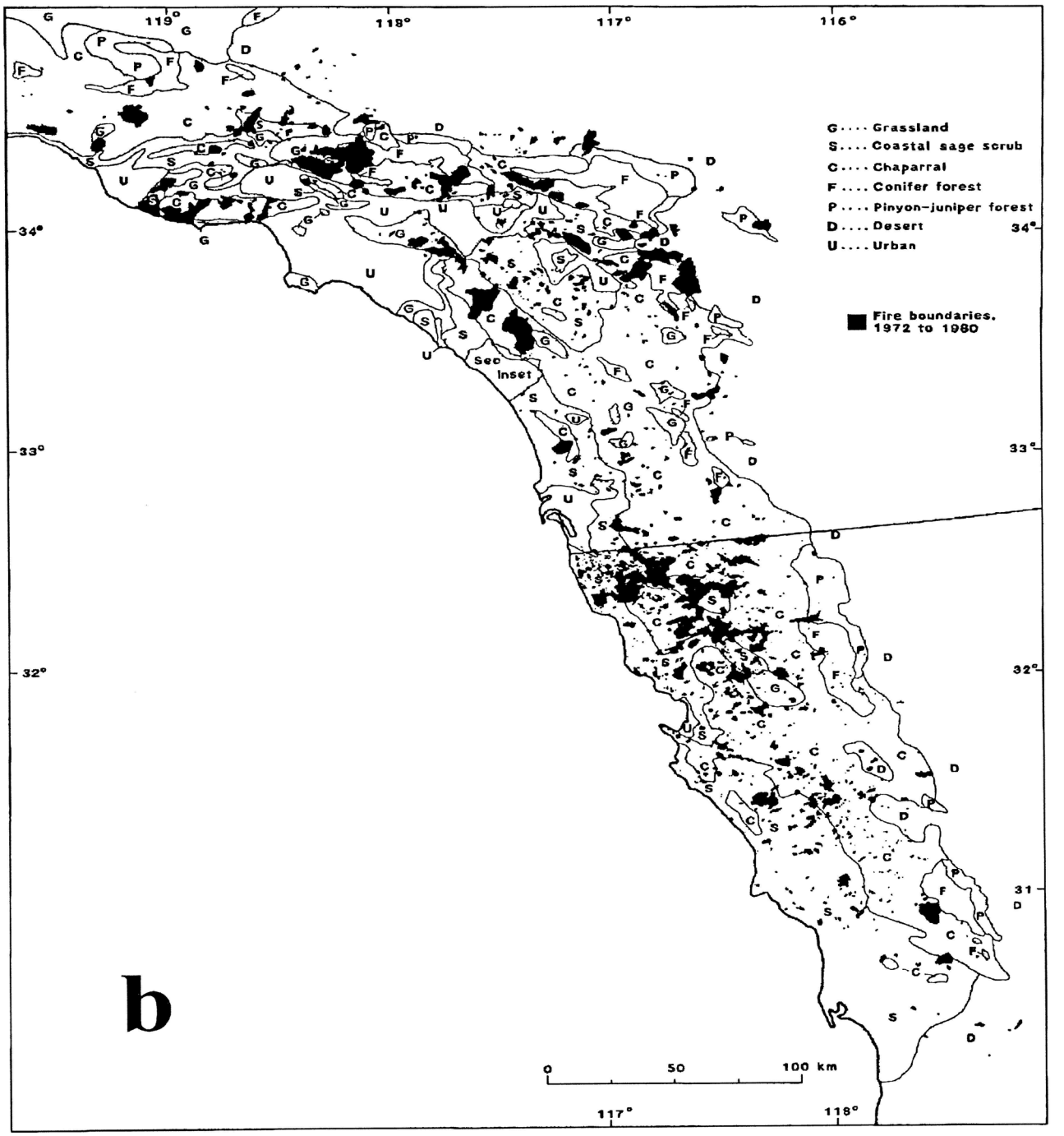


*Figure 1. continued*

able 16–18 years after a fire. At the very least, many researchers would require proof of such detective ability before drawing inferences about fire history. Such evidence is particularly important because several authors have reported large fires in northern Baja California (e.g., Henderson 1964; Haiman 1973; Amaya 1991).

In general, historical data for Baja California do not approach the quality of the written records available north of the border, so, beyond recent Landsat records, we know relatively little about the fire history of that region (Fig. 1b). Further, it is debatable whether or not the Landsat images demonstrate significant differences between southern California and northern Baja California (e.g., Strauss et al. 1989; c.f. Chou et al. 1993). But assuming, for the sake of argument, that one accepts the inference that differences exist, there is still much room for doubt as to the explanation for them. Minnich (1983, 1989, 1995, 1998) assumes that fire suppression policy is the only relevant

difference between southern California and Baja California, but this contention has never been demonstrated rigorously. More important, this conclusion is unwarranted in the absence of consideration of potential differences in landscape, climate, and land use between southern California and Baja California.

Factors that need serious consideration before one can accept the contemporary Baja California burning regime as representative of the "natural" southern California fire regime include the following: (1) There is an extraordinary difference in fire frequency between regions north and south of the border. (2) Fire climates are not entirely comparable north and south of the border. (3) Climates and soils differ between the two regions in ways that could affect patterns of fuel production. (4) Landscape characteristics in Baja California may be less conducive to large fires such as those that occasionally occur north of the border. (5) There are many differences in land use between these regions, some of which could contribute to differences in patterns of burning.

### Difference in Fire Frequency

Fire prevention is much less effective in Baja California and thus, due to human ignitions, fire frequency is up to five times greater there than in southern California (Minnich 1989, 1995; Minnich & Dezzani 1991; Henderson 1964; Haiman 1973; Keeley 1982; Freedman 1984). North of the border, the only place one sees a similar number of human-caused fires is on Camp Pendleton Marine Base, and these data were excluded from the earlier analysis of southern California because of "anomalously high ignition rates" (Minnich 1983). Higher ignition rates in Baja California are reflected in the marked differences observed in the amount of burning immediately north and south of the border (Fig. 1b).

Minnich et al. (1993) argue that in Baja California the larger number of human-caused ignitions is irrelevant in determining the mosaic pattern of burning because, even without this human subsidy, ignitions from lightning would be saturating. They reported approximately one lightning strike per 1000 ha per year in shrubland ecosystems of northern Baja California. No data were presented on the percentage of these strikes that ignite fires, and there was no direct evidence of saturation per se. Relative to other regions such as the southwestern United States (Reap 1986), northern Baja California experiences a low density of lightning strikes.

Saturation implies that additional ignitions will not affect fire frequency and burning patterns. Inconsistent with the notion of saturation is Haiman's (1973:174) report that in surveys of residents in the Sierra Juárez of northern Baja California, the major complaint was "directed towards the traditional ranchero activity of burning the montane ranges during the summer months." If lightning-ignited fires were "saturating," then the ranchero activities would not add to the fire regime and pose a risk to the local residents. It is implied by Minnich et al. (1993) that lightning saturates the environment north of the border as well, which would be evident if fire suppression did not extinguish these natural fires. But countless examples of humans subsidizing natural ignitions are noted to have occurred long before active fire suppression in southern California, beginning with the nineteenth-century settlement period (Barrett 1935; Brown & Show 1944; Lee & Bonnicksen 1978). Also, the assumption that lightning ignitions are saturating in the southern California environment is called into question by the fact that area burned is correlated with number of fires ($r^2 = 0.71$), which is correlated with population density (Keeley et al. 1999). Humans affect fire frequency, and this effect appears to be much greater south of the border. Even if lightning-ignited fires were saturating in Baja California, humans ignite fires far outside the natural fire season (Henderson 1964; Haiman 1973; Freedman 1984), and this alone could greatly alter natural burning patterns.

### Comparability of Fire Climates

Massive fires in southern California are commonly driven by foëhn-type Santa Ana winds, but these winds diminish south of the border (Henderson 1964; Mitchell 1969; Markham 1972; Pyke 1972; Haiman 1973; Freedman 1984). Although these winds are controlled by regional synoptic patterns that include a Great Basin high-pressure cell and Pacific Coast trough of low pressure (Schroeder et al. 1964), their ultimate manifestation is a result of local topography (Fosberg et al. 1966; Schroeder & Buck 1970). For example, the steep eastern escarpment and lack of low passes precludes such foëhn winds on the western slopes of the southern Sierra Nevada. In Los Angeles County, these winds are funneled through passes in the east-west trending Transverse Ranges and thus are predominantly northern or northeastern winds (Edinger et al. 1964; Weide 1968). In San Diego County they are strictly eastern winds (Campbell 1906; Sommers 1978) because of the north-south orientation of the peninsular ranges. These ranges extend southward into Baja California, where the sharp eastern escarpment of the Sierra Juárez and the San Pedro Mártir, coupled with the Gulf of California to the east, limit the formation of foëhn winds (Henderson 1964).

Most fires in northern Baja California are driven by onshore northwestern breezes (Minnich 1983, 1989, 1998), and these have a different capacity for fire spread than fires driven by Santa Ana winds. Minnich contends that the absence of Santa Ana wind-driven fires south of the border is due to the lack of contiguous older stands of vegetation with fuel sufficient to carry fire. This conclusion is disputed by the fact that these winds diminish the further south of the border one goes, and the fact that in

southern California Santa Ana winds will drive fire through nearly any age class of fuel (Keeley et al. 1999).

### Factors Affecting Fuel Production

Annual precipitation is substantially different between the regions we compared. The "fire suppression zone" of southern California considered by Minnich (1983) extends northward to Santa Barbara and may have up to double the precipitation observed at comparable elevations in the "nonsuppression zone" of northern Baja California (Markham 1972; Pyke 1972; Haiman 1973) (Fig. 2). Haiman (1973) showed that winter cyclonic systems were more predictable in southern California than in Baja California, and that, for similar elevations and distance from the coast, only one out of six storms produced comparable precipitation at sites in northern Baja California. Also, half of the storms deposited more than 75% greater precipitation in San Diego County (Table 1). In addition, there is an earlier cut-off of late winter and early spring precipitation the further south of the border one goes (Pyke 1972). Although summer monsoon rains are more predictable south of the border, this input is of marginal importance because it comprises a small fraction of the annual precipitation. In addition, higher summer evaporative demand is thought to make much of it unavailable to shrubs (Minnich & Franco-Vizcaino 1999), as has been demonstrated for Arizona chaparral subject to similar summer monsoon rains (Vankat 1989).

Differences in precipitation between southern California and Baja California could have profound effects on primary productivity and rates of fuel production. Less fertile soils in Baja California chaparral (Franco-Vizcaíno & Sosa-Ramirez 1997) would further exacerbate differences in primary production. Although precise comparisons of primary production are not available, Freedman (1984) estimates that similar-aged chaparral stands have 40% less cover in Baja California than "comparable" sites north of the border. The positive correlation between precipitation and fire occurrence within the chaparral type north of the border in San Diego County is direct evidence that precipitation affects fire regime (Krausmann 1981). Slower fuel accumulation in Baja California could have profound effects on rates of fire spread and patterns of burning.

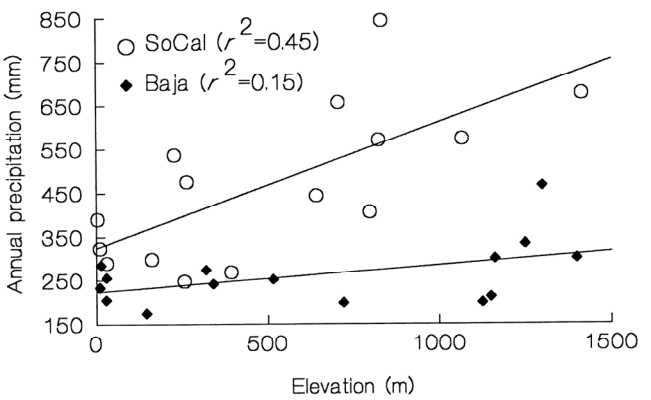


*Figure 2. Precipitation for selected sites at different elevations in southern California (SoCal) and northern Baja California (Baja). Relationship between precipitation and elevation is significant ($p < 0.01$) for southern California but not significant ($p > 0.05$) for Baja California (data from Henderson 1964; Haiman 1973; and National Oceanic and Atmospheric Administration, climatological data, annual summary).*

### Landscape Features

Differences in landscape have not been considered. Immediately south of the interior border crossing at Tecate, the topography changes and much of the chaparral-dominated landscape is a plateau, which lacks the topographic heterogeneity present north of the border (Haiman 1973). This is important in terms of both direct and indirect effects on fire regime. Rugged topography directly affects rate of fire spread through heating of adjacent fuels as well as creation of wind turbulence. Indirectly, rugged terrain in semiarid regions may lead to greater primary production and thus greater fuel production. For example, a plateau receives three times greater solar insolation than north-facing slopes, and this difference is not offset by south-facing slopes, which at these latitudes differ from flat surfaces by only 12% (Frank & Lee 1966). Higher solar insolation in this region likely translates into greater evaporative loss and less production on the Sierra Juárez plateau than in the adjacent San Diego County. Also, vegetation on slopes commonly receive underground water subsidies from upslope drainage (Rowe et al. 1954). These differences could have profound effects on primary production, fuel accumulation, and ultimately on fire regimes.

Also, in Baja California chaparral comprises about one-third less area than it does north of the border (Minnich 1989), and it typically is bordered by less flammable pinyon communities on the east (Minnich & Franco-Vizcaíno 1998). In all of northern Baja California there are few if any areas of contiguous chaparral the size of the massive Santa Ana–driven Matilija or Laguna fires recorded in southern California (Fig. 1a).

### Patterns of Land Use

Differences in land use may affect burning patterns. Working ranches north of the border are significantly larger than the legally mandated patchwork of small farms and ejidos south of the border (Henderson 1964), and on ejidos fire is used regularly to remove brush and expand grazing lands (Henderson 1964; Freedman 1984). In contrast, despite the thousands of permits issued by the State of California for brush burning since 1945, few ranch-

**Table 1. Comparison of precipitation in six storms during the winter of 1970-1971 among southern California and comparable sites in northern Baja California (from Haiman 1973).**

| *Location* | *Distance to coast (km)* | *Elevation (m)* | *Precipitation (mm)* |
|---|---|---|---|
| California (lat. 32°35′–32°55′) | | | |
| San Diego | 0 | 0 | 102 |
| Barrett Dam | 50 | 585 | 168 |
| Cuyamaca | 60 | 1305 | 201* |
| Baja California (lat. 31°50′–32°10′) | | | |
| Ensenada | 0 | 0 | 86 |
| Ojos Negros | 30 | 700 | 77 |
| San Juan Dios | 62 | 1250 | 84 |

*n = 5.

ers in southern California have applied for such permits (California Division of Forestry 1978). In addition, in many parts of Baja California such as the Sierra Juárez, cattle graze over much of the chaparral lands (Henderson 1964), reducing fine fuels and physically trampling the shrubs (Freedman 1984), both of which affect fire spread.

## Model of the Natural Fire Regime in Southern California Shrublands

Parameters of a fire regime include the mean and variance in fire frequency, fire intensity and severity, and fire season. In California chaparral and coastal sage scrub, the contemporary fire regime is reasonably well documented (Rogers 1942, Keeley 1982, 1992, 1998; Minnich 1983, 1989, 1998; Dunn 1989; Moritz 1997; Conard & Weise 1998; Keeley et al. 1999). Fire-rotation intervals, which are regional averages, are 30–40 years, and the range is illustrated by site-specific fire-return intervals, which vary from $<5$ to $>100$ years. They are always crown fires, and although the number of fires peaks in the summer, the bulk of the area is burned in autumn (Fig. 3). Fire intensity and severity are variable, depending upon fuels, weather, and topography. The majority of contemporary fires are small ($10–10^3$ ha), and only a tiny percentage become large ($10^5–10^6$ ha). These large fires are usually coincident with weather conditions generated by foëhn winds known as Santa Anas in southern California, Mono winds in central California, northeastern winds in northern California (Schroeder et al. 1964), or more localized "sundowner" winds in coastal Santa Barbara County (Ryan 1996).

It is questionable whether or not these parameters are representative of natural (pre-human influence) conditions because of the opposing anthropogenic impacts of fire suppression and increased fire ignitions. It is our intent to start with this contemporary regime and evaluate the extent to which the natural fire regime may have deviated from this pattern.

Based on the highly significant relationship between wildfire ignitions and increasing population density during the twentieth century (Fig. 4), it is apparent that the contemporary fire frequency is markedly higher than what would be experienced in the absence of human subsidy. This human influence is spatially variable, being most prominent in wildland areas adjacent to coastal population centers and decreasing in influence in the in-

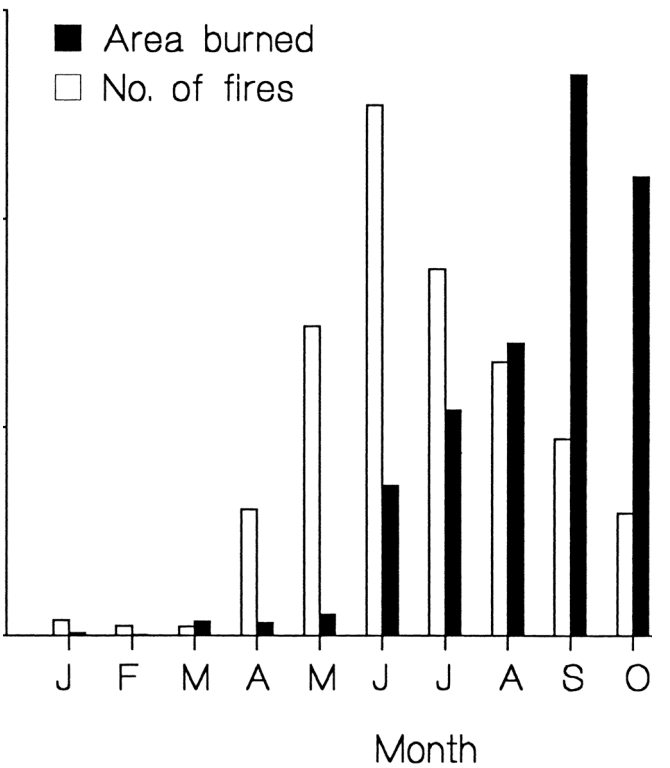


*Figure 3. Monthly distribution of fire frequency and area burned (1910 –1999) for Los Angeles County (data from the California Fire History Database, California Division of Forestry and Fire Protection, Fire and Resource Assessment Program, Sacramento).*

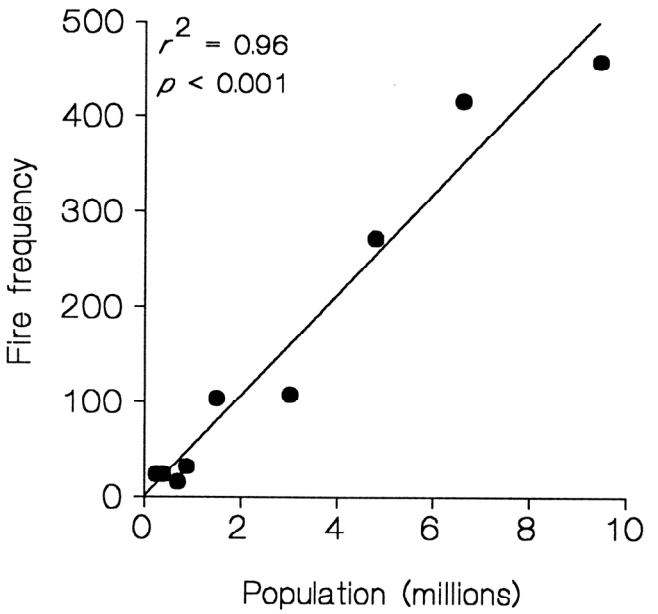


*Figure 4. Fire frequency each decade since 1910 versus population density at the beginning of each decade for Riverside and Los Angeles counties in southern California (data from Forstall 1998; Keeley et al. 1999).*

terior and at higher elevations (Keeley 1982; Keeley et al. 1999; Moritz 1999). This relationship between population density and number of fires has been noted since the early decades of the twentieth century (Brown 1945; Clar 1959).

Human fire subsidy began with the Native American occupation of California (Knowles 1953; Timbrook et al. 1982; Wickstrom 1987). Patterns of spatial variation were similar to those of contemporary anthropogenic effects, but, relative to contemporary California, were likely limited due to low population density and reduced mobility. Native Americans increased fire-return intervals in areas near coastal communities and surrounding slopes, but may have had limited effect on the broader landscape (Cooper 1922; Bolton 1927).

Under natural conditions, lightning is the only predictable source of ignition, but its importance varies spatially throughout the state in a pattern nearly opposite that of human-ignited fires (Keeley 1982). Thunderstorms are rare near the coast and most frequent at higher elevations in the interior. In the coast ranges east of Monterey, a 50-year record for the chaparral-dominated Pinnacles National Monument indicates only a single lighting-ignited fire (Greenlee & Moldenke 1982). In the coastal Santa Monica Mountains of southern California, no lightning-ignited fires have been recorded in the 60-year fire record (National Park Service fire records on file at the Santa Monica Mountains National Recreation Area Headquarters); lightning-ignited fires have been observed in this range (M. Morais, personal communication), but clearly they are not common.

In southern and central coastal California, lightning-ignited fires increase with distance from the coast and with elevation (Table 2). For example, the San Bernardino National Forest, the most interior forest with the highest elevation, has the highest density of lightning-ignited fires, most of which originate in coniferous forests. Even here, the density is not extraordinarily high, with an average of one lightning-ignited fire per year per 10,000 ha, which is more than an order of magnitude greater than the density in coastal foothills (Table 2).

### Model of the Natural Fire Regime

Lightning-ignited fires are spawned by thunderstorms concentrated in interior mountains in July and August. Historical accounts of fire in the San Gabriel and San Bernardino mountains of southern California during the latter quarter of the nineteenth century (Minnich 1978, 1987) give some insight into fire behavior that was unabated by active fire suppression. Although these fires were not necessarily all natural lightning-ignited fires (e.g., Leiberg [1899*c*] was certain that miners were responsible for much of this burning), they nonetheless provide some insight into fire behavior in the absence of fire suppression.

Several conclusions can be drawn from this record: (1) Presuppression chaparral fires were always stand-replacing fires that burned with "irregular" behavior, sometimes creeping through brush and other times raging, so fire intensity and severity were variable. (2) Fires would commonly burn for months before being extinguished by rain or natural barriers, but despite this long period of activity they often covered a relatively modest area (e.g., the 1898 Mt. Lowe Fire burned for 3 months and consumed only 2300 ha). (3) Fires occasionally would "hold over" in logs, even during rainstorms, to be reignited at a later time.

The lightning-ignited fires that burned slowly for months or "held over" in logs would certainly have been a ready source of ignition when the predictable Santa Ana winds began in September. Although this juxtaposition may not have occurred frequently, when it did occur it likely would have resulted in a massive landscape-scale burn. Indeed, these Santa Ana winds of 100 km per hour, coupled with extremely low relative humidity, can generate fires that may cover 30,000 ha in a day (Phillips 1971), and often such fires will burn for days at a time (Chandler 1963; Schroeder et al. 1964; Countryman 1974). Thus, we hypothesize that the majority of fires were small in the pre-suppression landscape, but the bulk of the landscape burned in a few large fires that occurred at unpredictable intervals in association with autumn foëhn winds.

Site-specific fire-return intervals were almost certainly highly variable, with some montane lightning hotspots experiencing fires every few decades and coastal sites

**Table 2. Total number of fires and hectares burned and percentage due to lightning during the 1970s for lower-elevation foothills (California Division of Forestry [CDF] jurisdiction) and higher-elevation interior mountains (U.S. Forest Service [USFS] national forests) in southern and central-coastal California (from Keeley 1982).**

| *CDF ranger unit / USFS national forest* | *Total no. of fires* (per $10^6$ hectares per decade) | *Total area burned (ha)* (per $10^6$ hectares per decade) | *No. due to lightning (%)* | *Area due to lightning (%)* |
|---|---|---|---|---|
| Foothills (CDF) | | | | |
| Monterey/San Benito | 3,140 | 53,570 | 2 | <1 |
| San Luis Obispo | 3,310 | 44,130 | 2 | <1 |
| San Bernardino | 9,680 | 12,240 | 4 | 11 |
| Riverside | 17,620 | 332,950 | 1 | 5 |
| Orange | 42,900 | 120,830 | <1 | <1 |
| San Diego | 9,450 | 20,930 | 3 | 6 |
| Mountains (USFS) | | | | |
| Los Padres | 2,340 | 49,720 | 9 | 56* |
| Angeles | 4,980 | 214,460 | 15 | 4 |
| San Bernardino | 4,400 | 41,030 | 24 | 6 |
| Cleveland | 4,870 | 121,370 | 11 | <1 |

**Much of this is due to a single lightning-ignited fire (Marble Cone fire) in 1977.*

remaining fire-free for a century or more. Regional rotation intervals were likely longer than at present, perhaps 70 years or more for interior regions (Minnich 1989, 1998; Conard & Weise 1998) and presumably much longer near the coast. In short, the fire regime was one of localized fires, punctuated by periodic massive fires, a pattern predicted by modeling studies of the central coastal chaparral (Greenlee & Langenheim 1990).

### Pros and Cons of the Fire Model

It could be argued that, despite the potential temporal juxtaposition of lightning-ignited fires prior to the severe autumn fire-weather conditions, frequent lightning fires that burned under moderate weather conditions would create a fine-grained mosaic of young age classes, capable of acting as a barrier to the spread of large Santa Ana–driven fires (Minnich 1989, 1995, 1998). Often cited in support of such a model are the nineteenth century forest-reserve surveys made by U.S. Geological Survey scientist John Leiberg in the San Gabriel, San Bernardino, and San Jacinto mountain ranges. These documents are extremely important because they represent some of the few descriptions of chaparral shrublands prior to fire control. One quote by Leiberg (1899*a*) is often cited in support of the age-mosaic model: "Recent fires—that is to say, within the last eight or ten years—have burned over about 14,000 or 15,000 acres [approximately 5920 ha] scattered throughout the reserve in small tracts."

At a landscape scale, however, Leiberg's comments do not describe a fine-grained age mosaic capable of preventing Santa Ana–driven fires. Indeed, Leiberg was reporting on the total burning observed across the 214,575 ha of brush on the San Jacinto Reserve (Leiberg 1899*a*, 1900*c*). Thus, according to his estimate, only about 2.8% had burned during the last decade of the nineteenth century (similar proportions appear to apply to the San Gabriel and San Bernardino reserves [Leiberg 1899*b*, 1900*a*, 1900*b*; Kinney 1887]). At this rate of burning it is estimated that, at any point in time, over 90% of the chaparral in the San Jacinto Reserve would have been three or more decades old, which surely describes a landscape capable of fueling a large, catastrophic Santa Ana–driven fire. Any lack of large fires at the turn of the century was not due to limited fuels but more likely to limited ignitions coincident with severe fire weather. Today, higher population density in the San Jacinto Range produces a greater number of ignitions, resulting in a rate of burning more than three times that observed by Leiberg (U.S. Forest Service, unpublished data).

It is hypothesized that, given sufficient time—half a century or more—most chaparral regions would have experienced the proper juxtaposition of lightning-ignited fires followed by severe fire-weather conditions to result in massive landscape-scale fires. On the time scale of centuries, fire-rotation intervals likely varied due to stochastic factors, although on longer time scales changes in climate might have altered return intervals as well (e.g., Swetnam 1993).

Illustrative of the natural pattern is the 72,400-ha Marble Cone fire ignited by lightning on the Los Padres National Forest in 1977 (Davis 1977). Some suggest that this fire resulted from unnatural fuel accumulation due to half a century of fire suppression. There was nothing unnatural about the Marble Cone Fire, however, because a similar-sized fire (60,700 ha) occurred in the same area in 1906, prior to active fire suppression (Greenlee & Moldenke 1982), and other large fires were recorded even earlier (Talley & Griffin 1980). Although the Marble Cone fire was not driven by foëhn-type winds, it did occur under severe fire-weather conditions. Another lightning-ignited

fire on the Los Padres Forest in 1999 (the Kirk Complex Fire) illustrates that, under severe weather conditions, fires are not blocked by young stands of chaparral, because the Kirk Fire reburned much of the Marble Cone burn (M. Borchert, personal communication).

Other massive chaparral fires are also known from historical records prior to effective fire suppression. For example, one of the largest fires in Los Angeles County (24,000 ha) occurred in 1878 (Keeley et al. 1999). The largest fire in Orange County's history burned over a quarter million hectares in 1889 (Lee & Bonnicksen 1978); Kinney (1900), Barrett (1935), Brown and Show (1944), and Brown (1945) provide further examples of large chaparral fires prior to fire suppression. As is the case today, some of these historical fires were of sufficient intensity to severely denude slopes, resulting in catastrophic flooding, and this occurred often enough to be the primary impetus for the creation of California's first federal forest reserve—the San Gabriel Timberland Reserve—in 1892 (Lee & Bonnicksen 1978).

Paleoecological records reveal that these large fires driven by Santa Ana winds were a prominent feature of the landscape long before European settlement (Mensing et al. 1999). In the Santa Ynez Range of Santa Barbara County, massive Santa Ana–driven fires have occurred several times per century over the past 560 years, a frequency that did not change during the settlement period or following fire suppression.

The contemporary fire regime in southern California shrublands mirrors the natural fire regime far more closely than is generally credited (c.f., Bonnicksen & Lee 1979; Minnich 1983, 1995, 1998; Davis 1995; Pyne 1995). As is the case today, the natural fire regime was likely characterized by many small fires and a few large fires that consumed the bulk of the landscape. Fire intensity and severity were variable, as is the case today. The majority of fires occurred in summer, but in all likelihood the bulk of the landscape burned during autumn, when fuels were at their driest and weather conditions the most severe. This pattern has not changed today (Fig. 3). The primary change in the fire regime has been the marked increase in fire frequency in areas of high population density such as southern and central coastal California (Moritz 1997, 1999; Conard & Weise 1998; Keeley et al. 1999). One consequence of this shorter fire-return interval has been widespread conversion of shrublands to non-native annual grassland (Keeley 1990; Minnich & Dezzani 1998). Today, fire suppression is required just to maintain some semblance of the natural fire regime (Conard & Weise 1998).

## Implications for Fire Management

Fire-management plans in southern California national forests have placed inordinate stock in the notion that fire suppression has been sufficiently effective to allow unnatural fuel accumulation, which has led to an unnatural fire regime that includes large, catastrophic wildfires. Fire suppression, however, has not effectively reduced the area burned (Conard & Weise 1998; Keeley et al. 1999; Moritz 1999). Also, large Santa Ana–driven fires are not dependent on an unnatural accumulation of fuel; rather, they appear to be a natural feature of this landscape (Mensing et al. 1999). The important implication of these findings is that we have not, through fire management policies, created the contemporary fire regime.

Nevertheless, nearly every decade in the twentieth century has been characterized by increased expenditure for fire suppression and greater losses of property and lives (California Department of Forestry and Fire Protection 1999). We propose that both increased fire-suppression costs and increased property loss are best explained by changes in human demography.

For much of this century, wildland fire frequency has been driven by population density (Fig. 4): more people on the landscape equals more fires. Because both state and federal fire-suppression funds are available on an as-needed basis (Mutch 1997), every decade requires more fire suppression just to maintain some semblance of status quo. In short, increased expenditure on fire suppression is a direct result of increased fire ignitions, coupled with increasingly sophisticated and expensive fire-fighting technology.

The determining factor in whether or not a fire becomes large is the coincidence of an ignition with severe fire weather. Indeed, nationwide, weather during fire is considered the most important determinant of the costs of suppression (Schuster et al. 1997). Fires ignited under severe weather conditions defy suppression, however, and thus fire managers have made limited progress in reducing the number of catastrophic fires. To their credit, though, the number of such fires has not greatly increased either. Indeed, fire suppression has become increasingly effective when measured as the area burned per number of fire starts (Keeley et al. 1999).

Why then does the loss of property and lives increase every decade? The primary culprit is the fact that growth in southern California cities has not come from changes in density but rather from expansion of boundaries, a pattern evident in cities in other parts of the United States and the world (Knight & Gappert 1989). Consequently, there has been an extraordinary expansion of the urban-wildland interface and a changing pattern of mixed urban and wildland patches (Davis 1989). During the twentieth century, changes in the fire regime have been dwarfed by changes in land-development patterns, which have made more people vulnerable to the natural forces long present on the landscape (Zivnuska & Arnold 1950; Davis 1965; Bradshaw 1987). Illustrative of this is the fact that in the 60-year period prior to 1980, 3802 structures were destroyed by wildfires in California; in the subse-

quent 14 years the number more than doubled (Coleman 1996). Further adding to the financial losses is the steady increase in property values attendant with economic inflation.

Management plans that call for widespread prescription burning to "recreate" a landscape mosaic of different age classes of vegetation will not stop large, catastrophic fires (Moritz 1997, 1999; Conard & Weise 1998; Keeley et al. 1999). We do not suggest that prescription burning is no longer an effective management tool. Under moderate weather conditions, young vegetation age classes may play a critical role in enhancing effective fire suppression, and fire suppression under moderate weather conditions will not lead to catastrophic fires if weather conditions change abruptly. In light of the many limitations to prescription burning in California shrublands (Conard & Weise 1998), increasing demands will be placed on the most cost-effective use of such fire-management practices and will require further study as to the most strategic placement of prescribed burns. Across the California shrubland landscape, however, fire suppression is still one of the most important tools in the fire manager's arsenal.

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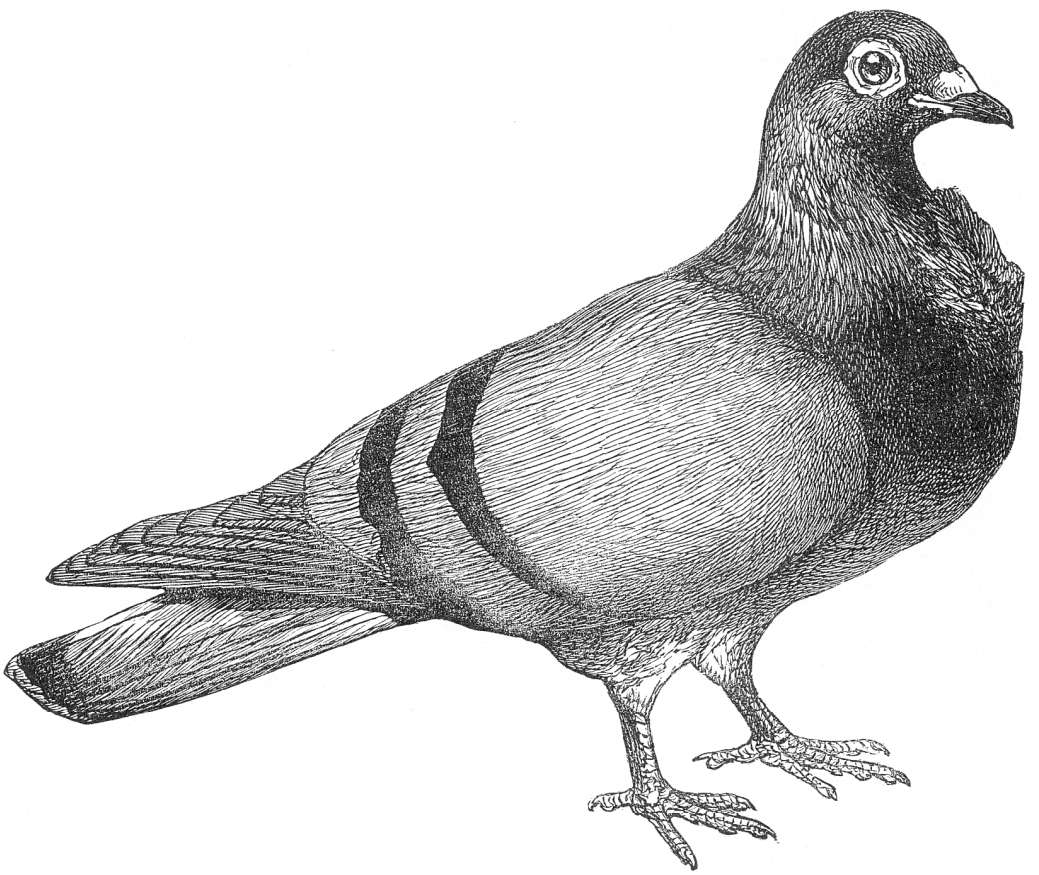

# 8. Impact of Past, Present, and Future Fire Regimes on North American Mediterranean Shrublands

Jon E. Keeley and C.J. Fotheringham

Mediterranean shrublands occur in five regions of the world, under a climate of mild wet winters and hot summer–fall droughts lasting six months or more. In California they dominate landscapes below 2000 m in the central and southern coastal ranges and foothills of the Sierra Nevada. One consequence of this distribution is that these shrublands, more than any other vegetation type, interface with urban areas (Fig. 8.1). These shrublands are subject to periodic massive wildfires (Fig. 8.2) that account for 40% of all wildland acreage burned in the United States (Lillard 1961), creating a particularly hazardous urban–wildland interface. Contributing to this fire hazard are the moderate temperatures during the rainy winter and spring, which prolong the growing season and generate broad bands of dense contiguous fuels. The long drought makes these fuels readily ignitable and the autumn foëhn winds that come each year at the end of the dry season produce the worst fire climate conditions in the country (Schroeder et al. 1964).

This chapter examines the past, present, and future fire regimes in California shrublands, particularly chaparral and coastal sage scrub. Although shrublands are recorded from nearly all counties in the state (Callaham 1985), this review will focus on those in the central and southern coastal ranges with the largest expanses of contiguous shrubland (Fig. 8.3). Of particular concern are the extent to which humans have altered this regime in the past and the extent to which future global change will affect fire regimes and vegetation patterns.

Humans directly influence fire regimes in two ways: they ignite fires and they suppress fires. Evaluating the net effect of these impacts is not simple because

**Figure 8.1.** Interface between urban environments and evergreen chaparral (*right*) and semi-deciduous coastal sage scrub (*left*) in southern California (by J.E. Keeley).

their relative importance varies across the landscape. For example, in the montane coniferous forests of the Southwest, lightning-ignited fires are abundant and human ignitions are far less important than in lower-elevation shrublands of southern California where lightning is uncommon and humans cause the majority of fires (Fig. 8.4). Also fire suppression has been far more effective in western coniferous U.S. forests, often achieving nearly complete fire exclusion (Skinner and Chang 1996; Agee 1993), but this "fire-suppression = fire-exclusion" equation does not apply to shrublands of southern and central coastal California (Keeley and Fotheringham 2001b).

## Determinants of Brushland Fire Regimes

Fire regimes are determined by the temporal and spatial pattern of ignitions, fuels, weather, and topography (Pyne, Andrews, and Laven 1996), and with regard to Californian shrublands there are two schools of thought on their relative importance. One is based on deductions from Rothermel's fire behavior model (Rothermel 1972) and argues that fire regime is a highly deterministic process driven by fuel load (Rothermel and Philpot 1973; Philpot 1974a,b, 1977). Under this model fire occurrence is unaffected by external drivers such as ignitions or weather, rather it is viewed as entirely dependent on community patterns of fuel accumulation (Minnich 1989, 1995,1998, 2001; Minnich and Cho 1997). The

**Figure 8.2.** Crown fire in chaparral (photo by USFS, Riverside Fire Lab).

alternative model argues that the fire regime is controlled by the coincidence of ignitions occurring under severe current and antecedent weather conditions that influence fuel flammability (Phillips 1971; Keeley et al. 1989; Davis and Michaelson 1995; Keeley and Fotheringham 2001a,b). Under this model any of these factors may be limiting, and the importance of each varies spatially and temporally with external drivers such as severe fire weather being of paramount importance in coastal California. These models have very different implications for fire management and affect our perception of anthropogenic impacts on fire regime and our ability to sort out future climatic signals.

## Patterns of Ignition

In order to appreciate fully the role humans play in shrubland fire regimes, we need to first examine how ignitions, fuels, and weather interact to determine fire behavior. In California humans have been a source of ignitions for more than

**Figure 8.3.** Central and southern California regions considered in this chapter. Central coastal California includes Monterey, San Luis Obispo, Santa Barbara, and Ventura counties, and southern California includes Los Angeles, San Bernardino, Riverside, Orange, and San Diego counties. Collectively these nine counties comprise nearly two million hectares of shrubland (Table 8.1).

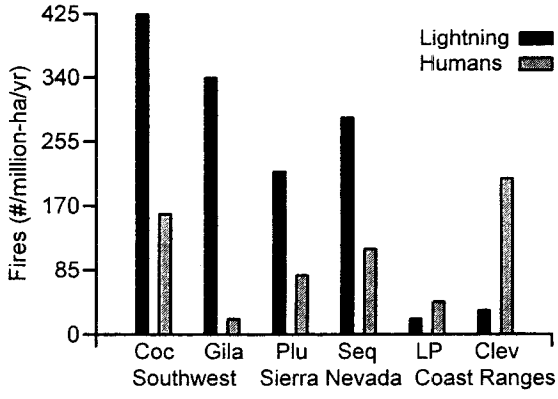


**Figure 8.4.** Regional comparison of lightning- and human-caused fires on USFS national forests. The Southwest includes the Coconino (Coc) in Arizona and Gilia in New Mexico. In California the Sierra Nevada forests are the Plumas (Plu) and Sequoia (Seq), and the California coastal ranges national forests are the Los Padres (LP) and Cleveland (Clev). Fire occurrence data from the published U.S. Forest Service, National Forest Fire Reports, 1970–1979, and forest area from (*http://www.fs.fed.us/land/*).

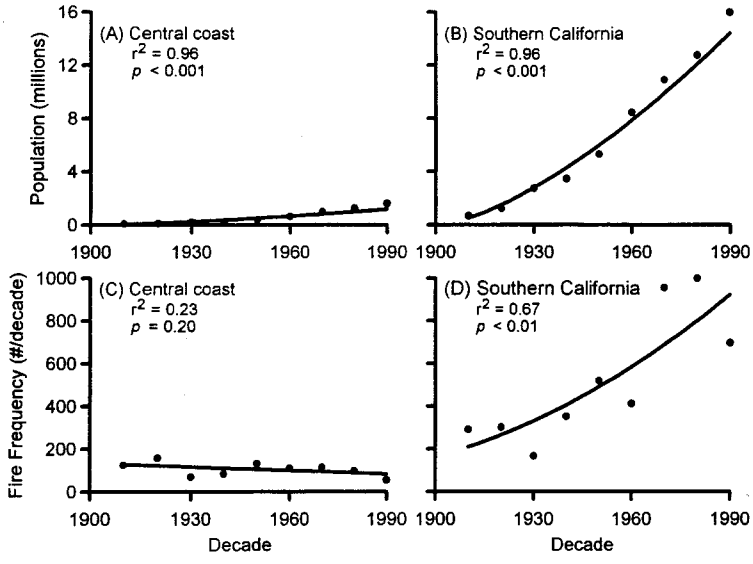


**Figure 8.5.** Decadal variation in population density (A–B) and fire frequency (C–D) for central coastal and southern California. Population data from the U.S. Department of Commerce, *http://www.census.gov/populations/cencounts/ca190090.txt.* (Fire data from the Statewide Fire History Data Base, California Department of Forestry, Fire and Resource Assessment Program (FRAP), Sacramento, CA, which includes historical fire records from the U.S. Forest Service national forests, California Division of Forestry ranger units and other protected areas, plus city and county records; minimum fire size recorded varied between 16 and 40 ha, depending on the agency).

10,000 years, but they likely have had a greater influence in the twentieth century due to the near exponential rise in population density and fire frequency in the southern part of the state (Fig. 8.5).

Under natural conditions lightning is a source of ignition but far less predictable than in other parts of the Southwest (Fig. 8.4). Within the state, lightning-ignited fires vary spatially because thunderstorms are rare near the coast and most frequent at higher elevations in the interior (Radtke, Atndt, and Wakimoto 1982; Keeley 1982; Greenlee and Moldenke 1982; Knipper 1998). Lightning is the dominant ignition source in the Sierra Nevada, but it is a far less common ignition source in the coastal ranges. Within the coastal ranges lightning varies with elevation; for example, in San Diego County lightning strikes are 10 times more abundant above 1800 m than below 500 m, and they vary temporally with 85% occurring between July and September (Wells and McKinsey 1994, 1995). Similar patterns are evident further south in Baja California (Minnich et al. 1993). The annual density of lightning discharges in this region is roughly 1 per 100 ha (Michael L. Wells, personal communication; Minnich et al. 1993). Based on the frequency of fires ignited by lightning in this region (Keeley 1982; Minnich et al. 1993), it would appear that only 2% to 5% of all lightning dis-

charges ignite a wildfire. In other words, 95% of all lightning discharges strike inadequate fuels, or are extinguished by rain, before they reach a detectable size.

Lightning ignitions in coastal and southern California shrublands account for a highly variable amount of burning, ranging from less than 1% to more than 50% of the landscape per decade (Table 8.1). Both spatial and temporal factors are involved. Considering all of California, lightning ignitions account for an increasing fraction of burning from the coast to the interior and from south to north (Keeley 1982). Occasionally lightning may coincide with severe weather and fuel conditions and result in massive fires such as the Marble Cone Fire in 1977 on the Los Padres National Forest (Table 8.1). Longer-term data sets for the Los Padres show this to be an infrequent event (Davis and Michaelsen 1995), suggesting that lightning fires in these coastal ranges are capable of reaching extraordinary size but the temporal variance is high.

Lightning is more predictable in the higher interior Sierra Nevada Range (Fig. 8.4), and it varies inversely with elevation (van Wagtendonk 1992). In Sequoia National Park (located in the southern Sierra Nevada, Fig. 8.3) lightning-ignited fires reach a peak at elevations between 2000 and 3000 m and are considerably less frequent in the lower-elevation shrubland-dominated foothills (Parsons 1981; Vankat 1985). Within the park the lower-elevation shrublands experience fewer lightning-ignited fires than would be expected based on shrubland area ($p < 0.001$ with $\chi^2$ test), and the opposite is true for higher-elevation mixed-coniferous forests. This pattern is repeated throughout the Sierra Nevada;

**Table 8.1.** Total number of fires and hectares burned and percentage due to lightning during the 1970s decade for lower-elevation foothills (California Division of Forestry Jurisdiction) and higher-elevation interior mountains (U.S. Forest Service national forests) in southern and central–coastal California

| CDF Ranger Unit/USFS National Forest | Total fires ($10^6$ ha/ decade) | Total area burned (ha) | Fires due to lightning (%) | Area due to lightning (%) |
|---|---|---|---|---|
| Foothills (CDF) | | | | |
| Monterey/San Benito | 3,140 | 53,570 | 2 | <1 |
| San Luis Obispo | 3,310 | 44,130 | 2 | <1 |
| San Bernardino | 9,680 | 12,240 | 4 | 11 |
| Riverside | 17,620 | 332,950 | 1 | 5 |
| Orange | 42,900 | 120,830 | <1 | <1 |
| San Diego | 9,450 | 20,930 | 3 | 6 |
| Mountains (USFS) | | | | |
| Los Padres | 2,340 | 49,720 | 9 | 56[a] |
| Angeles | 4,980 | 214,460 | 15 | 4 |
| San Bernardino | 4,400 | 41,030 | 24 | 6 |
| Cleveland | 4,870 | 121,370 | 11 | <1 |

*Source*: Keeley 1982.

*Note*: Sites are arranged from north to south, and national forest locations are shown in Figure 3. All of these ranger units or forests are dominated by chaparral, but they also include mixtures of grassland, sage scrub, woodlands, and forests.

[a]Much of this is due to a single lightning-ignited fire (Marble Cone Fire) in 1977.

foothill shrublands average about 10 lightning-ignited fires per year per million hectares and the higher-elevation montane forests experience 100 to 200 per year per million ha (Keeley 1982). Of course, making predictions about the elevational patterns of burning by lightning alone (i.e., in the absence of anthropogenic interference) is complicated by the likelihood that along this elevational gradient, conditions conducive to fire spread are inversely related to lightning fire frequency. Modeling is perhaps the only means of understanding the natural fire regimes in these ecosystems (e.g., Greenlee and Langenheim 1980; Davis and Burrows 1993; Davis and Michaelsen 1995; Zedler and Seiger 2000).

In general, rain or high humidity accompanies lightning fires, and there is often a time lag between ignition and changes in weather conducive to rapid fire spread. Thus, in forested ecosystems where lightning is the dominant ignition source (e.g., the Southwest, Fig. 8.4), fire suppression has been extraordinarily effective. Fire detection has become increasingly more reliable (Chandler 1960), and there is reason to believe that many suppressed lightning-ignited fires, in both forests and shrublands, would have burned out if never detected. This is supported by a greater number of reports of lightning-ignited wildfires in the latter half of the twentieth century (Keeley 1977, 1982; Greenlee and Moldenke 1982; Vankat 1985); however, it could reflect changes in fuel structure as well (Weatherspoon and Skinner 1996).

In the coniferous forests of the Sierra Nevada, lightning-ignited fires peak in the summer months of July and August and match closely the monthly distribution of human-ignited fires (Parsons 1981; Vankat 1985; van Wagtendonk 1992). Throughout the chaparral-dominated coastal ranges lightning-ignited fires are also concentrated in the summer months of July and August (Keeley 1982). However, humans are the dominant source of ignition (Fig. 8.4), and their impact on fire season varies from apparently very little effect in the central coast, as illustrated by a summer peak in burning to a much greater impact in the south, where anthropogenic fires result in a longer fire season and greater autumn burning (Fig. 8.6). Thus, in contrast to the situation in forests throughout the western United States where lightning is the dominant source of ignition and humans have successfully suppressed most fires, the vast majority of fires in chaparral and coastal sage scrub in the coastal ranges are ignited by humans (Keeley, Fotheringham, and Morais 1999; Keeley and Fotheringham 2001b). In short, fire suppression has not eliminated burning on this shrubland landscape. Human impact is most pronounced at lower elevations and in proximity to metropolitan areas. On shrubland landscapes under natural conditions, lightning is a predictable source of ignition but variably distributed in time and space.

## Fuels and Weather

The spatial and temporal arrangement of fuels is a critical determinant of fire behavior, and fuel loading is determined largely by differences in site productivity and vegetation age. The extent to which fire will propagate across a landscape

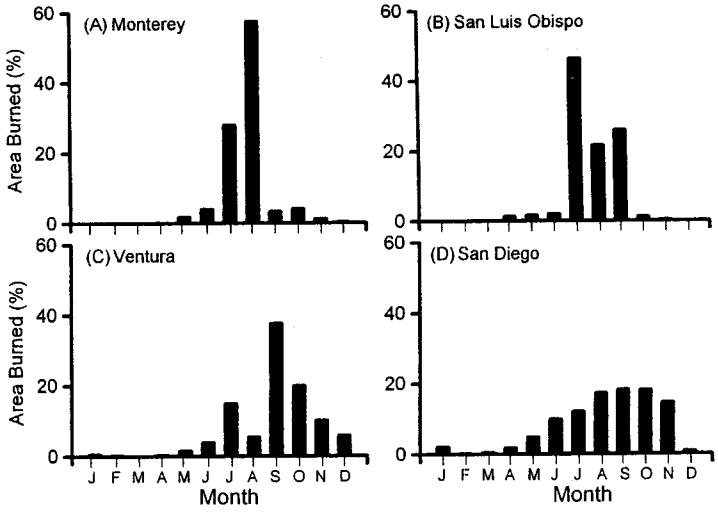


**Figure 8.6.** Seasonal distribution of burning reported for 1970 to 1999 for selected counties (data from the California Statewide Fire History Database; see Fig. 5).

is determined by the spatial arrangement of fuels and weather conditions prior to and during the fire. Fuel structure needs to be considered at different scales. In a stand of vegetation on a single slope face, the important fuel characteristics are the vertical and horizontal placement of fuels, fuel surface-area/volume ratio, and the moisture status of leaves and stems. At this scale shrubs are of uniform age and may be rather coarse grained in monotypic stands, becoming finer grained as the mixture of species increases. At the landscape level fuels are fine grained, and large expanses of homogeneous fuels are the exception. Barriers of reduced fuel loading, which could include rocks, rivers, alluvial fans, young age classes, or less flammable vegetation types, may inhibit fire spread. As seasonal drought progresses, different portions of the landscape are added as potential fuels, further contributing to inherent landscape heterogeneity of fuels. This interaction among landscape structure, fuels, and moisture limits the ability of models to predict fire spread, and the fine-grain nature of fuels leads to potentially large errors (Kessell and Cattelino 1978).

## Fuel Structure and Fuel Moisture

In mature shrublands, surface fuels are insufficient to carry fire, and thus fires propagate through the canopy as crown fires. Recently burned sites have sufficient herbaceous growth to carry surface fires (Haidinger and Keeley 1993), and this may be exacerbated by artificial seeding of nonnative grasses (e.g., Zedler,

Gautier, and McMaster 1983). However, sufficient herb biomass to carry surface fires is unlikely following dry winters or on highly infertile coarse-textured soils, such as occur in certain coastal sites (e.g., Lompoc, CA) or the interior ranges of Baja California (Franco-Vizcaino and J. Sosa-Ramirez 1997).

Normally, following a wet winter, high fuel moisture in chaparral shrubs makes them relatively resistant to fire in spring and early summer. However, as the amount of herbaceous matter in the stand increases, the seasonal window of burning increases. Dead herbaceous fuels dry rapidly and are capable of carrying fire within days of a rainfall event (Chandler 1963), and species composition plays a role as nonnative grasses typically die many weeks earlier than native herbs (Keeley, personal observations). As a result certain herbaceous fuels greatly extend the length of the fire season.

Shrublands that have been partially or fully type-converted to grasslands (e.g., Bentley 1967) have a greater probability of igniting but do not represent an extreme fire hazard as fire intensities are low and the fine herbaceous fuels fail to sustain embers or create the vortexes that carry the fire ahead of the moving front (Regelbrugge 2000). Even so, fires in a dense growth of non-native herbs, such as mustards (*Brassica nigra* and *Hirschfeldia incana*) on steep slopes, have been known to generate fire intensities sufficient to destroy homes (J. Keeley, personal observation).

For intact shrublands, two factors affect woody fuel moisture: the physiological activity (water potential) of live foliage and the quantity of dead fuels (Green 1981). Shrub species differ markedly in moisture status of foliage due in part to differences in rooting depth (Davis, Kolb, and Barton 1998)—shallow-rooted shrubs, such as chamise (*Adenostoma fasciculatum*) and *Ceanothus* spp., typically experience water potentials two to three times lower than more deeply rooted shrubs such as scrub oak (*Quercus berberidifolia*). Under prescription weather conditions fires may readily spread through *Adenostoma*-dominated chaparral but extinguish when they encounter patches of scrub oak (Chandler 1957; Green 1981). However, under extended drought, foliage moisture in scrub oak may drop to levels conducive to rapid-fire spread (Olsen 1960; Pirsko and Green 1967; Green 1981).

Dead fuels lack an internal water source and respond rapidly to changes in humidity; small diameter stems can dry completely within hours and larger fuels within days of experiencing low humidity (Chandler 1963; McCutchan 1977). Dead fuels not only combust readily, but as the proportion of dead/live material increases, there is an elevated potential for dead fuel combustion to cause drying of living foliage to a level sufficient for combustion. Because dead fuel carries fire and live fuel absorbs energy, the ratio of dead/live fuel is critical. This increase in combustibility of live fuels is enhanced by the common position of dead fuels beneath the living foliage. Topography plays a similar role. On steep terrain, head fires burning upslope enhance the combustion of fuels ahead of the front and may spread two to three times faster than on level ground—fire spread will roughly double for each 13 degree rise in slope (Green 1981).

## Fuel Structure and Wind

At low wind speed, fuel structure and arrangement plays a critical role in fire spread. For example, fine-textured, low, compact fuels—particularly subshrubs with extremely high levels of volatiles, for example *Salvia* spp. (sage)—may readily combust and spread fire rapidly. However, under the same weather conditions, fire might naturally extinguish in a taller chaparral stand in which fuels are more widely scattered in the canopy, and there is little continuity with ground-level fuels (Green 1981). Under low to moderate wind conditions species-specific fuel characteristics in chaparral can promote fire spread. Many characteristics of *Adenostoma fasciculatum* (chamise) make it far more flammable than associated shrub species. About two-thirds of the plant is composed of twigs <25 mm diameter and thus has a stem surface area–volume ratio greater than that of other species (Conard and Regelbrugge 1994). Individual chamise leaves have a relatively low surface area/volume ratio, but they have an extremely high content of volatile compounds that vaporize and increase combustibility (Philpot 1969). On a whole plant basis, *Adenostoma* leaves have a very high surface area/volume ratio; they comprise 67% of surface area but only 16% of plant volume, reflecting the loose packing of foliage (Countryman and Philpot 1970; Barro and Conard 1991).

One of the key factors affecting flammability of *Adenostoma* is the fact that it does not self-prune dead twigs and branches; instead, they are held aloft in the canopy and increase canopy porosity (shrub canopy volume/leaf and stem volume), which often exceeds 99% (Rundel, Parsons, and Baker 1980). High canopy porosity increases flammability and extends the seasonal window of flammability. Also experimental studies demonstrate that this natural retention of dead branches substantially increases fire intensity over an artificial treatment of clipping and leaving as surface fuels (Schwilk 2000). Species with more densely packed fuels, and that self-prune dead branches and have thicker twigs and stems (e.g., scrub oak, *Quercus*, or chaparral holly *Heteromeles arbutifolia*), often will not burn under conditions suitable for fire spread in *Adenostoma*-dominated chaparral. It has been hypothesized that characteristics enhancing flammability have adaptive value (Mutch 1970) and shrubs with seedling recruitment restricted to postfire environments (*Adenostoma, Ceanothus, Arctostaphylos*) have significantly higher flammability than species that recruit independently of fire (*Prunus, Rhamnus, Quercus*) (Bond, unpublished data).

While high-canopy porosity increases flammability, it leads to lower bulk density (mass/volume) and fuel loading (mass/area), reducing the total energy available for combustion. Thus the *Adenostoma* fuel structure increases flammability under a wide range of conditions, whereas the *Quercus* fuel structure is limited in the range of conditions suitable for burning, but under the severest conditions *Quercus* fuels should be expected to generate the highest intensities.

Fuel structure appears to play a less deterministic role under windy conditions, but there is a complex interaction of wind, humidity, fuels, temperature, and

topography. Cool moist marine air will extinguish fires (Coffin 1959), whereas warm dry air will lead to fire spread in fuels that otherwise would not burn. Wind accelerates oxygen supply and thus combustion (Green 1981) and is the primary mode of heat transfer. It carries heated air to adjacent fuels on the downwind side, raising the fuel temperature and driving off moisture. Wind also carries away water vapor as well as firebrands, which often occur when gusts are greater than 16 km/hr (Green 1981). Topographic features frequently cause unstable and erratic changes in velocity and direction as winds adapt to the topography. On coastal-facing slopes onshore winds are channeled up-canyon and produce eddies at ridgelines that may become turbulent and erratic. The typical pattern is for local daytime up-canyon wind and nighttime down-canyon winds, and on coastal slopes in the central coastal region extraordinarily strong down-canyon winds known as Sundowners are occasionally experienced (Ryan 1996).

Overriding synoptic-scale winds can upset these local wind patterns, e.g., foëhn winds known as "north winds" or "mono winds" in central California (Greenlee and Langenheim 1980) and Santa Ana winds further south (Lessard 1988) (Fig. 8.7). These winds are controlled by regional synoptic patterns that include a Great Basin high-pressure cell and Pacific Coast trough of low pressure, but their ultimate manifestation is a result of local topography (Schroeder and Buck 1970; Fosberg et al. 1966). For example, in the southern Sierra Nevada, the steep eastern escarpment and lack of low passes keeps these winds aloft (Mitchell 1969), and thus foëhn winds are not experienced on the lower western slopes. In Ventura and Los Angeles counties these winds are funneled through passes in the east west trending Transverse Ranges and thus are predominantly northern or northeastern winds (Weide 1968; Schroeder et al. 1964). In San Diego County they are strictly eastern due to the north–south orientation of the Peninsular Ranges winds (Campbell 1906; Sommers 1978). These ranges extend southward into Baja California where their sharp eastern escarpment, coupled with the Gulf of California to the east, limit the formation of foëhn winds on the west slopes of the Sierra San Pedro Mártir (Keeley and Fotheringham 2001a,b).

In southern California these hot, dry Santa Ana winds often have less than 10% relative humidity and may exceed 100 km per hour (Fosberg et al. 1966; Ryan 1969). Although referred to as "desert winds," the high temperatures and low humidity are the result of compression as air descends to form the "basin air mass" (Mitchell 1969), and on a local scale as it descends through coastal passes (Krick 1933). Santa Ana winds are most common in the autumn (Fig. 8.8). They have a mean life of about three days but may last two (Fosberg 1965) or three weeks (Campbell 1906), a critical factor since fire size is often determined by the duration of high wind conditions (McCutchan 1977). Under Santa Ana wind conditions fire spread is rapid. For example, the Kanan fire in the Santa Monica Mountains of southern California consumed 10,121 ha in 3 hours (Franklin 1987), and such fires may exceed 30,000 ha in a single day (Phillips 1971). Such fires are unimpeded by many potential barriers, since firebrands may be carried as much as 8 km beyond the front, igniting numerous new spot fires (Countryman

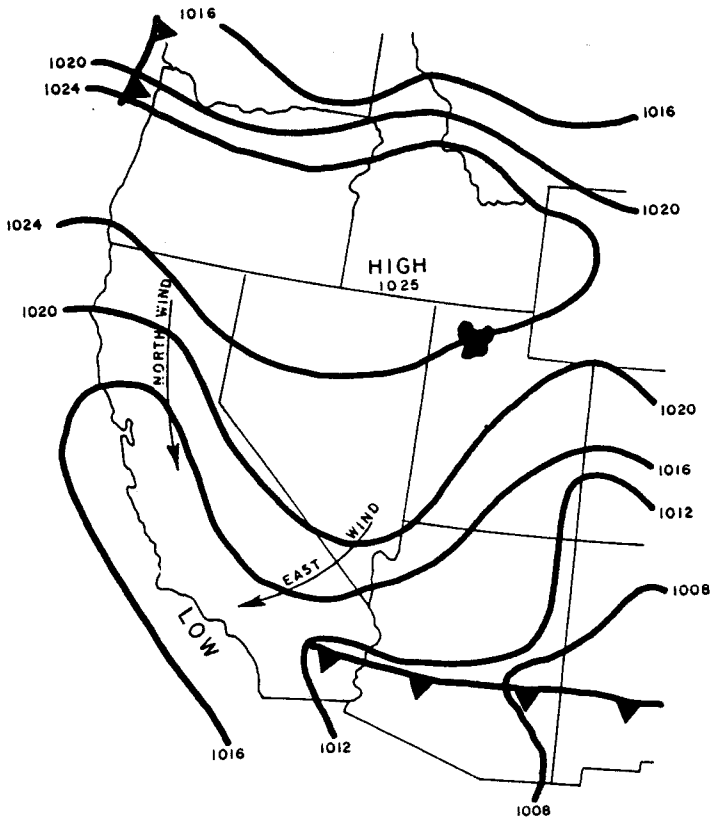


**Figure 8.7.** Surface weather map during the Great Basin high-pressure air mass that generates foëhn winds in central and southern California (from Phillips 1971).

1974). Under these conditions stands may burn regardless of stand age or species composition (Keeley, Fotheringham, and Morais 1999).

## Fuel Mass and Stand Age

It has long been held that fuel mass increases with stand age (Philpot 1977), but this has been criticized as oversimplistic because it ignores tremendous species-specific variability in rates of biomass accumulation (Fig. 8.9). For example, some *Ceanothus* species may accumulate many times more biomass in less than 20 years than *Adenostoma fasciculatum* does in 60 years (Riggan et al. 1994; Regelbrugge 2000). Also at 10 years of age north-facing aspects may have greater biomass accumulation than drier south-facing slopes do at 80 years of age (Black 1987). This fact alone makes landscape-scale predictions of flammability based on stand age extremely difficult. Complicating the prediction of flammability with stand age is the increasing proportion of biomass in large diameter stems that

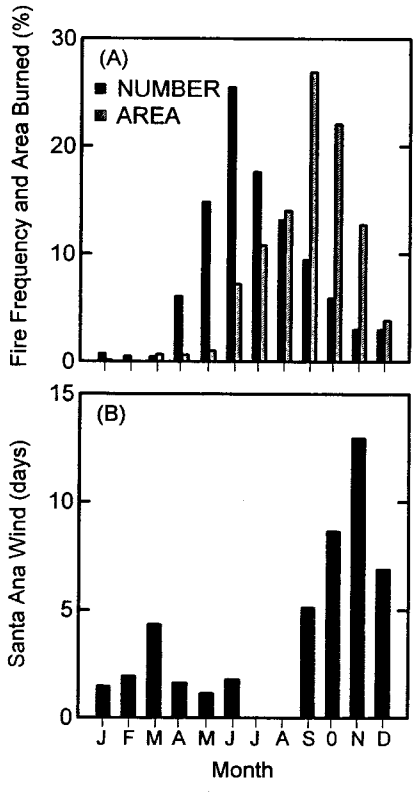


**Figure 8.8.** Seasonal distribution of fire occurrence and area burned during the twentieth century in Los Angeles County (data from Statewide Fire History Database; see Fig. 8.5) and seasonal distribution of Santa Ana winds (from Weide 1968).

combust only under the most extreme burning conditions. Also highly productive stands are often more mesic sites, and this, plus greater fuel density and higher fuel moisture, may reduce flammability. However, under extreme conditions, once ignited, productive sites sustain greater energy release than less productive stands (Riggan et al. 1988).

Successional changes in biomass (live and dead kg/ha) range from 1200 to 9000 in the first postfire year to 8000 to 13,000 after a decade, and 30,000 to 66,000

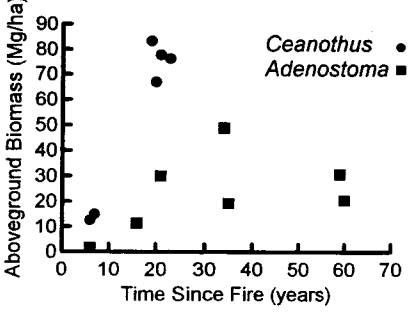


**Figure 8.9.** Live and dead aboveground biomass for chaparral shrubs at different times since fire based on several studies (data from Regelbrugge 2000).

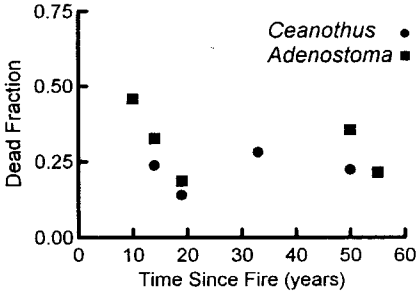


**Figure 8.10.** Fraction of total biomass comprising dead material for chaparral shrubs at different times since fire based on several studies (data from Paysen and Cohen 1990; Regelbrugge 2000).

(sometimes 100,000) in mature stands (Specht 1969, 1981; Green 1970; Keeley and Keeley 1984). Specht (1969) reported that the proportion of dead biomass exceeded 50% in mature chamise chaparral, and Green (1970) found 66% dead in mature *Cercocarpus betuloides*. These early reports led to the generalization of 1% dead for each year after canopy closure (Green 1981). However, more extensive studies (Fig. 8.10) report 30% dead/live ratios across the span from 20 to 60 years and no significant relationship with age (Paysen and Cohen 1990; Conard and Regelbrugge 1994; Regelbrugge 2000). It is apparent that dead/live ratios are a complicated function of many aspects of site composition and history. For example, unusually severe soil droughts may dramatically increase mortality, particularly of shallow-rooted *Ceanothus* shrubs, and this can occur in young or old stands (Keeley 2000; Davis et al. 2002). Also prior fire history may play a role; for example, chaparral stands burned by light fires leave large volumes of standing dead biomass that can produce very high dead/live ratios in young successional stands where high volume of dead fuels is not expected (e.g., Fig. 8.10).

In general, chaparral less than 25 years old has less than 20% dead, and this is insufficient to carry fire under "prescribed fire weather conditions" (Green 1981). Under severe weather conditions stand age (and total biomass and proportion dead) is less important in determining fire spread (Dunn 1989; Keeley, Fotheringham, and Morais 1999; Zedler and Seiger 2000).

The conclusion that older stands of chaparral generate fires of greater intensity needs to be viewed with caution. Fire intensity, which is often measured as fireline intensity or energy released per meter of fire front (Borchert and Odion 1995), can vary greatly depending on the interaction between weather and fuels. Sometimes intensity is equated with fire severity, which is defined as the ecological impact of the fire, and is often measured by mortality or the amount of plant biomass consumed, or alteration of nutrient cycles. However, a fast-moving fire that consumes little fuel and a slow-moving fire that consumes more fuel can achieve the same fireline intensity, and thus intensity and severity can not always be equated. In general, fire intensity is important to understanding options for fire suppression (Countryman 1974), whereas fire severity is most relevant to post-fire ecosystem recovery (Keeley 1998b). Lastly, large fires often are equated with fires of high intensity, but they need not be. Large fires or mass fires are often described as catastrophic fires, but this latter term best refers to the impact of fire upon property and lives.

## Past and Present Shrubland Fire Regimes

Understanding the extent of human impact on chaparral ecosystems requires that we reconstruct historical fire regimes. Stand-replacing crown fires typical of shrublands (Fig. 8.2) are not conducive to the formation of a tree-ring record of fires, as with surface fire regimes in montane coniferous forests. Thus reconstructing historical burning patterns for chaparral requires alternative approaches such as interpretation of sedimentary charcoal records.

Charcoal deposits in varved sediment cores from the Santa Barbara Channel have generated estimates of prehistoric fire frequency. Byrne, Michaelsen, and Soutar (1977) calibrated this procedure by comparison of annual varves from modern cores with U.S. Forest Service fire records. They found a significant correlation between large charcoal deposition events and incidence of large fires (>20,000 ha) in the adjacent mountain range less than 50 km from the core site. Using a core for the period from AD 730 to 1505, they were able to detect significant charcoal deposition but less than in the modern period, suggesting a lack of frequent small fires, unlike the contemporary pattern (Moritz 1997). They did, however, find two major peaks approximately 100 years apart with smaller peaks at 20- to 60-year intervals, and suggested this period had few fires, widely spaced, which became large conflagrations capable of generating large pulses of charcoal. Mensing, Michaelsen, and Byrne (1999) analyzed similar cores at a finer resolution and concluded that large fires were a feature of this region long before modern fire suppression.

## Native American Impacts

Tree-ring records of fire scars from the coastal ranges and the Sierra Nevada have been interpreted to suggest that during the few hundred years prior to Euro-American colonization fire frequencies exceeded the level expected from lightning alone (Reynolds 1959; Greenlee and Langenheim 1990). From historical records and ethnographic accounts there can be no doubt that California Indians regularly utilized fire to manage their environment (e.g., Lewis 1973; Timbrook, Johnson, and Earle 1982; Wickstrom 1987; Anderson and Moratto 1996). The extent to which this management practice altered landscapes is a matter of debate. Due to the naturally high fire frequency of lightning fires in the coniferous forests of the Sierra Nevada, Vale (1998) has argued that the additional burning by Indians did not alter landscapes except in localized areas (but cf. Anderson, Barbour, and Whitworth 1998). On the other hand, it has been hypothesized that direct use of fire by Native Americans greatly altered landscape patterns in the lower elevation coastal range foothills, primarily through type conversion of shrublands and woodlands to grasslands and other herbaceous associations (Cooper 1922; Wells 1962; Huenneke 1989; Keeley 1990, 2002; Hamilton 1997). This hypothesis is supported by the low lightning activity, high Indian popula-

tions, shrub-dominated landscapes, limited resources for Native Americans in undisturbed shrublands, and weak resilience of shrublands to high fire frequency (Keeley, in review).

## Euro-American Settlement Impacts

Euro-American settlers further increased fire frequency during the nineteenth century, primarily for the purpose of expanding rangeland into chaparral and coastal sage scrub dominated landscapes. The economy of the Spanish and later Mexican period was primarily based on pastoralism, and most historical sources indicate extensive grasslands at the time of colonization and limited need for immediate rangeland expansion (Keeley, 2002). Nonetheless, there are historical reports of these early pastoralists using fire to open up shrublands and increase forage (Kinney 1887), and this is reflected in increases in grass pollen from sediment cores (Russell 1983).

By the middle of the nineteenth century there was increasing pressure for rangeland expansion, and this was felt most severely in the coastal ranges south of San Francisco where 80% of livestock production was confined (Ewing et al. 1988). Following the Gold Rush of 1849, with an influx of American settlers, brush burning for the improvement of grazing became extensive throughout California. Ranchers in the foothill regions regularly burned large areas of brushland, and it became the practice of itinerant sheepherders, after leaving a grazing area, to set fires (Brown 1945; Bauer 1974; Nichols, Adams, and Menke 1984). Burcham (1957) contends that all rangelands in the state were fully occupied by 1880. A similar perspective is that of Brown and Show (1944) who stated, "It is generally conceded that what is known as the 'pastoral era' of California ended in 1870. In that year, good pasture land, which was also agricultural in character, rose to a price of from 75 cents to $6.00 per acre." In the succeeding decades there was extensive pressure to utilize fire for the purpose of opening up shrublands and increasing forage (Lee and Bonnicksen 1978). The burning by these stockmen in mountain watersheds of southern California were thought to be responsible for damaging floods on both the coastal and interior sides of the San Gabriel Mountains, leading to its designation as the first forest reserve in California (Lockmann 1981).

One factor contributing to the use of fire in the opening up of shrublands was apparently the homestead laws that allowed acquisition of 65-ha parcels from public domain land (Lee and Bonnicksen 1978). Such parcel sizes were generally sufficient to maintain a homestead based on stock production, but this plan did not work in the rugged hills of southern California, where homesteads were centered in small valleys known as *potreros*, surrounded by impenetrable chaparral. "Since the potreros were too small to support an economically sound cattle operation, stockmen supplemented meadow grazing with forage produced by periodically burning the adjacent chaparral" (Lee and Bonnicksen 1978). Since

brush burning was an essential resource use practice for stockmen, they burned extensive areas of chaparral (Barrett 1935; Brown and Show 1944; Brown 1945). For instance, in 1887 it was reported, that in the southern portion of San Diego County that "at least one third of the land covered with brush, grass and oak timber has been burnt off by settlers in the past eighteen months" (Lee and Bonnicksen 1978). As a consequence of early settler burning, fire control laws were enacted soon after statehood in 1850 (Clar 1959). Not surprisingly, in the early part of the twentieth century, ranchers were often the primary opponents to fire exclusion policies, which in southern California was prompted by the need for watershed protection in the coastal plain (Lee and Bonnicksen 1978).

In summary, it is apparent that during this settlement period the primary alteration in fire regime was to increase the frequency of fires on shrubland landscapes. This was an era of very limited fire suppression, and yet fires were much as they are today in that large crown fires covering tens of thousands of hectares were not uncommon (Kinney 1900; Barrett 1935; Brown and Show 1944; Brown 1945; Minnich 1987). For example, one of the largest fires in Los Angeles County (24,000 ha) occurred in 1878 (Keeley, Fotheringham, and Morais 1999), and the largest fire in Orange County's history was over a quarter million hectares and occurred in 1889 (Lee and Bonnicksen 1978).

## Twentieth-Century Patterns of Burning

Burning patterns during the twentieth century are shown for the nine counties in central and southern coastal California (Fig. 8.11). Most counties exhibited little or no change in area burned except for Los Angeles and Riverside counties in southern California, which exhibited highly significant increases in area burned during the twentieth century. In contrast to the situation in western U.S. coniferous forests, fire suppression clearly has not excluded fire from these shrubland landscapes. Collectively the 1920s, 1940s, and 1970s were high decades, and the 1930s and 1960s were low. Possible explanations for these patterns are that they result from (1) decadal-scale variation in climate, (2) natural cycles resulting from fuel buildup, and/or (3) human demographic patterns.

### Role of Climate/Weather

There are numerous suggestions in the literature of extended droughts contributing to extraordinarily severe fire seasons, but with a few notable exceptions, most lack statistical rigor. Minnich (1983) reported that there was a significant positive relationship between precipitation and area burned in coastal sage scrub of southern California and adjacent Baja California, but he presented no statistics to support this contention. He also inspected patterns of chaparral burning over this time period and concluded no such relationship existed with chaparral. However, others have reported a relationship between precipitation and burning

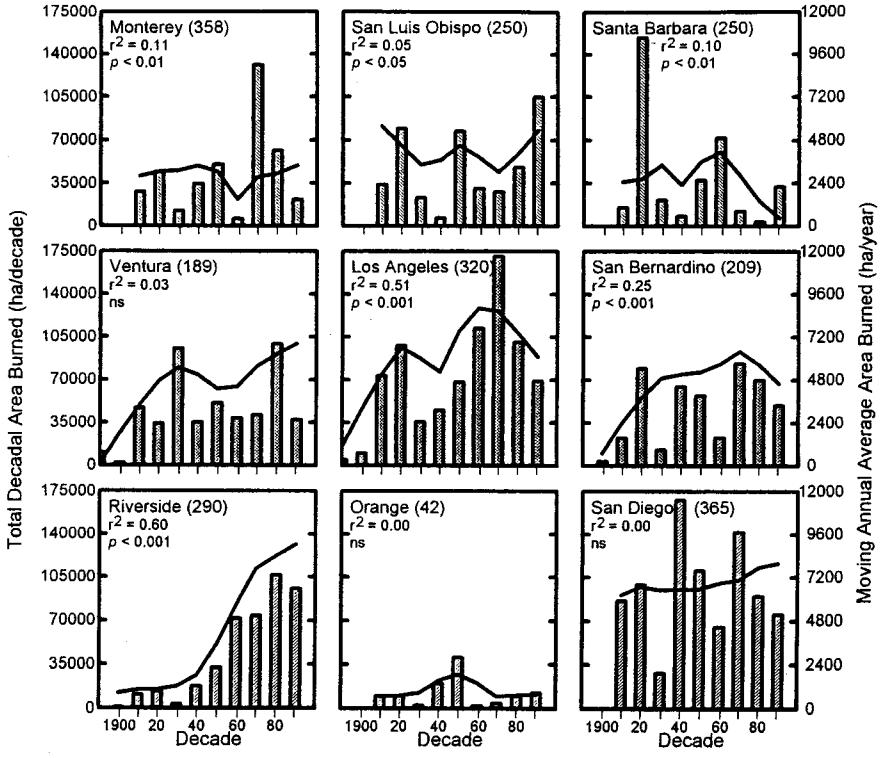


**Figure 8.11.** Area burned per decade and 10-year running annual average during the twentieth century for nine counties in central and southern California (data from the Statewide Fire History Database; see Fig. 8.5). Shrubland area in thousands of hectares shown in parentheses following the county name (from Callaham 1985).

in chaparral. One line of evidence is the spatial relationship between average precipitation and fire occurrence within the chaparral zone of San Diego County (Krausmann 1981). Another line of evidence is the demonstration that chaparral burning varies temporally with changes in precipitation; little area is burned following rainfall years where spring precipitation is >200 mm (Davis and Michaelsen 1995). These observations have been interpreted to mean that more rain translates into more biomass and thus greater fuels for burning in the subsequent fire season.

Using the FRAP data set (Fig. 8.11), we found few statistically significant correlations between patterns of rainfall and burning for chaparral and coastal sage shrublands combined. For each county separately, or all counties collectively, there was no significant relationship between total acreage burned per year and the nearest station with long-term records for:

1. total annual (January–December) precipitation,
2. growing season (November–June) precipitation,

3. spring (January–May) precipitation,
4. summer (June–August) precipitation, or
5. previous growing season's precipitation.

There was, however, a weak, but significant negative correlation ($p < 0.05$, $r^2 = 0.05$–$0.06$, $n \geq 88$) between October precipitation and area burned in each of the southern California counties, indicating that early autumn rains cut short the fire season at its peak.

Weather conditions affecting autumn foëhn wind-driven fires are most critical in determining area burned. Santa Ana wind conditions are largely responsible for fires becoming large and is reflected by the strong correlation between fire size and high temperatures. On the Los Padres National Forest fires generally ignite on days when the temperature is 3 to 5°C greater than the monthly average, and large fires never originate on days where temperatures are <25°C at the Santa Barbara airport (Davis and Michaelsen 1995; Moritz 1997). Moritz (1999) examined this relationship between severe fire weather (defined as days with maximum temperatures at the Santa Barbara airport ≥32°C) and extreme fire events in the central portion of the Los Padres National Forest. He found that large fires (>4000 ha) were strongly associated with severe fire weather. In this part of California severe fire weather is often, but not always, associated with foëhn winds (Schroeder et al. 1964; Dunn and Piierto 1987; Ryan 1996). However, farther south, for example, in the Santa Monica Mountains, all large fires appear to be driven by Santa Ana winds (NPS, Santa Monica Mountains National Recreation Area, unpublished data). In general, the largest wildfires in the central and southern coastal region are during severe fire weather conditions that include high temperatures, coupled with low humidity and high winds (Coffin 1959; Pirsko 1960; Schroeder et al. 1964; Weide 1968; Countryman, McCutchan, and Ryan 1969; Phillips 1971; Countryman 1974; Dunn and Piierto 1987; Gomes et al. 1993; Davis and Michaelson 1995; Minnich and Chou 1997).

## Role of Fuel Cycles

Fuel accumulation was implicated in burning patterns in California shrublands by modeling studies published in the 1970s (Rothermel and Philpot 1973; Philpot 1974a,b). Based on untested assumptions about rates of fuel accumulation and effectiveness of fire suppression, it was concluded that large fires were increasingly more common because of an accumulation of older age classes of vegetation (Fig. 8.12). In support of this idea are many anecdotal references that fire fighters and fire researchers often relate about the tendency of fires to stop upon encountering young age classes of fuels (e.g., Philpot 1974a,b; Minnich 1998). An example of how these anecdotes are often used is the story about the 1970 Laguna Fire (one of the largest in California's history), in which it is claimed the fire died out when it encountered young age classes of vegetation (Rich Minnich, public communication, National Public Radio's "All Things Considered" radio broadcast, June 10, 1999). While that observation may be true, the deduction that

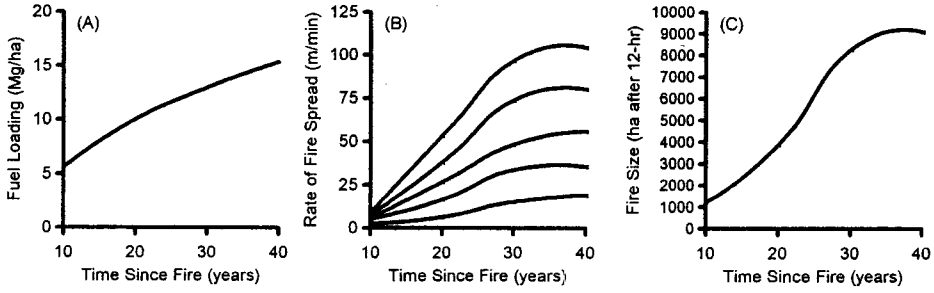


**Figure 8.12.** Modeling studies by Philpot (1974a, 1974b). (A) Assumed successional changes in fuel loads, (B) predicted rate of fire spread at increasing wind speeds from 10 to 50 kph, and (C) predicted fire size after 12 hours burning under sustained 50 kph wind speed. From these models it was concluded that as chaparral stands increase in age due to fire exclusion, there is a resultant increase in fuels, fire spread rate, and fire size. Following suggestions by Countryman (1974), these models were interpreted to support a fire management policy that relied heavily on prescription burning to produce a landscape comprising a mosaic of age classes.

there is a causal relationship is doubtful because the Laguna Fire burned over 10,000 ha of young vegetation (5–20 years) prior to its being extinguished (Dunn 1989), and the fire was contained only after a week of very severe Santa Ana winds subsided (Keeley, personal observations). In this fire, as well as other catastrophic fires, changes in fire behavior leading to containment often have had more to do with temporal changes in weather than spatial changes in fuels (Dunn and Piirto 1987). Although one can point to various fire perimeters that suggest fuel age is a barrier to fire spread (e.g., Philpot 1974), there are others that indicate it is not, such as half of the 5900 ha Romero Fire that burned above Santa Barbara in 1971 consumed seven-year old fuels from the 1964 Coyote Fire (Gomes et al. 1993). In short, there is no statistical evidence to support the notion that southern California landscapes supporting young vegetation are effective barriers to the spread of catastrophic fires. This of course is not meant to suggest that stand age has no effect on fire spread, only that its effectiveness is strongly controlled by weather (see the section below on Future Fire Management Strategies).

Fire history data also have been used to support the idea of fuel-driven fire behavior. Radtke, Arndt, and Wakimoto (1982) observed that peak decades of burning were followed by decades of very little burning in the Santa Monica Mountains of Ventura and Los Angeles counties. It was suggested that these decadal variations in burning represented a cyclical pattern driven by fuel loading. Their confidence in this model is illustrated by their future prediction that for the Santa Monica Mountains, the 1980s decade would be a peak and would be followed by a decline in burning during the 1990s. In retrospect we now know that, although the 1980s were high, the 1990s were even higher (Santa Monica Mountains Recreation Area, unpublished data). The primary weakness in explaining

**Table 8.2.** Shrubland area,[a] population density,[b] and estimated fire rotation intervals[c] for the shrub-dominated counties in California, arranged north to south

| County | Brush ($10^3$ ha) | People/ $10^6$ ha brush | Fire rotation interval (yr) pre-1951 | Fire rotation interval (yr) post-1950 |
|---|---|---|---|---|
| Monterey | 358 | 0.99 | 115 | 64 |
| San Luis Obispo | 250 | 0.87 | 60 | 48 |
| Santa Barbara | 250 | 1.48 | 47 | 81 |
| Ventura | 189 | 3.54 | 121 | 34 |
| Los Angeles | 320 | 27.69 | 44 | 30 |
| San Bernardino | 209 | 6.79 | 46 | 37 |
| Riverside | 290 | 4.04 | 225 | 38 |
| Orange | 42 | 57.39 | 36 | 29 |
| San Diego | 365 | 6.84 | 35 | 41 |

[a] Area as of 1985, from Callaham 1985.
[b] Population density for 1990, from *http://www.census.gov/population/cencounts/ca190090.txt.*
[c] From Keeley et al. 1999.

decadal variations in burning by changes in fuel loads is the fact that the total burning during a decade comprises only a fraction of the fuels on the landscape and substantial fuel loads are available for burning every decade. For example, fire rotation intervals (Table 8.2) indicate that in most counties only 20% to 30% of the landscape burned in any given decade; thus decades of peak burning should not automatically be assumed to alter the future course of burning by leaving the landscape with limited fuels.

For southern and central coastal California, fire history data refute the contention made by Minnich (1989, 1998, 2001; Minnich and Cho 1997) that chaparral fire occurrence is constrained by the rate of fuel accumulation. Fire hazard estimates are either independent of age (Moritz 1999) or only weakly dependent up to 20 years of age (Schoenberg et al. 2001; Peng and Schoenberg 2001). In addition stand-age classes burned in the eight largest wildfires in the Santa Monica Mountains illustrate that these extreme events are not dependent on accumulations of older fuels (Keeley, Fotheringham, and Morais 1999). Indeed, in this range the greatest proportion of burned vegetation is in the younger aged stands, for both coastal sage scrub and chaparral (Fig. 8.13). Also vegetation type, which has a profound influence on fuel distribution (e.g., Fig. 8.9), has been shown to have little influence on fire history in the Los Padres National Forest (Moritz 1999).

Alterations in the landscape distribution of fuels have also been implicated in changes in fire size. It has been proposed that due to fire suppression, there has been an increase in the age and homogeneity of fuel distribution leading to larger and higher-intensity fires (e.g., Minnich 1989, 1995, 1998; Minnich and Cho 1997). The only data in support of this model are the high frequencies of small fires south of the U.S. border, which are interpreted as solely the result of natural burning cycles in the absence of fire suppression. However, north of the border

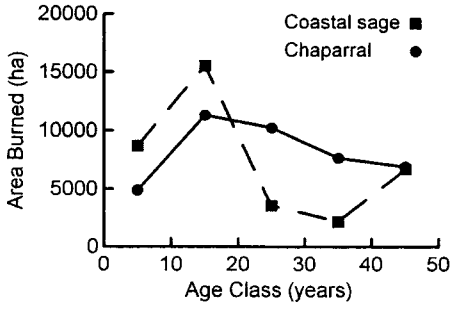


**Figure 8.13.** Age classes of chaparral and coastal sage scrub stands burned by all fires over 5000 ha from 1967 to 1996 in the Santa Monica Mountains (data from the U.S. National Park Service, Santa Monica Mountains National Recreation Area, Thousand Oaks, CA). Greater burning of young age classes of coastal sage scrub is likely due to more flammable fuels, longer fire season, and the concentration of this vegetation adjacent to urban centers, which are major sources of ignition.

fire suppression activities have not resulted in fire exclusion (Moritz 1997; Conard and Weise 1998; Keeley, Fotheringham, and Morais 1999; Weise et al., in press). Thus the patterns north and south of the border, while interesting, cannot be held up as an example of what happens to landscapes subjected to a fire suppression policy. Such fire management policies can not be held responsible for large destructive wildfires (Keeley and Fotheringham 2001a,b) as large fires have been a common feature of the southern California landscape throughout the nineteenth and twentieth centuries (Keeley, Fotheringham, and Morais 1999; Keeley and Fotheringham 2001a). Additionally sediment cores show the frequency of large fires has not changed during the past 450 years (Mensing, Michaelsen, and Byrne 1999), and colorful, but less authoritative, is the Digueño Indian legend of a large catastrophic fire sufficient to lead to migrations of tribes in San Diego County at about the time of Columbus (Odens 1971, p. 8). All of these observations suggest large fires are not a modern artifact of fire suppression as proposed elsewhere (Minnich 1989, 1995, 1998; Minnich and Dezzani 1991; Minnich and Chou 1997).

We now know that although the models developed by Philpot and others may be sound, their conclusions were flawed by incorrect assumptions. The assumption of a steady increase in fuels was inaccurate (Figs. 8.9 and 8.10), and the assumption that fire suppression was effectively excluding fire from shrubland landscapes was wrong (Fig. 8.11). In short, patterns of burning on shrubland landscapes cannot be explained solely by changes in accumulation of fuels (Moritz 1997, 1999; Conard and Weise 1998; Keeley, Fotheringham, and Morais 1999; Peng and Schoenberg 2001). Indeed, modeling studies that consider landscape patterns of fire spread conclude that stand age alone cannot constrain fire size (Zedler and Seiger 2000). If that were true, then just a single large Santa Ana wind-driven fire would reset the landscape to the same age class, which would

forever be doomed to burn as a single large unit. Zedler and Seiger's model shows that even in the absence of Santa Ana fires, if stand age were the only controlling factor, over time, burn units would coalesce and become larger and larger with each fire cycle.

## Role of Human Demography

Clearly, humans have perturbed shrubland fire regimes, but unlike the situation in many western U.S. forests, the primary impact has been through increased fire frequency (Table 8.1, Figs. 8.4 and 8.5c–d) and not through fire exclusion (Fig. 8.11). Collectively, across all counties considered in Figure 11, there was a significant correlation between fire frequency and population density and between fire frequency ($r^2 = 0.51$, $p < 0.05$, $n = 9$) and area burned ($r^2 = 0.71$, $p < 0.01$, $n = 9$). Southern California (defined in Fig. 8.3 legend), with the highest rate of population growth (Fig. 8.5b), also has had the greatest increase in wildfire ignitions (Fig. 8.5d). In contrast, the central coastal region has far fewer human ignitions (Figs. 8.4 and 8.5c), which is in line with the much lower population (Fig. 8.5a).

Indirectly the public infrastructure of roads contributes to patterns of burning. The central coastal region has substantial portions of its landscape lacking public roads, which is in stark contrast to the vast highway network connecting most parts of southern California. Fully one-third of all human-caused fires on Forest Service and CDF protected lands in southern California occur along roads (Gee 1974; Conard and Weise 1998). On shrubland landscapes near metropolitan areas, such as the Santa Monica Mountains, the vast majority of fires originate along roadways (Los Angeles County Fire Department, unpublished data).

In light of these considerations it seems probable that some portion of the decadal variation in burning during the twentieth century (Fig. 8.11) may have a human dimension. In the early part of the twentieth century populations in many parts of California were increasing rapidly (Fig. 8.5a–b). With this influx of people, came increased anthropogenic impact on the natural fire regime, driven largely by the increased mobility the automobile afforded; car registrations in California rose from 191,000 in 1915 to 1,500,000 in 1925 (Davis 1967). During the period 1908 to 1920, every county in southern California voted large bonds for road building (Davis 1967). Roads provided increased access to wildland areas. For example, a doubling in wildland use between 1916 and 1920 (Show and Kotok 1923) coincided with a marked increase in wildfire incidence in southern California (Fig. 8.5d). This rapid population growth and increased mobility strained the ability of fire protection in California during the early part of the twentieth century (Clar 1959). With the expanding population came an expansion of development at the urban–wildland interface, which then increased public susceptibility to wildfire impacts. As a consequence the decade of the 1920s witnessed some particularly destructive wildfires that increased public pressure for fire protection and prevention (Clar 1959).

In response, during the 1930s fire management agencies stepped up their attack on wildland fires by the introduction of lookout towers and aircraft for better

reconnaissance, which decreased the size of some fires due to early detection (Clar 1969; Pyne 1982). During this period various innovations were introduced to suppress fires, although effective suppression was elusive due to the inaccessibility of remote wilderness areas (Brown and Show 1944; Pyne 1982). A system of fuel breaks was one early answer to this problem, and creation of 200 CCC (Civilian Conservation Corp) camps throughout the state during the Depression contributed significantly to this network. Increased fire suppression activities due to an excess of man power from federal relief programs (Clar 1969 described it as a "forced feed" of the California Division of Forestry), coupled with reduced "motor touring" (e.g., AAA memberships dropped 40% in the five years following 1929; Davis 1967) perhaps contributed to the drop in area burned during the Great Depression in many counties.

Diversion of resources to the "war effort" during the first half of the 1940s contributed to diminished fire suppression capacity (Brown 1945; Clar 1969) and may account for the peak burning that occurred in some counties during that decade (Fig. 8.11). San Diego County stands out because its worst decade for wildfires was the 1940s. Zahn (1944) suggests the extraordinary fires of this era were the result of the aircraft industry, which had concentrated a great deal of the war effort in San Diego County. He described the situation at the time as follows: "Bootleg fuel, high payrolls and a yen for the open spaces have resulted in hundreds of aircraft workers motoring to the hills—night or day—between work shifts. Most of these workers are newcomers to California, unfamiliar with the tinder-box potentialities of local brush."

The modern era of effective fire suppression was introduced in the 1950s with the development of air tankers for fire fighting (Pyne 1982), and this impact was evident in a 10-fold drop in burning across the country (Dombeck 2001). However, in California these techniques have not proved very successful in halting fires during extreme Santa Ana wind conditions (Countryman 1974).

In short, despite innovations, fire suppression has not diminished the wildland fire problem in California. Indeed, since the 1950s, there has been an increase in the allocation of funds to the California brushfire problem (Bonnicksen and Lee 1979; Kinney 1984), and an increase in the loss of property and lives (Rogers 1982; Martin and Sapsis 1995). Additionally, due to television, there has been increased public awareness of large-scale wildfires. Over this period there have been a number of workshops, conferences, and proceedings volumes published on this wildland fire problem—roughly one every 5 to 10 years since 1950—and these offer a diversity of opinions on the role of fire in the California landscape. Although not a popular view, it has been frequently suggested that the problem stemmed in large part to the burgeoning population and poor zoning regulations attendant with urban sprawl into the foothills. The problem was evident 50 years ago. For example, Zivnuska, Amold, and Arment (1950) warned of this "potentially explosive situation," and noted "it is known that one of the significant trends in recent population changes has been the increase in number of residences in the flash-fuel types adjacent to primary watersheds." Under these conditions catastrophic fires are not necessarily the largest fires, as witnessed by the rather small

Oakland Hills Tunnel Fire in October 1991 (725 ha) that burned nearly 3000 structures and killed 25 people (Booker, Dietrich, and Collins 1995).

In summary, severe fire weather occurring each autumn coupled with human demographic patterns would seem to explain patterns of burning (Fig. 8.11) far better than changes in available fuels. During the twentieth century any changes in the fire regime have been dwarfed by the changes in land development patterns, which have increasingly placed more people at risk to the natural forces long present on the landscape (Davis 1965; Bradshaw 1987). This pattern continues—for example, in the 25 years prior to 1980, 2408 homes and other structures were destroyed by wildfires in California but in the subsequent 14 years the number tripled (*http://www.prefire.ucfpl.ucop.edu/wildfire.htm*). Preference for a rural lifestyle and the skyrocketing cost of suburban housing in large metropolitan areas has progressively increased the urban–wildland interface. Of particular concern is the prediction that rural population will exceed urban growth in the foreseeable future (Bradshaw 1987). For both economic and political reasons the notion that urban sprawl is responsible for natural wildfires becoming catastrophic fires is unpopular, in part, because it seems to defy the inherent belief that it is possible to engineer solutions to all environmental problems.

## The Contemporary Versus Natural Fire Regime

There is reason to believe that the contemporary fire regime in these shrublands mirrors the natural crown fire regime far more than is generally accepted (cf. Bonnicksen and Lee 1979; Minnich 1983; Pyne 1982). Today in southern California, fire incidence peaks in the summer, but most area burned is from autumn fires (Fig. 8.8a). Likewise the natural fire regime was probably characterized by many small summer lightning-ignited fires and a few large autumn fires driven by Santa Ana or Mono winds that burned large areas (Keeley and Fotheringham 2001a). This model would seem to be contradicted by the fact that Santa Ana or Mono winds are northeast winds, whereas summer thunderstorms are associated with south winds, and the two do not commonly coincide (Coffin 1959). Consequently today it is rare for Santa Ana wind-driven fires to be other than anthropogenic in origin. However, under natural conditions the fact that lightning fires burned for months (Minnich 1987), coupled with the relatively close temporal juxtaposition of the July–August lightning fire season (Keeley 1982) with the September–November Santa Ana winds (Fig. 8.8b), makes it inevitable that lightning ignitions would occasionally have been spread by these foëhn winds (Keeley and Fotheringham 2001a). While such events could not have been frequent, we know from historical documents that summer lightning-ignited fires can burn for more than a month and consume on the order of $10^3$ ha (Minnich 1987). This pales in comparison to the $10^4$ ha that are often covered in a single day by a Santa Ana wind-driven fire (Phillips 1971).

Davis and Burrows (1993, 1994) modeled the long-term fire regime in chaparral by linking physical models based on fire spread equations to fuel models of

stand senescence. Their simulations predicted a prehistoric fire regime of variable sized fires that produced a landscape mosaic of different age classes. With one ignition every 10 years (typical lightning-ignited fire frequency for coastal California; Keeley 1982) their model predicted that most fires would be large and over 80% of the landscape would burn at ages greater than 95 years. These conclusions are supported by other evidence that points to a natural fire regime of large fires and long fire return intervals for these coastal range landscapes (Greenlee and Langenheim 1990; Byrne, Michaelsen, and Soutar 1977; Mensing, Michaelsen, and Byrne 1999; Keeley and Fotheringham 2001a).

Alternatively, it has been argued that prior to the current fire suppression policy, landscapes were immune to Santa Ana wind-driven fires because lightning fires kept the shrublands in a fine-scale mosaic of young age classes (Minnich 1989, 1995, 1998). It is presumed that this mosaic was quickly erased by highly effective fire suppression during the first couple decades of the twentieth century (Minnich 1990). However, historical records do not support this notion. For example, 90% of the 214,000 ha of shrublands on the San Jacinto Forest Reserve were estimated to be 30 years or older when surveyed at the end of the nineteenth century, which represent far older age classes then present today (Keeley and Fotheringham 2001a). Clearly, this landscape was not a fine-scale mosaic immune to large fires. In addition the early history of forest protection does not support the idea that highly effective fire suppression was present in the opening decades of the twentieth century (Clar 1959; Lockmann 1981). Minnich and Chou's (1997) suggestion that fire suppression activities "culminated in extensive fire outbreaks as early as 1919" is contradicted by historical documentation that reports large fires in the region long before this date, and before any fire suppression activities (e.g., Kinney 1900; Barrett 1935; Brown and Show 1944; Brown 1945; Lee and Bonnicksen 1978; Radtke, Arndt, and Wakimoto 1982). Nationwide there is no evidence of substantive reductions in area burned due to fire suppression until midway through the twentieth century (Dombeck 2001).

Historically fire intensity was variable, and there is no credible evidence that it has increased during the era of fire suppression (Keeley, Fotheringham, and Morais 1999). The primary changes in the fire regime are that humans have replaced lightning as the primary source of ignition and fire frequency has increased, particularly in areas of high population density such as southern California (Figs. 8.4 and 8.5). Because fire prevention has been ineffective at eliminating human fires, presently and for the foreseeable future, fire suppression is required just to maintain some semblance of the natural fire regime.

## Impacts on Vegetation

In contrast to the paradigm suggested for many western U.S. forests, ecosystem health of shrublands is threatened not by a lack of fire but by high fire frequencies that exceed the resilience of many species. Examples of high fire frequency induced extirpations are numerous (e.g., Gause 1966; Zedler et al. 1983;

Haidinger and Keeley 1993; Zedler 1995; Keeley 2000). Generally, the threat of high fire frequency is lessened on very low nutrient soils where postfire annual biomass is limited and less likely to carry a repeat fire. Where fires occur more than once in a decade, nonsprouting chaparral shrubs are entirely lost from the system. Commonly exotic grasses and forbs will take their place, and as these increase in importance, they appear to competitively displace the native annuals. A similar course is evident in coastal sage scrub under higher fire frequency. In both of these crown fire ecosystems, high fire frequency favors annuals over woody plants, and this advantage increases with increasing soil aridity (Wells 1962).

As fire frequency increases, fuel structure changes and subsequent fire behavior changes. With increasing exotic herbaceous cover, the seasonal window of flammability increases (Radtke, Arndt, and Wakimoto 1982), and fire behavior becomes a mixture of crown and surface fires. This has two very important consequences. Surface fires connect the woody fuels where otherwise they might be too widely spaced to carry a crown fire, and thus exotic herbs shorten the fire return interval. Another important consequence is that fire intensity is lower where surface fires occur and this contributes to increased survivorship of exotic annual seed banks (Fig. 8.14). With continued disturbance these nonnative invasives may replace the entire ecosystem (Keeley, 2001), and type conversions of shrublands to exotic grasslands are well documented (e.g., Cooper 1922; Bentley 1967; CDF 1978; Biswell 1989; Minnich and Dezzani 1998). As a consequence exotic grasslands tend to replace shrublands in the proximity to urban environments, where the higher ignition sources in the company of flashy fuels have the potential for even greater fire frequency. Evidence of this is seen in the substantially shorter fire return interval in grassland vegetation at the urban–wildland interface than observed for shrublands at the interface (J. Spero, California Division of Forestry, personal communication, 1999).

The extent of such type conversion is unknown because of past disturbances, which includes Indian burning throughout the Holocene and burning coupled with intensive livestock grazing in the past 200 years. In the coastal counties from Monterey southward (Fig. 8.3) exotic annual grasslands cover nearly two million hectares or 25% of the wildland landscape, and less than 1% has significant patches of native perennial bunchgrass (Huenneke 1989). Although it is often taken as a matter of faith that these landscapes have always been grassland (Heady 1977), there is evidence that many exotic grasslands were formerly dominated by woody associations (Cooper 1922; Wells 1962; Oberbauer 1978; Huenneke 1989; Keeley 1990, Hamilton 1997). Today these landscapes comprise a mosaic of vegetation patterns (Fig. 8.15) that appear to be disturbance induced (Wells 1962). Grasslands on this modern landscape comprise a new quasi-equilibrium of nonnative annuals that are somewhat resistant to recolonization by native shrubs. It is a dynamic process whereby as disturbances increase or wane, vegetation physiognomy shifts between exotic grassland and shrubland/woodland (Hobbs 1983; Freudenberger, Fish, and Keeley 1987; Callaway and Davis 1993).

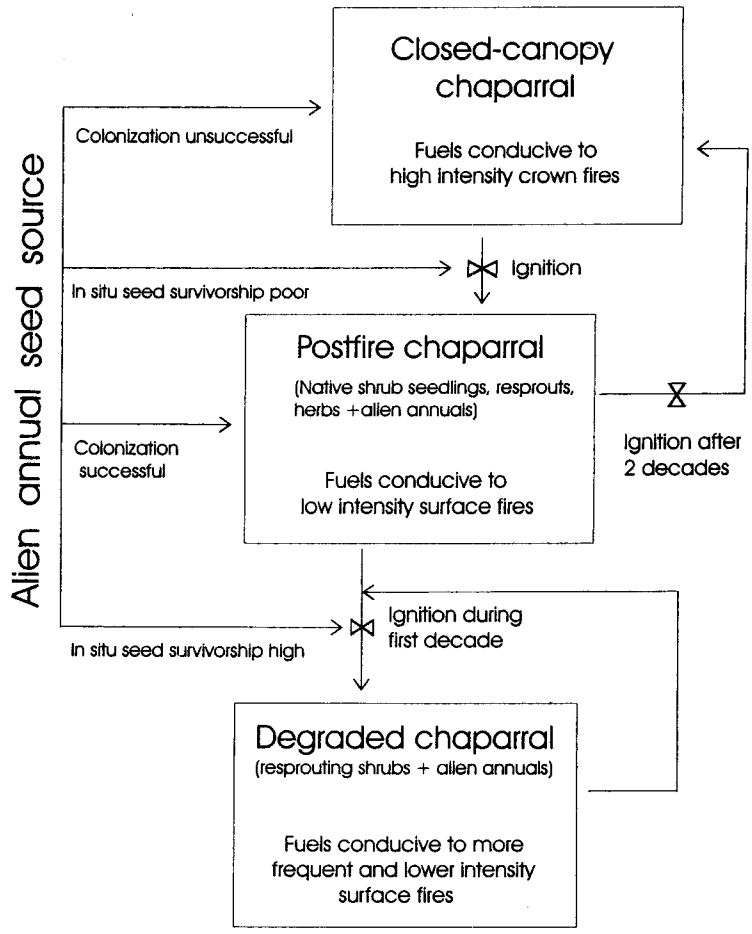


**Figure 8.14.** Schematic diagram of how rate of fire ignitions in chaparral affects alien plant invasion and how alien invasions affect fuel loads, which in turn alter fire frequencies, making sites more conducive to further invasion (from Keeley, 2001).

## Future Fire Management Strategies

It has been suggested that "after nearly a century of suppression" there is a need for a reintroduction of fire into chaparral through prescribed burning (Minnich and Dezzani 1991; Minnich and Franco-Vizcaíno 1999). However, fire history data do not support this management strategy. On most shrubland landscapes there is an abundance of fire, and 60- to 70-year-old stands, considered to be the normal age for burning (Minnich 1989), are rare at the present time (Keeley 1992). Indeed, the current fire rotation interval of 30 to 40 years is shorter than

**Figure 8.15.** Vegetation mosaic of nonnative annual grassland and shrublands in the central coastal ranges of California (photo by J. Keeley).

that calculated for the early part of the twentieth century (Keeley, Fotheringham, and Morais 1999). In light of the expected trends in population growth in California, and the close association between population density and fire incidence (Fig. 8.5), increased fire prevention is far more important to protecting natural resources than prescription burning or other methods of "fire restoration."

Consequently there is a need to reevaluate prescribed burning strategies for California shrubland landscapes. There are two common motivations for prescription burning: (1) for the benefit of natural resources and (2) as a fuel manipulation technique, primarily to reduce fire hazard but also to reduce the threat of soil erosion or air quality hazards, which may be worse under wildfire conditions. In many western U.S. forests, prescription burning provides both resource benefits and a reduction in fire hazard However, the reality for some ecosystems is that prescriptions reducing fire hazard, may not always enhance resource values and sometimes may detract (Johnson and Miyanishi 1995; Keeley and Fotheringham 2001b).

## Prescription Burning for Resource Benefit

There may be little justification for using fire for resource benefit, since vast portions of shrubland landscape currently experience a higher than normal fire frequency. Lack of fire does not appear to pose a risk because postfire studies

demonstrate that both chaparral and coastal sage scrub regeneration are highly resilient to even the most extreme fire events occurring after a long hiatus of burning (Keeley 1998, 2000).

One proposed benefit of prescribed burns is that they are done under more moderate weather conditions than are typical for wildfires, leading to less intense fires and less severe impacts on plant and soil resources (Green 1981; Moreno and Oechel 1991; Riggan et al. 1994; Wohlgemuth, Beyers, and Conard 1999). However, some of the experimental work demonstrating fire intensity effects on seed banks and soils have been done on piles of cut fuels, which do not accurately represent the fuel structure under natural conditions and are likely to generate unnaturally high soil temperatures. More importantly, however, even the most extreme fire wildfire events today probably do not fall outside the natural range of variation for these ecosystems.

Other resource benefits from prescription burning include invasive plant control, but the primary invasive problems involve herbaceous species, which invade shrublands when fire frequency increases (Fig. 8.14). It is not likely that prescription burning would displace these invasive species, unless the target is vulnerable to a particular seasonal window of burning. In shrublands there are no such windows of opportunity that are not equally damaging to some native species. Nonnative legume shrubs known as brooms (*Cytisus scoparius* and *Genista monspesulanus*) are sometimes targeted for removal with prescription burning, but these are inevitably replaced by exotic grasses (D'Antonio 2000). However, prescription burning for restoration of shrubland communities may be useful if accompanied by vigorous revegetation with native shrubs and herbs.

In general, there are few places where fire-dependent shrublands are threatened by the lack of fire and few instances where prescription burning is needed for natural resource benefits. The primary justification for prescription burning is for fire hazard reduction. However, in these ecosystems any additional fire carries with it the potential for negative impacts on resources. Negative impacts may arise not just from burning but can be associated with other fuel manipulations. For example, fuel breaks are possible corridors for bringing nonnative invasive species into wildland areas (Keeley, 2001).

## Prescription Burning for Fire Hazard Reduction

Prescription burning carries with it a risk of fires escaping, and escaped fires are quite hazardous in crown fire ecosystems, most particularly chaparral landscapes with a complex urban–wildland interface. In order to ensure successful containment of a prescribed burn, there are strict limitations on the acceptable wind speed, air temperature, relative humidity, and fuel moisture—typically wind speeds below 17 kph (10 mph), relative humidities above 30%, air temperature below 32°C (95°F), and fuel moisture above 75% (Fenner, Arnold, and Buck 1955; Green 1981). This, of course, varies with the fuel load and landscape, and various combinations will produce acceptable prescriptions (Paysen,

Narog, and Cohen 1998). One approach to reducing the risk of escaped fires is to burn in the spring, assisted by pretreatment of mechanical crushing and drying. Thus the target fuels are surrounded by less flammable living vegetation (Wolfram 1962). This procedure is expensive, and it has the potential for producing resource damage. For example, unseasonable application of fire inhibits postfire vegetation recovery (Florence 1985; Rundel, Parsons, and Baker 1987; Parker 1990) and is correlated with increased soil erosion (Turner and Lampinen 1983).

Because prescriptions are designed for safety, they are often marginal for burning. Under prescription weather conditions, fire spread is markedly influenced by fuel structure, and fire spread is often inhibited in stands less than 20 years of age (Green 1981; Paysen and Cohen 1990; Conard and Regelbrugge 1994). This is largely due to the lack of sufficient dead fuels required to spread fire to live foliage, and to the lack of fuel continuity between the ground and the shrub canopy and between adjacent canopies, factors that are extremely critical to fire spread under low wind and high humidity. Controlled burning of younger stands requires either prescriptions with risky weather conditions or pretreatment with biodegradable herbicides (which increase the dead fuels) coupled with seeding of exotic grasses that increase flashy (readily ignitable) fuels and increase surface fire spread.

Evaluating the effectiveness of prescribed burning at reducing fire hazard is complicated by the fact that such fuel management practices are never going to be fully effective against all fires. Wildfires are often more readily contained when they encounter young stands of vegetation, largely because lower fire intensities allow for safer access by fire suppression forces (Countryman 1974). However, landscape age mosaics created by rotational burning will not pose a barrier to wildfires ignited under severe fire weather, since the high winds readily push fires through young age classes (e.g., Fig. 8.13). Under these conditions young vegetation is of minimal value in halting the forward spread, and also firebrands are capable of spreading the fire kilometers beyond the front. Containment of shrubland fires burning under severe weather conditions usually requires a change to more favorable weather (Rogers 1982; Dunn and Piirto 1987; Gomes et al. 1993).

Thus prescription burning presents a catch-22 situation. It can only be done safely under weather conditions that require mature chaparral, 20 years of age or more, but stands of vegetation this age and younger will not form effective barriers to fire spread under severe weather conditions. Modeling studies indicate that to be effective even under moderate weather conditions requires a substantial portion of the landscape be treated (Mark Finney, public communication, 2001). Thus, while landscapes managed by rotational burning may contribute to easier containment of fires burning under moderate weather conditions, they are of limited value during severe weather. However, these latter fires are the ones that become truly catastrophic and are responsible for the greatest losses. Consequently National Forest Service policy of landscape-scale rotational burning to produce a mosaic of age classes needs to be reconsidered (Conard and Weise

1998). This type of fuel management is extremely expensive, unlikely to prevent catastrophic wildfires, and has little resource benefit.

Future fire management policy needs to steer away from extensive landscape-scale prescription burning and focus on intensive and strategic use of fire hazard reduction techniques, both to minimize negative impacts of high fire frequency on natural resources and to maximize fire hazard reduction. The marked differences observed between the central coastal ranges and southern California (Fig. 8.5) suggests that regions may require different fire management strategies. Greater focus needs to be given to transportation corridors as roadways are primary sites of ignitions, and since roadways are required to connect developments, as the urban/wildland interface increases, these fire hazards increase. Roads could also play a role in minimizing the negative impacts of fire hazard reduction programs, since many of the negative impacts of fuel reduction techniques (e.g., aesthetic impacts, promoting invasive plants and animals) are also shared by roadways. Thus greater attention needs to be given to co-locating roads and fuel manipulations such as fuel breaks.

Considering the psychology of many who inhabit the urban–wildland interface, it is questionable whether or not education can play a substantive role in reducing future losses from wildfires (Gardiner, Cortner, and Widaman 1987). Regulations requiring fire "safe" construction have been implicated in reducing property losses in the past and will possibly reduce the degree of future losses (Cohen 2000). It seems inevitable that fire management policy will increasingly require involvement of city and county planners in order to solve the primary fire hazard problem of how to constrain the ever-expanding urban–wildland interface. Fire managers can play a key role in providing accurate analytical models of causal factors driving extreme fire events and educating planners on the limitations to fire hazard reduction (e.g., Sapsis 2001).

## Global Change Impacts on Future Fire Regimes

Fire regime is an emergent property of landscapes arising from the interaction of vegetation, weather, topography, and land management (Davis and Michaelsen 1995). Fire regime is influenced directly by vegetation through flammability characteristics and the structural distribution of fuels. Weather affects fire regimes through timing of ignitions, and through frequency and severity of burning conditions as well as direct effects on vegetation distribution. Topography affects rates of natural lightning ignitions and wind patterns that ultimately control fire behavior. Land management affects the distribution of vegetation types and thus landscape patterns of fuels. Land management, in the broad sense, also controls the extent and pattern of the urban–wildland interface, which acts as a porous boundary where fires diffuse across in both directions. Wildland fires may diffuse out from the urban–wildland interface, but the most catastrophic fires result from wildfires burning into the urban environment. Global changes, including direct effects of increased atmospheric $CO_2$ levels, climate changes, and changing land

use, all have the potential for changing fire regimes by altering vegetation, weather, and land management.

Future increases in atmospheric $CO_2$ levels may directly affect plant growth and potentially alter patterns of fuel distribution. In chaparral the effects are predicted to be variable and strongly dependent on levels of other resources (Oechel et al. 1995). Along gradients of increasing soil fertility we might expect increased biomass production, but the increased leaf area may place greater demands on the limited soil water resources in this semi-arid region, dampening potential increases in primary production. Further exacerbating this dampening effect is the expected increase in summer temperature. However, this could be offset by increased water use efficiency expected with elevated $CO_2$.

Climate change in California shrubland landscapes over the next half-century is predicted to increase winter and summer temperatures by 3°C and 1°C, respectively, and to increase winter precipitation by 25% (Field et al. 1999). Warmer and much wetter winter conditions will almost certainly contribute to higher primary production, although the magnitude is likely to decline with decreasing soil nutrients. It is assumed that this increased production will lead to higher fuel accumulation and more intense fires. However, these climate changes may also accelerate decomposition of dead fuels, which are critical to fire spread, and the importance of this dampening effect on fuel accumulation has not been evaluated. Expected increases in C:N ratios of dead fuels imply variations in rates of decomposition along soil fertility gradients, paralleling expected increases in primary production. Thus sites with the greatest increases in fuels may also experience the greatest increases in decomposition. Even if the net effect is an increase in rate of fuel accumulation, this should not automatically be assumed to lead to major changes in the fire regime. This is based on the fact that currently rates of fuel accumulation do not play a highly deterministic role in shrubland fire regimes (Moritz 1999; Schoenberg et al. 2001; Peng and Schoenberg 2001).

Expected changes in climate will affect vegetation structure through changes in energy balance as well as nutrient cycling, but this involves such complexity that presently one can only speculate what the future holds (Oechel et al. 1995). Attempts to understand how changes in precipitation and temperature will affect vegetation composition include documentation of contemporary climatic responses (Westman 1991) and growth simulations (Malanson and Westman 1991a, b; Westman and Malanson 1992; Malanson and O'Leary 1995). Realistic parameterization of these models is one limitation to their current usefulness, and thus the primary conclusion one can draw at this point is that changes in the relative abundance of species are to be expected. Another possibility is that changes in fire intensity due to greater fuel loads may affect changes in postfire recovery, although shrublands currently exhibit extraordinary resilience to a wide range of fire intensities (Keeley 1998). Ecotones are expected to be sites of greatest sensitivity to climate change (Peteet 2000), and the complex vegetation mosaic of California landscapes (e.g., Fig. 8.15) presents many opportunities for shifts in vegetation distribution. Considering the large role played by human interference,

it seems likely that the greatest alteration in fire regimes will occur at the urban–wildland ecotone.

In general, GCM predictions for twenty-first-century climates in California are of limited value in understanding future fire regimes. Patterns of burning are driven by extreme events (Moritz 1997), and these are not well modeled (Field et al. 1999). One of the primary determinants of area burned is the coincidence of ignition with severe weather, and future changes in patterns of ignition might be expected to play a determining role in fire regimes. Climate-based models predict the California region will have a few percent increase in lightning fires (Price and Rind 1994), but this may not affect these shrubland landscapes where humans are the primary ignition source (Table 8.1, Figs. 8.4 and 8.5).

Future changes in land use are likely to have a more profound impact on shrubland fire regimes than other types of global change. Land use may also be the primary driver behind losses in biodiversity in California as well as in other Mediterranean-climate regions (Sala et al. 2000). Diversity loss is expected to result from increased population growth contributing to habitat loss, habitat fragmentation, and loss of corridors. Some of these factors will affect fire regimes, but, we expect that increased fire ignitions predicted from increased population growth will have a far more profound impact on these landscapes. As the fire return interval shortens, the native shrublands are degraded to mixtures of exotic grasses and forbs, and these invasives contribute to further decreases in fire return interval and loss of native plant diversity (Fig. 14). However, dampening this potential impact of shortened fire return intervals is the stepped-up rate of post-fire shrub recovery expected from predicted increases in winter temperature and precipitation. The impact of land-use changes on these landscapes makes it likely that it will far outweigh other global change impacts on fire regimes.

## Conclusion

Throughout much of the shrubland landscape humans play a dominant role in promoting fires beyond what was likely the natural fire cycle. Future climate change is expected to have a minor role in altering fire regimes relative to other global changes such as population growth and habitat fragmentation. Future fire management needs to take a strategic approach to fuel manipulations and move beyond evaluating effectiveness strictly in terms of area treated. Fire management should consider designing strategies tailored to different regions as there are marked differences between the central coastal region and southern California in source of ignition (e.g., Table 8.1, Fig. 8.4), season of burning (Fig. 8.6), and historical patterns of population growth (Fig. 8.5a–b) and burning (Figs. 8.5c–d and 8.11). Presently we know relatively little about fire regimes in shrublands in the foothills of the Sierra Nevada and interior foothills of the northern coastal ranges, and thus it would be prudent to not transfer the conclusions drawn here too broadly until we have a clearer understanding of the extent of regional

variation in shrubland fire regimes. One of the primary threats that all regions share is the increasing number of people being placed at risk to the natural wildfire threat because of the rapidly expanding urban–wildland interface. Fire management will need to play an increasingly active role in the planning process through critical analysis of causal factors driving fire regimes and the limitations to hazard reduction.

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*Review*

# Fire Management Impacts on Invasive Plants in the Western United States

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**Abstract:** *Fire management practices affect alien plant invasions in diverse ways. I considered the impact of six fire management practices on alien invasions: fire suppression, forest fuel reduction, prescription burning in crown-fire ecosystems, fuel breaks, targeting of noxious aliens, and postfire rehabilitation. Most western United States forests have had fire successfully excluded for unnaturally long periods of time, and this appears to have favored the exclusion of alien plant species. Forest fuel reduction programs have the potential for greatly enhancing forest vulnerability to alien invasions. In part this is due to the focus on reestablishing pre-Euro-American fire regimes on a landscape that differs from pre-Euro-American landscapes in the abundance of aggressive non-native species. We may be forced to choose between restoring "natural" fire regimes or altering fire regimes to favor communities of native species. Intensive grazing in many western forests may exacerbate the alien problem after fire and temporally decoupling grazing and fire restoration may reduce the alien threat. Many shrubland ecosystems such as the Intermountain West sagebrush steppe or California chaparral have a natural, high-intensity crown fire regime that is less amenable to forest restoration tactics. Historical use of prescribed fire for type conversion of shrublands to more useful grazing lands has played some role in the massive annual grass invasion that threatens these shrublands. Fuel breaks pose a special invasive plant risk because they promote alien invasion along corridors into wildland areas. Use of prescription burning to eliminate noxious aliens has had questionable success, particularly when applied to disturbance-dependent annuals, and success is most likely when coupled with ecosystem restoration that alters the competitive balance between aliens and natives. Artificial seeding of alien species as a form of postfire stabilization appears to cause more problems than it solves and may even enhance alien invasion.*

**Key Words:** exotic plants, fire suppression, fuel breaks, fuel reduction, non-native plants, postfire rehabilitation, prescription burning

Impactos de la Gestión de Fuego sobre Plantas Invasoras en el Oeste de Estados Unidos

**Resumen:** *Las prácticas de gestión de fuego afectan de diversas maneras a las invasiones de plantas. Consideré el impacto de seis prácticas de manejo de fuego sobre las invasiones: supresión de fuego, reducción de combustible forestal, quema prescrita en ecosistemas con fuego de dosel, guardarrayas, eliminación de invasoras dañinas y rehabilitación post fuego. En la mayoría de los bosques del oeste de Estados Unidos el fuego ha sido excluido exitosamente por largos períodos de tiempo no naturales y esto parece haber favorecido la exclusión de especies de plantas exóticas. Los programas de reducción de combustible forestal tienen el potencial para incrementar la vulnerabilidad de bosques a las invasiones de plantas exóticas. En parte, esto se debe al enfoque en el reestablecimiento de regímenes de fuego pre-Euroamericanos en un paisaje que difiere de paisajes pre-Euroamericanos en la abundancia de especies no nativas agresivas. Podremos ser forzados a elegir entre la restauración de regímenes de fuego "naturales" o la alteración de regímenes de fuego para favorecer a comunidades de especies nativas. El pastoreo intensivo en muchos bosques occidentales puede exacerbar el problema de invasoras después del fuego y la reducción temporal de pastoreo y gestión de incendios puede reducir la amenaza de las invasoras. Muchos ecosistemas con matorrales como la estepa de artemisa*

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*West Intermountain o el chaparral California tienen un régimen natural de fuego de alta intensidad que es menos dócil a las tácticas de restauración de bosques. El uso histórico de quemas prescritas para la conversión de terrenos con matorrales a tierras de pastoreo más útiles ha jugado un papel en la invasión masiva anual de pastos que amenaza a estos terrenos con matorrales. Las guardarrayas constituyen un riesgo especial porque promueven la invasión de áreas silvestres a lo largo de corredores. El éxito del uso de quemas prescritas para eliminar invasoras dañinas es cuestionable, particularmente cuando se aplica a anuales dependientes de perturbación, y el éxito es más probable cuando se combinan con restauración de ecosistemas que altera el balance competitivo entre invasoras y nativas. La diseminación artificial de semillas de especies invasoras como una forma de estabilización posterior al fuego parece causar más problemas que los que resuelve e incluso puede favorecer la invasión de exóticas.*

**Palabras Clave:** guardarrayas, plantas exóticas, plantas no nativas, quema prescrita reducción de combustible, rehabilitación post fuego, supresión de fuego

## Introduction

U.S. federal policies incorporate alien plant concerns into management of public lands. For example, the U.S. National Park Service policy (U.S. Department of Interior 2001) mandates that "exotic species will not be allowed to displace native species if displacement can be prevented." The chief of the U.S. Department of Agriculture Forest Service (USFS) has identified invasive species as one of the four significant threats to U.S. forest and rangeland ecosystems (U.S. Department of Agriculture Forest Service 2004), and the USFS manual states that "determining the risk of noxious weed introduction or spread as part of the NEPA process for proposed actions, especially for ground-disturbing and canopy-altering activities" is the explicit responsibility of managers (U.S. Department of Agriculture Forest Service 1995). Here I explore how these policies may be complicated, and sometimes compromised, by fire management practices. I examined impacts from six fire management practices: (1) fire suppression, (2) fuel reduction in forests, (3) prescription burning in shrublands, (4) fuel breaks, (5) prescription burning to target noxious aliens, and (6) postfire rehabilitation.

## Fire Suppression

Fire suppression policy over the past century has worked toward excluding fires from forests. For some forest types, such as Southwest ponderosa pine (*Pinus ponderosa* Laws.), the natural fire regime of frequent, low-intensity surface fires has been particularly amenable to fire suppression tactics. Consequently fires have been excluded over a significant portion of the landscape for much of the twentieth century (Allen et al. 2002). There is little debate about the critical nature of the fire hazard due to unnatural accumulation of understory fuels in these and many other western U.S. forest types. These fuels increase the probability of large, high-intensity wildfires and pose a threat to the long-term sustainability of these ecosystems (Graham et al. 2004).

Under this management policy of fire suppression, however, forests appear to have fared well in terms of minimal alien plant invasion (Pierson & Mack 1990*a*, 1990*b*; Weaver et al. 2001; Keeley et al. 2003). One of the major reasons for the resilience to invasion of undisturbed forests is that the closed forest canopy is highly inhibitory to aliens, most of which require high light levels (Rejmanek 1989; Pierson et al. 1990; Charbonneau & Fahrig 2004). Other factors that potentially play a role are the accumulation of surface litter, which diminishes sites for alien establishment, and reduced propagule sources (dense, closed canopy forests have little herbaceous growth to attract livestock).

## Fuel Reduction in Forests

The National Fire Plan (U.S. Department of Agriculture Forest Service 2001) addresses the threat of catastrophic fires by reducing fuels with prescription burning or mechanical thinning. The Healthy Forests Restoration Act of 2003 (House Resolution 1904) increases the ability of resource managers to perform necessary fuel reduction projects and is called forest restoration because one of its goals is to return forests to their prefire-suppression-era structure and function. Fire lines and firefighting equipment associated with prescription burning directly favor alien species by creating soil disturbances and introducing alien propagules (Harrod & Reichard 2001; Backer et al. 2004), but the impact is potentially much broader. There is growing evidence that these fuel reduction projects alter ecosystem structure in ways that promote alien plant invasion.

Ponderosa pine forests in the Cedar Grove section of Kings Canyon National Park in the southern Sierra Nevada of California have been managed with prescription burning for more than two decades. The primary goal is to return a quasi-natural fire cycle for the resource benefit of

these forests. In 1998, however, fire management voluntarily halted this program because of the recognition that associated with prescription burning was an explosion of cheatgrass (*Bromus tectorum* L.) in the burned forests (Caprio et al. 1999). Results of experiments on the interaction between cheatgrass and fire show that burning stimulates cheatgrass populations, regardless of whether it is late spring or early fall (T. McGinnis & J.E.K., unpublished data). Based on these studies, the only parameter with potential for inhibiting cheatgrass is accumulation of pine-needle litter, which suggests that lengthening the fire-return interval to significantly exceed the natural cycle may be one of the few options for controlling this alien invader.

Restoration includes restoring not only natural processes such as fire but also natural structure through mechanical thinning of forests, and these practices also may enhance alien invasion. Extensive forest restoration is currently under way in many western U.S. ponderosa pine forests. These treatments alone or in combination with burning of slash increase both the diversity and abundance of alien plant species (Griffis et al. 2001; Dodson 2004; Wienk et al. 2004). Longer-term studies are needed, however, to determine whether this is a short-lived invasion or whether such practices provide an opportunity for invasives to gain a foothold that will allow long-term persistence in these forests.

These examples suggest a potential conundrum. Forest restoration often has as one of its goals returning the system to historical fire regimes of high fire frequency (Covington & Moore 1994). These historical fires, however, occurred on a landscape that lacked a background of diverse alien species poised to take advantage of such disturbance regimes. This situation may force a choice between restoring "natural" fire regimes or altering those fire regimes to favor communities of native species. In reality, though, the question is not that simple because reducing the incidence of fire in these ecosystems has long-term impacts on forest structure, with potential cascading effects on alien species.

Many western U.S. forests have historically had rather complex fire regimes that included a mixture of surface fires and localized crown fires (Odion et al. 2004*b*). Low-intensity surface fires removed dead wood and thinned the sapling population, and localized patches of crown fire created gaps that were essential for reproduction (Keeley & Stephenson 2000). A century of fire suppression, coupled with other management activities such as grazing and logging, has added greatly to the amount and continuity of understory fuels such that now these perturbed forests face the reality that gaps created by high-intensity crown fire will be potentially orders of magnitude larger (Fig. 1). These canopy gaps are sinks for alien invasion (Keeley et al. 2003). Crawford et al. (2001) reported more than a dozen alien species in gaps produced by high-severity wildfires in northern Arizona ponderosa

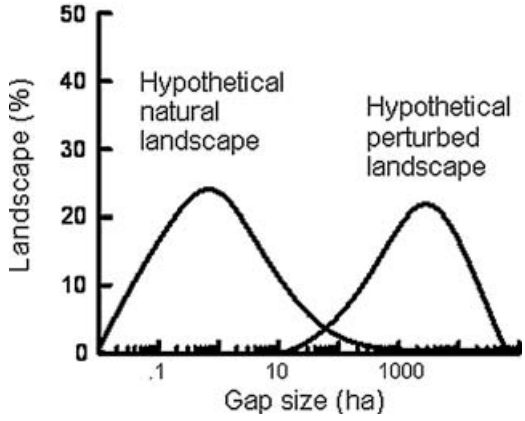


*Figure 1. Hypothetical distribution of fire-generated gaps expected for natural fire regimes and future fire regimes in Sierra Nevada mixed conifer forests perturbed by a century of fire exclusion (from Keeley & Stephenson 2000).*

forests, and these aliens constituted more than a quarter of the understory cover. These invasive species change the fuel structure of forests (Brooks et al. 2004) and are capable of setting back both natural and artificial regeneration of the dominant forest trees.

There are perhaps ways to minimize effects of alien species in fuel reduction projects. For example, many of the aliens Crawford et al. (2001) recorded in their burned sites were weeds that are often transported by cattle (Arnold 1950; Wuerthner & Matteson 2002); thus, prescription burning or logging, when coupled with grazing, may be a dangerous combination, exacerbating the alien invasion problem. This is supported by the report that wildfires in ungrazed ponderosa forests of northern Arizona have relatively few alien species (Laughlin et al. 2004). If there is a connection, then it could be rather large because 70% of the western United States is grazed, including wilderness areas, national forests, and some national parks (Fleischner 1994). I suggest that rotating grazing areas so that livestock are removed for an extended period of time before prescription burning might be one means of reducing alien species' response to necessary fuel reduction treatments.

Manipulating fire severity during prescription burning can also affect the alien response because high-severity gaps are more vulnerable to invasion than low-severity gaps (Keeley et al. 2003). This, however, is complicated by the requirement of many dominant trees in high-severity gaps for successful seedling recruitment (Keeley & Stephenson 2000).

Manipulating treatment patch size may be another way of altering the invasive threat. For example, the size of burned patches affects postfire colonization by opportunistic species (Turner et al. 1997). Small patches have a greater perimeter-to-area ratio, making the burned area

more vulnerable to invasion, whereas large burn patches have a smaller ratio, making the bulk of the burned area less susceptible to colonization from outside alien invaders. The landscape pattern of alien distribution, however, complicates drawing conclusions about community vulnerability to invasion. For example, forest patches adjacent to open habitat are much more susceptible to invasion than forests surrounded by more closed canopy forest (Charbonneau & Fahrig 2004). If aliens are sparsely distributed across the landscape, then small burn patches, despite their high perimeter-to-area ratio, are less likely to encounter alien populations, whereas large patches, with a greater absolute perimeter size, would have a higher probability of encountering alien populations.

In short, grazing history, alien distribution patterns, treatment size, and fire severity are all factors that might be manipulated to reduce the alien threat linked to necessary fuel-reduction projects. Roads and recreational use are other parameters that interact with fire and invasives (e.g., Gelbard & Belnap 2003) and could be manipulated in conjunction with fuel treatments to reduce alien invasion.

*Figure 2. Alien-grass-dominated scar in chaparral shrublands 10 years after an out-of-season winter burn in chaparral at Pinnacles National Monument (central coastal California) (photo by J. Keeley). A similar effect was also reported for another cool-season chaparral prescription burn in northern California (Parker 1987).*

## Prescription Burning in Shrublands

Many shrubland ecosystems such as the Intermountain West sagebrush steppe or California chaparral have a natural fire regime of high-intensity crown fires. These ecosystems provide fewer options for fuel reduction because mechanical treatments are both expensive and unlikely to provide commercial profit. Prescription burning is one of the more economically feasible treatments but there are increasing constraints on its widespread use in shrubland ecosystems because of the hazards of high-intensity fires on populated landscapes. One of the realities of doing prescription burning in crown-fire ecosystems is the difficulty of defining controllable prescriptions (Keeley 2002*a*). This is particularly problematic for burns in the normal late summer through autumn fire season. One approach is to conduct burns outside the normal fire season, but such manipulations have the potential for extreme resource damage, as illustrated by the poor recovery of the native community and massive alien invasion following a winter burn in one California park (Fig. 2).

For shrublands as well as forests, prescription burning is justified if it provides either resource benefits to the ecosystem or reduces fire hazard for people. In California chaparral, prescription burning is primarily justified on the basis of fire-hazard reduction, whereas in the Intermountain West sagebrush, the primary justification is benefit to ecosystem resources. The most commonly cited resource benefits are improved rangeland for wildlife (Beardall & Sylvester 1976; Holechek 1981) or livestock (Pechanec 1944; Sapsis & Kaufmann 1991). Other justifications include returning these ecosystems to their historical structure, which is considered by some to have been a landscape of more open sagebrush steppe vegetation. Indeed, rangeland literature commonly refers to the unnaturally dense stands of sagebrush in need of prescription burning (Blaisdell et al. 1982; Miller et al. 1994). In light of the massive cheatgrass invasion across much of this landscape (Mack 1981), coupled with the potential for burning to favor cheatgrass expansion (Harnis & Murray 1973; Knapp 1997; Young & Allen 1997), there is need for a closer examination of prescription burning in these Intermountain West ecosystems.

Prescription burning in sagebrush ecosystems is a highly effective method of improving rangelands for livestock grazing. The dominant shrub, *Artemisia tridentata* Nutt., is immediately replaced by more palatable herbaceous plants and recovers slowly over a period of decades (Stewart & Young 1939; Pechanec 1944; Ralphs & Busby 1979). On the other hand, prescription burning for enhancement of wildlife habitat appears to be justifiable in very few cases, and generally the loss of sagebrush following burning represents important habitat loss (Miller & Eddleman 2001; Welch & Criddle 2003). Restoring historical fire regimes is perhaps the weakest justification for prescription burning because many lines of evidence suggest fire-rotation intervals are currently at the low end of the historical range of variability (Menakis et al. 2003). The natural fire regime in sagebrush ecosystems appears to have been one of infrequent fires at 60- to 110-year intervals (Whisenant 1990; Welch & Criddle 2003; W. Baker, personal communication), although at the mesic end of the gradient it may have been shorter (Winward 1984). Thus, except on rangelands where livestock production

is the only goal, prescription burning may not be a desirable fire-management treatment because of the potential threat of exacerbating the cheatgrass invasion.

In California chaparral and sage scrub shrublands, a similar annual grass invasion has also occurred, although fire-management practices for rangeland improvement appear to have played a much bigger role. This began with burning by the Native Americans, largely to favor herbaceous vegetation over shrublands, which set much of the landscape in a quasi-disequilibrium vulnerable to rapid annual plant invasion upon the arrival of Europeans (Keeley 2002*b*). By the late nineteenth century rangelands were in short supply, widespread burning expanded the grazing lands, and the coastal analogues of cheatgrass, specifically *Bromus madritensis* L., *B. hordeaceous* L., and *B. diandrus* Roth., and forbs such as *Erodium cicutarium* (L.) L'Her., rapidly expanded to fill the void created by removing natural shrub dominants (Keeley 1990, 2001, 2004*b*). Initially these burning practices were unregulated, but in the mid-twentieth century organized efforts at rangeland expansion into shrublands was a state-sanctioned practice that resulted in substantial conversion to alien grasslands (Keeley & Fotheringham 2003).

Typically a repeat fire within the first postfire decade is sufficient to provide an initial foothold for aliens (Fig. 3). With the first entry of alien annuals into these shrubland ecosystems, there is a potential shift from a crown-fire regime to a mixture of surface and crown fires, where highly combustible grass fuels carry fire between shrub patches that have not yet attained a closed canopy capable of carrying crown fire under most weather conditions. As fire frequency increases there is a threshold beyond which the native shrub cover cannot recover (Zedler et al. 1983; Haidinger & Keeley 1993; Jacobson et al. 2004). Not only do alien grasses increase the probability of burning, but also the shift from crown fires to a mixture of surface and crown fires increases the probability of alien seed-

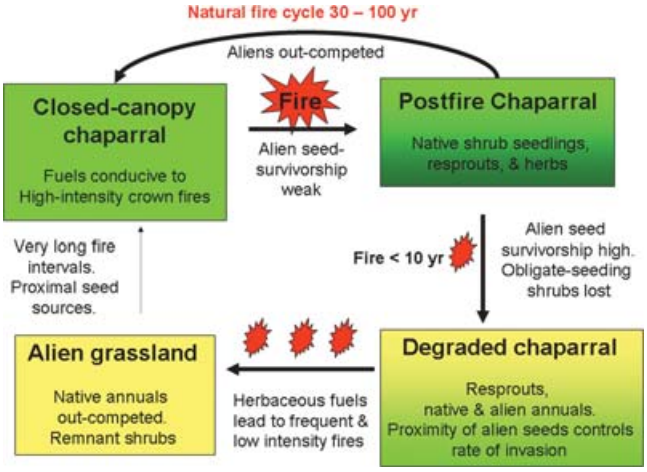


*Figure 3. Model of fire and alien species interactions in California chaparral.*

*Figure 4. Type conversion recorded for Malibu Canyon, Santa Monica Mountains, California: left, natural chaparral landscape representative of chaparral in Malibu Canyon (photo by Anna Jacobsen); right, landscape dominated by alien annual grass after three fires in 12 years (based on Jacobson et al. 2004; photo by Steve Davis).*

bank survivorship (Keeley et al. 2005) because grass fuels generate lower temperatures (Zschaechner 1985). In these shrublands and in other ecosystems, alien grasses alter fire regimes in ways that enhance their own success, in what has been described as a "grass/fire cycle" (D'Antonio & Vitousek 1992), "niche construction" (Keeley 2001), or "invasive engineering" (Cuddington & Hastings 2004).

In recent years ineffective fire prevention has allowed an unnaturally high number of wildfires on chaparral landscapes, which has resulted in conversion to alien-dominated grasslands (Fig. 4). Such type conversions not only affect biodiversity, but replacing slopes dominated by natural shrublands with grasslands also makes these landscapes highly vulnerable to major changes in hydrological processes. For example, experimental type conversions performed for fire hazard reduction have resulted in soil slips and other major geomorphological changes (Keeley 2002*a*).

On shrubland landscapes where the excessive load of anthropogenic fires has stressed natural ecosystems to the point of collapse, fire managers need to be prudent about adding further fire in the form of prescription burning. Currently this applies to much of the Great Basin and all of the lower-elevation foothills in southern California, where type conversion to alien grasslands is happening at an alarming rate (J.K., personal observations). To be avoided are prescription burning at fire-return intervals of 5 years in southern California chaparral (Loomis et al. 2003; Gonzalez-Caban et al. 2006), which are likely to lead to type conversion to alien grassland and even exacerbate the sedimentation problems they are supposed to reduce (Keeley et al. 2004).

## Fuel Breaks

Forests and shrublands, particularly in California, have had a long history of experimentation with different types of fuel breaks. They are constructed to create barriers to fire spread and to provide access and defensible space for fire-suppression crews during wildfires. These activities have the potential for creating suitable sites for alien plant invasion, and invasion is closely tied to the loss in overstory cover. In a recent study of 24 fuel breaks distributed throughout California, alien plants constituted as much as 70% of the plant cover and the proportion of aliens varied significantly with distance to roads, fuel break age, construction method, and maintenance frequency (Merriam et al. 2006). The association of alien species with fuel breaks raises two critical concerns. One is that the linear connectedness of these disturbance zones acts as corridors for alien invasion into wildland areas. Another is that these zones of reduced fuels produce lower temperatures and thus safe sites for alien propagules during wildfires, ensuring survivorship of seed banks (Keeley 2001, 2004*b*). Consequently, following fires these fuel breaks represent a major source area for alien invasion of adjacent wildlands (Fig. 5).

## Prescription Burning to Target Noxious Aliens

Fire has diverse effects on alien species, and except for a small handful of cases, it generally promotes persistence of aliens (e.g., Grace et al. 2001; Harrod & Reichard 2001; Brooks et al. 2004). Invasive species in the western United States that seem to be controlled by fire include Mediterranean Basin macchi shrubs known collectively as "brooms." Some of these are vigorous resprouters after fire and thus are not readily controlled by burning. Others (e.g., Scot's broom [*Cytisus scoparius* (L.) Link]) are weak resprouters, and burning shows promise of control. All have dormant, fire-stimulated seed banks; thus several repeat fires appear to be required to extirpate brooms from a site (Tveten & Fonda 1999; Alexander & D'Antonio 2003; Odion & Haubensak 2004), not unlike what happens to native shrublands in the face of repeat fires (Figs. 3 & 4). Burning, however, typically replaces these noxious woody aliens with herbaceous alien species (Keeley 2001).

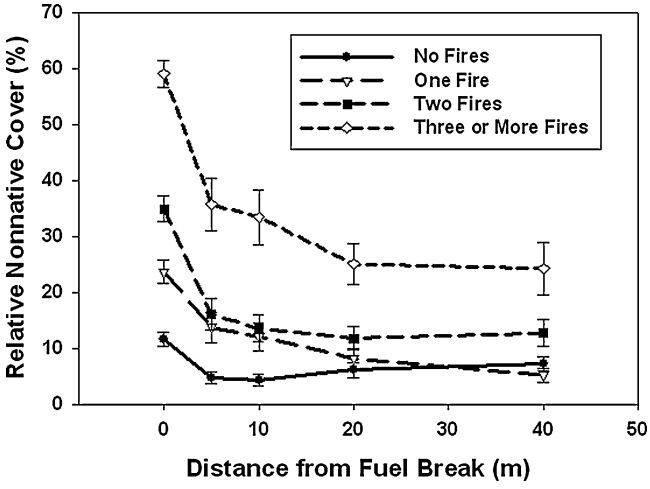


*Figure 5. Interaction between number of fires and distance from the fuel break. Error bars represent + 1 SE (from Merriam et al. 2006).*

Several lines of evidence point to precisely timed prescription burning as an effective treatment for eliminating certain noxious alien annuals with transient seed banks that are vulnerable to fire during spring seed dispersal. One example widely cited in recent alien plant review articles as a demonstration of such success is the application of spring burning in the control of yellow starthistle (*Centaurea solstitialis* L.). This European pest is distributed from Idaho to California and has been targeted as a particularly noxious alien because it alters range conditions and severely reduces soil water resources (Gerlach 2004). Confidence in prescribed burning treatment as a control for this species is based on the results of annual burning for 3 consecutive years in very dense stands that demonstrated 90–100% reduction in starthistle (DiTomaso et al. 1999; Odion et al. 2004*a*). Burn plans written by agencies undertaking prescribed burns in annual grasslands often use this as one of their primary goals (e.g., East Bay Regional Parks, http://www.ebparks.org/fire/rxfire). This species, however, like many aliens, has a relatively long-lived seed bank (Callihan et al. 1993), and longer-term study shows that this thistle rapidly reestablishes once burning is halted (Fig. 6). Clearly, prescribed burning provides only temporary reduction, does not effect sustainable control of this alien, and may exacerbate the alien situation.

Most alien herbs are opportunistic species that capitalize on disturbance. I offer the hypothesis that when it comes to eliminating such noxious aliens, control is most likely under conditions that limit the use of further disturbances such as fire (or grazing, mowing, or herbicides). In some cases prescribed fire may be appropriate if applied in a manner that affects the noxious target species more than potential native competitors and if coupled with active ecosystem restoration that alters the competitive balance between aliens and natives. Sustainable control of these aggressive weeds is most likely going to occur only when natural, intact ecosystems are restored. In the case of yellow starthistle, it invades annual grasslands that owe their origin to disturbance, either displacement of native perennial grassland or type conversion of shrublands and woodlands (Huenneke 1989; Keeley 1990; Hamilton 1997). In the absence of community restoration, prescription burning is likely to provide only temporary control of this, and other, noxious annual weeds, and not be cost-effective.

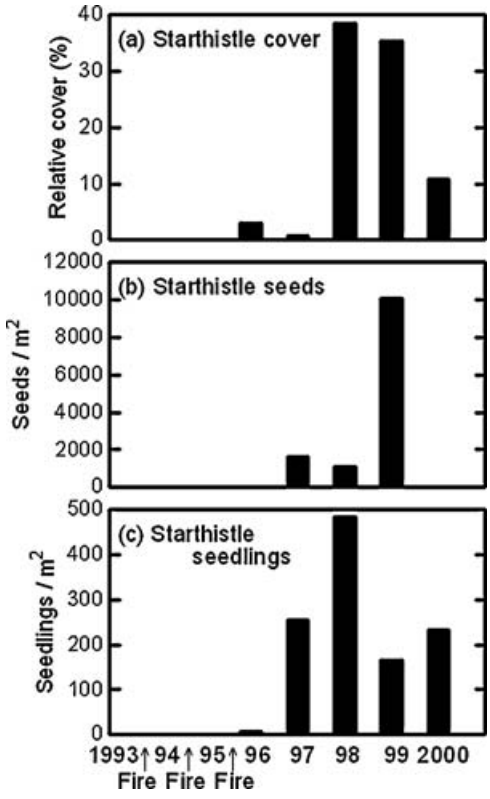


*Figure 6. Yellow starthistle (a) cover, (b) seed, and (c) seedling production following three consecutive annual burns applied to extremely dense populations of this noxious alien weed. Immediate postfire results were promising (DiTomaso et al. 1999), but follow-up studies indicate that burning destabilized these grasslands and allowed subsequent reinvasion once burning was stopped (Kyser & DiTomaso 2002).*

## Postfire Rehabilitation

Propagule source is often the limiting step in the invasion process (D'Antonio et al. 2001) and thus postfire management practices such as site stabilization by seeding of non-natives must be considered a potential influence on alien plant invasion. These postfire rehabilitation projects illustrate well the Severide Principle, after the newscaster Eric Severide, who is quoted as saying, "Most problems begin as solutions."

Early efforts at such revegetation projects may have played a role in the spread of some noxious weeds. For example, postfire seeding in southern California chaparral in the 1940s aerially seeded black mustard (*Brassica nigra* [L.] Koch and possibly related taxa) on steep southern California watersheds (Gleason 1948). These aggressive weeds soon found their way into citrus orchards and other agricultural fields and were eventually abandoned by fire managers as a suitable slope stabilizer. These species, however, produce polymorphic seed banks with dormant fire-stimulated germination (Went et al. 1952), and decades later on many of the previously seeded slopes in the Los Angeles Basin this species still figures prominently in the postfire flora as a ghost of seedings past (Keeley et al. 2005). Eventually postfire seeding projects replaced mustard with various grass species (e.g., ryegrass [*Lolium multiflorum* Lam.], zorro fescue [*Vulpia myuros* (L.) C. Gmelin], crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.]) that appear to lack persistent seed banks. Although these grasses are not persistent on chaparral or forested slopes (Barclay et al. 2004; Beyers 2004), they are capable of invading adjacent grassland and savanna communities.

Because they lack an ability to invade communities, "sterile" or "nonpersistent" cereal grains have been considered a more desirable species for reseeding (Beyers 2004). Although seeding of these species may have achieved some of the intended goals of slowing soil erosion, they have introduced other problems. In one study in the Sierra Nevada the success of wheat seeding was so extraordinary (Fig. 7) that it resulted in the loss of substantial native plant diversity and pine reproduction (Keeley 2004*a*), a pattern common in many seeding projects (Beyers 2004). Seeding nonpersistent species also carries with it the problem that a marked loss of plant cover in the second postfire year will create an ecological vacuum, and aggressive alien invaders are well suited to exploit this situation.

Increasingly it is apparent that mechanical rehabilitation treatments, including straw mulch and hay bales, are more predictable means of reducing soil erosion and other postfire hydrological problems (Robichaud et al. 2000). Mulching treatments, however, are particularly hazardous in terms of introducing and promoting alien establishment (Kruse et al. 2004). In fact, accidental introduction of alien propagules is possible with any "burned

*Figure 7. Postfire ponderosa pine forest reseeded with a nonpersistent variety of wheat after fire in the Giant Sequoia National Monument, Fresno County, California (photo by J. Keeley).*

area emergency rehabilitation" project. For example, following the 2000 Cerro Grande Fire it is estimated that contamination of aerial seeding sources was responsible for inadvertently broadcasting more than 1 billion cheatgrass seeds on recently burned sites (Keeley et al. 2006).

## Conclusions

Fire management practices could have widespread effects on invasions of alien species. This linkage is best understood when these problems are placed in a context of community ecology theory. Fire suppression and prefire fuel manipulations have ecological equivalents in that the former attempts to maintain ecosystem equilibrium by preventing disturbance and the latter introduces disequilibrium.

In western U.S. forests, a century of successful fire suppression policy has shifted the competitive balance in favor of long-lived trees that create ecosystem conditions unfavorable to alien invasion. Although greater ecosystem equilibrium appears to exclude alien plants, fire exclusion has set these forests on a trajectory of undesirable conditions for both forest sustainability and human fire hazard. Thus, forest thinning, fuel breaks, and prescribed burning are necessary and inevitable. But accompanying these management activities is a shift in ecosystem properties that favor early successional species, and when done in the context of a landscape with alien species it is likely to alter the balance of native and non-native species. The impact of these management practices may be altered by considering management practices that decouple grazing and burning practices and manipulate burning patterns in light of prefire alien presence.

In many western U.S. shrubland ecosystems, fire suppression policy—despite valiant efforts—has not kept up with an ever-increasing frequency of fires. These communities exhibit weak resilience to major deviations from the natural crown-fire regime and often the dominant life forms are lost, creating an ecological vacuum that is rapidly filled by alien weeds. In both the Intermountain West sagebrush and California chaparral (including sage scrub) this alien invasion has historically been exacerbated by fire management practices that included prescription burning for range improvement. Current infestations of annual grasses in both regions require enhanced efforts at fire prevention, fire suppression, and avoidance of prescribed burning under many situations.

## Acknowledgments

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# Historical patterns of wildfire ignition sources in California ecosystems

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**Abstract.** State and federal agencies have reported fire causes since the early 1900s, explicitly for the purpose of helping land managers design fire-prevention programs. We document fire-ignition patterns in five homogenous climate divisions in California over the past 98 years on state Cal Fire protected lands and 107 years on federal United States Forest Service lands. Throughout the state, fire frequency increased steadily until a peak *c.* 1980, followed by a marked drop to 2016. There was not a tight link between frequency of ignition sources and area burned by those sources and the relationships have changed over time. Natural lightning-ignited fires were consistently fewer from north to south and from high to low elevation. Throughout most of the state, human-caused fires dominated the record and were positively correlated with population density for the first two-thirds of the record, but this relationship reversed in recent decades. We propose a mechanistic multi-variate model of factors driving fire frequency, where the importance of different factors has changed over time. Although ignition sources have declined markedly in recent decades, one notable exception is powerline ignitions. One important avenue for future fire-hazard reduction will be consideration of solutions to reduce this source of dangerous fires.

**Additional keywords:** arson, debris burning, equipment, lightning, powerlines, smoking.

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## Introduction

Increasing concern over wildfires has prompted a re-emphasis by the federal government to stop this trend (https://www.doi.gov/pressreleases/secretary-zinke-directs-interior-bureaus-take-aggressive-action-prevent-wildfires, accessed 1 April 2018; Bedard 2017). For many decades, the focus of fire management has been on fuel modification with success on certain landscapes (Kalies and Kent 2016) but limited improvement on others (Keeley and Safford 2016). Because humans are a dominant ignition source over the majority of North America (Balch *et al.* 2017; Syphard *et al.* 2017) there is reason to believe improvements in fire prevention may be a key to reducing fire impacts. Indeed, the United States Forest Service (USFS) has been reporting fire causes since it began collecting systematic data on fires in 1905, with the explicit purpose of helping land managers design fire prevention programs (Donoghue 1982*a*).

Effective fire-prevention requires a sound understanding of the patterns and causes of fire ignitions, which are closely aligned with both human and biophysical-landscape characteristics (Syphard *et al.* 2008). Prestemon *et al.* (2013) suggested a conceptual model that linked ignitions to changes in biophysical, societal, prevention and management variations that illustrates the complexities of ascertaining relationships between different sources and how they change over time.

An important characterisation of anthropogenic ignitions is that the most abundant ignition sources are not always associated with the greatest area burned (Syphard and Keeley 2016). Thus, a topic in need of further study is how to sort out those ignition sources that are most damaging, how those have changed over time, and in light of future needs, how climate change is likely to affect different ignition sources and losses. For example, it has been demonstrated for the state of Victoria, Australia, that some ignition sources, such as electrical distribution lines, may be limited in number but result in much more severe fire consequences (Miller *et al.* 2017). In addition, these fires are more likely during periods of elevated fire danger. If some ignition sources play a larger role in area burned, these might be targets for closer scrutiny and fire-management planning. This potential has been demonstrated for parts of southern California over recent decades, where powerlines have been shown to cause a substantial amount of area burned in both subregions in southern California (Syphard and Keeley 2015). Other important factors were arson in one subregion and equipment in another.

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The goal of the present research is to expand that approach to include the entire written history of fires in the state. Our focus was on the spatial and temporal patterns of different ignition sources and the relationship between type of ignition and area burned. We took a long-term historical approach utilising data from 1910 to 2016 for USFS lands and from 1919 to 2016 for state protected Cal Fire lands. First, we examine the spatial and temporal patterns of natural lightning-ignited fires *v.* human fires in the state, and their contribution to area burned. Next, we investigated which anthropogenic causes are most frequent, their distribution within the state, their change over time and their contribution to area burned. Based on a study of state-protected lands in California, Syphard *et al.* (2007) found that fires increased from 1931 to the 1980s, but then decreased over the subsequent decades. A similar pattern for the whole state was also reported by Keeley and Syphard (2017) on both Cal Fire and USFS lands. Thus, the present study contrasts fire-ignition patterns within climatically homogenous sub-regions for the period before 1980 and for the period 1980–2016.We also investigated the extent to which seasonal climate parameters could explain patterns of ignitions and area burned for each type of ignition source.

## Methods

Fire-history data for numbers of fires and area burned, by cause, were analysed separately for state-protected Cal Fire and federal USFS lands. Data for counties, forests and climate divisions were all normalised by the area protected each year and within each unit and expressed as number of fires, or hectares burned, per million hectares.

Cal Fire data included 51 of the state's 58 counties (see Fig S1, available as Supplementary material to this paper) as 7 counties had limited fire activity or records. Fire statistics were from direct protection areas (DPA), which are mostly state-responsibility lands with smaller amounts of federal lands, and included the years 1919–2016, summarised by county. The term DPA was first used in 1986 and the area included was equivalent to what was called State Zone (1972–1985), Zones I and II (1945–1971) and Zones 1, 2, 3 (1919–1944). Cal Fire data from 1919 to 1930 are unpublished and were only available as typed reports at the California State Archives in Sacramento. Data from 1931 to 2016 were available in annual reports variously named, Forest Fire Summary, Fire Statistics, Fire Activity Statistics, and Wildfire Activity Statistics, often referred to as the *Redbook* series, available from research libraries or directly from the agency. Only 30 counties had complete data (excluding 1927 for nearly all counties and a few additional years in other counties) beginning in 1919, and an additional 21 counties had continuous data beginning in 1945 (or slightly later in a few cases) (see Table S1 for years of records for each county). Area protected has changed through this period of record and thus data were normalised to the hectares protected for that year presented with the annual reports. There was a period from 1941 to 1952 area where protected-area data were not included in annual reports and, as best we can determine, those data are no longer available, so we used the areas protected in 1940. In all cases, the changes between 1940 and 1953, when such data were again available, were minor.

USFS fire data covered 17 national forests (Fig S2) and included the years 1910–2016 (see Table S2, two forests were created after 1910 carved out of area from adjoining forests). Area protected has changed through this period of record and thus data were normalised to the hectares protected for that year. Data for USFS lands through the 1980s were from annual fire statistics reports for Region 5, available in the Forestry Library (most of which was transferred to the Bioscience Library) at the University of California, Berkeley. More-recent data, 1970 to 2016, were from the National Wildfire Coordinating Group (see http://fam.nwcg.gov/fam-web/weatherfirecd/state_data.htm, accessed 1 June 2017).

Most investigators are unfamiliar with these historical fire records and are sometimes sceptical of their accuracy. For example, Stephens (2005) contended that USFS data before 1940 were inaccurate, but cited a source (Mitchell 1947) that provided no evidence of this. Likely, the idea comes from Donoghue's (1982*b*) comment '1940 marked the modern era of fire reporting'. However, that comment was in reference to the fact that 'the report issued at this time was the first designed for automated data processing and easy readability' and was not in reference to reliability.

Historians have generally been confidant in these early California fire records (Brown 1945; Show 1945; Clar 1969; Cermak 2005). The first author, J. E. Keeley, examined all of the California fire-related materials stored at the state and federal archives and believes collectively they show managers have always been conscientious about reporting accuracy and completeness. For example, beginning in 1905, USFS record-keeping required 15 items of information on the fire reporting Form 944, including the specific cause (Donoghue 1982*b*). On state-protected lands there was an incentive in that the 1911 *Federal Weeks Law* provided fiscal aid to states based on statistics of fire protection (see http://www.calfire.ca.gov/about/about_calfire_history2, accessed 23 May 2018). In 1919, the California state legislature appropriated money for fire prevention and suppression, and records in the state archive show that, by 1920, there were more than 400 fire wardens distributed throughout the state who were charged with fire-fighting and fire reporting. In 1920, there were 800 flights of the Army's 9th Aero Squadron fire patrol that covered 426 500 km during the 5-month California fire season (Cermak 1991).

One complication in studying ignition sources is that reported categories have changed over time. Certain causes have persisted over the entire period of record, including lightning, smoking and camping, but other categories have changed their names. For example, arson fires are a relatively new category as intentionally set fires have, in the past, been labelled as 'incendiary', and seem to have been more rural than contemporary urban arson fires (Kuhlken 1999) and in this paper they are all recorded as arson fires. Other changes include the term 'brush burning' being changed to 'debris burning', and the categorisation of brush burning has been folded into debris burning. Causes that were unknown or represented minor categories have been included as miscellaneous fires (Donoghue 1982*a*), but are not addressed here.

Cal Fire data were spatially explicit at the level of the county and USFS data at the level of the individual forest. However, for analysis, these were grouped into climatically homogenous

areas as defined by the National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center (NCDC) California Climate Divisions (Fig. 1), comprising the main fire-prone landscapes in the state (see http://www.ncdc.noaa.gov/temp-and-precip/time-series/index.php?parameter=pdsi&month=1&year=2008&filter=p12&state=4&div=5, accessed 15 June 2016). These include, from north to south, Division 1 (North Coast), 2 (North Interior), 5 (Sierra Nevada), 4 (Central Coast), and 6 (South Coast). Where boundaries did not match precisely, counties or forests were placed in the climate division comprising the majority of land area in that unit.

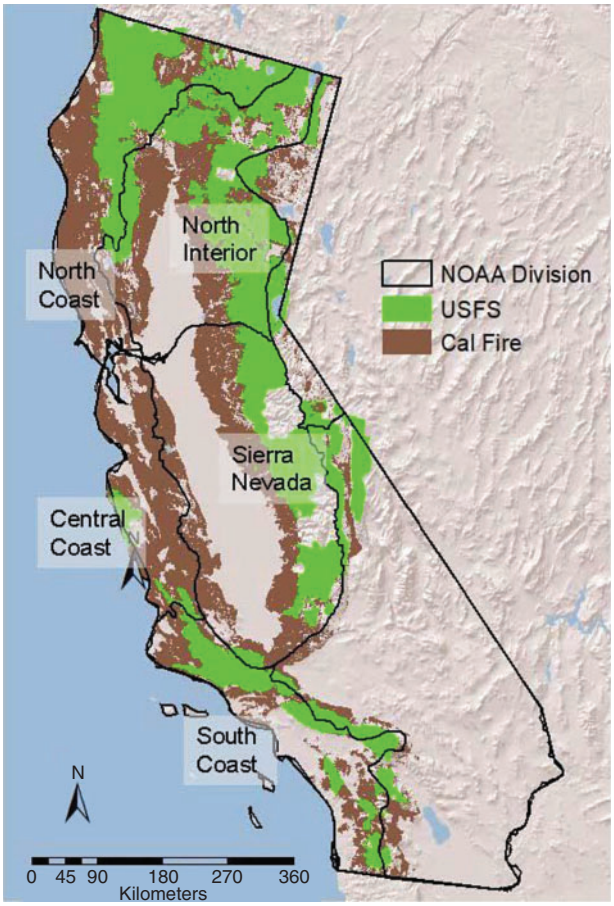


**Fig. 1.** NOAA climate divisions and Cal Fire protected and USFS protected lands in California for the five climate divisions with long-term fire history.

In 1919, Cal Fire-protected lands were $11.7 \times 10^6$ ha and increased to $12.5 \times 10^6$ ha in 2016. USFS lands comprised $9.8 \times 10^6$ ha in 1919 and decreased to $9.5 \times 10^6$ ha in 2016. Vegetation on state lands was dominated by grasslands and shrublands in the south and with significant woodlands and coniferous forests farther north (see Keeley and Syphard 2017 for more detailed vegetation data). USFS lands were dominated by coniferous forests, except in the southern part of the state where they were dominated by shrublands.

To evaluate climate impact on fire activity, we utilised PRISM climate for each county on Cal Fire-protected lands and each forest on USFS lands (Fig. 1). For every year in the analysis, we extracted 2.5 arc-minute PRISM data (PRISM Climate Group, Oregon State University, see http://prism.oregonstate.edu, accessed 15 February 2017) for areas within the boundaries of the Cal Fire and USFS lands. For each county and forest, we computed area-weighted averages of monthly mean precipitation and temperature, summarised by season – winter being December (prior year), January and February, spring being March, April and May, summer being June, July and August, and autumn being September, October and November.

Analysis was conducted with Systat software (ver. 11.0, Systat Software, Inc., San Jose, CA, http://www.systat.com/). For the climate analysis, we developed multiple regression models explaining area burned for USFS and Cal Fire based on seasonal temperature, precipitation and prior-season precipitation variables. To ensure multicollinearity would not be an issue, we calculated correlation coefficients among all potential explanatory variables and eliminated those that were strongly correlated ($P < 0.05$) with other variables in the model.

## Results

Long-term averages show that on a per-unit-area basis fires were approximately twice as frequent or more on Cal Fire lands as on USFS lands in all five NOAA climate divisions (Table 1). However, the relationship between ignitions and area burned varied markedly between Cal Fire and USFS lands and between divisions. In the North Coast division, Cal Fire dealt with twice as many fires as the USFS but the average area burned was very similar. In contrast, in the interior from the Sierra Nevada northward, Cal Fire experienced approximately double the number of fires and nearly double the area burned. In the coastal

**Table 1. Fire frequency and area burned on state and federal lands in California**

| NOAA division | Cal Fire (1919–2016) | | USFS (1910–2016) | |
|---|---|---|---|---|
| | Fire frequency ($n$/year/$10^6$ ha) | Area burned (ha/year/$10^6$ ha) | Fire frequency ($n$/year/$10^6$ ha) | Area burned (ha/year/$10^6$ ha) |
| North Coast | 317 | 7780 | 150 | 7559 |
| North Interior | 421 | 9642 | 207 | 5914 |
| Sierra Nevada | 356 | 8436 | 169 | 4709 |
| Central Coast | 277 | 5496 | 66 | 18860 |
| South Coast | 656 | 15278 | 369 | 24442 |

**Table 2. Cal Fire counties total fires, percentage due to human ignitions and regression coefficients for population density *v.* number of fires (per year per million ha) for years 1919–2016**

| Division | County | Total | Percentage human | <1980 | | ≥1980 | |
|---|---|---|---|---|---|---|---|
| | | | | *r* | *P* | *r* | *P* |
| North Coast | Del Norte | 330 | 97 | 0.39 | 0.007 | 0.07 | 0.667 |
| | Humboldt | 219 | 93 | 0.31 | 0.018 | −0.62 | 0.000 |
| | Lake | 446 | 98 | 0.72 | 0.000 | −0.66 | 0.000 |
| | Marin | 1155 | 100 | 0.10 | 0.526 | −0.07 | 0.699 |
| | Mendocino | 255 | 94 | 0.46 | 0.000 | −0.46 | 0.004 |
| | Napa | 493 | 99 | 0.79 | 0.000 | −0.83 | 0.000 |
| | Siskiyou | 256 | 63 | 0.44 | 0.000 | −0.07 | 0.681 |
| | Sonoma | 488 | 99 | 0.90 | 0.000 | −0.71 | 0.000 |
| | Trinity | 229 | 75 | 0.05 | 0.709 | −0.27 | 0.102 |
| North Interior | Butte | 929 | 95 | 0.89 | 0.000 | −0.51 | 0.001 |
| | Colusa | 115 | 95 | 0.44 | 0.003 | −0.60 | 0.000 |
| | Glenn | 87 | 93 | 0.28 | 0.069 | −0.64 | 0.000 |
| | Lassen | 178 | 50 | 0.55 | 0.000 | −0.39 | 0.017 |
| | Modoc | 113 | 51 | 0.42 | 0.020 | 0.04 | 0.811 |
| | Nevada | 936 | 97 | 0.72 | 0.000 | −0.80 | 0.000 |
| | Placer | 1645 | 98 | 0.88 | 0.000 | −0.89 | 0.000 |
| | Plumas | 489 | 74 | 0.67 | 0.000 | 0.08 | 0.654 |
| | Shasta | 469 | 90 | 0.77 | 0.000 | −0.38 | 0.020 |
| | Solano | 406 | 99 | 0.55 | 0.000 | −0.54 | 0.000 |
| | Tehama | 196 | 93 | 0.90 | 0.000 | −0.48 | 0.000 |
| | Yolo | 226 | 97 | 0.61 | 0.000 | −0.32 | 0.051 |
| | Yuba | 723 | 97 | 0.49 | 0.000 | −0.26 | 0.118 |
| Sierra Nevada | Amador | 507 | 99 | 0.60 | 0.000 | −0.47 | 0.003 |
| | Calaveras | 337 | 99 | 0.59 | 0.000 | −0.57 | 0.000 |
| | El Dorado | 213 | 98 | 0.77 | 0.000 | −0.26 | 0.123 |
| | Fresno | 100 | 96 | 0.84 | 0.000 | −0.69 | 0.000 |
| | Inyo-Mono | 255 | 98 | 0.67 | 0.002 | −0.63 | 0.000 |
| | Kern | 804 | 99 | 0.84 | 0.000 | −0.51 | 0.002 |
| | Kings | 321 | 99 | 0.29 | 0.146 | −0.32 | 0.107 |
| | Madera | 823 | 99 | 0.65 | 0.000 | −0.48 | 0.003 |
| | Mariposa | 617 | 97 | 0.70 | 0.000 | −0.45 | 0.005 |
| | Merced | 602 | 95 | 0.21 | 0.180 | −0.42 | 0.010 |
| | San Joaquin | 850 | 97 | 0.05 | 0.789 | −0.46 | 0.005 |
| | Stanislaus | 237 | 95 | 0.35 | 0.024 | −0.20 | 0.244 |
| | Tulare | 180 | 93 | 0.77 | 0.000 | −0.33 | 0.048 |
| | Tuolumne | 280 | 93 | 0.89 | 0.000 | −0.23 | 0.174 |
| Central Coast | Alameda | 117 | 98 | 0.65 | 0.000 | −0.68 | 0.000 |
| | Contra Costa | 447 | 93 | 0.59 | 0.000 | −0.21 | 0.213 |
| | Monterey | 306 | 93 | 0.84 | 0.000 | −0.83 | 0.000 |
| | San Benito | 151 | 93 | 0.62 | 0.000 | −0.81 | 0.000 |
| | San Luis Obi | 322 | 99 | 0.77 | 0.000 | −0.64 | 0.000 |
| | San Mateo | 158 | 97 | 0.74 | 0.000 | −0.08 | 0.055 |
| | Santa Clara | 242 | 93 | 0.38 | 0.002 | −0.63 | 0.000 |
| | Santa Cruz | 814 | 97 | 0.80 | 0.000 | −0.57 | 0.000 |
| South Coast | Los Angeles | 778 | 98 | 0.41 | 0.007 | −0.53 | 0.001 |
| | Orange | 1198 | 100 | 0.85 | 0.000 | −0.62 | 0.000 |
| | Riverside | 790 | 98 | 0.82 | 0.000 | −0.82 | 0.000 |
| | San Bernardi | 791 | 96 | 0.73 | 0.000 | −0.81 | 0.000 |
| | San Diego | 576 | 97 | 0.63 | 0.000 | −0.60 | 0.000 |
| | Santa Barbar | 347 | 99 | 0.70 | 0.000 | −0.64 | 0.000 |
| | Ventura | 713 | 99 | 0.84 | 0.000 | −0.42 | 0.010 |

areas from San Francisco to San Diego, there were substantially more fires on Cal Fire-protected lands but the area burned was substantially greater on USFS lands.

For Cal Fire-protected landscapes, the area-based average number of fires per year (1919 to 2016) varied from 1645 in Placer County to 87 in Glenn County (Table 2). Humans were

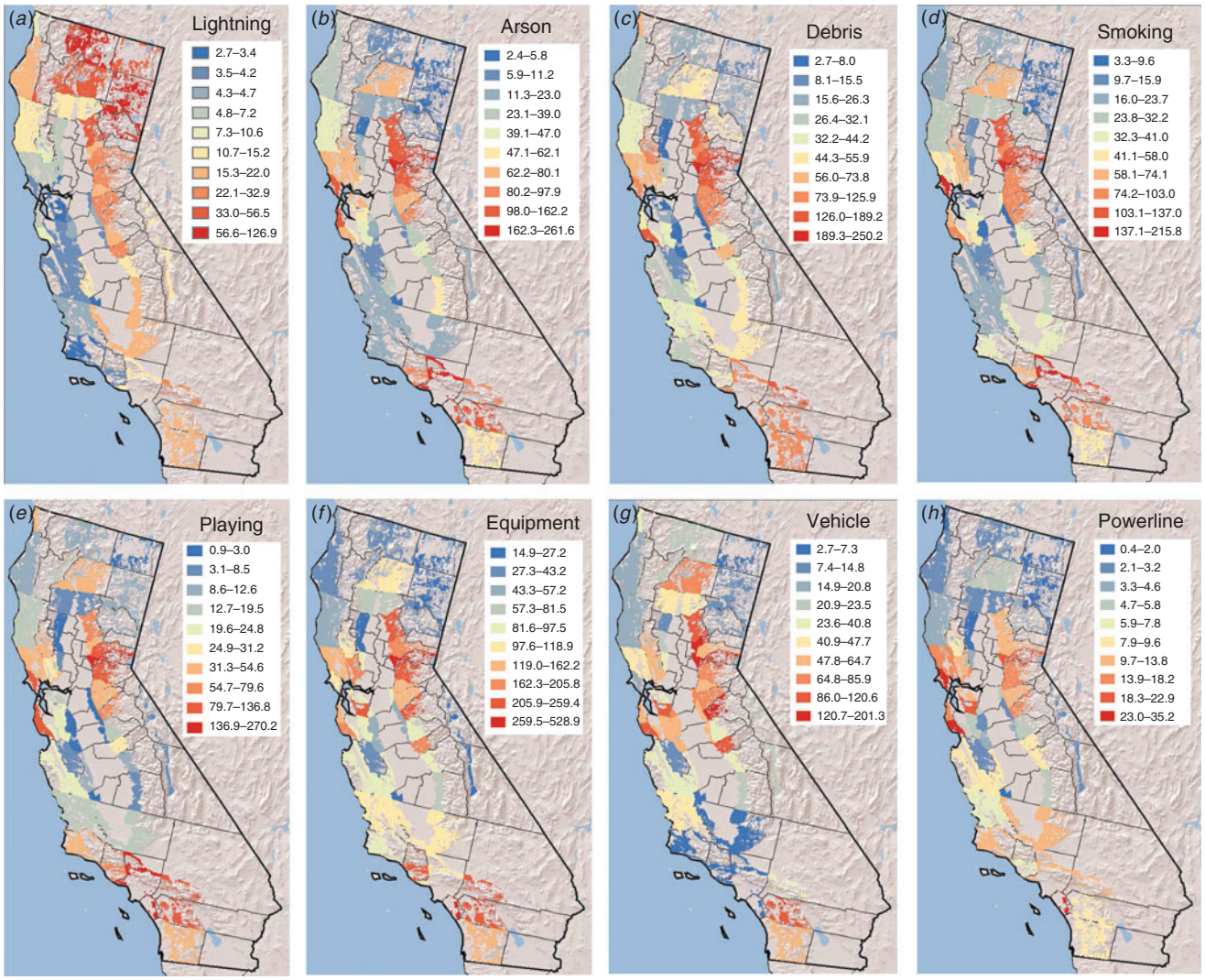


**Fig. 2.** Fire frequency for different ignition sources on Cal Fire protected lands in California for the years 1919–2016 ($n$/year/$10^6$ ha); note change in scales for each source.

responsible for most of fires, accounting for 95% or more of the ignitions in two-thirds of the counties. However, certain northern California counties stood out as notable exceptions, e.g. in Siskiyou, Trinity, Lassen, Modoc and Plumas counties lightning accounted for one-quarter to more than half of all ignitions, patterns illustrated in Fig. 2*a*. Regions with the lowest lightning-ignited fires extended through the coastal ranges from north of San Francisco to Santa Barbara. Area burned by lightning-ignited fires generally followed a similar pattern, although it was the source for significant burning in the San Bernardino County of southern California (Fig. 3*a*).

For USFS lands, the area-based average number of fires per year (1910 to 2016) varied from 478 in San Bernardino to 67 in Eldorado National Forest (Table 3). Humans accounted for far fewer fires than on Cal Fire lands. In the South Coast division, humans were responsible for 74–88%; however, in half of the other forests, humans accounted for less than 50% of the fires. As with Cal Fire landscapes, USFS lightning-ignited fires were most common in the north-east part of the state and declined markedly in coastal central and southern California (Fig. 4*a*). Area burned by lightning-ignited fires generally followed a similar pattern with the exception that parts of the North Coast and Central Coast, despite having few such ignitions, had substantial area burned by this source (Fig. 5*a*).

On both Cal Fire- and USFS-protected lands, humans played a substantial role in fire ignitions. During the first two-thirds of the 20th century there was a very strong positive relationship between population density and fire frequency in nearly 90% of the counties (Table 2) and more than 75% of the forests (Table 3). However, from 1980 to 2016, although population growth continued throughout the state, in most counties and forests, population density exhibited a highly negative relationship with fire frequency (Tables 2, 3).

On both Cal Fire- and USFS-protected lands, human-ignited fires derived from both intentional and accidental causes. The highest number of fires was from equipment, arson, debris

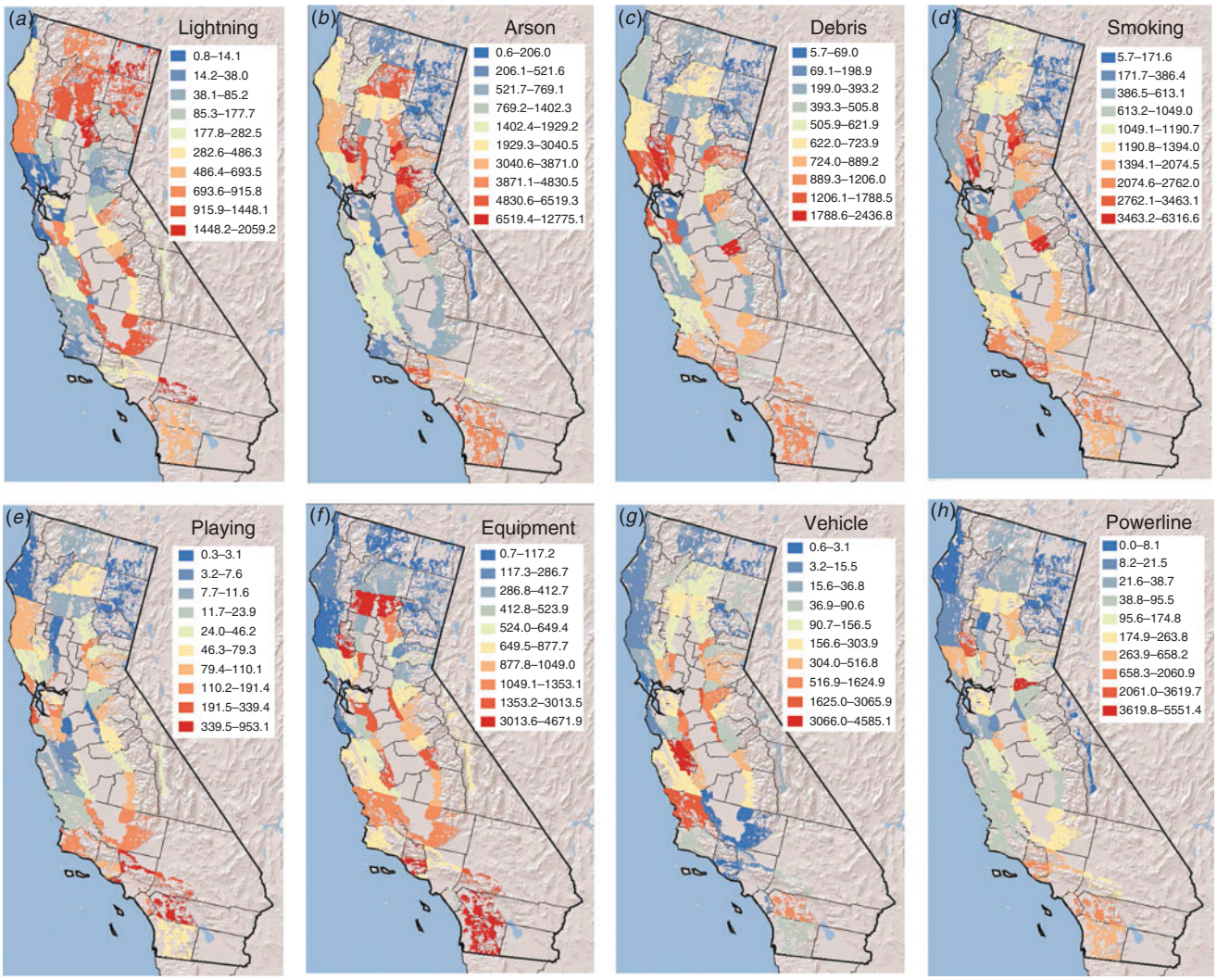


**Fig. 3.** Area burned by different ignition sources on Cal Fire protected lands in California for the years 1919–2016 (ha burned/year/$10^6$ ha); note change in scales for each source.

burning, children playing with fire, smoking, vehicles and powerlines (Tables S3–S6). Sources, such as railroads and lumber practices, did cause many fires in the early part of the record, but are of minor significance today (this change not shown).

These ignition sources exhibited marked geographical variation in their importance (Fig. 2–5). On lower elevation Cal Fire landscapes, arson was responsible for much of the area burned in the northern Sierra Nevada Mountains. (Fig. 3*b*), whereas debris burning was responsible for much of the area burned north and south of San Francisco (Fig. 3*c*), vehicles were the cause of much of the burning in the central coastal ranges (Fig. 3*g*) and equipment fires in southern California (Fig. 3*f*). Powerlines were responsible for significant number of fires in the north bay area of San Francisco and coastal communities from Santa Barbara south to the border (Fig. 3*h*).

In USFS forests, area burned in the South Coast was most heavily affected by arson and powerlines (Fig. 5*b*, *h*), but equipment and debris burning dominated in the Central Coast (Fig. 5*c*,*f*). Forests adjacent to high density metropolitan areas in Los Angeles and western San Bernardino counties had substantial burning due to smoking, children playing with fire, and powerlines (Fig. 5*d*, *e*, *h*).

### *Changing ignition patterns over time*

The historical pattern of fire frequency on lower elevation Cal Fire-protected lands for 97 years and USFS lands for 107 years is illustrated in Fig. 6 for the five climate divisions. There was a common pattern across both Cal Fire and USFS lands and consistent within each of the five climate divisions – a highly significant increase in fire frequency from the beginning of records to 1979, and a switch to a highly significant decline in fires from 1980 to 2016 (Fig. 6), the single exception being the South Coast USFS lands (Fig. 6*r*). Despite a significant fit of these data to the linear regression models, there were some marked departures on Cal Fire lands during the early record. Plotting of linear regression residuals from 1919 to 1979 shows

**Table 3. USFS forests total number of fires, percentage ignited by humans and regression coefficients for population density *v.* number of fires (per year per million ha) for years 1910–2016**

| Division | Forest | Total | Percentage human | <1980 | | ≥1980 | |
|---|---|---|---|---|---|---|---|
| | | | | *r* | *P* | *r* | *P* |
| North Coast | Klamath | 192 | 28 | 0.23 | 0.057 | −0.33 | 0.045 |
| | Mendocino | 97 | 51 | 0.26 | 0.032 | −0.36 | 0.030 |
| | Six Rivers | 137 | 65 | 0.46 | 0.007 | 0.11 | 0.528 |
| North Interior | Lassen | 271 | 38 | 0.66 | 0.000 | −0.43 | 0.008 |
| | Modoc | 118 | 21 | 0.42 | 0.000 | −0.06 | 0.730 |
| | Plumas | 280 | 46 | 0.36 | 0.002 | −0.37 | 0.024 |
| | Shast-Trinity | 188 | 50 | 0.15 | 0.142 | −0.41 | 0.012 |
| | Tahoe | 257 | 54 | 0.22 | 0.067 | −0.44 | 0.007 |
| Sierra Nevada | Eldorado | 67 | 58 | 0.43 | 0.000 | −0.25 | 0.129 |
| | Inyo-Mono | 237 | 40 | 0.85 | 0.000 | −0.67 | 0.000 |
| | Sequoia | 79 | 39 | 0.75 | 0.000 | −0.76 | 0.000 |
| | Sierra | 213 | 48 | 0.63 | 0.000 | −0.68 | 0.000 |
| | Stanislaus | 201 | 49 | 0.50 | 0.000 | −0.55 | 0.000 |
| Central Coast | Los Padres | 203 | 82 | 0.51 | 0.000 | −0.50 | 0.002 |
| South Coast | Angeles | 367 | 87 | 0.58 | 0.000 | 0.49 | 0.002 |
| | Cleveland | 292 | 88 | 0.71 | 0.000 | 0.05 | 0.773 |
| | Sbernardino | 478 | 74 | 0.89 | 0.000 | −0.50 | 0.002 |

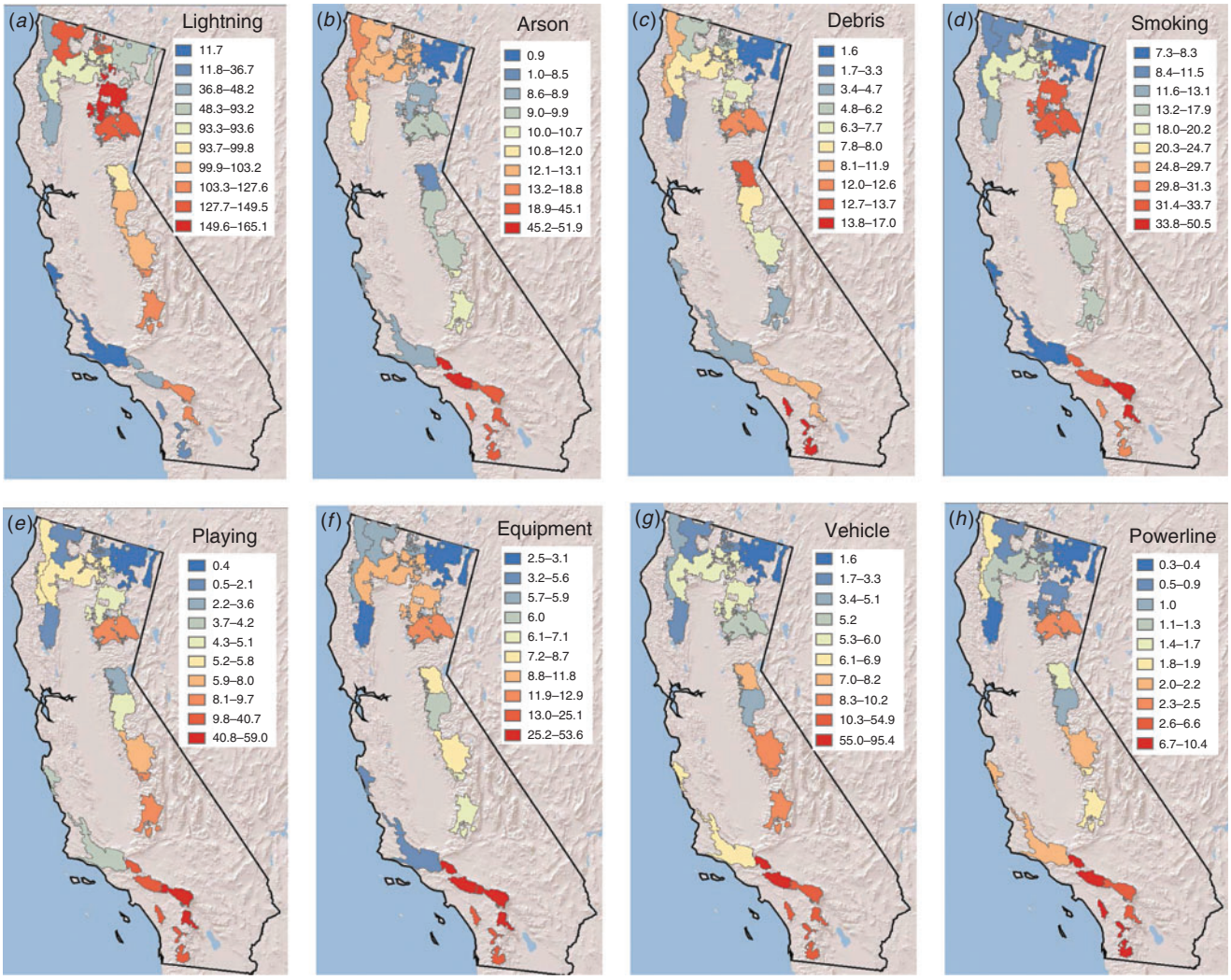


**Fig. 4.** Fire frequency for different ignition sources on USFS protected lands in California for the years 1910–2016 ($n$/year/$10^6$ ha); note change in scales for each source.

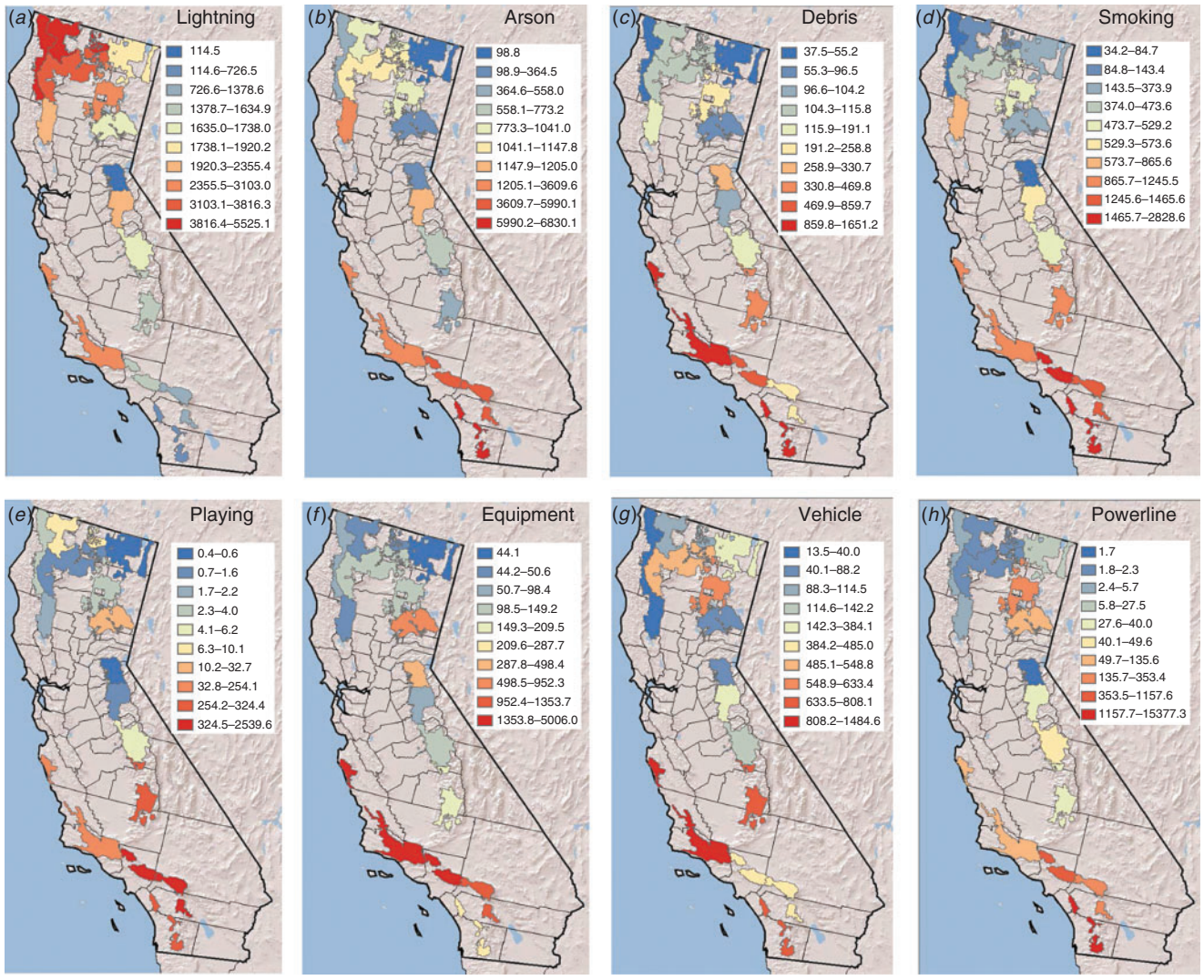


**Fig. 5.** Area burned by different ignition sources on USFS protected lands in California for the years 1910–2016 (ha burned/year/$10^6$ ha); note change in scales for each source.

marked and consistent diversions in most divisions (Fig. 7). Although the residuals early in the record are closely aligned with the regression line, during the 1920s and 1930s from the Sierra Nevada north there was a marked increase in ignitions. This pattern was less obvious in coastal central and southern California. In the 1950s and 1960s, there was a marked depression in ignitions in all climate divisions. It is worth noting that in the former period it was drier than the long-term average and in the latter period wetter (Fig. S3).

Changes in area burned did not closely follow changes in fire frequency (Fig. 6) – while fire frequency increased in the first three-quarters of the 20th century, area burned declined or stayed more or less constant. USFS forests in the northern part of the state showed a tendency for increased area burned in the last 4 decades (Fig. 6*d*, *l*) but in general there were no strong trends in area burned after 1980.

Of particular interest is how specific ignition sources have changed and, in order to simplify this presentation, we have consolidated climate divisions in the north (North Coast, North Interior and Sierra Nevada) and in the south (Central Coast and South Coast), which is justified by the marked similarities in ignition patterns within these two regions (see Fig. 2–5).

On Cal Fire-protected lands, it is noteworthy that changes in number of ignitions for lightning-ignited fires matched that of many human ignition sources, specifically increased ignitions during the first part of the record and decreased ignitions in recent decades (Fig. 8*a*, *e*). Numbers of lightning ignitions were more than double in the north than in the south, and substantially fewer than the leading anthropogenic causes. On USFS forests, lighting fire frequency (Fig. 9*a*, *e*) followed a temporal pattern similar to Cal Fire lands but were ~3 times more abundant than on Cal Fire landscapes and were one of the dominant ignition sources in forests. Despite changes in number of lightning-ignited fires, the area burned by this source did not exhibit consistent trends, although, in northern California forests, area burned by lightning-ignited fires has increased since 1980 (Fig. 8*i*, *m*, 9*i*, *m*).

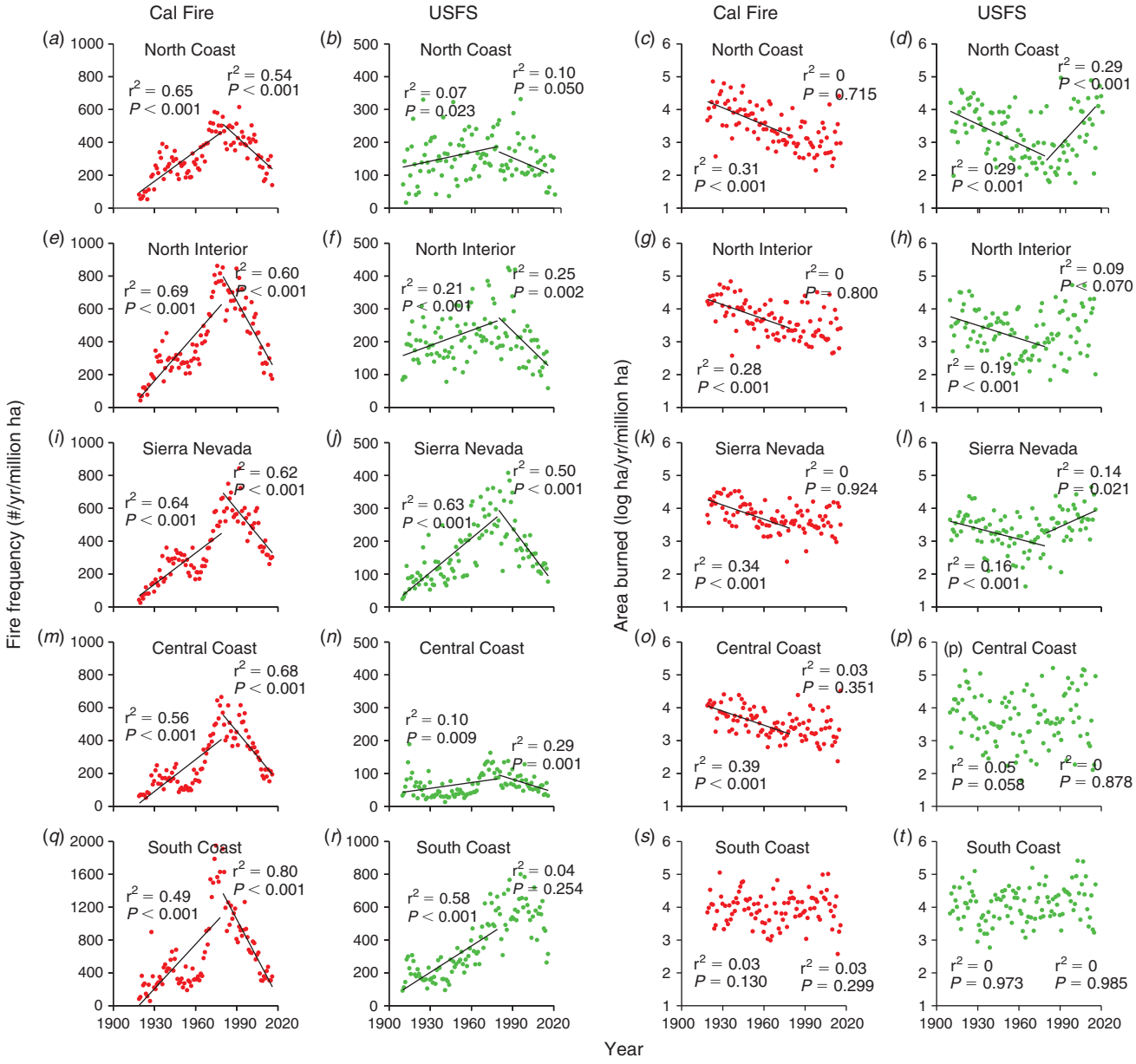


**Fig. 6.** Fire frequency for Cal Fire protected lands (*a*, *c*, *i*, *m*, *q*) and USFS lands (*b*, *f*, *j*, *n*, *r*) and area burned on Cal Fire (*c*, *g*, *k*, *o*, *s*) and USFS (*d*, *h*, *l*, *p*, *t*) lands. Note for frequency the change in scale between the South Coast and other divisions and between Cal Fire and USFS lands.

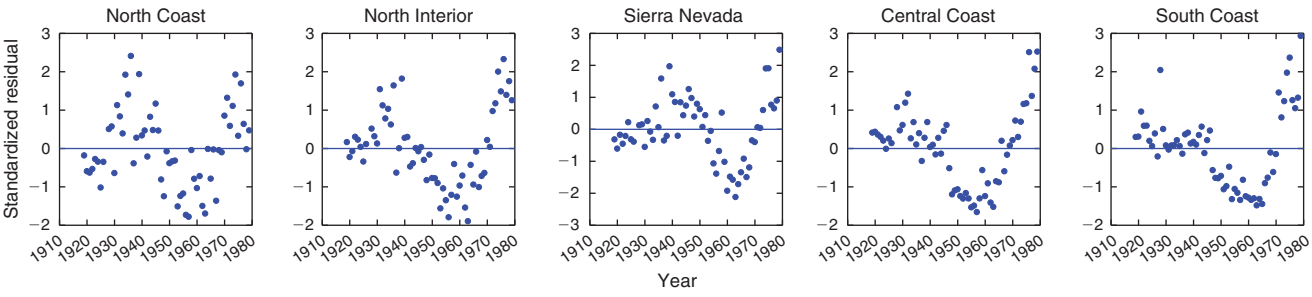


**Fig. 7.** Ignition sources recorded throughout the period 1919–2016 on Cal Fire protected lands by frequency (*a*–*h*) and area burned (*i*–*p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions from 1919 to 1979 and from 1980 to 2016; note the change in scale between lightning and anthropogenic sources for fire frequency.

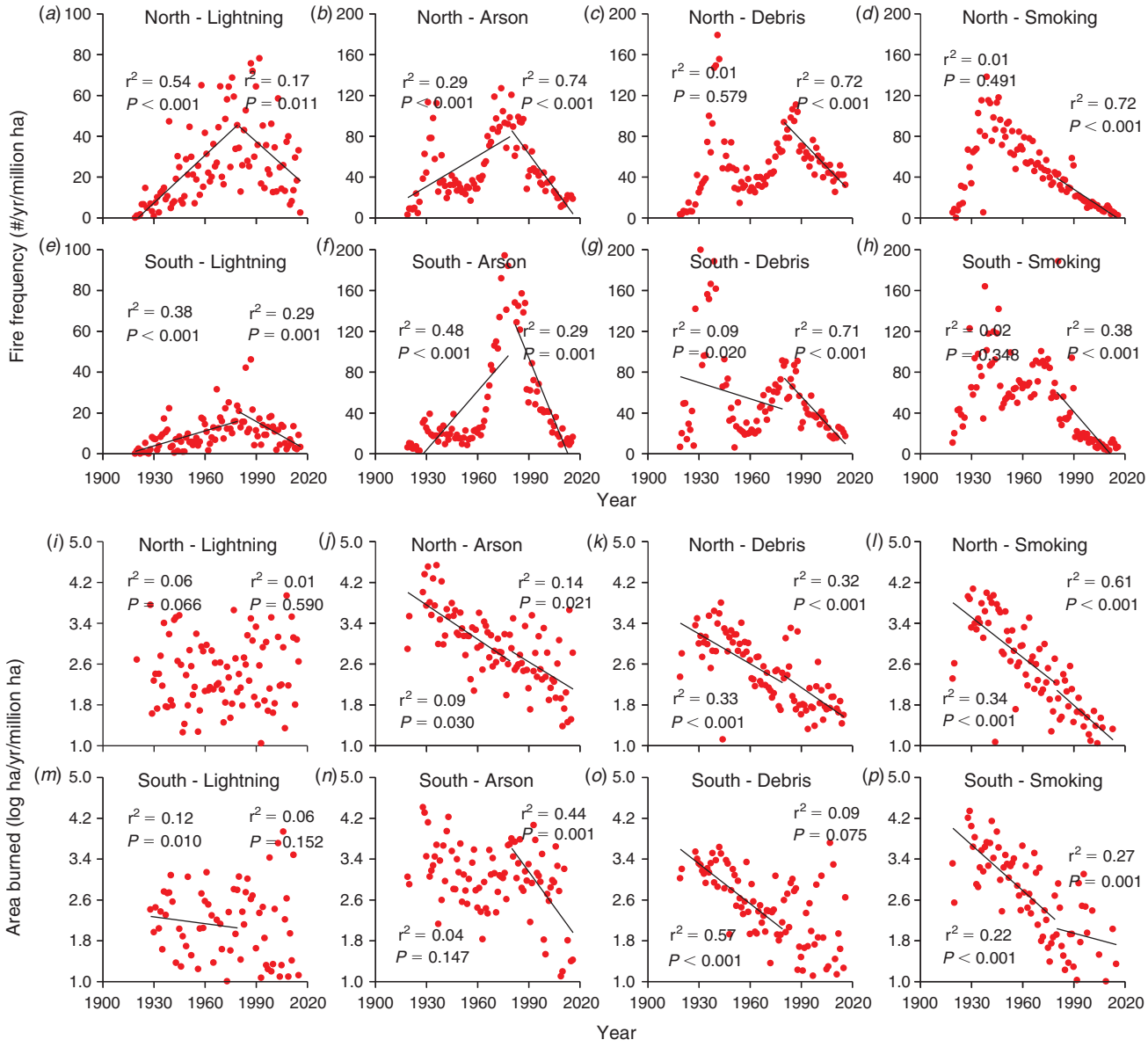


**Fig. 8.** Ignition sources not reported separately before 1960 on Cal Fire protected lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions before 1980 and 1980–2016; note the change in scale for fire frequency.

The main anthropogenic ignition sources on Cal Fire lands were arson, debris burning and smoking, and all showed a significant decrease in recent decades (Fig. 8*b–d*, *f–h*). Also, area burned by these ignition sources mostly showed a marked decrease in recent decades (Fig. 8*j–l*, *n–p*).

On USFS lands, arson and smoking were very important but camping was also a significant cause (Fig. 9). Arson fires exhibited remarkable similarity in the south of both jurisdictions with a marked decline in frequency and area burned since 1980 (Fig. 9*f*, *n*).

On both Cal Fire and USFS lands, some ignition sources, such as children playing with fire, equipment, vehicles and powerlines, were not specifically recorded during the early years (Fig. 10, 11). Children playing with fire declined significantly in both jurisdictions in the north and south (Fig. 10*a*, *b*, 11*b*, *f*) as did area burned by this source (Fig.10*i*, *m*, 11*j*, *n*). Equipment-ignited fires increased markedly between 1960 and 1979 on Cal Fire lands (Fig. 10*b*, *f*) but, during the same period, declined on USFS lands (Fig. 11*c*, *g*). Since 1980, this source of ignitions has declined sharply on Cal Fire lands in the north and south (Fig. 10*b*, *f*) but increased on USFS lands in the south (Fig. 11*g*). In contrast to all other ignition sources, powerline fires on Cal Fire and USFS lands in both the north and south have not declined in the last 4 decades (Fig. 10*d*, *h*, 11*d*, *h*) nor has area burned by this ignition source (Fig. 10*p*, 11*p*).

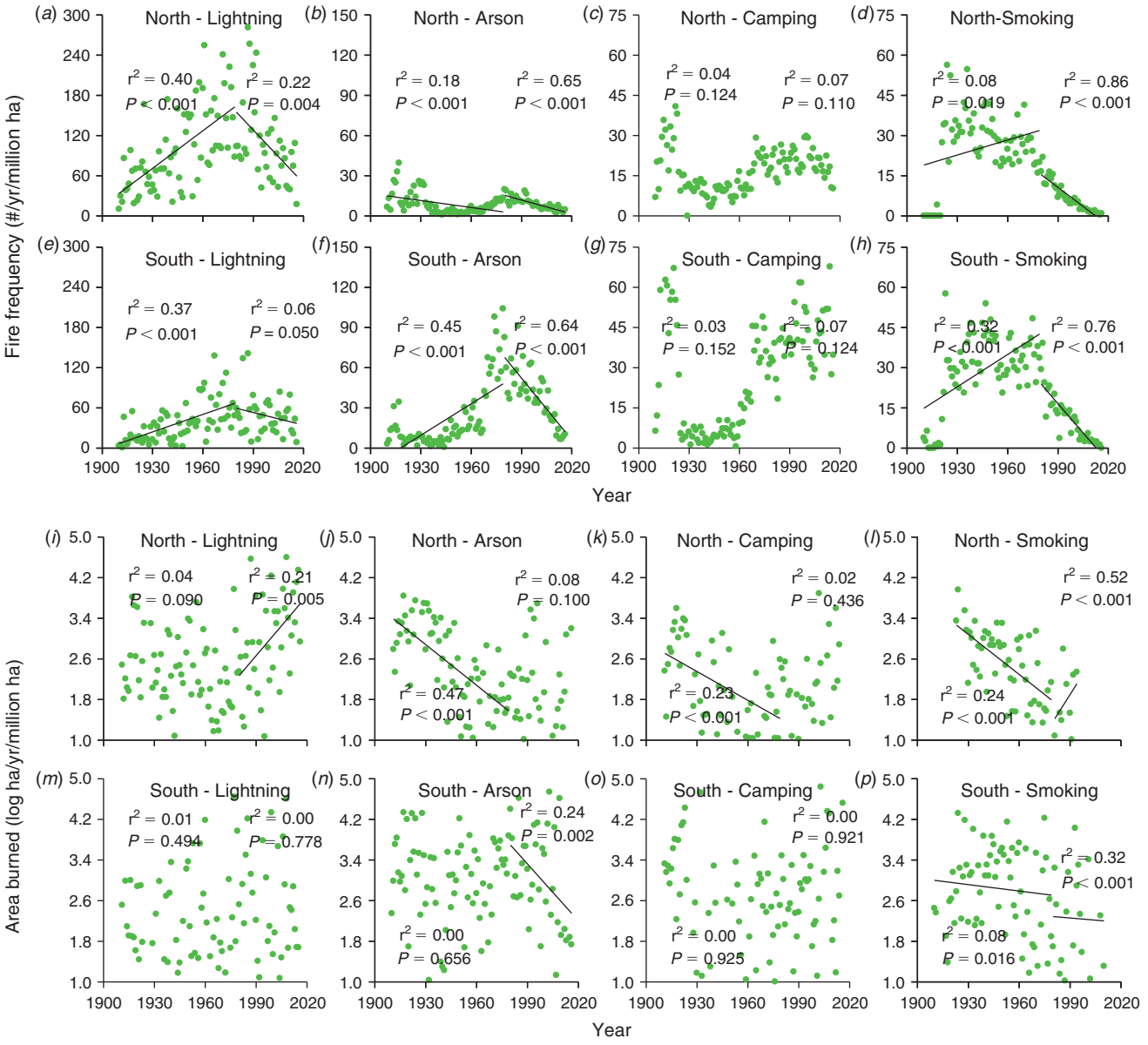


**Fig. 9.** Ignition sources recorded throughout the period 1910–2016 on USFS protected lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions from 1910 to 1979 and from 1980 to 2016; note the change in scale between lightning and anthropogenic sources for fire frequency.

### *Climate relationships to ignitions*

Based on the sharp change in ignition patterns through the period of record, it is critical to understand to what extent climate variation may have played a role. Considering the marked changes in climate over the period of this study (illustrated as decadal anomalies in seasonal temperature and precipitation in Fig S3), it is reasonable to expect climate variation has some explanatory value in understanding changes in ignition sources.

Multi-variate models used mean temperature and total precipitation for winter, spring, summer and autumn plus the prior-year winter–spring precipitation. Presented in Table 4 are those ignition sources with a significant $P < 0.05$ model. Not all ignition sources exhibited a significant climate mode and the models determining fire frequency were not the same as those for area burned. We note that, before 1980, the biggest driver of debris and railroad fires was prior-year precipitation. Since 1980, there was a negative relationship with summer temperature for debris burning, playing with fire, smoking and railroad fires. In the south, where lightning-ignited fires were uncommon (Fig. 2*a*), before 1980, they were strongly associated with high summer temperatures and autumn precipitation.

Total area burned on Cal Fire lands in the north before 1980 was significantly tied to low winter precipitation and high spring temperatures. In the south, area burned by both arson and powerlines was significantly tied to climate variation.

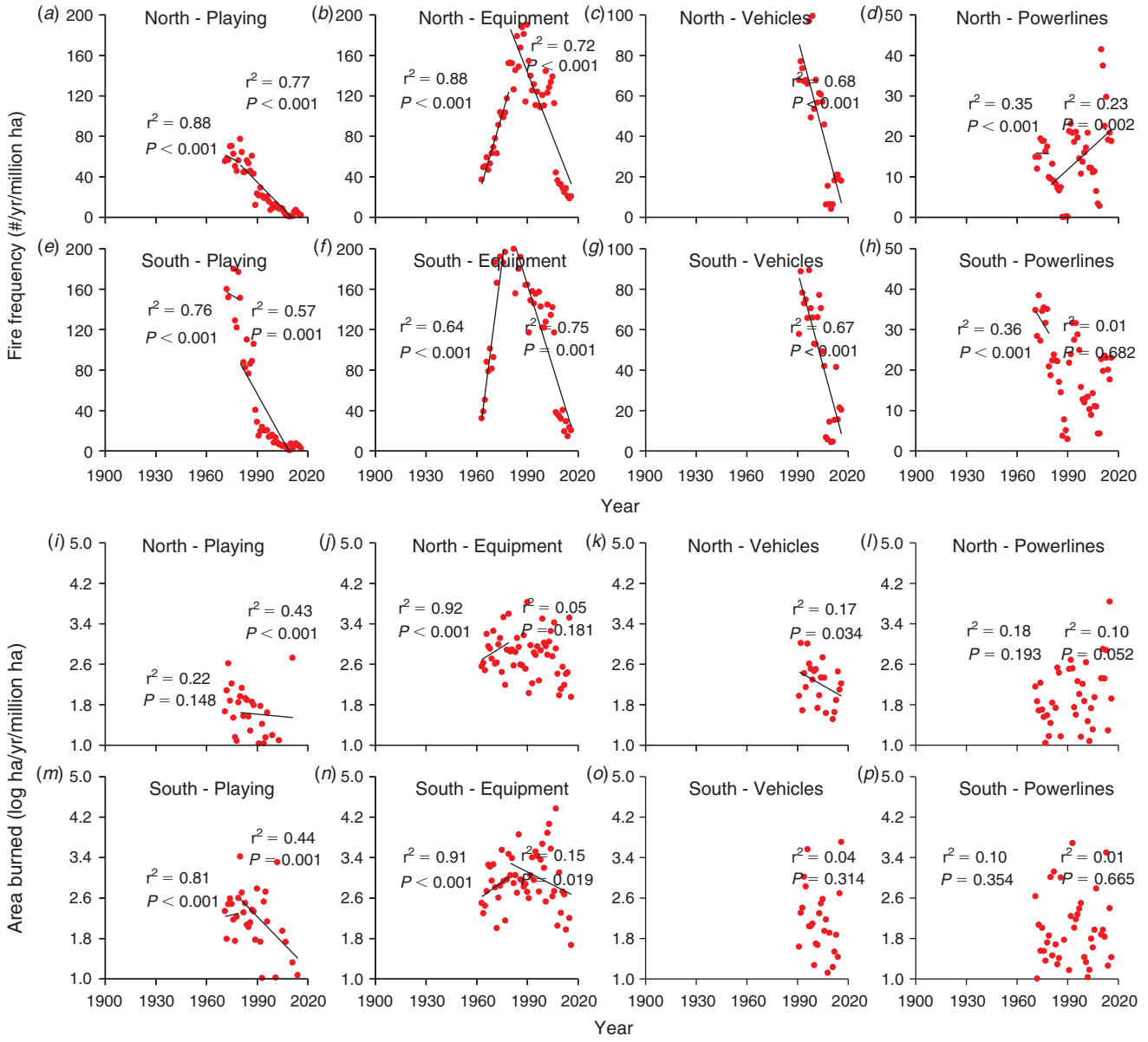


**Fig. 10.** Ignition sources variously recorded throughout the period 1910–2016 on USFS lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions before 1980 and 1980–2016; note the change in scale for fire frequency.

On USFS lands, total number of fires and area burned in both the north and south exhibited many significant climate models (Table 5). However, the patterns are complicated and not easily summarised as the specific climate models varied both spatially and temporally, as well as being different for different ignition sources.

For example, lightning fire frequency and area burned in both the north and south and before and after 1980 were significantly associated with climate variation, but, before 1980 in the north, the frequency of lightning fires was positively associated with summer precipitation, but the area burned was negatively associated with summer precipitation. After 1980 in the north, the model switched and there was a very strong effect of prior-year precipitation and summer temperature.

Since 1980, one of the strongest climate variables affecting both frequency and area burned was a positive relationship with prior-year precipitation. Although higher summer temperatures were associated with increased frequency of arson fires, it was noteworthy that lower summer temperatures were associated with an increased incidence of smoking, camping and children playing with fire in the north. Frequency of powerline fires were associated with elevated autumn temperatures and higher prior-year precipitation.

Cal Fire area-burned data were also presented by vegetation type and showed that in the north, forest and shrubland area

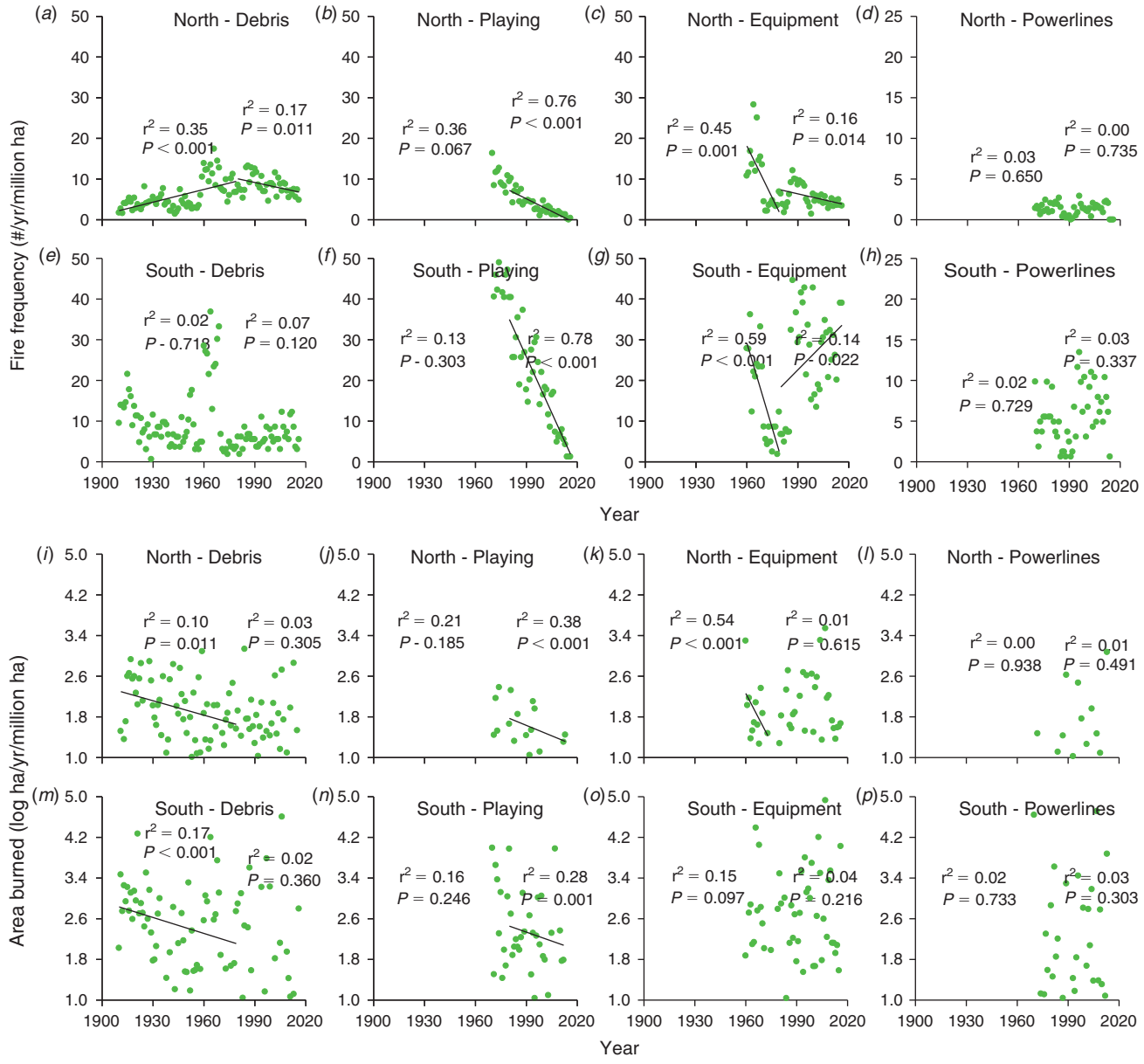


**Fig. 11.** Ignition sources variously recorded throughout the period 1910–2016 on USFS lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions prior to 1980 and 1980-2016; note the change in scale for fire frequency.

burned had significant relationships with climate variation before 1980 but not afterwards (Table 6). In the south, grasslands had a significant climate model after 1980.

## Discussion

Particularly striking about California ignitions is the steady increase in number of fires since the early 1900s until a peak *c.* 1980, followed by a marked drop in fire frequency up to 2016. This happened on both lower-elevation Cal Fire-protected lands and higher-elevation USFS lands, and in most climate divisions (Fig. 6). Despite a significant increase in fires during the first three-quarters of the 20th century, there were marked departures from this linear model, with accelerated ignitions during the 1920s and 1930s and a marked drop in the 1950s and 1960s (Fig. 7). Climate may have had some role in these changes since the former decade was drier and the latter was wetter (Fig S3) and during this period total fires on USFS lands did have a significant climate model largely driven by high summer temperatures and low summer precipitation (Table 4). What is particularly striking is the disconnect between number of ignitions and area burned; during the first three-quarters of the 20th century, although ignitions were increasing, area burned was steadily decreasing through much of the state.

In contrast, since 1980, ignitions have steadily declined, yet area burned has either not changed or, in some northern parts of the state, has increased. In short, the number of ignitions does not directly explain area burned. However, as discussed below, this conclusion does not apply to individual ignition sources, and, in this respect, there may be particular sources worth targeting for fire management purposes.

Factors that may have played a role in these historical patterns of ignitions and area burned are changes in: population density, infrastructure development, fire-prevention success, fire-suppression effectiveness, vegetation-management practices, climate, and possibly record-keeping accuracy. The drivers behind changes in ignition patterns are quite possibly different for different sources, different parts of the state and at different times. First, we consider the patterns for natural lightning-ignited *v.* human-caused wildfires.

### *Lightning-ignited fires*

In California, natural lightning-ignited fires decreased from north to south and from high (USFS) to low (Cal Fire) elevation (Fig. 2, 4). On USFS lands, Lassen and Plumas forests in the north-east averaged over 150 lightning-ignited fires per year per million hectares, whereas the coastal Los Padres Forest averaged one-tenth as many (Table S5). In northern California forests, such as the Klamath, Lassen, Modoc, Inyo-Mono and Sequoia, lightning accounted for the majority of fires, and on many others it is about equally important as human-ignited fires (Table 3). Notable exceptions are the coastal Los Padres and southern California Angeles, Cleveland and San Bernardino forests, where lightning accounted for less than one-quarter of all fires. In contrast, on lower-elevation Cal Fire-protected lands, lightning accounted for less than 10% of all fires in most counties, and in coastal areas from Sonoma County south, typically <1% of all ignitions (Table 2). These patterns closely follow the distribution of lightning strikes in the state (van Wagtendonk and Cayan 2008). In general, lightning-ignited fires in coastal California were substantially less than that observed over much of the USA (Prestemon *et al.* 2013). Thus, the report that extreme fire events driven by high winds are commonly due to human ignitions and not lightning (Abatzoglou *et al.* 2018) should not be too surprising in California because these extreme winds are largely restricted to coastal areas in southern California and the San Francisco Bay Area.

Area burned by lightning-ignited fires approximately paralleled these geographical patterns with a couple noteworthy exceptions. In the northern and central part of the state, more coastal USFS forests had low lightning-ignited fire frequency but these accounted for a substantial amount of area burned, although this was less evident on lower-elevation Cal Fire lands (Fig. 2–5). For interior forests where lightning is the dominant ignition source, fires have proven to be reasonably easy to extinguish, in large part because they typically occur in forests with a low-intensity surface-fire regime, and during lightning-storm weather conditions (van Wagtendonk and Cayan 2008), are conducive to rapid fire control. As a consequence, less than 1% of these forest lands burn each year and these landscapes have a fire-rotation interval of 100–200 years (Table 1), very different with what is believed to be the natural fire interval (Stephens 2005; Van de Water and Safford 2011; Safford and Van de Water 2014). In coastal central and southern California, lightning accounts for very little area burned, in large part because lightning strikes are very low, but also because human-ignited fires often occur under weather conditions more conducive to fire spread, contributing to a shorter fire-rotation interval, e.g. 40–50 years on southern California forest lands (Table 1).

**Table 4. Significant climate models ($P < 0.05$) explaining frequency of ignitions and area burned for the period <1980 and ≥1980 for Cal Fire protected lands**

Models tested mean temperature and total precipitation in winter, spring, summer and autumn, and prior year winter + spring precipitation (<1PptWinSpr)

| Variable | Era | Adjusted $R^2$ | $P$ | Model |
|---|---|---|---|---|
| Frequency in North | | | | |
| Debris | <1980 | 0.18 | 0.021 | <1PptWinSpr |
| Debris | ≥1980 | 0.24 | 0.050 | - TempSum |
| Playing | ≥1980 | 0.27 | 0.035 | - TempSum + TempWin |
| Smoking | ≥1980 | 0.32 | 0.016 | - TempSum |
| Railroad | <1980 | 0.18 | 0.020 | <1PptWinSpr + PptSpr |
| Railroad | ≥1980 | 0.25 | 0.045 | - TempSum + TempWin |
| Frequency in South | | | | |
| Lightning | <1980 | 0.40 | 0.001 | TempSum + PptAut |
| Debris | <1980 | 0.18 | 0.021 | <1PptWinSpr – PptAut |
| Area in North: | | | | |
| Total | <1980 | 0.23 | 0.007 | - PptWin + TempSpr |
| Area in South: | | | | |
| Arson | ≥1980 | 0.25 | 0.045 | - TempWin |
| Powerlines | <1980 | 0.99 | 0.046 | - TempSum – PptSpr – PptAut |
| Powerlines | ≥1980 | 0.24 | 0.050 | - TempAut |

Lightning fires have increased markedly over most of the 20th century on both Cal Fire and USFS lands, in the north and south (Fig. 8, 9). A possible explanation for this pattern is improvement in detection, as lightning-ignited fires often occur in remote areas and detection may have been less effective in the early part of the 20th century and improved in the latter part of the 20th century. However, there is there is reason to retain some level of scepticism that this pattern is an artefact of reporting (see the 'Methods' section), primarily because state and federal agencies have put in extraordinary effort at fire detection since the early 1900s (Clar 1969; Cermak 2005), including hundreds of thousands of kilometres of wilderness aircraft fire patrols beginning in 1919 (Cermak 1991).

Another reason for not simply dismissing historical patterns as an artefact of reporting is that there are physical factors that could account for such changes. For example, one potential factor for a 20th-century rise in lightning fires could be changes in forest fuel structure, which has been shown to affect lightning-ignited fire frequency on other landscapes (Krawchuk *et al.* 2006). In California, this would be expected based on the marked drop in area burned following the burning peak in the 1920s – for both Cal Fire and USFS lands, three times more area burned in that decade relative to the decadal average burned from 1950 to 1980 (Keeley and Syphard 2017). Thus, during the mid-20th century there was potentially an increase in fuels that

**Table 5. Significant climate models ($P < 0.05$) explaining frequency of ignitions and area burned for the period <1980 and >1980 for USFS protected lands**

Models tested mean temperature and total precipitation in winter, spring, summer and autumn, and prior year winter + spring precipitation (<1PptWinSpr)

| Variable | Era | Adjusted $R^2$ | $P$ | Model |
|---|---|---|---|---|
| Frequency in North | | | | |
| Total | <1980 | 0.27 | 0.001 | TempSum – PptSum + PptAut |
| Lightning | <1980 | 0.21 | 0.005 | TempSum + PptSum + PptAut |
| Arson | <1980 | 0.13 | 0.040 | –PptAut – PptSpr |
| Arson | ≥1980 | 0.28 | 0.030 | TempSum |
| Smoking | ≥1980 | 0.46 | 0.001 | –TempSum – PptSum |
| Debris | ≥1980 | 0.43 | 0.002 | – PptWin – TempAut – PptSum |
| Camping | ≥1980 | 0.26 | 0.039 | –TempSum |
| Playing | ≥1980 | 0.47 | 0.001 | –TempSum – PptSum |
| Railroad | < 1980 | 0.28 | 0.007 | PptAut |
| Railroad | ≥1980 | 0.32 | 0.017 | –PptWin + PptSpr |
| Equipment | ≥1980 | 0.32 | 0.016 | –TempSum – PptWin – PptSum |
| Powerlines | ≥1980 | 0.35 | 0.010 | <1PptWinSpr |
| Frequency in South | | | | |
| Total | ≥1980 | 0.29 | 0.026 | Ppt–1WinSpr |
| Lightning | <1980 | 0.18 | 0.012 | TempSum + PptAut |
| Powerlines | ≥1980 | 0.28 | 0.029 | TempAut + PptWin |
| Area in North: | | | | |
| Total | <1980 | 0.35 | <0.001 | –PptWinSpr – PptSum |
| Total | ≥1980 | 0.63 | <0.001 | <1PptWinSpr + TempSum – PptAut |
| Lighting | <1980 | 0.17 | 0.018 | –PptSum |
| Lighting | ≥1980 | 0.64 | <0.001 | <1PptWinSpr + TempSum |
| Arson | <1980 | 0.38 | <0.001 | –PptWin – PptAut – TempAut – TempWin |
| Debris | <1980 | 0.15 | 0.031 | – PptWin –PptAut |
| Smoking | <1980 | 0.16 | 0.022 | TempAut + TempSpr |
| Playing | ≥1980 | 0.34 | 0.010 | –TempSum –TempAut |
| Equipment | ≥1980 | 0.28 | 0.030 | <1PptWinSpr |
| Vehicles | ≥1980 | 0.37 | 0.007 | <1PptWinSpr |
| Powerlines | ≥1980 | 0.47 | 0.001 | –TempWin + <1PptWinSpr |
| Area in South | | | | |
| Total | <1980 | 0.20 | 0.006 | – PptAut – PptWin |
| Total | ≥1980 | 0.24 | 0.048 | TempSum – TempWin |
| Lighting | ≥1980 | 0.25 | 0.043 | –TempSpr – PptSpr |

may have contributed to a greater chance of lightning strikes igniting fires.

Changes in reporting standards is also not likely to explain the pattern of decreased lightning-ignited fires from 1980 to 2016 (Fig. 8, 9). On Cal Fire and southern USFS lands, this did not produce any significant trend in area burned by this fire source, although northern California (including the Sierra Nevada) USFS lands showed an increase in area burned by this source, a pattern also seen in the northern Rocky Mountains (Stephens 2005). Climate is strongly implicated in this change (Table 5) as two-thirds of the annual variation in area burned by lightning-ignited fires is explained by a combination of prior-year precipitation and current-year summer temperature. Although the latter variable most likely affects fuel moisture at the time of fire, the former is thought to increase fires through its effect on herbaceous fuels in the following year (Littell *et al.* 2009; Crimmin and Comrie 2011; Keeley and Syphard 2016). A similar conclusion was drawn by Knapp (1995) for the climatic control of lightning-ignited fires in the Intermountain West.

The future projections are that lightning strikes will increase 50% over this century (Romps *et al.* 2014), but this is not easily translated into future lightning fire risks in California. Some landscapes, such as forests in the northeastern part of the state, may already be saturated with lightning ignitions and coastal landscapes have very few strikes and thus a 50% increase may not significantly change lightning-ignited fire risk. In addition, changes in lightning-strike frequency will have very different impacts dependent on which season those changes occur in as well the state of future fuel conditions.

### *Human-ignition sources*

The fact that in all climate divisions, the number of ignitions is not a monotonic function of time over the past 100 years suggests a complex model of how ignition sources affect burning activity. Prestemon *et al.* (2013) presented a conceptual model of biophysical, social, prevention and management drivers in controlling human ignition sources. These factors are not static,

as illustrated by Guyette *et al.*'s (2002) dynamic anthropogenic fire regime model for the Ozark Mountains in Missouri. In their model, they found that the landscape changed over time from being ignition limited to fuel limited followed by stages dependent on fuel fragmentation and ultimately a culture-dependent stage. These temporal changes in drivers could explain a lot about the temporal changes observed in California ignitions.

It may be that the marked rise in ignitions during the first three-quarters of the 20th century in California is the result of increasing effectiveness of reporting, but this seems unlikely because the steepest rise in ignitions was in the latter part of the 20th century, i.e. 1960–1980 (Fig. 6). The 20th-century increase in ignitions was very strongly correlated with population growth (Tables 2, 3), but we believe that more is involved than just increasing population growth translates into more fires. This early–mid-20th-century growth spurt was correlated with road expansion throughout the state, which was bringing more people in contact with highly flammable fuels (Show 1945; Lockmann 1981; Keeley and Fotheringham 2003). In addition, because of migration patterns, growth included populations from less fire-prone parts of the US, and thus a population relatively naïve about the dangers of fire use in wildland areas (e.g. Zahn 1944; Show 1945). In addition, fire-prevention education was in its infancy and the population was slow to recognise their role in the fire problem. Included too is the widespread use of outdoor equipment that contributed to the sharpest rise in fires on Cal Fire landscapes between 1960 and 1980 (Fig. 10). On top of that, development of fire-response actions were far from perfect (Clar 1969). Also, during the period from 1940 to 1970 the State Resources Agency was actively involved in promoting burning of chaparral shrublands for the express purpose of type-converting native shrublands to exotic grasslands of greater economic value as rangelands (unpublished records in the State Archives). Indeed, the state was funding type conversion of private lands as this was perceived as a fire hazard reduction strategy, with an economic incentive of increasing rangeland.

Not directly related to changing demography is the significant decline in fires in the last several decades – while populations continued to grow after 1980, fire frequency was negatively related to population density (Tables 2, 3). This is consistent with the pattern of fire activity peaking under intermediate population density (Syphard *et al.* 2009). That is, the relationship between population density and ignition frequency is likely a function of finer-scale spatial processes regulating the degree of interspersion between development patterns and wildland vegetation. In other words, as both population and development expand into wildland areas, ignitions increase up to a point at which the area of development, or, impervious surface, far exceeds the area of wildland, and at that point, the relationship becomes negative. However, the timing of this switch varies with regions, e.g. south-east Australia continues to see a positive relationship in between population density and fire frequency (Collins *et al.* 2015).

Thus, these broad-scale patterns observed across the state may be reflecting macro-scale urbanisation trends over time. Massive areas of wildland vegetation have been developed and fragmented in California over the course of the 20th century (Hammer *et al.* 2007; Syphard *et al.* 2017), and the resulting extent and fragmentation of fuel surely has affected ignition trends and area burned. It may therefore be important to monitor areas that are becoming newly developed, as these may be the most fire-prone areas on the landscape, with sufficient people to start fires and wildland vegetation to carry fires (Radeloff *et al.* 2018).

Patterns such as these have been interpreted as indicating fires are not limited by human ignitions (Knorr *et al.* 2013; Moritz and Knowles 2016). This has prompted some to conclude that fire activity during the last several decades has been driven largely by climate change (Westerling *et al.* 2011). It is apparent that in mid–high-elevation forests in California seasonal climate variation has been an important factor in determining annual area burned (Table 5) and that global warming may exacerbate the fire situation on those landscapes (Keeley and Syphard 2016). However, in coastal California, climates are capable of generating large fire events most years (Keeley and Syphard 2017), with one exception being years with anomalous late spring rains (e.g. Dennison *et al.* 2008). In these coastal locations, big fire events occur during extreme wind events, however, these Santa Ana, Diablo or North Wind events occur predictably every year and yet big fires occur at unpredictable intervals, being determined by the coincidence of a human ignition with a wind event (Keeley and Zedler 2009).

During the first two-thirds of the 20th century more people translated into more fires, and greater fire activity. However, in recent decades the relationship between human population growth and fire activity has become more complex, nicely captured in Prestemon *et al.*'s (2013) model. In California in recent decades, increasing population density has increased the probability of ignitions under the worst weather conditions, either intentionally by arson for example or accidentally by powerline failures. This appears to be a widely seen situation throughout the USA where human-related ignitions are associated with conditions resulting in large wildfires (Nagy *et al.* 2018).

Decreasing ignitions over the last 4 decades is potentially reflective of increasing efficiency of fire prevention. However, it also likely reflects changes in human infrastructure; new roads in this era were tied to development projects that required demonstration of adequate fire response capabilities. In addition, an important factor behind declining ignitions is quite possibly the emergence of the California Fire Safe Council in the early 1990s (http://www.cafiresafecouncil.org/about-us/, accessed 11 August 2016), which made significant contributions to fire-safety education.

Arson has long been a major source of intentional human ignitions on both Cal Fire (Fig. 8) and USFS (Fig. 9) lands and on both jurisdictions arson ignitions increased during the first part of the 20th century and then dropped markedly in recent decades. Arson fires have always been one of the largest sources of area burned, although it was much higher in the early 20th century than in recent decades. This category comprises ignitions motivated for diverse reasons. Early in the 20th century, these were termed incendiary fires and were often motivated by goals of maintaining traditional burning practices (Coughlan 2016). As such practices became less socially (and legally) acceptable, the category was labelled arson fires. Arson fires exhibit interesting distribution patterns. On low-elevation Cal Fire lands they are a major ignition source in the northern Sierra Nevada (Fig. 2, 3) but on USFS lands they dominate in the

southern part of the state (Fig. 4, 5), suggesting a need for more concentrated anti-arson prevention measures in those regions. This clustering of arson fires has been observed in parts of the Mediterranean basin and has prompted an early alert system (Gonzalez-Olabarria *et al.* 2012).

One of the real success stories illustrated by these data is the marked decline since 1980 in frequency and area burned by arson fires on both Cal Fire and USFS lands (Fig. 8, 9). This reduction in arson fires is a pattern observed for other parts of the country (Prestemon *et al.* 2013). In California, this may be attributed to better neighbourhood-watch programs, which include patrols during red-flag warnings, but broadcasted fire prevention messaging may also be a factor. Another factor may be increased penalties for arson; e.g. the person found guilty of starting the 2003 Old Fire in southern California was sentenced to death, as was the arson convicted of the 2006 Esperanza Fire (Gabbert 2012).

Another source of burning on both Cal Fire and USFS lands has been smoking. This was a significant cause in the earliest records, recording even ignitions from cigarettes thrown from open cockpit planes. Throughout the first half of the 20th century, smoking was a major cause of wildfires and was the focus of one of the earliest fire prevention campaigns. In 1942, over 100 000 'fag bags' were distributed to persons entering the Angeles National Forest, bright red bags designed to carry smoking materials and with a prominent fire-safety reminder stamped on them (Show 1945). The late 20th-century decline in smoking caused such fires to decline at a much faster rate (Fig. 8, 9) than due to simple reduction in smoking (Prestemon *et al.* 2013). Reductions in smoking-caused fires are due to a combination of less smoking, more fire-resistant cigarettes, and improved fire prevention (Butry *et al.* 2014).

Children playing with fire has been an important ignition source and it has exhibited a marked decline in frequency in recent decades on both Cal Fire (Fig. 10) and USFS (Fig. 11) lands. Increased fire-prevention effectiveness through better messaging and development of childproof lighters are potential factors. Perhaps stricter ordinances in power-tool usage in wildlands under red-flag warnings may be a factor as well as requirements for more effective spark arrestors.

Vehicles present another accidental fire source that has declined sharply on Cal Fire protected lands. Catalytic converters, which were first required in 1975, are thought to have been a significant ignition factor (Bertagna 1999; http://www.cbs8.com/story/35871110/how-a-cars-catalytic-converter-can-spark-a-massive-fire, accessed 1 June 2017) when they overheated, igniting roadside vegetation. However, modern vehicles have warning lights when they overheat, which has the potential for reducing vehicle fires and could be a factor in the decline of such fires. Another factor potentially reducing vehicle fires is improved vegetation treatment along roadside verges.

Electrical powerlines have been reported ignition sources since 1905 (Show 1945). In the present study, this source of ignition stands out in that, unlike many other human ignition sources, powerline fires and area burned by this ignition source have not declined in recent decades (Fig. 10, 11). Although powerlines do not account for many fires, they often account for substantial area burned, and some of substantial size (Keeley *et al.* 2009; Syphard and Keeley 2015). One reason that powerline fires are so dangerous is that they commonly occur during high winds and there are three effects of these winds: tree contact, line arcing, and metal fatigue resulting in lines down (Mitchell 2009). These winds create extremely dangerous fires capable of rapid spread over long distances. This is a serious problem in other regions such as southern Australia where it was found that electricity-caused wildfires are over-represented when fire danger is high (Miller *et al.* 2017) and similar conclusions were drawn by Ganteaume and Guerra (2018). Powerline distribution tends to follow roads and this may be part of the reason burning patterns are closely correlated with road distribution in southern California (Faivre *et al.* 2014). Also, they burn larger areas than fires ignited by most other causes and are associated with more significant impacts on lives and property (Collins *et al.* 2016).

Because these powerline failures typically occur in known extreme-wind corridors, it has been proposed that wiring these corridors with underground power could minimise the problem (Keeley *et al.* 2009). However, utility companies have shown a reluctance to accept this solution. One company in southern California, San Diego Gas & Electric, has opted for an alternative plan whereby they monitor weather throughout the county and use these data to shut down portions of the power grid when that area experiences high winds (https://www.cnbc.com/2017/12/13/southern-california-utilities-shut-off-power-to-prevent-wildfires.html, accessed 1 June 2017). In initial attempts to deal with fire hazards there have been significant complaints about the process of shutting down the power grid as it creates many unanticipated problems (https://www.nbcsandiego.com/news/local/Supervisor-Demands-State-Investigation-of-Power-Shut-offs-During-Lilac-Fire-467782743.html, accessed 1 June 2017). Other approaches have been to replace wooden poles with metal poles, however, this seems to be a distraction since wooden poles have not been blamed for starting fires (https://www.voiceofsandiego.org/topics/science-environment/sdge-environmentalists-are-at-opposite-poles-on-one-fire-prevention-method/, accessed 1 June 2017).

Climate change impacts on anthropogenic ignitions is rather difficult to parse out because climate affects both fire behaviour and human behaviour. For example, in forests, fire activity is enhanced by higher spring and summer temperatures through effects on fuel moisture (Westerling *et al.* 2006; Littell *et al.* 2009; Keeley and Syphard 2017). However, in the present study, fires started by camping, children playing with fire, and smoking were negatively correlated with summer temperatures, suggesting the possibility that cooler temperatures may have encouraged greater outdoor activity.

In general, climate variation exhibited a closer relationship with fire activity in the higher-elevation USFS lands in the northern part of the state, consistent with the flammability limited fire regimes in these regions (Keeley and Syphard 2017). Of particular significance is the importance of prior-year rainfall as this is well known to be due to increased fuel production in grass dominated ecosystems (Crimmins and Comrie 2004; Keeley and Syphard 2016). We found that this climate variable was strongly tied to powerline fires, suggesting perhaps that fine flashy fuels may be a marked hazard in association with powerlines and may be an additional management target.

## Conclusions

Throughout California, fire frequency has increased steadily until a peak *c.* 1980, followed by a marked drop to the present. There was not a tight link between frequency of ignition sources and area burned by those sources and the relationships changed over time. Natural lightning-ignited fires decreased from north to south and from high to low elevation. Throughout most of the state human-caused fires dominated the record and were positively correlated with population density for the first two-thirds of the record, but this relationship reversed in recent decades. Most ignition sources have declined markedly in recent decades with one notable exception, powerline ignitions. One important avenue for future fire hazard reduction will be consideration of solutions to reduce this source of dangerous fires.

## Conflicts of interest

The authors declare that they have no conflicts of interest.

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# EFFECT OF STAND WIDTH AND ADJACENT HABITAT ON BREEDING BIRD COMMUNITIES IN BOTTOMLAND HARDWOODS

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***Abstract:*** Bottomland hardwood forests support an abundant and diverse avifauna, but area of this forest type has been reduced, and current projections indicate continued declines. We compared breeding bird abundance indices and species richness among bottomland hardwood stands ranging in width from <50 m to >1,000 m and enclosed by forested habitat. We also compared avian abundance indices and richness among stands enclosed by pine (*Pinus* spp.) forest and stands enclosed by field-scrub habitats. Total species richness and species richness of Neotropical migrants were associated positively ($P < 0.05$) with stand width in all years. Total bird counts differed among width classes in all years, with counts generally greatest in width classes <50 m and >1,000 m. Counts of Neotropical migrants differed ($P < 0.05$) among width classes in 1993 and 1995 and followed the same general trend as total bird count. Acadian flycatcher (*Empidonax virescens*), blue-gray gnatcatcher (*Polioptila caerulea*), and red-eyed vireo (*Vireo olivaceous*) were more abundant in smaller width classes ($P < 0.05$), whereas the opposite was true for white-eyed vireo (*Vireo griseus*) and northern parula (*Parula americana*). Probability of occurrence was associated positively ($P < 0.05$) with stand width for 12 species and negatively with stand width for 1 species. Total bird count and the counts of blue-gray gnatcatcher in 1995 and of northern cardinal (*Cardinalis cardinalis*) in both years were higher in field-enclosed stands (FES) than in pine-enclosed stands (PES). No species analyzed was more abundant in PES than in FES. We conclude that even narrow riparian zones can support an abundant and diverse avifauna, but that conservation of wide (≥500 m) riparian zones is necessary to maintain the complete avian community characteristic of bottomland hardwood forests in South Carolina.

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***Key words:*** bottomland hardwoods, breeding birds, landscape management, minimum area requirement, South Carolina, species richness.

Bottomland **hardwood forests (hereafter,** bottomland **hardwoods) are seasonally inundated floodplain forests dominated by oak** (*Quercus* **spp.), gum** (*Nyssa* **spp.), and cypress** (*Taxodium* spp.), **and they support an abundant and diverse avifauna (Dickson 1978,** Hamel **1989) that includes approximately 70 breeding species (Pashley and Barrow 1993). Furthermore, up to 65% of the species at any given site may be Neotropical migrants (Pashley and Barrow** 1993), **including many forest interior species experiencing population declines** (Askins **et al. 1990, Peterjohn et al. 1995). However, the** pre-**Columbian (15th century) extent of bottomland hardwoods has undergone considerable reduction, largely because of agricultural conversion and construction of hydroelectric reservoirs (Harris and Gosselink 1990). Approximately 50% of the area existing in 1940 had been lost by 1985 (Harris and Gosselink 1990).**

**Currently, bottomland hardwoods are an important source of hardwood lumber, and demands on these forests likely will increase. Hardwood timber removals by the year 2030 are projected to have increased by 64% over 1984 levels (U.S. Forest Service 1988). During the same period, acreage of bottomland hardwoods in the Southeast is projected to decrease from about 5.5 million ha to about 4.7 million ha, a decline of** 15% **(U.S. Forest Service 1988). Much of the remaining bottomland hardwoods exist in narrow** (<50 m) **drainages and** streamside **management zones. Although narrow stands may contain substantial area because of their length, their utility to forest birds may be compromised because of a lack of interior habitat conditions.**

**Species richness and abundance of forest bird communities are associated positively with**

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stand area (Galli et al. 1976, Whitcomb et al. 1981, Blake and Karr 1987). However, recent research attention has focused on width of riparian zones rather than area (Keller et al. 1993, Darveau et al. 1995, Dickson et al. 1995, Thurmond et al. 1995, Hodges and Krementz 1996) because of difficulties associated with defining area when riparian zones are interconnected. Further, species richness of some avian guilds is correlated positively with riparian zone width (Keller et al. 1993). However, most research on the effect of width on bird communities in Southeastern bottomland hardwoods has been restricted to narrow stands surrounded by young pine plantations. Although these studies are applicable in most forest management contexts, research addressing the range of stand widths encompassed in bottomland hardwood systems is necessary to assess the habitat requirements of area-sensitive species. We compared avian abundance indices and species richness among bottomland hardwood stands of various widths (<50 to >1,000 m) that were surrounded by closed-canopy pine (*Pinus taedu, P. palustris*) forest. We also compared abundance indices and species richness among stands enclosed by pine forest and stands enclosed by-field-scrub habitats.

## STUDY AREA

The study was conducted on the U.S. Department of Energy's Savannah River Site, a 78,000-ha tract in Aiken, Bamwell, and Allendale counties, and on private property in Allendale County. This region lies in the Upper Coastal Plain of westcentral South Carolina and is bounded on the west by the Savannah River. Topography is characterized by gently rolling ridges, broad flat regions, and interspersed stream courses (Soil Survey Staff 1977). Elevation ranges from <25 m at the Savannah River to 80 m at first-order streams. Bottomland hardwoods are found along stream courses and may be flooded seasonally, usually during late winter-early spring. Dominant canopy species of bottomland hardwoods include sweetgum (*Liquidambar styraciflua*), swamp tupelo (*Nyssa sylvatica* var. *biflora*), red maple (*Acer rubrum*), water oak (*Quercus nigra*), laurel oak (Q. *laurifolia*), overcup oak (*Q. lyrata*), and cherrybark oak (Q. *falcata* var. *paegodifolia*). The midstory is composed of American holly (*Ilex opaca*), sweet bay (*Magnolia virginiana*), and red bay (*Persea borbonia*). Switchcane (*Arundinaria gigantea*) and dog hobble (*Leucothoe axillaris*) dominate the shrub layer, and Christmas fern (*Polystichum acrostychoides*) and netted-chain fern (*Woodwardia areolata*) are the dominant ground cover (Workman and McLeod 1990).

## METHODS

We used a completely randomized design with repeated measures across years. We selected 4 replicates of bottomland hardwood stands in each of 5 width classes: <50 m, 50–150 m, 150–300 m, 300–1,000 m, and >1,000 m. We used width classes rather than size classes because the forested watershed in which we worked was nearly continuous throughout the study area. Thus, first-order streams (narrow floodplains) were continuous with second- and third-order streams (wider floodplains), which made delineation of stand boundaries (and therefore determination of area) impossible. We believe that width was a good index to area because wider stands contained more area; hence, width was more useful in a forest management context. We used aerial photographs to locate sites from which we measured width of the entire floodplain, including both sides of a creek or drainage. The 2 largest sites were located on the Savannah River floodplain; width of these sites refers to 1 side only because the Savannah River constituted a significant break in the canopy (≥100 m) and likely served as an effective barrier to cross-stream movement of birds (Hodges and Krementz 1996). All sites were on different creeks, except those on the Savannah River, which were separated by >1 km to ensure independence of replicates. We selected sites characterized by Zone III, IV, and V vegetation types (Wharton et al. 1982) in an attempt to control for differences in vegetation among sites. Larger sites encompassed a greater diversity of habitat types, and a few plots slightly overlapped communities of baldcypress (*Taxodium distichum*)-water tupelo (*Nyssa aquatica*).

We measured habitat characteristics in 5 circular 0.04-ha plots (James and Shugart 1970) per stand in 1994. We measured canopy coverage with a densiometer and vegetation profile with a 3-m density board (Noon 1981); each measurement was from the cardinal points on the perimeter of each plot. We recorded species and size class of all trees in the plot (James and Shugart 1970). For analysis, we selected vegetation profile (PROFILE) as a measure of un-

derstory structure, basal area of hardwood pole timber (POLE), which we defined as hardwood stems 8-23 cm dbh and which provided a measure of midstory structure, canopy coverage (CANOPY), and basal area of hardwood sawtimber (SAW), which we defined as hardwood stems >23 cm diameter at breast height (dbh). This approach minimized the number of vegetation variables, yet provided measures of structure for 3 primary habitat layers and also included 2 variables commonly inventoried by forest managers. We subjected these data to principle components analysis (PCA; PROC PRINCOMP; SAS Institute 1990) to reduce the number of habitat variables included in the bird-habitat analyses (Hodges and Krementz 1996). We selected for inclusion in analyses of bird-habitat relations only those principal components (PC) that had eigenvectors ≥1.0. We used I-way analysis of variance (ANOVA; PROC GLM; SAS Institute 1990) to compare PC scores among width classes.

We used 5-min, fixed-radius (50 m) point counts (Hutto et al. 1986, Ralph et al. 1995, Smith et al. 1995) to sample the bird population for each stand. Within each stand, 2 points were spaced 200 m apart along a transect centered within each corridor and oriented parallel to the general bearing of the drainage. To aid in estimation of distance, we placed high-visibility flagging tape on trees at the perimeter of each plot in each of the cardinal directions. We visited each stand at approximately equal intervals 3 times per year between mid-May and late June 1993-95, once each during early, middle, and late morning. This design yielded 72 point counts in each width class during the study (4 stands X 2 points X 3 visits X 3 years). Smith et al. (1995) suggested 50 counts per factor level were sufficient to detect most biologically meaningful variation.

We conducted counts from sunrise to 3.5 hr after sunrise, except during periods of high wind or rain (Ralph et al. 1995). We only recorded birds once, if they were detectable from both points in a stand (Ralph et al. 1995). Birds flying over the stand were not recorded (Ralph et al. 1995). Species detected within the stand but beyond the 50-m radius or within ±3 min of the count period while en route to points were recorded for evaluation of species richness We took the high count for each species per point and averaged values from both points to obtain an index of relative abundance for each site (Blondel 1981, Blake and Karr 1987). For stands with widths <100 m (i.e., too narrow for a plot of 50-m radius, $n = 4$), counts were adjusted by extrapolation based on the fraction of a 50-m-radius plot that each plot comprised. We assumed any bias in bird detection among points was minimal because vegetation characteristics did not differ among sites (see below), only 2 observers were used, weather conditions were standardized, and timing of counts within day and season was stratified.

We evaluated the effect of stand width (log-transformed), habitat variables (i.e., PC), and year on species richness via a generalized linear model (PROC GLM; SAS Institute 1990). We used the same procedure to evaluate the effect of corridor width on species richness of Neotropical migrants (forest interior and interior-edge species only; Whitcomb et al. 1981). We compared the slopes of our regressions of species richness by stand width to slopes from species-area relations of other studies to test the null hypothesis that the species-width slopes did not differ from species-area slopes. Because we were aware of no published species-area relations from bottomland hardwood habitats, we used slopes from studies in upland hardwood forests in South Carolina (Kilgo 1996) and Illinois (Blake and Karr 1987).

We tested the null hypotheses that total bird count, total Neotropical migrant count, and counts of each species did not differ among width classes. We analyzed only those species for which we recorded an average of ≥20 observations/year. We made comparisons among width classes with repeated-measures (3 yr) analysis of covariance (RM-ANCOVA; PROC GLM; SAS Institute 1990). The linear model included the following terms: width class, site (width class), year, year x width class, PC1, PC2, and PC3, where PC1-PC3 were PC scores. Before analysis, we converted covariates to deviations from the mean. We tested covariates and width class with the site-within-width class as the error term. When the year x width class interaction was significant ($P < 0.05$), we analyzed years separately. When covariate effects were nonsignificant, they were eliminated. When RM-ANCOVA revealed significance ($P < 0.05$), we separated covariate-adjusted means via the least significant difference, calculated with site-within-width class as the error term.

We used logistic regression (PROC LOGISTIC; SAS Institute 1990) to model the effect of

year and width on the probability of occurrence for each species. We analyzed only species recorded in ≥5% of the 60 stand-years (20 stands sampled 3 yr). The year effect was nonsignificant for all species, so we pooled data among years. Significance of the model was assessed with the score statistic (SAS Institute 1990). When the linear model was not significant, we added a quadratic term, $B_2x_i^2$, (Robbins et al. 1989), and accepted the model with the greatest significance.

To examine the effect of adjacent habitat type, we added 4 stands in 1994 with field-scrub habitat adjacent on both sides: 2 in the width class of 50-150 m and 2 in the width class of 150-300 m. Vegetation was sampled in 1994, and birds were sampled in 1994–95. We compared data from these FES with those from the 8 PES in the same width classes. Habitat data from the 12 stands were subjected to PCA, and PC scores were compared between treatments with incomplete block design ANOVA, blocking on width class. We compared total species richness, species richness of Neotropical migrants, total bird count, Neotropical migrant count, and species counts between treatments (i.e., surrounding habitat type) with RM-ANCOVA as described above, but with the addition of the treatment term and associated interactions.

## RESULTS

Each of the first 3 PC from the analysis of vegetation in the 20 PES had eigenvectors >1.0, and they accounted for 91% of the variation in vegetation measured among sites: PC1 = 35.3%, PC2 = 30.3%, and PC3 = 25.2%. High scores on PC1, which was correlated positively with PROFILE and SAW and negatively with POLE and CANOPY (Table 1), represented stands with an open midstory and canopy, dense understory, and high basal area of hardwood sawtimber. High scores on PC2, which was correlated positively with PROFILE and POLE and negatively with SAW (Table 1), represented stands with well-developed understories and midstories, but low basal area of hardwood sawtimber. Finally, high scores on PC3, which was correlated positively with SAW and CANOPY (Table 1), reflected stands with large trees and a closed canopy. The PC scores did not differ among width classes ($P > 0.05$).

We detected 56 species of birds in the 20 PES of which 23 (41%) were forest-dwelling Neotropical migrants. No edge-scrub or field-edge Neotropical migrants (Whitcomb et al. 1981) were detected because we sampled at the centers of forested stands. We analyzed species richness data by year because both total and Neotropical migrant species richness differed among years ($P < 0.001$), with highest values ($P < 0.05$) in 1993. Total species richness and species richness of Neotropical migrants were associated positively ($P < 0.05$) with the natural log of stand width in all years (Fig. 1). The slope of the species-width relation did not differ in any year from that of species-area relations in upland hardwoods of South Carolina (slope = 3.5, Kilgo 1996; 1993: $F_{1,1} = 1.20$, $P = 0.471$; 1994: $F_{1,1} = 1.79$, $P = 0.409$; 1995: $F_{1,1} = 3.02$, $P = 0.332$) and Illinois (slope = 5.2, Blake and Karr 1987; 1993: $F_{1,1} = 0.05$, $P = 0.862$; 1994: $F_{1,1} = 0.24$, $P = 0.709$; 1995: $F_{1,1} = 0.50$, $P = 0.609$).

Table 1. Eigenvectors for variables included in principal components (PC) analysis of 20 bottomland hardwood stands enclosed by pine forest in South Carolina, 1993–95. The PC1–PC3 (only components with eigenvalues >1.00) accounted for 91% of the variation in the variables measured among sites.

| Variable | PC1 | PC2 | PC3 |
|---|---|---|---|
| Vegetation profile | 0.58 | 0.57 | 0.09 |
| canopy coverage | -0.63 | 0.03 | 0.59 |
| Basal area: hardwood pole timber[a] | -0.29 | 0.80 | 0.10 |
| Basal area: hardwood sawtimber[b] | 0.43 | -0.18 | 0.80 |

[a] Defined as all hardwood stems 8–23 cm dbh
[b] Defined as all hardwood stems >23 cm dbh.

Total species richness was associated positively with PC2 in 1993 ($P = 0.018$), indicating that number of species increased with increasing understory and midstory development. Similarly, species richness of Neotropical migrants was associated positively with PC2 in 1993 ($P = 0.021$) and 1995 ($P = 0.051$) but was associated negatively with PC1 in 1993 ($P = 0.032$) and 1995 ($P = 0.019$), indicating a positive association with canopy coverage.

Because the year × width class interaction was significant for both total bird count ($F_{8,59} = 3.02$, $P = 0.014$) and Neotropical migrant count ($F_{8,59} = 3.08$, $P = 0.012$), we analyzed years separately. Total bird count was not associated with PC in any year ($P > 0.05$) but differed among width classes in each year (1993: $F_{4,19} = 26.18$, $P < 0.001$; 1994: $F_{4,19} = 4.54$, $P = 0.013$; 1995: $F_{4,15} = 3.62$, $P = 0.030$; Fig. 2); counts generally were greatest in width classes <50 m and >1,000 m (Fig. 2). Neotropical migrant

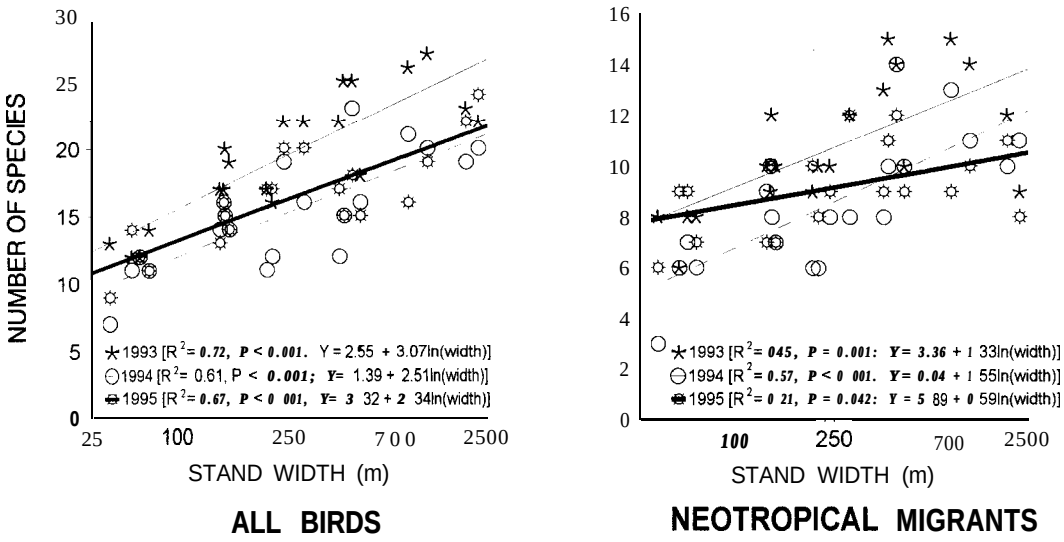


Fig. 1. Relation between breeding bird species richness and width of bottomland hardwood stands in South Carolina, 1993–95.

count differed among width classes in 1993 ($F_{4,19}$ = 28.41, $P < 0.001$) and 1995 ($F_{4,15}$ = 3.43, $P = 0.035$) and followed the same general trend as total bird count (Fig. 2). Neotropical migrant count also was associated negatively with PC3 in 1993 ($F_{1,12}$ = 6.91, $P = 0.022$).

Eight species had sufficient data for individual analysis: Acadian flycatcher, Carolina wren (*Thryothorus* ***ludovicianus),*** blue-gray gnatcatcher, white-eyed vireo, red-eyed vireo, northern parula, hooded warbler (*Wilsonia citrina*), and northern cardinal. Only blue-gray gnatcatcher count was associated with a habitat covariate (positively with PC3; $F_{1,12}$ = 7.20, $P = 0.020$). The year x width class interaction was significant for northern cardinal ($F_{8,59}$ = 3.21, $P = 0.009$), so years were analyzed separately; northern cardinal counts generally were greatest in width classes <50 m and >1,000 m (Fig. 2). Counts differed among width classes for the following species: Acadian flycatcher ($F_{4,15} = 9.53$, $P = 0.001$), blue-gray gnatcatcher ($F_{4,12}$ = 10.51, $P = 0.001$), white-eyed vireo ($F_{4,15}$ = 5.54, $P = 0.006$), red-eyed vireo ($F_{4,15}$ = 11.99, $P < 0.001$), and northern parula ($F_{4,15}$ = 4.11, $P = 0.019$). Counts of Acadian flycatcher, blue-gray gnatcatcher, and red-eyed vireo were greatest in smaller width classes (Fig. 3), whereas counts of white-eyed vireo and northern parula were greatest in wider width classes (Fig. 3).

Probability of occurrence was associated positively with stand width for 12 species and negatively with stand width for 1 species (Table 2). The best model for 6 species contained a quadratic term, but only 3 of these models were significant ($P < 0.05$; Table 2). Acadian flycatcher was detected in every site in every year, and we failed to detect blue-gray gnatcatcher in only 1 site in 1 year.

The PC analysis of the vegetation characteristics in the 12 stands used to evaluate the effect of adjacent habitat type on the bird community revealed that PC1 and PC2 had eigenvectors >1.0 and together accounted for 70% of the variation among stands (PC1 = 40.4%, PC2 = 29.2%). High scores on PC1 represented stands with a closed canopy and high basal area of sawtimber but a poorly developed understory, and high scores on PC2 represented stands with a high basal area of sawtimber and a well-developed understory but poorly developed midstory (Table 3). We found no difference between width class or treatment scores along either PC1 or PC2 ($P > 0.05$).

The year x treatment interaction was significant for total species richness ($P < 0.001$); richness was greater in PES in 1994 and greater in FES in 1995 (Table 4). Total species richness was not related ($P > 0.05$) to habitat covariates in either year. Species richness of Neotropical migrants did not differ between treatments (Table 4) but was positively associated with PC1 ($F_{1,6}$ = 6.09, $P = 0.049$). Total bird count,

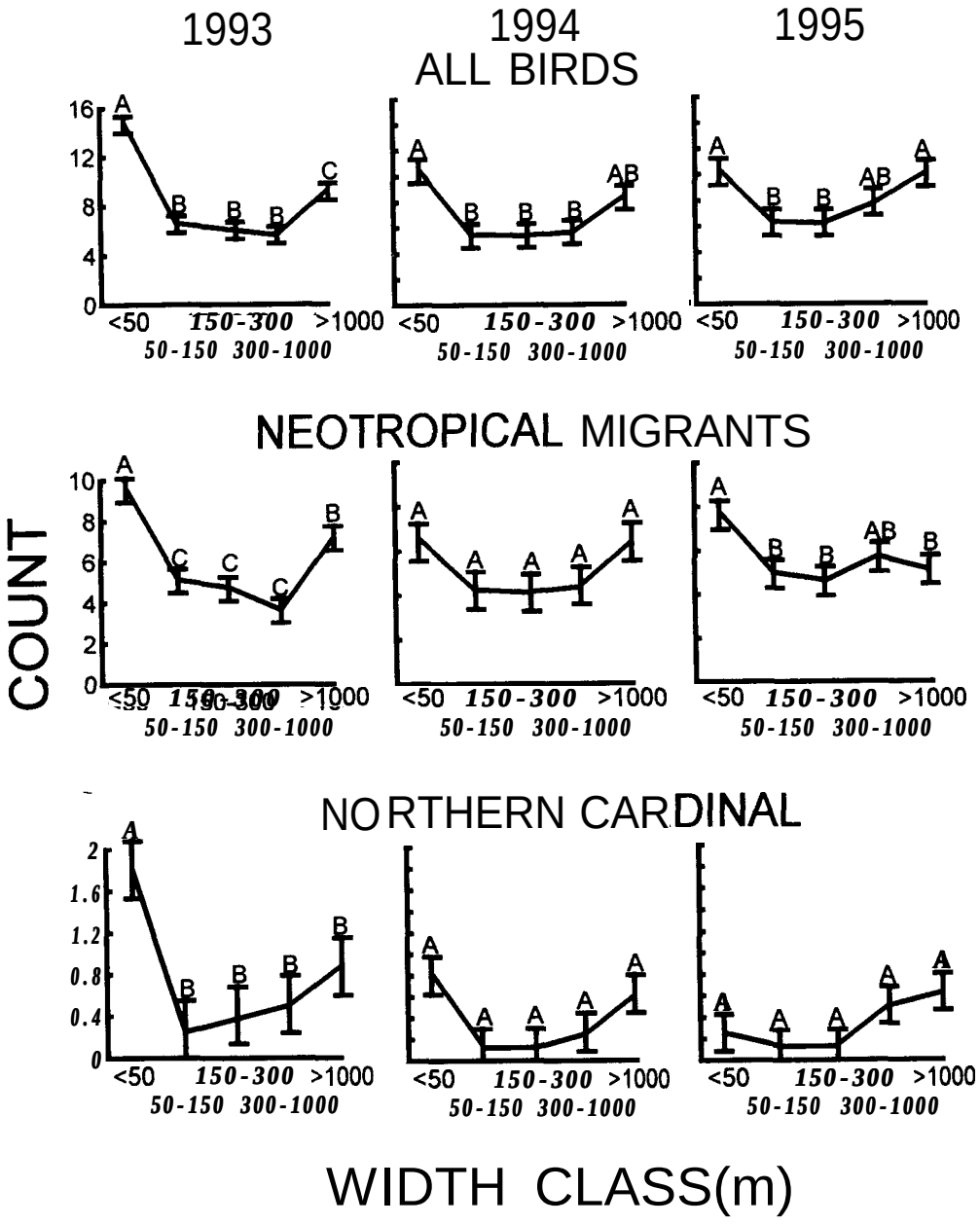


Fig. 2. Counts (mean ± SE) of breeding birds in 5 width classes of bottomland hardwood forests in South Carolina, 1993-95, analyzed by year because the year x width class interaction was significant ($P < 0.05$). Means with the same letter above them are not different ($P > 0.05$).

counts of blue-gray gnatcatcher in 1995, and counts of northern cardinal were greater in FES than in PES (Table 4). No species analyzed was significantly more abundant in PES than FES (Table 4), and no species' count was associated with PC1 or PC2 ($P > 0.05$).

## DISCUSSION

Species richness exhibited a strong positive relation with bottomland forest width (Fig. 1). This relation existed although the adjacent habitat also was forested. Hence, there was a less abrupt ecotone in our study than in previous

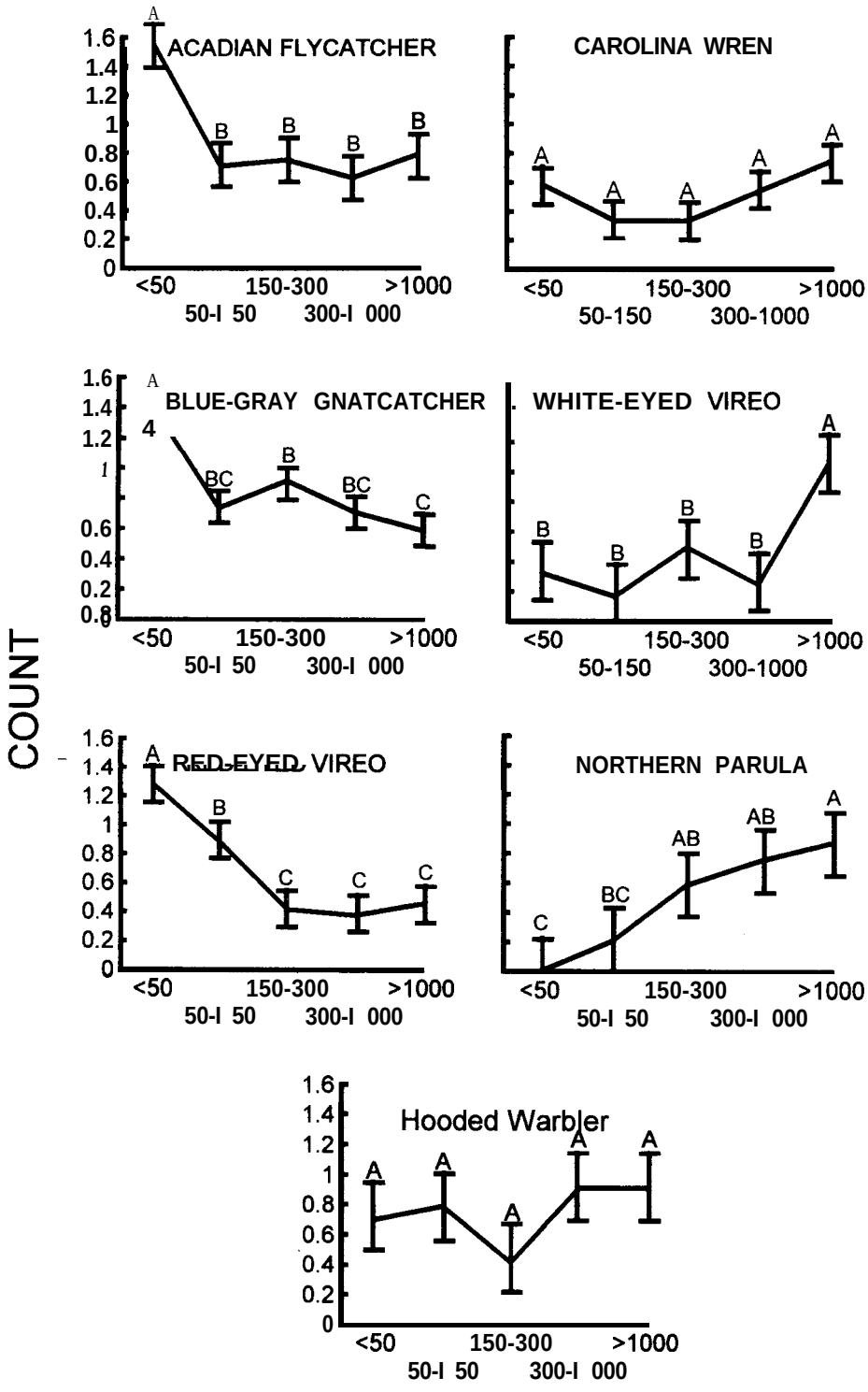
ACADIAN FLYCATCHER
CAROLINA WREN
BLUE-GRAY GNATCATCHER
WHITE-EYED VIREO
RED-EYED VIREO
NORTHERN PARULA
Hooded Warbler
COUNT
<50
150-300
>1000
50-150
300-1000
WIDTH CLASS(m)

Table 2. Probabilities of detecting species in bottomland hardwood forests of various widths, as estimated by logistic regression analysis of data from 20 stands measured from 1993 to 1995, in South Carolina. Species are ordered from those with the strongest positive relation with forest width to those with the most negative relation. Only species detected in ≥5% of the sites over all years are included.

| Species[a] | Bottomland forest width (m) | | | | | | | Wald $X^2$ | $P$ |
|---|---|---|---|---|---|---|---|---|---|
| | 25 | 50 | 100 | 200 | 500 | 1,000 | 2,500 | | |
| Swainson's warbler | **0.05** | 0.05 | 0.06 | 0.07 | 0.14 | 0.36 | 0.95 | 23.86 | **0.000** |
| American crow | **0.13** | 0.14 | 0.15 | 0.19 | 0.30 | 0.56 | 0.97 | 17.08 | **0.000** |
| Prothonotary warbler | **0.13** | 0.14 | 0.15 | 0.18 | 0.28 | 0.51 | 0.95 | 16.02 | 0.000 |
| Northern parula | **0.07** | 0.12 | 0.28 | 0.78 | 1.00 | 1.00 | 1.00 | 13.60 | 0.000 |
| Barred owl | **0.05** | 0.06 | 0.06 | 0.07 | 0.11 | 0.22 | 0.76 | 13.38 | 0.000 |
| Pileated woodpecker | **0.40** | 0.41 | 0.43 | 0.47 | 0.60 | 0.78 | 0.98 | 7.40 | 0.01 |
| Red-bellied woodpecker | **0.32** | 0.36 | 0.44 | 0.60 | 0.92 | 1.00 | 1.00 | 6.33 | 0.01 |
| White-eyed vireo | **0.52** | 0.55 | 0.60 | 0.69 | 0.88 | 0.98 | 1.00 | 6.26 | 0.01 |
| Summer tanager[b] | **0.27** | 0.29 | 0.33 | 0.42 | 0.65 | 0.82 | 0.24 | 7.61 | 0.02 |
| Kentucky warbler[b] | **0.56** | 0.59 | 0.65 | 0.75 | 0.90 | 0.95 | 0.09 | 7.52 | 0.02 |
| Yellow-billed cuckoo | **0.54** | 0.55 | 0.57 | 0.61 | 0.73 | 0.86 | 0.99 | 4.97 | 0.03 |
| Red-shouldered hawk | **0.19** | 0.19 | 0.20 | 0.21 | 0.25 | 0.34 | 0.66 | 4.25 | 0.04 |
| American redstart" | **0.10** | 0.11 | 0.14 | 0.20 | 0.39 | 0.46 | 0.00 | 5.65 | 0.06 |
| Downy woodpecker | **0.28** | 0.29 | 0.29 | 0.31 | 0.36 | 0.45 | 0.73 | 3.39 | 0.07 |
| Northern cardinal | **0.71** | 0.72 | 0.75 | 0.79 | 0.89 | 0.97 | 1.00 | 3.22 | 0.07 |
| Black-and-white warbler[b] | 0.12 | 0.13 | 0.16 | 0.21 | 0.37 | 0.09 | 0.01 | 4.88 | 0.09 |
| Hooded warbler | **0.65** | 0.74 | 0.86 | 0.97 | 1.00 | 1.00 | 1.00 | 2.67 | 0.10 |
| Yellow-throated vireo[b] | **0.23** | 0.24 | 0.27 | 0.33 | 0.50 | 0.63 | 0.09 | 4.25 | 0.12 |
| Tufted titmouse | **0.86** | 0.90 | 0.95 | 0.99 | 1.00 | 1.00 | 1.00 | 1.00 | 0.32 |
| Red-eyed vireo | **0.83** | 0.95 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.57 | 0.45 |
| Great-crested flycatcher | **0.45** | 0.45 | 0.45 | 0.46 | 0.48 | 0.52 | 0.62 | 0.47 | 0.49 |
| Carolina wren | **0.83** | 0.95 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.40 | 0.53 |
| Yellow-throated warbler | **0.11** | 0.11 | 0.11 | 0.11 | 0.12 | 0.13 | 0.17 | 0.14 | 0.71 |
| Ruby-throated hummingbird | **0.04** | 0.04 | 0.04 | 0.05 | 0.07 | 0.10 | 0.35 | 0.07 | 0.78 |
| Carolina chickadee | **0.29** | 0.29 | 0.29 | 0.29 | 0.30 | 0.31 | 0.35 | 0.06 | 0.80 |
| Common yellowthroat | **0.14** | 0.14 | 0.15 | 0.15 | 0.15 | 0.16 | 0.17 | 0.03 | 0.87 |
| Acadian flycatcher | **1.00** | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.00 | 1.00 |
| Blue-gray gnatcatcher[c] | **0.98** | 0.98 | 0.98 | 0.98 | 0.98 | 0.98 | 0.98 | **N/A** | **N/A** |
| Blue jay | **0.23** | 0.23 | 0.22 | 0.21 | 0.18 | 0.13 | 0.05 | **1.00** | **0.32** |
| Pine warbler | **0.14** | 0.13 | 0.11 | 0.07 | 0.02 | 0.00 | 0.00 | **1.00** | **0.32** |
| Mourning dove[b] | **0.02** | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | **2.32** | **0.31** |
| Louisiana waterthrush | **0.44** | 0.43 | 0.42 | 0.39 | 0.31 | 0.21 | 0.05 | **3.36** | **0.07** |
| wood thrush | **0.70** | 0.70 | 0.69 | 0.67 | 0.60 | 0.49 | 0.19 | **4.75** | **0.03** |

[a] Scientific names of species not mentioned in text: American crow (*Corvus brachyrhynchos*); prothonotary warbler (*Protonotaria citrea*); barred owl (*Strix varia*); pileated woodpecker (*Dryocopus pileatus*); summer tanager (*Piranga rubra*); red-bellied woodpecker (*Melanerpes carolinus*); yellow-billed cuckoo (*Coccyzus americanus*); red-shouldered hawk (*Buteo lineatus*); American redstart (*Setophaga ruticilla*); downy woodpecker (*Picoides pubescens*); black-and-white warbler (*Mniotilta varia*); yellow-throated vireo (*Vireo flavifrons*); tufted titmouse (*Parus bicolor*); great-crested flycatcher (*Myiarchus crinitus*); yellow-throated warbler (*Dendroica dominica*); ruby-throated hummingbird (*Archilochus colubris*); Carolina chickadee (*Parus carolinensis*); common yellowthroat (*Geothlypis trichas*); blue jay (*Cyanocitta cristata*); pine warbler (*Dendroica pinus*); mourning dove (*Zenaida macroura*).

[b] The best-fit logistic regression equation included a quadratic term (width$^2$)

[c] Because we failed to detect blue-gray gnatcatcher in only 1 site in 1 year, convergence could not be attained in logistic regression analysis Therefore, the probability of detection reported is the proportion of all stands, by year, in which the species was detected. This represents the maximum-likelihood estimate appropriate when probability of detection is not related to width (Robbins et al. 1989).

studies relating species richness to area (Blake and Karr 1987, Robbins et al. 1989) or width (Keller et al. 1993). However, the slope of this relation did not differ from slopes of species-area relations, indicating that our wider stands did not exhibit a greater increase in species richness than was expected from simple species-area regressions. The general lack of associations between the bird community and habitat features is likely attributable to the general similarity of vegetation among the study sites; stands were selected because of their apparent similarity of vegetation. Thus, the observed relation of species richness to stand width is due

←

Fig. 3. Counts (mean ± SE) of 7 breeding bird species in 5 width classes of bottomland hardwood stands in South Carolina, 1993-95. Means with the same letter are not different ($P > 0.05$).

Table 3. Eigenvectors for variables included in principal components (PC) analysis of 12 bottomland hardwood stands, 8 enclosed by pine forest and 4 enclosed by fields, in South Carolina, 1994-95. The PC1 and PC2 (only components with eigenvalues >1.00) accounted for 70% of the variation in the variables measured among sites.

| Variable | PC1 | PC2 |
|---|---|---|
| Vegetation profile | -0.44 | 0.52 |
| Canopy coverage | 0.72 | -0.12 |
| Basal area: hardwood poletimber[a] | -0.04 | -0.64 |
| Basal area: hardwood sawtimber[b] | 0.53 | 0.55 |

[a] Defined as all hardwood stems 8–23 cm dhh
[b] Defined as all hardwood stems >23 cm dhh.

either to a response to width per se or to unmeasured features of the habitat. Pashley and Barrow *(1993)* described several aspects of bottomland hardwood habitats important to birds. These included scour channels, Spanish moss (*Tilandsia usneoides*), canebrakes (i.e., switchcane thickets), vine tangles, and thickets of palmetto (*Sabal minor*). The wider a stand, the more likely it is to contain each of these features, yet all are difficult to quantify with the conventional techniques we used to sample avian habitat.

Both total and species-specific counts generally were greatest in the narrowest and widest width classes. This U-shaped pattern in total bird count was inconsistent with our expectation that fewer species in narrow stands would mean fewer birds. We suggest that the observed pattern might better be understood by examining the 2 segments of this relation separately (i.e., the portion of the abundance-width curve for which the relation is negative vs. that for which the curve is positive). Three factors may have contributed to the negative relation that characterized the narrow stands. First, the relation potentially resulted from the combined effects of species positively associated with width (e.g., nor-them parula, white-eyed vireo), and of species negatively associated with width (e.g., Acadian flycatcher, blue-gray gnatcatcher, red-eyed vireo). Second, a greater amount of edge habitat was censused in the narrow stands because census plots in these stands overlapped both stand edges. Consequently, edge species such as northern cardinal and Carolina wren were more abundant in the narrowest width classes than in the medium width classes (this trend was nonsignificant for Carolina wren). Finally, densities in our narrowest stands potentially were high simply because birds were confined within a smaller area, whereas territories were not as packed in medium width stands, because space was not limited. Previous studies reported that bird density decreased with increased width of the riparian zone, whereas species richness increased with width (Darveau et al 1995, Thurmond et al. 1995). Such a pattern is consistent with our results for the narrow width classes, which encompassed the widths

Table 4. Comparison of breeding birds in bottomland hardwood stands enclosed by pine forest (PES; $n = 8$) and enclosed by fields (FES; $n = 4$) in South Carolina, 1994-95.

| Variable | PES | | FES | | P |
|---|---|---|---|---|---|
| | $\bar{x}$ | SE | $\bar{x}$ | SE | |
| Species richness | | | | | |
| All birds[a] | | | | | |
| 1994 | 18.75 | 0.73 | 14.50 | 1.03 | 0.007 |
| 1995 | 14.63 | 0.82 | 19.00 | 1.16 | 0.012 |
| Neotropical migrants[b] | 8.42 | 0.54 | 8.02 | 0.76 | 0.530 |
| Count | | | | | |
| All birds | 5.88 | 0.45 | 9.03 | 0.63 | 0.015 |
| Neotropical migrants | 4.50 | 0.29 | 5.20 | 0.41 | 0.356 |
| Acadian flycatcher | 0.81 | 0.45 | 0.78 | 0.10 | 0.879 |
| Carolina wren | 0.34 | 0.07 | 0.59 | 0.10 | 0.301 |
| Blue-gray gnatcatcher[a] | | | | | |
| 1994 | 0.69 | 0.09 | 0.90 | 0.13 | 0.216 |
| 1995 | 0.56 | 0.07 | 1.15 | 0.10 | 0.001 |
| White-eyed vireo | 0.25 | 0.05 | 0.25 | 0.07 | 1.000 |
| Red-eyed vireo | 0.69 | 0.11 | 0.64 | 0.15 | 0.801 |
| Northern parula | 0.47 | 0.08 | 0.71 | 0.11 | 0.426 |
| Hooded warbler | 0.59 | 0.08 | 0.25 | 0.11 | 0.237 |
| Northern cardinal | 0.13 | 0.03 | 0.84 | 0.04 | 0.001 |

[a] Year × treatment interaction was significant ($P < 0.05$). so years were analyzed separately.
[b] Species richness was positively correlated with PC1 ($P = 0.049$).

reported in these studies. For example, Thurmond et al. (1995) reported higher bird densities but fewer species in narrow (16-20 m) versus wide (53-58 m) streamside management zones in Georgia. Similarly, Darveau et al. (1995) reported that 20-m-wide riparian strips in Quebec contained greater bird densities but fewer species than 40- and 60-m-wide strips, although the wider strips supported a greater number of territories because they contained greater areas. Thus, the negative relation between count and width for narrow stands may be related to area and sampling effects, whereas counts from wider stands, for which no comparison from the literature is available, actually may reflect superior habitat conditions that support higher densities of birds.

Some species generally considered to be area sensitive (Robbins et al. 1989) exhibited unexpected patterns of occurrence and abundance. The probabilities of occurrence for wood thrush ***(Hylocichla mustelina)*** and Louisiana waterthrush (*Seiurus motacilla*) were negatively related to width. Capture rates of wood thrush in a concurrent mistnetting study (R. A. Sargent et al., unpublished data) also were negatively related to width. Keller et al. (1993) found these species positively associated with riparian zone width in the mid-Atlantic states. Counts of red-eyed vireo, also considered an area-sensitive species (Robbins et al. 1989, Keller et al. 1993), declined as width increased, although this species' probability of occurrence increased (non-significantly) with width. Similarly, Acadian flycatcher was detected even in our narrowest stands, and their counts declined in wider stands. Conversely, counts of white-eyed vireo, an edge species, were positively related to width. Our results for Acadian flycatcher and white-eyed vireo are corroborated by those of Hodges and Krementz (1996) from the Altamaha River basin, a tributary of the Savannah River. Reasons for lower densities in sites where a species is more likely to occur are unclear but may be related to the species' sociobiology. Density also is not necessarily an accurate reflection of habitat quality (Wiens 1989:306).

We failed to detect a consistent effect of adjacent habitat on species richness. We hypothesized that more species would be found in PES than in FES because the presence of an adjacent, closed canopy forest might serve as a buffer against negative edge effects (Harris 1984, Kilgo et al. In press), and thereby increase the functional width of the stand. Such an effect was evident in 1994, but the pattern was reversed in 1995. Similarly, we failed to detect an effect of adjacent habitat on the counts of area-sensitive species. The northern cardinal, an edge species, was more abundant in FES, but counts of the area-sensitive northern parula and white-eyed vireo (this study) were not affected negatively by the presence of field habitat adjacent to the stand. The expected pattern may have been evident had we sampled narrower FES (i.e., some species may be sensitive to external fragmentation below the range of widths we sampled).

## MANAGEMENT IMPLICATIONS

We concur with the conclusion of Thurmond et al. (1995) that even retention of narrow streamside buffer zones can benefit local bird assemblages. Several area-sensitive species (e.g., Acadian flycatcher, wood thrush, red-eyed vireo, Louisiana waterthrush, Kentucky warbler [*Oporornis formosus*], hooded warbler) were common in our narrowest stands. However, because we sampled a broad range of widths, we detected several species that were highly area-sensitive and apparently would benefit only from conservation of very wide stands. For example, the narrowest stand in which we detected Swainson's warbler ***(Limnothlypis swainsonii)*** ***was 475*** m wide. Although we could not include them in our analysis, Mississippi kite ***(Ictinia mississippiensis)*** was recorded only in stands 21,000 m wide, and swallow-tailed kite (*Elanoides forficatus*) was recorded only in stands 21,900 m wide. Keller et al. (1993) and Hodges and Krementz (1996) recommended that a minimum forested buffer zone of ≥100 m be maintained adjacent to drainages to provide habitat for forest interior species. In our study, the width at which probability of occurrence was 50% of its maximum (i.e., a conservative estimate of the minimum amount of habitat required by a species for breeding; Robbins et al. 1989) exceeded 100 m for 8 species (pileated, red-bellied, and downy woodpeckers, yellow-throated vireo, northern parula, American redstart, black-and-white warbler, summer tanager) and exceeded 500 m for 6 additional species (barred owl, red-shouldered hawk, ruby-throated hummingbird, American crow, prothonotary warbler, Swainson's warbler). Thus, although narrow riparian stands are extremely valuable avian habitat, we feel that the complete avian

**community characteristic of bottomland hardwoods in South Carolina can be maintained only in the few remaining riparian zones that are extremely wide** (>500 m).

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Conservation Biology

*Review*

# Effects of Road Networks on Bird Populations

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**Abstract:** *One potential contributor to the worldwide decline of bird populations is the increasing prevalence of roads, which have several negative effects on birds and other vertebrates. We synthesized the results of studies and reviews that explore the effects of roads on birds with an emphasis on paved roads. The well-known direct effects of roads on birds include habitat loss and fragmentation, vehicle-caused mortality, pollution, and poisoning. Nevertheless, indirect effects may exert a greater influence on bird populations. These effects include noise, artificial light, barriers to movement, and edges associated with roads. Moreover, indirect and direct effects may act synergistically to cause decreases in population density and species richness. Of the many effects of roads, it appears that road mortality and traffic noise may have the most substantial effects on birds relative to other effects and taxonomic groups. Potential measures for mitigating the detrimental effects of roads include noise-reduction strategies and changes to roadway lighting and vegetation and traffic flow. Road networks and traffic volumes are projected to increase in many countries around the world. Increasing habitat loss and fragmentation and predicted species distribution shifts due to climate change are likely to compound the overall effects of roads on birds.*

**Keywords:** bird populations, roads, road mortality, roadway lighting, surface transportation, traffic noise

Efectos de las Redes de Caminos sobre Poblaciones de Aves

**Resumen:** *El incremento en la prevalencia de caminos, que han tenido varios efectos negativos sobre aves y otros vertebrados, es un potencial contribuyente a la declinación mundial de poblaciones de aves. Sintetizamos los resultados de estudios y revisiones que exploran los efectos de los caminos sobre las aves, con énfasis en caminos pavimentados. Los bien conocidos efectos directos de los caminos sobre las aves incluyen la pérdida y fragmentación de hábitat, mortalidad causada por vehículos y envenenamiento. Sin embargo, los efectos indirectos pueden ejercer una mayor influencia sobre poblaciones de aves. Estos efectos incluyen ruido, luz artificial, barreras al movimiento y bordes asociados con caminos. Más aun, los efectos indirectos y directos pueden actuar sinérgicamente para causar decrementos en la densidad poblacional y en la riqueza de especies. De los muchos efectos de los caminos, parece que la mortalidad y el ruido del tráfico tienen los efectos más significativos sobre las aves en relación con otros efectos y grupos taxonómicos. Las medidas potenciales para mitigar los efectos perjudiciales de los caminos incluyen estrategias de reducción de ruido y cambios en la iluminación y vegetación de los caminos y en el flujo de tráfico. Se proyecta que las redes de caminos y los volúmenes de tráfico incrementen en muchos países en el mundo. Es probable que el incremento en la pérdida y fragmentación de hábitat y los cambios pronosticados en la distribución de especies debidos al cambio climático compliquen los efectos de los caminos sobre las aves.*

**Palabras Clave:** caminos, iluminación en caminos, poblaciones de aves, mortalidad en caminos, ruido de tráfico, transportación terrestre

## Introduction

Bird populations are declining around the world (BirdLife International 2008*a*). In North America the abundances of at least 20 species previously categorized as common have declined more than 50% in the last 40 years (Butcher & Niven 2007; BirdLife International 2008*b*). Additionally, abundances of over half the species of Neotropical

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migrants have declined substantially. The reasons for these declines are not fully understood (Butcher & Niven 2007; BirdLife International 2008*c*). One likely contributor is the expansion of paved roads, mostly in terms of widening (National Research Council 2005), and corresponding increases in the speed and volume of vehicles on those roads (Ritters & Wickham 2003). We synthesized these effects on birds to balance the much greater attention that has hitherto been paid to the effects of roads on mammals and to examine the potentially negative effects of roads on birds worldwide.

Reduced breeding success is correlated with proximity of birds to roads and road density for species ranging from passerines (Catchpole & Phillips 1992; Reijnen & Foppen 1994) to vultures (Donazar et al. 1993). In some cases, avian communities adjacent to roads differ from nearby avian communities (Glennon & Porter 2005), presumably because of some combination of the direct and indirect effects of roads on animals in general (Forman & Alexander 1998; Trombulak & Frissell 2000; Fahrig & Rytwinski 2009).

There is a little understanding of whether declines in persistence of birds are more affected by direct or indirect effects. If this could be determined in urban areas, it may be possible to increase bird abundance and species richness. It is also important to identify and mitigate any negative road effects in protected areas, which are assumed to buffer populations of wild animals from human activities.

Many of the negative effects of roads on other vertebrates (e.g., mortality, habitat fragmentation, and audiovisual disturbance, chemical pollution) also apply to birds (Forman et al. 2003; Jacobson 2005). There are a few ways roads can benefit birds. For example, roads retain heat that can reduce metabolic costs for birds that rest on road surfaces (Whitford 1985), associated road infrastructure (e.g., poles and bridges) can create nesting sites (Forman 2000), and verges increase availability of food sources (Lambertucci et al. 2009) and link patches of habitat (Meunier et al. 1999; Huijser & Clevenger 2006; Reijnen & Foppen 2006). We reviewed recent reports and peer-reviewed articles focused primarily on direct and indirect negative effects of roads on bird populations and identified some potential forms of mitigation. Much of the literature we reviewed concerns paved roads because they have been the subject of more study and because their ecological effects are assumed to be greater than gravel, dirt, or ice roads (Forman et al. 2003; National Research Council 2005).

## Direct Threats Posed to Birds by Roads and Traffic

For bird populations the most visible direct negative effects of roads are habitat loss and mortality due to collisions with vehicles. Because the effects of habitat loss on birds have been comprehensively reviewed elsewhere (Andren 1994), we did not focus on this effect here. Nonetheless, roads have other effects that are related to habitat loss. For example, maintenance activities in the right-of-way can further reduce habitat quality and destroy nests, which may reduce population viability for rare species (e.g., Burrowing Owl [*Athene cunicularia*]) (Catlin & Rosenberg 2006). We focused on the negative effects associated with vehicular traffic.

### Vehicle-Caused Mortality

For individual birds and other vertebrate groups, a direct threat of roads is death due to collisions with vehicles (Erritzoe et al. 2003). In the United States, vehicles are estimated to cause approximately 80 million bird fatalities each year (Erickson et al. 2005). Despite the high number of mortalities each year, vehicle-caused mortality has been assumed to have less of an effect on persistence than some indirect effects of roads (Forman & Alexander 1998; Reijnen & Foppen 2006). Only three bird species found in the United States appear to suffer population declines as a result of them: Florida Scrub-Jay (*Aphelocoma coerulescens*) (Mumme et al. 2000; IUCN 2008), Audubon's Crested Caracara (*Polyborus plancus audubonii*), and Hawaiian Goose (*Branta sandvicensis*) (Huijser et al. 2007; IUCN 2008). A greater understanding of what makes some species more susceptible to vehicle collision and population decline as a result of vehicle-caused mortality is needed, but some generalities emerge from the literature.

First, birds are more likely to collide with vehicles if they forage, roost, or nest near roads (Erritzoe et al. 2003; Huijser et al. 2007). Collision frequency can increase near watercourses (Erritzoe et al. 2003; Ascensao & Mira 2006) and houses (Ascensao & Mira 2006). Collisions are also more likely to occur at lower elevations (Clevenger et al. 2003) and in open areas than in forests (e.g., Clevenger et al. 2003; Ascensao & Mira 2006; Ramp et al. 2006).

Several other factors have less consistent effects on vehicle-induced bird mortality. For many species, vehicle-induced mortality increases during breeding and migration (Fulton et al. 2008; Gryz & Krause 2008), but for other species it increases during winter (Loos & Kerlinger 1993; Boves 2007). Collisions can increase (Jackson 2003) or decrease as roadside lighting increases (Hernandez 1988). Roadside trees, hedgerows, and other features that cause birds to fly higher across roads typically decrease collision frequency (Pons 2000; Bard et al. 2002; Clevenger et al. 2003; Erritzoe et al. 2003; Taylor & Goldingay 2004; Orlowski 2005), but they can also increase it (Ramp et al. 2006; Varga et al. 2006). Birds also vary in their responses to roads. Some individuals appear to learn to avoid vehicles (Mumme et al. 2000), whereas others do not (Loos & Kerlinger 1993; Jackson 2002).

It is difficult to measure the true extent of vehicle-induced mortality because estimates are typically far lower than the actual number of birds killed (Erickson et al. 2005). Estimation accuracy is reduced by variation in searcher efficiency, scavenger bias (Erickson et al. 2005; Boves 2007), and incorrect attribution of cause of death (Kerlinger & Lein 1988). Even long-term studies in which 100% of individuals are marked, researchers can fail to detect all instances of vehicle-caused mortality (Mumme et al. 2000). Vehicle collisions may also cause nonfatal injuries that increase the probability birds will die from other causes (Orlowski & Siembieda 2005). In addition, inaccurate estimates of vehicle-induced mortality can result if only carcasses are studied in the absence of data on species abundance (Hernandez 1988; Aebischer et al. 2005). Missing information about population size makes it difficult to compare rates of mortality in different areas, especially on different continents (Erritzoe et al. 2003).

### Pollution and Poisoning

Deicing agents, petroleum-based organic compounds, nutrients, sediments, agricultural chemicals, and other substances regularly run off paved roads during construction, maintenance, and use (Buckler & Granato 1999). Road salt is a common deicing agent that attracts birds. Its ingestion can lead to death, which dispels the notion that road salt has a negative effect only because it attracts birds to the road surface, making them subject to collisions with vehicles (Mineau & Brownlee 2005). Dust on unpaved roads can change the composition of vegetation (Walker & Everett 1987), which can affect birds (Kalisz & Powell 2003). Gravel roads are frequently treated with dust suppressants, the environmental and toxicological effects of which are not well understood (Fay & Kociolek 2009). Despite the ubiquity of road contaminants from vehicles and maintenance activities, toxic effects of roads appear to be rare, even in areas with high traffic volumes (Buckler & Granato 1999), and pollution appears to have fewer effects on birds than other road-related effects (Reijnen & Foppen 2006).

## Indirect Threats Posed to Birds by Roads and Traffic

Even in the absence of direct deleterious effects, many bird species appear to avoid roads purposely (e.g., Bollinger & Gavin 2004; Balbontin 2005; Gavashelishvili & McGrady 2006). Some species may be present near roads for a time, but they are more likely to abandon nests near roads (Gorog et al. 2005). For birds, road avoidance appears to be associated with the physical barrier to movement roads present, noise, artificial light, and edge effects.

### Physical Barriers

Of the indirect threats of roads, the barriers to movement roads present may have the greatest effect on vertebrates (Forman & Alexander 1998). Several forest-dwelling bird species are unlikely to cross gaps in forest cover $\geq$50 m in areas dominated by agriculture (Desrochers & Hannon 1997), timber harvesting (Awade & Metzger 2008), and urban infrastructure (Tremblay & St. Clair 2009). Some species exhibit reluctance to cross dirt roads that are 10–30 m wide (Develey & Stouffer 2001). Nonetheless, the barriers caused by roads may be a simple function of the width of the gap they create in the surrounding habitat, unless the roads are also noisy (St. Clair 2003; Tremblay & St. Clair 2009) or are associated with tall features such as power lines (Pruett et al. 2009).

### Noise

Traffic noise probably has the most widespread and greatest indirect effect on birds (Reijnen et al. 1995 (Table 1). Noise likely causes reductions in population densities that have been reported for several bird species that are present near roads (Reijnen & Foppen 2006; Patricelli & Blickley 2006). In grasslands the effects of noise appear to extend farther from roads than in forests (Forman et al. 2002), perhaps because grasslands have less vegetation to absorb sound. In addition to the effects of traffic volume and its associated noise, there may be synergistic effects of noise, habitat loss and fragmentation (Forman & Deblinger 2000), and edge effects (Habib et al. 2007).

Birds may be affected by anthropogenic noise because they rely extensively on acoustic communication (Table 1). Chronic industrial noise can reduce species richness, alter population age structure, and change avian predator–prey dynamics (Francis et al. 2009). Like industrial noise, chronic traffic noise appears to produce younger age structures and reduces population densities in several bird species (Reijnen & Foppen 2006). These effects may occur because anthropogenic noise masks the frequencies of calls used to attract mates (Rheindt 2003; Pohl et al. 2009), communicate with flock members (Lohr et al. 2003; Slabbekoorn & Ripmeester 2008) or offspring (Leonard & Horn 2005), defend territories (Habib et al. 2007; Mockford & Marshall 2009), and detect predators (Slabbekoorn & Ripmeester 2008; Francis et al. 2009) (Table 1). Effects of noise on both birds and anurans seem to depend on the frequencies and amplitudes of species-specific signals (Lengagne 2008; Slabbekoorn & Ripmeester 2008; Hu & Cardoso 2009). Some species seem unaffected by roads or traffic (Kaseloo 2005; Reijnen & Foppen 2006), and others may not come near roads when traffic volume is high (Bautista et al. 2004). Several urban-dwelling songbird species appear to counteract the masking effects of traffic noise (Table 1) by singing at a higher pitch (Slabbekoorn & Peet 2003), increasing song amplitude (Brumm 2004b), or singing

**Table 1. The effects of anthropogenic noise on avian communities and communication.**

| *Category* | *Effect* | *References* |
|---|---|---|
| Community | | |
| species richness | reduced as noise increases | Stone 2000 |
| density & abundance (all species) | reduced as noise increases | Reijnen et al. 1995, 1996; Kuitunen et al. 1998; Bayne et al. 2008 |
| | no overall reduction | Peris & Pescador 2004 |
| densities & abundance (specific species) | reduced as noise increases | Reijnen & Foppen 1994; Reijnen et al. 1995, 1997 |
| | dependent on species | Kuitunen et al. 1998; Peris & Pescador 2004 |
| | higher abundance of birds with higher song pitch near roads | Rheindt 2003 |
| age structure | younger at noisy sites | Reijnen & Foppen 1994; Habib et al. 2007 |
| physiology | increased stress at higher noise levels | Campo et al. 2005 |
| | no stress difference at higher noise levels | Byers et al., unpublished data |
| Breeding cycle | | |
| pairing and mate retention | decreased time devoted to courtship behavior | Goudie & Jones 2004 |
| | reduced pairing success | Habib et al. 2007 |
| | reduced mate preference | Swaddle & Page 2007 |
| territory and nest-site selection | farther from noise sources | Francis et al. 2009 |
| nest success | increased as noise increases for some species | Francis et al. 2009 |
| Foraging | | |
| begging calls | reduced parental discrimination in noisy locations | Leonard & Horn 2005 |
| prey location and probability of predation | predator reduction increases nest success in noisy locations | Francis et al. 2009 |
| | potential alterations to interspecies interactions | Slabbekoorn & Halfwerk 2009 |
| | increased vigilance as noise increases | Quinn et al. 2006 |
| Communication | | |
| temporal adjustment | sing more at night in noisy locations | Fuller et al. 2007 |
| amplitude increase | sing louder as noise increases (Lombard effect) | Cynx et al. 1998; Brumm 2004a, 2004b; Brumm et al. 2009; Osmanski & Dooling 2009 |
| | louder begging calls in noisy locations | Leonard & Horn 2005 |
| pitch modification | increased pitch in noisy locations | Slabbekoorn & Peet 2003; Fernandez-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Wood & Yezerinac 2006; Parris & Schneider 2009; Kirschel et al. 2009; Nemeth & Brumm 2009 |
| redundancy | no correlation between pitch and road noise | Skiba 2000 |
| detection of con- and heterospecific vocal signals | more repetition in noisy locations | Brumm & Slater 2006 |
| | reduced detection probability of signals in noisy locations | Langemann et al. 1998; Lohr et al. 2003 |
| response to signals | strongest response to played-back signals when ambient noise levels are similar to local environment | Mockford & Marshall 2009 |
| reviews | effects of noise and implications | Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Barber et al. 2010 |
| Brain response | immediate early-gene ZENK | Vignal et al. 2004 |
| gene activation | expression in the neural pathway of the avian brain not modified by noise playback | |

during periods of low traffic noise (Fuller et al. 2007). Other species may be unable to adapt their songs to accommodate chronic noise (Slabbekoorn & Ripmeester 2008; Barber et al. 2010), and pairing success of birds with relatively high amplitude songs is reduced when they are exposed to high levels of chronic noise (Habib et al. 2007).

### Artificial Light

Light from roadways can have negative effects on many animals (Rich & Longcore 2006), including birds (Ogden 1996; Van De Laar 2007). Some lighting structures attract migrating bird species, which increases the probability they will be preyed on or collide with structures and often causes them to redirect flight paths and thus deplete energy stores (van de Laar 2007). Artificial lighting can also affect avian patterns of nestling development, singing, breeding, molting, and migration (De Molenaar et al. 2006). There is some evidence that roadway lighting may reduce habitat quality and change the timing of breeding for the Black-tailed Godwit (*Limosa limosa*), a species associated with grasslands in Africa, Europe, and Asia (De Molenaar et al. 2006). American Robins (*Turdus migratorius*) sing earlier in the morning in areas with more anthropogenic light (Miller 2006), but this response may be difficult to disentangle from the associated effect of road noise, which is more important than light for explaining nocturnal singing by European Robins (*Erithacus rubecula*; Fuller et al. 2007).

### Edge Effects

Positive and negative effects of edges on breeding birds have been documented in many studies (Stephens et al. 2003). The edge effects of roads may be particularly acute when introduced species, such as rats (*Rattus rattus*), prey on ground-nesting birds (Delgado et al. 2001) or parasitic species, such as Brown-headed Cowbirds (*Molothrus ater*), target the nests of species of conservation concern (Chace et al. 2003). In some cases, these edge effects are contradictory (Bergin et al. 2000; Lariviere 2003).

## Mitigation

Paved roads are a pervasive feature across much of North America, and existing roads are being widened, new roads are being built, and, and traffic volume is increasing (Forman et al. 2003; National Research Council 2005) throughout the world (Urban Land Institute 2007; Bhattacharya 2008). Efforts to mitigate road effects are most likely to increase probabilities of persistence of birds when applied across extensive areas (Stutchbury 2009).

New information about the ubiquity of the effects of noise on birds suggests reducing road noise may be cost-effective because it can benefit both birds and humans (Bluhm et al. 2007; Slabbekoorn & Ripmeester 2008; Barber et al. 2010). Promising measures to reduce road noise include temporal adjustments to traffic flow (Reijnen & Foppen 2006) and increased reliance on mass transit (Barber et al. 2010). The unvegetated area created by light-rail train tracks is more permeable to bird movement than roads of equivalent sizes, perhaps because they are quieter (Tremblay & St. Clair 2009). New tire designs (Carstens 2003) and noise-absorbing porous asphalt (Piepers 2001) can substantially reduce levels of highway noise (Elvik & Greibe 2003). Other noise-reducing strategies include the use of earth berms and vegetation that, unlike walls (Varga et al. 2006), do not create vertical barriers to animal movement, although this may depend on the animal. These features typically also increase quality of life and property values for human residents.

Changing roadway lighting may also benefit both birds and people through reductions in energy consumption and increases in safety (De Molenaar et al. 2006). Replacing red or white lights with green lights greatly reduces the negative effect of artificial lights on oil platforms on birds (van de Laar 2007). Such lighting could be used on highway (Poot et al. 2008).

Edge effects might be partially mitigated with vegetation management and restoration. Poisoning and nonpoint source pollution can be mitigated, in part, by policy aimed at encouraging use of nontoxic agents to maintain safe driving conditions. A practice that would reduce vehicle-induced bird mortality would be to refrain from planting along roadsides fruit-bearing vegetation that attracts birds.

## Future Implications

In the United States road area is expected to increase by 27,900 $km^2$ by 2030, and lanes added to existing roadways to accommodate increased traffic volume is projected to increase road area by an additional 94,100 $km^2$ (Theobald 2010). Exponential increases in the road network and traffic volume are anticipated to occur in large, densely populated, countries such as China and India (Bhattacharya 2008). Among the factors studied to date, it appears that traffic noise has the greatest potential to reduce population abundance and species richness of birds (Reijnen & Foppen 2006; Barber et al. 2010). Although vehicle-caused mortality does not appear to affect persistence for most populations, it is a problem for some species (Huijser et al. 2007) and may exacerbate other anthropogenic threats to birds (Erickson et al. 2005). Given global traffic projections and in light of losses due to collisions, road-induced mortality of birds should be examined more systematically and comprehensively. Other road-related disturbances such as light and chemical

pollution appear to have minor effects at the population level, but their spatial extent may still generate a large collective effect on birds. Finally, increasing habitat loss and fragmentation, in addition to predicted species distribution shifts due to climate change, are likely to compound the overall effect of roads (Heller & Zavaleta 2009).

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Los Angeles Times

# Where SoCal Edison may shut off power in California

By PRIYA KRISHNAKUMAR, BEN WELSH AND RYAN MURPHY

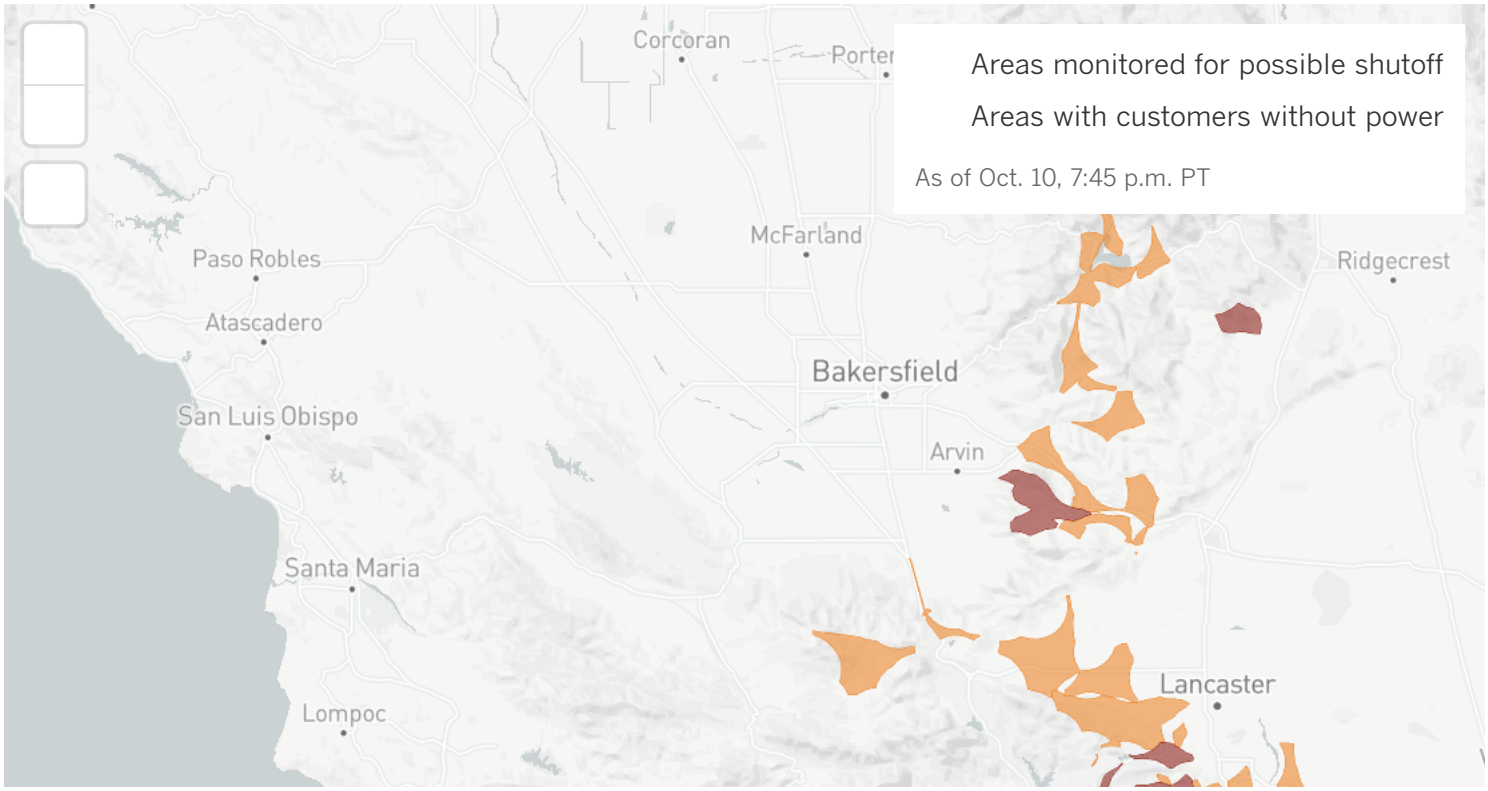
OCT. 9, 2019

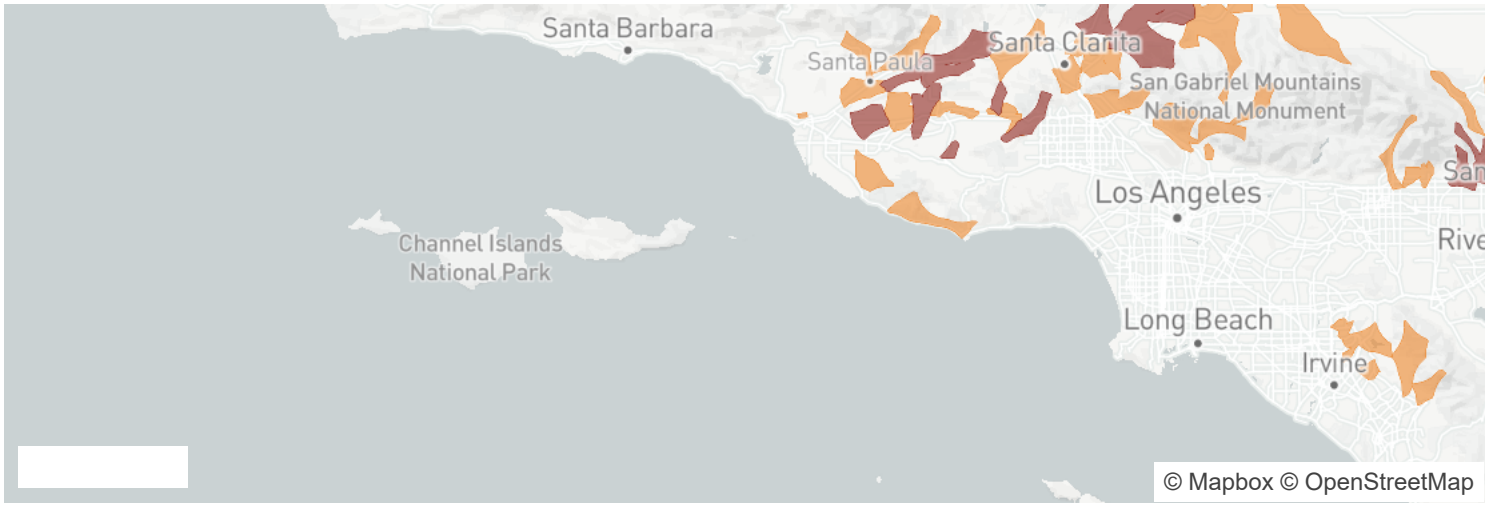
Southern California Edison has cut power to nearly 13,000 customers as firefighters battle several growing blazes fueled by strong Santa Ana winds. With forecasts for strong winds in the area, the utility said power could be cut off to more than 173,000 customers in parts of eight counties.

Edison's announcement follows a precautionary power outage in Northern California by Pacific Gas & Electric that began early Wednesday.

In the map below are the areas where Edison says the power has been and could potentially be turned off. Look up your address to see if you could be affected.

Search






Edison outages may occur in the following areas:

## Los Angeles County (about 49,439 customers)

- Lancaster
- Palmdale
- La Cañada Flintridge
- Malibu
- Pasadena
- Chatsworth
- San Fernando
- Santa Clarita
- Unincorporated areas including Acton, Agua Dulce, Boiling Point, White Heather, Sunland, Tujunga, La Crescenta, Montrose, Wildwood, Canyon Country, Newhall, Forest Park, Sleepy Valley, Del Valle, Leona Valley, Plum Canyon, Alpine, Merrie Dell, Indian Springs, Jumper Hills, Valencia, Stevenson Ranch, Mount Wilson, Valyermo, Paradise Springs, Humphreys, Placerita Canyon State Park, Little Rock, Pearblossom, Quartz Hill, Lake Hughes, Green Valley, Elizabeth Lake, Sylmar, Portal Ridge, Three Points, Upper Big Tujunga Canyon, and near Antelope Valley and unincorporated areas of Chatsworth and Sylmar

## San Bernardino County (about 40,978 customers)

- Big Bear
- Calimesa
- Fontana
- Hesperia

- Rancho Cucamonga
- Rialto
- San Bernardino
- Yucaipa
- Yucca Valley
- Unincorporated areas, including the communities of Doble and Upper Holcomb Valley, Cajon Pass, Devore, Etiwanda, Lucerne Valley, Lytle Creek, Running Springs, Lake Arrowhead, Cedar Pines Park, Valley of Enchantment, Crestline, Valley View Park, Joshua Tree, Homestead Valley, Oak Hills, Muscoy, Green Valley Lake, Morongo Valley and unincorporated areas near Yucca Valley

### Ventura County (about 23,139 customers)

- Fillmore
- Camarillo
- Simi Valley
- Santa Rosa Valley
- Ventura
- Unincorporated areas, including Sespe, Oak Village, north of Moorpark, Piru, Elkins Ranch Golf Course, Leesdale, north Fillmore, Santa Susana, Stauffer, Sycamore Canyon, Solromar, unincorporated areas near Piru and communities near Telegraph Road

### Riverside County (about 21,366 customers)

- Banning
- Beaumont
- Calimesa
- Hemet
- San Jacinto
- Menifee
- Moreno Valley
- Perris
- Unincorporated Riverside County, including the communities of Whitewater and Bonnie Bell, Banning Pass, Cabazon, Owl, portions of Desert Hills Outlet Mall, North Palm Springs, Gilman Hot Springs, Lakeview, Nuevo, Mons, Mead Valley, Eden Hot Springs, Mountain Center, Good Hope and unincorporated areas near Beaumont and Banning

### Orange County (about 7,250 customers)

- Rancho Santa Margarita
- Orange
- Unincorporated areas, including North Tustin

### Kern County (about 19,313 customers)

- Tehachapi
- Unincorporated areas, including Frazier Park, Lake of the Woods, Pine Mountain Club, Bodfish, Kernville, Wofford Heights, Lake Isabella, Camp Owens, Lebec, Bear Valley Springs, Stallion Springs, Keene, Golden Hills, Sand Canyon, Alpine Forest, Manolith, Weldon, Bella Vista, Monolith, Onyx, Canebrake, and unincorporated areas of Walker Basin and Kernville

### Mono County (about 13,963 customers)

- Mammoth Lakes
- Unincorporated areas near Bishop, including the community of Paradise and portion of Swall Meadows, Sunny Slopes, Mammoth Lakes (Trails, Core, North, Slopes), June Lake Village, Loop, Crestview, Mono Lake, Mono City, North Conway, Willow Springs, Bridgeport, Old Mammoth, Mammoth Lakes Basin, Lee Vining, Lee Vining Canyon, Falls Creek Tract and Bridgeport Valley to Twin Lakes Inyo County (about 131 customers)
- Unincorporated areas near Bishop, including Aspendell and Round Valley

### Tulare County (about 108 customers)

- Unincorporated areas, including Fairview and Johnsondale

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## More fire coverage from the Los Angeles Times

*L.A. County faces critical fire danger, possible power cuts as Santa Ana winds blow in*

*What makes the Santa Ana winds blow?*

*California's huge, humiliating power outages expose the vulnerabilities of PG&E's power grid*

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PLOS ONE

RESEARCH ARTICLE

# Identifying riparian climate corridors to inform climate adaptation planning

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## Abstract

Riparian habitats have been frequently identified as priority areas for conservation under climate change because they span climatic gradients and have cool, moist microclimates relative to surrounding areas. They are therefore expected to act as dispersal corridors for climate-induced species range shifts and to provide microclimatic refugia from warming. Despite recognition of these values, rigorous methods to identify which riparian areas are most likely to facilitate range shifts and provide refugia are currently lacking. We completed a novel analysis across the Pacific Northwest, USA, that identifies potential riparian corridors featuring characteristics expected to enhance their ability to facilitate range shifts and provide refugia. These features include large temperature gradients, high canopy cover, large relative width, low exposure to solar radiation, and low levels of human modification. These variables were used to calculate a riparian climate-corridor index using a multi-scale approach that incorporates results ranging in scale from local watersheds to the entire Pacific Northwest. Resulting index values for potential riparian corridors in the Pacific Northwest were highest within mountainous areas and lowest within relatively flat, lowland regions. We also calculated index values within ecoregions, to better identify high-value riparian climate corridors within the relatively flat, degraded areas where they may most contribute to climate adaptation. We found that high-value riparian climate-corridors are least protected in flat, lowland areas, suggesting that such corridors should be high priorities for future conservation effort. Our analysis provides critical information on valuable riparian climate-corridors to guide climate adaptation efforts (and riparian management and restoration efforts) in the Pacific Northwest, while offering a novel approach that may be applied to similar efforts in other geographies.

## Introduction

As climate change progresses and concern grows over the ability of species and ecosystems to adapt [1–2], considerable effort has been devoted to identifying areas on the landscape expected to promote biological resilience to change [3–5]. Riparian areas have been frequently

design, data collection and analysis, decision to publish, or preparation of the manuscript.

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identified as important features to conserve for climate adaptation [6–9], because they span the climatic gradients species are likely to follow as they track shifting areas of climatic suitability [10–12] and contain microclimates that are significantly cooler and more humid than immediately surrounding areas [13]. For these reasons, they are expected to provide dispersal corridors for species undergoing climate-induced range shifts [7,9] and microclimatic refugia from warming for species with limited movement capacities [14,5–6]. Riparian areas may also offer especially effective conservation umbrellas under climate change, because they disproportionately contribute to regional species richness [15–16], provide habitat for many upland species as well as riparian specialists [15–16], and directly contribute to the climate resilience of adjacent freshwater aquatic habitats [17–18]. Despite this recognition, few methods have been proposed for identifying priority riparian areas for climate adaptation.

Riparian areas are frequently prioritized in conservation planning efforts (e.g., [19–20]), but there are few examples of approaches aimed at identifying those that are most likely to promote climate adaptation. Available approaches for identifying riparian corridors to promote climate-induced range shifts include a conservation planning analysis for South Africa that included riparian corridors constructed by applying a fixed buffer around rivers connecting coastal to inland habitats to promote elevational species range shifts [21]. Similarly, riparian areas associated with 2$^{nd}$ order streams linking the Pacific Ocean to high elevations were prioritized in a climate adaptation analysis for California, USA [22]. In another analysis, a land facet corridor analysis aimed at promoting species range shifts in Arizona, USA, connected large blocks of natural habitat using riparian corridors identified by applying a fixed buffer around expert-identified streams and riparian habitats [23]. Most of these analyses used rivers as coarse proxies for riparian habitat, and none rigorously accounted for variability in riparian area quality, which we argue strongly influences the degree to which riparian areas may facilitate range shifts and provide refugia.

To address the need for a rigorous approach to identify priority riparian areas for climate adaptation, we completed a novel analysis that identifies potential riparian corridors expected to promote the ability of biodiversity to respond to climate change. Specifically, we developed a riparian climate-corridor index to quantify the degree to which riparian areas may promote range shifts and provide refugia, identifying those riparian areas that: 1) span large temperature gradients, 2) have high levels of canopy cover, 3) are relatively wide, 4) have low solar insolation, and 5) exhibit low levels of human modification. These variables were derived from the theoretical and empirical literature on species' responses to observed and projected climatic change. For example, riparian corridors that span large climatic gradients may help promote climate-induced range shifts from warmer to cooler areas [11–12]; riparian areas are already used as movement corridors for both riparian and upland species [24–26], and those spanning climatic gradients may offer particularly effective conduits for range migration, particularly across flat, degraded landscapes [27]. The effectiveness of such corridors would be further enhanced by high levels of canopy cover and greater riparian area width, features that have been shown to increase wildlife use of riparian areas as movement corridors [25], and to help moderate temperatures within riparian areas and promote the resilience of neighboring aquatic systems [17, 28]. Riparian corridors with lower exposure to solar insolation may also feature cooler temperatures and greater moisture [13, 29], increasing their value as microclimatic refugia [30–32]. Finally, riparian corridors with lower levels of human modification are likely to be more permeable to wildlife movement [33], while also being less vulnerable to exotic species invasion and other stressors that may inhibit species movements and reduce refugia quality [34].

Because these characteristics are likely to vary by the scale of analysis, and because scales of climate-induced range shifts and microclimatic refugia are likely to vary among species and

over time [35,14], we developed a multi-scale approach to calculating riparian climate-corridor index values that incorporates results ranging in scale from local watersheds to the entire Pacific Northwest, USA. We also evaluated the protected status of riparian climate-corridors to help inform potential conservation action for maintaining riparian climate-corridor networks. Our analysis may thus provide critical information for guiding riparian management and climate adaptation efforts in the Pacific Northwest, while offering a novel approach that may be applied to similar efforts in other geographies.

## Materials and methods

### Study area

We completed our analysis for the Pacific Northwest, USA (USGS Water Resource Region 17; Fig 1). The Pacific Northwest includes a relatively cooler, moister region between the Pacific Coast and Cascade Range that is dominated by evergreen temperate forest; and a relatively drier region between the Cascade Range and Rocky Mountains that experiences more pronounced seasonality in temperature and features more diversity in vegetation types, from mixed forest at higher elevations to sagebrush-steppe in more arid lowlands.

**Fig 1. Analysis extent.** We completed our analysis for the Pacific Northwest hydrologic region (Water Resource Region 17, in dark gray).

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## Analysis inputs

To identify high value riparian climate-corridors, we used a map of potential riparian areas identified by Theobald et al. [36], rather than a map of riparian vegetation. The potential riparian area map identifies the physical template where the dynamics of riparian vegetation are expected to occur, based on hydrological (stream discharge) and geomorphological (valley bottom shape) information rather than the (current) presence of riparian vegetation [36]. This 30 m data layer thus provides a comprehensive and consistent estimate of potential riparian area while avoiding many of the data gaps and inconsistencies [37] associated with existing maps of riparian vegetation derived from land cover (e.g., US LANDFIRE, US Fish & Wildlife Service National Wetland Inventory), which often have difficulty distinguishing riparian from non-riparian vegetation at 30 m resolution [37]. The potential riparian area dataset also provides key additional data layers (e.g., flow direction; see below) required by our analysis.

Our analysis aimed to identify the extent to which riparian corridors span large temperature gradients, have high levels of canopy cover, are relatively wide, have low exposure to solar radiation, and exhibit low levels of human modification. Our analysis thus included the following five variables (Table 1): mean annual temperature, canopy cover, riparian area width, potential relative radiation, and landscape condition.

We calculated mean annual temperature ($T$) as the 30-year mean of mean annual temperatures from 1961–1990, using a 90 m digital elevation model and the ClimateWNA tool [38], which extracts and downscales PRISM [39] monthly data and calculates climate variables for specific locations based on latitude, longitude, and elevation. For canopy cover ($C$), we used the percent tree canopy cover dataset for 2011 from the National Land Cover Dataset [40, 41]. We calculated potential riparian area ($A$), a measure of the width of potential riparian areas, directly from the 30 m potential riparian area data layer from Theobald et al. [36]. We used the 30 m National Elevation Dataset [42] to calculate potential relative radiation ($R$), a unitless measure of solar radiation that takes into account temporal changes in solar orientation as well as topographic shading from adjacent landforms [43]; such shading has been shown to contribute to lower temperatures in complex terrain [13–14]. We used the landscape condition ($L$) model [44] as a measure of the degree to which potential riparian areas have been affected by human activities. Although a more recent and higher-resolution dataset on human modification was available [45], we used $L$ to be consistent with the Western Association of Fish and Wildlife Agencies Crucial Habitat Assessment Tool [46].

**Table 1. Analysis variables and source data.**

| Analysis Variable | Base Layer | Base Layer Resolution | Year Represented by Base Layer | Base Layer Sources |
|---|---|---|---|---|
| Mean Annual Temperature ($T$) | PRISM Mean Annual Temperature (downscaled using Climate WNA) | 90 m | 1961–1990 (mean historical temperature) | Daly et al. [39] (http://prism.oregonstate.edu/), Wang et al. [38] (http://climatewna.com/) |
| Canopy Cover ($C$) | NLCD Percent Canopy Cover | 30 m (resampled to 90 m using bilinear interpolation) | 2011 | National Land Cover Dataset [40] |
| Riparian Area ($A$) | Potential Riparian Area | 90 m | 2009 (digital elevation model) | Theobald et al. [36] |
| Potential Relative Radiation ($R$) | Potential Relative Radiation (calculated using digital elevation model) | 30 m (resampled to 90 m using bilinear interpolation) | 2009 (digital elevation model) | This study, following methods of Pierce et al. [43], and using a digital elevation model from the National Elevation Dataset (http://ned.usgs.gov/). |
| Landscape Condition ($L$) | Landscape Condition | 270 m (resampled to 90 m using bilinear interpolation) | 2010 (roads); 2006 (development); 2001 and 2006 (landcover) | Western Association of Fish and Wildlife Agencies Crucial Habitat Assessment Tool [46], based on the NatureServe Landscape Condition Model [44] |

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## Calculating a riparian climate-corridor index

We calculated an index of riparian climate-corridor quality for individual, ecologically-relevant spatial units that we call "potential riparian corridors," which we define as the potential riparian area that runs longitudinally along a stream/river from the stream outlet (or mouth) up through the hydrologic network of a watershed, ending at the stream initiation point (or headwater). For each potential riparian corridor, we calculated a riparian climate-corridor index using three main steps.

First, we accumulated the values of four variables (*C*, *A*, *R*, *L*) from locations (cells) within potential riparian areas laterally (i.e., orthogonal to the neighboring stream) to the nearest cell along the central flow path that follows the mid-line of streams/rivers (Fig 2a).

Second, we accumulated the values longitudinally along the central flow path within the stream/river, from its outlet to its headwater (Fig 2b). We accumulated values upstream rather than downstream to simulate the process of upward range movement along riparian corridors, from watershed outlets toward higher-elevation headwaters. Accumulating upstream also allowed us to calculate index values for individual riparian corridors adjacent to a stream/river reach running between its headwater and watershed outlet, because accumulating downstream would result in a single accumulated index value for an entire watershed. Third, we used these accumulated variable values to calculate an index of climate adaptation quality for the riparian climate-corridor from the outlet to headwater. Representing potential riparian corridors using a raster representation (rather than stream line vectors) allowed us to account for subtle gradients and variations within potential riparian areas—vital information lacking in previous

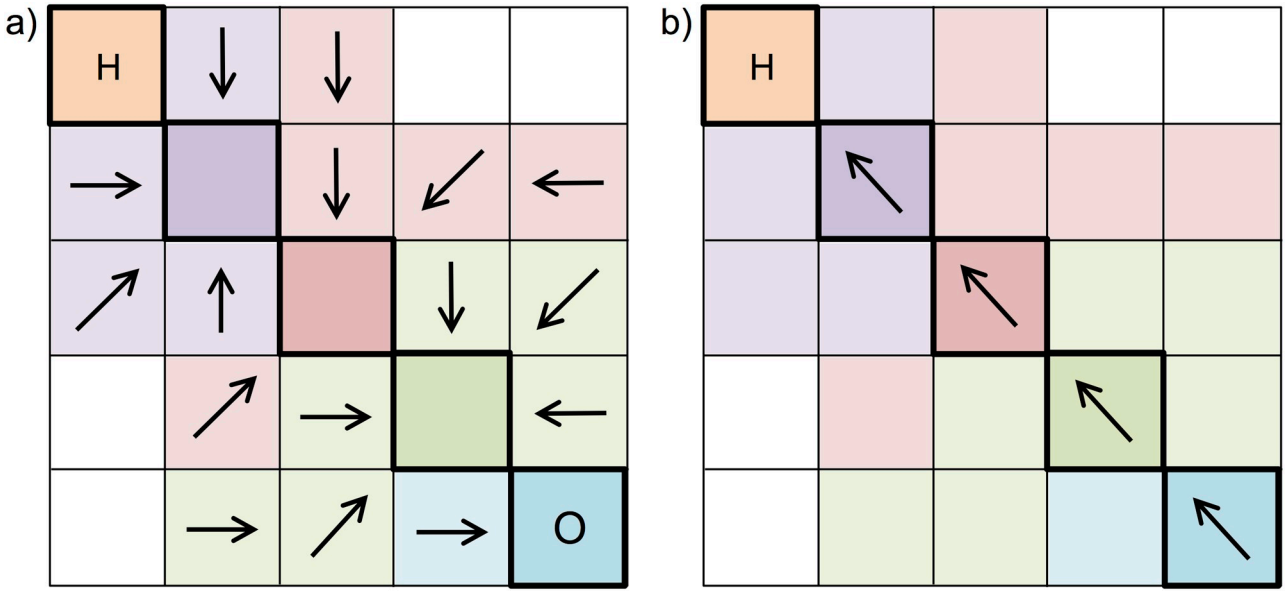


**Fig 2. Using Flow Direction, Flow Accumulation, Flow Length tools to calculate the riparian climate-corridor index for a potential riparian corridor.** a) For all potential riparian cells draining into a given cell in the streamline (outlined in bold, with it and all cells draining into it shown in the same color), we calculate, for each variable (*C*, *R*, *L*), the average value across the cells that contribute (accumulate) to the stream flow cell, and attribute this average value to the streamline cell (or the midline cell, for larger water bodies) using the Flow Direction and Flow Accumulation tools in ArcGIS. We calculate *A* as the number of potential riparian cells draining into the streamline cell. b) We then calculate, for each variable (*C*, *R*, *L*, *A*), the average value across all streamline cells from the outlet (O) to the headwater (H), and attribute this average value to the headwater using the Flow Length tool in ArcGIS. We also attribute a value for *T*, calculated as the absolute difference in temperature between the outlet and headwater cells. We then standardize (0–1) the average value for each variable (for equal weighting) and calculate the index, attributing this index value to the headwater cell. This is repeated for each downstream outlet until reaching the ocean, each time attributing the index value to the headwater cell. Each streamline cell is then given the average index value attributed to its upstream headwaters.

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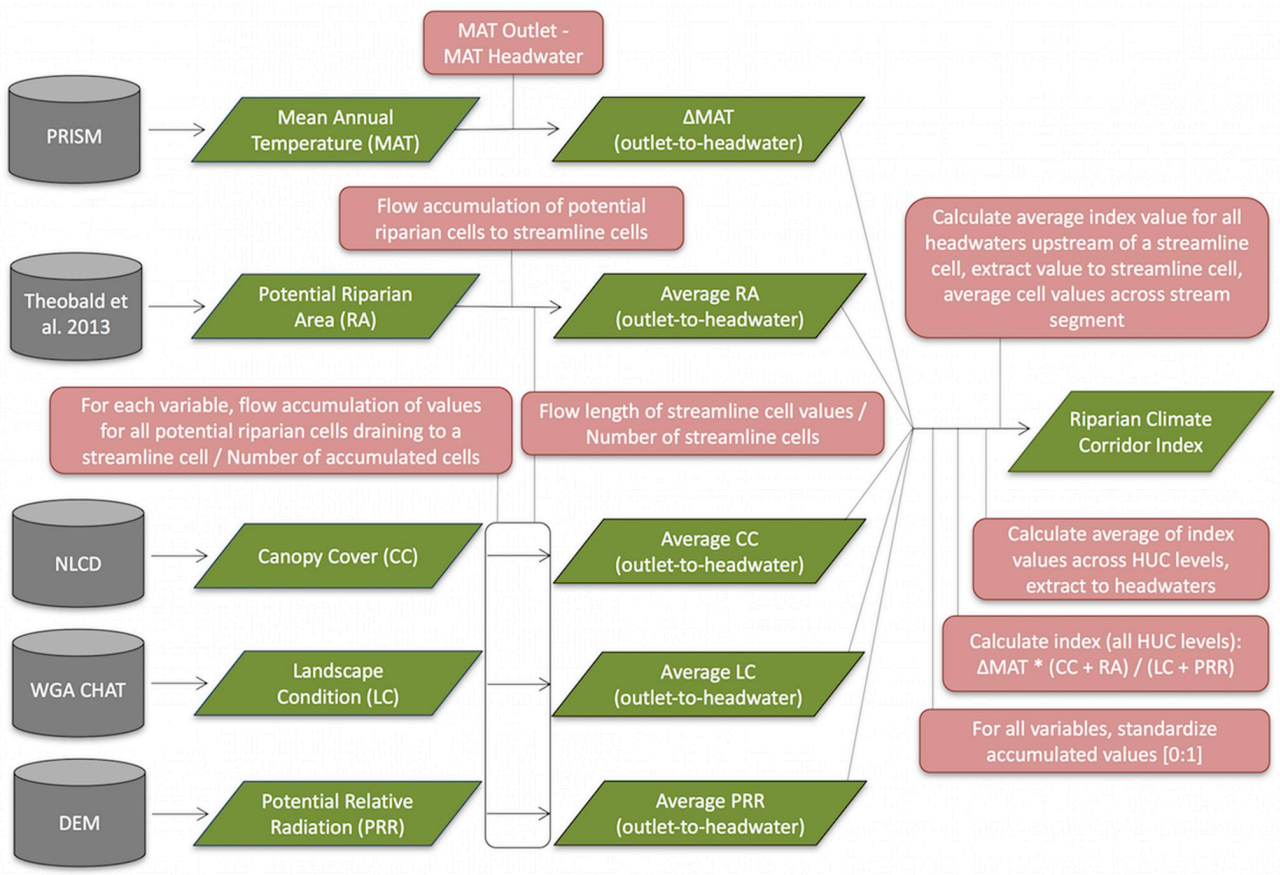


**Fig 3. Summary of modeling approach, including key inputs, outputs, and analysis steps.** Data sources are shown in gray, processing steps in pink, and inputs and outputs in green.

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studies. For rivers wider than 90 m, we excluded water cells when calculating variable values. Note that we represented spatial features, such as elevation and land cover, at 30 m resolution, but accumulated the up-scaled data at 90 m for computational purposes. A more detailed description of our analysis is provided below, and summarized in Fig 3.

**1. Accumulate values within potential riparian corridors laterally to the stream line.** We clipped the *C*, *R*, and *L* rasters to the extent of the potential riparian area. We then accumulated C, R, and L values along flow paths for all potential riparian cells draining into a given cell that represents the center of the stream line (i.e. the central flow path). That is, each cell located along the central flow path was attributed with the sum of the values for that variable for all the potential riparian cells that drain into it, using hydrologic tools in ArcGIS v10 software [47]. We then divided the accumulated value for each variable by the number of accumulated cells, so that, for each variable, each central flow path cell in the adjacent stream/river was ultimately attributed with the average variable value for its contributing potential riparian cells. The flow-accumulated area for the potential riparian area (*A*) was calculated in a similar manner, by accumulating the number of potential riparian cells draining into each central flow path cell in the adjacent stream/river. In cases where no potential riparian area cells drained into a central flow path cell, values for each variable were measured for only the central flow path cell itself, which was given an *A* value of 1.

**2. Accumulate values for each variable longitudinally from stream/river outlet to headwater.** We accumulated values along individual streamlines running from the watershed outlet to a stream's headwater, for each of the four variables (*C*, *A*, *R*, *L*). These accumulated values were then extracted to the central flow path cell at the stream/river's headwater, and divided by the number of contributing central flow path cells, to provide an average value for each variable for the associated potential riparian corridor. Mean annual temperature (*T*) was also extracted at each watershed outlet (or sink, in the case of closed basins) and for each headwater, and the difference between the two calculated and extracted to each stream/river's headwater. The average value for each variable was then divided by the largest value for that variable within the full study region, to standardize values to the range 0:1.

**3. Calculate riparian climate-corridor index for each watershed-scale riparian corridor.** We used the averaged, standardized values for each variable to calculate a Riparian Climate-Corridor Index for each watershed-scale riparian corridor, using the following formula:

$$Riparian\ \ Climate - Corridor\ \ Index = \Delta T \times [(C + A)/(R + L)]$$

Index values will thus be highest for those riparian corridors with the largest change in temperature (*T*) from outlet to headwater, highest percent canopy cover (*C*), greatest width (*A*), lowest exposure to solar radiation (*R*), and lowest level of human modification (*L*). Where $\Delta T$ was negative (indicating a higher temperature at the headwater than at the outlet), the index value was set to 0, to maintain higher index values for corridors leading from warmer to cooler areas across scales (see description of multi-scale approach, below). Our analysis is thus similar to other climate-gradient corridor approaches [11–12] in that it prioritizes corridors connecting warm areas to cool (in this case, headwater and outlets) using pathways that follow monotonic gradients (i.e., moving along gradients in only one direction, from warm to cool). All index values were extracted to the headwater associated with each potential riparian corridor.

**4. Account for scale effects.** We calculated a multi-scale, riparian climate-corridor index using the above procedure for riparian corridors within 6$^{th}$, 5$^{th}$, 4$^{th}$, 3$^{rd}$, 2$^{nd}$, and 1$^{st}$ field HUCs (i.e., nested watersheds, from smallest to largest, respectively). HUCs are hierarchical hydrologic unit codes (HUC) assigned to all watersheds in the US [48]; the watershed cataloguing system nests watersheds into progressively larger units, similar to Pfafstetter codes that are also used globally. Our method should thus be applicable to any similar watershed cataloguing system in other countries. This procedure resulted in up to six index values being extracted to each headwater, corresponding to the index values of progressively longer downstream potential riparian corridors adjacent to each stream/river from its headwater to its outlet for progressively larger watersheds, eventually terminating at the ocean (or sink, in the case of closed basins). We scaled each of these nested index values to the range (0:1) and averaged them (equally-weighted), so that the final index value extracted to each headwater would reflect the climate adaptation value of all of its downstream riparian corridors. Finally, we calculated, for each individual central flow path cell within streams/rivers, the average of the index values attributed to all of its upstream headwaters. The final index values for each flow path cell within streams/rivers thus reflect the degree to which its adjacent potential riparian area cells are expected to help facilitate range shifts and provide refugia, from local to regional scales.

We also calculated a measure of riparian climate-corridor quality for entire watersheds by calculating the average of index values for all riparian climate-corridors within a given HUC. To account for differences in index values among ecoregions, and to more easily identify the highest quality riparian climate-corridors within each ecoregion, we binned all index values into 5 equal-area quintiles within each Level III ecoregion [49].

### GAP analysis and sensitivity testing

We evaluated the degree to which high-value riparian climate-corridors identified by our analysis fall within currently designated protected areas by measuring the GAP status of riparian climate-corridors within 1) the top quintile of index scores, 2) the top two quintiles, and 3) all quintiles, for both the entire Pacific Northwest and within ecoregions. GAP status codes are provided by the US Geological Survey's Gap Analysis Program (GAP), and measure the degree to which lands in the US are managed for conservation [50]. Code 1 and 2 denote the highest degree of management for conservation (and meet the IUCN definition of protected), while Code 3 is given to lands that support multiple uses, including resource extraction. Code 4 lands are unprotected or have unknown management intent.

We also tested the sensitivity of the riparian climate-corridor index to the inclusion of individual input variables by removing individual variables one at a time, re-calculating the index, and measuring resulting differences across the study area. We also calculated correlation coefficients among these index values, as well as correlation coefficients among individual variables, to aid in interpretation of results.

## Results

### Riparian climate-corridor index values

We found that the climate adaptation potential of riparian corridors varies considerably, both across the Pacific Northwest (Fig 4) and within individual watersheds (Fig 5). Index values ranged from 0 to 0.83 (Fig 6), with the highest index values found in mountainous areas (e.g., the Cascade Range), and the lowest index values found in relatively flat, lowland regions such as the Columbia Plateau. Mountainous areas exhibited higher $\Delta T$ scores, on average, as well as higher canopy cover ($C$), solar insolation ($R$), and landscape condition (S1–S4 Figs). These effects were amplified by positive correlations among all input variables but riparian area (S5 Fig): relatively flat areas with low $\Delta T$ tended to also have lower canopy cover ($C$), were in poorer landscape condition ($L$), and had higher solar insolation ($R$). Indeed, removing $\Delta T$ from the index calculation resulted in a spatial pattern similar to that seen when the calculation included $\Delta T$ (Fig 7); including $\Delta T$ generally reinforced the pattern of lower values in areas with gentler topographic relief (often near outlets) and higher values in mountains (often near headwaters).

Most potential riparian corridors had relatively low index values (Fig 6). The relatively high number of potential riparian corridors with index values equal to 0 is due in large part to the relatively cool temperatures of the Pacific Northwest coast; many interior headwaters have warmer mean annual temperatures than their streams' coastal outlets. Because negative $\Delta T$ values were converted to zero and $\Delta T$ is multiplied by the rest of the index, such potential riparian corridors receive a zero value, though they may otherwise be of high quality (Fig 7). For example, the low index scores received by otherwise high-quality riparian areas in the western Olympic Peninsula were due to negative or relatively low $\Delta T$ between coastal stream outlets and headwaters (Fig 7, S1 Fig).

Areas with no headwaters (and thus no index scores) were seen in regions lacking surface water due to high aridity and/or high soil permeability (Fig 4).

### GAP analysis and sensitivity testing

We found that riparian climate-corridors varied regionally in their level of protection (Fig 8). For riparian climate-corridors with the highest 20% of index scores, 35.5% were fully protected (GAP status 1–2) and 50.4% were partially protected (GAP status 3) across the Pacific

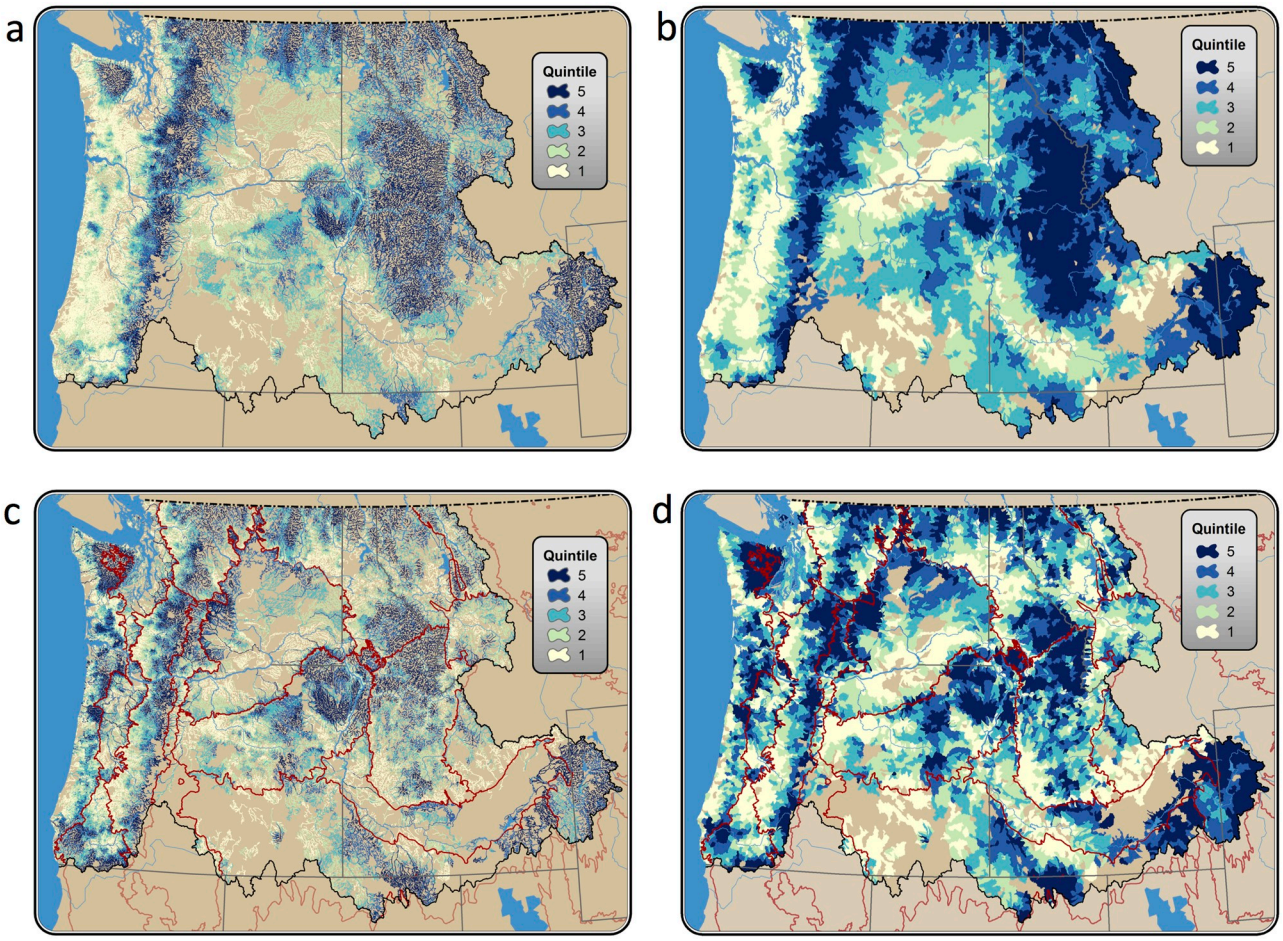


**Fig 4. Riparian climate-corridor index values for the Pacific Northwest.** Values are averaged across nested watershed scales (6th to 1st field HUCs), attributed to streamlines associated with potential riparian corridors. Values are shown by quintile for the Pacific Northwest, USA (panels a and b), and within ecoregions (panels c and d); and for both individual riparian corridors (panels a and c) and averaged across 6th field HUCs (panels b and d).

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Northwest. Within ecoregions, GAP status of riparian climate-corridors with the highest 20% of index scores varied from 83.8% fully protected and 14.6% partially protected in the North Cascades, to 1.3% fully protected and 18.8% partially protected in the Columbia Plateau.

We found that riparian climate-corridor index values were relatively insensitive to individual input variables (Fig 7). Removal of individual variables from the index calculation resulted in little change to index scores across the study area, resulting in an average change in index values of -0.0126 for removal of mean annual temperature ($\Delta T$), +0.0051 for landscape condition (L), -0.0168 for canopy cover ($C$), -0.0607 for riparian area ($A$), and -0.1154 for potential relative radiation ($R$). Given the strong correlations among index variable values and elevation (i.e., that relatively flat areas with low $\Delta T$ also have lower canopy cover ($C$) and landscape condition ($L$), and higher solar insolation ($R$)), variable exclusion generally resulted in decreased values in mountainous areas and increased values in lower-elevation areas. Exclusion of $R$ had a slightly stronger effect on index values in mountainous areas (lowering index values), and exclusion of $T$, $C$, and $L$ had a slightly stronger effect on lower-elevation coastal areas (increasing values).

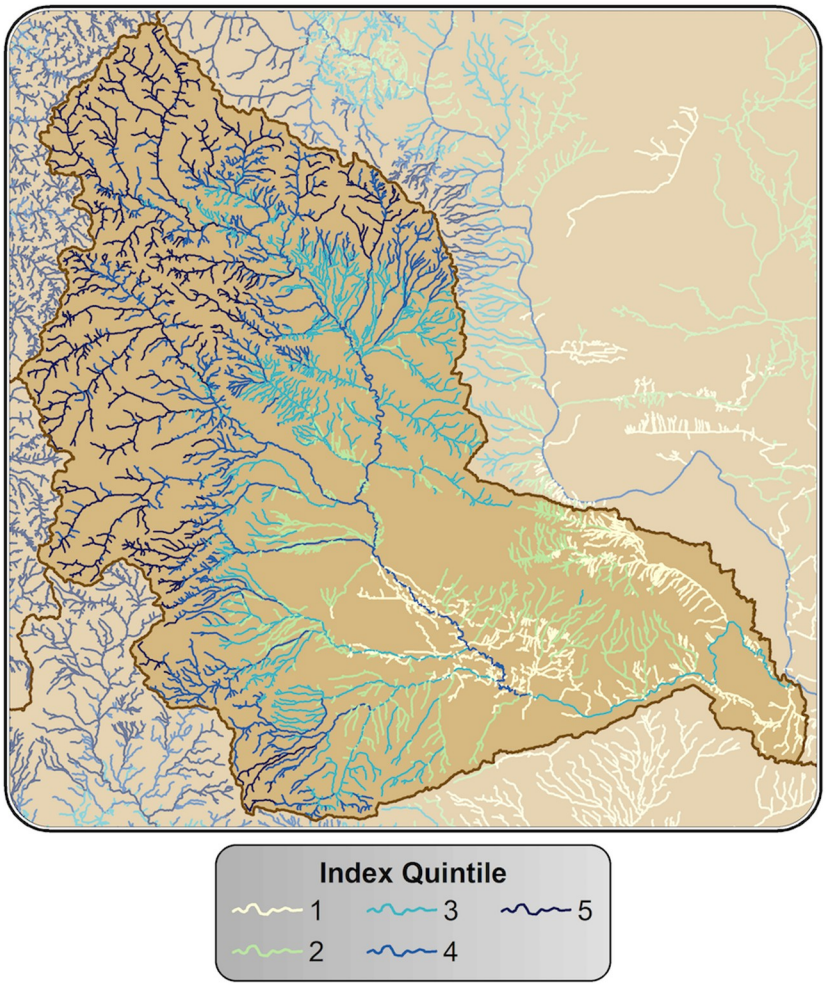


**Fig 5. Riparian climate-corridor index values shown for an individual watershed.** Values are shown by quintile and attributed to streamlines associated with potential riparian corridors.

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## Discussion

Our analysis identified potential riparian corridors that span climatic gradients, have high canopy cover, low levels of solar exposure, low levels of human modification, and are relatively wide—characteristics expected to facilitate climate-induced range shifts and provide micro-climatic refugia. Not surprisingly, we found that potential riparian corridors in mountainous regions—which tend to be steep, forested, topographically shaded, and have low levels of human modification—had the highest riparian climate-corridor index values. We also found that potential riparian corridors in lowland areas—which tend to be flat and have low canopy cover, less topographic shading, and high levels of human modification—had the lowest values (Fig 4a and 4b). Because of the correlations of temperature with other variables, change in temperature—which we had expected to be a key variable for identifying riparian corridors with strong climatic gradients—in fact had a relatively modest impact on index scores (Fig 7), generally reinforcing the pattern of lower index values in areas with gentler topographic relief and higher values in mountains. The index is thus robust to our coarse approach to measuring temperature gradients along riparian corridors.

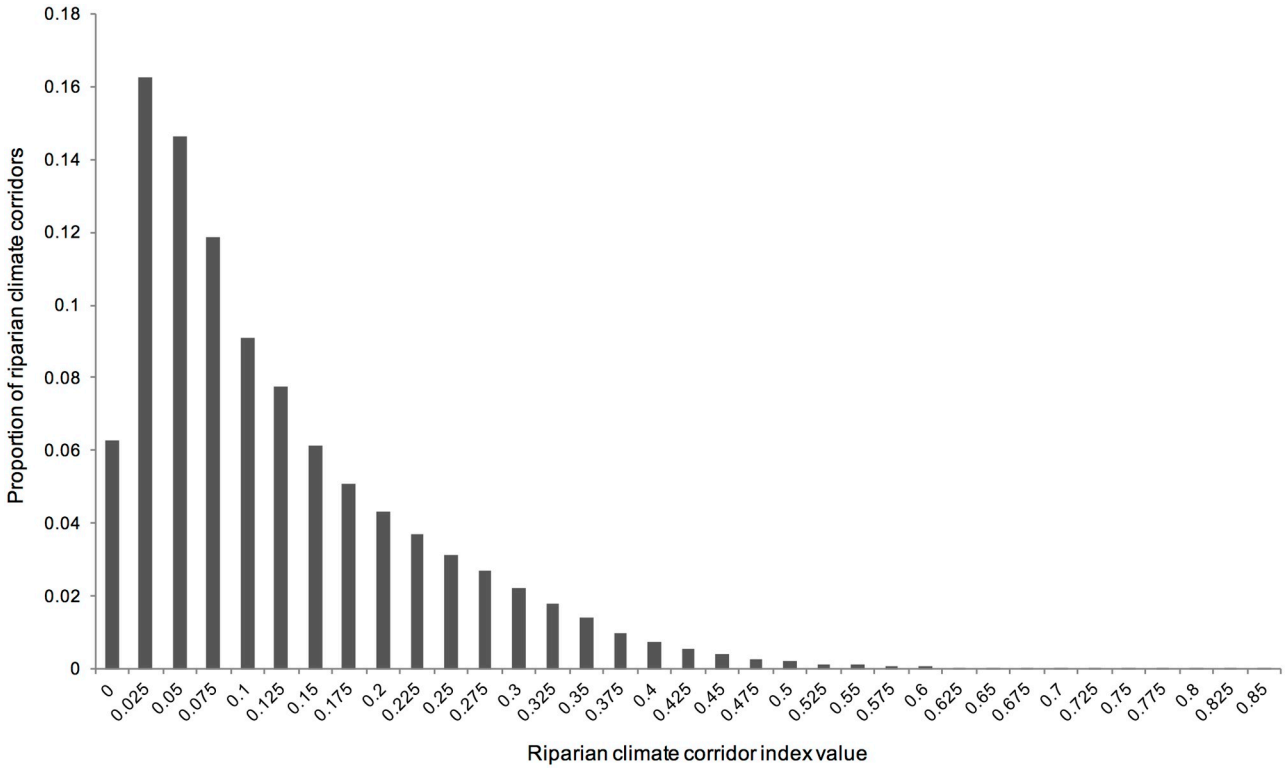


**Fig 6. Distribution of riparian climate-corridor index values.** Shown for all watershed-scale riparian corridors in the Pacific Northwest.

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We also found that relatively flat and highly modified ecoregions (e.g., the Columbia Plateau and Puget Lowlands ecoregions; Fig 4c and 4d) had the least protected high-scoring riparian climate-corridors among Pacific Northwest ecoregions (Fig 8). High-scoring riparian climate-corridors in these areas thus suggest immediate priorities for conservation action (e.g., protection or restoration), as they may provide some of the best adaptation opportunities in flat, highly modified landscapes that may limit species range movements and persistence in microclimatic refugia. We also found that a large number of otherwise high-quality potential riparian corridors along the coast received low index scores, because their interior headwaters have warmer mean annual temperatures than their streams' cooler, coastal outlets. These results emphasize that our index is designed to identify riparian climate-corridors expected to promote species range shifts from warmer to cooler areas, which may in some cases result in low scores for corridors that have high conservation value under static or current climates.

Index values for riparian climate-corridors along large rivers (e.g., the Columbia River) often had higher values than corridors within nearby lower-order streams (e.g., headwater streams). This is because higher-order streams frequently have tributaries at higher elevations; riparian climate-corridors associated with these higher-elevation tributaries tend to have relatively high index values, and the index values of riparian climate corridors along higher-order streams incorporate these upstream values. The high index values of riparian climate-corridors along higher order streams thus reflect their connectivity to high-scoring upstream corridors, and thus their capacity to promote range shifts and provide access to climatic refugia at a regional scale. Indeed, shorter riparian corridors, such as those that would be found along headwater streams, have been shown to be more effective at promoting species movements [51]. Thus, the trade-off of this multi-scale approach—designed to accommodate diverse

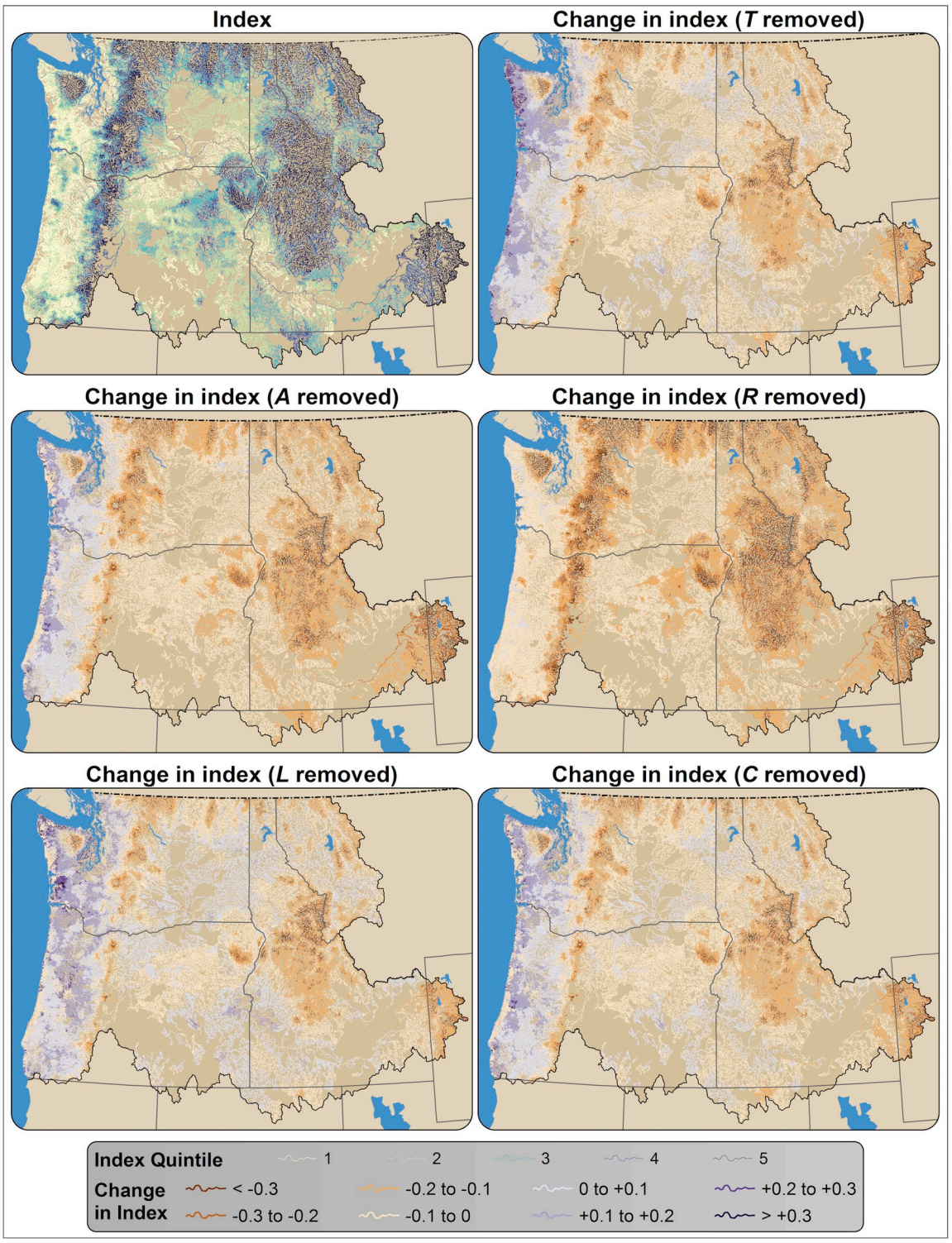


**Fig 7. Sensitivity of riparian climate-corridor index values to individual analysis variables.** Panels show the index with all variables included (top left), and the index with change in mean annual temperature (*T*) removed, with riparian area (*A*) removed, with potential relative radiation (*R*) removed, with landscape condition (*L*) removed, and with canopy cover (*C*) removed.

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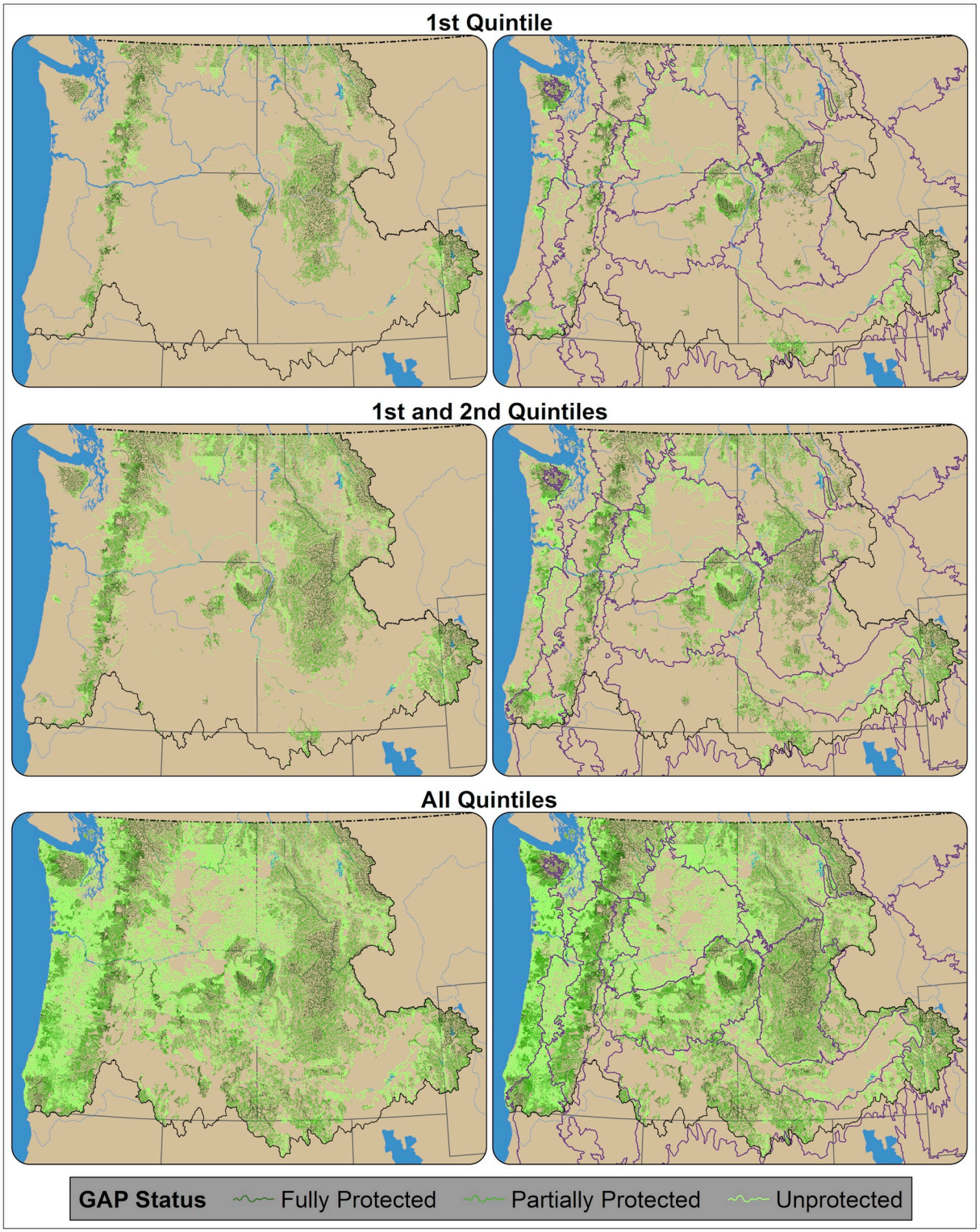


**Fig 8. GAP status of riparian climate-corridors.** GAP status is shown for riparian corridors within the top quintile of riparian climate-corridor index values (top row), top two quintiles (middle row), and all quintiles (bottom row); by both the entire Pacific Northwest (left column) and within ecoregions (right column). GAP status is shown for fully protected (GAP status 1 and 2; forest green), partially protected (GAP status 3; kelly green), and unprotected (GAP status 4; lime green) riparian climate-corridors.

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species with needs for movement and refugia at a range of scales—is its potential to overlook riparian climate-corridors that may be valuable at a more local scale, but do not meaningfully contribute to broader-scale, regional adaptation. Identifying riparian climate-corridors with high index values within ecoregions (Fig 4c and 4d) or local watersheds (S6–S10 Figs) may help address needs for more local-scale prioritization.

We recommend considering several caveats when applying the riparian climate-corridor index. First, this approach only indirectly accounts for connectivity along riparian corridors; while index values will decrease with increasing human modification along a corridor, the effect of local but severe movement barriers (e.g., towns, cliffs) on index values could be muted if human modification is low elsewhere along the corridor, particularly at broader scales. The analysis could thus be improved by incorporating explicit connectivity measures that sufficiently penalize high-resistance, local barriers that could sever connectivity; a range of connectivity modeling approaches could be adapted for this purpose (e.g., [52]). The analysis could also be improved by further validating analysis inputs and assumptions, such as empirically measuring canopy cover and solar insolation across riparian areas and testing their influence on temperature, and, ultimately, range shifts and refugia. Future comparison of our index to other indices of riparian quality (e.g., [53]) would also aid in interpretation of results. Thus, we recommend using this analysis as a means of identifying priority riparian areas for additional evaluation (e.g., field validation, comparison with other data sets, integration with other conservation values) before making decisions regarding conservation action.

We also recognize the scaling challenges in mapping riparian vegetation and modeling potential riparian areas. Our analysis provides estimates of potential riparian climate-corridors at (>90 m) due to data resolution and computation limitations. Future work can apply our approach using high resolution data that have (or will likely) become available. An additional caveat is the risk of unintended negative consequences (e.g., spread of invasive species or disease) by protecting or restoring riparian climate corridors to promote species movements. Our analysis reduces this risk by prioritizing those riparian areas that are in good condition, and therefore expected to be less vulnerable to invasion. Further, previous research has shown that the benefits of corridors outweigh potential negative effects [54], including potential risks related to climate-induced range shifts [55]. Indeed, the synergistic threats of habitat loss, fragmentation and climate change present an urgent need to restore landscape features such as riparian corridors that have historically provided natural conduits for species movement.

Although riparian areas are expected to provide critical movement corridors and refugia under climate change [6–7,9], they are also among the most threatened habitats in many regions [56]. Our analysis offers a first step toward identifying, for large regions, those riparian areas most likely to promote species' ability to respond to climate change, as well as those that may be most vulnerable to climate change and in need of restoration measures. Such information may offer valuable guidance for future investments in riparian protection and restoration as part of climate adaptation efforts.

## Supporting information

**S1 Fig. Mean annual temperature (*T*), based on the 30-year mean of mean annual temperatures from 1961–1990, using a 90 m digital elevation model and the ClimateWNA tool [34], which extracts and downscales PRISM [35] monthly data and calculates climate variables for specific locations based on latitude, longitude, and elevation.**
(TIFF)

**S2 Fig. Canopy cover (*C*), based on the percent tree canopy cover dataset from the National Land Cover Dataset [36].**
(TIFF)

**S3 Fig. Potential relative radiation (*R*), a unit-less measure of solar radiation that takes into account temporal changes in solar orientation as well as shading effects from neighboring topography [38], based on a 30 m digital elevation model from the National Elevation Dataset [36].**
(TIFF)

**S4 Fig. Landscape condition (*L*), provided by the Western Governors' Association's Crucial Habitat Assessment Tool (WGA 2013) as a measure of the degree to which potential riparian areas have been affected by human activities using the landscape condition model [39], where higher values correspond to lower landscape intactness.**
(TIFF)

**S5 Fig. Riparian area (*A*), based on the potential riparian area data layer from Theobald et al [32].**
(TIFF)

**S6 Fig. Riparian climate-corridor index values averaged across individual watersheds ($6^{th}$ field HUCs).**
(TIFF)

**S7 Fig. Riparian climate-corridor index values averaged across individual watersheds ($5^{th}$ field HUCs).**
(TIFF)

**S8 Fig. Riparian climate-corridor index values averaged across individual watersheds ($4^{th}$ field HUCs).**
(TIFF)

**S9 Fig. Riparian climate-corridor index values averaged across individual watersheds ($3^{th}$ field HUCs).**
(TIFF)

**S10 Fig. Riparian climate-corridor index values averaged across individual watersheds ($2^{nd}$ field HUCs).**
(TIFF)

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**Project administration:** Meade Krosby.

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**Visualization:** Robert Norheim.

**Writing – original draft:** Meade Krosby, David M. Theobald.

**Writing – review & editing:** Meade Krosby, David M. Theobald, Robert Norheim, Brad H. McRae.

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# Health Effects of the 2003 Southern California Wildfires on Children

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*Rationale:* **In late October 2003, Southern California wildfires burned more than 3,000 km$^2$. The wildfires produced heavy smoke that affected several communities participating in the University of Southern California Children's Health Study (CHS).**

*Objectives:* **To study the acute effects of fire smoke on the health of CHS participants.**

*Methods:* **A questionnaire was used to assess smoke exposure and occurrence of symptoms among CHS high-school students (n = 873; age, 17–18 yr) and elementary-school children (n = 5,551; age, 6–7 yr), in a total of 16 communities. Estimates of particulate matter ($PM_{10}$) concentrations during the 5 d with the highest fire activity were used to characterize community smoke level.**

*Main Results:* **All symptoms (nose, eyes, and throat irritations; cough; bronchitis; cold; wheezing; asthma attacks), medication usage, and physician visits were associated with individually reported exposure differences within communities. Risks increased monotonically with the number of reported smoky days. For most outcomes, reporting rates between communities were also associated with the fire-related $PM_{10}$ levels. Associations tended to be strongest among those without asthma. Individuals with asthma were more likely to take preventive action, such as wearing masks or staying indoors during the fire.**

*Conclusions:* **Exposure to wildfire smoke was associated with increased eye and respiratory symptoms, medication use, and physician visits.**

**Keywords:** air pollution; asthma; sore throat; wheezing

**AT A GLANCE COMMENTARY**

**Scientific Knowledge on the Subject**

Adverse effects of fire smoke are known, but results in children are inconsistent due to a lack of large population-based studies.

**What This Study Adds to the Field**

The study quantifies effects of fire smoke on eye, upper, and lower respiratory symptoms. It gives first evidence of benefits of preventive actions.

In October 2003, a series of devastating wildfires burned in Southern California. The hot and dry Santa Ana winds encouraged the spread of fires across several locations to the north, east, and south of the Los Angeles metropolitan area, and dense plumes of smoke dominated much of the area for several days. Local air-quality monitors recorded hourly particulate matter concentrations approaching 1,000 μg/m$^3$ particles of aerodynamic diameter up to 10 μm ($PM_{10}$); these levels were 10 to 20 times the typically observed ambient levels (1, 2). The fires occurred over a wide geographic area, over a 480-km swath affecting six Southern California counties (Ventura, Los Angeles, San Bernardino, Riverside, Orange, and San Diego). The fires consumed more than 3,100 km$^2$ (750,000 acres) and destroyed 3,640 homes, 33 commercial properties, and 1,141 other structures (including several regional air-monitoring stations).

Most wildfire investigations focus on short-term changes in hospital admissions or on segments of the population believed to be especially sensitive to respiratory stress, such as patients with chronic obstructive lung disease (COPD) or asthma, or on those individuals especially prone to exposure, such as firefighters (3, 4). Medical surveillance data from San Diego County revealed significant increases in hospital emergency room visits for asthma, respiratory problems, and eye irritation during the 2003 fire period (5). Population-based investigations of the acute respiratory health effects of fire smoke on children's health have been limited and based on small samples. The lack of data may be contributed, in part, to the logistical challenge of implementing population-based studies during fire emergencies. Australian researchers investigated the health effects of bush fires and reported increased evening wet cough among a panel of 32 children with asthma but nonsignificant results for wheeze and β-agonist use (6). $PM_{10}$ peaks were much lower (130 μg/m$^3$) than in the 2003 California fires. Associations of fire smoke and evening peak flow were also not conclusive (7). In Asia, the large 1997 fires resulted in an increased use of health services (4) and higher mortality rates both among infants and adults (8).

The Southern California fires offered a unique opportunity to conduct a population-based, large-scale investigation of the health consequences of the smoke from wildfires on children's health. The region affected by the wildfires included several communities participating in a long-term ongoing health study of California schoolchildren, the University of Southern California Children's Health Study (CHS) (9, 10). The goal of the CHS is to understand the contribution of long-term or lifetime exposure to ambient air pollution to children's respiratory health (9–11). Initial cohorts of children were recruited (1993 and 1996) from 12 communities across six Southern California counties. In 2002, an additional cohort of kindergarten and first-grade children

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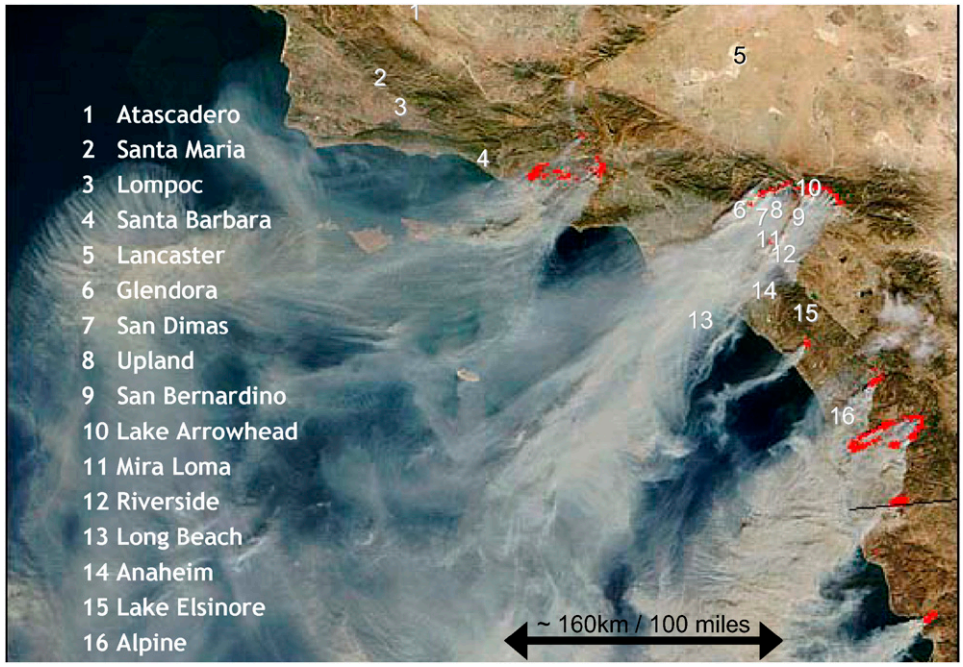


*Figure 1.* Satellite image of Southern California taken on October 24, 2003, showing the smoke plumes from numerous fires. Locations of the 16 Children's Health Study communities participating in the fire study are *highlighted*. Image courtesy of MODIS Rapid Response Project at NASA/GSFC.

(aged 5 to 6 yr) were enrolled from 13 partly overlapping communities (10). At least 12 of the 16 cohort communities were either directly affected by the fire (i.e., the community was the site of fire damage and human evacuation) or indirectly affected (by dense smoke covering the community). Figure 1 presents the cohort study towns in a satellite image of the wildfire areas taken in late October 2003.

To assess the effects of the wildfires, we implemented a questionnaire-based investigation of fire smoke exposure and symptoms for two of the existing and accessible study cohorts (12th-grade high-school students, and first- and second-grade elementary-school children). The availability of extensive sociodemographic and health data among this large sample of children offered a unique opportunity to efficiently investigate and quantify the health consequences of fire smoke exposure in both children with asthma and nonasthmatic children. Some of the results of this study have been previously reported in the form of an abstract (12).

## METHODS

The CHS methods have been published elsewhere. Details about the fire study are provided online. In brief, the CHS consists of repeated annual health assessments to monitor the course of respiratory health. The fire questionnaire study focused on participants of two ongoing CHS cohorts, including one cohort of high-school students (17 to 18 yr old during the fire), originally enrolled in 1996, and a cohort of elementary-school children (aged 6 to 7 yr), recruited in 2002. The older student cohort included high schools from the 12 (9, 10) original CHS communities and the elementary-school cohort involved 13 communities (nine of which were the same) (10). The study protocol was approved by the institutional review board for human studies at the University of Southern California, and written, informed consent was provided by participating students and a parent or legal guardian of minors.

The 2003 Southern California fires peaked between October 20 and November 2. During November–December 2003, the high-school students and the parents of the elementary-school children received the fire questionnaire by mail (*see* online supplement) and/or during the first 6 mo in 2004 as an annex activity of the ongoing CHS. The reporting period referred to the "two weeks of the October 2003 fire period." Although the first page of the fire questionnaire asked about health-related problems, the second page referred to exposure to fire smoke and personal measures taken to modify this exposure (including evacuation, wearing of masks, reduction in time spent outdoors, and changes in physical activity). To quantify exposure duration, questionnaire response categories included the following: "not at all," "1–2 d," "3–5 d," "6–10 d," or "all days" (i.e., up to 2 wk).

Objective smoke measurements (i.e., $PM_{10}$ [U.S. Environmental Protection Agency–approved Federal Reference Methods to quantify $PM_{10}$]) were available only on the community rather than on an individual level. $PM_{10}$ was the strongest marker of fire smoke pollution (1, 2). High concentration periods lasted approximately 5 d; thus, we used the 5-d mean $PM_{10}$ level to characterize fire smoke. Missing air-quality data required estimation procedures of the 5-d average $PM_{10}$. Five-day average $PM_{10}$ concentrations were estimated for 5 of the 16 communities. San Dimas, Glendora, and Anaheim had all 5 d (October 24–28) estimated, and San Bernardino had 4 d (October 25–28) estimated. Because Alpine was directly affected by the fires from October 26 to 28, $PM_{10}$ concentrations at Alpine were averaged over the 3 fire days with 2 d estimated (October 27–28). For more details, *see* text and Table E1 in the online supplement and Reference 1.

### Statistical Analyses

To investigate the association between fire smoke exposure and symptoms, we chose multilevel approaches to distinguish within-community differences in exposure from the contrasts between communities. We used the reported "smell of fire smoke indoors" as the primary measure of exposure. We created two components of reported exposure response. The first was a between-community measure, derived from the community-specific mean response. The second was a within-community response, created by subtracting the community mean from the individual response, using a mixed-effects model with a logistic link. As described in the online supplement, the five exposure categories were combined into three levels, providing comparison across the following groups of "fire smoke smelled": no fire smoke, fire smoke smelled 1 to 5 d, and fire smoke smelled 6 d or more.

The first set of analyses was based on the reported levels of fire smoke smelled at home indoors, reflecting the change in symptoms due to an increase in the duration of (perceived) fire smell. In a second set of models, we replaced the reported community mean fire smoke response with the ambient 5-d mean $PM_{10}$. Thus, these between-community estimates reflected the change in symptoms for a change in ambient $PM_{10}$ during the 5 most extreme days of fire smoke.

**TABLE 1. HIGH-SCHOOL STUDENTS AND PARENTS (ELEMENTARY-SCHOOL CHILDREN) RESPONDING TO THE FIRE QUESTIONNAIRE WITHIN 8 WEEKS OF THE FIRE (EARLY RESPONSE, NOVEMBER/DECEMBER 2003) AND TOTAL RESPONSE (INCLUDING JANUARY TO JUNE 2004 DURING CHILDREN'S HEALTH STUDY HEALTH VISITS)**

| | High-School Students (17–18 yr old) | | | Elementary-School Children (6–7 yr old) | | |
|---|---|---|---|---|---|---|
| Community | Baseline Population | Early Response (2003), n (%) | Total Response (2003/04), n (%) | Baseline Population | Early Response (2003), n (%) | Total Response (2003/04), n(%) |
| Alpine | 75 | 35 (46.4) | 70 (93.3) | 397 | 165 (41.5) | 299 (75.3) |
| Anaheim | — | — | — | 419 | 90 (21.4) | 251 (59.9) |
| Atascadero | 74 | 68 (91.8) | 70 (94.5) | — | — | — |
| Glendora | — | — | — | 466 | 228 (48.9) | 374 (80.2) |
| Lake Arrowhead | 70 | 28 (40.5) | 67 (95.7) | 401 | 163 (40.6) | 301 (75.0) |
| Lake Elsinore | 66 | 23 (35.3) | 62 (93.9) | 386 | 254 (65.8) | 254 (65.8) |
| Lancaster | 64 | 27 (41.5) | 61 (95.3) | — | — | — |
| Lompoc | 80 | 32 (40.0) | 78 (97.5) | — | — | — |
| Long Beach | 85 | 35 (41.6) | 79 (92.9) | 366 | 87 (23.7) | 239 (65.3) |
| Mira Loma | 64 | 51 (78.4) | 62 (96.8) | 510 | 280 (54.9) | 286 (56.0) |
| Riverside | 69 | 53 (76.8) | 67 (97.1) | 439 | 150 (34.1) | 285 (64.9) |
| San Bernardino | — | — | — | 410 | 94 (22.9) | 255 (62.1) |
| San Dimas | 74 | 39 (52.7) | 74 (100) | 393 | 169 (43.0) | 213 (54.1) |
| Santa Barbara | — | — | — | 468 | 166 (35.4) | 360 (76.9) |
| Santa Maria | 66 | 25 (39.0) | 62 (93.9) | 470 | 125 (26.5) | 311 (66.1) |
| Upland | 86 | 39 (46.4) | 82 (95.3) | 426 | 198 (46.4) | 347 (81.4) |
| Total | 873 (100) | 455 (52.4) | 834 (95.5) | 5,551 (100) | 2,169 (39.0) | 3,775 (68.0) |

The final models included those covariates that were independent predictors and/or confounders in the models of at least one symptom, namely sex, ethnicity, educational level of parents, asthma status before the fire (physician-diagnosed asthma), and cohort (high-school vs. elementary-school cohort). A p value of 0.05 or less was considered statistically significant. In addition, all analyses were stratified by asthma status. All analyses were conducted with the statistical software SAS/STAT, version 9 (2002; SAS Institute, Cary, NC).

## RESULTS

Table 1 summarizes the study populations and participation. High-school students' participation rates during the first 8 wk (2003) reached 52.4%, whereas only 39.0% of the parents (younger cohort) returned the mail-in questionnaire. The extended distribution of the fire questionnaire during 2004 strongly improved response rates, ultimately reaching 95.5% in the older and 68.0% in the younger cohort.

Table 2 summarizes the distribution of reported fire exposure and the ambient levels of measured or estimated $PM_{10}$ (*see* Methods). Both the subjective and objective measures of fire smoke showed that communities not directly affected by local fires suffered substantial smoke exposure (e.g., Mira Loma, Riverside, and Anaheim).

Table 3 summarizes the prevalence of the reported outcomes, by cohort and asthma status. As expected, prevalence rates were much higher among individuals with asthma. Dry cough, medication, and physician visits were more frequently reported by parents of elementary-school children, whereas high-school students were more likely to report eye symptoms. Home loss due to fire was reported by 35 (0.75%) study participants. In Alpine and

**TABLE 2. PREVALENCE OF REPORTED SMELL (%) OF FIRE SMOKE INDOORS (BY COHORT), 5-DAY MEAN $PM_{10}$ DURING THE FIRE PERIOD,* AND LONG-TERM AMBIENT $PM_{10}$ IN THE 16 COMMUNITIES**

| | High-School Students (*n = 834*) | | | | Elementary-School Children (*n = 3,775*) | | | | $PM_{10}$ in $\mu g/m^3$ | |
|---|---|---|---|---|---|---|---|---|---|---|
| Town | Not at All | 1–2 d | 3–5 d | ⩾ 6 d | Not at All | 1–2 d | 3–5 d | ⩾ 6 d | 5-d Mean (fire period) | 1992–2003, Mean |
| Alpine | 27.1 | 21.4 | 20.0 | 31.4 | 21.1 | 23.8 | 19.1 | 33.6 | 201 | 25.3 |
| Anaheim | — | — | — | — | 64.4 | 10.2 | 6.4 | 13.6 | 132 | 36.9 |
| Atascadero | 97.1 | 1.4 | 0 | 0 | — | — | — | — | 52 | 21.3 |
| Glendora | — | — | — | — | 54.4 | 20.9 | 8.4 | 13.9 | 158 | 32.5 |
| Lake Arrowhead | 63.6 | 14.6 | 12.1 | 10.6 | 57.7 | 20.1 | 10.4 | 9.4 | 172 | 19.8 |
| Lake Elsinor | 64.5 | 17.7 | 3.2 | 9.7 | 59.0 | 16.1 | 10.8 | 11.7 | 104 | 35.6 |
| Lancaster | 45.9 | 29.5 | 11.5 | 9.8 | — | — | — | — | 45 | 29.0 |
| Lompoc | 88.5 | 2.6 | 1.3 | 5.1 | — | — | — | — | 32 | 14.4 |
| Long Beach | 63.3 | 17.7 | 11.4 | 5.1 | 62.2 | 15.9 | 5.2 | 11.6 | 135 | 36.8 |
| Mira Loma | 54.1 | 16.4 | 13.1 | 16.4 | 47.1 | 13.2 | 13.2 | 23.2 | 250 | 66.3 |
| Riverside | 52.2 | 13.4 | 14.9 | 16.4 | 47.1 | 16.4 | 12.9 | 16.4 | 172 | 42.3 |
| San Bernardino | — | — | — | — | 24.2 | 15.3 | 13.3 | 41.1 | 199 | 51.0 |
| San Dimas | 55.6 | 19.4 | 11.1 | 12.5 | 45.5 | 15.8 | 18.7 | 16.8 | 191 | 36.7 |
| Santa Barbara | — | — | — | — | 80.3 | 9.7 | 2.9 | 2.6 | 30 | 28.2 |
| Santa Maria | 90.3 | 6.5 | 0 | 1.6 | 90.8 | 2.6 | 0.3 | 1.6 | 51 | 22.0 |
| Upland | 26.6 | 7.6 | 24.1 | 39.3 | 20.1 | 18.6 | 20.4 | 39.0 | 252 | 40.7 |

* Rows do not add up to 100% due to rounding and a few "don't know" answers.

**TABLE 3. PREVALENCE (%) OF SYMPTOMS REPORTED FOR THE FIRE PERIOD, BY STUDY COHORT AND BY ASTHMA STATUS (BASED ON THE LAST CHILDREN'S HEALTH STUDY QUESTIONNAIRE AVAILABLE PRIOR TO THE FIRE)**

| | High-School Students (*n = 834*) | | | Elementary-School Children (*n = 3,775*) | | | Both Cohorts (*n = 4,609*) | | |
|---|---|---|---|---|---|---|---|---|---|
| Symptom | No Asthma (*n = 616*) | Asthma (*n = 218*) | All | No Asthma (*n = 3,287*) | Asthma (*n = 488*) | All | No Asthma (*n = 3,903*) | Asthma (*n = 706*) | All |
| Itchy/watery eyes | 41.1 | 47.7 | 42.8 | 29.9 | 51.6 | 32.8 | 31.7 | 50.4 | 34.6 |
| Irritated eyes | 41.6 | 50.9 | 44.0 | 30.9 | 51.8 | 33.6 | 32.6 | 51.5 | 35.5 |
| Sneezing/blocked nose | 38.6 | 49.3 | 41.4 | 37.6 | 65.8 | 41.3 | 37.7 | 60.7 | 41.3 |
| Cold | 26.0 | 27.5 | 26.4 | 24.4 | 33.9 | 25.7 | 24.7 | 31.9 | 25.8 |
| Sore throat | 32.3 | 41.3 | 34.6 | 30.8 | 42.5 | 32.3 | 31.0 | 42.1 | 32.7 |
| Dry cough at night | 14.3 | 22.5 | 16.4 | 24.1 | 49.3 | 27.4 | 22.6 | 41.0 | 25.4 |
| Dry cough first in morning | 13.0 | 19.3 | 14.6 | 20.7 | 43.5 | 23.7 | 19.5 | 36.0 | 22.0 |
| Dry cough other times | 17.5 | 28.4 | 20.3 | 19.3 | 43.8 | 22.4 | 19.0 | 39.0 | 22.0 |
| Wet cough | 13.7 | 16.2 | 14.5 | 12.9 | 24.0 | 14.3 | 13.0 | 21.6 | 14.3 |
| Wheeze/general | 7.3 | 18.9 | 10.4 | 6.8 | 39.9 | 11.0 | 6.8 | 33.3 | 10.9 |
| Wheeze/disturbed sleep | 2.3 | 7.0 | 3.5 | 3.5 | 21.9 | 5.8 | 3.3 | 17.3 | 5.4 |
| Wheeze/ limited speech | 1.0 | 1.9 | 1.2 | 0.9 | 4.3 | 1.3 | 0.9 | 3.5 | 1.3 |
| Asthma attack | 1.0 | 11.0 | 3.6 | 1.3 | 17.4 | 3.3 | 1.2 | 15.4 | 3.4 |
| Bronchitis | 3.3 | 2.8 | 3.1 | 3.7 | 9.9 | 4.5 | 3.6 | 7.7 | 4.2 |
| Medication* | 12.9 | 23.6 | 15.7 | 23.7 | 50.6 | 27.2 | 22.0 | 42.3 | 25.1 |
| Visit a doctor* | 5.6 | 9.7 | 6.7 | 9.8 | 22.0 | 11.4 | 9.2 | 18.2 | 10.6 |
| Missed school* | 9.8 | 14.7 | 11.1 | 11.8 | 24.8 | 13.5 | 11.5 | 21.7 | 13.1 |

* For above problems.

Lake Arrowhead, more than 3% of study participants lost their homes (n = 15 and 10, respectively).

The main results are summarized in Table 4. Six or more days of fire smell indoors was significantly associated with all outcomes, and the smaller risk estimates for 1 to 5 d of exposure reached statistical significance in all but two outcomes (asthma attacks and bronchitis). Having fire smoke smell indoors for more than 6 d was associated with more than fourfold higher rates of eye symptoms, approximately threefold increased rates of dry cough and sneezing, and more than twofold higher rates of cold, sore throat, wet cough, medication use, physician visits, and missed school due to symptoms. The three types of wheezing (general, sleep-disturbing, and speech-limiting) occurred 3.5, 4.9, and 5.5 times more often, respectively, among those with 6 or more days of fire smell indoors. Asthma attacks increased 63%. The trend across the different levels of fire smell duration was highly significant for all outcomes except for asthma attacks ($p = 0.12$).

The between-community comparisons were analyzed with two different metrics, namely $PM_{10}$ and the community mean

**TABLE 4. MAIN EFFECT OF FIRE SMOKE ON ALL OUTCOMES (ODDS RATIOS AND 95% CONFIDENCE INTERVALS)**

| | Within-Community (reported) | | | | Between-Community ($PM_{10}$) | |
|---|---|---|---|---|---|---|
| Symptom | OR 1–5 d | 95% CI | OR ⩾ 6 d | 95% CI | OR 210 | 95% CI |
| Itchy/watery eyes | **2.26** | 1.90–2.68 | **4.11** | 3.36–5.02 | **2.97** | 2.00–4.40 |
| Irritated eyes | **2.38** | 2.01–2.82 | **4.42** | 3.61–5.41 | **3.13** | 2.15–4.55 |
| Sneezing; runny/blocked nose | **1.98** | 1.68–2.33 | **2.79** | 2.30–3.39 | **1.94** | 1.44–2.61 |
| Cold | **1.50** | 1.25–1.81 | **2.13** | 1.73–2.63 | 0.92 | 0.67–1.25 |
| Sore throat | **1.81** | 1.53–2.14 | **2.50** | 2.05–3.05 | **1.79** | 1.45–2.20 |
| Dry cough at night | **2.25** | 1.87–2.71 | **3.35** | 2.71–4.15 | **1.92** | 1.38–2.67 |
| Dry cough first thing morning | **2.24** | 1.85–2.72 | **2.91** | 2.33–3.63 | **1.93** | 1.36–2.73 |
| Dry cough other times | **2.67** | 2.20–3.24 | **3.27** | 2.61–4.09 | **2.49** | 1.86–3.33 |
| Wet cough | **1.42** | 1.13–1.79 | **2.15** | 1.67–2.77 | 1.01 | 0.72–1.41 |
| Wheezing or whistling | **2.15** | 1.63–2.83 | **3.53** | 2.62–4.75 | 1.37 | 0.86–2.20 |
| Wheeze/disturbed sleep | **2.29** | 1.56–3.37 | **4.94** | 3.33–7.33 | 0.89 | 0.56–1.42 |
| Wheeze/limited speech | **2.23** | 1.03–4.83 | **5.49** | 2.63–11.48 | 0.78 | 0.29–2.10 |
| Asthma attack | 1.32 | 0.84–2.07 | **1.63** | 1.00–2.67 | 1.03 | 0.58–1.80 |
| Bronchitis | 1.33 | 0.87–2.02 | **2.23** | 1.45–3.43 | 0.79 | 0.39–1.59 |
| Medication for above problems | **1.82** | 1.51–2.19 | **2.33** | 1.89–2.88 | **1.38** | 1.03–1.84 |
| Visit a doctor for above problems | **1.33** | 1.02–1.74 | **2.03** | 1.53–2.71 | 0.81 | 0.59–1.12 |
| Missed school for above problems | **1.59** | 1.25–2.02 | **2.24** | 1.72–2.91 | 0.96 | 0.72–1.27 |

*Definition of abbreviations*: CI = confidence interval; OR = odds ratio.

Within-community ORs are based on individually reported smell of fire smoke indoors (no fire smell = reference, OR = 1.0; not shown; 1-5 d; and ⩾ 6 d of fire smell). Between-community ORs show the associations scaled to the contrast in $PM_{10}$ between the communities with the highest and lowest levels, respectively ($\sim$ 210 vs. 30 $\mu g/m^3$). Models are adjusted for baseline asthma, ethnicity, parental education, and study cohort. Statistically significant estimates ($p \leqslant 0.05$) are in bold type.

response to the fire smell question. Results are presented for the former only (Table 4) as they were similar for both metrics. The community mean of the reported level of fire smoke indoors and the estimates of the 5-d mean $PM_{10}$ were highly correlated ($r = 0.81$) in both high-school and elementary-school students. Comparing highest with lowest community exposures, the between-community results were statistically significant and similar for both metrics in case of dry cough, eye, nose, and throat symptoms, as well as for medication. Eye symptoms were approximately three times as frequent in the communities most affected by fires as compared with lesser-affected communities. The between-community estimate for wheezing was significant only with the mean reported smoke (odds ratio [OR], 1.37 per unit change) but not with $PM_{10}$ (Table 4). The other outcomes were not significantly associated with either community-level metric.

The model presented in Table 4 also adjusted for asthma status before the 2003 fire period ("physician-diagnosed asthma"). Therefore, the model also estimates the contribution of physician-diagnosed asthma to symptom frequency in the end of October 2003, independent of the fire smoke. We present these effects (ORs) in Table E3 to highlight the much higher symptom rates among children with asthma (*see also* Table 3). Children with asthma were two to three times more likely to report symptoms than nonasthmatic children. Thus, the effect of having asthma was similar to the effects of fire smoke. In the case of wheezing, asthma status was more strongly related to the symptom (OR = 7.4; *see* Table E3.) than fire smoke (OR = 3.5; *see* Table 4).

The effect of fire smoke was, however, not restricted to children with asthma. Results of Table 4, stratified by asthma status, are presented in the online supplement (Tables E4 and E5). In fact, among nonasthmatic children, coefficients were either very similar or stronger (wheezing) than in children with asthma (n = 706) in whom point estimates tended to be smaller and not statistically significant for speech-limiting wheezing, asthma attacks, bronchitis, cold, wet cough, physician visits, and missed school. The between-community estimates followed a similar pattern as in nonasthmatic children, with significant associations among nine questionnaire items.

To evaluate the joint effects of fire and asthma status on reported symptoms, we examined five indicator variables for the combinations of fire smell (none, 1–5 d, ⩾ 6 d) and asthma status (yes/no) using nonasthmatic children without fire exposure as the reference group. Figure 2 presents the effects of fire smoke among children with and without asthma.

### Preventive Action and Fire-related Health Outcomes

We distinguished those who took action such as wearing masks, spending less time outdoors, or using air conditioners for at least 1 to 2 d from those not reporting preventive strategies. Those taking action also reported higher rates in almost all outcomes, and in many cases, these differences were statistically significant. For example, those reporting "wearing a mask" had symptom rates more than twice as high as those not using masks, whereas those reporting the use of air conditioners or spending "less time outdoors" during the fire had 1.2- to 1.6-fold rates in symptoms. Of particular interest is the interaction between preventive actions and reported duration of fire smell indoors (*see* Table 5). As a general pattern, we observed larger risk gradients related to fire smoke among those who did not take preventive action as compared with those who did. The interaction term reached statistical significance in several models (*see* Table 5). Compared with those who reported no fire smell, subjects with 1 to 5 d of smoke smell indoors who did not wear a mask were twice as likely to report sneezing (OR = 2.02 [1.7–2.4]). For those who did wear a mask (and reported 1–5 d of smoke), sneezing rates were only 25% higher. In the most exposed subgroup (> 6 d of smoke), those without masks had an OR of 2.8 [2.3–3.5], whereas the OR among those with a mask was only 1.67.

## DISCUSSION

To our knowledge, this is the largest investigation of acute effects of wildfire smoke on children's health. We confirmed very substantial effects of wildfire smoke exposure on eyes as well as upper and lower respiratory symptoms, in both children with asthma and nonasthmatic children. The study was population based; thus, findings may be generalized more broadly to other comparable populations. Our findings are consistent with other studies conducted after wildfire outbreaks and occupational studies among firefighters, which suggest that wildfire smoke leads to acute exacerbations of respiratory and eye symptoms and increased demand for health services (13). Like ambient urban air pollution, wildfire smoke contains numerous primary and secondary pollutants, including particles, polycyclic aromatic hydrocarbons, carbon monoxide, aldehydes, organic acids, organic compounds, gases, free radicals, and inorganic materials with diverse toxicologic properties (14), which may explain the wide range of acute symptoms observed in our survey (15).

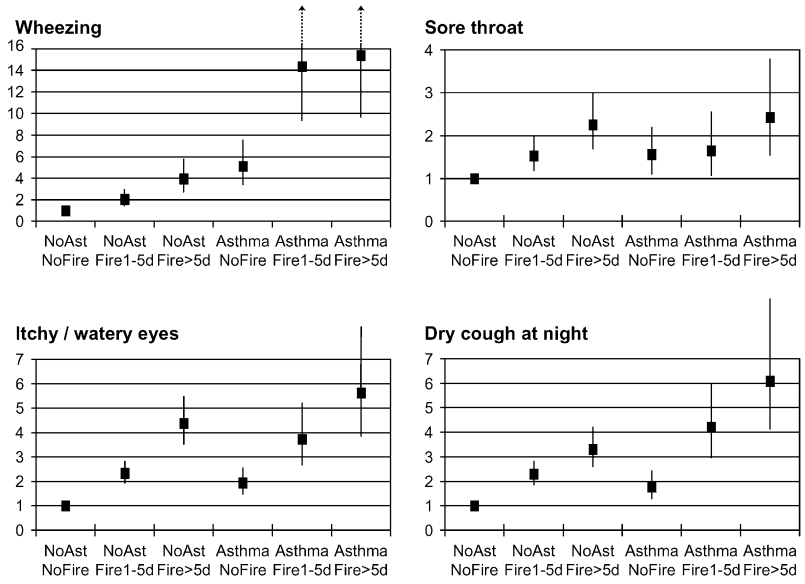


*Figure 2.* Effect of reported smell of fire smoke indoors (during 1–5, > 5 d, respectively) for four symptoms among children with and without asthma. Odds ratios and 95% confidence intervals from models with interaction terms for asthma and fire, adjusted for sex, ethnicity, educational level of parents, and cohort. No asthma (No Ast), no fire = reference.

**TABLE 5. ODDS RATIOS FOR SYMPTOMS AMONG THOSE WITH AND WITHOUT PREVENTIVE ACTIONS AND WITH NO REPORTED SMOKE EXPOSURE (REFERENT GROUP), 1–5, OR ⩾ 6 DAYS OF FIRE SMOKE SMELL INDOORS**

| | Use of Mask | | Air Conditioner Use | | Less Outdoors | |
|---|---|---|---|---|---|---|
| Symptom Exposure Level | No OR (*95% CI*) | Yes OR (*95% CI*) | No OR (*95% CI*) | Yes OR (*95% CI*) | No OR (*95% CI*) | Yes OR (*95% CI*) |
| Sneezing or runny/blocked nose, n | 3,673 | 396 | 3,158 | 911 | 1,371 | 2,698 |
| No fire smell (referent) | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| 1–5 d fire smell | 2.01 (1.70–2.39) | 1.58 (0.86–2.91) | 2.14 (1.77–2.59) | 1.75 (1.26–2.43) | 1.84 (1.25–2.73) | 1.76 (1.46–2.11) |
| 6 or more days fire smell | 2.81 (2.27–3.47) | 2.30 (1.22–4.31) | 3.05 (2.42–3.85) | 2.23 (1.52–3.25) | 2.54 (1.60–4.01) | 2.47 (1.98–3.09) |
| Wheezing, n | 3,630 | 387 | 3,111 | 906 | 1,357 | 2,660 |
| No fire smell (referent) | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| 1–5 d fire smell | 2.05 (1.51–2.79) | 1.50 (0.68–3.31) | 2.29 (1.64–3.18) | 1.79 (1.79–3.07) | 4.80 (2.51–9.20) | 1.76 (1.28–2.42) |
| 6 or more days fire smell | 3.47 (2.49–4.85) | 2.23 (1.52–3.25) | 3.46 (2.41–4.98) | 3.00 (1.71–5.27) | 7.65 (3.74–15.63) | 2.91 (2.06–4.09) |

For definition of abbreviations, *see* Table 4.

Total n varies between 4,017 and 4,069 due to varying number of "don't know" answers). The interactions of fire smell and preventive actions were statistically significant (likelihood ratio test, $p < 0.05$) for mask and air conditioner use in case of sneezing/blocked nose, and for "less outdoors" in case of wheezing. Note that in each exposure category, those taking preventive action had higher symptom rates than those not taking action (*see* text).

Biases require particular attention in the interpretation of these findings. Because many parents and students completed the fire questionnaire several months after the fire (from 1 to 7 mo later), and because both exposure and outcome are reported by participants, the study may be subject to interrelated reporting, recall, and selection biases. Due to the lack of individual-level $PM_{10}$ data, we were able to compare effects of objective ($PM_{10}$) and subjective (reported) markers of exposure in the between-community comparison only. We used the community mean of reported fire smoke as the subjective aggregate exposure.

For reported fire smoke, the estimates for individual and community mean were similar for most outcomes. However, between-community estimates using the mean reported fire smell were not entirely consistent with those based on $PM_{10}$. The latter showed no clear association with cold, cough, asthma symptoms, physician visits, and missing school. There are several possible reasons for these inconsistencies.

First, the exposure metrics are inherently different and measure different domains of exposure. $PM_{10}$ estimates the average concentration during the 5 most extreme days. In contrast, the questionnaire-based approach relates to the duration (i.e., number of days of observed smoke) rather than the level of the smoke in the community. Duration may characterize the true contrasts in exposure better than the 5-d average $PM_{10}$ because some communities experienced fire smoke for longer or shorter periods.

Second, $PM_{10}$ levels had to be estimated for five fire communities (*see* METHODS and online supplement). The unknown errors in these estimates may lead to under- or overestimation in the between-community effects. Thus, the results based on "objective" measures of community-level exposure are not necessarily unbiased.

Third, $PM_{10}$ community levels are not sensitive to spatial differences in smoke densities that may have occurred within communities. Therefore, $PM_{10}$ concentrations at the monitor may not represent the mean of the true, but unknown, home outdoor $PM_{10}$ levels. We have no objective data to validate the reported diversity on the individual level. Wu and colleagues estimated $PM_{10}$ distributions all across the Southern California area during the wildfire period, using PM measurements, light extinction, meteorologic data, and smoke information from satellite images (1) (*see* Figure E1). We used these results to investigate the range of daily mean $PM_{10}$ concentrations for small areas representing size and location of several CHS communities. For example, the $PM_{10}$ concentration estimates for a $1 \times 1$–km grid within a 10-km buffer around San Dimas indicated substantial temporal differences during the fire period, with daily means ranging from 115 $\mu g/m^3$ (October 28) to 220 $\mu g/m^3$ (October 26) as well as large spatial gradients across the grid points. For example, on October 25, the point estimates ranged from 54 to 250 $\mu g/m^3$, and from 90 to 337 $\mu g/m^3$ the next day, with spatial standard deviations up to 50% of the daily means (*see* Figure E1). Although these $PM_{10}$ estimates may be associated with significant uncertainties at the neighborhood scale, they demonstrated substantial spatial heterogeneity, which corroborates the notion that smoke concentrations may vary substantially within communities. The distribution of reported smoke—and thus the community mean of the reported conditions—may reflect these distinct spatial gradients that are influenced by topography and wind patterns (1, 2).

Fourth, the community-level $PM_{10}$ does not take into account $PM_{10}$ levels in locations to which the children might have been evacuated, nor does it account for other individual preventive action taken during the fire period. Thus, the monitor $PM_{10}$ value may again be offset from the true, but unknown, mean $PM_{10}$ across children.

Fifth, the reported fire smell related to the indoor environment where most of the time was spent, whereas outdoor $PM_{10}$ levels are not sensitive to differences among children's indoor environments.

The community mean of the reported fire smell was highly correlated with measured $PM_{10}$. However, others have shown that community mean reported annoyance of ambient air pollution correlates highly with objective measurements, whereas individual scores may poorly correlate with the home outdoor $NO_2$ measurements (16). Reporting was associated with health status and sex. A recent review also concluded that reported exposure to traffic was poorly associated with objective data (17). It is not clear whether findings for reported ambient air pollution also apply to fire smoke perception. Reporting of fire smoke may be less affected by personal attitudes than reported ambient air pollution, given the strong smell of fire smoke, the visibility of the problem, and the exceptional situation of the fire period. Reporting was also associated with sex. Eye symptoms, cold, medication, and physician visits were significantly more often reported among girls, whereas boys were more likely to report wheezing (data not shown). However, sex did not confound nor modify the main effects of fire smoke.

In conclusion, although it is neither possible to dismiss the possibility of biases nor to quantify their effects on our results,

we believe that the arguments outlined above support the questionnaire-based results.

### Effect of Fire Smoke on Children with Asthma

With the exception of bronchitis, we consistently observed larger coefficients of reported fire smoke among the nonasthmatic children, a general pattern also true for the between-community comparison. However, the smaller effect sizes in children with asthma must be seen in light of the much higher baseline rates for all symptoms among these children (*see* Tables 3 and 4). Therefore, a small increase in the relative risk may constitute a much larger effect in the children with asthma than in the nonasthmatic children. This is apparent in Figure 2. Symptom rates among children with asthma with no fire smoke were generally as high as those among nonasthmatic children with 1 to 5 d of fire smoke.

Children with asthma were usually treated and may have had better access to medical treatment. A Centers for Disease Control and Prevention surveillance reported increased over-the-counter sales of medication after this 2003 fire period (13). The fire questionnaire did not ask about specific treatments such as steroids.

We also have evidence that children with asthma were more likely to change their behavior (data not shown). For example, 15% of children with asthma reported to have worn a mask for at least some days, whereas only 2% of nonasthmatic children reported taking this personal protective measure. More children with asthma reported reduction in time spent outdoors, outdoor sports, and indoor physical activity due to the fire than did nonasthmatic children. This is in line with results from a previous California fire study indicating that those with preexisting conditions were more likely to follow public advisories to prevent smoke exposure (18). The use of air cleaners in that study was twice as high among those with preexisting health problems.

During a 1987 fire period in California, emergency room visits due to asthma and a range of upper and lower respiratory problems increased significantly beyond the expected rates (19). This was also observed in San Diego County during this 2003 wildfire (5). Large fires in Lithuania also affected crude rates of asthma exacerbation (20). Australian scientists found inconclusive results in their investigation of bushfire effects among a panel of 32 children with asthma. Only evening wet cough was associated with fire smoke (21). Interaction with medication use was not assessed (7), but statistical power may have been a major limitation.

We conclude that the much higher background rates of symptoms was the major reason for the weaker effect estimates observed among children with asthma, and that limitations in the assessment of asthma activity, severity, and medication added further random error to the assessment of effects in children with asthma.

We did investigate effects of fire on boys and girls separately (data not shown). Although baseline frequencies differed by sex for some symptoms, sex did not confound nor did it modify the effects of fire smoke.

### Long-term Ambient Air Pollution and Fire Smoke

Some of the CHS communities with high long-term ambient pollution were heavily affected by fire; thus, we investigated confounding by long-term exposure to air pollution (data not shown). Communities with high long-term pollution had significantly higher reporting of "bronchitis" and "missed school." However, the long-term mean ambient PM did not confound the association between fire smoke and fire-related outcomes. Regular exposure to wood smoke has been reported to be a risk factor for chronic respiratory diseases (22). Tan and colleagues (23) and van Eeden and colleagues (24) have shown that acute exposure to wildfire smoke was associated with the stimulation of the bone marrow to release polymorphonuclear leukocytes in men, which reflects a systemic response that may be relevant to subsequent lung injury. However, the long-term relevance of a single wildfire exposure is not clear. Follow-up of the CHS fire study participants may allow an investigation of the long-term consequences of this unusual episode.

We stratified the analyses by cohort to investigate age-related differences in the effect of fire smoke. Results among the (larger) cohort of elementary-school children were more often statistically significant than in the cohort of high-school students. Coefficients tended to be larger in the latter, however, in particular for the between-community estimates (data not shown). It is difficult to assign these differences to age, given the differences in the study methods, with parents reporting for their young children and high-school students self-reporting symptoms.

Participation rates immediately after the fires in 2003 were low in some cities, so the presence of possible selection bias based on exposure and/or symptoms might have been an issue. However, survey administration efforts during 2004 resulted in increased response rates. We evaluated the effect of time elapsed since the fire on reported symptom prevalence. For some symptoms, the likelihood of reporting steadily decreased as time elapsed between the fire and answering the questionnaire (results not shown). Reporting of eye-related symptoms increased with elapsed time. This analysis demonstrates the importance of obtaining symptom-related information from study subjects in as timely a manner as possible after an unexpected natural event or emergency. Attempts to maximize early responses are important strategies for future studies. Inclusion of some control outcome not believed to be affected by fire smoke (e.g., stomach or digestive complaints) could have enhanced the assessment of reporting biases.

Our study suggests there was a beneficial effect of wearing masks, spending less time outdoors, and/or using air conditioning—actions that were recommended during the fire by public health agencies and the media. As recently shown in a fire smoke intervention study conducted in Colorado, ventilation patterns including the use of air filters can have substantial effects on the indoor levels of fire-related PM (25); thus, our results are plausible. However, because our assessment of exposure, symptoms, and preventive action were cross-sectional and self-reported, caution is appropriate in the interpretation of these results.

In summary, this investigation indicates substantial effects of fire smoke on children's health. The study provides suggestive evidence for protective health benefits of simple strategies, such as staying indoors, wearing a mask, or the use of air conditioners during wildfire smoke periods.

***Conflict of Interest Statement***: None of the authors has a financial relationship with a commercial entity that has an interest in the subject of this manuscript.

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# Gene flow and pathogen transmission among bobcats (*Lynx rufus*) in a fragmented urban landscape

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## Abstract

**Urbanization can result in the fragmentation of once contiguous natural landscapes into a patchy habitat interspersed within a growing urban matrix. Animals living in fragmented landscapes often have reduced movement among habitat patches because of avoidance of intervening human development, which potentially leads to both reduced gene flow and pathogen transmission between patches. Mammalian carnivores with large home ranges, such as bobcats (*Lynx rufus*), may be particularly sensitive to habitat fragmentation. We performed genetic analyses on bobcats and their directly transmitted viral pathogen, feline immunodeficiency virus (FIV), to investigate the effects of urbanization on bobcat movement. We predicted that urban development, including major freeways, would limit bobcat movement and result in genetically structured host and pathogen populations. We analysed molecular markers from 106 bobcats and 19 FIV isolates from seropositive animals in urban southern California. Our findings indicate that reduced gene flow between two primary habitat patches has resulted in genetically distinct bobcat subpopulations separated by urban development including a major highway. However, the distribution of genetic diversity among FIV isolates determined through phylogenetic analyses indicates that pathogen genotypes are less spatially structured—exhibiting a more even distribution between habitat fragments. We conclude that the types of movement and contact sufficient for disease transmission occur with enough frequency to preclude structuring among the viral population, but that the bobcat population is structured owing to low levels of effective bobcat migration resulting in gene flow. We illustrate the utility in using multiple molecular markers that differentially detect movement and gene flow between subpopulations when assessing connectivity.**

*Keywords*: carnivores, disease ecology, gene flow, habitat fragmentation, microsatellites, viral phylogenetics

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## Introduction

Habitat loss and degradation are the leading causes of species declines around the world (http://www.iucnredlist.org/). Urbanization, an extreme form of habitat degradation, results in immediate displacement of wildlife from developed areas, followed by the increasing isolation of groups of animals confined to shrinking natural areas (McKinney 2002; McDonald *et al.* 2008). A common effect of urbanization is the fragmentation of once contiguous landscapes into smaller patches of non-contiguous habitat.

Maintaining functional connectivity, the extent to which organisms and genetic material move between

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habitat patches, can be essential for population persistence in fragmented landscapes (Crooks & Sanjayan 2006). Reduced functional connectivity between habitat patches can result in physically and genetically isolated subpopulations prone to inbreeding and to the loss of genetic diversity through genetic drift (Frankham 2006). However, measuring functional connectivity can be difficult, especially for cryptic solitary species such as large carnivores (Crooks 2002). One commonly used method of evaluating functional connectivity involves characterizing patterns of gene flow using molecular markers to evaluate the distribution of genetic diversity within and among groups of individuals (Frankham 2006; Balkenhol & Waits 2009; Ruell *et al.* in press). Populations with high connectivity should exhibit homogenous distributions of genetic diversity. Populations with low connectivity will be genetically structured, exhibiting localized variations in genetic diversity as a consequence of reduced gene flow among isolated groups of individuals.

Microsatellites are neutral heritable molecular markers commonly used to evaluate genetic structure, and hence connectivity, among natural populations (Avise 2004; Hedrick 2005a). These polymorphic, codominant markers provide a powerful means for assessing gene flow. However, microsatellite markers only reflect individual movement within structured populations if a migrant is sampled or if a migrant successfully reproduces and at least one offspring is sampled. Transient movements between subpopulations, or migrants that do not reproduce, may not be detected by analysing microsatellites (Riley *et al.* 2006). Therefore, while powerful, host genetic markers may not accurately characterize connectivity when individual movements do not result in gene flow.

Because directly transmitted obligate pathogens are inextricably linked to their hosts, pathogens can serve as alternative or additional markers for studies of wildlife population dynamics (Nieberding & Olivieri 2007; Liu *et al.* 2008). Feline immunodeficiency virus (FIV), a retrovirus that naturally infects many felid species (Troyer *et al.* 2005; Vandewoude & Apetrei 2006), has many characteristics that render it potentially useful as a marker of population dynamics in wild cats. First, the mutation rate of FIV is significantly faster than that of host genetic markers (approximately $\mu = 1$–$3\%$ every 10 years in mountain lions) (Biek *et al.* 2003). Also, infection with FIV is life-long because an obligatory step in viral replication involves the permanent insertion of a copy of the viral genome into the host's chromosomal DNA. Therefore, FIV genotypes have the capacity to serve as life-long molecular markers for each infected individual. Furthermore, the virus cannot be transmitted by insect vectors, nor is it stable in the environment, and thus, transmission events are indicators of direct contact between individuals.

Finally, the strains of FIV, which infect domestic cats, are genetically distinct from the strains isolated from wild felids. The domestic cat strains have never been documented to infect nondomestic felids in the wild, and therefore, the genetic diversity of FIV among nondomestic felids is only influenced by the distribution, movement and contact rates among conspecifics across the landscape.

Indeed, previous studies have demonstrated that patterns of FIV relatedness closely reflect the geographical distribution of bobcats, mountain lions and African lions at various geographical scales (Biek *et al.* 2006; Franklin *et al.* 2007a; Antunes *et al.* 2008). Specifically, Franklin *et al.* (2007a) demonstrated that the FIV isolates infecting bobcats north and south of Los Angeles, CA are genetically distinct, having diverged since the isolation of the two host populations. Because of these characteristics, viral genetic analyses may provide novel and powerful techniques for assessing connectivity and population structure with improved resolution, supplementing that which is currently possible using host genetic markers.

Bobcats (*Lynx rufus*), with large home ranges and high resource requirements, are susceptible to the effects of habitat loss and fragmentation in urbanizing systems (Crooks 2002; Riley *et al.* 2003, 2006, 2010). We investigated patterns of genetic diversity among bobcats and FIV isolates from a fragmented landscape in southern California to evaluate how urbanization affects connectivity among bobcats in this region. We specifically evaluated the extent to which several large freeways, and the developed areas surrounding them, are barriers to gene flow and pathogen transmission between habitat patches. We predicted that decreases in connectivity would lead to significant genetic structure among both host and pathogen populations. We performed standard population genetics analyses using 16 unlinked microsatellite loci from 106 bobcats. We also constructed phylogenetic trees to assess patterns of relatedness among FIV isolates from 19 of these individuals infected by the virus.

Our findings, presented below, demonstrate that two spatially structured, genetically distinct bobcat subpopulations exist. However, the pathogen phylogeny revealed no association between FIV relatedness and bobcat population structure, suggesting movements, contacts and disease transmission between subpopulations continue despite very low levels of host gene flow. This finding was inconsistent with our hypothesis that decreased gene flow among bobcats would lead to similar genetic structure among the virus population. However, these results are consistent with other studies that have found major roads and urban development to

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be more permeable to transient bobcat movements than to effective migration, allowing for the potential movement of pathogens in the absence of gene flow (Riley *et al.* 2006; Ruell *et al.* in press). We illustrate the utility in using multiple molecular markers, each with different determinants of movement throughout populations, to assess complex questions of connectivity.

## Methods

### *Location and field sampling*

This study was located south and west of Los Angeles, CA and included four habitat patches divided by three large freeways—Interstate-5 (I-5), the Riverside Freeway (SR-91) and the San Joaquin Hills Transportation Corridor (SR-73) (Fig. 1). I-5 through this region was constructed from 1944 to 1958 and has an average annual daily traffic volume (AADT) of ~262 000 cars per day (California DOT 2009). SR-91 was originally completed in 1971 and underwent a major expansion in 1995. The AADT of this freeway is ~264 000 cars per day (California DOT 2009). SR-73 was constructed in 1996 and has an AADT of ~73 000 cars per day (California DOT 2009). Aside from these roads and adjacent urban development, the only potential natural barrier to bobcat movement is the Santa Ana River, which flows about 100 m to the north of SR-91. No other natural barriers to gene flow (i.e. major mountain ranges) exist between these habitat patches, which are primarily characterized by chaparral, coastal scrub and grassland vegetative communities.

A total of 106 bobcats were included in this study. The majority of bobcats ($n = 75$) were live-captured between December 2002 and March 2009 using wire cage traps baited with visual and odour attractants (Lyren *et al.* 2006, 2008a,b). Animals were anesthetized, and blood samples were collected. Animals were captured, sampled and released with permission of cooperating agencies after approval by all appropriate animal care and use committees. The remaining individuals ($n = 31$) were opportunistically sampled postmortem; when possible, heart blood clots, thoracic fluid, ear punch and hair samples were collected from these bobcats. Blood and tissues were stored at USGS facilities in Irvine, CA, and aliquots were sent to Colorado State University for analysis as described below.

### *Putative subpopulation assignments*

Bobcats were assigned to one of four putative subpopulations based on the GPS coordinates of the capture or road kill location relative to freeways I-5, SR-91 and SR-73 (Fig. 1). These three freeways were the focus of our investigation because they completely traverse the study area (i.e. animals cannot move between habitat fragments without crossing one of these freeways), and these roads represent a gradient of permeability to bobcat movements based on previous studies [see discussion and also Lyren *et al.* (2008a,b)]. The San Joaquin Hills west subpopulation [SJH-west ($n = 29$)] was located between the coast and SR-73, which merges with I-405 to the north and I-5 to the south. The San Joaquin Hills east subpopulation [SJH-east ($n = 20$)] included individuals sampled between SR-73 and I-5. The North Irvine Ranch [NIR ($n = 44$)] subpopulation comprised individuals captured east of I-5 and south of SR-91, whereas the Chino Puente Hills [CPH ($n = 12$)] subpopulation consisted of individuals captured east of

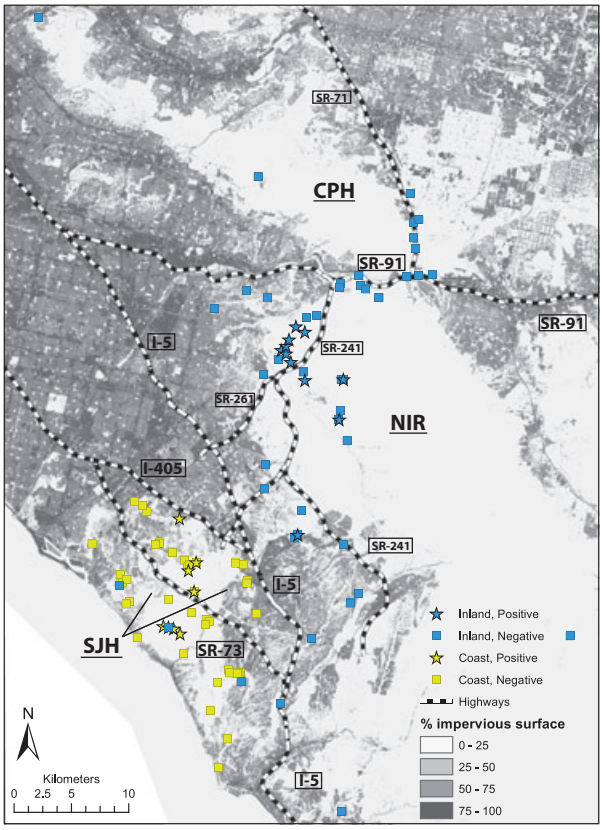


**Fig. 1** Map of study locations southeast of Los Angeles, California. GPS capture locations of 105 bobcats indicated by squares [feline immunodeficiency virus (FIV) negative] or stars (FIV positive). Blue or yellow fill of each symbol represents the genetic assignment of an individual to an inland (east of I-5) or coastal (west of I-5) subpopulation, respectively (see Fig. 2). The a priori assignment of individuals to putative subpopulations (SJH-W: San Joaquin Hills West; SJH-E: San Joaquin Hills East; NIR: North Irvine Ranch; CPH: Chino Puente Hills) was based on the capture location of bobcats relative to the focal roads SR-73, I-5 and SR-91, which were investigated as potential barriers to gene flow. Degree of urban development (% impervious surface) is represented by grey shading.

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I-5 and north of SR-91. One individual did not have a recorded capture location, and thus, it was not included in analyses that required the above subpopulation assignments. The following population genetics analyses were, except where noted, performed using this a priori assignment of individuals to putative subpopulations and the multilocus microsatellite genotype data for each individual.

### *Genotyping microsatellites*

Bobcat genomic DNA was extracted from whole blood, peripheral blood mononuclear cells (PBMCs) or tissue using QIAamp® DNeasy blood and tissue kit (Qiagen Inc., Valencia, CA, USA). Seventeen microsatellite loci (Table 1) were amplified using primer pairs for polymerase chain reaction (PCR) developed by Menotti-Raymond *et al.* (1999): FCA008, FCA023, FCA026, FCA031, FCA043, FCA045, FCA077, FCA090, FCA096, FCA132, FCA149, FCA559; Menotti-Raymond *et al.* (2005): FCA740, FCA742; and Faircloth *et al.* (2005): BCE5T, BCD8T, BCG8T. Primers BCE5T and BCG8T were modified to contain the M-13 sequence instead of the CAG sequence as published. We selected these primer pairs from the above publications based on the following criteria: longer repeat units, efficiency of amplification and maximal heterozygosity. The 5′ end of the forward primer of each primer pair was modified with a 16-bp tail comprising the M-13 sequence (5′–GTA AAA CGA CGG CCA G–3′). Reverse primers were not modified. All microsatellite PCR products were fluorescently labelled using a second forward primer consisting of the above M-13 sequence with 6-FAM on the 5′ end.

PCR methodologies were adapted from Boutin-Ganache *et al.* (2001) and Riley *et al.* (2006). PCR reaction conditions included 94 °C for 3 min followed by 22 cycles of (94 °C for 30 seconds; 59 °C for 30 seconds; and 72 °C for 45 seconds), followed by 10 cycles of (94 °C for 30 seconds; 53 °C for 30 seconds; and 72 °C for 45 seconds), and a final cycle of 72 °C for 10 min. Randomly selected PCR products as well as the negative control for each reaction were visualized under UV light using gel electrophoresis with ethidium bromide in 2% agarose gel to confirm the presence of amplicons of appropriate length. Precise PCR product fragment lengths were determined using an ABI 3730xl DNA Analyzer and Peak Scanner 1.0 software (Applied Biosystems, Foster City, CA, USA). PCR and genotyping were repeated in ten per cent of randomly chosen bobcat samples for each microsatellite locus to confirm genotypes and prevent scoring errors. All duplicated genotypes were consistent with the primary analysis, demonstrating a high degree of assay reproducibility and reducing the likelihood of genotyping errors owing to false alleles or allelic dropout.

**Table 1** Characterization of 17 microsatellite loci in 106 bobcats

| Locus | Size range | No. of alleles | Repeat | Chromosome | $H_O$ | $H_E$ | PIC | References |
|---|---|---|---|---|---|---|---|---|
| FCA008 | 140–156 | 8 | di | A1 | 0.71 | 0.77 | 0.73 | 1 |
| FCA023 | 144–158 | 6 | di | B1 | 0.67 | 0.72 | 0.67 | 1 |
| FCA026* | 138–166 | 13 | di | D3 | 0.79 | 0.83 | 0.81 | 1 |
| FCA031 | 237–255 | 8 | di | E3 | 0.78 | 0.80 | 0.77 | 1 |
| FCA043† | 131–139 | 5 | di | C2 | 0.78 | 0.73 | 0.68 | 1 |
| FCA045* | 147–173 | 7 | di | A1 | 0.63 | 0.83 | 0.81 | 1 |
| FCA077† | 130–140 | 6 | di | C2 | 0.77 | 0.74 | 0.70 | 1 |
| FCA090* | 108–126 | 7 | di | A1 | 0.41 | 0.52 | 0.48 | 1 |
| FCA096 | 189–209 | 8 | di | A2 | 0.80 | 0.77 | 0.75 | 1 |
| FCA132* | 182–194 | 7 | di | D3 | 0.66 | 0.78 | 0.74 | 1 |
| FCA149 | 133–149 | 9 | di | B1 | 0.76 | 0.78 | 0.75 | 1 |
| FCA559 | 115–135 | 6 | tetra | B1 | 0.64 | 0.67 | 0.60 | 1 |
| FCA740 | 333–353 | 6 | tetra | C1 | 0.84 | 0.79 | 0.76 | 2 |
| FCA742 | 104–134 | 7 | tetra | D4 | 0.65 | 0.67 | 0.61 | 2 |
| BCD8T | 156–180 | 5 | tetra | Unknown | 0.21 | 0.21 | 0.20 | 3 |
| BCE5T | 256–280 | 7 | tetra | Unknown | 0.70 | 0.75 | 0.71 | 3 |
| BCG8T | 275–299 | 11 | di | Unknown | 0.73 | 0.78 | 0.74 | 3 |

$H_O$, observed heterozygosity; $H_E$, expected heterozygosity; PIC, polymorphic information content.
*Null alleles may exist in one subpopulation.
†FCA077 and FCA 043 were found to be in linkage disequilibrium; FCA043 was not used in population genetics analyses.
References: (1) Menotti-Raymond *et al.* (1999); (2) Menotti-Raymond *et al.* (2005); and (3) Faircloth *et al.* (2005).

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### *Validating and characterizing microsatellite data*

Microsatellite data were screened for genotyping errors because of stuttering, null alleles and large allele dropout at all loci in MICROCHECKER 2.2.3 (Van Oosterhout *et al.* 2004). There was no evidence of errors because of stuttering or large allele dropout at any loci. The following three loci showed evidence of null alleles when testing across all individuals with no subpopulation information: FCA045, FCA090 and FCA132. The null alleles at these loci correspond to NIR (FCA045 and FCA090) and SJH-west (FCA132) when the same analysis was run with a priori subpopulation assignments.

Tests for linkage disequilibrium among loci were performed in GENEPOP 4.0 (Raymond & Rousset 1995; Rousset 2008). The results for linkage disequilibrium varied greatly between subpopulations with seven significant tests in SJH-west (120 total tests; $\alpha = 0.009313$), four significant tests in SJH-east (120 total tests; $\alpha = 0.009313$), two significant tests in NIR (136 total tests; $\alpha = 0.009102$) and one significant test in CPH (104 total tests; $\alpha = 0.009567$). Loci FCA077 and FCA043 were in linkage disequilibrium in all four putative subpopulations, and therefore, FCA043 was eliminated from further analyses.

Hardy–Weinberg equilibrium probabilities were calculated using GENEPOP 4.0 (Raymond & Rousset 1995; Rousset 2008). Three of four subpopulations significantly deviated from Hardy–Weinberg equilibrium at one unique locus: FCA023 in SJH-west (15 tests; $\alpha = 0.015068$), FCA045 in NIR (16 tests; $\alpha = 0.014790$) and BCE5T in CPH (16 tests; $\alpha = 0.014790$). The remaining loci in each subpopulation did not deviate from HW equilibrium, and therefore, all subpopulations were assumed to be in HW equilibrium. Observed and expected heterozygosity and the polymorphic information content (PIC) for each locus were determined using the program CERVUS 3.0 (Table 1) (Kalinowski *et al.* 2007).

### *Assessment of population structure*

Population differentiation based on allele frequencies was calculated for each pair of putative subpopulations using GENEPOP 4.0 (96 tests; $\alpha = 0.0097$) (Raymond & Rousset 1995; Rousset 2008). Allelic richness, estimated using rarefaction to avoid bias caused by differences in sample size (Leberg 2002), was calculated for each putative subpopulation using FSTAT 2.9.3.2 (Goudet 1995). Allelic richness results were confirmed to be normally distributed using a Ryan Joiner Test in Minitab Student Version 14.11.1 (Ryan Joiner test; $P > 0.1$). Analysis of variance (ANOVA) was used to determine whether allelic richness differed significantly between subpopulations ($\alpha = 0.05$). Estimates of subpopulation differentiation ($D_{est}$) were calculated using the online program Software for Measurement of Genetic Diversity (Jost 2008; Crawford 2010). Fst values were calculated in FSTAT (Goudet 1995). The use of $F_{ST}$ values as measures of population differentiation has recently been criticized (Hedrick 2005b; Jost 2008). Therefore, we include them here as supplemental information only to allow a general comparison among similar, previously published studies (Table S1, Supporting information).

Bayesian clustering in program STRUCTURE 2.3.3 was used to infer the number of genetically distinct subpopulations ($K$) and to assign each individual to the subpopulation with which they share the highest genetic similarity. Parameters were set to include 50 000 burn-in and 500 000 Markov Chain Monte Carlo iterations (Pritchard *et al.* 2000). Data were first analysed without a priori source population information for individuals. Independent allele frequencies among subpopulations and genetic admixture were included as parameters so as not to introduce an upward bias in the estimation of $K$ (Pritchard *et al.* 2000). This analysis was repeated five times for each $K$ to verify the consistency of likelihood values between runs. $K$ was varied from $K = 1$ to 5, representing a range of greater than expected $K$ values to ensure our analysis included all ecologically plausible values of $K$.

This was followed by additional analyses with the data set divided into two groups: coastal animals (SJH-west and SJH-east) and inland animals (NIR and CPH) to more closely evaluate possible substructure within each of these two groups (Pritchard *et al.* 2010). The parameters of this model were the same as above, with each analysis repeated five times for each $K$ from $K = 1$ to 3 for each group. For all of the above analyses, posterior probability values were computed for each $K$ according to Pritchard *et al.* (2010). Additionally, $\Delta K$ values, which have been shown to accurately reflect the actual number of genetic clusters, were calculated according to Evanno *et al.* (2005).

Structure was also used to identify individuals that were captured in one subpopulation but genetically assigned to another and thus represent migrants. The parameters for this analysis were the same as described above except subpopulation assignments were included in the analysis with the migration prior set to 0.05. Individuals with a probability of assignment to their source population ≤0.01 were considered migrants. Individuals with ambiguous assignment probabilities were considered hybrids.

An individual pairwise relatedness test was performed after correction for null alleles using the program Maximum-likelihood (ML)-Relate (Kalinowski *et al.* 2006; Wagner *et al.* 2006; Carlsson 2008). The

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average pairwise relatedness of each subpopulation was compared using a *t*-test.

### *Detection of FIV infection*

All bobcats for which serum samples were available ($n = 91$) were screened for antibodies to FIV by Western blot as previously described (Franklin *et al.* 2007b). Of these, 24 (26.4%) were scored as 'weak positive' or 'positive' for FIV antibodies. PCR was used to confirm FIV infection in these samples (two to four PCR attempts per seropositive individual) using DNA extracted from whole blood or PBMCs. We used a set of degenerate nested primers, which was previously shown to amplify a region of the *RT-pol* gene from a diverse set of FIV isolates (Troyer *et al.* 2005). All bobcats that were not screened by Western blot ($n = 15$) were screened for FIV infection by the PCR method only. In total, 19 individual bobcat FIV isolates were amplified by PCR and included in the FIV genetic analyses.

### *FIV pol and env PCR amplification and sequencing*

Two gene regions were analysed to evaluate viral phylogeny using both a highly conserved region (*RT-pol*, encoding the essential viral polymerase) and a region that is less evolutionarily constrained (*env*, encoding the surface envelope protein) (Pecon-Slattery *et al.* 2008). PCR amplification of a region of the *RT-pol* gene was performed using degenerate primers as previously described (Troyer *et al.* 2005). Primers to amplify a region of the *env* gene were designed by first performing an alignment of two previously published FIV sequences: PLV-14 [GeneBank (accession no. U03982)] isolated from a Florida panther (*Puma concolor coryi*) and PLV-1695 [GenBank (accession no. DQ192583)] isolated from a puma (*Puma concolor cougar*) in British Columbia. Degenerate nested primer pairs were designed from regions of homology including first-round primers mJLenvF1 (5′–GTG CAI GTC ATI AGA TGT AGA G–3′) and mPLVenvR7 (5′–GGG GTG TCA TTA TAA IIA GTA AAA TT–3′), amplifying a fragment of ~700 bp, and second-round primers mPLVenvF8 (5′–GGG TGC ATT IGT IAA AGA ICC ATT TTT AG–3′) and mPLVenvR6 (5′–GGT GCI TTG AAI GGA CAC ATT CC–3′), which amplified a 570-bp product. Underlined bases indicate 5′ tail sequences added to the primers to lengthen primers and increase strength of primer binding to the template DNA.

Fifty microlitre PCR reaction mixtures contained 25 μL iQSuperMix (Qiagen), 400 nM of each primer and 10 μL DNA. DNA concentrations varied among samples resulting in a range of ~100–500 ng template per reaction. PCR reaction conditions for both rounds included a hot start at 94 °C followed by 20 cycles of melting at 94 °C for 30 seconds, touchdown annealing temperatures ranging from 55 to 46 °C decreasing by 1 °C every 2 cycles for 30 seconds, extension at 72 °C for 30 seconds, followed by 25 cycles of melting at 94 °C for 30 seconds, annealing at 52 °C for 30 seconds and extension at 72 °C for 30 seconds with a final extension at 72 °C for 3 min. This protocol successfully amplified proviral *env* fragments from three FIV-positive bobcats.

The resulting sequences were aligned, and the regions of highest homology were used to develop the following nested primer pairs that successfully amplified *env* fragments from all remaining bobcats with amplified *pol* sequences ($n = 16$). First-round primers were envfw201 (5′–TTT CTC ATG TTC CTT GAA TGG TAC–3′) and envrv202 (5′–CAC ATT CCA CTT AAT TGG TAT TG–3′), resulting in approximately a 450-bp amplicon. Second-round primers were envfw202 (5′–TGG TAC ATT CTG GGT GTT TAA ATC–3′) and envrv201 (5′–CTA TTT TGG TCA CTC TCT GAT GC–3′), resulting in approximately a 400-bp product. PCR reagents and reaction conditions were the same as above with the exception that touchdown annealing temperatures ranged from 58 to 49 °C and the annealing temperature for the last 25 cycles was 54 °C. PCR products were visualized under UV light using gel electrophoresis with ethidium bromide in 2% agarose gel to confirm the presence of product bands.

PCR products were purified using the QIAquick PCR Purification Kit (Qiagen Inc.) prior to sequencing. Forward and reverse sequences were aligned using BLAST (National Center for Biotechnological Information, Bethesda, MD, USA), and a single consensus FIV sequence was produced for each infected bobcat. All sequences were verified manually. All sequences are available in the NCBI GenBank under accession numbers JN383436–JN383465.

### *Genetic alignments and phylogenetic analyses*

Sequences were trimmed at the 5′ and 3′ ends resulting in all sequences having the same length (*pol* = 427 bp, *env* = 347 bp). Trimmed consensus sequences for each gene fragment ($n = 19$ *pol* & *env*) were converted to coding frame using an online DNA translator tool (Swiss Institute of Bioinformatics; http://www.isb-sib.ch/), prior to alignment in CLUSTAL X2 (Larkin *et al.* 2007). Alignments were input into JMODELTEST (Posada 2008) to estimate the best-fit model of nucleotide substitution, which was the TPM2uf model with among-site rate variation for both gene segments (Kimura 1981). The estimated model parameters used for *pol* were [Lset base = (0.4030 0.1312 0.1592) nst = 6 rmat = (7.3755

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50.7381 7.3755 1.0000 50.7381) rates = gamma shape = 0.2280 ncat = 4 pinvar = 0]. The model parameters for *env* included [Lset base = (0.3707 0.1869 0.1840) nst = 6 rmat = (4.2249 11.3706 4.2249 1.0000 11.3706) rates = gamma shape = 0.2250 ncat = 4 pinvar = 0].

Maximum-likelihood phylogenetic analyses were conducted in Phylogenetic Analysis Using Parsimony (PAUP) (Sinauer Associates, Sunderland, MA, USA) (Swofford 2003). The corresponding *pol* and *env* gene regions from an FIV isolate sequenced from a Florida panther in 1994 were included to provide a root for each tree (Langley *et al.* 1994). ML trees were constructed using an NJ starting tree, followed by a heuristic search using the tree-bisection-reconnection branch-swapping algorithm. The *pol* and *env* trees were found to be congruent, and therefore, a single *pol-env* concatenated sequence was used to construct the final phylogenetic tree for analysis. Bootstrap analyses were performed with 100 iterations for all trees. Viral isolates were divided into four 'FIV Groups' based on clusters of related isolates arising from a basal node supported with an ML bootstrap value of 70 or greater.

We estimated the number of FIV migration events between coastal and inland bobcat subpopulations by calculating the *s* statistic for the observed ML phylogenetic tree in Mesquite 2.75 (Maddison & Maddison 2011). The *s* statistic reflects the minimum number of parsimony steps that explain the discord between subpopulations as monophyletic groups on the tree (Slatkin & Maddison 1989).

To estimate the timeline of past virus transmissions within and between subpopulations, the concatenated viral sequence data were analysed in the coalescent framework as implemented by the program BEAST 1.6.2 (Drummond & Rambaut 2007). The SDR06 substitution model was used with a relaxed uncorrelated lognormal molecular clock (Drummond *et al.* 2006). The tree model included a piece-wise linear Bayesian Skyline prior with five groups and a randomly generated starting tree (Drummond *et al.* 2005). An initial run of 10 000 000 Markov chain Monte Carlo (MCMC) iterations, sampled every 1000 runs, was performed to estimate model parameter values. The first 10% of logged values were discarded as burn-in. From this analysis, the following model parameter priors were changed from default settings: (i) the relative rate parameters were set to vary from 0 to 10; (ii) the Bayesian Skyline population size was set to vary from 0 to 500; and (iii) the mean rate for the uncorrelated relaxed molecular clock was set to vary from 0 to 10.

The final analysis included the above settings with 50 000 000 MCMC iterations sampled every 1000 runs. The first ten per cent of logged values were again discarded as burn-in. The estimated values and associated effective sample size (ESS) for each model parameter were viewed in TRACER 1.5 (Rambaut & Drummond 2007). ESS values for all parameters were >500. The maximum clade credibility tree was produced in TREEANNOTATOR 1.6.2 (Rambaut & Drummond 2002). The resulting tree was viewed in FIGTREE 1.3.1 (Rambaut 2006), and the mean posterior probability heights with 95% highest posterior density (HPD) intervals were labelled on internal nodes.

## Results

### *Bobcat population structure*

*Distribution of alleles.* An analysis of population differentiation performed in GENEPOP indicated that the distribution of alleles among bobcats from the two coastal subpopulations, SJH-west and SJH-east, differed significantly ($P = 0.0064$) at only the FCA008 microsatellite locus. Therefore, the coastal bobcats, regardless of whether they were captured east or west of SR-73, had a similar distribution of alleles at 15 of the 16 microsatellite loci examined. Similarly, the two inland subpopulations, NIR and CPH, significantly differed in allelic distribution at only FCA026 ($P = 0.0025$) and FCA077 ($P = 0.0048$). This finding demonstrates that bobcats captured north and south of SR-91 had a similar distribution of alleles at 14 of the 16 microsatellite loci we analysed. However, the distribution of alleles differed greatly between the coastal and inland subpopulations. SJH-west bobcats significantly differed from NIR and CPH bobcats at 13 and 10 microsatellite loci, respectively, and SJH-east bobcats differed from both NIR and CPH bobcats at 13 loci ($P < 0.01$ all significant pairwise tests). These results indicate a high degree of genetic differentiation exists between bobcats separated by I-5 and its associated urban development.

*Genetic diversity.* No pairwise difference existed in allelic richness (Table S2, Supporting information) when comparing the two coastal subpopulations ($F_{1,29} = 2.59$, $P = 0.118$) or the two inland subpopulations ($P = 0.982$, $F_{1,30} = 0.00$). However, the coastal bobcats (combined SJH-W and SJH-E) had significantly lower allelic richness than the inland bobcats (combined NIR and CPH) ($P < 0.001$, $F_{1,62} = 12.62$). This further suggests that coastal and inland bobcats are genetically distinct and indicates that coastal bobcats have lower genetic diversity than inland bobcats. Interestingly, the BCD8T locus appears to have drifted to fixation in coastal bobcats as only one allele was sampled at this locus from all 49 coastal bobcats. Although the frequency of this allele was also high in NIR (0.82) and CPH (0.67), four and

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five alleles, respectively, were present at this locus in these subpopulations.

*Departures from random mating.* The overall estimate of genetic differentiation among the four putative subpopulations, $D_{est}$ = 0.11, indicates a moderate amount of genetic structure exists within this population. Pairwise $D_{est}$ values were lowest when comparing the two coastal subpopulations ($D_{est}$ = 0.008, SJH-west:SJH-east) or the two inland subpopulations ($D_{est}$ = 0.014, NIR:CPH) and highest between the coastal and inland subpopulations ($D_{est}$ = 0.11, SJH-west:NIR; $D_{est}$ = 0.13, SJH-west:CPH; $D_{est}$ = 0.14, SJH-east:NIR; $D_{est}$ = 0.19, SJH-east:CPH). The estimated differentiation between the coastal bobcats (combined SJH-W and SJH-E) and the inland bobcats (combined NIR and CPH) was $D_{est}$ = 0.14. Locus-specific $D_{est}$ values are reported in Table S2 (Supporting information).

We found no evidence of inbreeding within the overall population ($F_{IS}$ = 0.013; 95% CI: −0.29–0.065), nor in any of the putative subpopulations [$F_{IS}$ = (0.011, SJH-W; −0.045, SJH-E; 0.029, NIR; 0.034, CPH)].

*Individual assignment tests.* Bayesian clustering indicated the assumption of two genetically distinct subpopulations ($K$ = 2) best explained the variation in our microsatellite data (Fig. S1, Supporting information). This result was the same regardless of whether or not source population information was used as a prior in the analysis. All bobcats caught east of I-5 (NIR and CPH bobcats $n$ = 56) were assigned to one 'inland' subpopulation, while 46 of 49 bobcats caught west of I-5 (SJH-west and SJH-east bobcats) were assigned to a 'coastal' subpopulation (Fig. 2). Three individuals captured west of I-5 were genetically assigned to the inland subpopulation and thus represent possible migrants. However, no bobcats captured east of I-5 were genetically assigned to the coastal subpopulation. If any additional human development and/or freeways in this region (i.e. SR-91, SR-73, SR-241, SR-261) were causing genetic structure, a population model with $K$ > 2 should have had the highest support. Therefore, the I-5 corridor is the only human development in this region implicated as a cause of genetic structure among bobcats during our period of sample collection.

Three individuals were identified as first-generation migrants as they were captured in the coastal area but had assignment probabilities of 1.00 to the inland population when capture locations were included in the Structure analysis (denoted by * in Fig. 2b). Three other bobcats captured in the coastal area had the genetic profile of hybrids with partial assignment to both subpopulations (denoted by # in Fig. 2b). No individuals sampled from the inland area were identified as migrants or hybrids from the coastal area.

*Relatedness of individuals.* The average relatedness of bobcats in the coastal population ($R$ = 0.096; SE = 0.0037)

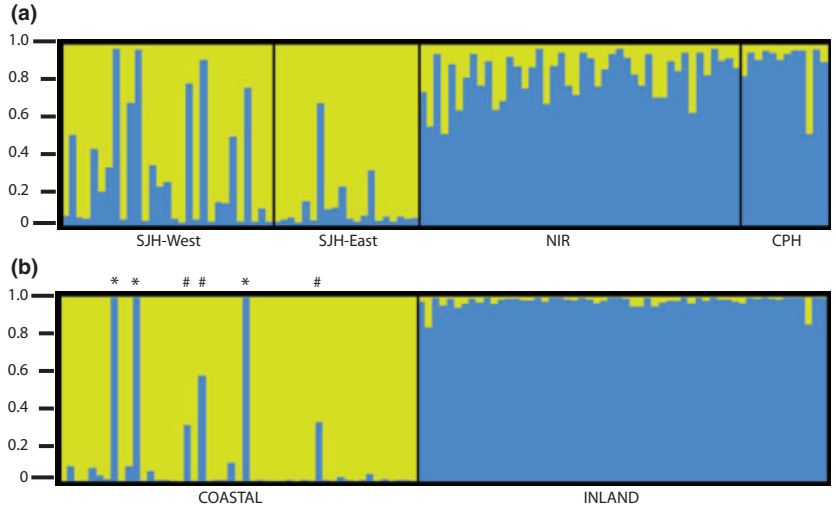


**Fig. 2** Individual bobcat genetic assignments to each of two distinct subpopulations. Each vertical bar represents one individual. Values on the $y$-axis are the probability of assignment of each individual to one of the two genetic groups identified (Fig. S1). The shading of each bar corresponds to the probability of genetic assignment to either the coastal group (yellow) or the inland group (blue) of bobcats. (a) Results for simulation of $K$ = 2 without including a priori capture locations. The majority of individuals captured west of I-5 had strong assignment to one subpopulation (coastal—yellow), while all of the individuals captured east of I-5 had a high probability of assignment to a second subpopulation (inland—blue). (b) Three migrants (*) and three hybrids (#) were identified in Structure using a priori assignments to coast or inland subpopulations based on capture locations. All gene flow was detected from the inland to the coastal subpopulation.

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was significantly higher ($t_{5634}$ = 7.23; $P$ < 0.001) than in the inland population ($R$ = 0.064; SE = 0.0026).

### *FIV phylogenetic analyses*

We amplified a 427-bp region of *pol* and 347-bp region of *env* by PCR from 19 bobcats (four in SJH-west, four in SJH-east and 11 in NIR) bobcats. These included 17 of the 24 (70.8%) bobcats putatively seropositive by Western blot, one bobcat that was negative by Western blot and one bobcat that was screened by PCR only. The inability to amplify FIV sequences from a subset of putatively seropositive bobcats is similar to the findings of previous studies (Troyer *et al.* 2005; Franklin *et al.* 2007b). This is probably the result of a difference in the sensitivity and specificity of these two assays and/or a relatively low FIV proviral load present in a subset of infected animals.

The demographic information for 18 of the 19 FIV-positive bobcats was known: 13 were adult males, one was a yearling male, two were adult females and two were yearling females. The age-specific prevalence of FIV was 14.2% (3/21) for yearlings and 23.8% (15/63) among adults.

The ML phylogenetic tree built from *pol-env* concatenated gene sequences (Fig. 3) shows no evidence of association between capture location (coastal vs. inland) and FIV relatedness (see also Fig. 4). The basal nodes have low bootstrap support, suggesting little overall genetic structuring within the virus population. The number of parsimony steps (*s* statistic) that best explains the discord of FIV relatedness between subpopulations indicates a minimum of three FIV transmission events have occurred between the coastal and inland subpopulations (Slatkin & Maddison 1989).

We estimated the past timeline of virus movement within and between bobcat subpopulations using a coalescent Bayesian model (Drummond *et al.* 2005; Drummond & Rambaut 2007). Figure 5 illustrates the maximum clade credibility tree with labels representing the estimated year of coalescence (mean posterior node ages) for each internal node. The age of the basal nodes is difficult to interpret because of large 95% HPD intervals (analogous to 95% confidence intervals). Therefore, it is impossible to reconstruct a precise timeline of ancestral divergence into the observed FIV groups. However, the more terminal nodes are insightful as they depict the estimated year of recent FIV coalescent events. FIV Group 4, the largest supported group of isolates, comprises six isolates from inland bobcats (x23, x24, x27, x31, x37 and x55) and two isolates from coastal bobcats (x240 and x46). The two coastal isolates in this group share a common ancestor with two of the

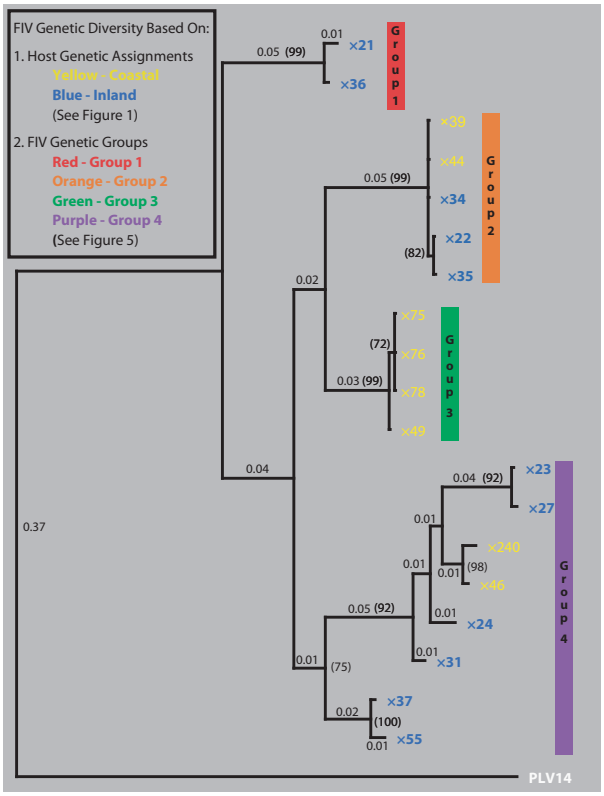


**Fig. 3** Maximum-likelihood phylogenetic tree of feline immunodeficiency virus (FIV) concatenated *pol-env* sequences from 19 infected bobcats. The tree was constructed using a single 774-bp sequence (427 bp from *pol*, 347 bp from *env*) of proviral DNA from each individual. All sequences are in coding frame. Bootstrap values >70 are indicated in parentheses. Branch lengths ≥0.01 are also indicated. Individuals have been coloured to represent their genetic assignment based on the results of the *Structure* analysis (see Figs 1 and 2). Because no migrants were infected with FIV, the colour of an individual also represents whether an individual was captured west (yellow) or east (blue) of I-5. FIV isolates were assigned to groups based on the four most basal supported nodes to illustrate the distribution of FIV genetic diversity across the landscape (See Fig. 4). The tree is rooted with PLV-14, a viral sequence from the same FIV clade, which was sequenced from a Florida panther in 1994.

inland isolates (x23 and x27) in *c.* 1990 (Fig. 5; 95% HPD: 1967–2003). Similarly, FIV Group 2, with 99% bootstrap support, contains nearly identical sequences from three inland bobcats (x22, x34 and x35) and two coastal bobcats (x39 and x44), which share a common ancestor in approximately the year 2000 (Fig. 5; 95% HPD: 1995–2003).

Feline immunodeficiency virus Group 3 contains four closely related viral isolates (Fig. 3; x75, x76, x78 and x49) from related coastal bobcats ($r$ > 0.25). To our knowledge, this is the first evidence of FIV familial transmission among bobcats. Familial transmission of

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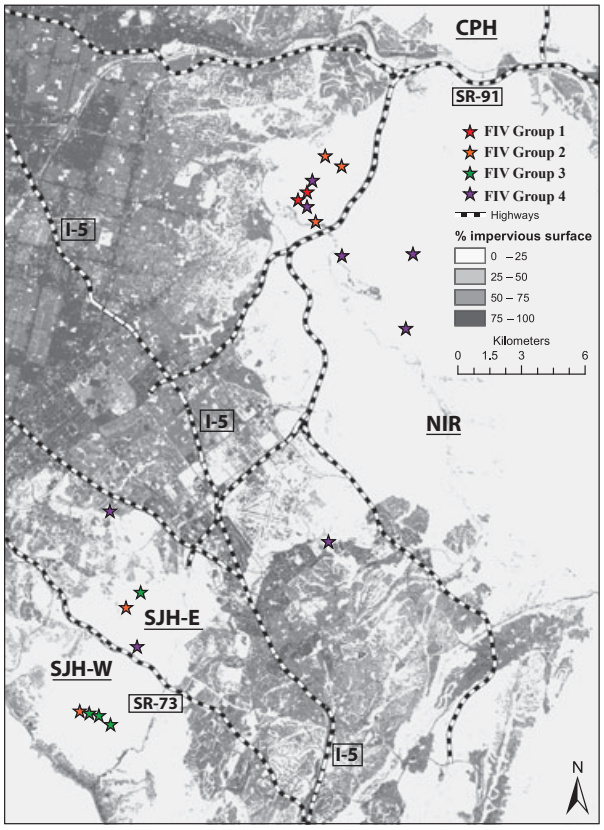


**Fig. 4** Geographical distribution of feline immunodeficiency virus (FIV) genetic diversity among inland and coastal bobcats. Each star indicates the capture location of one FIV-positive bobcat. The stars are coloured corresponding to which of the four groups of related FIV isolates was sampled from each bobcat (See Fig. 3). FIV Groups 1 (red) and 3 (green) contain isolates sampled only from inland or coastal bobcats, respectively. FIV Groups 2 (orange) and 4 (purple), containing both inland and coastal bobcats, resulted from the movement of FIV across Interstate-5. Degree of urban development (% impervious surface) is represented by grey shading.

FIV has been previously documented in mountain lions (Poss *et al.* 2008).

## Discussion

### *Bobcat population structure*

Understanding the degree of connectivity among populations in heterogeneous landscapes is an important goal of ecology, population genetics and conservation biology (Taylor *et al.* 1993; Crooks & Sanjayan 2006; Fischer & Lindenmayer 2007). We evaluated host and pathogen genetic markers to investigate connectivity among bobcats throughout a fragmented urban landscape in southern California. Our results indicate that two genetically distinct groups of bobcats existed in our study area, defined as coastal and inland subpopulations, separated by urban development including Interstate-5 (Figs 1 and 3). This finding is in agreement with other analyses performed previously with a small subset of these bobcats and four of the 16 microsatellite loci utilized in this report (Ruell *et al.* in press).

Our results indicate that the coastal and inland bobcat subpopulations had a different distribution of alleles at most of the microsatellite loci examined and a low, unidirectional pattern of migration from the inland to the coastal area. We also observed reduced genetic diversity and increased relatedness among individuals in the coastal population. These findings suggest the observed genetic differentiation is because of decreased migration through the urban matrix between the inland and coastal habitat patches. We therefore conclude that urban development, including I-5, has been a physical barrier that has reduced bobcat movement and gene flow between isolated groups of individuals.

We did not detect substructure among bobcats separated by the two other freeways that we specifically evaluated, SR-91 and SR-73 and nor did we find evidence of genetic structure because of any other freeways (i.e. SR-241, SR-261) or human development in the region. The maintenance of gene flow across SR-91 and SR-73 is probably explained by the fact that these roadways are perforated by more functional wildlife underpasses and are bordered by more natural habitat than I-5. Therefore, the distance between habitat patches is shorter across SR-91 and SR-73 than across I-5, a factor that has been shown to be an important determinant in carnivore movement among habitat fragments in this region (Crooks 2002). It is possible that because SR-91 and SR-73 are newer roads, any isolation these may be causing has not yet resulted in detectable genetic structure.

Our findings, revealed by analyses of empirical genetic data, are supported by observations from remotely triggered cameras placed near underpasses of all three focal roadways. Cameras placed near the only potential wildlife corridor under I-5 that directly links SJH-E to NIR did not document any movement of bobcats between these habitat patches during 204 consecutive days of observation (Lyren *et al.* 2008a). Cameras, however, did not monitor another potential path across I-5 connecting NIR to SJH-W to the south; road kill carcasses and models of connectivity both suggest this path may be utilized by bobcats (Lyren *et al.* 2008a). In contrast to the lack of remote camera observations of bobcat movement across I-5, a similar duration of camera monitoring of potential wildlife corridors under SR-91 documented many successful movements between NIR and CPH (E. E. Boydston, unpublished data). Likewise, multiple bobcat movements between

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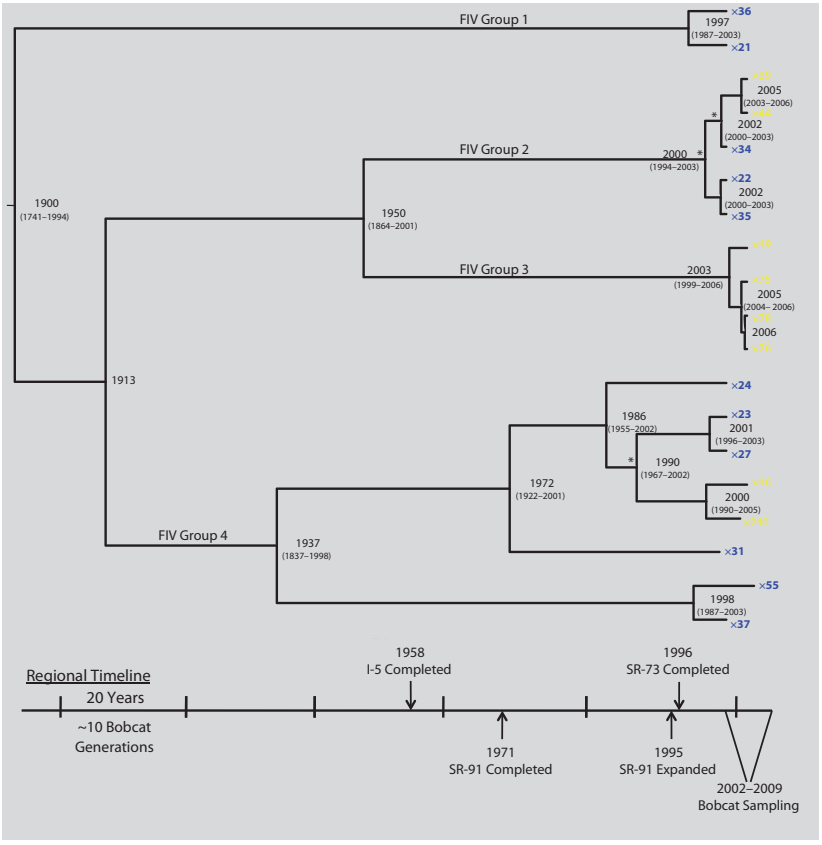


**Fig. 5** The estimated timeline of viral coalescent events. Maximum clade credibility Bayesian phylogenetic tree of *pol-env* concatenated sequences constructed using dated tips. Internal node labels correspond to the highest mean posterior probability estimate [with 95% highest posterior density (HPD) interval] for the year of coalescence. The estimated dates on basal nodes lack precision; therefore, it is impossible to accurately reconstruct the timeline of ancestral diversification into the current four-group structure of feline immunodeficiency virus (FIV). Estimates of recent coalescent events are more precise and depict contemporary FIV transmission within and between bobcat subpopulations. *Indicates common ancestor to contemporary isolates sequenced from both inland and coastal bobcat isolates. Viral movement across I-5 has probably occurred since the estimated date of these coalescent events, resulting in the presence of related viral strains sampled in both subpopulations (See Fig. 4).

SJH-W and SJH-E were also recorded during 358 days of camera observations near SR-73 (Lyren *et al.* 2008b).

Interstate-5 and the surrounding urban matrix have greatly increased in size over time since the original construction was completed in 1958. While it is difficult to know when I-5 became a 'barrier' to bobcat movement, Crooks (2002) estimated that the coastal San Joaquin Hills might have become effectively isolated from inland natural areas around 1980. Given the generation time of bobcats (*c.* 2 years) (Knick *et al.* 1985), between 12 (*c.* 1980) and 25 (*c.* 1958) generations have passed because the inland and coastal bobcat subpopulations became physically isolated.

### *FIV phylogenetic analyses*

Directly transmitted pathogens are inextricably linked to their hosts, and therefore, the geographical distribution of pathogens reflects the movement and contacts of their hosts throughout the landscape. We analysed two gene sequences from FIV, a retroviral pathogen of bobcats, to evaluate whether the gene flow (transmission) of the virus revealed information about bobcat movement not discernable from traditional host genetic analyses. We hypothesized that urban development, which limits bobcat gene flow, would also limit viral transmission between bobcat subpopulations. Given that only one in five bobcats are infected with FIV, the expected virus migration rate is five times lower than the host migration rate. Thus, we expected each of the two bobcat subpopulations would be infected with a genetically distinct viral strain, divergent from one another owing to years of isolation, low viral migration rates and the high mutation rate of FIV.

This prediction is consistent with previous literature demonstrating that geographical or social barriers,

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which prevent mixing between neighbouring host subpopulations, result in genetically structured retrovirus populations (Franklin *et al.* 2007a; Liu *et al.* 2008; see also Fig. S2, Supporting information—demonstrating clear divergence between FIVs isolated from bobcats north or south of Los Angeles). However, the phylogenetic trees constructed in this study from FIV gene segments demonstrated a pattern that differs from these previously published findings. The relatedness of FIV isolates is mixed among coastal and inland bobcat subpopulations, indicating that there is no association between FIV relatedness and the geographical/genetic structure of its host (Figs 3 and 4). While this finding differs from our prediction based on the ecology of FIV, it is consistent with previous studies of urban bobcats in southern California, which have found that individual movements (and thus opportunities for disease transmission) between fragmented habitat patches occur more frequently than predicted by observed levels of gene flow (Riley *et al.* 2006; Ruell *et al.* in press).

The topology of the ML phylogenetic tree (Fig. 3) illustrates that neither the coastal nor the inland bobcats are infected with a monophyletic cluster of viruses. Instead, we identified four groups of related FIV isolates but found no evidence to suggest these groups developed because of the population structure of bobcats. While two of the four groups contained only coastal or inland isolates (FIV Groups 1 and 3), these were the smallest groups sampled and the other two FIV groups did not follow this pattern. Instead, FIV Groups 2 and 4 contained closely related viruses arising from both bobcat subpopulations. The coastal isolates within each of these two groups shared recent common ancestry with inland viruses (Fig. 5), and thus, we conclude that FIV-infected bobcat migration events across I-5 are responsible for the observed mixing of isolates. Half of the viruses infecting coastal individuals (4/8) recently originated from, or were transmitted to, inland bobcats. The former is likely to have occurred in FIV Group 2 as suggested by the presence of multiple inland isolates basal to the two coastal isolates and evidence of a long Group 2 residence time within the inland subpopulation.

### *Utilizing host and pathogen genetics*

The presence of related FIV strains on both sides of I-5 suggests that the intervening urban development is somewhat permeable to bobcat movement and disease transmission, despite the presence of distinct genetic structure among the host population. There may be several explanations for the discrepancy between the population structure of FIV and its host. One hypothesis is that a recent increase in bobcat migration across I-5 has led to the observed mixing of viral genotypes, but not enough time has passed for this recent increase in migration to counteract previously established genetic structure among the bobcats. While possible, we consider this unlikely as human development along the I-5 corridor has increased over time, and no notable changes have been made in the area (e.g. underpasses, culverts) that would account for a recent increase in connectivity between the two subpopulations.

An alternative hypothesis is that FIV exchange between the two subpopulations is not necessarily linked to bobcat gene flow. Transient movements of individuals across a semi-permeable barrier such as I-5 may not result in the exchange of genetic material, but may involve sufficient contact between individuals to allow for disease transmission. Under this hypothesis, the contrasting patterns of population structure may reflect differences in the underlying ecology of the two molecular markers.

Microsatellite markers are useful for detecting host gene flow, the specific process involving animal movement which results in the exchange of genetic material from one group of individuals to another (Endler 1977). According to this definition, gene flow is dependent upon successful mating after migration. FIV transmission, however, can occur both vertically *and* horizontally, allowing FIV isolates to move between individuals and subpopulations in the absence of gene flow. For example, Biek *et al.* (2003) reported that for one population of mountain lions, horizontal transmission among adults resulted in the majority of new FIV infections and accounted for the observed increasing prevalence of FIV with age. Vertical transmission, resulting in a cohort of young individuals infected prior to adolescence, was equally important in explaining the dynamics of FIV in the population.

Given that bobcats and mountain lions share many life history characteristics, it is probably that similar FIV transmission dynamics occur in bobcats. Indeed, the relative prevalence of FIV in yearlings (14%) vs. adults (24%) in this study is similar to the age–prevalence relationship described in Biek *et al.* (2003). Young infected individuals may therefore play an important role in the maintenance and spread of FIV in this population. At adolescence, juvenile (usually male) bobcats often make transient movements during dispersal from their natal range while attempting to establish a new home range (Kitchings & Story 1984; Knick 1990; Hansen 2007). Young bobcats infected prior to dispersal therefore represent a potentially important mode of virus movement within and between subpopulations.

In fragmented landscapes such as southern California, where urban development and freeways act as boundaries limiting animal movement, bobcat home

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ranges may shrink, and the amount of overlap between neighbouring home ranges may increase (Riley 2006; Riley *et al.* 2006). This pattern of 'home-range pile-up' has been described in other bobcat populations in California (Riley *et al.* 2006). This phenomenon decreases the probability that juveniles dispersing to a neighbouring subpopulation will successfully mate. Under these conditions, the actual rate of bobcat movements, contacts and opportunities for disease transmission between subpopulations would be higher than expected based on migration rates estimated from gene flow.

The low level of gene flow we detected across I-5 occurred in a unidirectional pattern from the inland area towards the coast. The coastal population, while reduced in overall genetic diversity, contains both migrants and hybrids from the inland population. This suggests that, while rare, inland bobcats can successfully migrate to and breed in the coastal population, while the reverse was not seen. However, inland FIV isolates do not form a monophyletic group; two of the three FIV groups infecting coastal bobcats also infect inland bobcats. There are two possible explanations to this pattern. One is that movement of FIV has occurred repeatedly one-way from the inland subpopulation to the coast, causing the diversity among coastal isolates to closely mirror that observed inland. This hypothesis is consistent with the one-way pattern of bobcat movement we detected from the microsatellite analysis.

The other possibility is that a coastal virus population diverged from inland viruses after the two groups were isolated by urban development and has since been transmitted back into the inland subpopulation multiple times via transient movements and contacts resulting in disease transmission but not gene flow. Tracking the movements of individual bobcats, evaluating FIV diversity in other neighbouring bobcat populations and utilizing spatially explicit phylogeographic analyses may help to distinguish between these alternatives.

In conclusion, our findings indicate that bobcats inhabiting this fragmented landscape in southern California are physically isolated and genetically structured. This pattern is consistent with decreased connectivity across urban development, resulting in low levels of migration and/or a low probability that migrants establish a home range and successfully mate. However, movements are apparently made, allowing for disease transmission between these habitat fragments. This conclusion carries with it conservation implications as populations with these characteristics are susceptible to decline as a result of a continued loss of genetic diversity from genetic drift and decreased individual fitness because of inbreeding depression (Frankham 2006). In addition, both subpopulations should be managed as a unit when considering treatment and prevention interventions during future disease outbreaks. Habitat conservation and restoration as well as connectivity enhancements such as functional underpasses to better facilitate movement of bobcats under roadways may help safeguard their persistence in the face of substantial ongoing threats posed by humans in this region.

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The authors are interested in research involving ecology, conservation, and/or infectious diseases of carnivores. They share particular interest for topics relating to the effects of human activities on carnivores.

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## Data accessibility

DNA sequences—GenBank accession numbers JN383436–JN383465. Microsatellite data—DRYAD entry doi:10.5061/dryad.mm317th7.

## Supporting information

Additional supporting information may be found in the online version of this article.

**Table S1** $F_{ST}$ values calculated from 16 bobcat microsatellite loci.

**Table S2** Measures of genetic structure among bobcats calculated from 16 microsatellite loci.

**Fig. S1** Estimating the number of genetic subpopulations (*K*) of bobcats.

**Fig. S2** Maximum-likelihood phylogenetic tree built from *pol* sequences using the same model parameters as those described to produce the Maximum-likelihood tree in Fig. 4 (see Methods).

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COMMENTARY | ENVIRONMENT | MY TURN

# My turn: Here's how rooftop solar can combat wildfires

BY GUEST COMMENTARY

PUBLISHED: FEBRUARY 13, 2019

Workers installing solar panels on a residential homes roof.

**By Audrey Lee**, Special to CALmatters

U.S. District Court Judge William Alsup recently issued an unprecedented directive to Pacific Gas & Electric: Inspect its entire electric grid in the coming months and turn off power during fire-prone weather if its equipment has not been deemed safe for those conditions.

After the terrible losses caused by wildfires in recent years, this dramatic turn of events portends greater challenges to utilities in the face of a changing climate.

The Fourth National Climate Assessment reports that climate change and extreme weather events are going to make power disruptions and related wildfires even more common.

Californians deserve real solutions to reduce fire risk while meeting their energy needs. PG&E, other utilities, and the rooftop solar industry should partner to design wildfire mitigation plans that truly protect communities and address the concerns identified by state residents, policymakers, advocates, and the courts.

Local solar power paired with batteries can provide reliable energy and keep electricity running for communities in need, particularly at times when a power line needs to be turned off for safety reasons. This technology might also reduce the chances of electric sparks on overhead lines, which could result in dangerous wildfires.

Electrical lines can only safely carry a certain amount of power without getting too hot. When an electric line heats up with too much energy running through it, the line can sag and drop closer to potential hazards.

Currently, utilities can manage higher power flows for a short time to carry out limited repairs without transmission and distribution lines reaching extreme temperatures, but it may not be enough to handle increased wildfires.

If communities were to deploy more local solar and batteries, we could reduce the amount of power flowing through electricity lines, and coordinate with utilities in real time, leading to an improved scenario for utilities to carry out maintenance, reroute power in case of problems, and ensure overall safety of fire-prone communities.

I have been working to promote energy innovation for decades, first with the U.S. Department of Energy, then at the California Public Utilities Commission, and now as the head of Energy Services at Sunrun.

Let me paint a picture of how this could work.

Consider a community of 500 homes, each using about 5 kilowatts of power, which is roughly the profile of a significant number of homes in fire-prone areas in California.

All these homes are currently connected to the wider network by a single electricity line. For a small community such as this, as few as five to 10 houses with rooftop solar and batteries could



at the required level for safe conditions during times of high demand.

Even in the case that this community were to require more energy and the electricity line supporting it reaches 100 percent capacity, this community would only need 50 to 100 homes with rooftop solar and storage to return to safe conditions.

Naturally, local solar and batteries  are more useful as more homes have them. But the minimum threshold to be valuable to engineers can be as low as a handful of customers, depending on how the electricity system in that area has been designed and built, as well as the needs of the supported community.

Home solar and batteries can provide for more resilient energy solutions in high-risk fire areas serviced by electric lines. More importantly, they can help reduce or even prevent power outages for homes, businesses, and other critical facilities.

We have a short period of time until the next fire season hits us. Californians are demanding better solutions from their utilities, now.

Sustainable business models and partnerships with solar leaders looking to protect fire-prone communities are a start. Let's use this opportunity to come together—state leaders, regulators, local policymakers, the rooftop solar industry and utilities—to swiftly bring more solar and batteries to the communities that need them when it matters most.

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Audrey Lee is vice president for energy services, Sunrun, based in San Francisco, with services in 23 states plus Washington, D.C., and Puerto Rico. audrey.lee@sunrun.com. She wrote this commentary for CALmatters.

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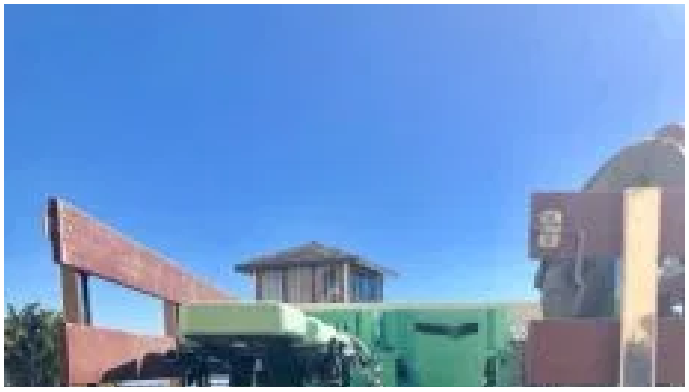

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# A systematic review of the physical health impacts from non-occupational exposure to wildfire smoke

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## Abstract

**Background—**Climate change is likely to increase threat of wildfires, and little is known about how wildfires affect health in exposed communities. A better understanding of the impacts of the resulting air pollution has important public health implications for the present day and the future.

**Method—**We performed a systematic search to identify peer-reviewed scientific studies published since 1986 regarding impacts of wildfire smoke on health in exposed communities. We reviewed and synthesized the state of science of this issue including methods to estimate exposure, and identified limitations in current research.

**Results—**We identified 61 epidemiological studies linking wildfire and human health in communities. The U.S. and Australia were the most frequently studied countries (18 studies on the U.S., 15 on Australia). Geographic scales ranged from a single small city (population about 55,000) to the entire globe. Most studies focused on areas close to fire events. Exposure was most commonly assessed with stationary air pollutant monitors (35 of 61 studies). Other methods included using satellite remote sensing and measurements from air samples collected during fires. Most studies compared risk of health outcomes between 1) periods with no fire events and periods during or after fire events, or 2) regions affected by wildfire smoke and unaffected regions. Daily pollution levels during or after wildfire in most studies exceeded U.S. EPA regulations. Levels of $PM_{10}$, the most frequently studied pollutant, were 1.2 to 10 times higher due to wildfire smoke compared to non-fire periods and/or locations. Respiratory disease was the most frequently studied health condition, and had the most consistent results. Over 90% of these 45 studies reported that wildfire smoke was significantly associated with risk of respiratory morbidity.

**Conclusion—**Exposure measurement is a key challenge in current literature on wildfire and human health. A limitation is the difficulty of estimating pollution specific to wildfires. New

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methods are needed to separate air pollution levels of wildfires from those from ambient sources, such as transportation. The majority of studies found that wildfire smoke was associated with increased risk of respiratory and cardiovascular diseases. Children, the elderly and those with underlying chronic diseases appear to be susceptible. More studies on mortality and cardiovascular morbidity are needed. Further exploration with new methods could help ascertain the public health impacts of wildfires under climate change and guide mitigation policies.

**Keywords**

Wildfire; Air pollution; Health; Smoke; Forest Fire

## 1. Introduction

Much remains unknown regarding the public health impacts of forest fire smoke, but interest in the topic is growing as forest fire incidence rises in many parts of the world (Dimopoulou and Giannikos 2004). There is broad consensus that climate change is increasing the threat of forest fires (Albertson *et al.*, 2010; Balling *et al.*, 1992; Flannigan and Vanwagner 1991; Keeton *et al.*, 2007; Malevsky-Malevich *et al.*, 2008; Spracklen *et al.*, 2009), with fires that burn more intensely, occur more frequently, and can spread faster (Fried *et al.*, 2008; Fried *et al.*, 2004; Parry *et al.*, 2007; Westerling and Bryant 2008). The U.S. Forest Service noted that forest fires have already become more intense and that the forest fire season has expanded (U.S. Forest Service 2009). While an increasing frequency of forest fires has often been attributed to many factors including changes in land use, higher spring and summer temperatures may be more relevant (Westerling *et al.*, 2006). The Intergovernmental Panel on Climate Change (IPCC) anticipates that climate change will lengthen the window of high summertime forest fire risk in North America by 10–30%, and result in increased frequency of forest fires in many other parts of the world (Parry *et al.*, 2007). As a result, exposure to air pollution from forest fires is anticipated to increase in coming decades (Interagency Working Group on Climate Change and Health 2010).

The U.S. Forest Service recognizes forest fire smoke as a hazard to human health and identifies airborne particulate matter (PM) as the component of greatest concern for the public (U.S. Forest Service 2010). Numerous studies have demonstrated links between airborne particles and health outcomes including mortality and hospital admissions (Lepeule *et al.*, 2012; Medina-Ramon *et al.*, 2006; Peng *et al.*, 2008; Pope and Dockery 2006). However, not all particles appear to be equally toxic as research indicates that the size and chemical composition of airborne particles affect its impact on health (Ebisu and Bell 2012; Franck *et al.*, 2011; Zanobetti *et al.*, 2009). In general, effects are stronger for smaller particles, which can deposit deeper in the respiratory tract (Valavanidis *et al.*, 2008). The specific mechanistic pathways to adverse health outcomes remain unclear, but chemical composition, particle size, number, and shape have been identified as of putative importance. As the chemical composition of forest fire smoke is likely to differ from those of other sources (e.g., vehicles) (Mao *et al.*, 2011; Pio *et al.*, 2008; Robinson *et al.*, 2011), the observed health associations for more commonly studied air pollutants and sources, such as particulate matter in urban settings, may not be generalizable to pollution from forest

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fires. Thus, scientific evidence is needed on the health burden from forest fire smoke specifically.

Understanding how forest fire smoke affects public health has the potential to inform intervention-focused policies to protect public health in the present day, climate change mitigation policies, research on health impacts from a changing climate, and economic estimates of the health costs of forest fires. We reviewed and summarized the published literature regarding the public health impacts of forest fire smoke with the goals of synthesizing existing information and identifying gaps in scientific knowledge.

## 2. Methods

### Eligibility criteria

We reviewed peer-reviewed journal articles on the topic of forest fire/wildfire smoke and health, published between 1 Jan 1986 and 30 May 2014. We included studies written in English or Portuguese (with English abstract), and excluded papers written in other languages. We considered all papers relevant to non-occupational exposure to wildfire smoke and physical health impact. We excluded experimental/chamber studies because it is not clear how relevant the exposure level/composition is to those experienced by the community. We excluded conference abstracts, unpublished studies, and non-research publications, such as commentaries. Natural fires were included and controlled prescribed burns were excluded. We did not exclude studies based on type or diversity of vegetation, such as trees peat bog or savannah. All fires are referred to as ‘wildfire’ hereon. We excluded studies of indoor and outdoor wood burning for heating or cooking purposes. Studies that investigated occupational exposures were excluded, as the focus of this review was impacts on communities or broader populations. Therefore, we excluded studies of fire fighters. Since mental health issues are not direct physical health consequences from exposure to wildfire smoke, we excluded studies that investigated only mental health outcomes. As this review focussed on wildfire smoke we also excluded studies that investigated non-smoke related morbidities, such as burns and accidents. Thus, we focused on wildfire smoke and its physical health impacts on the general population.

### Information sources

We considered papers indexed in PubMed, a database of biomedical literature and life science journals, managed by the U.S. National Library of Medicine (NIH 2011) and Scopus, a comprehensive database of research literature (Elsevier 2013). References of the resulting papers were examined to better ensure a complete assessment of the literature.

### Search terms

Detailed information on the search terms is provided in the supplemental material. Briefly, key words included “wildfire”, “forest fire”, or “bushfire” with any of the following: “health”, “hospital*”, “respir*”, “pulmon*”, “asthma*”, “cardiac”, “cardiovascular”, or “mortality”, where “*” stands for any combination of letters (*e.g.*, hospital* can represent hospitalizations or hospital) (Appendix A).

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### Summary measures

We summarized the papers with respect to study setting, study design, exposure and outcome assessment, participant vulnerability, key findings, and estimates of association (*e.g.*, odds ratios) when provided.

### Study assessment

As exposure assessment is a critical challenge in the study of health impacts from wildfire smoke, we described the approaches used by identified studies to estimate exposures. We assessed the overall state of scientific evidence on associations between wildfire smoke and health outcomes for respiratory morbidity, cardiovascular morbidity, mortality, and other outcomes. The approaches to assess health outcomes are diverse, and we summarized the sources of health data for each study. We grouped the studies by health outcomes and summarized the results on health effects. We described factors that might have influenced the summary of evidence based on the studies reviewed. Finally, we highlighted the limitations of these studies and identified needs for future research.

## 3. Results

The database searches identified 926 papers. We then excluded 277 duplicates (i.e., papers identified by more than one search). We eliminated papers that did not meet the inclusion criteria, by first screening the titles and abstracts (526 papers excluded) and then by a review of the full articles (62 papers excluded). We also excluded studies for which wildfire smoke exposure was not a dominant component relative to other ambient sources (e.g. Sarnat *et al.*, 2008). The final review included 61 studies of human health impacts of wildfires in community populations (Table 1).

### Study setting

More studies were identified for more recent years, with 4 studies published before 2000 and 35 studies published in the last 5 years. Most studies focused on the Brazilian Amazon, Southeast Asia and the Pacific, the North American West, and the Mediterranean, where wildfires are common. The U.S. and Australia were the most frequently studied countries (18 U.S. studies, 15 Australian studies). Southeast Asia was also frequently studied (9 studies). No studies were set in Africa. Geographic scales ranged from a single small city (population about 55,000) (Huttunen *et al.*, 2012) to the entire globe (Johnston *et al.*, 2012). Most studies focused on cities or regions close to fire events.

### Study design

The majority of studies were based on either spatially or temporally aggregated populations, such as ecological studies (37 of 61 studies). There were relatively fewer cohort or panel studies (14 of 61 studies). Most of the studies compared the risk of health outcomes between 1) periods with no fire events and periods during or after the fire events, or 2) regions not affected by wildfire smoke and regions affected by wildfire smoke. The selection of model adjustment variables was not universal, but can be classified as 1) meteorological; 2) air pollutants other than the pollutants of interest; 3) community-level socio-demographics; and 4) temporal effects (seasonal or secular trend). Of these, meteorological factors were the

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most prevalent adjustment variables. Some studies controlled for individual variables, such as age group and sex, by stratification (Analitis *et al.*, 2012; Castro *et al.*, 2009; Delfino *et al.*, 2009; Frankenberg *et al.*, 2005; Henderson *et al.*, 2011; Mott *et al.*, 2005; Nunes *et al.*, 2013; Prass *et al.*, 2012; Rappold *et al.*, 2011; Sarnat *et al.*, 2008)

### Health outcomes investigated and outcome assessment

Respiratory disease was the most frequently studied outcome (45 studies (74% of 61 studies)) (Supplementary Table A.4). The outcomes included contacts with emergency departments (ED), hospitals or other primary care providers (33 studies (54%)), respiratory symptoms or lung function measurements (9 studies (15%)), and dispensation or consumption of medication (three studies (5%)). Relatively few studies examined cardiovascular morbidity (14 studies) or mortality (13 studies) (Table 2).

Other outcomes investigated were diarrhea due to power outage after wildfire events (identified from surveillance records), birth weight (obtained from hospital birth records), blood biomarkers for systemic inflammation and bone marrow content. The studies of lung-function, blood biomarker concentration and bone marrow content were all cohort studies measuring subjects' lung function or blood samples both before and after fire events.

The most common source of information for health outcomes was the use of datasets maintained by governmental agencies or statistical bureaus (32 studies), followed by hospital admission records or billing records (19 studies), interviews or surveys (10 studies), and subject tests such as lung function or blood samples (seven studies). Some studies used multiple methods to assess health outcomes. All mortality data came from governmental agencies or bureaus. Use of individual surveys (*e.g.*, "smell of wildfire smoke indoors" (Kunzli *et al.*, 2006)) was the most employed method in assessing personal exposure and self-reported symptoms for short-term studies.

### Exposure assessment

The most commonly used method for either designating a fire period or area, or assessing exposure for previously designated fire and non-fire periods or areas, was use of measurements from land-based air pollutant monitors (35 studies), followed by satellite-based imagery or models (11 studies), air quality modelling (six studies) and personal exposure from individual surveys, personal reports, or personal photometers (three studies) (Supplementary Table A.3). Of the 61 studies, seven studies used other methods to assess exposure, such as air sample analysers. Satellite-based methods became popular in studies from recent years.

Pollutant data from air monitors were usually obtained by governmental agencies or research institutions and were used as the exposure variable in statistical models. The monitoring data usually covered pre-, during- and post-fire periods. Most of the studies determined "exposed period" based on the start/end dates of fire events but did not specify how the start/end days were identified. Some studies used thresholds of air monitoring data to categorize days, for example, high PM days with aerodynamic diameter <2.5μm ($PM_{2.5}$) >40μg/$m^3$, low PM days with $PM_{2.5}$<10μg/$m^3$ (*e.g.*, Johnston *et al.*, 2002). Personal surveys

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and reports generally asked questions such as “did you smell any smoke?” or “did you have any health symptoms?” plus the respondents’ personal characteristics, such as age and education. Personal photometers were used to measure personal exposure to $PM_{2.5}$ (Huttunen *et al.*, 2012).

Satellite-based imagery or models are increasingly common in the recent studies to aid exposure assessment. Some satellite-based studies used satellite images to detect “hotspots”, which were used as indicators of fire events (*e.g.*, Castro *et al.*, 2009; de Mendonca *et al.*, 2006)). Some studies determined “exposed region” based on either satellite images or proximity to fire events (*e.g.*, Kunii *et al.*, 2002). The majority of the studies using satellite-based methods measured exposure for at least 5 years. In contrast, studies using individual photometers or reports usually investigated individual-specific exposure among subjects of a prospective cohort for a shorter period of a few days to a few months (Frankenberg *et al.*, 2005; Kunii *et al.*, 2002; Kunzli *et al.*, 2006).

The length of exposure measurement varies from a few days to over a dozen years. Huttunen *et al.* assessed daily average exposure of $PM_{2.5}$ and PM with aerodynamic diameter < 10μm ($PM_{10}$) during a 12-day fire that occurred in Kotka, Finland from Apr. 25 to May 6, 2006 (2012). Many studies compared longer-term exposure across months or seasons (Hanigan *et al.*, 2008; Johnston *et al.*, 2007; Smith *et al.*, 1996). Elliott *et al.* (2013) measured exposure during fire seasons (Apr. 1 to Sep. 30) in each year (2003–2010) and compared the health risk during fire seasons with non-fire seasons. Evaluation of long-term exposure was more common in regions with distinct fire seasons, such as Australia (*e.g.*, Hanigan *et al.*, 2008; Johnston *et al.*, 2011; Morgan *et al.*, 2010; Smith *et al.*, 1996) and Canada (Elliott *et al.*, 2013). Johnston *et al*. (2011) investigated long-term mortality effect by measuring $PM_{10}$ exposure attributed to wildfires over 13.5 years, from 1994 to 2007 in Sydney, Australia.

Other studies compared exposure and health during the period when forests were burning to the periods before and/or after the fire (Supplementary Table A.3). Of these studies, Duclos *et al.* (1990), Frankenberg *et al.* (2005), and Moore *et al.* (2006) compared exposure and health during the fire events or seasons with control periods in preceding and/or subsequent years. Many studies estimated short-term (*e.g.*, a few days to one or two weeks) exposure under a certain fire event and compared the health risk during the fire event with that during short pre- or post-fire periods (*e.g.*, Schranz *et al.*, 2010; Sutherland *et al.*, 2005; Vora *et al.*, 2011). This exposure timeframe was common in studies based on local populations and a single fire event. Many studies compared longer-term exposure across months or seasons (*e.g.*, Hanigan *et al.*, 2008; Johnston *et al.*, 2007; Smith *et al.*, 1996).

Almost all studies mentioned that air pollutant levels, especially particulate matter levels, increase dramatically during wildfire events. Figure 1 shows estimated air pollutant levels during fire periods compared with levels in control periods. $PM_{2.5}$ levels in most studies exceeded the U.S. EPA National Ambient Air Quality Standard for 24-hour $PM_{2.5}$ ($35\mu g/m^3$). Some studies indicated particulate levels during fire periods over 100 $\mu g/m^3$ for $PM_{2.5}$ and over 500 $\mu g/m^3$ for $PM_{10}$ (*e.g.* Hänninen *et al.*, 2009; Holstius *et al.*, 2012; Kolbe and Gilchrist 2009; Kunii *et al.*, 2002)

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### 3.1 Association between wildfire smoke and health outcomes

**3.1.1 Respiratory morbidity—**Of the health outcomes examined, respiratory morbidity had the strongest evidence of an association with wildfire smoke, with a statistically significant adverse association reported for 43 of the 45 respiratory studies (Supplementary Table A.4). Analysis of respiratory-related contacts with primary care providers constituted 31 studies that reported associations and 2 studies that did not detect an adverse association. ED contacts for asthma in Darwin, Australia were 2.4 (95% confidence interval 1.5–3.9) times greater on a fire day ($PM_{10}$>40μg/$m^3$) than on a non-fire day ($PM_{10}$<10 μg/$m^3$) (Johnston *et al.*, 2002). Two other Australian studies reported greater risk of hospital admission for elevated exposure two days before the hospital admission day (Morgan *et al.*, 2010) and five days before the admission day (Chen *et al.*, 2006). Associations for longer lags (greater than five days) between exposure and hospitalization were not directly investigated in any study. From cross-sectional studies there were increases in primary care contacts for a 12-week period of exposure to wildfire smoke in California (Lee *et al.*, 2009) and a five-week exposure period in Canada (Moore *et al.*, 2006) compared to the same period in previous years when there were no fires. However, it remains unclear as to whether admissions increased due to high acute exposures over short periods (days) and/or lower levels accumulated over a longer period (months). Associations were consistently reported between wildfire related exposure and respiratory symptoms or dispensation/use of medication (all 12 studies). Adverse associations were observed for cough, wheeze and eye irritation (Supplementary Table A.4).

A statistically significant association between exposure to wildfire smoke and hospital or emergency room admissions for respiratory diseases was not reported in two of the 45 studies (Azevedo *et al.*, 2011; Smith *et al.*, 1996). A study of Sydney compared ED records in seven hospitals during a two-week fire period with that during the same period in the previous year. The researchers found no difference in asthma ED visits during the two periods (Smith *et al.*, 1996). The Northern Portugal study reported that high ozone level (greater than 100μg/$m^3$) during the three-month fire period was not associated with respiratory disease admissions.

**3.1.2 Cardiovascular morbidity—**Of the 14 studies that assessed the relationship between wildfires and cardiovascular morbidity, six reported a statistically significant increase in risk of cardiovascular outcomes with exposure to wildfire smoke. Some authors reported change in risk per unit (such as per 100 μg/$m^3$) increase in daily measurement of certain wildfire-promoted pollutants, such as ozone, $PM_{10}$ or $PM_{2.5}$ (Azevedo *et al.*, 2011; Lee *et al.*, 2009; Rappold *et al.*, 2012). Others reported changes in risks comparing regions or time periods of wildfires with non-wildfire regions or times (Delfino *et al.*, 2009; Rappold *et al.*, 2011). $PM_{10}$ was the most commonly studied pollutant for cardiovascular diseases and most of the $PM_{10}$-CVD studies (eight out of nine) did not find any significant association. Other air pollutants from wildfires were less studied and their impact on cardiovascular illness remains unclear. Study findings varied geographically, with no report of a statistically significant cardiovascular impact of wildfire smoke in any study from Australia and Canada (seven out of 14) (Crabbe 2012; Hanigan *et al.*, 2008; Henderson *et al.*, 2011; Johnston *et al.*, 2007; Martin *et al.*, 2013; Moore *et al.*, 2006; Morgan *et al.*,

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2010). Contrastingly, five out of six U.S. studies reported that exposure to wildfire smoke was associated with hospital admissions for cardiovascular diseases, such as cardiac arrests, or symptoms such as chest pain (Delfino *et al.*, 2009; Lee *et al.*, 2009; Rappold *et al.*, 2012; Rappold *et al.*, 2011). All studies assessed cardiovascular disease by hospital admissions or emergency room visits. A U.S. study found that a 100μg/$m^3$ increase in wildfire smoke-related $PM_{2.5}$ was associated with a significant 42% (95%CI: 5%–93%) increase in emergency room visits for congestive heart failure (CHF) (Rappold *et al.*, 2012). However, there were too few studies on specific cardiovascular endpoints, such as ischemic heart disease (*e.g.*, Azevedo *et al.*, 2011; Crabbe 2012; Moore *et al.*, 2006) to establish consistency of associations.

**3.1.3 Mortality—**Mortality was associated with wildfire smoke for nine of 13 studies. Only three of these studies assessed non-accidental mortality (Analitis *et al.*, 2012; Johnston *et al.*, 2011; Vedal and Dutton 2006). Two investigated cause-specific mortality for respiratory and COPD (Castro *et al.*, 2009; Nunes *et al.*, 2013). Other studies examined total all-cause mortality. The increase in mortality under exposure to wildfire smoke, compared with periods of no fires, ranged from 1.2% for children during the fire event (Jayachandran 2009) to 92.0% for respiratory mortality during days with large fires (Analitis *et al.*, 2012). Large fires (>3000 hectares burned) had larger estimated associations with mortality than smaller fires (Analitis *et al.*, 2012). As wildfire events occur more often in summer, Shaposhnikov *et al.*, (2014) examined the interaction between heat and wildfire smoke. They found that temperature and $PM_{10}$ (largely due to wildfires) collectively contributed to over 2000 deaths. One of the three studies that investigated shorter-term exposure and did not report a statistically significant association did not provide numeric results (Vedal and Dutton 2006) while the effect estimates reported in the other two studies were in the positive direction, i.e., adverse mortality effects (Hänninen *et al.* (2009) and Morgan *et al.* (2010)).

**3.1.4 Other health outcomes—**Eleven studies investigated other health outcomes in relation to wildfire smoke. These included studies on birth weight (Holstius *et al.*, 2012; Prass *et al.*, 2012), bone marrow content (Tan *et al.*, 2000), systematic inflammation (Huttunen *et al.*, 2012), physical strength and overall health (Frankenberg *et al.*, 2005), diarrhea (Viswanathan *et al.*, 2006), diabetes (Lee *et al.*, 2009), and injuries (Cameron *et al.*, 2009; Cleland *et al.*, 2011). For the two studies that investigated birth weight, results were inconsistent (Holstius *et al.*, 2012; Prass *et al.*, 2012). All three cohort studies reported significant adverse associations between wildfires and health: systemic inflammation (Huttunen *et al.*, 2012), bone marrow content (Tan *et al.*, 2000), and physical strength and overall health (Frankenberg *et al.*, 2005). Diarrhea and diabetes were mentioned as health outcomes of interest in multiple studies (Aditama 2000; Jalaludin *et al.*, 2000; Lee *et al.*, 2009; Viswanathan *et al.*, 2006), but only two reported the results (Lee *et al.*, 2009; Viswanathan *et al.*, 2006). Exposure to wildfire smoke did not show discernible effects on either diarrhea or diabetes.

**Vulnerable sub-populations:** A limited number of studies assessed whether some populations face higher health risk from exposure to wildfire smoke than others, examining population characteristics such as age categories. The age cut-offs for age categories varied

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by study. Larger positive associations between wildfire smoke and cardiorespiratory morbidities were observed for middle-aged adults (Henderson *et al.*, 2011) and older adults compared to other age groups (Analitis *et al.*, 2012; Castro *et al.*, 2009; Delfino *et al.*, 2009; Frankenberg *et al.*, 2005; Morgan *et al.*, 2010; Nunes *et al.*, 2013; Shaposhnikov *et al.*, 2014). Elevated levels of wildfire smoke had larger risk estimates for asthma hospitalizations among adults aged 40–64 years (Mott *et al.*, 2005), 15–64 years (Morgan *et al.*, 2010), and 19–64 years (Rappold *et al.*, 2011) compared to other age groups. Risk of respiratory-related hospital contacts associated with wildfire smoke was higher for children (<5 years) compared with other age groups (Ignotti *et al.*, 2010).

Men and women may have different health risks when exposed to wildfire smoke. Risks for asthma-related symptoms or visits in relation to wildfire smoke were greater for women than men (Lee *et al.*, 2009; Rappold *et al.*, 2011). However, Henderson *et al*. (2011) and Prass *et al.* (2012) did not find differences in wildfire effect estimates between men and women in respiratory and cardiovascular physician visits, and birth weight, respectively.

Three studies reported effect modification by socio-economic status (SES), race, or co-morbidities. Larger risk estimates between wildfire smoke and risk of asthma and congestive heart failure were observed among counties of lower SES compared to higher SES counties (Rappold *et al.*, 2012). Aboriginal Australians had higher risk of respiratory admissions and emergency admissions than other races when exposed to $PM_{10}$ (Hanigan *et al.*, 2008; Johnston *et al.*, 2007). Johnston *et al.*, (2007) did not detect an association between $PM_{10}$ and cardiovascular admissions for the general population, but restriction of analyses to the Aboriginal population with ischemic heart disease resulted in findings of the greatest risk of respiratory-related hospital admissions three days after exposure (Johnston *et al.*, 2007). It is plausible that associations at longer lags might have only been observable for such high-risk sub-populations, most susceptible to wildfire. Lee *et al.* (2009) and Mirabelli *et al.*, (2009) reported that adults with pre-existing respiratory conditions or weakness (i.e. small airway size) were more likely to seek care or have additional symptoms after wildfire exposure than persons without those conditions. However, Künzli *et al.* (2002) reported opposite results, as children without pre-existing asthmatic conditions had greater increase in respiratory symptoms under exposure than did other children. The authors suggested that children with pre-existing asthmatic conditions tended to be on medication and have better access to care, hence their smaller increase in symptoms when exposed to wildfire smoke. In an Australian study, no adverse association was observed between wildfire related $PM_{10}$ and lung function (peak expiratory flow) except when analysis was restricted to children with no bronchial hyper-reactivity (Jalaludin *et al.*, 2000).

## 4. Discussion

Overall, wildfire smoke exposures, as measured by proxies such as criteria air pollutants, were consistently associated with mortality and respiratory morbidities. Respiratory-related effects of wildfire smoke included increases in risk of hospitalization, use of respiratory medication, cough, wheeze and eye irritation. In one study, risk of emergency department contact for asthma could be more than two times greater after exposure to wildfire smoke (Johnston *et al.*, 2002). As most mortality studies investigated all-cause mortality, further

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research is needed to better identify the specific causes of mortality most strongly associated with wildfire smoke exposures. The magnitude of the effects on mortality varied by study. Respiratory mortality almost doubled from exposure to a wildfire in Greece (Analitis *et al.*, 2012), but some wildfires were not associated with changes in the mortality rate (Morgan *et al.*, 2010). The only global study posited that 339,000 deaths per year were attributable to wildfires, with Sub-Saharan Africa and Southeast Asia the most affected regions (Johnston *et al.*, 2012). However, this review highlighted disproportionately fewer studies in Southeast Asia and no other studies conducted in Sub-Saharan Africa. Some parts of the world such as Sub-Saharan Africa are affected by wildfire events but have not been studied. Those places, usually the less-developed regions, may contribute the most to the global burden of many diseases. It is also unlikely that these parts of the world can respond to such risk as well as more developed nations. Therefore, more studies are needed in these less studied countries.

Although our review of studies on forest fires and health is the most extensive to date, past reviews on related topics have also contributed substantially towards knowledge on the health effects of wildfire smoke. An early review by Naeher *et al.* (2007) focused on the toxicity of wood smoke, thereby establishing biological plausibility of the association, and called for further studies on the topic. Two later reviews investigated effects on respiratory outcomes of bushfire smoke (Dennekamp and Abrahmson 2011) and on respiratory outcomes for forest fires (Henderson and Johnston 2012). Dennekamp and Abramson (2011) identified that elevated PM concentrations from bushfire smoke explained associations with increased respiratory morbidity. Henderson and Johnston (2012) confirmed consistency of associations with acute respiratory outcomes and identified the need for studies in equatorial regions with rainforest depletion. Finlay et al. (2012) included non-respiratory outcomes and focused on demonstrating the current stage of investigation on this issue in the U.K. and identified literature gaps for the U.K. Finlay et al. identified the potential burden on cardiovascular and ophthalmic outcomes. Our review confirms that there still remain too few studies on these endpoints to establish consistency. The findings of our comprehensive review add to those of the previous reviews that focused on specific types of wildfire, health outcomes, or countries. Our review also quantified the substantial increase in exposure levels from wildfires and how these increases differed across studies. This was the first review to identify the dearth of studies from sub-Saharan Africa and paucity of studies in Southeast Asia, which are regions that experience a large health burden and are less able to respond to the increasing frequency and intensity of wildfires that accompany climate change. Our review also identified the shift in exposure assessment from the dominant use of measurements from ground-based air monitors to use of satellite imagery and chemical transport models.

In our review we found that results were most consistent among cohort studies, as almost all cohort studies found significant impact of wildfire smoke on health in at least one of the health outcomes and part of the population studied. Studies involving direct physiological measurements on recruited patients, such as bone marrow (Tan *et al.*, 2000) and Peak Expiratory Flow Rates PFFR (e.g. Jalaludin *et al.*, 2000), also tend to discern significant impacts. Ecological studies generally had inconsistent results. However, it is difficult to draw conclusions as to how study design and methods affected the reported associations

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because of heterogeneity in these and other design factors across studies, significant difference between pollutant levels during wildfire and non-wildfire periods, and how this difference varied across studies.

Studies consistently reported substantially higher levels of air pollution during fire periods and locations compared to non-fire periods and areas. Daily average $PM_{10}$ levels in an exposed city (Jambi, Indonesia) exceeded 1800μg/$m^3$ during fire events (Kunii *et al.*, 2002), which was 12 times the WHO interim target-1 standard (150μg/$m^3$ 24-hour) and 36 times the WHO air quality guideline (50μg/$m^3$ 24-hour). Daily average $PM_{2.5}$ levels during wildfires exceeded 150μg/$m^3$, more than 6 times greater than the WHO air quality guideline (25μg/$m^3$ 24-hour) (Moore *et al.*, 2006). Levels of carbon monoxide can increase 30–40% during wildfire periods compared with periods with no fires (Sutherland *et al.*, 2005; Tan *et al.*, 2000). These results indicate that wildfire events can result in severe levels of exposures. In addition to high levels, the chemical composition of wildfire smoke is distinctive. Wildfire smoke is accompanied by elevated levels of black carbon (Crabbe 2012), and polycyclic aromatic hydrocarbons can be 15 times higher than background levels (Aditama 2000).

### 4.1 Methods used to assess exposure to wildfire smoke

This review identified assessment of exposure as a key challenge in health studies of wildfires, with a range of methods applied. It is difficult to identify a direct marker that can represent air pollutants only from wildfires. Studies used indicators such as criteria air pollutants, aerosol optical depth or area burnt as indirect proxies. Although use of indirect proxies can be a useful approach, it is difficult to ascertain the fraction of health morbidity due to wildfire smoke excluding health morbidities due to those proxies in non-wildfire periods and from other sources during wildfire periods. The most commonly used marker for wildfire smoke used in the reviewed studies was particulate matter (PM) (Phuleria *et al.*, 2005). Although the fine fraction of particulate matter ($PM_{2.5}$) has been more consistently associated with adverse health effects than larger particles in studies of particulate matter more generally (Pope and Dockery 2006), fewer studies investigated the health effects of wildfire smoke-related $PM_{2.5}$. Notably, in all countries, the measurement of $PM_{2.5}$ began more recently than $PM_{10}$. A further exposure-related limitation of many of the reviewed studies was the coarse spatial resolution of exposure, due primarily to the use of ground-based ambient air monitors and the available monitoring network. An exception to this was studies that used remotely sensed satellite-derived imagery of area burnt (de Mendonca *et al.*, 2006). However, it is unclear as to whether area burnt is a suitable proxy for wildfire smoke exposure because it must be interpreted relative to population's distance to the wildfire, wind speed and direction, and atmospheric mixing depth (Naeher *et al.*, 2007; Ward 1990). Wildfire smoke also varies with vegetation type as, for example, wood from eucalypt forest has more oil content and releases higher concentrations of $PM_{10}$ than pine, acacia or cork oak (Goncalves *et al.*, 2010).

Exposure assessment is an ongoing challenge in epidemiological studies of wildfire smoke. Ground-based monitors do not measure the complicated mixture of pollution from the source of wildfires specifically. Monitors measure the level of a specific pollutant, such as

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$PM_{2.5}$, and cannot measure the pollution solely from fires as opposed to other sources. Therefore, it is difficult to separate the health effect of wildfire-emitted pollutants from that of pollutants from other sources. Moreover, ground-based air pollution monitors are not located in all places or time periods with affected populations. Exposure estimates based on satellite data provide more comprehensive spatial coverage (Kloog *et al.*, 2011; Lee *et al.*, 2011), but do not address the issue of specificity of the exposure estimates for wildfire smoke. It is critical to better understand the levels of wildfire smoke-specific pollutants (e.g., particulate matter from wildfires), as the range of health responses to the chemical signature specific to wildfire smoke is currently unclear (Wegesser *et al.*, 2009). Recent developments in chemical transport models may help address this limitation in future work. Chemical transport models, such as GEOS-Chem models, can estimate air pollutants specifically from wildfires (e.g. Singh *et al.*, 2010). Johnston et al (2012) employed this method to estimate the global exposure to wildfire-emitted $PM_{2.5}$. They found that 339,000 deaths could be attributed to wildfires annually. One limitation of using chemical transport models is that the wildfire-specific pollutant estimates may be difficult to validate. Modeled data could also be computationally expensive and requires collaboration efforts of atmospheric scientists (Kleeman *et al.*, 2009).

### 4.2 Health outcomes affected by wildfire smoke

The health endpoints investigated by the reviewed studies mainly focused on mortality and respiratory morbidity. Over 90% of the studies on respiratory morbidity and about 70% of the studies on mortality found significant association with wildfire smoke. There was insufficient evidence to conclude a consistent association between wildfire smoke and cardiovascular morbidities due to the relatively fewer number of studies. Despite the inconsistent association for cardiovascular morbidities globally, the association was mostly consistent in North America (five out of six studies found significant impact), where prevalence of cardiovascular diseases are higher than many other study areas. Causal links have been established between $PM_{10}$ more generally and a range of cardiovascular endpoints (Brook *et al.*, 2010). Other potential health endpoints that have been studied in the context of air pollution are hypertensive disorders (*e.g.* van den Hooven *et al.*, 2011), ophthalmic outcomes (*e.g.* Versura *et al.*, 1999), adverse pregnancy outcomes (*e.g.* Ritz *et al.*, 2002), and non-respiratory atopic disease (Morgenstern *et al.*, 2008). Future studies on the health impacts from wildfires may investigate these outcomes.

### 4.3 Susceptibility/Vulnerability

Among other factors, variation in the magnitude and statistical significance of observed effect estimates across the reviewed studies was likely attributable, in part, to differences in the underlying characteristics of the study population, including biological susceptibility, sociodemographic vulnerability, or other factors. Air pollution research more broadly has acknowledged population characteristics that can lead to greater biological susceptibility or sociodemographic vulnerability (Gouveia and Fletcher 2000). However, for wildfire smoke exposure, our review identified a paucity of studies on potentially vulnerable/susceptible subpopulations. There was some indication of elevated vulnerability to adverse health-effects of wildfire smoke among certain sub-populations: young children, older adults, and individuals of lower socioeconomic status. It is plausible that individuals with pre-existing

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respiratory morbidities are more susceptible to the respiratory effects of wildfire smoke possibly due to elevated sensitivity to environmental hazards by weaker immune systems. Pre-existing morbidities, such as asthma, that may not be fully controlled by medication might lead to greater susceptibility to adverse health effects of wildfire smoke. Although not specific to wildfire smoke, $PM_{10}$ has been associated with poorly controlled asthma among adults (Jacquemin *et al.*, 2012) and the effect of air pollutants on respiratory exacerbation among asthmatic children appears to be greater for those not on anti-inflammatory medication (Delfino *et al.*, 2002).

In the identified studies, five of six U.S. studies reported associations between wildfire smoke and cardiovascular hospital admissions, whereas associations were not observed in studies for other locations, including Australia and Canada. Cardiovascular diseases are more prevalent in U.S. adults (more than 1 in 3 adult Americans have cardiovascular diseases) (Lloyd-Jones *et al.*, 2010) than in Australia (about 1 in 6) (The Heart Foundation 2011). The mortality rates due to cardiovascular diseases are also higher in the U.S. than in Canada or Australia (Lloyd-Jones *et al.*, 2010). The different findings by region may result from higher risk for cardiovascular responses from wildfire smoke for population with high CVD prevalence.

### 4.4 Recommendations for future research

More studies in wildfire-affected but less-developed regions, such as Africa and Southeast Asia are needed. These regions face the highest health risk to wildfire smoke because they lack well-developed health care infrastructure and resources (Watson *et al.*, 2007). They are also less able to adapt to climate change compared to the developed world (Matthes 2008), leading to even higher risk to wildfires in the future. The populations are particularly vulnerable because behavioral interventions are complex (e.g., remaining indoors might increase exposure due to use of solid fuels, and chronic exposure to indoor solid fuels can lead to higher susceptibility to respiratory diseases (Po *et al.*, 2011)) (Smith *et al.*, 2004).

More large-scale studies are needed to obtain more reliable results on health impact of wildfires. Most of the identified studies were based on single-episode fire events, with fewer long-term studies. Studies based on multiple-episode fire events might be useful to identify consistency of an association over time or change in vulnerability or behavioral adaptation (*e.g.*, remaining indoors) to wildfire smoke exposure. Similarly, most studies focused on local regions, with few studies at national or other large geographic scales. Investigating larger geographies will introduce greater sociodemographic variation that might reveal communities at the greatest risk of wildfire smoke-related health responses. Large-scale studies can also help policy-makers by identifying the most vulnerable communities and populations for policy reference.

In addition, future studies could also adapt more new technologies to advance exposure assessment. Chemical transport models, dispersion models and satellite-based models could help address the limitations of assessing wildfire smoke exposure using air monitors. Moreover, as wildfire potential has been projected to increase in the future (Liu *et al.*, 2010), studies that estimate future wildfire-related health impact are needed. In our review, no identified studies projected the future health risk from wildfires under climate change, or

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identified high-risk regions or populations under future conditions. Studies projecting future health impact of wildfires can raise awareness of the health impact of wildfires in communities, promote preventive public health programs in high-risk communities, and aid in our understanding of the health consequences of a changing climate.

## 5. Conclusion

Our review indicates that wildfire events have potential to induce a substantial health burden. As wildfires are likely to occur more frequently and intensely under the impact of climate change, this health burden may increase in the future. Air pollution from wildfires was consistently associated with respiratory outcomes, and more studies are needed to investigate cardiovascular morbidity and mortality in community populations. Most of the current studies were based on single episodes and local populations. Conducting multiple episode and larger scale studies may reveal effects of wildfire smoke and help elucidate changes in wildfire frequency and possible adaptation. It was not possible to separate completely the health effect of wildfires from that of other ambient sources for the reviewed studies. Key challenges in current research include the assessment of exposure of wildfire-specific pollutants and the health risk modelling for source-specific air pollutant estimates. More research is needed to investigate the health effects of fine particulate matter from wildfires in Africa and Southeast Asia, the susceptible/vulnerable populations under exposure to wildfire smoke, and future health burden from wildfires under climate change.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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## Highlights

- Wildfire smoke dramatically increased ambient air pollutant levels
- Wildfire smoke consistently associated with increased risk of respiratory disease
- Suggestive evidence wildfire smoke linked with cardiovascular diseases & mortality
- Key challenge of exposure assessment: estimating fire-specific pollutants

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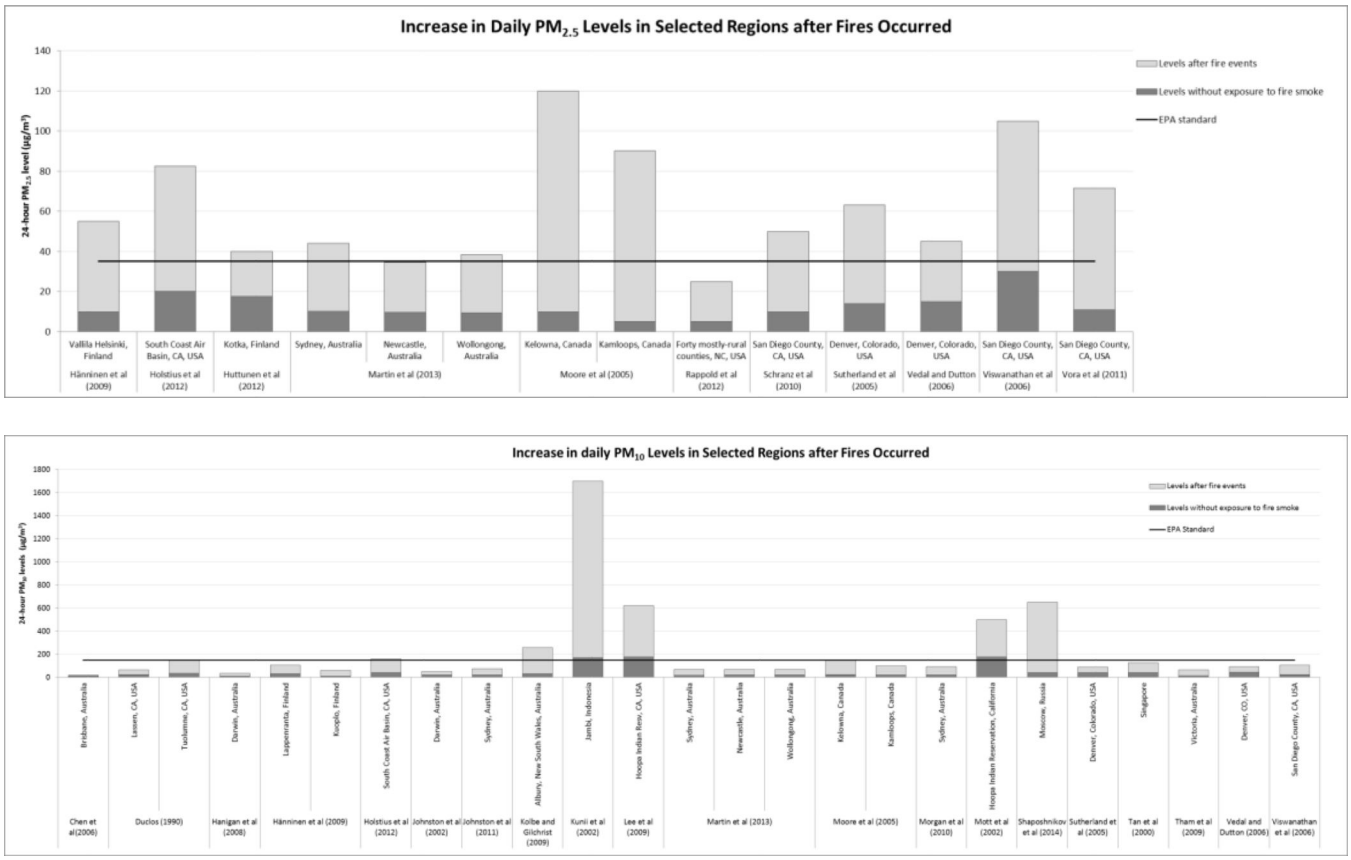


**Figure 1.**

$PM_{2.5}$ (top) and $PM_{10}$ levels (bottom) during wildfire events and non-fire periods

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**Table 1**

Summary of studies on wildfire smoke and population health

| Study | Location | Background population or cohort size | Time of fire | Major health outcome | Exposure metric |
|---|---|---|---|---|---|
| Aditama (2000) | Multiple provinces in Indonesia | 12,360,000 residents exposed to smoke | major fire: July–Oct. 1997 | Respiratory symptoms | CO, $SO_2$, $PM_{10}$, TSP, NOx, $O_3$, organic compounds |
| Analitis *et al*., (2012) | Athens, Greece | More than 3 million residents | 1994–2004 | Mortality | Sizes of area burned |
| Azevedo *et al*., (2011) | Northern coast of Portugal | Elderly among Porto (total population 1.4 million) | June to Aug. 2005 | Cardiovascular (CVD), respiratory admissions | $O_3$ |
| Caamano-Isorna et al., (2011) | Galicia, Spain | About 2 million inhabitants | Summer 2006 | Respiratory medicine usage | Exposure classified into three categories based on number of fires |
| Cameron *et al*., (2009) | Victoria, Australia | 5.2 million residents | Feb. 2009 | Injuries | Not specified |
| do Carmo *et al.*, (2010) | Alta Floresta municipality, Mato Grasso, Brazil | 51,136 residents in Alta Floresta, Mato Grosso (9% children <5y, 5% elderly >64y) | Jan. 2004 – Dec. 2005 | Respiratory admissions | $PM_{2.5}$ |
| Castro *et al*., (2009) | State of Rondônia, western Brazil | 1.6 million residents | 1998–2005 | Mortality | Number of fire “hotspots” |
| Centers for Disease Control and Prevention (CDC) (1999) | Central Florida | Not specified | Jun.– Jul. 1998 | Respiratory and cardiovascular Emergency Room (ER) visits | Wildfire v. non-wildfire periods |
| Centers for Disease Control and Prevention (CDC) (2007) | Panhandle region and 9 other counties, Texas, U.S. | Not specified | March 12–20, 2006 | Mortality | Presence of wildfire smoke |
| Centers for Disease Control and Prevention (CDC) (2008) | San Diego Co., California, U.S. | Not specified | Oct. 22–26, 2007 | Respiratory ER visits | Wildfire v. non-wildfire periods |
| Chen *et al*., (2006) | Brisbane, Australia | Not specified | Fire seasons 1997–2000 | Respiratory admissions | $PM_{10}$ |
| Cleland *et al*., (2011) | Melbourne, Australia | Not specified | Feb. 2007 | Injuries | Not specified |
| Crabbe (2012) | Darwin, Australia | 110,000 residents | 1993–1998 | Respiratory, CVD ER visits | $PM_{10}$, black carbon |
| Delfino *et al*., (2009) | Southern California, U.S. | 20.5 million residents | Oct. 21–30, 2003 | CVD, respiratory admissions | $PM_{2.5}$ |
| Dohrenwend *et al*., (2013) | San Diego Co., California, U.S. | Not specified | Oct 21–Nov 6, 2007 | Respiratory ER visits | Wildfire v. non-wildfire periods |
| Duclos *et al*., (1990) | 6 counties in California, U.S. | Residents in 6 counties (population size not specified) | Aug. 30–Sep. 3, 1987 | Respiratory ER visits | $PM_{10}$, TSP |

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| Study | Location | Background population or cohort size | Time of fire | Major health outcome | Exposure metric |
|---|---|---|---|---|---|
| Elliott *et al.*, (2013) | British Columbia (BC), Canada | Residents from 29 local health areas (LHA) in BC; population ranges 7,024–352,783 people | Fire seasons 2003–2010 | Respiratory medicine usage | $PM_{2.5}$, $PM_{10}$ |
| Emmanuel (2000) | Singapore | > 3 million residents | End of Aug. to early Nov. 1997 | Respiratory admissions; all-cause mortality | $PM_{10}$, $SO_2$, $NO_2$, $O_3$, CO, total hydrocarbon |
| Frankenberg *et al.*, (2005) | Kalimantan and Sumatra, Indonesia | 10,869 subjects > 30y | July–Oct., 1997 | Respiratory illness/symptoms; physical strength, overall health | Aerosol |
| Hanigan *et al.*, (2008) | Darwin, Australia | 110,000 residents | Dry seasons (Apr. – Nov.) of 1996–2005 | Respiratory, CVD admissions | $PM_{10}$ |
| Hänninen *et al.*, (2009) | 11 provinces in southern Finland | 3.4 million residents | Aug. 26–Sep. 8, 2002 | Mortality | $PM_{2.5}$, $PM_{10}$ |
| Henderson *et al.*, (2011) | Southeastern corner of BC, Canada | 281,711 subjects | Summer 2003 | CVD, Respiratory admissions | $PM_{10}$ |
| Holstius *et al.*, (2012) | South Coast Air Basin, California, U.S. | 886,034 infants in exposed group; 747,590 infants in control group | Oct. 2003 | Birth weight | Exposed or unexposed to fire during pregnancy |
| Huttunen *et al.*, (2012) | Kotka, Finland | 52 elderly people (>50 y) with ischemic heart disease | Apr. 25–May 6, 2006 | Blood concentration of inflammatory markers | $PM_{2.5}$ |
| Ignotti *et al.*, (2010) | Microregions in northern states of Brazilian Amazon, with Mato Grosso and Maranhão | 24 million inhabitants affected; subpopulations: Children (<5 y), elderly (>64), and an intermediate age group (5–64 y) | 2004–2005 | Respiratory admissions | $PM_{2.5}$ |
| Jalaludin *et al.*, (2000) | Sydney, Australia | 32 children | Jan. 1994 | Peak expiratory flow rates (PEFR) | $PM_{10}$, $NO_2$, $O_3$ |
| Jayachandran (2009) | Indonesia | ~1.3 million children (<3 y), infants or fetuses | Aug.–Oct. 1997 | Mortality | Aerosols |
| Johnston *et al.*, (2002) | Darwin, Australia | 115,000 residents | Apr. 1–Oct. 31, 2000 | Asthma ER visits | $PM_{10}$ |
| Johnston *et al.*, (2006) | Darwin, Australia | 251 asthmatic adults and children, about half < 18y | 7 months in 2004 | Asthmatic symptoms | $PM_{2.5}$, $PM_{10}$ |
| Johnston *et al.*, (2007) | Darwin, Australia | 110,000 residents | Fire seasons of 2000, 2004, 2005 | Respiratory, CVD admissions | $PM_{10}$ |
| Johnston *et al.*, (2011) | Sydney, Australia | ~ 4 million residents | 1994–2007 | Mortality | $PM_{10}$, $O_3$ |
| Johnston *et al.*, (2012) | Global | Not specified | 1997–2006 | Mortality | $PM_{2.5}$ |
| Kolbe and Gilchrist (2009) | Albury, New South Wales, Australia | 389 interviewees | Jan–Feb, 2002 | Respiratory symptoms | $PM_{10}$ |
| Kunii *et al.*, (2002) | Jambi, Sumatra (affected) and Jakarta, Java (control), Indonesia | 543 subjects in Jambi | July–Oct. 1997 | Respiratory symptoms | CO, $CO_2$, $SO_2$, $NO_2$, $O_3$, $PM_{10}$, inorganic ions, PAHs |

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| Study | Location | Background population or cohort size | Time of fire | Major health outcome | Exposure metric |
|---|---|---|---|---|---|
| Kunzli *et al.*, (2006) | 16 communities in Southern California, U.S. | 873 high school students, 5551 elementary school students | Oct. 2003 | Respiratory symptoms | $PM_{10}$ |
| Lee *et al.*, (2009) | Hoopa Indian Reservation, California, U.S. | 2,633 residents | Late summer and fall 1999 | Respiratory, CVD, diabetes admissions | $PM_{10}$ |
| Martin *et al.*, (2013) | Sydney, Newcastle and Wollongong, Australia | About 4.5 million residents | Fire seasons 1994–2007 | All non-trauma admissions | $PM_{10}$, $PM_{2.5}$ |
| Mascarenhas *et al.*, (2008) | Rio Branco, Brazil | 19,581 ER visits | Sep. 1–30, 2005 | Respiratory ER visits | $PM_{2.5}$ |
| de Mendonca *et al.*, (2006) | 261 districts in Brazilian Amazon | Residents in Amazon regions (population size not specified) | Fire seasons 1996–2000 | Respiratory admissions | hot pixels from satellite data |
| Mirabelli *et al.*, (2009) | 12 counties in California, U.S. | 465 non-asthmatic students (16–19 y) in the Children's Health Study | Oct. – Nov. 2003 | Respiratory symptoms | Number of days subjects smelled smoke |
| Moore *et al.*, (2006) | Kelowna and Kamloops regions in British Columbia, Canada | 146,199 residents in Kaelowna; 100,548 residents in Kamloops | Aug. 2003 | Respiratory, CVD | $PM_{10}$, $PM_{2.5}$ |
| Morgan *et al.*, (2010) | Sydney, Australia | ~ 3.48 million residents | Jan. 1994–June 2002 | Respiratory admissions; Mortality | $PM_{10}$ |
| Mott *et al.*, (2002) | Hoopa Reservation, California | 289 residents in Humboldt Co. interviewed (26% of population) | Aug. 23–Nov. 3, 1999 | Respiratory admissions | $PM_{10}$ |
| Mott *et al.*, (2005) | Kuching, Malaysia | ~400,000 residents affected | Aug. 1–Dec. 31, 1997 | Respiratory symptoms | $PM_{10}$ |
| Nunes *et al.*, (2013) | 107 micro areas in Brazilian Amazon | Not specified | Dry season 2005 | Mortality due to circulatory diseases | Annual % hours with $PM_{2.5}$ greater than 25μg/$m^3$ |
| Prass *et al.*, (2012) | Porto Velho, Amazon region | 22,012 live births | 2001–2006 | Birth weight | Number of fires |
| Rappold *et al.*, (2011) | 42 contiguous counties in eastern North Carolina, U.S. | Not specified | June 2008 | Respiratory, CVD ER visits | Aerosol optical depth (AOD) |
| Rappold *et al.*, (2012) | 40 mostly rural counties, North Carolina, U.S. | Not specified | June to July, 2008 | Asthma, CVD ER visits | $PM_{2.5}$ |
| Sastry (2002) | Kuala Lumpur and Kuching, Malaysia | Not specified | July–Dec. 1997 | Mortality | $PM_{10}$ |
| Schranz *et al.*, (2010) | San Diego Co., California, U.S. | Not specified | Oct. 21–24. 2007 | Respiratory ER visits | $PM_{2.5}$ |
| Shaposhnikov *et al.*, (2014) | Moscow, Russia | 11.5 million residents | Jul–Aug 2010 | Mortality | $PM_{10}$, $O_3$ |
| Shusterman *et al.*, (1993) | Alameda Co., California, U.S. | Not specified | Oct. 20–21, 1991 | Respiratory, injury ER visits | Not specified |
| Smith *et al.*, (1996) | Western Sydney, Australia | 907,450 residents | Jan. 5–12,1994 | Respiratory, asthma ER visits | $PM_{10}$, $NO_2$ |

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| Study | Location | Background population or cohort size | Time of fire | Major health outcome | Exposure metric |
|---|---|---|---|---|---|
| Sutherland *et al.*, (2005) | Denver, Colorado, U.S. | 21 residents who are >40 y, smoke, and with pre-existing COPD | June 8 to July 18, 2002 | Respiratory symptoms | $PM_{2.5}$, $PM_{10}$, CO |
| Tan *et al.*, (2000) | Singapore | 30 male volunteers | Sep.–Oct. 1997 | Bone marrow content | $SO_2$, $PM_{10}$, $NO_2$, $O_3$; CO |
| Tham *et al.*, (2009) | Northeastern and Alpine district, Victoria, Australia | Not specified | Jan.–March, 2003 | Respiratory ER visits | $PM_{10}$ |
| Thelen *et al.*, (2013) | San Diego Co., California, U.S. | Not specified | Oct. 2007 | Respiratory ER visits | $PM_{2.5}$, $PM_{10}$ |
| Vedal and Dutton (2006) | Denver, Colorado, U.S. | ~ 2 million residents | June 9–18, 2002 | Mortality | $PM_{2.5}$, $PM_{10}$ |
| Viswanathan *et al.*, (2006) | San Diego Co., California, U.S. | 2.8 million residents | Oct. 2003 | Respiratory, CVD, diarrhea admissions | $PM_{2.5}$, $PM_{10}$, $O_3$, $NO_2$, $SO_2$, CO |
| Vora *et al.*, (2011) | San Diego Co., California, U.S. | 8 subjects in downtown San Diego with asthma | Oct. 2007 | Respiratory function, rescue medication use | $PM_{2.5}$ |
| (Wiwatanadate and Liwsrisakun (2011)) | Chiang Mai, Northern Thailand | 1.7 million residents | Aug. 2005 – June 2006 | PEFR, asthma symptoms | CO, $O_3$, $NO_2$, $SO_2$, $PM_{2.5}$, $PM_{10}$ |

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## Table 2

Summary of studies based on health outcome and observed associations

| | Total number of studies | Statistically significant associations observed | No statistically significant associations observed | Studies that found significant association |
|---|---|---|---|---|
| Blood biomarker concentration | 1 | 1 | 0 | Huttunen *et al*. (2012) |
| Asthma | 5 | 4 | 1 | Johnston *et al.* (2006); Martin et al (2013); Rappold *et al.* (2012); Johnston *et al.* (2002) |
| Birth weight | 2 | 1 | 1 | Holstius *et al*. (2012) |
| Bone marrow content | 1 | 1 | 0 | Tan *et al*. (2000) |
| Cardiovascular | 14 | 6 | 8 | Azevedo *et al*. (2011); CDC (1999); Delfino *et al.* (2009); Lee *et al.* (2009); Martin et al (2013); Rappold *et al*. (2011); Rappold *et al.* (2012) |
| Diabetes | 1 | 0 | 1 | |
| Diarrhea | 1 | 0 | 1 | |
| Injuries | 3 | 3 | 0 | Cleland *et al.* (2011); Cameron *et al.* (2009); Shusterman *et al.* (1993) |
| Mortality | 13 | 9 | 4 | Analitis *et al.* (2012); CDC (2007); de Castro, *et al.* (2009); Jayachandran (2009); Johnston *et al.* (2011); Johnston *et al.* (2012); Nunes et al, (2013); Sastry (2002); Shaposhnikov *et al.* (2014) |
| Opthalmic symptoms | 5 | 5 | 0 | Aditama (2000); Hänninen et al, (2009); Kunzli *et al.*,(2006); Mirabelli et al (2009); Viswanathan et al (2006) |
| PEFR | 2 | 2 | 0 | Jalaludin *et al.* (2010); Wiwatanadate and Liwsrisakun (2011) |
| Physical strength and overall health | 1 | 1 | 0 | Frankenberg *et al.* (2005) |
| Rescue medication use | 3 | 3 | 0 | Vora *et al.* (2011); Elliott *et al.* (2013); Caamano-Isorna (2011) |
| Other Respiratory diseases | 37 | 35 | 2 | Aditama (2000); Cardoso de Mendonça (2006); CDC (2008); Chen *et al.* (2006); Delfino *et al.* (2009); do Carmo *et al.* (2010); CDC (1999); Dohrenwend *et al*, (2013); Duclos, (1990); Emmanuel, (2000); Hanigan *et al.* (2008); Henderson *et al*. (2011); Ignotti *et al.* (2010); Kolbe and Gilchrist (2009); Kunii *et al.* (2002); Künzli *et al.* (2006); Lee *et al.* (2009); Martin *et al* (2013); Mirabelli *et al.* (2009); Moore *et al.* (2005); Morgan et al. (2010); Mott *et al.* (2002); Mott *et al*. (2005); Schranz *et al.* (2010); Sutherland *et al.* (2005); Viswanathan *et al.* (2006); Crabbe (2012); Frankenberg *et al.* (2005); Johnston *et al.* (2007); Mascarenhas *et al.* (2008); Shusterman et al. (1993); Tham *et al.* (2009); Thelen *et al* (2013); Rappold *et al.* (2011); Vora *et al.* (2011) |

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# FORECASTING RELATIVE IMPACTS OF LAND USE ON ANADROMOUS FISH HABITAT TO GUIDE CONSERVATION PLANNING

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*Abstract.* Land use change can adversely affect water quality and freshwater ecosystems, yet our ability to predict how systems will respond to different land uses, particularly rural-residential development, is limited by data availability and our understanding of biophysical thresholds. In this study, we use spatially explicit parcel-level data to examine the influence of land use (including urban, rural-residential, and vineyard) on salmon spawning substrate quality in tributaries of the Russian River in California. We develop a land use change model to forecast the probability of losses in high-quality spawning habitat and recommend priority areas for incentive-based land conservation efforts. Ordinal logistic regression results indicate that all three land use types were negatively associated with spawning substrate quality, with urban development having the largest marginal impact. For two reasons, however, forecasted rural-residential and vineyard development have much larger influences on decreasing spawning substrate quality relative to urban development. First, the land use change model estimates 10 times greater land use conversion to both rural-residential and vineyard compared to urban. Second, forecasted urban development is concentrated in the most developed watersheds, which already have poor spawning substrate quality, such that the marginal response to future urban development is less significant. To meet the goals of protecting salmonid spawning habitat and optimizing investments in salmon recovery, we suggest investing in watersheds where future rural-residential development and vineyards threaten high-quality fish habitat, rather than the most developed watersheds, where land values are higher.

*Key words: conservation targeting; ecological thresholds; exurban development; forecasting land use change;* Oncorhynchus *spp.; Russian River, California; salmonid spawning habitat; urban sprawl; watershed risks.*

## INTRODUCTION

Land use change is a primary driver of habitat loss and ecosystem degradation at local-to-global scales (Foley et al. 2005), yet our ability to forecast the influence of landscape attributes and future impacts on ecosystems has lagged behind other advances in environmental sciences (Harte 2001). To reduce future losses of biodiversity and ecosystem function, resource managers, decision-makers, and conservation organizations are increasingly requesting information and tools to identify where species and ecosystems are most vulnerable to future land use conversion (Newburn et al. 2005, 2006, Armsworth et al. 2006). Developing spatially explicit projections of land use changes and their consequences has thus emerged as one of the eight grand challenges in environmental science (Clark et al. 2001, National Research Council 2001). In this study, we explore nonlinear thresholds beyond which land use change will result in the degradation of aquatic ecosystems, and then forecast future land use change and its effects on these systems.

Aquatic ecosystems are particularly sensitive to land use activities within their watersheds (e.g., Roth et al. 1996, Harding et al. 1998), and rapid land use changes have contributed to disproportionately high numbers of endangered aquatic species and the decline of economically valuable fisheries, such as anadromous salmonids (Richter et al. 1997, Ricciardi and Rasmussen 1999). The mechanisms by which land use activities affect aquatic ecosystems include elevated production and delivery of fine sediment to streams, which diminish water quality, alter channel morphology, and degrade habitat conditions for organisms ranging from invertebrates to fish (ASCE Task Committee on Sediment Transport and Aquatic Habitats 1992, Soulsby et al. 2001, Greig et al. 2005). The scale of influence and relative contribution of land use activities remain debated (e.g., Strayer et al. 2003), but recent work from Pacific temperate to mediterranean climate watersheds points to watershed-scale rather than local influences driving changes in sedimentation (Pess et al. 2002, Opperman et al. 2005).

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While many factors can limit salmonid spawning and rearing habitat, embeddedness, the extent to which grains of fine sediment (particle size <2 mm) surround spawning-sized substrate, is a key attribute of spawning gravel quality (see Kondolf 2000 for review) that can be affected by watershed-scale land use patterns (e.g., Opperman et al. 2005). Successful incubation requires spawning gravels that have low concentrations of fine sediment, which can fill a redd's interstitial framework and thereby reduce exchange rates of oxygen and metabolic wastes and impede fry emergence (Phillips et al. 1975, Everest et al. 1987, Groot and Margolis 1991). Kondolf (2000) concluded from his review of the literature that salmonid survival and emergence are reduced by 50% when fines exceed 30%. Thus, research elucidating the relative impacts of different land uses on levels of fine sediment in streams can inform management of salmonid populations, and forecasts of future land use changes can be invaluable for species recovery programs. Moreover, forecasts can provide ecological support for rural land use planning (Theobald et al. 2005) and guide conservation programs and planning (Van Sickle et al. 2004, Chan et al. 2006, Newburn et al. 2006).

Forecasting the environmental consequences of land use change requires addressing several challenges, including limited data availability and resolution (Clark et al. 2001, Nilsson et al. 2003, Rindfuss et al. 2004). For example, natural scientists often rely on land-cover classifications derived from remotely sensed imagery, such as Landsat TM, to classify urban development (<1 acre per house; 1 acre = 0.405 ha) and intensive agriculture; however, this imagery cannot distinguish rural-residential development (>1 acre per house; see Plate 1) from more extensive land covers such as forest (Sutton et al. 2006). The omission of low-density development in previous studies may therefore have led to biased parameters in statistical models overestimating the effects of urban development and agriculture as the effects from rural-residential land use were incorrectly attributed to adjacent urban development and agriculture.

Assessing the specific impacts of rural-residential development is particularly important because rural-residential development is the fastest growing land use type in the United States (Heimlich and Anderson 2001, Theobald 2003, Brown et al. 2005; see Plate 1) and is expanding in Canada and Europe (Dubost 1998, Azimer and Stone 2003). Using nighttime satellite imagery, Sutton, Cova, and Elvidge (2006) found that exurban development occupies 14% of U.S. land area, whereas the urban footprint was only 1.7%. Further studies are needed evaluating the impact of rural-residential development given recent documented impacts of exurban development on wildlife abundance, including carnivores (Odell and Knight 2001) and bird communities (Merenlender et al. 1998, Odell et al. 2003, Parsons et al. 2003). More importantly, rural-residential development has recently been shown to be a fundamentally different type of growth than urban development (Newburn and Berck 2006). Specifically, urban development requires sewer and water infrastructure before higher-density development (<1 acre per house) can be built. Conversely, rural-residential development (1–40 acres per house) is almost invariably serviced by private wells and septic systems and thus not bound to existing or planned sewer and water service areas (SWSA). These differences between urban and rural-residential development extend the possible range and associated environmental impacts of rural-residential development, such as sedimentation, but also temperature and nutrient loading from septic systems, well beyond the urban fringe (Hansen et al. 2005, Newburn and Berck 2006). These findings together suggest that biophysical models must explicitly determine the relative effects of rural-residential vs. urban development, and land use change models must distinguish between these different residential densities to forecast land use development patterns.

Finally, projection of the environmental consequences of land use change requires an understanding of biophysical thresholds, the amount of disturbance that an ecosystem can withstand without changing the processes and variables that control its structure (Gunderson and Holling 2002). A growing body of theoretical and empirical research suggests that ecosystems often display nonlinear responses to stressors (Scheffer et al. 2001, Carpenter 2003, Folke et al. 2004), necessitating the use of nonlinear models and extensive data on the response variables (e.g., Yuan and Norton 2004, Donohoe et al. 2006). Understanding how responses vary with initial land use conditions is also important to minimize the marginal losses to ecological systems from expected future land use conversion.

Here we assess the impacts of existing and projected future land use on spawning-substrate quality in tributaries of the Russian River in Sonoma County, California, and discuss the implications of future land use conversions on salmonid spawning habitat. Specifically, we analyze the relative impacts of three different land uses (urban, rural-residential, and vineyard) on the levels of fine sediment in streams. In Sonoma County, almost all intensive agriculture is vineyard for premium wine production. Urban development consists mainly of single-family residences (<1 acre per house) and here also includes paved roads, commercial, and industrial uses. Rural-residential development is defined as parcels with 1–40 acres per house. We hypothesized that low-density rural-residential development is a significant predictor of elevated levels of fine sediment in streams and differs in its severity of impact on stream conditions compared to higher-density urban development.

Our analysis integrated several modeling improvements for the first time. First, we developed an ordinal logistic response model to estimate the relative impact of each land use type on the probability distribution of levels of fine sediment in these watersheds. Ordinal logistic regression is designed to detect nonlinear threshold responses (Neter et al. 1996): in this case, the

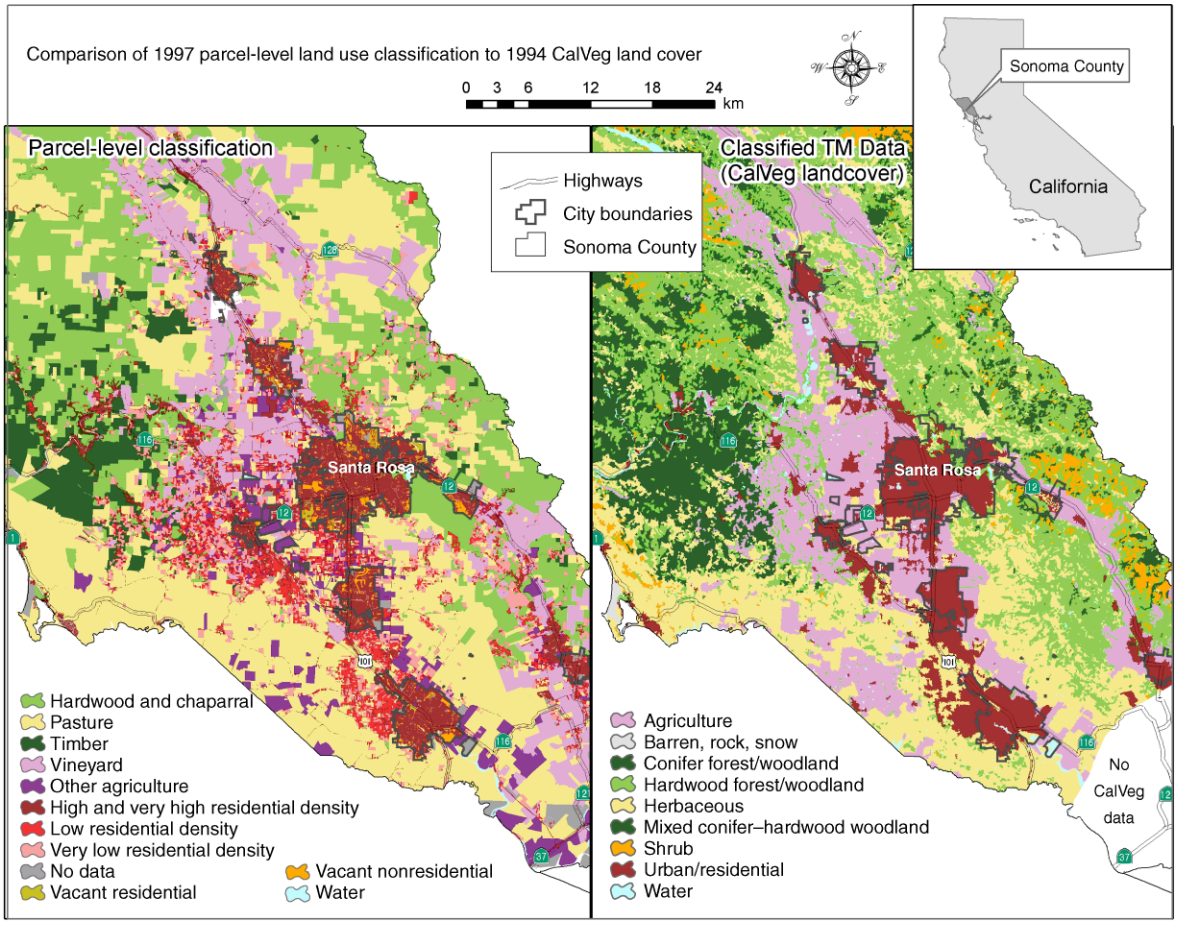


FIG. 1. Comparison of parcel-level and LANDSAT TM imagery land use (based on CalVeg classification) in the study region in Sonoma County, California. Parcel-based land use classification for 1997 shows rural-residential development (1–40 acres per structure; 1 acre ≈ 0.4 ha) and urban development (<1 acre per structure). Residential densities were based on parcel records obtained from the Sonoma County tax assessment office. Vineyard land use was digitized from aerial photographs in 1997.

probability of a spawning site within a given reach declining in spawning-substrate quality with increases in different land uses. Second, we develop a spatially explicit land use change (LUC) model using individual owner land use conversion decisions (including rural-residential, urban, and vineyard development) as a function of the parcel-level characteristics. The LUC model was used to calculate the expected probability of future conversion for each land use type on all remaining developable parcels, which was then integrated with the biophysical model to forecast the expected loss in substrate quality in each watershed. We performed the last critical step of forecasting land use change and its impacts on future levels of fine sediment to aid planners and other decision-makers in preventing further damage to salmonid spawning sites in the Russian River Basin. After combining our forecasts on the expected impacts to spawning habitat with hedonic models for estimating land costs, we conclude with recommendations of priority areas for land conservation efforts and for future development.

## METHODS

### *Study basin*

The Russian River basin is 3850 km$^2$, and is located in Sonoma and Mendocino Counties in northern California. The basin is underlain primarily by the Jurassic-Cretaceous age Franciscan Formation and experiences a mediterranean climate, with cool, wet winters and hot, dry summers; mean annual rainfall ranges from 69 to 216 cm. Natural vegetation consists mostly of mixed-hardwood forests, oak savannas, and grassland, with conifer-dominated forests occurring near the coast and on north-facing slopes throughout the basin. Primary land uses include vineyards, orchards, and other agriculture, sheep and cattle grazing, timber harvest, and urban and residential development.

We focused our studies on tributaries of the Russian River in Sonoma County that (1) support anadromous salmonid spawning habitat, and (2) where stream habitat and digital parcel-level land use data were available (Fig. 1). Focal tributaries included Green

Valley, Mill, Willow, Mark West, Dutch Bill, Maacama, Atascadero, Ward, and Austin Creeks. In the Russian River, three species of anadromous salmonids, including the Central California Coast steelhead (*Oncorhynchus mykiss*), Central California Coast coho (*Oncorhynchus kisutch*), and California Coastal chinook (*Oncorhynchus tshawytscha*), have been listed as threatened under the Federal Endangered Species Act.

### *Indicator of spawning gravel quality*

We used a database from the California Department of Fish and Game (CDFG) for spawning streams in the Russian River Basin to characterize the levels of fine sediment in salmonid spawning habitat. Field crews working for CDFG evaluated the degree of embeddedness of spawning habitat in surveys conducted from 1994 to 2002. Embeddedness was defined as the extent to which fine sediment (particle size $<2$ mm) surrounded spawning-sized substrate (i.e., gravel and cobbles). Each potential spawning site in a stream reach was ranked for the level of fine sediment surrounding the appropriate spawning substrate, using a four-level ordinal system. Rank 1 indicates low levels of fine sediment (0–25%) surrounding spawning-sized substrate, and Rank 4 indicates very high levels of fine sediment (75–100%) surrounding the substrate. We estimated the distribution of substrate quality for each reach surveyed from 1994 to 1997, and used the rank level of each spawning site as our dependent variable. We employed a geographic information system (GIS) to segment these data by stream reach (Byrne 1996, Radko 1997). We restricted our analyses to depositional reaches (gradient $<0.03$) most likely to be impacted by sediment. This data set included 93 stream reaches with an average of 54 spawning sites per reach.

To examine the relationship between land use and embeddedness as a measure of spawning habitat quality, we used a 10-m Digital Elevation Model (DEM) and the ArcView extension FlowZones (ESRI 2002) to delineate watersheds above the downstream end of each surveyed reach that had a minimum of five spawning sites. Ten spawning sites per reach, representing the actual distribution of rankings observed at each reach, were used in model development to avoid overrepresentation of sites in particularly long reaches. For example, if a reach had 100 spawning sites and 70, 20, 10, and 0% of the spawning sites were Rank 1, 2, 3, and 4, respectively, then we represented this distribution in the model as 7, 2, 1, and 0 spawning sites (10 total) with Rank 1, 2, 3, and 4, respectively, for that given reach. No more than five reaches nested in the same drainage area were used to reduce overrepresentation of any given watershed and to minimize spatial autocorrelation. Watersheds ranged in size from 500 to 18 165 ha. Finally, we excluded those few watersheds in the study area that currently or historically supported extensive timber harvesting to avoid problems associated with the land use legacies (Harding et al. 1998). Other extensive uses such as historic livestock grazing, orchards, and other agriculture were treated as baseline land uses. In total, 93 watersheds were used for model development; 58 reaches were excluded to reduce overrepresentation of different watersheds and/or land use legacies, resulting in a model based on 922 spawning sites.

### *Parcel-based land use classification*

For land use classifications, we used tax assessment parcel-level data linked to a digital parcel map within a GIS to provide information on residential development density classes. This approach provides more accurate residential classification than LANDSAT TM imagery, which was used in our previous work in the Russian River basin (Opperman et al. 2005), because tax assessment parcel data provide information on residential density. Specifically, the Sonoma County tax assessment data contain information on the number of housing units and lot size for each landowner, and therefore they can be used to determine housing density. By comparison, LANDSAT data do not indicate residential density; they only classify areas as either urban, or extensive uses such as agriculture or hardwood forest. We note to planners and managers that LANDSAT still has better spatial resolution and accuracy for vegetation cover than parcel level data.

For this study, residential development was categorized into four density classes: very high density ($<0.25$ acres per structure), high density (0.25–1 acres per structure), low density (1–5 acres per structure), and very low density (5–40 acres per structure). These four residential density classes were used in the land use change model described below. For the biophysical model, however, very low and low classes were later combined into the rural-residential class for the ordinal logistic regression in order to reduce multicollinearity, because these two classes were highly correlated within watersheds ($r^2 = 0.68$). Similarly, very high and high-density classes were combined into urban development. The urban classification also included paved roads, parking lots, and commercial uses (industrial uses were relatively uncommon within the CDFG-surveyed watersheds). The specific distinction between urban ($<1$ acre per structure) and rural-residential (1–40 acres per structure) was made at 1 acre per structure because this density is the typical limit on residential development serviced by septic systems (Newburn and Berck 2006). To obtain the amount of vineyard land use in each watershed, we digitized vineyard boundaries from 1997 aerial photographs. Vineyard parcels were classified as vineyard if the parcel had $\geq 10\%$ vineyard or $\geq 5$ ha of vineyard, based on the intersection of the parcel and aerial photo vineyard classification. A comparison of land use classification by parcel-level data and LANDSAT TM imagery is provided in Fig. 1.

### *Model development*

We developed ordinal logistic response models (cumulative proportional odds) using the rank level of

substrate quality at each spawning site as our response variable (Hosmer and Lemeshow 2000). Explanatory variables included existing areal percentages of vineyard, urban, and rural-residential land use in 1997 within each watershed and biophysical watershed variables as controls (Hosmer and Lemeshow 2000). These watershed variables included continuous variables such as stream-power index (product of stream gradient and watershed size), road density, soil particle size, a hillslope stability index from a shallow landslide model, SHALSTAB (Dietrich et al. 2001) (*available online*)[5] as well as categorical variables including channel type, dominant geology type (Franciscan mélange, volcanic, and sedimentary), and bank substrate material (bedrock, boulder, silt/clay, cobble). Other extensive land uses including historic livestock grazing, orchards, and other agriculture were thus treated as baseline uses in our model; the impact of an additional 1% of specified land use (e.g., vineyard, urban, rural-residential) is the amount of impact above the baseline impact of extensive uses.

Given the response variable $y$ taking on ordinal values from 1 to $J$ and the $1 \times K$ vector of explanatory variables $X^i$ for watershed $i$, the proportional odds model is expressed as

$$\log(P_j^i/1 - P_j^i) = \alpha_j + \beta X^i, \quad j = 1, 2, \ldots, (J-1)$$

where $\beta X^i = \beta_1 X_1^i + \beta_2 X_2^i \cdots \beta_k X_k^i$ and $P_j^i$ denotes the probability that a spawning site in watershed $i$ falls into rank category $j$ or lower. The cumulative proportion odds specification indicates a nonlinear relationship between the probability of each rank level and the explanatory variables. Furthermore, $\alpha_j$ provides the threshold parameters between the rank categories $j$ and $j + 1$. The models were constructed such that Rank 1 corresponded to the highest substrate quality and Rank 4 corresponded to the lowest. Therefore, a negative sign in the parameter estimates indicates reduced substrate quality, because in this case, a marginal change in the variable would lower the probability of observing a high-quality spawning site with Rank 1.

Log-likelihood (LL) ratio tests were used to test the difference between a given model and any nested model and decide which variables to drop from or add to the model. Chi-square is the difference in log-likelihood ratios (−2LL) for the two models. If the computed chi-square was equal to or greater than the critical value of chi-square for the given degree of freedom, then the models were significantly different and the dropped variable in the nested model was considered significant in predicting the dependent. For category variables (dominant geology and bank substrate quality), we assessed the significance of these variables by comparing the chi-square difference of the full model and a model with all the variables in a dummy set dropped (e.g., bedrock, boulder, cobble/gravel, and silt/clay). Thus we treated the dummy variables associated with the categorical variable as a block (Hosmer and Lemeshow 2000).

We evaluated the goodness of fit and performance of the biophysical model on an additional data set of watersheds not used previously for model building. First, we refitted the model including the additional data set. Second, the full model, which included all variables, was compared with a partial model that excluded rural residential development. The partial and full models were used to predict substrate quality based on additional streams surveyed from 1998 to 2002 ($n = 45$ reaches) and updated 2002 parcel-level data and aerial photos of vineyard. We evaluated the capability of both the partial and full model to predict the values observed in the validation set of watersheds using the mean square prediction error (sum of squared errors/number of watersheds in the validation set) (Neter et al. 1996).

### *Land use change model*

A parcel-level LUC model was constructed for the period 1994–2002, using the tax assessment data to determine residential development and aerial photos to determine vineyard development. The data were initially compiled to determine the set of developable parcels in 1994, and then used to assess whether the developable parcels were converted to either vineyard or one of several housing densities from 1994 to 2002. A parcel was considered developable if there was no vineyard use in 1994 and the existing housing density in 1994 was less than one structure per 40 acres. Hence, the set of developable parcels excluded those parcels protected in parks and reserves and already converted to vineyard or residential development before 1994. Residential development was categorized into the four density classes described above. Land use conversion was defined as transitions from developable parcels into vineyard development or one of the four residential density classes during the period 1994–2002.

A multinomial logit model was developed to explain land use transitions as a function of parcel-site characteristics, including average slope, growing degree-days (microclimate), 100-year floodplain, accessibility to major employment centers, designated sewer and water services, and minimum lot size zoning. The 1989 General Plan was used because it was in effect as the planning document during 1994–2002 and therefore guided new development location and type. An indicator variable was used to specify whether a given parcel is located outside the existing 1989 sewer and water service area. Urban development is expected to be less likely in places without access to public water and sewer service. However, it should be noted that rural-residential homes built in the unincorporated areas are often privately serviced by groundwater wells and septic systems, and thus are still likely to occur outside the sewer service area. Zoned minimum lot size is included as another

[5] ⟨http://socrates.berkeley.edu/geomorph/⟩

proxy for potential residential development, represented in natural log form.

Average percentage slope and elevation in meters were calculated for each parcel. Growing degree-days, summed over the April to October vineyard growing season, served as a proxy for microclimate. A dummy variable was used to represent whether a given parcel was situated within the 100-year floodplain. An optimal routing algorithm within the GIS was used to calculate the minimum travel time in minutes between each parcel and San Francisco along the road network, utilizing weighted travel speeds of 55 mph (88 km/h) on major highways and 25 mph (40 km/h) on county roads. The distance in kilometers from each parcel centroid to the nearest major highway was calculated. This variable represents access to local employment centers within Sonoma County, because all incorporated cities are located along these transportation corridors.

We used the estimated coefficients from the multinomial logistic regression to predict the site-specific conversion probabilities for each land use type on each developable parcel remaining in 2002, given that the site characteristics were already known for all parcels within the GIS. Zoning variables and sewer water service area boundaries were updated to the 2001 General Plan. We note that although the county had a relatively high population growth rate, 2–3% annually, the zoning and sewer and water service area boundaries changed by a very small amount from 1989 to 2001. We then used the LUC model to simulate the expected amount and location of development for each land use type within each watershed. According to the site-specific conversion probabilities, each parcel may remain developable or become converted to one of the five developed land use types in a given simulation. We repeated the simulations 1000 times to obtain average expected watershed area converted to each land use type. The amount of future development from the LUC model spanned an eight-year period, 2002–2010, because the LUC model was calibrated over an eight-year development period, 1994–2002. Over this short planning horizon period, we assumed no additional changes in urban zoning and boundaries. Hence, the forecasted amounts of land use change from 2002 to 2010 represent a "business-as-usual" scenario. The two rural residential classes were then grouped, and two urban classes were also grouped, to simplify the ordinal logistic model on spawning-substrate quality. We then calculated the percentages of the three land uses in each watershed (percentage of total watershed area) for 2002–2010. To obtain the forecasted land use in 1997–2010, the amount of forecasted change in 2002–2010 was added to the actual extent of land use change measured from aerial photos and tax assessment data.

### *Hedonic price model for estimating land values*

We used a hedonic price model to determine the market value for developable land as a function of the site-specific characteristics. Specifically, recent property transactions of developable parcels were used to estimate the actual sales price as a function of the parcel land characteristics. The Sonoma County Tax Assessor's database provides the necessary information on individual parcels for the land value, current land use, and other property characteristics. Using the GIS, we used a similar set of explanatory variables for each parcel, including characteristics for land quality (slope, elevation, microclimate, 100-year floodplain), accessibility (travel times to urban centers, sewer and water service), neighboring land use externalities (percentage of protected open space and urban), and zoning (land use designations, minimum lot size).

Coefficients in the hedonic equation are interpreted as the marginal implicit value of a unit change in the explanatory variable. For example, the hedonic coefficient on travel time to San Francisco estimates the gradient in land values as one travels away from the urban center. We are then able to estimate the value of developable land for each developable parcel, since key site characteristics are known within the GIS. The predicted value of developable land was observed to range over several orders of magnitude. The large degree of variation in land prices highlights why priority setting should include the spatial heterogeneity in land values. See Newburn et al. (2006: Table 2) for more details on the hedonic model used here to estimate the land value of developable parcels in Sonoma County.

### *Forecasting environmental consequences of land use change*

We forecasted the probability distribution of spawning-substrate quality based on the expected percentages of each land use type in 2010 and the estimated parameters in the ordinal logistic model. To estimate the relative impact of each land use type in 2010, we calculated the change in the probability distribution of substrate quality in response to each land use type in 2010, conditional on holding the other two land use types at the existing amount in 1997. Furthermore, in order to demonstrate how nonlinear responses to future land use development is sensitive to the initial levels of land use in each watershed, we categorized watersheds into quartiles (most developed, moderate, less, least developed) based on the summed percentages of all three types of existing development in 1997 (87 watersheds with forecasts).

A targeting rule was used to identify priority areas for protection based on the expected loss of high-quality spawning substrate from future land use conversion and the average land costs in each watershed. Hence, we maximized conservation goals based on the objective of minimizing the expected loss in environmental benefit per unit cost (Newburn et al. 2006). Applying this targeting rule to our results, we identified priority areas by summing the relative probabilities of loss of Ranks 1

TABLE 1. Average existing development (1997) and forecasted changes in land use (1997–2010) in the least to most developed watersheds (as a percentage of the watershed) and across all watersheds ($n = 87$ watersheds).

| Variable | Land use | Land use in watershed (%) | | | | |
|---|---|---|---|---|---|---|
| | | Least | Less | Moderate | Most | All watersheds |
| Existing development, 1997 | urban | 0.06 | 0.48 | 0.64 | 5.05 | 1.56 |
| | rural-residential | 0.10 | 1.74 | 6.43 | 22.59 | 7.71 |
| | vineyard | 0.36 | 1.07 | 4.29 | 2.41 | 2.03 |
| | total | 0.52 | 3.28 | 11.36 | 30.05 | 11.30 |
| Change 1997–2010 | urban | 0.10 | 0.05 | 0.10 | 0.21 | 0.11 |
| | rural-residential | 1.66 | 1.71 | 1.14 | 1.64 | 1.54 |
| | vineyard | 1.58 | 1.98 | 2.85 | 2.82 | 2.31 |
| | total | 3.35 | 3.73 | 4.08 | 4.67 | 3.96 |

and 2 and dividing by the average cost per acre for that watershed.

## RESULTS

The parcel-level land use classification in Sonoma County revealed that urban (<1 acre per structure) and vineyard land use represented only 1.56% and 2.03% of the land area in 1997 within the CDFG-surveyed watersheds, respectively, while rural-residential development (1–40 acres per structure) represented 7.71% (Table 1). Indeed, rural-residential development constituted >80% of the total land area developed for residential use, although it only represented <20% of the total population in the area. The spatial distribution of these land uses was extremely variable among the study watersheds (Fig. 1). On average, the most-developed watersheds had an order of magnitude more development than the least-developed watersheds (Table 1).

Ordinal logistic regression models (cumulative proportional odds) were used to estimate the probabilities for observing each of the four spawning-site quality levels within a given reach as a function of the percentages of watershed-scale land uses in 1997 and biophysical variables. Thus, each reach had a unique set of four probabilities, corresponding to the watershed characteristics for the specific reach. The best ordinal logistic regression model on spawning-substrate quality included land use variables for the percentages of urban, rural-residential, and vineyard use within each watershed and biophysical watershed variables for stream power index, geology, and bank substrate material (Table 2). The model results showed that all three land use variables were negatively and significantly associated with spawning-substrate quality. Partial likelihood ratio tests excluding rural-residential indicated that this land use type significantly improved the model fit ($G = 16.55$, $P < 0.0001$), supporting the hypothesis that increased rural-residential development is a significant predictor of elevated levels of fine sediment in streams. An index of stream power, the product of watershed size and stream gradient, and stream bank substrate material were the only significant biophysical watershed variables. Strict adherence to conventional levels of statistical significance would have dictated that we consider a smaller model deleting dominant geology. However, due to the fact that geology is an important control variable on

TABLE 2. Final model for projection of spawning habitat quality under land use change.

| Term | Estimate | SE | Lower 95% confidence limit | Upper 95% confidence limit | Chi-square | $P$* |
|---|---|---|---|---|---|---|
| Intercept [1]† | −0.859 | 0.313 | | | 7.53 | 0.0061 |
| Intercept [2]† | 1.268 | 0.314 | | | 16.27 | <0.0001 |
| Intercept [3]† | 2.524 | 0.323 | | | 61.19 | <0.0001 |
| Stream power index | −1.764 | 0.617 | −2.925 | −0.608 | 8.18 | **0.0042** |
| Urban 1997 (%) | −0.120 | 0.033 | −0.189 | −0.059 | 12.96 | **0.0003** |
| Rural-residential 1997 (%) | −0.034 | 0.008 | −0.051 | −0.018 | 17.01 | **<0.0001** |
| Vineyard 1997 (%) | −0.055 | 0.022 | −0.099 | −0.013 | 6.38 | **0.0115** |
| Substrate [bedrock] | −0.173 | 0.231 | −0.651 | 0.296 | 0.56 | 0.4541 |
| Substrate [boulder] | 1.169 | 0.431 | 0.278 | 2.124 | 7.36 | **0.0067** |
| Substrate [cobble/gravel] | −0.226 | 0.210 | −0.668 | 0.206 | 1.16 | 0.2819 |
| Geology [Franciscan] | 0.398 | 0.260 | −0.058 | 0.935 | 2.34 | 0.1260 |
| Geology [sedimentary] | −0.167 | 0.271 | −0.647 | 0.384 | 0.38 | 0.5381 |
| Geology [volcanic] | 0.381 | 0.265 | −0.084 | 0.923 | 2.07 | 0.1501 |

*Notes:* Estimated ordinal logistic regression terms, coefficients and standard errors (SE), and confidence limits are reported. Chi-square is the likelihood-ratio chi-square test for the hypothesis that all regression parameters are zero, and $P$ value is the probability of obtaining a greater chi-square value by chance alone if the specified model fits no better than the model that includes only intercepts. $N = 922$ pools; −2 log-likelihood = 199.9.

* The values in boldface type indicate significance at the $P < 0.05$ level.

† The ordinal logistic model fits a different intercept, but the same slope, for each of $r - 1$ cumulative logistic comparisons, where $r$ is the number of response levels. There are three intercept parameters because there are four response categories.

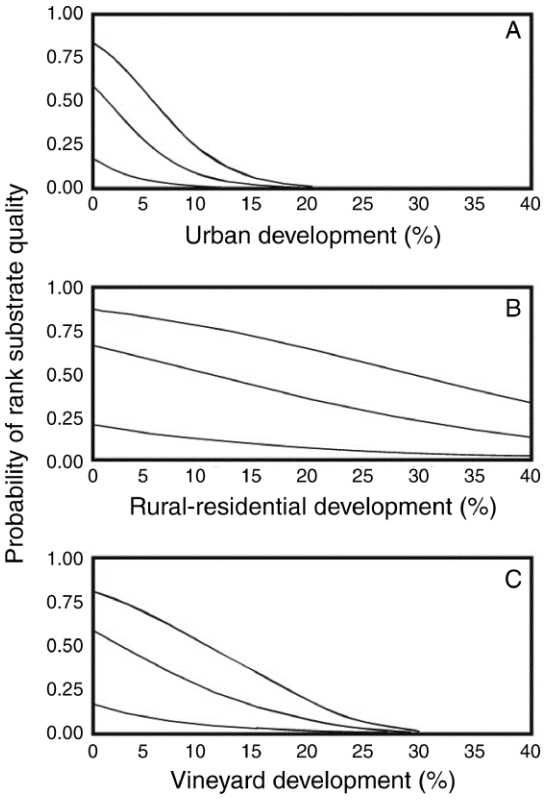


FIG. 2. Ordinal response regression models for (A) the percentage of urban development, (B) the percentage of rural-residential development, and (C) the percentage of vineyard development in the watershed.

sediment production and delivery, dominant geology was retained to control for this factor across watersheds (Hosmer and Lemeshow 2000). Significance of stream bank substrate material indicated more local-scale influences on spawning gravel quality.

The probability of observing low levels of fine sediment in spawning gravels decreased as the percentage of different types of development increased in the watershed (Fig. 2). The marginal effects of urban development (i.e., the change in the probability of substrate quality with 1% increase in urban development) were larger than either vineyard or rural-residential development in lesser-developed watersheds (Fig. 2). However, the marginal effect of urban land use decreased when there was already a high percentage of existing development. In the least-developed watersheds, >65% of spawning sites were high quality (Ranks 1 and 2), whereas >70% of the sites in the most-developed watersheds were highly embedded with sediment (Ranks 3 and 4) (Fig. 3). Thus, prior development had already impacted the majority of spawning sites in the most-developed watersheds.

Estimating the model with all the data (1994–2002) did not significantly alter the coefficient estimates in the final model indicating goodness of fit. Results from projecting the effects of land use change from 1997 to 2002 on stream conditions on the test set of watersheds ($n = 45$) showed that the mean prediction error only decreased 7% with the full model compared to the partial model. Biased parameter estimates for urban and vineyard could help to explain why there were only minor differences in the mean squared prediction errors between the models; the partial model overestimated the effects from urban and vineyard because it had mistakenly attributed the effect from the omitted exurban variable to urban and vineyard.

### *Forecasting land use change*

The estimation results from the LUC model indicated that urban and rural-residential development responded very differently to land use regulations. Designation of sewer and water service area boundaries was the most important determinant of urban development (Table 3). Calculating the odds ratios for the two urban classes showed that very high and high-density development were respectively 44.5 and 4.5 times less likely to occur outside of sewer and water service area boundaries compared to areas with existing and planned sewer service. In contrast, designation of sewer and water service areas did not affect rural-residential development, as development at this density only requires the installation of private groundwater wells and septic systems. The odds ratios for the two rural-residential classes show that very low and low-density development are actually 5.9 and 2.7 times more likely outside of sewer and water service area boundaries. Hence, because of these different responses to land use controls, the LUC model showed that rural-residential development actually leapfrogged into less-developed areas well beyond sewer and water service area boundaries. Furthermore, urban development at high and very high densities was less likely on steeper slopes, within the 100-

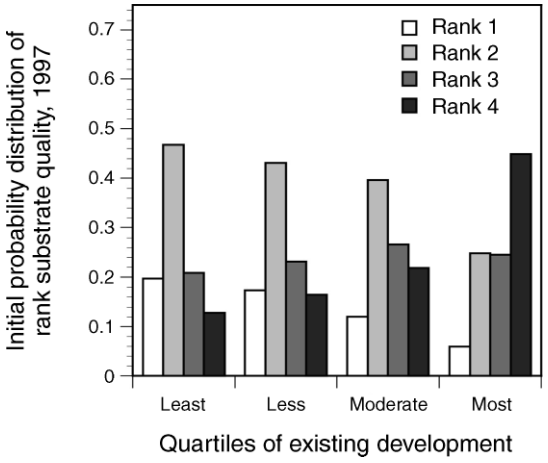


FIG. 3. Estimated probability distribution of quality levels of spawning habitat within stream reaches, grouped according to the quartiles of existing land use development in 1997 (least, less, moderate, and most developed).

TABLE 3. Estimated coefficients of multinomial logit model for land use conversion (to very high, high, low, and very low housing density, or vineyard) during 1994–2002 on undeveloped parcels in Sonoma County, California.

| Variable | Housing density classes | | | | |
|---|---|---|---|---|---|
| | Very high | High | Low | Very low | Vineyard |
| Outside sewer service areas | −3.797** | −1.510** | 1.006** | 1.781** | 2.469** |
| | (0.199) | (0.153) | (0.176) | (0.372) | (0.324) |
| Travel time to San Francisco | −0.015** | 0.008* | −0.022** | −0.0294** | 0.011** |
| | (0.003) | (0.003) | (0.004) | (0.006) | (0.003) |
| Distance to nearest highway | −0.304** | −0.146** | −0.041 | 0.004 | −0.112** |
| | (0.055) | (0.047) | (0.031) | (0.030) | (0.018) |
| Slope | −0.053** | −0.052** | −0.036** | 0.001 | −0.049** |
| | (0.006) | (0.005) | (0.005) | (0.005) | (0.004) |
| Growing degree-days | 0.198 | −0.059 | −0.154 | 0.696** | 1.796** |
| | (0.144) | (0.152) | (0.156) | (0.198) | (0.115) |
| Floodplain | −1.111** | −1.811** | −1.116** | −1.066 | −0.500* |
| | (0.252) | (0.416) | (0.345) | (0.589) | (0.199) |
| Elevation | −0.008** | 0.0026** | 0.002** | 0.002** | −0.001 |
| | (0.002) | (0.001) | (0.001) | (0.001) | (0.001) |
| ln(zoned minimum lot size) | 0.089** | −0.177** | −0.112** | 0.085 | 0.539** |
| | (0.029) | (0.0379) | (0.038) | (0.049) | (0.034) |
| Constant | −0.603 | −2.092** | −2.672** | −7.282** | −11.669** |
| | (0.494) | (0.552) | (0.568) | (0.755) | (0.506) |

*Notes:* "Remain undeveloped" is the baseline alternative. Standard errors are in parentheses. For the ordinal logistic model in Table 2, the very high and high-density classes were combined into urban development, while the very low and low-density classes were combined into rural residential development. $N = 20\,487$ parcels; log likelihood = −8732.04.

* $P < 0.05$; ** $P < 0.01$.

year floodplain, and farther from major highways. (See Newburn and Berck [2006] for more details on differences between urban and rural-residential development.) Finally, vineyard development was more likely on areas with lower slope and higher growing degree-days (warmer microclimate).

We used the LUC model to forecast development for the period 1997–2010. Although urban development resulted in the largest marginal change in probability in substrate quality per unit increase in development (Fig. 2), the amount of future urban development was relatively small, largely due to no changes in urban zoning and boundaries. For the forecast period 1997–2010, the area developed as urban in CDFG watersheds was estimated to increase only 0.11%, whereas rural-residential and vineyard development were estimated to increase by 1.54% and 2.31%, respectively (Table 1).

### *Forecasting land use impacts on spawning-substrate quality*

Future vineyard and rural-residential development had larger relative impacts on spawning-substrate quality than future urban development across all watersheds (Fig. 4). Initial conditions of the watersheds largely determined which watersheds had the most to lose with respect to good-quality spawning substrate (Ranks 1 and 2) (Fig. 5). The amount and type of expected land use change also factored into which watersheds were expected to lose good spawning habitat (decreases in Ranks 1 and 2) and to be impaired by sedimentation (increases in Ranks 3 vs. 4) (See Fig. 6, but also the Appendix for forecasts for all watersheds.) The interplay between these two factors, initial conditions and expected land use change, was observed across the watersheds in Sonoma County. Specifically, watersheds near Cloverdale, farthest from the San Francisco Bay area, were less disturbed and generally responded to expected land use change with declines in the probability of observing high-quality spawning sites (declines in Rank 1; Fig. 6a). In watersheds near Healdsburg, particularly to the east near Napa County, high amounts of projected vineyard development and, to a lesser extent, rural-residential development, led to large expected losses of Rank 1 and Rank 2 sites and large increases in Rank 4 sites (Fig. 6b). Whereas the southern most-developed watersheds near Santa Rosa showed little change in the probable loss in Rank 1 spawning sites because spawning-substrate quality was already low, watersheds showed large probable gains in Rank 4 sites from expected losses of Ranks 2 and 3 sites (Fig. 6c).

The average land cost per acre varied widely across watersheds in the study area and generally decreased from south to north (Fig. 5). Based upon land costs and the likelihood of future development, watersheds in the northern and central part of the study area (shaded in red and orange, Fig. 6) had the highest probability of loss of good substrate quality per unit land cost. Watersheds colored red represent the highest benefit-cost option for conserving habitat. In contrast, watersheds in the south (yellow watersheds, Fig. 6) had relatively low probable loss of good substrate quality per unit land cost.

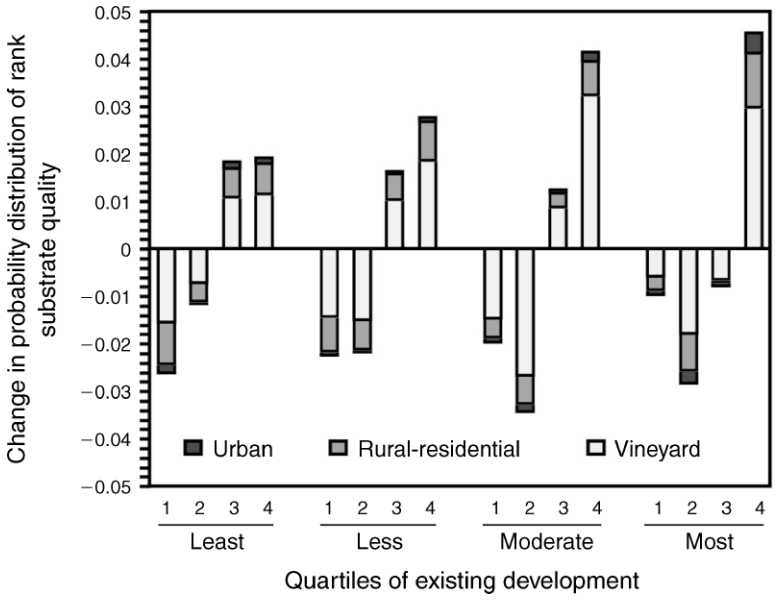


FIG. 4. Average change in the probability distribution of spawning site quality (Rank 1–4) in least to most developed watersheds. Shading in bars indicates the relative impacts of forecasted rural-residential, urban, and vineyard development on the change in spawning site quality.

## DISCUSSION

We quantified nonlinear relationships between land use (including low-density residential development) and relative levels of fine sediment in streams and then forecasted the expected impacts of land use change on spawning habitat for endangered salmon. Elevated inputs of fine sediment from land use conversion can negatively impact salmonid populations through the degradation of both spawning and rearing habitat (Reiser and White 1988, O'Connor and Andrew 1998, Kondolf 2000, Suttle et al. 2004), aggradation of pools (McIntosh et al. 2000), simplification of habitat (McIntosh et al. 2000), and suppression of invertebrate prey base for juvenile fish (Osmundson et al. 2002, Suttle et al. 2004). Taken together, results presented here and the linkages between fine sediment and salmonid population decline suggest that steelhead trout and coho salmon, already listed as threatened, are vulnerable to future increases in fine sediment loads due to expected land use conversions.

In this study, urban and vineyard land use were significant predictors of in-stream levels of fine sediment, consistent with our previous work (Opperman et al. 2005) and other studies (Wang et al. 2001, Pess et al. 2002, Morse et al. 2003, Donohoe et al. 2006). Unlike previous studies, however, we were able to distinguish and evaluate the effects of rural-residential development based on a spatially explicit, parcel-level land use change model. We found that the proportion of high-quality spawning sites decreased significantly with the percentage of rural-residential development in the watershed (see Plate 1). Findings suggest that previous studies relying on Landsat TM for land-cover data likely have omitted an important type of development that adversely impacts aquatic ecosystems (Fig. 1). As the amounts of urban and rural-residential development were more likely to occur within the same watershed (correlation coefficient = 0.52 in our watersheds), omission of the rural-residential variable in the regression model would have mistakenly attributed much of its effect to urban development. As a result, decision-makers might adopt policies to curb or redirect urban development, such as urban-growth boundaries (UGB) on sewer infrastructure expansion, while allowing rural-residential development to continue unabated (Newburn and Berck 2006). While our findings point to the previously omitted impacts of rural-residential development, the use of parcels as the spatial reporting unit likely overestimated the percentage of the watershed impacted by this type of land use because the entire parcel may not be impacted by the developed area. More research is needed to quantify the actual area of development associated with low-density residential development. We have begun to use pixel-based and object-based remote sensing to calculate the development footprint around existing rural residences, and have found that these methods effectively delineate the developed areas as long as tree cover does not hide structures and roads. Beyond the actual developed area, indirect impacts associated with the presence and use of roads for rural-residential development remain poorly characterized and likely extend the disturbance footprint of rural-residential development (Havlick 2002, Forman et al. 2003). Research in this area is underway to calculate the development areas for a large number of parcels, as

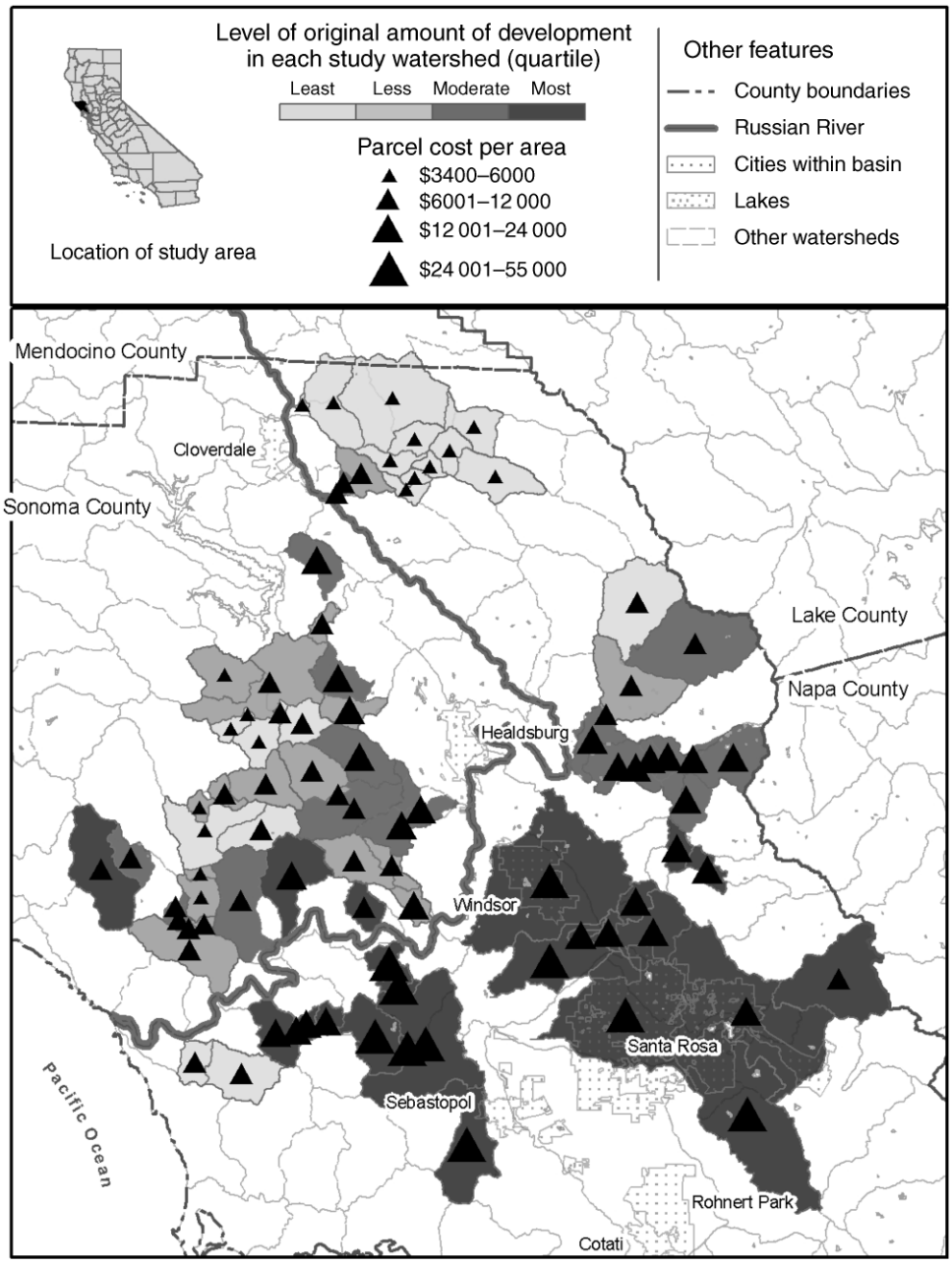


FIG. 5. Initial conditions of land use development in the study watersheds and cost per parcel area (see *Methods: Hedonic price model* for description of estimating land values from tax assessor's database on parcels).

there appears to be a high level of variability that can in part be explained by parcel size.

Our results also indicate that urban, rural-residential, and vineyard development differed in their severity of impact on streams. While urban development had the largest marginal effects (greatest response per unit of land use change), our data suggest that future rural-residential may have a greater overall impact than urban development on spawning-substrate quality. We expect this greater impact because the LUC model predicts 10 times as much land to be converted to rural-residential compared to urban development. In addition, the model projects rural-residential development to occur in watersheds ranging from the least to the most developed, and thus will affect reaches that currently have suitable habitat to support salmon reproduction. In contrast, the LUC model predicts future urban development to be more likely in areas that already have high levels of urban land use and low-quality spawning habitat (Fig. 6c). Finally, our results indicate that future

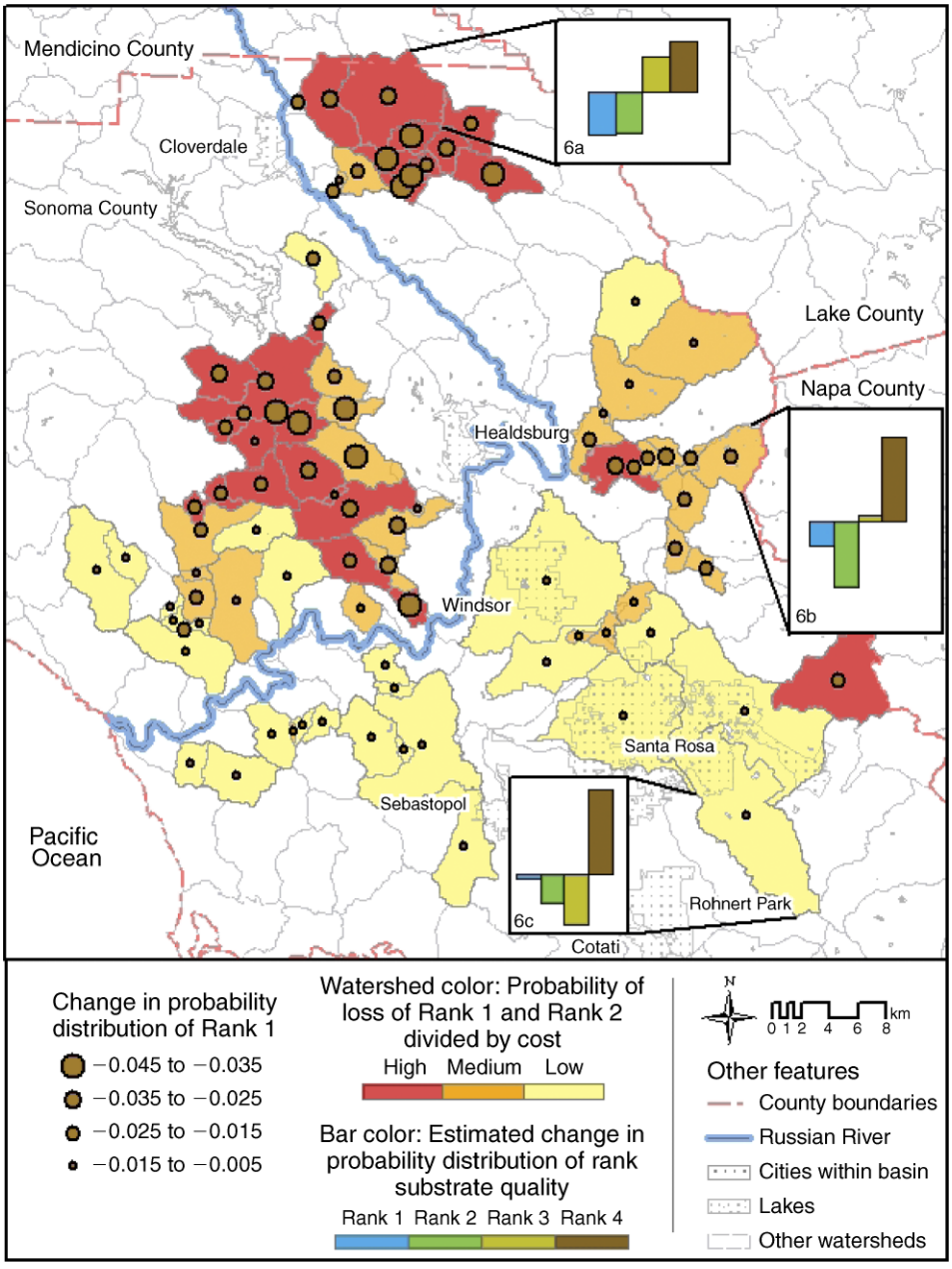


FIG. 6. Change in probability distribution of high-quality spawning sites (Rank 1) with forecasted land use change (key with circles) and probability of loss of high-quality substrate ÷ land cost in least to most developed watersheds in the Russian River Basin (watershed color). The watersheds colored red represent the lowest cost option for conserving high-quality spawning habitat. Inset bar color graphs show examples of estimated change in probability distribution of substrate quality within that rank for (6a) least, (6b) moderate, and (6c) most developed watersheds.

vineyard conversion could lead to high levels of sedimentation, and hence have a larger relative impact than urban development. Together, our findings suggest that fundamentally different land use types should not be aggregated in risk-assessment models.

Due to the nonlinearity of the responses, watersheds that differed in their level of initial development conditions had varying vulnerability to degradation of spawning habitats from future development. Based on the forecasting model, watersheds with lower percentages of existing development showed relatively large declines in the probability of high-quality spawning habitat (Ranks 1 and 2) (Fig. 6a). This sensitivity declined within the most-developed watersheds largely because these reaches initially had a small proportion of high-quality spawning habitat (Fig. 6c). Watersheds with large amounts of expected land use change (particularly agriculture) also showed large gains in the

PLATE 1. Example of rural-residential development in Sonoma County, California, USA. Photo credit: A. M. Merelender.

highest sediment levels (Fig. 6b). High sensitivity to development emphasizes the need to protect salmon habitat very early in the development process (or trajectory), often before many regulations designed to protect water from land use activities are triggered.

In this study, we forecasted changes over a short planning horizon (only about a decade) because the LUC model was calibrated over an eight-year development period, 1994–2002. Over longer planning horizons, market forces and urban service boundaries may change, making land use change projections more uncertain and assumptions underlying the models invalid. In a detailed study of exurban and urban development scenarios, Newburn and Berck (2006) showed that the probability of urban development increased 10-fold if they extended a sewer and water service area boundary, but rural-residential development did not change. We expect that the impacts of urban development in our model results would have been larger if sewer and water service areas were extended. Nonetheless, the impacts would still have been felt mostly in watersheds of already low-quality habitat. Thus, altered urban boundaries would not have likely changed the priority of conservation targets. Over a longer time frame (25–50 years), we expect the projected losses of habitat quality would be much larger due to urban expansion but also to rural-residential development in lesser-developed watersheds. Again, we expect conservation priorities would be similar to our short-term forecasts because priorities are based on relative rankings, in this case, the relative probabilities of loss of good spawning substrate divided by the average cost per acre for that watershed. Longer range forecasts are a topic of ongoing research.

The nonlinear relationships between various land uses and fine sediment described here can provide decision-makers with information on vulnerability of high-quality spawning habitat to different development pressures. Because resources for land conservation are limited, this forecasting approach can be used to prioritize areas for conservation efforts intended to reduce sediment loading to streams, such as purchasing conservation easements, reconnecting streams to floodplains, and reducing the sediment production from road networks. Funding for land conservation will likely be more fiscally efficient if areas with low-to-moderate threat to land use conversion are targeted rather than land at the urban fringe with the highest threat. Land costs at the urban fringe are several orders of magnitude higher than low-threat areas, making compensation to landowners for forgoing development far more costly (Fig. 5) (Newburn et al. 2005, 2006). Such a process will also identify locations where existing land use development may overwhelm the future efficacy or marginal benefit of conservation programs.

Through local zoning and other land use policies, decision-makers can work to influence the density and location of future residential development. Transfer of development rights (TDR) programs, for example, can be used to create a market between properties with existing rural-residential development rights located in environmentally sensitive areas (sending areas) and regions that are already serviced for denser urban development (receiving areas). For instance, local

planners in Montgomery County, Maryland downzoned properties with 5-acre minimum lot sizes and credited the landowners with the development rights. These development rights were then sold to developers who wanted to build urban housing at high densities within areas that already had SWSAs (Johnston and Madison 1997). In the context of our study, we recommend that a TDR program be implemented to curtail lower-density rural-residential development within moderate- and less-developed watersheds (sending areas in red and orange, Fig. 6), while encouraging higher-density infill urban development to take place in areas already highly disturbed (receiving areas in yellow watersheds, Fig. 6) (Johnston and Madison 1997, Nilsson et al. 2003, Merenlender et al. 2004).

In concert with these more transformative planning tools, effective runoff and construction control techniques can be employed when development does occur in sensitive watersheds. Best management practices for road construction and maintenance include guides for environmentally sensitive maintenance of dirt and gravel roads, as well as basic road design elements (Roads, Highways, Bridges–NPS categories) (*available online*).[6] Other low-impact development (LID) strategies for storm water management are also available to use at a local scale (Low-Impact Development) (*available online*).[7] The next research steps in spatial targeting include spatial prioritization within targeted watersheds that will begin to meet the needs of conservation groups who require finer scale spatial information on the relative value of individual parcels. On this research front, Newburn et al. (2006) have taken the first step toward parcel-level targeting within these watersheds, but had the simplicity of a linear benefit function in their model. Our future research will work toward integration of a dynamic optimization of the economic and land use change model with our biophysical model encompassing cumulative and nonlinear threshold effects.

While we effectively assessed the nonlinear response of spawning habitat to land use change, we still need a better understanding of hysteresis, as the conditions under which spawning sites shift to higher fine-sediment levels may differ from those that will shift the system back to lower levels. Reductions in fine sediment may occur through punctuated changes in stream flow or shifts in stream geomorphology. In general, a better understanding of the mechanism of sediment transport in these watersheds is desirable; we need to address questions about how water extraction and channel incision and other changes to stream geomorphology associated with development influence sediment dynamics. This increased understanding would inform management efforts to improve the quality of stream habitat where existing conditions fall below desired thresholds.

[6] ⟨http://www.epa.gov/owow/nps/roadshwys.html⟩
[7] ⟨www.EPA.gov/owow/nps/lid/⟩

## Conclusions

It is well recognized that urban development and intensive agriculture can increase sediment production and delivery to downstream stream reaches, rendering them unsuitable for successful fish spawning. In this study, we were also able to examine the impacts of exurban land use and found that increases in the percentage of total exurban development in a watershed significantly reduced the probability of observing high-quality stream habitat. In fact, results from this study suggest that exurban development may have a greater relative impact than urban development on stream conditions in the next decade because 10 times as much land is expected to be developed in exurban than urban areas, and exurban development has the ability to leapfrog into less-developed watersheds, which contain high-quality habitat, compared to urban development, which is typically constrained by urban growth boundaries. As exurban development now takes up 15 times the area of higher-density development (Brown et al. 2005) and is the fastest-growing type of land use in the United States (Theobald 2001), these findings raise concern for other areas where low-density residential development is on the rise.

Results from our study also demonstrate that urban and rural residential development are fundamentally different and thus require different land use policies to reduce their impacts on stream ecosystems and upland areas. Future urban development will tend to be clustered in areas that already have high levels of urban development and little high-quality spawning habitat. In contrast, exurban development is more likely to leapfrog into remote areas well beyond sewer water service areas and impact watersheds with good habitat quality. Hence, limits on the sewer service extension, a key objective of an urban growth boundary, will likely be effective in curbing urban expansion. However, it would have little or no influence on rural residential development. The application of our findings demonstrates the need to target conservation efforts in watersheds with the lowest cost option for protecting high-quality habitat. This approach directs resources away from those watersheds with the greatest threat of future development, which tend to have the highest land costs, and toward watersheds with low to moderate threat of future development. These watersheds contain high-quality habitat and have significantly lower land costs and are still at risk of low-density development in the near future. We recommend that local governments implement purchase and transfer of development rights programs as a primary strategy for influencing patterns of rural-residential development. In addition, we need to inform planners about the potential impacts of this type of land use and its consequence for environmental degradation because few existing policies, regulations, and incentive-based conservation programs are in place to adequately address the problem.

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## APPENDIX

A figure showing the change in probability distribution of spawning site quality with forecasted land-use change in the study watersheds (*Ecological Archives* A018-013-A1).

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*Review*

# Estimation of Bird-Vehicle Collision Mortality on U.S. Roads

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**ABSTRACT** Roads have numerous direct and indirect ecological impacts on wildlife. Vehicle collisions are a top impact of roads on birds, with tens of millions of birds thought to be killed each year in the United States. However, currently available mortality estimates are extrapolated from a single study. We reviewed the literature and used 20 mortality rates extracted from 13 studies to systematically quantify data-driven estimates of annual U.S. mortality from bird-vehicle collisions. We generated 4 separate estimates along with uncertainty using different subsets of data deemed to be rigorous enough to contribute relatively little bias to estimates. All of our estimates of vehicle mortality are higher than previous U.S. figures. When averaging across model iterations, we estimated that between 89 and 340 million birds die annually from vehicle collisions on U.S. roads. Sensitivity analyses indicated that uncertainty about survey-related biases (scavenger removal and searcher detection of carcasses) contributes the greatest amount of uncertainty to our mortality estimates. Future studies should account for these biases to provide more accurate local estimates of mortality rates and to inform more precise national mortality estimates. We found relatively little information available to quantify regional, seasonal, and taxonomic patterns of vehicle collision risk, and substantial uncertainty remains about whether collisions contribute to large-scale impacts on bird populations. Nonetheless, the large magnitude of bird mortality caused by vehicle collisions combined with evidence that collisions can contribute to local population declines for some species highlights the need for implementation of conservation and management actions to reduce this mortality. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** anthropogenic mortality, automobiles, birds, detection probability, roadkill, roads, scavenger removal, systematic review, United States, vehicles.

The global proliferation of road networks has led to a multitude of ecological impacts that affect biological diversity. In the United States, the greater than 6.5 million kilometers of roads (U.S. Department of Transportation 2012) ecologically affect at least 22% of the nation's land area (Forman 2000), causing loss and fragmentation of habitat; pollution with chemicals, light, and noise; alteration of animal movement and behavior; and direct mortality of wildlife from vehicle collisions (Forman and Alexander 1998, Trombulak and Frissell 2000, Forman et al. 2003, Coffin 2007). For birds, vehicle collisions are one of the greatest threats posed by roads (Kociolek et al. 2011), with as many as 80 million birds thought to be killed annually in the United States (Erickson et al. 2005) and roughly 13 million birds estimated to be killed annually in Canada (Bishop and Brogan 2013). Moreover, roadkills have the potential to constitute the vast majority of total mortality for some bird species—most notably, barn owls (*Tyto alba*) (Moore and Mangel 1996, Newton et al. 1997). Roadkill mortality can also result in the creation of population sinks (Mumme et al. 2000, Boves and Belthoff 2012, Grilo et al. 2012) and may be an additive source of mortality that contributes to population declines (Bujoczek et al. 2011).

A large body of literature has identified numerous factors that influence bird-vehicle collision rates. Mortality rates have been found to increase with increasing traffic speed and volume (Case 1978) and rates are generally highest during spring and summer. Mortality rates are also greater for juvenile birds, in areas with favorable bird habitat in close proximity to the road, and where bird populations are abundant (Loos and Kerlinger 1993, reviewed by Erritzoe et al. 2003, Gunson et al. 2010, Boves and Belthoff 2012). In some cases, mortality rates have been found to increase with increasing width of the road corridor (Oxley et al. 1974) or to be greater along road segments that are elevated above the surrounding land (Baudvin 1997, Lodé 2000). Often, 2 or

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*Conflict of interest: The authors have no conflicts of interest to declare.*

more of the above factors are strongly correlated—i.e., wider roads usually have a higher traffic volume than narrow roads—making it difficult to dis-entangle the relative impact of each factor. Furthermore, exceptions to the above relationships occur and are illustrative of how mortality rate correlates are often region-, taxa-, and habitat-specific. For example, several studies have found no link between traffic volume and mortality rates (Massemin et al. 1998, Lodé 2000, Coelho et al. 2008, Kambourova-Ivanova et al. 2012).

Current estimates of annual U.S. bird mortality from vehicle collisions—ranging from 60 to 80 million—are highly speculative, based on extrapolation of mortality rates from a single British study (Hodson and Snow 1965) to the entire U.S. road network (Banks 1979, Erickson et al. 2005). Comprehensive meta-analyses of studies that quantify bird populations have concluded that roads are consistently associated with reductions in bird abundance (Fahrig and Rytwinski 2009, Benitez-Lopez et al. 2010), but no clear evidence exists that vehicle collision mortality is a significant driver of these road-related declines. In addition, no such comprehensive analyses have been completed to assess bird-vehicle collision mortality in the United States. When compared to speculative or extrapolative estimates based on small samples of data, such systematic and quantitative reviews provide a more rigorous approach to estimating mortality, an improved understanding of the sources of uncertainty associated with estimates (Loss et al. 2012, 2013*a*, 2014; Machtans et al. 2013), and a more valid evidence base on which to prioritize policy and management strategies and to identify major research needs (Calvert et al. 2013, Machtans and Thogmartin 2014).

We reviewed the North American and European bird-vehicle collision literature and defined inclusion criteria to screen and remove studies likely to bias our estimates substantially. Based on data extracted from the remaining studies, we 1) systematically quantified the magnitude of bird mortality (along with uncertainty) caused by collisions with vehicles on U.S. roads by combining probability distributions of mortality rates, the length of U.S. roads, and biases associated with surveys for dead birds; 2) used sensitivity analyses to quantitatively investigate factors contributing to estimate uncertainty and to identify major research needs; and 3) summarized the available species-specific data on bird-vehicle collisions in the United States.

## METHODS

### Literature Search and Inclusion Criteria

We used Google Scholar and the Web of Science database to search for publications about bird-vehicle collisions on roads. The search terms we used were "bird-vehicle collision," "bird-vehicle roadkill," the previous terms with "bird" replaced by "avian" and "vehicle" replaced by "automobile," "car," and "truck." We checked reference lists to locate additional sources, and we also referenced an annotated bibliography that included approximately 670 sources covering the impacts of roads on wildlife (Nietvelt 2002). For 5 North American studies (Nero and Copland 1981, Decker 1987, Smith et al. 1994, Sutton 1996, Potvin and Bishop 2010), we were unable to access full-text articles and instead extracted the data as summarized in a review of bird-vehicle collisions in Canada (Bishop and Brogan 2013). Because of the large quantity of international studies—many that are published in languages other than English or inaccessible online or through North American libraries—we could not exhaustively review this literature. However, our review of the North American literature was comprehensive, and we likely located all studies that included a systematic sampling component. We may have overlooked some North American publications containing descriptions of incidentally found roadkill victims; however, these studies would have been excluded from analyses based on our inclusion criteria described below.

We defined several criteria for studies to be included in our estimation models. We designed inclusion criteria to remove studies that were not useful for generating mortality rate estimates or that were likely to substantially bias estimates. We excluded studies prior to in-depth review if they included no original data; were conducted in a region other than the United States, Canada, or Europe; or were published in a language other than English. In addition, because we sought to generate mortality estimates that were relevant to relatively modern road types and traffic patterns, we arbitrarily selected 1970 as the earliest date for which publications could be included in analyses (see also Bishop and Brogan 2013). Following in-depth review of the remaining 53 studies, we also excluded studies that 1) were retrospective, based on assessment of opportunistically collected data sets or recoveries of banded or radio-tagged birds, 2) focused on particular bird species or groups without sampling or presenting data for all species and groups, 3) included an experimental component without presenting control and treatment data separately, 4) were prospective but also included incidentally collected data without presenting it separately, 5) did not provide information about the proportion of the year covered by sampling, 6) did not present the length of road corridor sampled or a per kilometer mortality rate, 7) were based on a single survey or a series of surveys that covered less than 1 month, and 8) did not separately report fatalities from vehicle collisions and other collision sources (e.g., roadside fences). After implementing the above inclusion criteria, 16 of the 53 reviewed studies remained (9 U.S. and 7 European studies; Table 1; see Table S1 for excluded studies).

For the summary of species representation of mortality, we included data from U.S. studies meeting criteria 1–4 and 7–8 above. We considered criteria 5 and 6 unnecessary for producing unbiased species summaries. We used 7 of the 9 U.S. studies meeting inclusion criteria for the mortality estimate for the species analysis. The 2 excluded studies did not provide data at the species level (Oxley et al. 1974, Gerow et al. 2010).

### Data Extraction

From most studies meeting the above inclusion criteria, we extracted a single mortality rate. However, for studies that

**Table 1.** Meta-data and mortality rates for studies meeting inclusion criteria for 1) estimation of annual bird-vehicle collision mortality on U.S. roads and/or 2) species mortality summary.

| Location | Sampling coverage | Used? | | Road type | Mortality per km[c] | Study |
|---|---|---|---|---|---|---|
| | | Total[a] | Species[b] | | | |
| United States | | | | | | |
| Southern Idaho | Yr-round | Yes | Yes | 4-lane paved | 2.01 | Boves and Belthoff (2012) |
| Bow River Valley, AB | Apr–Nov | Yes | Yes | 2-lane paved | 0.38 | Clevenger et al. (2003)—Bow Valley Parkway |
| Bow River Valley, AB | Apr–Nov | Yes | Yes | 4-lane paved | 0.37 | Clevenger et al. (2003)—Trans-Canada Highway |
| Tippecanoe County, IN | Yr-round | Yes | Yes | 2-lane paved | 6.54 | Glista et al. (2008)—South River Road |
| Tippecanoe County, IN | Yr-round | Yes | Yes | 2-lane paved | 5.69 | Glista et al. (2008)—State Road 26 |
| Tippecanoe County, IN | Yr-round | Yes | Yes | 2-lane paved | 4.85 | Glista et al. (2008)—U.S. Highway 231 |
| Central California | 25 May–26 Nov | Yes | Yes | 4-lane paved | 1.20 | Moore and Mangel (1996) |
| Athens County, Ohio | Yr-round | Yes | Yes | 4-lane paved | 6.56 | Seibert and Conover (1991) |
| Southern Ontario/Quebec | 31 May–23 Sep | Yes | No | Unpaved | 0.23 | Oxley et al. (1974)—Gravel unpaved road 1 |
| Southern Ontario/Quebec | 31 May–23 Sep | Yes | No | Unpaved | 2.11 | Oxley et al. (1974)—Gravel unpaved road 2 |
| Southern Ontario/Quebec | 31 May–23 Sep | Yes | No | 2-lane paved | 2.96 | Oxley et al. (1974)—2-lane paved highway |
| Southern Ontario/Quebec | 31 May–23 Sep | Yes | No | 4-lane paved | 3.22 | Oxley et al. (1974)—4-lane paved highway |
| Long Point, ON | Apr–Oct | No[d] | Yes | 2-lane paved | 91.43 | Ashley and Robinson (1996) |
| Tippecanoe County, IN | Yr-round | No[d] | Yes | 2-lane paved | 24.44 | Glista et al. (2008)—Lindberg Road |
| Alachua County, FL | Yr-round | No[d] | Yes | 4-lane paved | 43.44 | Smith and Dodd (2003) |
| Saguaro Nat. Park, AZ | Yr-round | No[e] | No | ? | NA | Gerow et al. (2010)—Rincon Mountain |
| Saguaro Nat. Park, AZ | Yr-round | No[e] | No | ? | NA | Gerow et al. (2010)—Tucson Mountain |
| Europe | | | | | | |
| Northeast France | Yr-round | Yes | No | 2-lane paved | 1.54 | Baudvin (1996) |
| Northeast Poland | Yr-round | Yes | No | 2-lane paved | 11.55 | Gryz and Krauze (2008) |
| Galanta, Slovakia | Yr-round | Yes | No | ? | 17.09 | Hell et al. (2005) |
| Belovo, Bulgaria | Mar–Oct | Yes | No | ? | 3.00 | Kambourova-Ivanova et al. (2012)—1st-class road |
| Belovo, Bulgaria | Mar–Oct | Yes | No | ? | 8.09 | Kambourova-Ivanova et al. (2012)—Trakia highway |
| Western France | Apr–Nov | Yes | No | ? | 8.80 | Lodé (2000) |
| Wroclaw, Poland | Mid-Mar–Oct | Yes | No | ? | 5.89 | Orlowski (2005) |
| Spain and France | Yr-round | Yes | No | ? | 0.65 | Pons (2000) |

[a] Whether we used the mortality rate to estimate bird-vehicle collision mortality on U.S. roads.
[b] Whether we used the source to calculate average proportional representation for individual species (excluded U.S. studies focused on particular bird group(s) without including all species; we excluded all international studies).
[c] We calculated mortality rates using raw data (i.e., we did not directly extract reported rates from studies because calculation approaches varied among studies and were not always calculated transparently). We first divided the total number of fatalities reported for a road segment by the length of road corridor covered by that segment. For rates representing >1 year of sampling, we then divided by the number of years sampled; we applied a partial-year sampling correction in the mortality estimation model (see Methods section in main text for details).
[d] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is a statistical outlier among studies meeting criteria.
[e] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is adjusted for biases associated with carcass surveys (detection probability and scavenger removal); these biases were separately accounted for in our mortality estimation model.

sampled along more than 1 road type (e.g., paved and unpaved roads and/or roads with different numbers of lanes) or used different sampling methods (e.g., different sampling intervals or survey types) for different portions of the study area, we extracted separate mortality rates. This resulted in extraction of 25 mortality rates (17 U.S. and 8 European rates; Table 1) from the 16 included studies. We calculated all rates as the number of dead birds found per kilometer of road corridor sampled. This approach is different than that of some studies that calculate mortality rates using the total length of lanes sampled (e.g., for a 2-lane road, lane-length is twice the length of the road corridor). Some studies did not provide enough information to clarify how they calculated mortality rates. Therefore, rather than directly extracting the reported rates, we recalculated rates based on the number of fatalities reported for a road segment divided by the length of road corridor covered by that segment. Because we recalculated rates using this raw data, the mortality rate we

calculated was sometimes different than that presented in the original study.

We then used one of several approaches to convert multi-year mortality rates to annual rates. For multi-year studies that sampled across the entire calendar year in every year of the study, we divided mortality rates by the number of years to generate the annual rate (Table 1). We also took this approach for multi-year studies that only sampled a portion of each year; we accounted for partial-year sampling coverage separately (see following subsection). For 4 studies that sampled at least 1 entire calendar year as well as an additional partial year (Seibert and Conover 1991, Baudvin 1997, Hell et al. 2005, Glista et al. 2008), we treated the partial year as a full year when calculating the annual rate. This approach led to conservative rate estimates because mortality was spread across a longer time period than it actually occurred in.

We excluded 3 mortality rates from the above data set for being statistical outliers and 2 for being adjusted for various sampling biases that we accounted for separately in the mortality estimation model (see Supplementary Methods, available online at www.onlinelibrary.wiley.com). The final data set used for estimation of mortality therefore included 20 mortality rates (12 U.S. and 8 international rates) extracted from 13 studies (6 U.S. and 7 European studies; Table 1).

## Quantification of Annual Bird Mortality

To increase the comparability of mortality estimates from different studies, mortality rates should ideally be standardized to account for varying proportions of the year being covered by sampling (Loss et al. 2012). Potential standardization approaches include 1) using mortality rates from year-round studies to proportionally correct partial-year studies (Longcore et al. 2012, Loss et al. 2013*a*), 2) including a correction factor in the mortality estimation model that accounts for partial-year sampling (Loss et al. 2014), or 3) using only full-year mortality rates to generate mortality estimates. We were unable to implement the first approach because year-round vehicle collision studies either do not present data separately for different portions of the year or only provide seasonal data for single bird species or taxa other than birds. Because the second and third approaches were both possible, we repeated mortality estimation using each approach. We expected the estimate generated using approach 2 would represent a maximum value because this approach assumed that mortality rates observed during the sampled portion of the year—typically the peak periods of vehicle collision mortality in spring, summer, and/or autumn —also applied to the un-sampled portion of the year (see Supplementary Methods).

Our approach for estimating mortality was to combine a mortality rate probability distribution with a probability distribution for the length of U.S. roads susceptible to that range of mortality rates. We defined the maximum susceptible road length to be the entire U.S. road network and the minimum susceptible length to be only the length of roads in rural areas (see Supplementary Methods). This approach assumes that mortality rates in urban areas are likely lower than in rural areas, but does not entirely discount mortality in urban areas. We also incorporated correction factors to account for sampling coverage of less than the entire calendar year (for estimates that included partial-year morality rates) and for biases associated with carcass surveys (all estimates), including removal of carcasses by scavengers and imperfect detection of carcasses by surveyors (Loss et al. 2013*a*, 2014). Because a preliminary analysis found little support for differences in mortality rates between 2-lane, 4-lane, and gravel roads, and because the sample of mortality rates was too small to generate separate probability distributions for different road types, we applied the same range of mortality rates across all U.S. road types. This simplified approach contributes uncertainty to our mortality estimate; however, we did not have enough available data to allow separate mortality estimates for different road types. In addition to repeating mortality estimation with and without inclusion of partial-year studies, we also estimated mortality with and without inclusion of European mortality rates. Thus, we generated 4 separate estimates of annual mortality using different subsets of data: U.S. year-round mortality rates, U.S. year-round and partial-year rates, U.S. and Europe year-round rates, and U.S. and Europe year-round and partial-year rates.

For the estimates based only on year-round mortality rates, we used the model:

$$\text{Mortality}_{\text{year-round studies}} = R \times K_{\text{year-round studies}} \times B \qquad (1)$$

where $R$ is the length of U.S. roads susceptible to the range of mortality rates in the mortality rate probability distribution ($K$), $K$ is the is the range of collision mortality rates per km of road corridor, and $B$ is a bias correction factor to account for removal of carcasses by scavengers prior to surveys and imperfect detection of carcasses remaining at the time of surveys.

For the estimates based on year-round and partial-year rates, we used the model:

$$\begin{aligned}&\text{Mortality}_{\text{year-round and partial-year}}\\ &\quad = R \times K_{\text{year-round and partial-year}} \times Y \times B\end{aligned} \qquad (2)$$

where $Y$ is a correction factor that accounts for the average proportion of the calendar year not covered by sampling in the studies used to develop the mortality rate distribution (Loss et al. 2014). The partial-year sampling correction factor was a fixed value; however, we defined all other parameters as uniform probability distributions (specific distributions shown in Table 2; rationale for distributions in Supplementary Methods). For all estimates, we used the runif function in Program R (R Version 3.0.1., <http://www.r-project.org/>. Accessed 14 Apr 2014) to draw random values from each probability distribution, and we calculated mortality using the above formulas. We repeated this calculation 10,000 times for each of the 4 estimation approaches to generate ranges of uncertainty for mortality estimates.

## Sensitivity Analyses

We used sensitivity analyses to quantitatively investigate the factors contributing to uncertainty in our mortality estimates.

**Table 2.** Probability distributions used for estimation of annual bird-vehicle collision mortality on U.S. roads.

| Parameter | Distribution type | Distribution parameters | Source |
|---|---|---|---|
| Total length of road corridors in the United States[a] | Uniform | Min. = 3.76 M; max. = 4.33 M | U.S. Department of Transportation (2012) |
| Morality rates (per km) | | | |
| U.S. studies (yr-round)[b] | Uniform | Min. = 3.48; max. = 6.78 | 95% CI across 5 rates meeting inclusion criteria |
| U.S. studies (all)[c] | Uniform | Min. = 2.78; max. = 6.73 | 95% CI across 12 rates meeting inclusion criteria |
| U.S. + Europe studies (yr-round)[b] | Uniform | Min. = 2.85; max. = 9.70 | 95% CI across 9 rates meeting inclusion criteria |
| U.S. + Europe studies (all)[c] | Uniform | Min. = 4.24, max. = 8.58 | 95% CI across 20 rates meeting inclusion criteria |
| Partial-yr sampling correction | | | |
| U.S. studies (all)[c] | NA[d] | Estimate = 1.49 | 1/average proportion of yr covered by mortality rates |
| U.S. + Europe studies (all)[c] | NA[d] | Estimate = 1.37 | 1/average proportion of yr covered by mortality rates |
| Bias correction factor | Uniform | Min. = 3.26; max. = 11.46 | Bruun-Schmidt (1994), Gerow et al. (2010), Santos et al. (2011), Boves and Belthoff (2012), Texeira et al. (2013) |

[a] Includes length in millions (M) of kilometers of all public roads in all states excluding Alaska and Hawaii.
[b] Estimate is based only on mortality rates from studies with year-round sampling coverage.
[c] Estimate is based on mortality rates from all studies meeting inclusion criteria.
[d] Parameter is a point estimate, not a probability distribution.

We defined univariate regression models with the 10,000 replicated mortality estimates as the dependent variable and randomly drawn values of model parameters as the independent variable. We repeated this analysis 4 times, once for each of the 4 mortality estimate models. We used the adjusted $R^2$ values for each independent variable (averaged across the 4 sensitivity analysis iterations) to interpret the percentage of estimate uncertainty attributable to each model parameter (Blancher 2013, Loss et al. 2013*a*).

### Vehicle Collision Mortality by Species

In addition to estimating total annual mortality for all U.S. birds, we also calculated the average proportional representation of each bird species (Longcore et al. 2013, Loss et al. 2013*a*). We used this calculation rather than estimating species-specific mortality because the data from studies meeting inclusion criteria only represented 100 bird species. This value is likely much lower than the actual number of species killed along U.S. roadways each year. Estimates of species-specific mortality would therefore be biased high for observed species and biased low for species killed but not reported in the literature. Therefore, we would be unable to draw unbiased conclusions about species-specific collision risk. Nonetheless, to provide a rough summary of the findings to date, we estimated average proportional representation of species by 1) calculating the proportion of each study's total count represented by each species (i.e., multiple proportions calculated for each species, 1 from each study), and 2) averaging each species' individual-study proportions across all studies. For averaging, we only included zero-values of proportions (i.e., species was not found in study) when a species could have been found, as determined by overlap of breeding, migration, and/or wintering ranges with study sites (Sibley 2000).

## RESULTS

We found considerable variation (41.8%) among median mortality estimates produced using the 4 models (Table 3). The model using only year-round mortality rates from the United States produced the lowest annual estimate (median = 145.7 million; 95% CI = 61.9–274.6 million), and the model including both year-round and partial-year mortality rates and rates from both the United States and Europe produced the highest estimate and the estimate with the greatest range of uncertainty (median = 250.5 million; 95% CI = 103.8–476.8 million). Averaging across all 4 models (i.e., averaging the 4 estimates produced in each model iteration and then averaging these values across 10,000 iterations) resulted in a median annual mortality estimate of 199.6 million birds (95% CI = 88.7–339.8 million). Regardless of the model used, sensitivity analyses indicated that the bias correction factor for scavenger removal and searcher detection contributed the greatest uncertainty to estimates (average variance explained = 63.2%), followed by the mortality rate (32.5%) and the road corridor length over which the mortality rate applies (1.3%).

Among the species documented in studies meeting inclusion criteria, the barn owl had the highest average proportional representation across studies, averaging 32.4% of total counts (all species proportions in Table S2). Four other species, including 3 in the Corvidae family, had average proportional representation of at least 5%: common raven (*Corvus corax*; 6.3%), gray jay (*Perisoreus canadensis*; 6.0%), black-billed magpie (*Pica hudsonia*; 5.0%), and European starling (*Sturnus vulgarus*; 5.0%). Several species were found in 3 or fewer studies, and these species' proportions were more likely to be biased by abnormally high or low counts documented in single studies. Given the small sample of

**Table 3.** Estimates of annual bird-vehicle collision mortality on U.S. roads.

| | Total mortality (millions) | | Mortality per km | |
|---|---|---|---|---|
| **Mortality data used** | **Median** | **95% CI** | **Median** | **95% CI** |
| United States | 145.7[a] | 61.9–274.6[a] | 36.0[a] | 15.3–68.0[a] |
| | 197.1[b] | 78.2–397.9[b] | 48.8[b] | 19.4–98.5[b] |
| United States + Europe | 171.0[a] | 59.6–381.5[a] | 42.3[a] | 14.8–94.4[a] |
| | 250.5[b] | 103.8–476.8[b] | 62.0[b] | 25.7–118.0[b] |
| Average across models | 199.6 | 88.7–339.8 | 49.4 | 22.0–84.1 |

[a] Estimate based only on mortality data from studies with year-round sampling coverage.
[b] Estimate based on data from all studies meeting inclusion criteria.

studies included in the species summaries (7 studies including 3,246 total fatality records), caution should be used when interpreting these results.

# DISCUSSION

### Annual Bird-Vehicle Collision Mortality on U.S. Roads

All of our estimates of annual bird-vehicle collision mortality exceed the previous estimates of between 60 and 80 million birds, which were produced by extrapolating the results of 1 British study (Hodson and Snow 1965) across the entire U.S. road network (Banks 1979, Erickson et al. 2005). We improved upon these earlier estimates by systematically incorporating 20 mortality rates from 13 studies that used a prospective sampling design and reported results for all potentially killed bird species. Even when considering the lowest estimate range (between 62 and 275 million birds), our results suggest that bird-vehicle collisions outrank many other sources of direct anthropogenic mortality. Among threats with estimates that are data-driven and systematically derived, only predation by free-ranging domestic cats (Loss et al. 2013*a*) and collisions with buildings and their windows (Loss et al. 2014) are estimated to cause greater annual bird mortality in the United States. Estimates of total numbers of birds killed by anthropogenic threats are useful for prioritizing conservation and management efforts. However, increased attention should also be given to documenting which species and regions are most vulnerable to vehicle collisions and other mortality sources (Longcore et al. 2013; Loss et al. 2013*b*, 2014).

As expected, estimates that incorporated both year-round and partial-year mortality rates were higher than those that used only year-round rates. This likely occurred because the partial-year correction factor was calculated under the assumption that mortality rates were constant across all seasons. Among the studies we used, sampling periods typically covered spring, summer, and/or autumn, seasons characterized by relatively high mortality rates for most species (Loos and Kerlinger 1993, Smith and Dodd 2003, Orlowski 2005, Gryz and Krauze 2008). Extrapolating mortality rates from these peak seasons to un-sampled seasons that are generally characterized by lower mortality rates may have inflated our estimates. Estimates from models including partial-year rates should therefore be viewed as maximum values. Additional year-round studies that present results separately by month and/or season are needed to clarify intra-annual variation in vehicle collision mortality rates.

Estimates that included European mortality rates were higher than those that used only U.S. rates. This may have occurred due to the inclusion of 2 European rates that were not statistical outliers but were higher than all U.S. rates meeting inclusion criteria (11.6 and 17.0 birds/km/yr; Hell et al. 2005, Gryz and Krauze 2008). Although exceptionally high annual mortality rates of up to 91 birds/km (Ashley and Robinson 1996) have been documented locally in the United States, such rates likely do not apply across most roads. Roadkill fatalities are often clustered in hotspots (e.g., Gunson et al. 2010), and these areas are often the focus of mortality studies. This tendency to focus on areas already known to experience bird mortality may have contributed positive bias to individual estimates of mortality rates and to our national mortality estimates. Nonetheless, we sought to minimize this source of bias by removing mortality rates that were identified as statistical outliers.

We were unable to assess regional variation in bird-vehicle collision mortality rates and to produce regional mortality estimates. Only 6 U.S. studies met our inclusion criteria; this sample was insufficient to allow for quantification of regional variation. Filling this data gap will require rigorous and prospective studies across a broad cross-section of the United States within numerous ecosystems, states, and regions. Individual studies that randomly sample roadkill mortality across a large spatial scale (e.g., entire states or regions) will also provide increased understanding of regional variation.

### Research Needs and Estimate Limitations

The relatively small sample of data meeting inclusion criteria resulted in substantial uncertainty in our mortality estimates. When assessing specific uncertainty contributions of individual model components, sensitivity analyses indicate that the model parameter contributing the greatest uncertainty to our estimates is the bias correction factor, which accounts for both scavenger removal and imperfect detection of carcasses. Further research on these biases may decrease the uncertainty associated with this correction factor and allow for increased precision of future mortality estimates. However, the magnitude of these biases depends on a suite of factors, including the local scavenger community, habitat type, traffic volume, and weather conditions (Santos et al. 2011, Boves and Belthoff 2012, Guinard et al. 2012, Texeira et al. 2013). Development of a

narrow distribution of bias correction factors that apply across a national scale may therefore not be possible. An alternative approach is for future studies to estimate scavenger removal and searcher detection rates to calculate adjusted mortality rate estimates. A large sample of locally adjusted mortality rates would obviate the need for post hoc correction factors (Loss et al. 2013*b*). Recent studies outline considerations for scavenger removal and detection trials (Santos et al. 2011, Texeira et al. 2013). Of particular promise are approaches that allow for estimation of both biases using a single experimental trial incorporated into standard fatality monitoring (Smallwood 2013) or using only the dead birds found during fatality monitoring, thus removing the need for separate experimental trials (Etterson 2013).

Mortality rate probability distributions also contributed substantial uncertainty to our estimates. The relatively small sample of studies meeting inclusion criteria along with the inherently variable nature of collision rates likely contributed to this uncertainty. To increase the number of mortality rates that can be used to estimate national mortality, future studies should seek to meet the level of rigor captured by our inclusion criteria. In particular, more studies are needed that sample and present data for all bird species. When summarizing average proportional representation of collision mortality, we found that a few species (particularly barn owls and several corvids) comprise a relatively large percentage of all fatalities that have been identified to species. However, sample sizes of usable studies and available data were small, and results of the species summary were likely biased by high detection probabilities for large species and by geographical biases in sampling. Taking a more species-inclusive approach to studying bird-vehicle collisions will improve understanding of species- and taxa-specific vulnerabilities to vehicle collisions. Because of the above limitations, species proportions should not be used to draw conclusions about national-scale vulnerabilities of bird species to vehicle collisions. Nonetheless, they provide a descriptive summary of the bird species that have been documented as roadkill victims along U.S. roads.

In addition to estimate bias caused by scavenger removal and imperfect detection of carcasses, an unknown number of birds that collide with vehicles fly out of detection range (i.e., crippling bias; Slater 2002, Texeira et al. 2013) or are destroyed or carried away by vehicles (Stewart 1973, Mumme et al. 2000). Because these biases have never been formally quantified in the context of vehicle collisions, substantial uncertainty remains about to what degree they contribute to under-estimation of roadkill mortality rates. Future research of these bias sources is necessary for fully understanding the magnitude of bird mortality caused by vehicle collisions.

Numerous biotic and abiotic factors influence bird collision mortality rates along roads. These correlates collectively result in bird fatalities being clustered along particular road segments (Clevenger et al. 2003, Smith and Dodd 2003, Glista et al. 2008, Gunson et al. 2010). Further research is needed to clarify the combination of factors that lead to carcass clustering (e.g., habitat, characteristics of the road and its cleared corridor, and community composition and population abundance of birds) and to assess how these correlates vary seasonally and regionally. When possible, studies should employ sampling designs that allow for separation of often-confounded mortality correlates (e.g., road width, traffic volume, and traffic speed).

The negative bias contributed to mortality rate estimates by scavenger removal is amplified with increasing time intervals between surveys. This occurs because—with all other factors held constant—more collisions occur between surveys, and a greater proportion of carcasses are removed by scavengers. Because carcass removal adjustment factors are less accurate across long search intervals (Smallwood 2013) and because carcass removal rates appear to be especially high along roadways (Bruun-Schmidt 1994, Antworth et al. 2005, Santos et al. 2011, Texeira et al. 2013), optimal search intervals for documenting roadkill mortality are very short (e.g., sampling on alternate days for large birds and daily for small birds; Santos et al. 2011). Because the search intervals in the studies we used were between 2 and 15 days, mortality rates in individual studies could have been substantially under-estimated. This under-estimation could have contributed negative bias to our mortality estimates.

In addition to using long search intervals for carcass surveys, the studies we used conducted surveys using various transportation methods, including foot, bicycle, and automobile. Because of the relatively high speed at which sampling is conducted, automobile surveys usually detect only a small fraction of carcasses (Slater 2002, Gerow et al. 2010, Guinard et al. 2012, Texeira et al. 2013). In the sample of mortality rates extracted from studies meeting our inclusion criteria, the majority of rates (15 of 20) were based on automobile surveys, and estimated mortality rates for automobile surveys averaged 2.3 times lower than for other survey types. Therefore, the use of automobile surveys may have contributed additional under-estimation bias to our mortality estimates. The use of automobile surveys may have also influenced our species summary, with surveys likely over-representing large-bodied species (e.g., raptors and corvids) that are relatively easy to detect from a fast-moving automobile.

## MANAGEMENT IMPLICATIONS

The large magnitude of mortality caused by vehicle collisions combined with the potential for impacts at the population level highlights the need for conservation and management attention to mitigate this threat. Mitigation efforts may be most relevant at areas known to experience exceptionally high rates of collision mortality (e.g., clear examples include the studies that were identified as statistical outliers for our mortality estimate). Following identification of mortality hotspots, potential options to reduce bird collision mortality along roads include (see also Boves and Belthoff 2012, Bishop and Brogan 2013) placing flight deflectors along roadsides to force birds to fly above vehicle height (Bard et al. 2001, Ramsden 2003, Gomes et al. 2009), locally reducing speed limits and erecting signage to alert drivers, reducing or removing the amount of favorable bird habitat

along roadsides, and using visual or auditory deterrents. All of these approaches have rarely been implemented and remain largely untested. Research is therefore needed to determine which combinations of the above approaches are most effective at reducing mortality and to clarify how responses vary by bird species, region, habitat, season, and road type. Identification and implementation of effective conservation measures is especially crucial given the increasing length of U.S. roadways, increasing traffic volume, and an increasing number of direct and indirect anthropogenic threats to bird populations.

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## SUPPORTING INFORMATION

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# Recent ecological responses to climate change support predictions of high extinction risk

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**Predicted effects of climate change include high extinction risk for many species, but confidence in these predictions is undermined by a perceived lack of empirical support. Many studies have now documented ecological responses to recent climate change, providing the opportunity to test whether the magnitude and nature of recent responses match predictions. Here, we perform a global and multitaxon metaanalysis to show that empirical evidence for the realized effects of climate change supports predictions of future extinction risk. We use International Union for Conservation of Nature (IUCN) Red List criteria as a common scale to estimate extinction risks from a wide range of climate impacts, ecological responses, and methods of analysis, and we compare predictions with observations. Mean extinction probability across studies making predictions of the future effects of climate change was 7% by 2100 compared with 15% based on observed responses. After taking account of possible bias in the type of climate change impact analyzed and the parts of the world and taxa studied, there was less discrepancy between the two approaches: predictions suggested a mean extinction probability of 10% across taxa and regions, whereas empirical evidence gave a mean probability of 14%. As well as mean overall extinction probability, observations also supported predictions in terms of variability in extinction risk and the relative risk associated with broad taxonomic groups and geographic regions. These results suggest that predictions are robust to methodological assumptions and provide strong empirical support for the assertion that anthropogenic climate change is now a major threat to global biodiversity.**

anthropogenic warming | elevated temperature | extinction crisis | climate warming

Many scientists argue that we are entering the sixth great mass extinction and that anthropogenic climate change is one of the major threats to global biodiversity (1–3). Comprehensive, multitaxon reviews suggest that 10–70% of plant and animal species assessed so far could be at increased risk of extinction from climate change (4) or that by 2050, climate-induced changes in habitat will commit 15–37% of species to extinction (1). Both these estimates are based on approaches that can be sensitive to ecological and methodological assumptions (5–8), and the latter study considers only geographical range shifts resulting from changes in temperature and rainfall (1). Many species are also expected to be adversely affected by changes in sea-level and ocean chemistry (9), and the impacts of climate change may include breakdowns in biological interactions as species respond individualistically to climate change (10), loss of habitat because of sea-level rise (11), and higher mortality because of increased ocean acidity (12). The spectrum of approaches used to predict ecological responses to climate change has also broadened in recent years, enabling more robust estimates of future changes to be made (13). Here, we use International Union for Conservation of Nature (IUCN) Red List Criteria (14) to derive estimates of extinction risk from a wide range of climate impacts, ecological responses, and methods of analysis. Importantly, the broad evidence base that now exists for realized ecological responses to recent climate change allows us to validate future predictions by comparison with responses that have already been observed.

We identified 130 observed and 188 predicted ecological responses to climate change using a robust review of 10 leading scientific journals from 2005 to 2009 (*Methods*). The responses included documented changes to extinction risk, population size, and geographic range size for 305 taxa from all major groups of organisms, covering a high proportion of the global terrestrial and marine surface (Table S1). All 318 climate change responses were expressed in terms of extinction risk using IUCN Red List criteria, which is possible, because the threshold values used to assign IUCN categories on the basis of population decline are linearly related to the logit transform of threshold extinction risk values (Fig. S1). Estimates of the mean extinction risk for taxa and the proportion subject to varying degrees of extinction risk were derived with an intercept-only generalized linear model with an inflated β-error distribution and logit link function (*Methods*).

A range of factors relating to the selection of study systems (climate impact type, taxon, and region) and the publication of results could influence whether the sampled climate change responses gave unbiased estimates of mean extinction risk. To determine whether there was publication bias, we investigated whether extinction risk was related to the journal in which the study was published and also, created a funnel plot of extinction risk against sample size (Fig. S2). The presence of asymmetry in a funnel plot signifies bias to the publication of significant results (15). To account for biases in the type of impact studied, we incorporated impact type as a factor into models and compared the results of averaging across impact types with those results obtained by averaging across studies. To account for possible phylogenetic nonindependence of extinction risk, we constructed a phylogenetic tree and added the residual of each tip relative to its branch to the mean across all tips in instances where branches were significant. Research carried out in regions where taxa are disproportionately threatened by climate change could also bias overall estimates of threat, and therefore, we controlled for spatial patterns in extinction risk by spatially averaging our results (*Methods*).

To examine whether there were consistent ecoregional and taxonomic patterns across studies making predictions and studies reporting empirical data, we subdivided our data into three major taxonomic groups (plants, invertebrates, and vertebrates) and four major ecoregions: (*i*) polar and boreal, (*ii*) temperate, (*iii*) tropical and subtropical, and (*iv*) marine; we compared observations with predictions.

## Results and Discussion

Across all studies, the mean extinction risk over 90 y (i.e., to 2100) was 11.2%. Separating projections of extinction risk based on predicted and observed responses yielded a mean extinction

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risk of 6.7% based on predictions but 14.7% based on observations (Table 1).

The proportion of taxa qualifying as threatened by 2100 using IUCN criteria would be 7.6% based on predictions and 31.7% based on observations. The proportion of taxa more likely to go extinct than not was 1.9% based on predictions but 12.0% based on observations (Table 1). The degree of variability in extinction risk across observations and predictions is similar (Fig. 1), with the majority of taxa (>80%) at low risk (<5%) of extinction; this finding suggests that predictions are not invalidated by methodological assumptions. The symmetry of the funnel plots of extinction risk against sample size (Fig. S2) suggests very little evidence of publication bias. However, extinction risk for both observations and predictions was affected by climate impact type. More studies reported threats from changes in temperature and rainfall, but the few studies on the effects of reductions in sea ice and changes in ocean circulation patterns showed higher predicted extinction risk (Table S2). More studies on effects such as changes in oceanic circulation patterns and acidity on marine organisms would improve estimates of extinction risk. Nevertheless, models that controlled for climate impact type did not lead to marked changes in mean extinction risk, either for empirical observations or predictions (Fig. 1 and Table 1).

There was evidence of phylogenetic nonindependence of extinction risk, with both observations and predictions suggesting high levels of threat to vertebrates and lower levels of threat to plants and invertebrates. This finding was also supported by comparisons of extinction risk within each of these three major taxonomic groups (Fig. 2). There was a high degree of consistency between observations and predictions, with most taxa observed to be at high risk also predicted to be highly threatened in the future. After accounting for phylogeny, estimated extinction risks from observations decreased to 14%, whereas those risks from predictions did not change (Table 1). Thus, observed responses may be slightly exaggerated by work on more threatened taxa. Spatial averaging of results did not alter estimates of

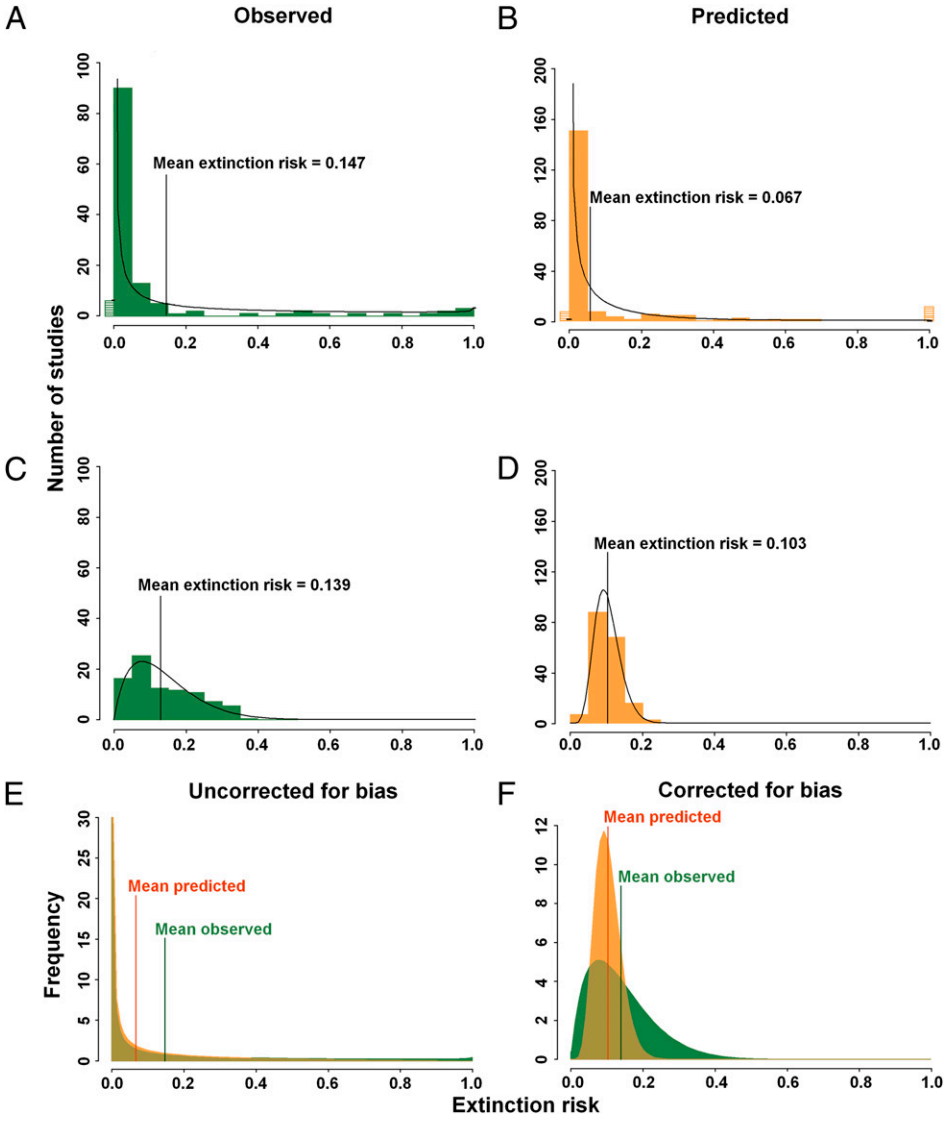


**Fig. 1.** Proportion of taxa subject to varying degrees of extinction risk by 2100. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The horizontal hatched bars (actual) and horizontal black lines (modeled) represent the number of studies with an extinction risk of zero or one. (*A* and *B*) Uncorrected estimates derived from observed (*A*) and predicted (*B*) data. (*C* and *D*) Estimates accounting for biases (*Methods*) derived from observed (*C*) and predicted (*D*) data. (*E* and *F*) Modeled probability density functions (green, observed; orange, predicted) overlaid to show that, when uncorrected (*E*), the variance in extinction risk derived from observed and predicted data is similar, and when corrected (*F*), the means are similar.

**Table 1. Projected extinction risk by 2100 based on observations and predictions**

| Method | Expected extinction risk | | | >50% probability of extinction | | | Threatened with extinction | | |
|---|---|---|---|---|---|---|---|---|---|
| | All | Observed | Predicted | All | Observed | Predicted | All | Observed | Predicted |
| Estimate derived from values given in each study | 0.112 | 0.147 | 0.067 | 0.069 | 0.120 | 0.019 | 0.291 | 0.318 | 0.076 |
| Estimate obtained by averaging across impact types | 0.116 | 0.158 | 0.061 | 0.073 | 0.132 | 0.035 | 0.298 | 0.333 | 0.204 |
| Estimate obtained by averaging across taxa | 0.104 | 0.140 | 0.061 | 0.051 | 0.104 | 0.049 | 0.296 | 0.329 | 0.375 |
| Estimate obtained by spatially averaging across the globe | 0.118 | 0.139 | 0.103 | 0.000 | 0.002 | 0.000 | 0.620 | 0.648 | 0.600 |

Expected extinction risk is based on the β-distribution of observed or predicted extinction risks ($n_{predicted}$ = 188; $n_{observed}$ = 130). Taxa categorized as threatened were those taxa exceeding a modeled extinction risk by 2100 of 0.09. IUCN categories: CR, critically endangered; EN, endangered; VU, vulnerable.

observed extinction risk (13.9%), whereas predicted risk increased (10.3%), implying that models of future effects of climate change may, to some extent, have neglected regions subject to higher levels of threat (Table 1). Comparisons of extinction risk in broad ecoregions suggest that marine taxa are particularly threatened and that taxa in the terrestrial tropics and subtropics are less threatened than those taxa in terrestrial temperate and high latitude areas, and the relative threat predicted for different regions was quite well-supported by empirical observations (Fig. 3). However, for both observations and predictions, there were few studies from the terrestrial tropics: the larger number of predictions from the subtropical and tropical category is mostly of tree responses in Mexico (16). In the marine environment, there is a bias to research on corals, which may be disproportionately affected by climate change. More research from tropical areas, where most species occur and are expected to have climates for which no current analog exists (17) and on a greater variety of marine taxa, would improve estimates of the realized threat to biodiversity from climate change.

Our approach, using IUCN criteria to translate between population or range changes and extinction risk, has allowed us to include more examples than simply population viability studies, which estimate extinction risk directly. We, thus, reduce possible bias in threat levels that could result, because particular methodologies might focus on endangered species. However, we make the assumption that the threshold values for criteria relating to decline and extinction risk are comparable (*SI Methods*). Although the rules used to assign taxa to IUCN categories represent inter-

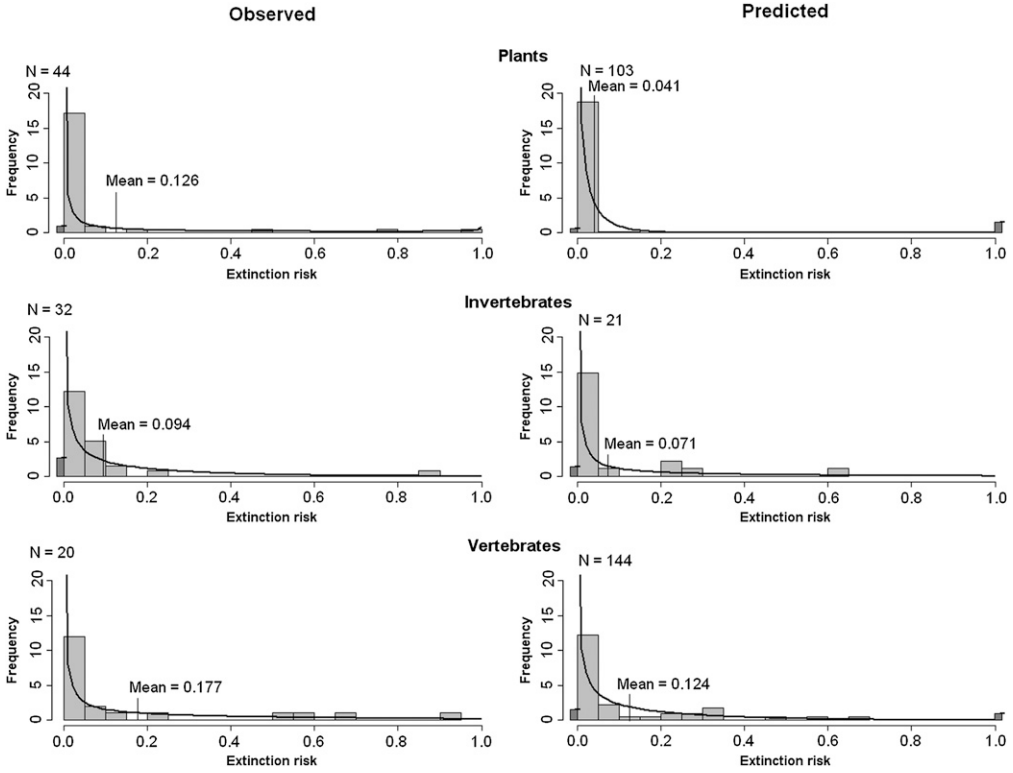


**Fig. 2.** Frequency distribution of extinction risk by 2100 in (*Left*) observed and (*Right*) predicted studies of taxa: (*Top Left* and *Top Right*) plants, (*Middle Left* and *Middle Right*) invertebrates, and (*Bottom Left* and *Bottom Right*) vertebrates. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The dark bars (actual) and horizontal black lines (modeled) represent the frequency of studies with an extinction risk of zero or one. Data are scaled such that the total area of histogram bars and under the modeled extinction risk line is equal to one. *N* is the number of samples in each category.

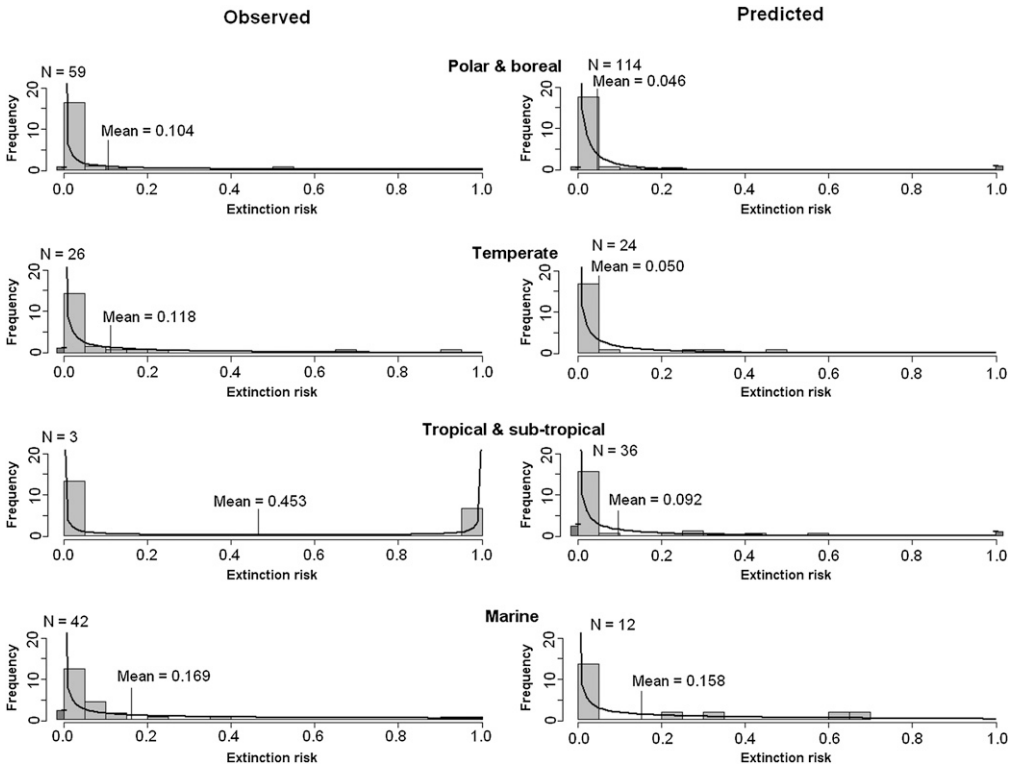


**Fig. 3.** Frequency distribution of extinction risk by 2100 in (*Left*) observed and (*Right*) predicted studies of ecoregions: (row 1) polar and boreal, (row 2) temperate, (row 3) tropical and subtropical, and (row 4) marine. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The dark bars (actual) and horizontal black lines (modeled) represent the frequency of studies with an extinction risk of zero or one. Data are scaled such that the total area of histogram bars and under the modeled extinction risk line is equal to one. *N* is the number of samples in each category.

nationally accepted decision tools in conservation biology (14, 18) and broad consistency between criteria was sought during their development (19), variation among species makes it difficult to validate the equivalence of thresholds for different criteria (20). Moreover, phylogenetic nonindependence of extinction risk could also reflect difficulties in assessments for poorly known taxa, with generally fewer experts and less data available (14). For example, the apparent low threat to invertebrates may partly reflect the lack of detailed understanding of climate threats facing most insects, with the majority of studies being on Lepidoptera (21). Direct predictions of extinction, as determined, for example, by population viability analyses, yielded higher estimates of extinction risk than estimates provided by changes in population and range size (Fig. S3). However, we suspect that this finding is primarily caused by these studies focusing on particularly endangered species. Our results were not unduly sensitive to the assumed relationship between range change, population change, and extinction risk (Table S3), suggesting that our overall estimates of extinction risk are relatively robust to any lack of equivalency among IUCN criteria. Furthermore, interactions between taxonomic group and method did not significantly affect estimates of extinction risk, suggesting that variation in the degree of difficulty in estimating extinction risk across categories is unlikely to invalidate our cross-taxonomic findings.

Estimated extinction risk was not related to the journal of publication or the time period over which observations were carried out or predictions were made. The sample size in each study could still influence the reliability of results, but we did not use formal metaregression techniques for two reasons. First, it was our intention to report means and variances in extinction risk across taxa rather than provide a single measure. Each estimate is derived from different taxa and could stem from any one of a number of different responses. Consequently, the effect being measured is not common across studies, and there is no reason to attribute a higher weighting to studies with larger sample sizes. Second, many studies do not report complete or comparable measures of uncertainty. Therefore, the use of metaregression to calculate the uncertainty in extinction risk across all studies would not be valid. Consequently, we attached the same weighting to all studies, irrespective of sample size. This weighting is unlikely to cause major bias in estimates of extinction risk, because there was no evidence of a consistent relationship of reported extinction risks with either sample size or the number of species studied (*SI Methods* and Fig. S3).

There are many unknowns when projecting declines in biodiversity, and the values here should be interpreted with caution. Nevertheless, our results were robust to publication, taxonomic, geographical, and impact-type biases, and assumed theoretical relationships between extinction risk, population decline, and range change. Furthermore, the degree of variance is also similar across observations and predictions, suggesting that predictions are not invalidated by methodological assumptions. Given that climate change is expected to accelerate and hence, exacerbate impacts, empirical evidence suggests that many predictions of extinction risk may be somewhat conservative. However, in terms of consistent phylogenetic and ecoregional patterns, the results suggest that realized ecological responses to climate change support predictions of future change. Our estimates of extinction risk are lower than previous estimates of the proportion of species committed to extinction by 2050 (1), but they are within the same order of magnitude. Moreover, commitment to extinction is not the same as extinction risk, because decades may elapse between habitat loss or climate change and the resultant species-level extinctions (22). Consequently, one would expect estimated extinction risk over a specified period to be lower.

Our results lend support to the contention, based on entirely different data and methods (1), that anthropogenic climate

warming at least ranks alongside other recognized threats to global biodiversity. Based on published results, we endeavor to distinguish between responses to climate and other drivers of change, although in many cases, the mechanisms behind species responses to climate change are not known. Several studies suggest that changes to biotic interactions have led to increased extinction risk for at least one interacting species (10, 23). Habitat degradation (24), invasive species (25), and overexploitation (26) play additional roles, and interactions among these threats and climate change will increasingly threaten populations of species. In addition, rapid climate change has the potential to overwhelm the capacity for adaptation in many populations, reducing the ability to resist and recover from other environmental stressors (27). Our metaanalysis showing high predicted levels of extinction, backed up by consistent data for changes that have already occurred, shows the need to give climate change high priority in conservation planning and to communicate its potentially wide-ranging consequences to policy makers and the wider public.

## Methods

Details of the studies and methods are provided in *SI Methods* and Table S1.

**Selection of Studies.** We reviewed 1,120 papers published from 2005 on in 10 leading journals focused on general science, ecology, or conservation. We searched all papers with climate change in the title, abstract, or keywords in *Biological Conservation*, *Conservation Biology*, *Ecological Applications*, *Ecology Letters*, *Journal of Applied Ecology*, *Nature*, *Proceedings of the Royal Society of London Series B Biological Sciences*, and *Science*, and all papers with climate change and biodiversity in *Global Change Biology* and PNAS. Those papers in which extinction probabilities, IUCN Red List categories, or a change in population size or range were reported were shortlisted for metaanalysis. We extracted data only from those articles in which changes could primarily be attributed to climate change or where climate was distinguished from other effects. From each paper, we recorded the taxon and number of species, the start and end of the study period, the type of climate change impact (changes in temperature and/or rainfall, ocean circulation patterns, ocean acidity, or sea ice, or responses to habitat change such as loss of habitat because of sea-level rise), and the number of spatial and temporal replicates. We also specified whether the response was observed or predicted. In all, we extracted data from 74 studies (32 observations and 42 predictions), providing 318 (130 observations and 188 predictions) taxon-specific climate change response estimates (*SI Methods* and Table S1).

**Estimating Extinction Risk.** We used IUCN Red List criteria to derive estimates of extinction risk from changes in population or range size, with a change in range size measured as the change in the area occupied. We assumed that a change in range is directly equivalent to a change in population size, an approach that is likely to give conservative estimates of population decline (28). Extinction risks can be standardized over any given period using multiple event probability theories (Eq. **1**):

$$E_s = 1 - (1 - E_t)^{\frac{s}{t}}, \quad [1]$$

where $E_s$ is the extinction probability of the desired time period $s$ and $E_t$ is the extinction probability over time period $t$. When extinction probabilities associated with each of the three IUCN Red List categories are standardized to 55.628 y and logit transforms are applied to ensure a continuous range of values, there is a perfectly linear relationship with the equivalent population size reductions over 10 y in each of the categories (Fig. S1). It is, thus, possible to infer extinction risk for any given change in population size, including increases. We also included studies where species had been assigned to IUCN Red List categories by assuming conservatively that their extinction risk corresponded to the threshold value for the category in which they had been placed. We assessed extinction risk over a 90-y period to give estimates for 2100. Full details of the method used to infer extinction risk from each study are given in Table S1. Because extinction estimates are constrained to values between zero and one and were zero- and one-inflated, estimates of the mean extinction risk for taxa and the proportion subject to varying degrees of extinction risk were derived by fitting a zero- and one-inflated β-error distribution to the data with a logit link function using the R (29) package GAMLSS (30).

To test for publication bias to studies that reported a high extinction risk, we examined the relationship between extinction risk and sample size. To test for researcher bias to species particularly threatened by climate change, we applied the same method using the number of species studied instead of sample size. There was no evidence of either researcher or publication bias (*SI Methods* and Fig. S2).

The potential effects of mean time of study, journal, and impact type on extinction estimates were assessed using a generalized linear model in R (29). All combinations of variables, including the null model, were tried, and the final model was selected using Akaike's Information Criterion (31). For both observed and predicted data, models in which impact type was included yielded the lowest Akaike's Information Criterion. We, thus, averaged across impact types to give a revised estimate.

To examine whether there were consistent taxonomic patterns across studies making predictions and empirical data, we subdivided our data into three major taxonomic groups: plants, invertebrates, and vertebrates. Bacteria, fungi, and taxa such as algae that were resolved to insufficient taxonomic detail were excluded from these analyses. To examine whether there were consistent ecoregional patterns across studies, we subdivided our data into four major ecoregions: (*i*) polar and boreal (ice sheets, tundra, and taiga), including studies of high altitude taxa at mid-latitudes, (*ii*) temperate (forest and steppe), (*iii*) tropical and subtropical, including xeric and Mediterranean habitats, and (*iv*) marine (all latitudes). Freshwater wetland taxa were assigned to the ecoregion in which the wetland was located. Studies spanning more than one ecoregion were excluded from these analyses.

**Phylogenetic Relationships.** A composite phylogeny of all study taxa was constructed using information contained in ref. 32, with branch lengths scaled to be approximately equal to time since divergence. Often, extinction estimates were for groups of species only, and in such instances, a dummy species was created that branched from the node encompassing all species within the group. Using the standardized normal residuals from the Generalized Linear Model (GLM) modeling, the mean residual value across all descendant terminal taxa was then calculated for each branch using the analysis of traits function in Phylocom 4.1 (33). The significances of branch values relative to the mean value across all terminal taxa were calculated by randomizing values for each taxon across all tips. To control for the extent to which particular taxa differed in terms of their extinction risk when calculating global estimates, the residual of the tip relative to the branch was added to the mean across all tips in instances where branches were significant. To test the robustness of our results to uncertainties associated with divergence time estimation, we also ran our analyses on the same tree but with branch lengths set to one. This change did not affect observed estimates of extinction risk, but predicted estimates increased from 6.1% to 6.5%.

**Spatial Relationships.** The geographical boundaries of all study sites from which extinction estimates were derived were mapped as polygons in ArcGIS 9.2 using a Cylindrical Equal Area projection (ESRI). The centroids of all study areas were then calculated, and spatial kriging with a spherical semivariogram model was performed using the Spatial Analyst tool in ArcGIS. Because it is not possible to define a projection that preserves true distances between all points on the globe, a North Pole Azimuthal Equidistant projection was used to perform spatial kriging in the northern hemisphere, and a South Pole Azimuthal Equidistant projection was used to perform spatial kriging in the southern hemisphere. The two hemispheres were then joined and converted back to a cylindrical equal area projection with a 1-km$^2$ resolution. The individual pixel values were then exported as an ASCII file, and a zero- and one-inflated β-error distribution with a logit link function was fitted to these data to estimate the mean extinction risk and the proportion of taxa subject to varying degrees of extinction risk.

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CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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# USING CIRCUIT THEORY TO MODEL CONNECTIVITY IN ECOLOGY, EVOLUTION, AND CONSERVATION

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*Abstract.* Connectivity among populations and habitats is important for a wide range of ecological processes. Understanding, preserving, and restoring connectivity in complex landscapes requires connectivity models and metrics that are reliable, efficient, and process based. We introduce a new class of ecological connectivity models based in electrical circuit theory. Although they have been applied in other disciplines, circuit-theoretic connectivity models are new to ecology. They offer distinct advantages over common analytic connectivity models, including a theoretical basis in random walk theory and an ability to evaluate contributions of multiple dispersal pathways. Resistance, current, and voltage calculated across graphs or raster grids can be related to ecological processes (such as individual movement and gene flow) that occur across large population networks or landscapes. Efficient algorithms can quickly solve networks with millions of nodes, or landscapes with millions of raster cells. Here we review basic circuit theory, discuss relationships between circuit and random walk theories, and describe applications in ecology, evolution, and conservation. We provide examples of how circuit models can be used to predict movement patterns and fates of random walkers in complex landscapes and to identify important habitat patches and movement corridors for conservation planning.

*Key words:* *circuit theory; dispersal; effective distance; gene flow; graph theory; habitat fragmentation; isolation; landscape connectivity; metapopulation theory; reserve design.*



## INTRODUCTION

Connectivity among habitats and populations is considered a critical factor determining a wide range of ecological phenomena, including gene flow, metapopulation dynamics, demographic rescue, seed dispersal, infectious disease spread, range expansion, exotic invasion, population persistence, and maintenance of biodiversity (Kareiva and Wennergren 1995, Ricketts 2001, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Moilanen et al. 2005, Crooks and Sanjayan 2006, Damschen et al. 2006, Fagan and Calabrese 2006). Preserving and restoring connectivity has become a major conservation priority, and conservation organizations are investing considerable resources to achieve these goals (Beier et al. 2006, Kareiva 2006).

Understanding broad-scale ecological processes that depend on connectivity, and making effective conservation planning decisions to conserve them, requires quantifying how connectivity is affected by landscape features. Thus, there is a need for efficient and reliable tools that relate landscape composition and pattern to connectivity for ecological processes. Many ways of predicting connectivity using landscape data have been developed (reviewed by Tischendorf and Fahrig 2000*a*, *b*, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Fagan and Calabrese 2006). Common approaches include the derivation of landscape pattern indices (e.g., Schumaker 1996), individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005), and analytic measures of network connectivity, such as graph theory and least-cost path models (Keitt et al. 1997, Urban and Keitt 2001, Adriaensen et al. 2003, Minor and Urban 2007). The latter have gained increasing attention in recent years and are widely

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applied in connectivity modeling and in conservation planning.

We propose that connectivity models from electrical circuit theory can make a useful addition to the approaches available to ecologists and conservation planners. Circuit theory has been applied to connectivity analyses in chemical, neural, economic, and social networks, and has recently been used to model gene flow in heterogeneous landscapes (McRae 2006, McRae and Beier 2007). The same properties that make circuit theory useful in these fields hold promise for ecology and conservation as well. Because connectivity increases with multiple pathways in circuit networks, distance metrics based on electrical connectivity are applicable to processes that respond positively to increasing connections and redundancy. Additionally, previous work has shown that current, voltage, and resistance in electrical circuits all have precise relationships with random walks (Doyle and Snell 1984, Chandra et al. 1997). These relationships mean that circuit theory can be related to movement ecology via random-walk theory, providing concrete ecological interpretations of circuit-theoretic parameters and predictions. Finally, because algorithms to implement circuit models are well developed, they can be applied to large networks and raster grids.

Here we present several ways in which circuit theory can be used to model connectivity in ecology and conservation. We describe ecological applications of previously developed theory relating resistance, current, and voltage in electronic circuits to random walks on analogous graphs (Doyle and Snell 1984, Klein and Randic 1993, Chandra et al. 1997). This theory can be applied to predict movement patterns and probabilities of successful dispersal or mortality of random walkers moving across complex landscapes, to generate measures of connectivity or isolation of habitat patches, populations, or protected areas, and to identify important connective elements (e.g., corridors) for conservation planning. Our approach does not require new ways of representing landscape data; rather, it takes advantage of graph-theoretic data structures, which are already familiar to many ecologists, and can be applied in traditional graph-theoretic or raster GIS frameworks. Coupled with applications of circuit theory to predict equilibrium patterns of gene flow (McRae 2006, McRae and Beier 2007), these new applications comprise a modeling framework that integrates spatial aspects of ecology, evolution, and conservation.

## Basic Concepts

### *Graph data structures and terminology*

Connectivity models from circuit theory are applied to *graphs* (Harary 1969), so we will use the terminology of graph theory here (see Urban and Keitt 2001 for a review). Briefly, graphs are networks comprised of sets of *nodes* (connection points which represent, e.g., habitat patches, populations, or cells in a raster landscape) connected by *edges* (Fig. 1). Edges reflect functional connections, such as dispersal, between nodes. The *weight* of each edge typically corresponds to the strength of the connection (e.g., the ease of movement or number of dispersers exchanged) between the nodes it connects.

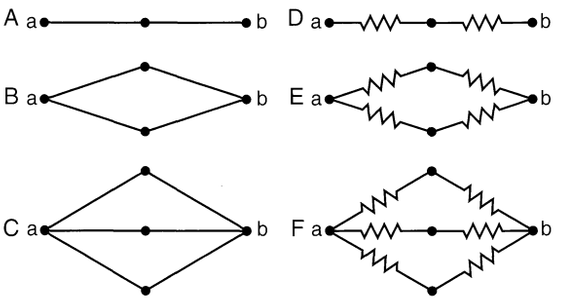


FIG. 1. Three graphs at left (A, B, C), with edge weights of 1. Traditional shortest path or geodesic distance, $d$, between nodes a and b is identical ($d = 2$) all three cases. At right (D, E, F), edges have been replaced with unit resistors to create analogous circuits. Effective resistance, $\hat{R}$, measured between nodes a and b decreases from top to bottom ($\hat{R} = 2$, 1, and 2/3, respectively), reflecting additional contributions from multiple pathways (figure modified from Klein and Randic [1993]).

### *Circuit theory*

In this paper, circuits are defined as networks of nodes connected by *resistors* (electrical components that conduct current) and are used to represent and analyze graphs (Fig. 1). The basic concepts of resistance, conductance, current, and voltage all apply, and their definitions and ecological interpretations are summarized in Table 1. Recall Ohm's law, which states that when a voltage $V$ is applied across a resistor, the amount of current $I$ that flows through the resistor depends on (1) the voltage applied and (2) the resistance $R$, such that $I = V/R$. The lower the resistance (or the higher the conductance, $G$, which is simply the reciprocal of resistance), the greater the current flow per unit voltage. Similarly, when a voltage is applied across two nodes in a resistive circuit (e.g., between nodes a and b in the circuits shown in Fig. 1), the total amount of current that flows across the circuit is determined by (1) the voltage applied and (2) the configuration and the resistances of the resistors the circuit contains. The *effective resistance* ($\hat{R}$) between the nodes is the resistance of a single resistor that would conduct the same amount of current per unit voltage applied between the nodes as would the circuit itself, i.e., $\hat{R} = V/I$.

In simple circuits, such as those shown in Fig. 1, effective resistance can be calculated using some basic rules. First, two resistors connected in series may be replaced by a single resistor with a resistance is that the sum of the two resistances. Thus, the effective resistance in the top circuit in Fig. 1D would be $\hat{R} = R_1 + R_2 = 2$ ohms. Conversely, connecting resistors in parallel decreases their effective resistance, such that they may be replaced by a single resistor whose conductance is



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TABLE 1. Electrical terms and their ecological interpretations.

| Electrical term (symbol, unit) | Ecological interpretation |
|---|---|
| Resistance ($R$, ohm), the opposition that a resistor offers to the flow of electrical current. | Opposition of a habitat type to movement of organisms, similar to ecological concepts of landscape resistance or friction. Graph edges or grid cells allowing less movement are assigned higher resistance. |
| Conductance ($G$, siemens), inverse of resistance and a measure of a resistor's ability to carry electrical current. | Analogous to habitat permeability. In random-walk applications, it is directly related to the likelihood of a walker choosing to move through a cell or along a graph edge relative to others available to it. In population genetic applications (see McRae 2006), it is a measure of migrants exchanged between neighboring populations. |
| Effective resistance ($\hat{R}$, ohm), the resistance to current flow between two nodes separated by a network of resistors. | Also known as the *resistance distance*, a measure of isolation between pairs of nodes on a graph or cells on a raster grid. Similar to ecological concept of effective distance, but it incorporates multiple pathways (Fig. 1D–F). It scales linearly with equilibrium genetic differentiation in population genetic applications. |
| Effective conductance ($\hat{G}$, siemens), inverse of effective resistance, a measure of a network's ability to carry current between two nodes. | A measure of connectivity between pairs of nodes on a graph or cells on a raster grid. It increases with additional available pathways and scales linearly with effective migration in population genetic applications. |
| Current ($I$, ampere), flow of charge through a node or resistor in a circuit. | Current through nodes or resistors can be used to predict expected net movement probabilities for random walkers moving through corresponding graph nodes or edges (Fig. 2). |
| Voltage ($V$, volt), the potential difference in electrical charge between two nodes in an electrical circuit. Related to current and resistance by $V = IR$. | Voltages can be used to predict the probability that random walkers leaving any point on a graph will reach a given destination (representing, e.g., successful dispersal) before another (representing, e.g., mortality; Fig. 3). |



given by the sum of the conductances of the two resistors, that is, $\hat{G} = G_1 + G_2$. (In terms of resistance, these quantities are given by: $\hat{R} = R_1R_2/[R_1 + R_2]$.) Applying these equations to the circuits shown in Fig. 1, the effective resistance declines from the top to the bottom circuit.

Applying circuit theory to graphs involves preserving the same graph structure with interconnected nodes, but replacing graph edges with resistors, as in Fig. 1. The conductance of each resistor is typically a function of the corresponding edge weight or probability of movement between the pair of nodes it connects. The resistance of a resistor is the reciprocal of its conductance and can be thought of as representing isolation or movement cost between nodes.

## INTERPRETATION OF RESISTANCE, CURRENT, AND VOLTAGE

### *Resistance and conductance*

The simplest connectivity measure from circuit theory is the *resistance distance* (Klein and Randic 1993), a distance metric defined as the effective resistance between a pair of nodes when all graph edges are replaced by analogous resistors (as in Fig. 1D–F). A convenient property of the resistance distance is that it incorporates multiple pathways connecting nodes, with resistance distances measured between node pairs decreasing as more connections are added. Hence, the resistance distance does not reflect the distance traveled or movement cost accrued by a single individual. Rather, it incorporates both the minimum movement distance or cost and the availability of alternative pathways. As additional links are added, individuals do not necessarily travel shorter paths, but have more pathways available to them. For example, in the three graphs in Fig. 1A–C, the minimum distance required to travel from node a to b (called geodesic distance in graph theory) is the same. However, the resistance distance decreases as more connections are added, reflecting increased flow capacities and levels of redundancy. In short, the resistance distance is small when two nodes are connected by many paths with low resistance (high conductance) edges and large when there are few paths with high resistance. Resistance distances can be calculated across irregular networks or with continuous landscape data, which are typically represented as discretized lattices or grids. On continuous surfaces, the resistance distance increases linearly with Euclidean distance in homogeneous one-dimensional habitats and with its log transformation in two-dimensional habitats, a property important for modeling gene flow (McRae 2006).

Resistance distances can also be related to random-walk times between nodes. For the theory and examples that follow, we assume that conductances are chosen so that the probability of moving from a node along any given edge is equal to the conductance assigned to the edge divided by the sum of the conductances of all edges connected to the node. For an organism moving through a habitat network (the main focus of this paper), this would correspond to a scenario where the individual chooses to move along an edge in proportion to the edge's conductance, a surrogate for habitat quality or (inverse) perceived risk, relative to the quality of all other choices of direction; this choice is then repeated at each subsequent step. For genes moving across a network of populations over many generations, this would correspond to a scenario where edge conductances correspond to per-generation migration rates (McRae 2006).

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Chandra et al. (1997) showed that, when resistors are parameterized in this way, the resistance distance between a pair of nodes is precisely related to the *commute time* between the nodes, i.e., the expected time for a random walker to move from one node to the other and back again. The commute time between any pair of nodes $u$ and $v$ can be calculated using the following formula:

$$\text{Commute time} = \hat{R}_{uv} \sum_{x=1}^{n} \sum_{y=1}^{n} (1/R_{xy}) \qquad (1)$$

where $R_{xy}$ is the resistance of the resistor connecting nodes $x$ and $y$ and $n$ is the number of nodes in the network. Note that Eq. 1 accommodates resistors connecting a node to itself, which would reflect a nonzero probability of staying at the node for any time step. Chandra et al. (1997) also provided formulas to calculate a commute *cost*, if there is a cost imposed for each step that is independent of the resistance (and thus independent of the behavior of a random walker). An interesting result of Eq. 1 is that if the goal is to minimize commute times between a pair of nodes, there is a penalty for adding connections which is offset by the degree to which the new connections help to lower effective resistance between the two nodes. Within a fixed network, commute times between different pairs of nodes will be directly proportional to the effective resistances measured between them. Another potentially useful way to apply resistance calculations across graphs is to compute upper and lower bounds for the *cover time*, or the expected number of steps of a random walk visiting all nodes in the graph (Chandra et al. 1997).

*"Functional" or "effective" distance.*—Used as an ecological distance metric, the resistance distance provides a conceptual complement to commonly used least-cost distances in two important ways. First, it integrates all possible pathways into distance calculations, whereas least-cost distances are measured along a single optimal pathway. Second, it offers a measure of isolation assuming a random walk, whereas least-cost distances presumably reflect the route of choice if a disperser has complete knowledge of the landscape it is traversing.

The resistance distance also provides a quantitative complement to least-cost distances. If only a single pathway between two nodes is available (e.g., in Fig. 1A or in any graph that is a tree), the resistance distance will equal the least-cost distance. On the other hand, when two identical and independent pathways connect a pair of nodes in parallel, the resistance distance will be half the least-cost distance. This suggests an interpretation of the resistance distance as an indicator of redundancy in connections relative to the least-cost distance:

$$\text{Redundancy} = (\text{least-cost distance})/(\hat{R}).$$

Thus, the two measures can be compared directly, their ratio providing a rough measure of parallel pathways available to dispersers.

The relationship between resistance distances and commute times is one way to link circuit and ecological theories and is the basis of using resistance distances to predict patterns of gene flow and genetic structuring in heterogeneous landscapes (McRae 2006). Calculating commute times directly may provide valuable additional information because commute times take into account how efficiently a given landscape configuration will channel dispersal between source and destination nodes. Additional pathways that primarily result in increased wandering behavior rather than directed movement may reduce resistance distances but will increase commute times. Low commute times and low resistance distances between pairs of nodes indicate that dispersers will be efficiently directed between them.

### *Current*

Currents in circuits can also be interpreted in terms of random walks on corresponding graphs. Consider again a graph in which the probability that a random walker will move from a node along any graph edge is proportional to its conductance. Doyle and Snell (1984) showed that when 1 A (ampere) of current is injected into one node (node a in Fig. 2A) and a second node (node e) is tied to ground, the current $i_{xy}$ flowing through the resistor connecting any pair of nodes $x$ and $y$ is equivalent to the expected net number of times that a random walker, starting at a and walking until it reaches e, will move along that branch. Because we are tallying net passages through the branch, movements from $x$ to $y$ are counted as positive, whereas movements from $y$ back to $x$ are counted as negative.

*Corridor identification and dispersal predictions.*—By predicting net movement probabilities along branches or through nodes, current density can be used to identify landscape corridors or "pinch points," i.e., features through which dispersers have a high likelihood (or necessity) of passing. High current through a node or branch indicates that removing or converting it will have a high impact on connectivity. In Fig. 2, all the current passes through node b; removing that node (or the link between nodes a and b) would completely disconnect nodes a and e, whereas removing node c, through which only half the current passes, would reduce redundancy but would still leave nodes a and e connected via the lower branch. In graph terminology, node b is a *cutnode*, and the resistor connected nodes a and b is a *cutlink*.

### *Voltage*

Doyle and Snell (1984) also showed that voltage can be related to random walk probabilities. Consider a graph in which a voltage source set to 1 V is connected to one node (or to a set of nodes), and another node (or set of nodes) is connected to ground (Fig. 3). The voltage measured at any remaining node on the graph will equal the probability that a random walker, starting at that



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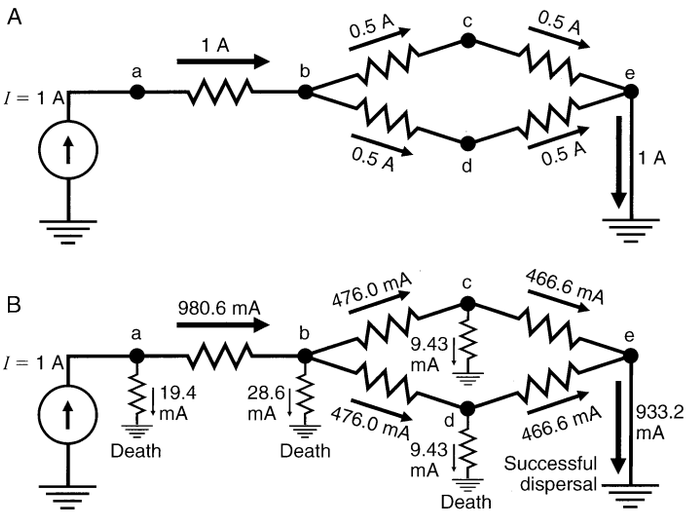


FIG. 2. (A) A simple circuit, with a 1-A (ampere) current source ($I$) placed at node a, and with node e tied to ground. Branch currents that would be observed with unit resistors are shown and reflect the net number of times that a random walker, starting at node a, is expected to pass along each branch before reaching node e. All random walkers must pass across the first branch, but half would be expected to take the upper pathway, and half the lower. Resistances connecting nodes were set to 1 ohm for this simple example; the methods we describe here can accommodate heterogeneous resistances with values from 0 to infinity. (B) The same circuit as in (A), but with ground resistors added to reflect a 1% probability of mortality as the random walker passes through each node. To achieve this, resistances to ground for nodes a–d were set to 99, 33, 49.5, and 49.5 ohms, respectively. Currents show the expected number of net movements along each branch, as well as the expected number of deaths at each node. For example, the proportion of dispersers leaving node a expected to successfully reach node e is 0.9332 (933.2 mA equivalent). Deaths at each node exceed 1% because nodes are visited multiple times by random walkers, with the highest numbers of deaths observed in nodes with the highest numbers of visits. Only one possible dispersal destination was included here, but the method can accommodate as many dispersal destinations as desired. Although we tied the destination node directly to ground, resistors could be added between destination nodes and ground, with their conductances set to reflect a finite probability that a walker would settle rather than continue walking once reaching a node.



node, will reach any of the nodes set to 1 V before reaching any node connected to ground. The most obvious application of this property is to predict the probability of successful dispersal via a random walk from any node on a graph. Suitable destination patches for dispersal can be set to 1 V, whereas mortality can be represented by resistors connected to ground, with their conductances reflecting probabilities of mortality (Fig. 3).

### APPLYING CIRCUIT ANALYSES TO RASTER GRIDS

Predicting connectivity using circuit theory requires translating spatial data sets into a graph structure, but that doesn't mean that primary landscape data must be in a patch-based or network-style format. In fact, we envision most landscape applications operating on raster data, with a graph extracted from these data as is done for least-cost path analyses (Adriaensen et al. 2003). Since well-developed computer algorithms allow millions of cells to be processed, large raster landscapes can be accommodated.

Analyzing a raster grid involves first assigning resistances to different habitat types in the grid. Fig. 4 shows a simple example with three different habitat types: assigned unit, infinite, and zero resistance. The last is useful when practitioners wish to measure connectivity or identify important connective elements between areas (representing, for example, habitat patches or reserves), rather than points on a landscape. To represent a grid as a circuit, cells with finite resistances are converted to nodes (gray), whereas cells with infinite resistance (i.e., those representing complete barriers, black) are dropped. Adjacent nodes are connected by resistors, with resistances reflecting a function (typically the mean) of the resistances of the cells they connect. Adjacent cells with zero resistance (open) are consolidated into a single node that is then connected by resistors to all nodes adjacent to the zero-resistance patch. Following this procedure, the 16-cell

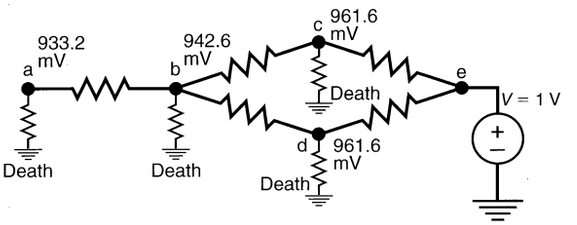


FIG. 3. The same circuit shown in Fig. 2B, but with a voltage source ($V$) of one volt at node e instead of a current source at node a. Node voltages reflect the probability that a random walker, starting at each node, will successfully reach node e. Consistent with the result from Fig. 2B, the probability of successful dispersal from node a to node e is 0.9332.

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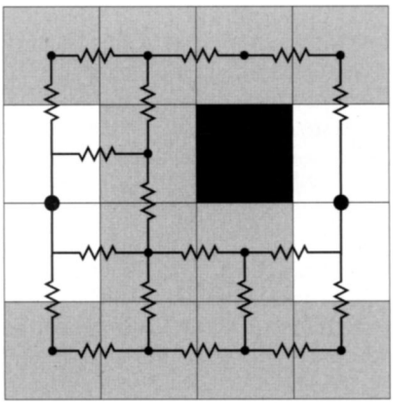

FIG. 4. A simple landscape represented as both a grid and a circuit. The landscape contains two contiguous patches of 0-resistance cells (open), dispersal habitat of finite resistance (gray), and one "barrier" cell with infinite resistance (black). Cells with finite resistance are replaced with nodes (small dots), and adjacent nodes are connected by resistors. Patches of cells with 0 resistance are each consolidated into a single node (large dots). Connections between diagonal neighbors and nonadjacent cells can also be incorporated, the latter representing "hops" over intervening cells. Current sources, voltage sources, and ground connections can be added as in Figs. 2 and 3.

grid in Fig. 4 is now represented as a circuit with 13 nodes and 18 resistors.

## COMPUTATION

Although simple circuits can be solved by hand, *nodal analysis* is typically used to analyze larger circuits, such as those derived from raster grids (McRae 2006). Given a circuit with current or voltage sources, nodal analysis uses Kirchoff's and Ohm's laws in matrix form to solve for a vector, specifying voltages at each node; once these are known, Ohm's law can be used to calculate currents passing through individual resistors or nodes. Effective resistance between a pair of nodes is given by the voltage between them when one is connected to a 1-A current source and the other is connected to ground (e.g., Fig. 2A). The method is described in standard circuit theory textbooks (e.g., Dorf and Svoboda 2003); an example of its use to calculate effective resistances is provided by McRae (2006).

Computer languages used for scientific computing such as Java, C, MATLAB, and Python include linear solver routines that can solve for effective resistances on graphs. Fast graph operations can be used to define connected components in a landscape and discard from a graph any components that are completely isolated. Very large graphs can be processed relatively easily and efficiently; we have solved for effective resistances, voltages, and current on landscapes containing over 1 million cells using Java (Sun Microsystems, Mountain View, California, USA), and up to 48 million cells using a parallel version of MATLAB (MathWorks, Natick, Massachusetts, USA) implemented using Star-P (Interactive Supercomputing, Waltham, Massachusetts, USA). Solving 1 million cells on a notebook computer with a 2-GHz processor and 2 GB of RAM took us 16 minutes using Java and only 20 seconds using MATLAB. This calculation must be repeated for each configuration of current sources and grounds, but typical connectivity applications will require a small number of calculations (e.g., for each pair of populations or reserves between which connectivity is to be modeled). Calculations between multiple pairs can be sped up considerably using matrix preconditioning and/or parallel processing. Software implementing many of the algorithms in this manuscript is available (B. H. McRae, *unpublished data*).

## EXAMPLE APPLICATIONS TO HETEROGENEOUS LANDSCAPES

Here we provide examples of the applications described above to predict connectivity and movement of random walkers across large raster grids. For the example analyses described next, we solved for effective resistances and node currents using code written in MATLAB R2007b. The example landscapes (i.e., resistance surfaces) were all created using ArcView GIS 3.2 (ESRI, Redlands, California, USA) and exported as ASCII raster grids, with cell values corresponding to resistances ranging from 0 to infinity (Fig. 5). For circuit analyses, cells with finite resistances were converted to nodes, whereas those with infinite resistances were dropped. Cells were connected to their eight neighbors such that the resistance between a pair of first-order neighbors was set to the mean of the two cells' resistances, and the resistance between a pair of second-order (diagonal) neighbors was set to the mean resistance multiplied by the square root of 2 to reflect the

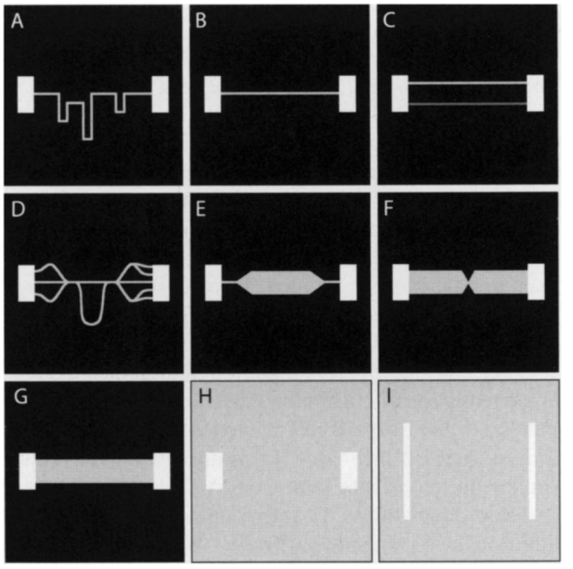


FIG. 5. Nine simple raster landscapes (A–I), consisting of $1000 \times 1000$ cells. Habitat patches (shown in white and assigned 0 resistance, or infinite conductance) are connected by different configurations of dispersal habitat (light gray, 10 ohms/cell; dark gray [lower corridor in panel C], 20 ohms/cell; black = infinite resistance or 0 conductance).



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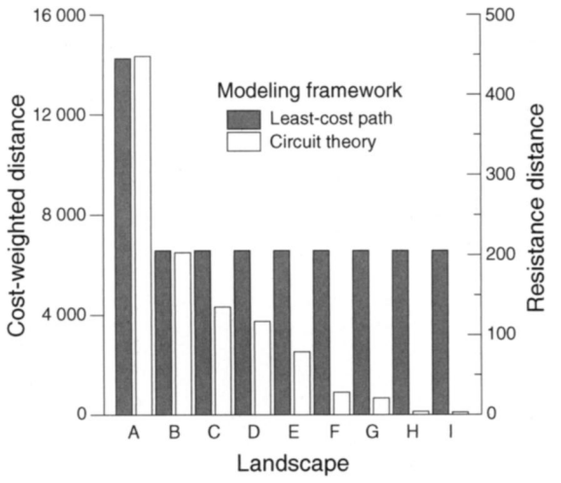


FIG. 6. Least-cost distances and resistance distances between habitat patches for the nine simple landscapes shown in Fig. 5. Least-cost distances decrease from (A) to (B) but are equivalent for all remaining maps. Effective resistances decrease not only from (A) to (B), but also from (B) to (I), reflecting the availability of more and wider pathways. Redundancy, defined here as the ratio of least-cost distance to effective resistance, would be roughly equal for cases (A) and (B) but would increase from (B) to (I). Cost-weighted distance (measured in cost units) were calculated using PATHMATRIX software. Resistance distances (measured in ohms) were calculated using Circuitscape software.



greater distance between cell centers. We converted individual cells to single nodes, except for cells in areas of zero resistance, i.e., open source/target patches; as in the simple landscape in Fig. 4, these cells were considered collectively and consolidated into a single node for the analyses. For all examples, we used the same resistance surfaces to calculate least-cost distances and map least-cost corridors using PATHMATRIX software (Ray 2005).

We started with nine simple landscapes (Fig. 5) meant to illustrate different properties of circuit models. The landscapes consisted of 1000 × 1000 cells each and contained two primary habitat patches, which were always the same distance from one another and always occupied the same total area. Least-cost and resistance distances calculated between habitat patches in the nine simple landscapes illustrate some advantages of the resistance distance (Fig. 6). Although least-cost distances correctly identify decreased isolation between habitat patches in landscape B relative to A, they were identical in landscapes B through I. Resistance distances show a similar decrease from landscape A to B, but they also decrease from B to I, reflecting the availability of additional, or wider, pathways. Note that between landscapes H and I, only the shape of the primary habitat patches has changed, and not their area or the distance separating them. Yet the resistance distance differs because the greater surface area of each habitat patch in landscape *I* acts as a "drift fence" to better intercept or release dispersers.

Commute times ranged from 1.2 million steps (landscapes B, C, and G) to 6.2 million steps (landscape A). They were intermediate for landscapes D, E, F, H, and I, which had commute times of 2.6, 3.0, 1.6, 2.7, and 2.0 million steps, respectively. Lower commute times reflect configurations in which dispersers are efficiently channeled between habitat patch pairs, minimizing wandering time.

These same simple landscapes also demonstrate how current maps (Fig. 7) can highlight connective elements in raster frameworks. As the availability of multiple pathways increases, current density—indicating cells through which dispersers are likely to pass moving from one patch to the other—decreases. Pinch points are highlighted in landscapes D–F, and the "drift fence" effect resulting from the more linear shape of the habitat patches in landscape I is evident as well. Fig. 7J shows a least-cost path map for the "braided stream" corridor configuration. The technique identifies the route with the lowest cumulative cost, but gives no information about the contribution of alternative pathways. By contrast, the current map (Fig. 7D) clearly indicates the importance of different corridor segments, with current densities at their highest in the two critical linkages and at their lowest in segments that are most redundant.

We can now illustrate how these models can be used to analyze connectivity in more realistic landscapes. Fig. 8A shows a complex landscape, with patches of high-quality habitat, lower quality "matrix" habitat, corridors, and complete barriers. Fig. 8B shows cumulative travel cost mapped between two high-quality patches using standard least-cost path techniques. The map highlights the most efficient pathway between the two patches, as well as low-cost detours that do not actually contribute to connectivity, e.g., into habitat cul-de-sacs or along "corridors to nowhere." By contrast, the current map between the same two habitat patches (Fig. 8C) highlights critical pinch points between the two patches. Habitat cul-de-sacs and corridors that do not contribute to connectivity have minimal current flow. The current map also indicates two broad routes linking the habitat patches, whereas only one is highlighted in the least-cost map. The current map thus gives important insight into the redundancy that would be lost if the second route were to be blocked.

Often it will be useful to summarize connectivity between many habitat patches or protected areas in a single map. Fig. 9A shows the result of adding 10 pairwise current maps calculated among all pairs of five habitat patches. These maps show which landscape elements are most important for overall connectivity among the five habitat patches, indicating the net number of times random walkers are expected to move through raster cells if one random walker moves from each patch to each other patch.

We could also extend the analyses of our raster maps in much the same way as the analyses in Fig. 2A were extended in Figs. 2B and 3. Ground resistors could be added to incorporate mortality or finite probabilities of

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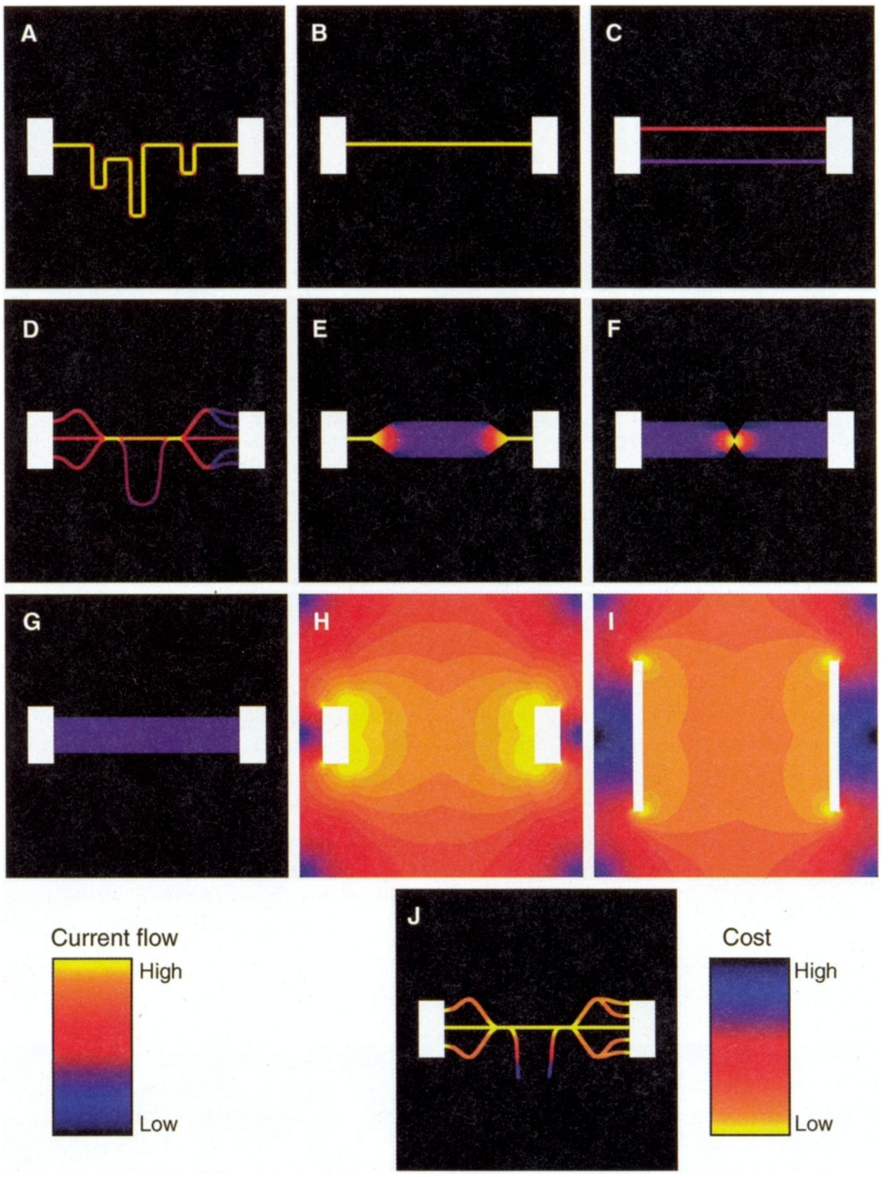


FIG. 7. Current flow through landscapes shown in Fig. 5 when 1 A (ampere) of current is injected into one habitat patch and the other is connected to ground. Current maps were log-transformed to facilitate display. Among the nine panels, three different quantitative scales are applied to the color schemes in order to most clearly illustrate differences in current densities. The three schemes are applied in panels (A)–(D), (E)–(G), and (H)–(I). Highest maximum current densities (indicating the greatest impact of habitat cell removal or conversion) are observed in (A), (B), and (D)–(E), where connectivity depends on single, narrow corridor segments. The lowest maximum current densities are observed in landscape (I), which provides the most redundancy and lowest effective resistance. This landscape also exhibits a drift-fence effect, in which the linear shapes of the habitat patches act to intercept dispersing individuals. (J) The least-cost path solution of the "braided stream" landscape shown in Fig. 5D. Whereas this technique highlights the most efficient travel path, it gives no indication of pinch points or effects of multiple parallel corridors.

settling once a disperser reaches a habitat patch or protected area. With multiple destination patches, a matrix of asymmetrical dispersal rates between all patch pairs could be generated. Or, target patches could be set to 1 V and probabilities of successful dispersal (or dispersal to one patch vs. others) from any point on the landscape could be mapped. Finally, additive maps (such as the one shown in Fig. 9A) could be adjusted to give greater weight to important source or destination patches, with more current released or absorbed by larger or higher quality habitat patches.

### *Model sensitivity to landscape scale*

Representing a landscape as a raster grid always involves choosing an appropriate scale of analysis (cell size and map extent). Because different species respond



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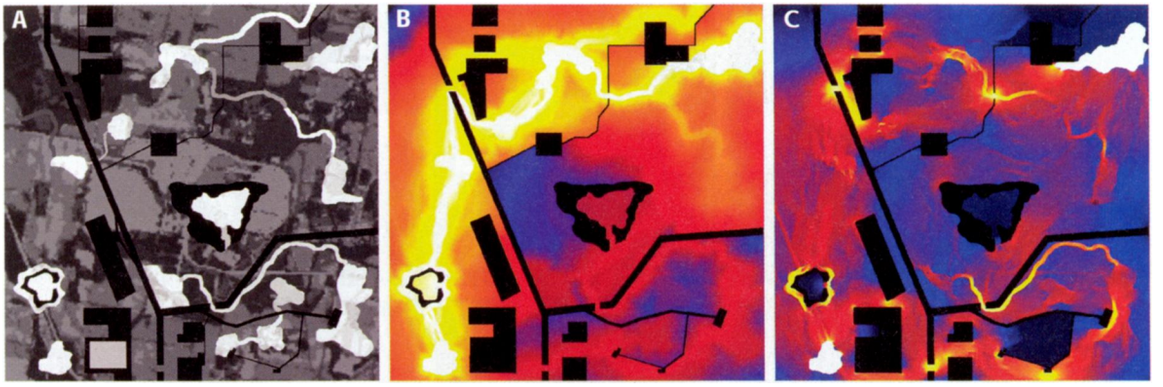


FIG. 8. Connective elements identified using least-cost path and circuit models in a complex landscape. (A) Map of the landscape, with resistances and costs for circuit and least-cost path analyses ranging from 1 (light gray) to 100 (dark gray) to infinite (black). (B) Results from least-cost modeling between habitat patches in lower left and upper right corners of the map. The value assigned to each cell indicates the cost accumulated moving along the most efficient possible route that passes through the cell from one habitat patch to the other; brighter areas indicate cells along the route of lowest cumulative cost. Some habitat cul-de-sacs are highlighted because the most efficient path connecting one patch to the other via the cul-de-sac has a low cost relative to most other features in the landscape. For the same reason, some "corridors to nowhere" are highlighted, such as the one leading off of the top of the map. (C) Current map between the same two habitat patches. Higher current densities indicate cells with higher net passage probabilities for random walkers moving from one patch to the other. The map highlights "pinch points," or critical habitat connections, between the two patches. Habitat cul-de-sacs have minimal current flow because they do not contribute new, independent pathways between habitat patches.



to landscape structure at different scales (Wiens 1985, Wiens and Milne 1989; Beier et al., *in press*), there will be no single correct approach to this. The extent of an analysis will obviously have important consequences, since map edges will constrain potential movement routes. Cell size is also important, but our analyses indicate that as long as it remains fine enough to capture relevant landscape elements, such as narrow corridors and barriers, there is considerable robustness in the technique to changes in cell size. Fig. 9B shows the same landscape as in Fig. 9A, but analyzed using cell sizes that are an order of magnitude larger. Notably, current densities and resistance distances calculated among habitat patches are highly correlated between the two scales, a consistent result in our analyses in a wide range of natural and artificial landscapes. However, these analyses also show that it is particularly important to capture absolute barriers to movement that may not easily be detected at coarser cell sizes. Such barriers (such as the narrow roads in Fig. 9A) were automatically

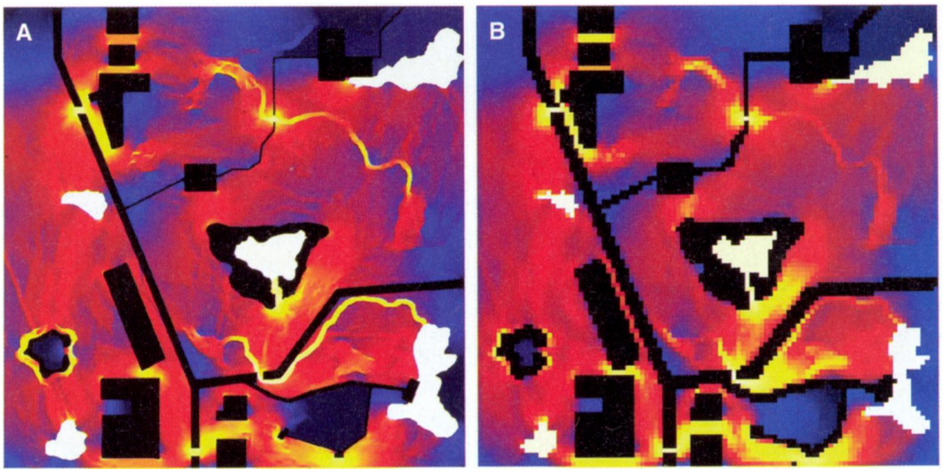


FIG. 9. Summed current from all pairwise current maps between five habitat patches, each shown in white. Calculations were performed (A) at the original 1000 × 1000 cell resolution and (B) at a reduced 100 × 100 cell resolution. To produce the coarser resolution habitat map, blocks of 10 × 10 cells were converted to single cells, with the resistance of each new cell set equal to the mean resistance of the 100 cells it contained. The current maps at the two resolutions identify the same pinch points and important corridors, and pairwise effective resistances measured between all habitat patch pairs at the two scales are highly correlated ($R^2 = 0.963$), illustrating the method's robustness to scale.

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PLATE 1. Puma mother and kitten in Caspers Wilderness Park, Orange County, California. Cirtuit theory is being applied to inform efforts to conserve connectivity for pumas in the region. Photo credit: Donna Krucki.

incorporated into our analyses in Fig. 9B because we averaged resistances among consolidated cells, with infinite resistances "trumping" all others.

## DISCUSSION

Although a wide variety of methods exists for predicting connectivity across landscapes, circuit-theoretic models provide some distinct advantages. First, the precise relationships between circuit theory and random walks lend theoretical justification to these models and mean that the metrics they generate can genuinely be considered to be process based. Second, these relationships also mean that circuit models will often be more straightforward to parameterize than other connectivity models because conductances and resistances assigned to edges or raster cells have clear interpretations in terms of movement probabilities. Third, unlike commonly applied least-cost path approaches, circuit methods incorporate multiple pathways, not only in generating metrics of connectivity and isolation, but also in identifying corridors and other important landscape elements connecting habitat patches or protected areas. An advantage of this property is that when dispersal pathways are lost, the predicted importance of remaining pathways increases. Finally, circuit models have an intuitive appeal in that the idea of using resistance and current to model connectivity across landscapes is readily understood by both practitioners and nonscientists. In effect, we find that the method objectively identifies important connective elements similar to those identified by the human eye, replicating expert opinion but removing potential sources of bias once relative resistance values and scales of analysis have been defined.

### *Niches for circuit models*

We envision several roles for circuit theory in evolution, ecology, and conservation. Circuit theory has already been shown to be useful for predicting patterns of gene flow in heterogeneous landscapes, particularly when data on absolute population sizes and migration rates are lacking, but relative population densities or permeabilities to movement are hypothesized for different landscape features (McRae 2006, McRae and Beier 2007). As discussed in the section below, the theory underlying gene flow modeling is similar to that described here, but relates resistance distances to random walks of genes over multiple generations rather than to random walks of individuals within single lifetimes.

In ecology, circuit models can be used as simple movement models, e.g., when data or time required for simulations are lacking or when the comparison of simple and complex model predictions is desirable. An example application would be to predict dispersal rates between populations based on simple landscape data in order to parameterize metapopulation models. Additionally, just as it can be used to predict gene flow, circuit theory may be useful in modeling other emergent



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processes that depend on dispersal. Some ecological phenomena, e.g., community similarity and diversity, may respond to dispersal not of one species, but of several species with only somewhat similar dispersal abilities or habitat requirements. Here, simulations may be prohibitive or inappropriate because of the large number of species involved. However, analytic approaches like ours may be able to adequately capture these processes without imposing prohibitive data or computational requirements.

Measurements of resistance distances, commute times, and current densities have clear applications in conservation planning, such as corridor design or predicting the effects of different land use practices on connectivity. Circuit theory should provide an especially powerful tool for designing robust reserve networks, i.e., those that still provide for connectivity in the face of uncertainty in species distribution data and/or future habitat loss (Moilanen et al. 2006*a*, O'Hanley et al. 2007; Pinto and Keitt, *in press*). Importantly, circuit methods can be applied to the same resistance surfaces that are commonly employed in least-cost path analyses, and with little added computational expense.

In this paper, we limited our examples of circuit-based analyses to accessible interpretations of resistance, voltage, and current. However, there should be a large number of tools that could be derived from these basic properties. For example, metrics that combine predictions of efficient travel paths, pinch points, and mortality risks could allow practitioners to map landscape features that most effectively contribute to connectivity while minimizing mortality rates. Or, metrics derived from shortest path or least-cost distances, such as the Harary index (Ricotta et al. 2000, Jordán et al. 2003) or the integral index of connectivity (Pascual-Hortal and Saura 2006) could be modified by substituting resistance distances for least-cost distances in their calculation. Additionally, algorithms like edge and node thinning, used to evaluate impacts to connectivity of habitat loss in graph theory (Urban and Keitt 2001), can also be applied using circuit-based measures.

### *A note about ecological vs. evolutionary applications*

It is important to be aware of subtle differences in assumptions behind applications of circuit theory to different processes. So far we have identified two distinct frameworks, one which models gene flow across population networks and the other focused on individual movement across habitat networks. The former assumes nodes (or cells) represent subpopulations (or occupied habitat for continuously distributed populations), with resistors representing numbers of migrants exchanged between adjacent nodes per generation (McRae 2006). By contrast, applications focused on individual movement will typically be implemented at finer temporal and spatial scales, with nodes (cells) mapped at the scale at which individual movement decisions are made. Thus, the two will often be applied at different scales and with (at least somewhat) different habitat models. Similarly, predictions from the two frameworks must also be interpreted differently. For example, in applications where nodes or cells represent occupied habitat exchanging migrants, a decrease in the resistance distance between two nodes corresponds to a proportional increase in gene flow predicted between them; however, when nodes represent dispersal habitat rather than subpopulations, a decrease in the resistance distance corresponds only to an increase in available dispersal pathways, and not necessarily a commensurate increase in individual movement rates or gene flow. It does, however, indicate that there will be more pathways available to dispersers, and presumably greater robustness of the network to future habitat loss. Conservation applications may be implemented using either framework, but it is important to specify the process being modeled.

### *Model parameterization*

A critical and challenging step in applying circuit models to landscape data will be assigning relative movement, mortality, and/or settlement probabilities to different land cover classes. Many of the same strategies for parameterizing least-cost path models using expert opinion, literature review or data on species occurrences, animal movement paths, or interpatch movement rates (reviewed by Beier et al., *in press*) will be useful in circuit modeling, particularly when viewed in light of the concrete interpretations of resistances in terms of random walk probabilities outlined here. Practitioners should also consider approaches taken to parameterize other models that consider habitat heterogeneity, such as diffusion and simulation models (e.g., Dunning et al. 1995, Schumaker 1996, Ovaskainen 2004; Arellano et al., *in press*; Ovaskainen et al., *in press*).

Connections between resistance distances and gene flow (McRae 2006, McRae and Beier 2007) should facilitate the use of genetic data to estimate relative resistances of different habitats. Still, because assumptions differ between evolutionary and ecological applications of circuit theory (as discussed here), using data from one to parameterize the other must be done with care.

Regardless of the method used to assign them, there will always be uncertainty in resistance values. We encourage uncertainty analyses to address how decisions at each modeling step affect results; Beier et al. (*in press*) reviewed strategies for conducting uncertainty analysis in least-cost path modeling, and these should be equally applicable to circuit theory. Additionally, for corridor and reserve designs, uncertainty in landscape resistances could be incorporated in much the same way as proposed by Moilanen et al. (2006*b*), with penalties that reflect modeled error incorporated into landscape resistance input maps.

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### *Limitations and alternatives*

As with other methods for describing connectivity in complex landscapes, there are limitations to our approach that should be considered when deciding if it is appropriate for a given problem. First, because resistors are isotropic, i.e., their resistance to current flow is the same in both directions, the methods described here cannot accommodate movement that is biased in one direction (as in directed graphs). This will limit applications in some systems, e.g., marine environments, where directional currents play a large role in determining dispersal rates. Second, circuit models are restricted to Markovian random walks, i.e., random walks in which each step is independent of previous moves. Random walkers thus have no "memory," and our framework cannot incorporate correlated random walks, changes in movement behavior with time, or mortality rates that increase with an organism's age. Even when the assumption of constant mortality with time is reasonable, incorporating mortality into circuit models must be done with care. Because they have no memory or long distance perception, random walkers can retrace their steps over and over, inflating mortality rates because travel time and exposure to mortality risks are increased (Fig. 2B).

Several other connectivity modeling frameworks provide complements to ours. The conceptually and computationally simplest are based on Euclidean distances, and can be quickly calculated on grids with millions of cells (e.g., Moilanen et al. 2005, Moilanen and Wintle 2007). Least-cost path models have been applied for over a decade in connectivity analyses and have proven useful in conservation planning efforts (e.g., Beier et al. 2006, Rouget et al. 2006). Although they do not have the theoretical foundation in random walk theory that circuit models do, their intuitive appeal and ability to identify efficient movement pathways make them useful counterparts to the applications we have described here. Recently, variants on these approaches have been developed that identify and rank the importance of multiple pathways across landscapes (Theobald 2006; Pinto and Keitt, *in press*).

More sophisticated analytical and simulation models can be used to derive results similar to those produced by circuit theory, with some advantages. Markov chain models use the same data structures as those described here, but can accommodate directionality in movement along edges, providing more flexibility for modeling, e.g., effects of directed dispersal, prevailing winds, or ocean currents. Still, although Markov chain models have been available for decades, ecologists and conservationists have been slow to adopt them, whereas simpler, more intuitive least-cost path models have been widely employed. Spatially structured diffusion models (Ovaskainen 2004) are promising because they also integrate over all movement paths and can approximate correlated random walks in their long-term behavior, but their mathematical formulation can be quite challenging. Of course, individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005) offer much more flexibility than analytic models, can incorporate subtle effects of dispersal behavior and other aspects of life history, and can simulate transient effects of landscape characteristics that evolve over time. However, the data and computational requirements of such models will likely continue to limit their use in many applications (Minor and Urban 2007). Our hope is that circuit models will fill a niche between simpler Euclidean or least-cost path analyses and more powerful analytic and simulation approaches.

### *Future prospects*

Our focus has been on measuring connectivity in heterogeneous landscapes using models from circuit theory. Even in this context, there remain many exciting applications to explore. Nonequilibrium circuit analyses may be applicable to ecological problems (McRae and Beier 2007), and nonlinear circuit elements show promise as well (for example, diodes would allow incorporation of movement probabilities with directional bias). Additionally, analytical techniques developed to minimize effective resistances across networks (Ghosh et al. 2006) may be useful in designing optimal networks for connectivity conservation. More broadly, circuit theory will likely benefit other areas of ecology that deal with networks, such as the analysis of community interactions, food web structure, exotic invasion, or disease transmission. In the meantime, circuit models are being actively applied to conservation planning for species of concern in rapidly developing landscapes, including pumas (*Puma concolor*; see Plate 1) in southern California.



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# Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits

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## Abstract

Landscape connectivity is crucial for many ecological processes, including dispersal, gene flow, demographic rescue, and movement in response to climate change. As a result, governmental and non-governmental organizations are focusing efforts to map and conserve areas that facilitate movement to maintain population connectivity and promote climate adaptation. In contrast, little focus has been placed on identifying barriers—landscape features which impede movement between ecologically important areas—where restoration could most improve connectivity. Yet knowing where barriers most strongly reduce connectivity can complement traditional analyses aimed at mapping best movement routes. We introduce a novel method to detect important barriers and provide example applications. Our method uses GIS neighborhood analyses in conjunction with effective distance analyses to detect barriers that, if removed, would significantly improve connectivity. Applicable in least-cost, circuit-theoretic, and simulation modeling frameworks, the method detects both complete (impermeable) barriers and those that impede but do not completely block movement. Barrier mapping complements corridor mapping by broadening the range of connectivity conservation alternatives available to practitioners. The method can help practitioners move beyond maintaining currently important areas to restoring and enhancing connectivity through active barrier removal. It can inform decisions on trade-offs between restoration and protection; for example, purchasing an intact corridor may be substantially more costly than restoring a barrier that blocks an alternative corridor. And it extends the concept of centrality to barriers, highlighting areas that most diminish connectivity across broad networks. Identifying which modeled barriers have the greatest impact can also help prioritize error checking of land cover data and collection of field data to improve connectivity maps. Barrier detection provides a different way to view the landscape, broadening thinking about connectivity and fragmentation while increasing conservation options.

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## Introduction

Landscape connectivity, or "the degree to which the landscape facilitates or impedes movement among resource patches" [1], is crucial for many ecological and evolutionary processes, including dispersal, gene flow, demographic rescue, and movement in response to climate change [2–7]. Many research and conservation planning efforts have focused on mapping areas important for connectivity using GIS models (e.g., [8–12]). The results of these analyses are guiding investments by governmental and non-governmental organizations to promote ecological connectivity across large areas. In the USA and Canada, for example, numerous broad-scale conservation efforts such as the U.S. Department of Interior Landscape Conservation Cooperatives, the Western Governors' Association's Initiative on Wildlife Corridors and Crucial Habitat, and the Yellowstone to Yukon Conservation Initiative are working to integrate and coordinate connectivity conservation actions spanning millions of acres and crossing many political and ecoregional boundaries.

Conservation practitioners employ two primary strategies to promote connectivity. The first focuses on conserving areas that *facilitate* movement; the second focuses on restoring connectivity across areas that *impede* movement (e.g., by removing a fence or building a wildlife-friendly highway underpass). Most connectivity analyses have focused on the former strategy by modeling and mapping areas important for movement under present landscape conditions. A wide array of tools have been developed for this purpose: least-cost corridor modeling [8,13,14], circuit theory [15], individual-based movement models (e.g., [16–18]), graph theory [19,20], and centrality analyses (e.g., [21,22]) have all been used to identify areas important for movement of plants and animals. Outputs from such models are now being used as inputs to reserve selection algorithms (e.g., [23]) to optimize actions to conserve connectivity.

In contrast, there has been little effort by conservation scientists towards identifying candidate areas for the second strategy: that is detecting restoration opportunities by mapping barriers that strongly reduce movement potential. We define a barrier as a

landscape feature that impedes movement between ecologically important areas, the removal of which would increase the potential for movements between those areas. Here we are concerned with movements important for access to resources, demographic rescue, gene flow, range shifts, and other ecological and evolutionary processes. In this context, barriers are distinguished from features that are impermeable but not situated such that they block biologically relevant movement routes. Barriers are thus the inverse of corridors, which delineate pathways facilitating movement. Barriers can either be complete (impermeable) or partial (e.g., land cover types that hinder movement relative to ideal conditions, but may still provide some connectivity value). Barriers may be human-made (e.g., roads, fences, or urban areas) or natural (rivers or canyons); they may be linear (e.g., highways) or span large areas (agricultural fields). As with traditional connectivity concepts [1,24], what constitutes a barrier, the impact it has, and whether it reduces connectivity through behavioral inhibition, increased mortality, or other means will differ among species.

Detecting barriers to movement would complement traditional connectivity analyses in several important ways. First, some barriers may be restorable. Knowing where barriers have the greatest impact would help practitioners decide where and how to invest scarce conservation resources to conserve and enhance connectivity. For example, it may be cheaper to restore a barrier that blocks a movement corridor through public land than to establish permanent protection of a functioning corridor that runs through private land [25]. Quantifying such trade-offs would be necessary to integrate connectivity restoration into systematic conservation planning analyses aimed at optimizing conservation investments [26–28], but tools to incorporate connectivity conservation and/or restoration into such efforts remain rare [29–31]. Second, consider that corridor modeling often produces corridors that may not be good enough to realistically support movement [32]. Barrier detection analysis could reveal such cases, allowing practitioners to 'triage' a landscape, focusing efforts on more viable movement routes. Finally, surprising results in a barrier analysis could alert analysts to situations in which poor land cover data or incorrect model parameterization may be causing spurious results.

In this paper, we introduce a new method to identify barriers and rank them by their impact on connectivity. Our method complements existing connectivity modeling approaches, is applicable in least-cost and other connectivity modeling frameworks, and can be extended to centrality analyses. The method can be readily applied across large landscapes, efficiently analyzing barriers among many locations and at different scales corresponding to different sizes of barriers and types of restoration activities. It also quantifies the extent to which restoration can be expected to improve connectivity. We provide example applications of the method, showing that the potential for connectivity conservation is not constrained to narrow corridors, but includes options spanning much more of the landscape when restoration options are considered. We also discuss how our approach can facilitate sensitivity analyses, data quality screening, and prioritization of areas for error checking of GIS base data.

## Method for Detecting Barriers and Restoration Opportunities

Our method identifies areas that most reduce connectivity between two locations on a landscape. Making these areas permeable to movement would therefore most increase connectivity between the locations. Thus, these are areas that practitioners should consider when implementing restoration to promote connectivity.

To illustrate the method, we use a least-cost corridor modeling framework [13,14,32], which is commonly used to map and prioritize areas important for connectivity conservation (e.g., [8–12]). However, our approach could also be used with other modeling frameworks capable of producing measures of effective distance, such as circuit theory and individual-based movement models (see Discussion).

As with least-cost corridor models, input data include locations to be connected (hereafter, "patches") and a raster resistance surface (Figure 1A). The former may consist of points or polygons, and typically represent natural landscape blocks, protected areas, or core habitat for a particular species or species guild [33]. The resistance surface represents the difficulty, energetic cost, or mortality risk associated with movement through each pixel (see [34] for a review of resistance surface development).

Least-cost methods calculate the cost-weighted distance (*CWD*) of all pixels to a source location, creating a raster of *CWD* values (Figures 1B and 1C). Adding together *CWD* rasters from two locations produces a corridor (Figure 1D), showing the pathways with the lowest cumulative movement cost between the locations [14]. The minimum value of the corridor raster is the least-cost distance (*LCD*); this represents the cumulative resistance encountered moving along the optimal path from one location to the other, and is a common measure of isolation in spatial ecology (e.g., [35,36]), landscape genetics (e.g., [37,38]), and related fields.

Our method is based on this simple assumption: if a certain area (the size is defined by the user) is restored such that the resistance across it is reduced, then the *LCD* of the best route connecting the patches through the restoration area will also be reduced. Systematically quantifying the potential reduction across a landscape will allow us to detect those areas where restoration would lead to the greatest reduction in least-cost distance.

The method begins with *CWD* calculations from two patches (Figures 1B and 1C). However, rather than adding the two *CWD* surfaces together to produce a corridor, we instead calculate the minimum value of each *CWD* surface within a localized area around each pixel location (e.g., within a 500 m radius). We then add the minimum values from both *CWD* surfaces to calculate the cumulative resistance that would be incurred moving between the patches and through the focal pixel assuming the area within the search window is restored:

$$LCD' = CWD1_{MIN} + CWD2_{MIN} + (L * R'), \qquad (1)$$

where $LCD'$ is the least-cost distance of the best path between the patches passing through the focal pixel after barrier removal, $CWDX_{MIN}$ is the minimum *CWD* value from patch $X$ within the search window, $L$ is the length of the longest axis of the search window, and $R'$ is the resistance value of the feature replacing (or cutting through) the barrier. We use a circular moving window to illustrate the method (Figure 2), but consider alternative search window shapes in the Discussion. Note that the longest axis of a circle is its diameter.

For each pixel, this formula yields the cost of the best corridor that would pass through that pixel if the resistance of a strip of land crossing the search window were changed to $R'$. Including $R'$ and the search window length accounts for the cost of moving across the search window, assuming restoration or removal of the intervening barrier.

If $LCD'$ is less than *LCD*, then restoration across the moving window (e.g., the circle in Figure 2) would reduce effective distance and increase connectivity between the two patches. When this is

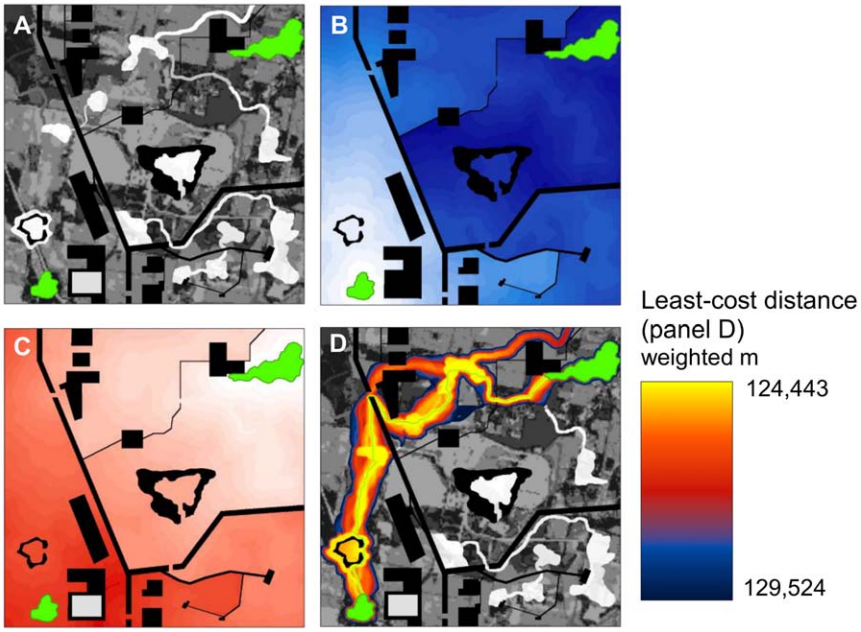


**Figure 1. Cost-weighted distance modeling.** (A) Example 3 km×3 km landscape with a pixel size of 3 m (from [15]). Two habitat patches (green) are embedded in a matrix of land cover types with differing resistance to movement. Resistances range from 1 (white) to 100 (dark grey); complete barriers with infinite resistance (e.g., linear features representing roads and highways) are shown in black. (B) Cost-weighted distance (*CWD*) from leftmost patch, with darker shades representing higher cumulative resistance from the patch. (C) *CWD* from rightmost patch, with darker shades representing higher cumulative resistance from the patch. (D) Modeled least-cost corridor produced by adding *CWD* surfaces shown in panels B and C (best 20% of study area shown). The least-costly path (traced in green) has a cumulative least-cost distance (*LCD*) of 124,443 weighted meters.
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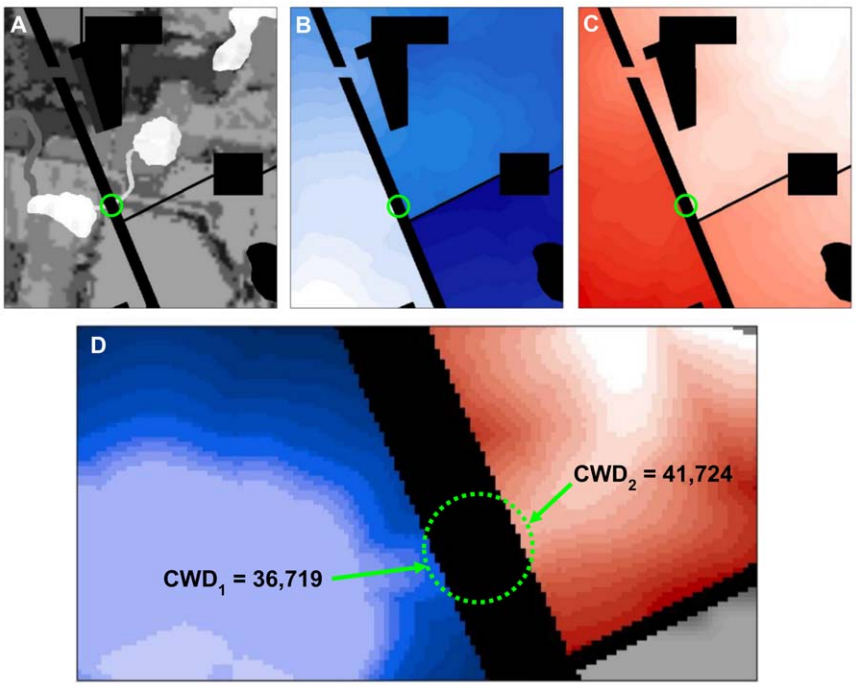


**Figure 2. Detail of resistance and *CWD* surfaces with circular moving window.** For a window with a diameter of 60 m (20 pixels) centered on the barrier, the arrows show the pixels in the window that have the lowest *CWD* to each patch (values shown are in weighted meters). Because the lowest *CWD* values from each patch will always be found on the edge of a moving window, only pixels on the perimeter need to be examined, increasing processing efficiency.
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the case, a simple metric of connectivity improvement that would result from restoration across the moving window is:

$$\Delta LCD = LCD - LCD' \quad (2)$$

Dividing $\Delta LCD$ by the search diameter gives the connectivity benefit per unit distance restored; dividing $\Delta LCD$ by $LCD$ gives the proportional improvement relative to unrestored effective distance.

To illustrate the method, we first apply it to the relatively simple landscape described in Figure 1 using a search window with a diameter of 60 m (20 pixels at 3 m resolution; Figure 2). The search window size is chosen to match the size of the barrier that one is interested in detecting: a diameter of 20 pixels will fully incorporate effects of barriers up to 20 pixels across. We assign a resistance of 1 to optimal movement habitat, so that the cumulative cost of movement is identical to the Euclidean distance traversed when no barriers are encountered. For the circular window centered on the highway in Figure 2, the lowest *CWD* values from the left and right patches are 36,719 and 41,724 weighted meters, respectively. Summing these values and adding 60 (the cost of crossing the circle if it were restored to optimal movement habitat with a resistance of 1), gives the least-cost distance of the path crossing through the restored area (36,719+41,724+60 = 78,503 weighted meters). Since this is considerably lower than the least-cost distance between the patches without restoration (124,443 weighted meters), this location is a potent barrier, and the center pixel is assigned an improvement value of 45,940 weighted meters. This is repeated for every pixel on the landscape using standard GIS neighborhood analyses, resulting in a raster surface of improvement scores (Figure 3A).

The removal of the barrier where the improvement score is maximal – for example, by constructing a wildlife crossing structure – would re-route the best movement path (Figure 3B) and lower the effective distance between the two patches by 37% (45,940/124,443). Once that improvement is carried out, a second barrier analysis with the altered landscape conditions suggests that additional restorations along the highway will not further reduce the *LCD* at this point (Figure 3C). The next priority would be a road crossing in the upper right of the panel (dark orange in Figure 3C), connecting the rightmost patch to high-quality movement habitat above the road. The method is computationally efficient enough that different restoration scenarios can be tested iteratively: a barrier analysis with a 20- pixel search diameter across a landscape with 1 million pixels takes less than 2 seconds using a 2.7 GHz notebook computer.

## Identifying barriers across scales and across large landscapes with multiple patches

The method described above can be extended across scales and across networks of patches, and we explore a few approaches to accomplish this here. By modifying the search diameter, the method can detect barriers of different sizes (Figure 4). Windows the width of a highway will best highlight where highways act as barriers, as in Figures 2 and 3. Larger windows will best detect barriers like agricultural fields, or cases in which narrow barriers run parallel to one another. Summary maps showing barrier effects across search window sizes may be created by first dividing improvement scores by the window size to produce maps of barrier strength per unit width, and then taking the maximum pixel score across scales (Figure 4B). This puts results from different analysis scales in the same units, allowing them to be summarized in a single map. Alternative summary metrics are possible, and we address some of them in the Discussion.

To summarize across multiple sets of patch pairs, we have implemented a similar approach in which the maximum or sum of improvement scores across all patch pairs is assigned to a pixel. Taking the maximum of improvement scores shows the features that have the greatest effect for any patch pair (Figure 4C). Summing improvement scores highlights those barriers that isolate multiple pairs of patches from one another, extending the method to quantify barrier centrality (Figure 4D).

The methods described in this paper have been implemented in Barrier Mapper software [39], freely available as a new addition to the Linkage Mapper Toolkit for ArcGIS [40].

## Example application in a landscape undergoing active conservation planning

The Washington Wildlife Habitat Connectivity Working Group, a collaboration of land and resource management agencies, non-governmental organizations (NGOs), universities, and Washington treaty tribes, recently completed a connectivity analysis across the Columbia Plateau Ecoregion in Washington, Oregon, and Idaho, USA [41]. The Working Group focused on the Columbia Plateau because the ecoregion is home to a large portion of Washington's sensitive plant and animal species but is also highly fragmented by agriculture and other anthropogenic activities. The Group modeled corridors to connect habitat for 11 focal species and also to connect natural landscape blocks scoring highly on an index of landscape integrity (i.e., large areas with relatively low levels human modification). Products from the analysis are being used to inform conservation planning efforts by several state and federal agencies and NGOs. Many of the corridors identified by the analysis pass through human-dominated landscapes, where roads, agricultural fields, and other human uses likely still act as barriers to movement.

We reanalyzed results for a corridor connecting two natural landscape blocks identified by the Working Group in Douglas County, Washington (Figure 5). We chose these blocks because they have been identified as important for many species of concern; for example, the blocks contain important habitat or corridors for 8 of 11 focal species analyzed by the Working Group. Moreover, both are occupied by greater sage-grouse (*Centrocercus urophasianus*, categorized as a Species of Greatest Conservation Need in Washington and a candidate for listing under the US Endangered Species Act), and both fall within a recovery area designated for the species by Washington State [42]. In addition, this landscape contains a complex mix of native systems and agricultural lands – the latter including both annual cropland and perennial vegetation cover – and includes roads, transmission lines, and other human-made features affecting animal movement [41].

To represent species with differing degrees of sensitivity to human modification, the Working Group used different resistance surfaces for landscape integrity analyses [41]. These surfaces all contained resistance values that increased with the degrees of human modification, differing only in the range of resistances assigned. Resistance scores of 1–100, 1–1000, and 1–10,000 were used for minimum, medium, and maximum sensitivity surfaces respectively (see [41] for details). We present results from a barrier analysis using the medium sensitivity resistance surface.

The modeled least-cost corridor connecting the patches dips south from the western patch, runs east to Banks Lake, and then north along a narrow strip of native vegetation and cliffs sitting between the lake and cropland (Figure 6A). A secondary and much longer corridor follows broad swaths of native vegetation through

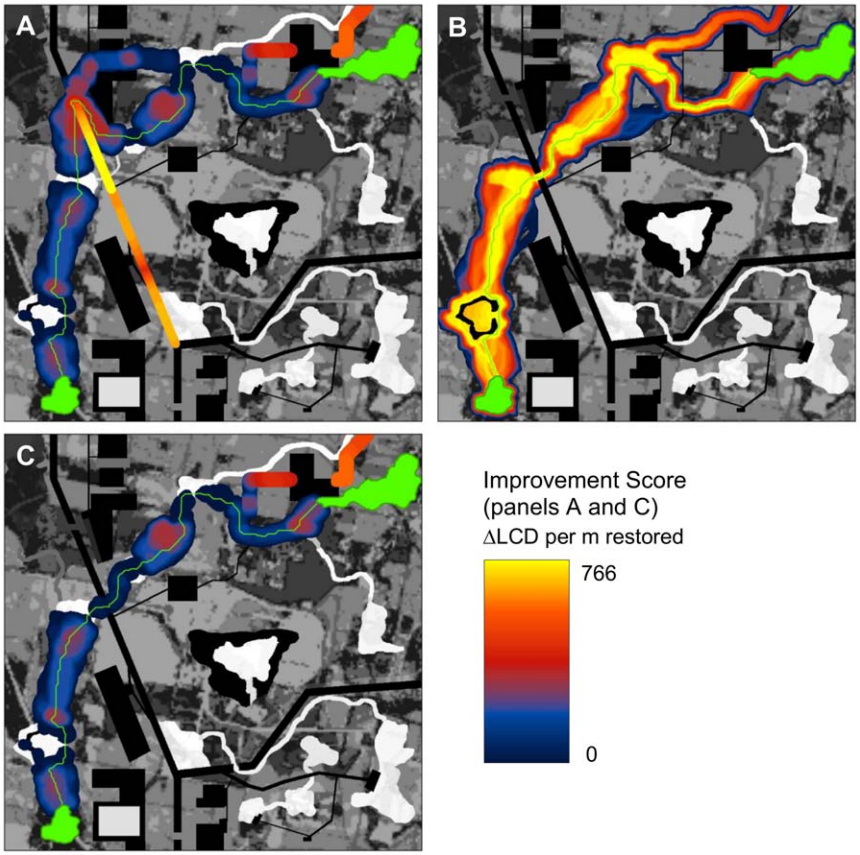


**Figure 3. Barrier analysis of landscape.** (A) Improvement scores (*ΔLCD*) for a 60 m search diameter using an enhanced version of Linkage Mapper software ([40]). Only positive values (indicating barriers whose removal would reduce isolation) are shown. To facilitate visualization of the barriers, scores were mapped so that they filled the search window (i.e. the maximum *ΔLCD* value within the search radius of each pixel is displayed). The greatest improvement potential was detected crossing the highway. Note that a natural corridor is bisected by the highway at the point with the highest improvement potential (see detail in Figure 2). (B) Creating a new gap in the barrier where restoration potential is highest re-routes the modeled least-cost corridor and greatly reduces resistance between the patches (*LCD* = 78,503 weighted meters compared with an *LCD* of 124,443 pre-restoration). Best 20% of study area shown. (C) Barrier detection at 60 m search diameter after restoration.
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Moses Coulee and Beezley Hills to the south. A barrier analysis indicates numerous opportunities for improving the least-cost corridor, particularly within its east-west segment (Figure 6B). There are also opportunities outside of the main corridor, occurring along the longer route to the south and to the north as well (Figure 6B). Restoring any of these latter areas would re-route the modeled least-cost corridor, causing it to occur in a different location than it did in the unrestored landscape.

Restoration of any of several barriers identified to the south would improve connectivity as measured by *LCD* (Figure 6B); however, this would result in a much longer least-cost corridor. Restoration to the north has the potential to both improve *LCD* and shorten the distance traversed by the corridor. We simulated a restoration by changing a 1 $km^2$ (500 m×2 km) swath of agricultural land (indicated by the arrow in Figure 6B) to a resistance of 1. We chose 2 km because the greatest improvement was detected at the 2 km scale, and we assumed 500 m was wide enough to accommodate movement. A second corridor analysis following the simulated restoration shows the new corridor to the north (Figure 6C). The corridor has 9.4% less cumulative resistance than the original (1348 weighted km *vs.* 1489 weighted km), and its least-cost path is 44% shorter in un-weighted length. A post-restoration barrier analysis indicates that the highest improvement scores now fall along the new corridor (Figure 6D); restoring a second 1 $km^2$ swath in this new corridor at the point indicated by the arrow would further reduce *LCD* by 50%.

## Discussion

Connectivity models have provided valuable guidance to conservation planning efforts, as well as predictions of movement, gene flow, and isolation important to landscape genetics and other fields concerned with movement ecology. Yet they have almost exclusively emphasized identifying features that facilitate, rather than impede, movement; this emphasis gives an incomplete picture of how landscape features affect connectivity, what connectivity management strategies might be appropriate, and the uncertainty underlying model predictions. We see considerable potential for barrier detection analyses to help practitioners overcome these limitations. In particular, the ability to identify restoration opportunities can provide valuable alternatives to traditional conservation efforts focused on existing movement corridors.

Our reanalysis of the Columbia Plateau data (Figure 6) illustrates these points, showing how detecting barriers can increase conservation options available to practitioners, improve understanding of analysis products, and result in more robust conservation plans. Without a barrier analysis, conservation

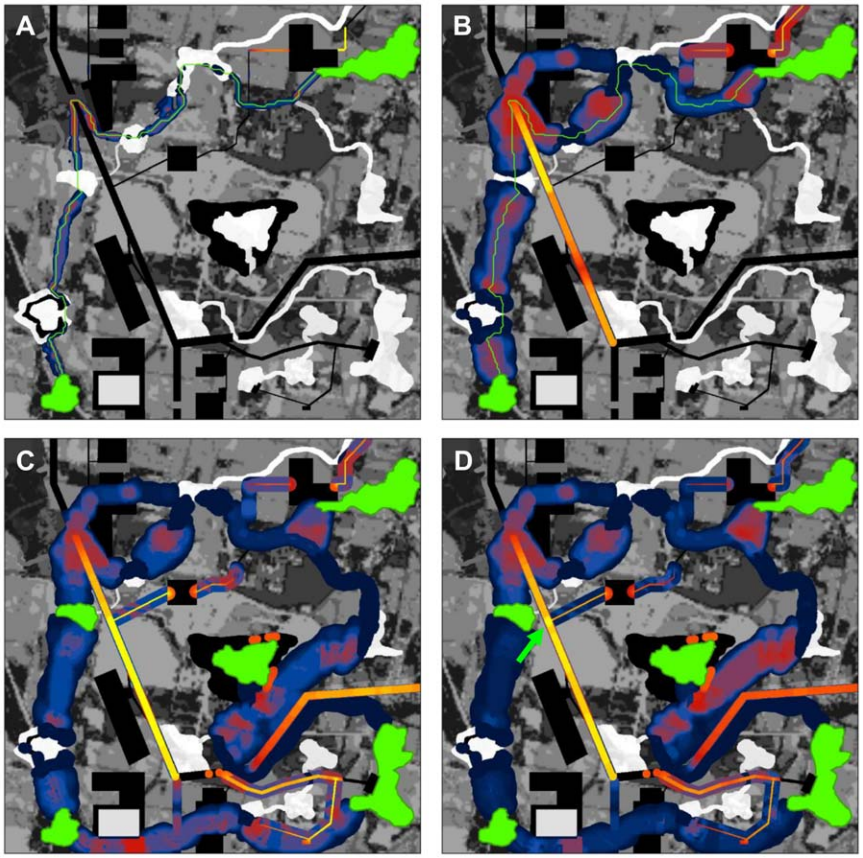


**Figure 4. Barrier analyses integrating across multiple scales and patch pairs.** (A) Results of barrier analysis with original patch pair at 12 m search diameter, which detects restoration opportunities equal to or less than 12 m across (e.g., local roads). (B) Maximum per-meter improvement value across 10 search window sizes (from 6 m to 60 m, with 6 m steps between search diameters). The map highlights where actions at different scales would have highest impact per meter restored. (C) Maximum per-meter improvement value across same window sizes and 5 patches, showing where greatest improvement could be achieved for any single pair of patches. (D) Sum of improvement scores among 5 patches (green). As in Panels A–C, the maximum per-meter improvement score was calculated for each patch pair at each scale. These were then summed across patch pairs to incorporate cumulative benefit for multiple patch pairs across multiple scales. The area scoring highest (bright yellow) had high improvement scores for multiple patch pairs; we interpret this area as having high 'barrier centrality,' i.e. being an important restoration opportunity for keeping the overall network connected. Note that the area occurs at a road intersection; if practical, placing a wildlife crossing structure here would re-route four corridors connecting the two leftmost patches to both the central and upper-right patch.
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planners would likely have focused on conserving land in or adjacent to the original least-cost corridor. Our analysis revealed numerous opportunities to improve this corridor, but also that restoration of a 1 $km^2$ swath of cropland would create a new corridor with several desirable characteristics. Specifically, the new corridor has a lower least-cost distance, is shorter in length, and appears to have fewer pinch-points (narrow sections) than the original corridor—all desirable characteristics for corridor design [15,32]. Moreover, if the two original corridors remain in place, the new, northern corridor adds redundancy to connections between the natural landscape blocks. This is important because organisms seldom follow a single optimal path [43], and because redundant connections help to ensure continued connectivity in the face of unpredictable environmental changes [15].

The analysis showed that connectivity conservation options need not be limited to a small portion of the landscape, opening up much more area for actions that could conserve or enhance connectivity and illustrating tradeoffs between different conservation strategies and target locations. Beyond the corridor quality differences cited above, we note that the original corridor runs along a narrow stretch of land bordering Banks Lake, sometimes traversing cliffs. The cliffs were assigned low resistance because the landscape integrity model used by the Working Group only quantified the degree to which pixels have been converted to human land uses. Practitioners, however, may consider cliffs to be impermeable for some species of conservation concern. The barrier analysis allows the user to quickly focus a more critical examination of corridor characteristics on areas influencing the results, and to identify options for alternative corridors that may better fit specific planning needs.

Similarly, the analysis underscored the potential sensitivity of corridor mapping to errors in GIS base data: our results show how the misclassification of a single agricultural field could have entirely altered the location of the original least-cost corridor shown in Figure 6A. The sensitivity of connectivity analysis results to landscape features at key locations has consequences for disciplines that depend on corridor maps (like conservation planning) and for disciplines that depend on connectivity measures (like landscape genetics). We discuss applicability of barrier detection methods to sensitivity analysis and error checking below.

Following the first barrier analysis and simulated restoration, a subsequent barrier analysis indicated that the restoration would

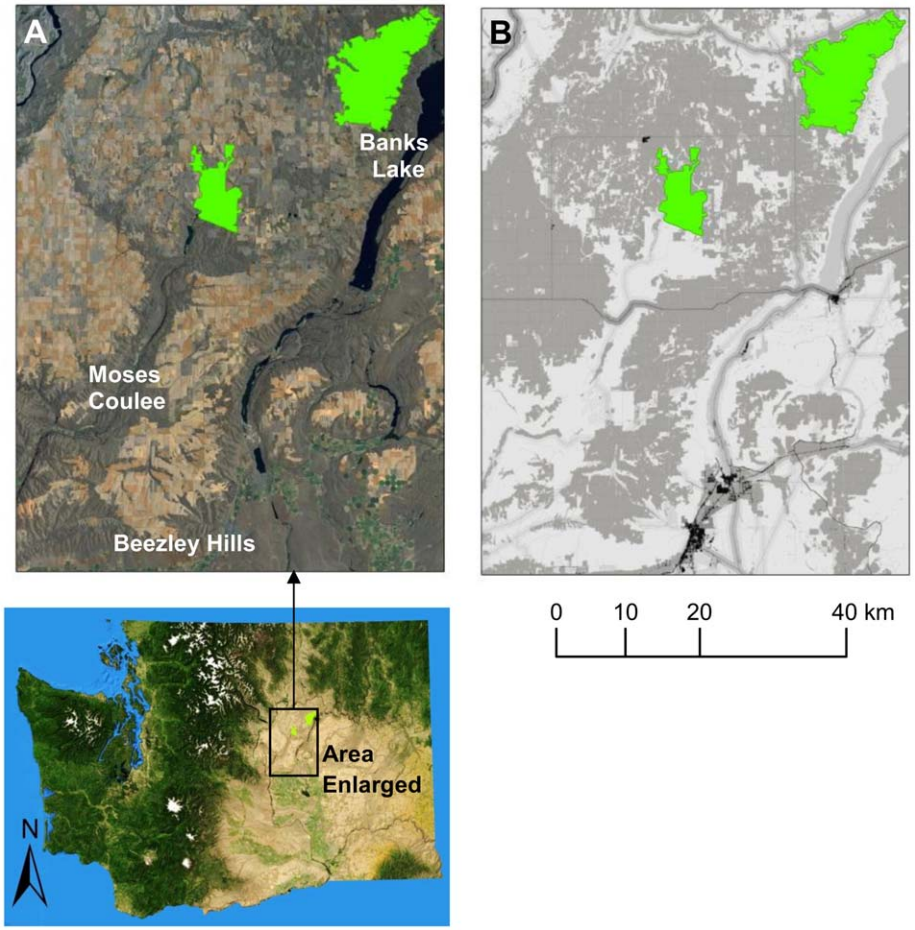


**Figure 5. Corridor analysis in a landscape undergoing active conservation planning.** (A) 60 km by 80 km study area in eastern Washington, USA, containing two natural landscape blocks to be connected (green). (B) Resistance map used to model corridors in a recent multi-partner connectivity analysis across the Columbia Plateau Ecoregion [41]; values range from 1 (white) to 1000 (black). Low resistance areas include native grassland and shrub-steppe, whereas high resistance areas include roads, developed areas, and agriculture.
doi:10.1371/journal.pone.0052604.g005

open up further restoration opportunities of considerable value, one of which would cut *LCD* values by half. Thus, simulating restorations and re-running corridor and barrier analyses will likely improve final conservation and restoration plans.

Although we are aware of no other efforts to automate identification of terrestrial connectivity restoration opportunities, least-cost corridor analyses have been used to guide placement of crossing structures across roads to restore connectivity for wildlife. For example, Beier et al. [44] assigned a single, finite resistance value to all segments of a highway between two protected areas, regardless of whether a segment contained wildlife crossing structures. The least-cost corridor between the areas crossed the highway at the location where a crossing structure would result in the lowest ecological cost of travel. If highway crossing structures were not located in this corridor, Beier et al. [44] recommended specific structures at particular locations. This approach is useful, but does not quantify the improvement compared to existing conditions, does not identify restoration opportunities outside of least-cost corridors, and cannot be readily applied to barriers more complex than roads.

In addition to overcoming these limitations, our method is also amenable to highlighting barriers that affect multiple corridors, introducing the concept of barrier centrality. As shown in Figure 4, barriers can be mapped across all patch pairs, and the results summed. This identifies barriers with high network centrality, similar to analyses that identify corridors or pathways with high centrality [21,22,45,46].

## Applications for error checking and sensitivity analyses

GIS land cover data used to develop resistance layers for connectivity analyses are typically based on satellite or aerial imagery and often suffer from high levels of classification error [34,47]. Although our method relies on these same base data, it can help to prioritize error checking of the data by highlighting mapped features that strongly influence corridor locations. If a permeable feature is misclassified as impermeable and identified as a barrier, the misclassification could entirely alter a corridor's location. We recommend examining detected barriers, either by manually checking aerial imagery or conducting field surveys. Similarly, impermeable features misclassified as permeable that occur along least-cost paths can change corridor locations as well. Examining features along least-cost paths in tandem with barriers could thus further reduce the effects of classification error in connectivity analysis products.

Barrier detection can also be applied to parameter sensitivity analyses, important because resistances are often assigned based on expert opinion, which can be unreliable [34,47,48]. For example, if a given land cover type fell along a corridor's least-cost

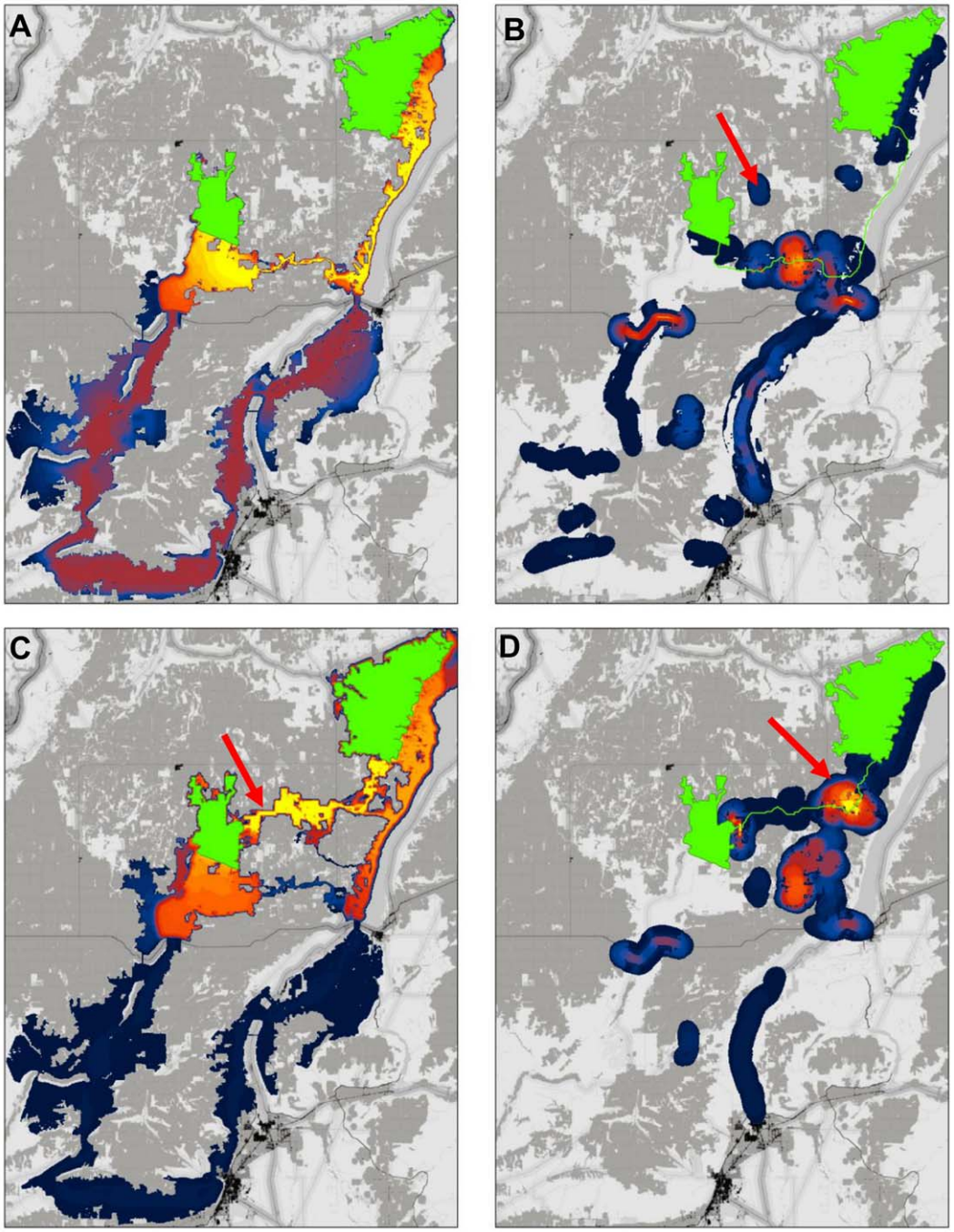


**Figure 6. Reanalysis of connectivity modeling results using barrier detection algorithm.** (A) Corridor connecting natural landscape blocks, showing least-cost movement routes. Best 20% of study area shown. (B) Barriers detected at diameters from 200 m to 2 km, with original least-cost path shown in green for reference. Mitigating barriers along the least-cost path (i.e., intersecting the green line) would improve the existing corridor without changing its location; mitigating barriers away from the path would re-route the best modeled corridor. (C) Restoring a 1 $km^2$ (500 m $\times$2 km) swath spanning the barrier indicated by the arrow establishes a new least-cost corridor to the North. (D) A barrier analysis incorporating the simulated restoration indicates opportunities to substantially improve the new corridor with additional restorations.
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path or encompassed an influential barrier outside of the corridor, the resistance assigned to that land cover type would be known to influence the corridor's location. The sensitivity of the corridor's location to the resistance value assigned the land cover type could then be analyzed using alternative parameterization methods as described by Beier et al. [47]. As with connectivity models, our method will depend on the grain size of the resistance raster; to adequately resolve features that potentially impede movement, we recommend pixels no larger than ½ the width of barriers one is interested in detecting.

## Potential enhancements

**Directionality of barrier effects.** Our methods could be improved to more precisely pinpoint barriers. For example,

elongated moving windows (search polygons) could perform better than circles to identify the best path for an improved corridor design. Measuring $\Delta LCD$ along elongate polygons placed at different angles, although more computationally complex than measuring across circles, would allow the attribution of directionality to barrier effects as well as adjustment of improvement scores at large search distances to reflect improvement achievable at smaller (nested) distances. New procedures to select the best orientation and width of such polygons could obviate the need to subjectively orient restoration polygons, like the 500 m×2 km polygon in our simulated restoration (Figure 6).

**Restoration cost.** We measured barrier strength by conservation improvement per meter restored because it was the simplest way to illustrate our approach. An alternative metric would be conservation improvement per restoration dollar; this would reflect, for example, that the cost per meter of a 10 m road crossing structure exceeds the cost per meter of a 50 m crossing structure, which in turn exceeds the cost per meter of restoring agricultural land. This enhancement would facilitate incorporation of connectivity restoration into return-on-investment analyses [49,50], helping managers to balance improvement potential, corridor importance, costs, and risk of conversion or degradation when deciding which parts of a landscape should be conserved or restored. The disadvantage, or course, is that this metric would require more data to calculate.

**Restoration efficacy.** Different $R'$ resistance values could be applied to different land cover types to reflect the fact that some barriers would be more permeable to movement following restoration than others. For example, a highway underpass installed to allow animal movement may still have considerable resistance, whereas a restored forest stand may have resistance similar to undisturbed forest.

**Other enhancements.** Just as areas that cannot be conserved can be removed from reserve selection algorithms [51], unremovable barriers, such as urban areas, could be excluded from barrier analyses. The metrics described in equation (2) could be modified to incorporate restoration costs that vary by feature type, or land prices mapped using parcel data. Metrics of corridor importance (e.g., link centrality) could be integrated by multiplying improvement scores by such metrics, which would highlight opportunities to restore the most potent barriers in the most important corridors. Or, rather than focusing on pairs of patches, the method could be altered to focus on the connectedness of each patch by summing barriers detected between each patch and all others. Lastly, improvement scores may be expressed in terms of absolute improvement or percent improvement relative to unrestored corridor resistance. An advantage of the latter approach is that it would favor restoration in corridors in which *LCD* values are already low, presumably meaning they are more viable.

Which of these enhancements are most valuable will depend on the objectives of individual users and projects.

## Application in other connectivity modeling frameworks

Although least-cost corridor models are by far the most commonly applied connectivity planning tool, they rely on simple assumptions about animal movement and other processes [43,48,52,53]. However, our approach can be applied in any connectivity modeling framework that produces measures of effective distance. For example, circuit-based connectivity analyses can model the relative proximity of each pixel to two patches by setting the voltage of one patch to 1 and the other to ground (see [15] for details on applying circuit modeling to landscapes). The resulting voltage surface gives the probability that a random walker will reach one patch before reaching the other [15,54]. Strong gradients in voltage indicate barriers that separate areas relatively accessible to one patch from areas relatively accessible to the other. If removed, such barriers would reduce effective resistance between the patches, an analog to *LCD* that takes into account the availability of multiple, parallel connections. A similar approach is widely used in microchip design: simulated voltage levels reveal areas with strong voltage gradients (known as IR drops) where electrical connectivity must be enhanced [55]. Thus barrier analysis using circuit theory can identify opportunities to provide valuable redundant connections even when *LCD* would not be reduced. In contrast, barrier analysis using least-cost methods will not identify these opportunities.

Individual-based movement models provide a more complex but also more powerful framework for modeling connectivity, capable of incorporating more biological realism and behavioral information than least-cost or circuit analyses [56]. As long as an individual-based model can produce maps of effective distance (e.g., based on the probability of, or energetic expenditure associated with, reaching different locations from a source patch), the approach described here could be applied to the model. Models such as PATH [16] and HexSim [17] can be used to derive such measures.

## Potential for integration with systematic conservation planning

Our method is not a substitute for algorithms like Marxan [57] or Zonation [51], which are designed to optimize selection of reserves or sets of conservation actions. Although our method identifies and ranks candidate areas for restoration actions, it does not select optimal *sets* or portfolios of conservation actions to achieve given conservation goals while minimizing cost. The same can be said for algorithms designed to map areas that most facilitate movement and connectivity (e.g., [22,40,46,58–60]); rather than incorporating optimization routines, such algorithms instead produce maps that must be interpreted by practitioners, who then make conservation decisions in light of costs, benefits, and other management objectives.

Although it has long been recognized as important to reserve network design [61], incorporating connectivity directly into optimization algorithms has proven difficult. Most such efforts can be characterized as minimizing local fragmentation by either considering the geographic proximity of candidate areas to other areas (e.g., [62–64]) or maximizing the compactness and contiguity of reserves by favoring selection of adjacent cells or using boundary quality or length penalties (e.g., [29,57,65,66]). Because these algorithms favor conserving or restoring contiguous natural areas, they may neglect areas that, although fragmented, contribute to connectivity between natural areas. Thus, relying solely on maximizing the proximity or contiguity of protected areas could lead to elimination of movement routes that cross human-dominated landscapes.

Progress toward synthesizing connectivity and optimization algorithms has likely been hampered by the 'network' nature of connectivity planning: conservation in one area can affect the function and value of distant areas, contingent upon the conservation status and characteristics of the intervening landscape. Incorporating this complexity into optimization algorithms becomes computationally prohibitive with large numbers of planning units [67]. Still, practitioners are beginning to use outputs of multi-species connectivity models as inputs to optimization algorithms like Zonation [23,68]. Such examples are promising, and should be equally applicable with restoration-oriented algorithms such as ours.

An alternative to our approach that would seek to develop a near-optimal set of conservation actions would be to employ a routine similar to that used by Zonation software, which begins with an intact landscape and iteratively removes grid cells with low conservation value [51,69]. Starting with a landscape in which all restorable barriers have been removed, different sets of barriers could be added back in and connectivity metrics recalculated at each iteration. As with traditional connectivity models, however, this would be computationally prohibitive with large numbers of patches or restoration sites because of the computational time required for recalculating connectivity metrics. A promising hybrid approach could be to use the method described in this paper to identify sets of pre-screened restoration opportunities, which could then be removed from a resistance surface and added back in using an algorithm like Zonation's.

### Practical considerations for improving conservation and restoration decisions

Managing for connectivity to facilitate gene flow, climate adaptation, and other processes is challenging without reliable maps to guide practitioners [33]. Connectivity analyses have provided valuable implementation guidance in the past; barrier mapping can increase the rigor of such analyses and the range of conservation options they reveal. It can help practitioners a) decide if connectivity conservation is a worthy investment in a landscape; b) identify opportunities to restore vs. conserve different areas; c) reduce uncertainty due to errors in GIS base data; and d) balance potential improvement against costs so that investments can be prioritized.

The goals of managers and planners can be used to guide applications of barrier detection methods. For example, if a transportation agency is interested in determining which highway segments are likely to have the greatest impact on wildlife movement, the search window should correspond to the width of highways, with outputs clipped to highways and the $R'$ value determined based on the estimated resistance of the kind of crossing structure (or alternative structures) being considered. If a land management agency is prioritizing restoration of degraded native vegetation, the search window should relate to the size of appropriate restoration projects, and outputs should be clipped to the eligible land base (e.g., limited to the type of vegetation the restoration would target). If an NGO is identifying landowners interested in obtaining voluntary incentive payments for wildlife-friendly management, the window should reflect the scale of such management. Summarizing barrier analyses across multiple scales will be desirable for collaborations among organizations with differing goals and mandates. As noted above, iterative application of the model with simulated restorations will likely provide the most informative results and most robust conservation plans.

Similarly, the method may have potential to help adapt results from coarse-filter connectivity assessments, such as landscape integrity/human modification-based connectivity maps, to more fine-filter objectives (see [70] for a review of coarse- and fine-filter conservation planning). Alternative corridors revealed by the method could be assessed for their suitability under different planning constraints (e.g., corridors for species that must avoid cliffs, as in the Columbia Plateau example). While not a replacement for species-specific connectivity analyses, such an approach could help land managers evaluate alternatives if a mapped corridor is deemed unsuitable for their particular needs.

Connectivity maps do not always identify functioning routes that need to be maintained and protected; rather, they frequently map routes that may not be currently viable, but appear to provide the best opportunities for future work toward enhancing connectivity. In this sense connectivity maps often represent visions and goals for desired future conditions [71]. Barrier detection can add insight into the practicality of these goals, and identify specific options for achieving them. It can also help practitioners to 'triage' a connectivity plan, identifying corridors that traverse numerous barriers – and therefore would require significant investment to fully restore – so that efforts may be focused on more viable movement routes.

Perhaps most importantly, the ability to detect options to re-route corridors also opens up a broader suite of potential actions to improve connectivity. It can help managers identify new corridors that add additional movement pathways in areas important to the overall connectivity of a landscape (i.e. linkages with high centrality). Combined with spatially explicit land cost data, the method could help to improve conservation efficacy while reducing costs.

We hope barrier analyses will expand conservation options available to managers, and broaden conversations about restoration of connectivity more generally. By identifying new ways to improve connectivity in a particular area, the method can allow managers to consider different suites of strategies, or engage with new sets of stakeholders with interests in different areas. Both from the perspective of entities mandated to carry out conservation actions, and from the perspective of stakeholders with interests in the lands that are the focus of such actions, broadening the suite of alternatives and tools can only increase the opportunities for finding common ground in pursuit of multiple objectives.

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## Author Contributions

Conceived and designed the experiments: BHM. Performed the experiments: BHM. Analyzed the data: BHM. Contributed reagents/materials/analysis tools: BHM. Wrote the paper: BHM SAH PB DMT. Suggested refinements to methods and analyses: SAH, PB, DMT.

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Improving the Success of Wetland Creation and Restoration with Know-How, Time, and Self-Design

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# IMPROVING THE SUCCESS OF WETLAND CREATION AND RESTORATION WITH KNOW-HOW, TIME, AND SELF-DESIGN[1,2]

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*Abstract.* The creation and restoration of new wetlands for mitigation of lost wetland habitat is a newly developing science/technology that is still seeking to define and achieve success of these wetlands. Fundamental requirements for achieving success of wetland creation and restoration projects are: understanding wetland function; giving the system time; and allowing for the self-designing capacity of nature. Mitigation projects involving freshwater marshes should require enough time, closer to 15–20 yr than 5 yr, to judge the success or lack thereof. Restoration and creation of forested wetlands, coastal wetlands, or peatlands may require even more time. Ecosystem-level research and ecosystem modelling development may provide guidance on when created and restored wetlands can be expected to comply with criteria that measure their success. Full-scale experimentation is now beginning to increase our understanding of wetland function at the larger spatial scales and longer time scales than those of most ecological experiments. Predictive ecological modelling may enable ecologists to estimate how long it will take the mitigation wetland to achieve steady state.

*Key words: achieving successful wetland mitigation; creating wetlands; ecological engineering; ecological modelling; freshwater marshes; functional analysis of wetlands; mitigation of wetland loss; Olentangy River Wetland Research Park, Ohio; wetland succession.*

## INTRODUCTION

The way in which we measure "success" of created or restored wetlands and our ability to achieve success are two issues that have come under increased discussion in recent years by wetland scientists and managers. Success in the general sense here means the establishment of a biologically viable and sustainable wetland ecosystem. Some call a wetland a success when it replaces the functions lost in a wetland that is being replaced; others would gauge success of a created or restored wetland against natural reference wetlands in the region. Unfortunately, there has been little formal published follow-up of the poorly named (see Renner 1994) "mitigation wetlands" that are constructed to replace wetlands that are unavoidably lost and there are few satisfactory methods for assessing replacement of the functions lost with the original wetland (Mitsch and Gosselink 1993). Regulators and consultants have chosen to use simple indicators of "success" to expedite the process and to keep monitoring costs low. Normally 3–5 yr of simple once- or twice-per-year monitoring is required, with easily measured parameters such as plant lists, animals witnessed, and percentage vegetation cover as the overall indicators. Assessing success is then based on comparing these easily measured parameters with a relatively simple set of criteria that were stipulated in the original permit for the project; these criteria may or may not accurately reflect wetland function.

After reviewing pertinent literature, we discuss three fundamental requirements for achieving success of wetland creation and restoration projects: understanding wetland function, giving the system time, and appreciating the idea of self-design. Our hypothesis is that most attempts to measure and achieve success of created and restored wetlands—caused by a lack of application of good wetland science to the problem and compounded by the existing construction-schedule-driven process—are flawed because of misunderstanding or misapplication of these factors. We then argue that ecosystem-level research and ecosystem modelling may provide better guidance on when created and restored wetlands can be expected to comply with criteria that measure their success.

## STUDIES ON WETLAND MITIGATION SUCCESS

Most studies suggest that there is much room for improvement in the building of wetlands. Maguire (1985) used area, vegetative cover, and implementation of permit conditions to estimate mitigation success in Virginia and found that only 50% of 23 mitigation wetlands were "successful." In most unsuccessful cases, the mitigation project had not been implemented. An additional study by Reimold and Cobler (1985) conducted for the U.S. Environmental Protection Agency (EPA) gave similar results. Glubiak et al. (1986) and Quammen (1986) both suggested the need for better management of mitigation wetlands. Additionally Glubiak et al. (1986) predicted that while the protection

[1] Manuscript received 10 June 1994; revised 3 April 1995; accepted 12 April 1995.

[2] For reprints of this group of papers on wetland mitigation, see footnote 2, page 33.



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of wetlands through a permit process—Section 404 of the Clean Water Act enacted by the U.S. Congress in 1972—was somewhat effective, it would not prevent wetland area losses as effectively as it should.

In the mid-1980s some scientists involved in wetland restoration and mitigation believed that mitigation was working (Harvey and Josselyn 1986), while others suggested that more research needed to be done and that, if not properly conducted, a wetlands mitigation project could easily fail (Race 1986). Kusler and Groman (1986) raised concerns about the granting of Section 404 permits to contractors when alternative sites are available. Many questions and issues were raised by Kusler and Groman (1986) and Golet (1986) regarding permitting processes and the actual success of wetland mitigation projects. Their major issues were: When should destruction/damage and subsequent creation/restoration be permitted? How is the damage to the original system measured and how is the creation/restoration deemed sufficient? Golet (1986) suggested that under no circumstances should damage to a wetland be allowed unless there is absolutely no alternative.

While there are many factors that could be used to monitor progress of mitigation wetlands, observing vegetation has often been the easiest and probably the most common method (see, e.g., Wentworth et al. 1988, Jarman et al. 1991, Atkinson et al. 1993). This concept has already been codified in several parts of the country. For example, in Massachusetts, vegetation cover of $\geq$75% is the major success criterion, even if vegetation composition is very different from that of the original wetland (Jarman et al. 1991). Reinartz and Warne (1993) argue that while vegetation cover may be an easy measure of success, it is a poor indicator of function.

Recent investigations of wetland mitigation projects, as a greater number of mitigation sites have become available for scrutiny, generally reinforce the early concerns. For example, Erwin (1991) found that, of 40 mitigation projects in south Florida involving wetland creation and restoration, only about half of the required 430 ha of wetlands had been constructed and that 24 of the 40 projects (60%) were judged to be incomplete or failures. The most significant problems identified with created wetlands were improper water levels and hydroperiod. Sifneos et al. (1992) collected information from permits on Louisiana, Alabama, and Mississippi wetland mitigation projects and found that in Louisiana (their primary area of interest) only 8% of areas impacted by dredge-and-fill activity was compensated for, and >50% of the areas receiving permits covered <0.4 ha. Additionally, only 10% of the mitigation wetlands were monitored by at least one site visit. The lack of standardized record-keeping from state to state made the study difficult. The study suggests that follow-up monitoring and information on wetland functions be required in future permit decisions. Kentula et al. (1992) investigated several mitigation wetlands in Oregon and Washington and found a net loss in wetland area of 43% for Oregon and 26% for Washington. Data were either incomplete or of poor quality and up-to-date standardized databases were recommended. In a similar study, but without field checks, Holland and Kentula (1992) examined >300 Section 404 permits issued in California from 1971 to 1987 and found that while 1260 ha of compensatory mitigation (wetland creation, restoration, or preservation) had been required for impacts to 1180 ha of wetlands over that period, there was little follow-up of the permits and fewer than one-third (31.5%) required any field monitoring. Confer and Niering (1992) found that when comparing five created freshwater marshes with five nearby natural ones, the created marshes generally had greater water depth and thus more open water. They state that most of their created wetlands were highly dependent on highway runoff as a water source. Roberts (1993), quoting several ecologists, summarizes the skepticism by calling wetland trading "a loser's game."

## Improving the Odds of Wetland Success

We propose three general concepts that will need attention of those involved in wetland mitigation if we are truly going to address the issue of creating and restoring viable wetland ecosystems: (1) Understand wetland function; (2) Give the system time; and (3) Allow for the self-designing capacity of nature. These points are discussed in detail below.

### *Understand wetland function*

Mitsch and Cronk (1992) proposed that the "know-how" of building and restoring wetlands is based on an empiricism with little scientific backing, and is learned and relearned every time a new wetland is built. Wetland restoration and creation are relatively new fields and few engineers are trained in ecology and few ecologists have any experience in engineering methods. Engineers, consultants, scientists, and landscape architects can, and frequently do, claim to be experts with little experience or little knowledge of wetland ecology; without any certification standards for individuals involved in wetland creation and restoration, projects are often carried out by organizations and individuals not well versed in wetland ecology. A relatively high number of "failures" of mitigation wetlands can be attributed to a general lack of understanding of first principles of wetland science.

For example, an understanding of wetland hydrology as the fundamental forcing function of wetlands is well understood conceptually (Mitsch and Gosselink 1993) yet not always put into practice by many of those involved in wetland mitigation. The importance of hydrology is discussed in detail in a companion paper by Bedford (1996). Erwin (1991) pointed out that a number of Florida wetlands were considered failures in his Florida study because they lacked suitable hydrology. In so-called "on-site mitigation," wetlands are devel-

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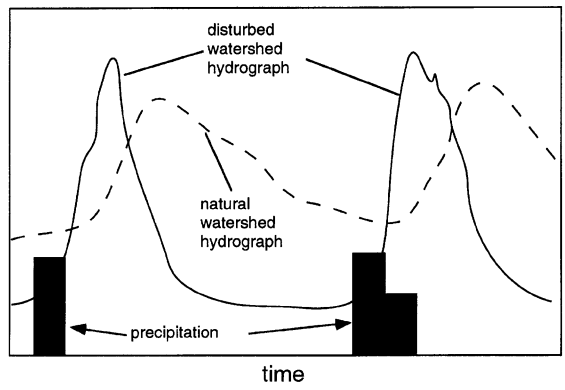


FIG. 1. Comparison of a hypothetical stream hydrograph in a natural watershed vs. one from a highly disturbed urban or suburban watershed. Placing the wetland in either of these two watersheds would probably lead to significantly different wetland structure and function.

oped in watersheds near the wetlands being drained or lost; their success is often problematic because of the usual proximity of the mitigation project to a human-altered landscape and the accompanying changes in hydrologic conditions. In these settings, created and restored wetlands can be subjected to "flashy" streams and human-regulated hydrologic conditions. In urban and suburban settings, floods are often greater and occur more quickly after precipitation; low-flow conditions are drier than in a "natural" hydrology (Dunne and Leopold 1978). Both of these conditions lead to generally greater water level fluctuations compared to those in more natural settings (Fig. 1). Unpredictable and rapidly fluctuating hydrology can lead to washouts, scouring, planting failure, and animal and macroinvertebrate emigration, leading to decreased biodiversity and even loss of water quality function.

### *Give the system time*

A flaw in the measurement of mitigation wetland success is the limited amount of time that regulators and the land development process allow for newly created wetlands to develop before passing judgment. The legal and economic necessities seem to dictate the ecological patterns of nature, encouraging "quick-fix" wetlands while not allowing for the stochasticity of nature. Engineers have long recognized the probabilistic nature of hydrologic events (e.g., precipitation and streamflow) yet relatively deterministic indicators such as wetland plant viability, open water area, endangered species, and waterfowl are expected to develop in a relatively short time span, usually 5 yr. The very best that we can have after 5 yr of monitoring a mitigation wetland is a general idea of the wetland's ecological trajectory and even less understanding of its function.

In one of the longest-running documentations of a constructed wetland in this country, an 8-ha freshwater tidal marsh (Windmill Point), was constructed in 1974–1975 within dikes in the James River in eastern Virginia, USA. Early indications, from 1978 to 1982, considered the wetland a success as it supported a diversity of herbaceous vegetation typical of tidal freshwater marshes (Newling and Landin 1985). At that time the monitoring was referred to as "long-term." But the dikes were breached in 1986 due to flooding on the James River, eliminating the vegetation and submersing the wetland in the river (Landin 1994, *personal communication*). Sixteen years after construction the project could be termed by some as a hydrologic and ecologic failure if long-term survival of the wetland was one if its goals.

Because of the stochastic nature of hydrologic events and the slow development of ecosystems, sometimes in spurts, sometimes in the slow process of recruitment and growth, the 5-yr time horizon can be viewed as arbitrary and probably much too short. As ecological models show (see e.g., Jørgensen 1994), the further initial conditions are from steady-state, the longer it will take for that system to reach or approach steady state (Fig. 2). Short monitoring times favor measuring success with transplanted vegetation and pioneer organisms; long-term success is less dependent on these initial conditions.

### *Allow self-design*

There are two general approaches for introducing vegetation (and other organisms) in wetland creation and restoration projects. One is the "designer" approach of introducing species and expecting their survival in Gleasonian zones, akin to gardening or landscape architecture. The other emphasizes the "self-design" or "self organization" capacity of Nature to both recruit species on its own and to make choices from those species introduced by humans (Odum 1989, Mitsch 1993). In self-design the emphasis is on the introduction of as many species as possible, knowing that natural forces will help in the ultimate design by choosing the most appropriate species. Self-design also recognizes the importance of natural colonization of species in wetlands.

In one of the few studies to make a preliminary comparison of these two general approaches, Reinartz and Warne (1993) compared 11 created wetlands in southeastern Wisconsin that were naturally colonized with 5 wetlands in the same region where 22 species were

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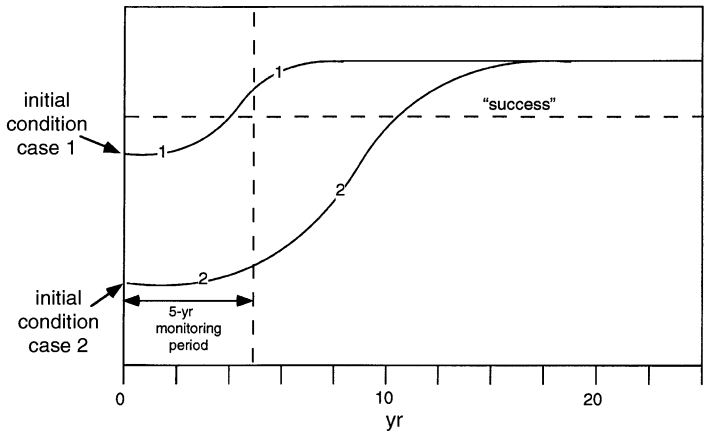


FIG. 2. Hypothetical comparison of the pattern of one wetland criterion for "success," e.g., percentage vegetation cover, for two different initial conditions at the same hypothetical wetland site. In Case 1 the wetland would be considered a "success" after 5 yr, while in Case 2 the wetland would be considered a "failure." Each wetland case could end up eventually at the same level, but well after 5 yr. In reality, a multiplicity of criteria would be used in this comparison.

introduced by seeding. The diversity and richness of plants in the colonized wetlands increased with age, size, and proximity to the nearest wetland source even though *Typha* spp. comprised 15% of the vegetation for 1-yr-old wetlands, and 55% for 3-yr-old wetlands. Seeded wetlands had a high species diversity and richness after 2 yr and *Typha* cover in the seeded sites was lower than in the naturally colonized sites after a 2-yr period.

Many studies to date (e.g., Confer and Niering 1992, McKnight 1992), especially those on restoration of non-coastal wetlands, have probably over-predicted—because of short time horizons and small spatial scales—the survivability of transplanted species in "designer" wetlands. (An exception to this short time horizon is the long-term observation of Frenkel and Boss [1988], through aerial photography, of the spread of *Spartina patens* in areas along Oregon's coastal wetlands.) With enough time and space, introduced species may be less successful than we initially believed. A better idea is to give the wetland system many possibilities through multiple-seeding, multiple-transplanting, and establishment of hydrologically open systems; this allows nature to participate in the wetland design.

## PROVIDING THE NEEDED RESEARCH TOOLS

In addition to the above suggestions for wetland managers and ecological engineers who are attempting to design and monitor wetlands, there are some important approaches that wetland scientists can use to reduce the uncertainty of wetland mitigation.

### *Select the proper experimental scale*

The limited ability of science as we generally practice it to both understand and solve our dilemmas in natural resource conservation was argued by Ludwig et al. (1993) and debated in the pages of *Ecological Applications* (Levin 1993). Taking the cue from Holling (1993) and Costanza (1993) in that discussion, we question whether reductionistic experimental science, with its short time scales (often the time required for a Ph.D. dissertation) and its small spatial scales (often in laboratories or small field plots) can correctly prescribe how to build large wetlands. A holistic systems approach, with the appropriate time and space scales, should at least have equal emphasis.

As one example, a number of studies of wetland function were carried out with four full-scale constructed wetlands at the Des Plaines River Wetland Demonstration Project in northeastern Illinois (Sanville and Mitsch 1994). Hydrologic conditions were varied for high- and low-flow conditions for entire wetlands (average size: 2.4 ha), not just experimental plots; the studies were carried out over 3 yr. Researchers had important findings in estimating detention and mixing (Kadlec 1994), water quality function (Hey et al. 1994, Phipps and Crumpton 1994), sedimentation (Brueske and Barrett 1994, Fennessy et al. 1994*a*), vegetation development (Fennessy et al. 1994*b*), aquatic metabolism (Cronk and Mitsch 1994*a, b*), and avian success (Hickman 1994) in created wetlands, most as a function of hydrology.

In a comparison of two natural tidal marshes with a 0.65-ha constructed marsh in coastal Virginia 5 yr after construction, Havens et al. (1995) found seasonal differences in fish and shellfish abundances between natural and constructed marshes, with lower numbers in the latter. They attribute the differences to relative lack of organic carbon and less morphometric heterogeneity (e.g., stream rivulets, microtopography) in the created marsh.

We recently initiated a full-scale comparison of "self-design" and "designer" approaches to wetlands at the Olentangy River Wetland Research Park at The Ohio State University (Fig. 3; Mitsch and Wu 1995, Mitsch 1995). In one newly constructed wetland basin (1 ha), we planted, in approximately the stratification that we would find in nature, ≈2500 individuals representing 14 species of wetland plants. In an identical constructed wetland basin nearby, we planted nothing. Hydrologic conditions are being maintained as similar as possible in the two basins and there is no predeter-

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FIG. 3. The Olentangy River Wetland Research Park at The Ohio State University in Columbus, Ohio, USA, is a whole-ecosystem long-term experiment begun on 14 May 1994 with the planting of one of the deep-water marshes shown in foreground (right basin) with ≈2500 plants representing 15 wetland species. The second deep-water marsh (left basin) remains unplanted. Each basin is 1 ha in size and water is supplied by pumps in the lower right-hand corner of the site to create a similar hydrology for each basin. The Olentangy River, shown flowing from bottom right to the top of the picture (with the university ≈0.5 km downstream of the site on the horizon of the picture), is the source of the water, which is pumped in proportion to the river flow in the same patterns for each wetland basin. The photo was taken in November 1993 prior to the introduction of water to the wetlands (photo by Mark Myers, Apex, Columbus, Ohio).

mined completion date to our experiment. We believe that our "experiment" is closer to the scale necessary for documenting the forces, e.g., plant recruitment, geese and muskrat invasions, etc., that influence ecosystem development. Working at this full scale precludes extensive replication because of land and construction costs, yet our understanding of ecosystem development and other wetland functions will come only

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from studying spatial scales and longer time scales to supplement traditional ecological experiments.

### *Develop predictive modelling*

Little attention has been paid to ecological modelling—the one tool that can expand the time horizon—in predicting success of created and restored wetlands. While this approach must be used with caution and proper qualifications, it enables ecologists to project into the future and estimate how long it will take the mitigation wetland to achieve some type of steady state. A few publications (Costanza and Sklar 1985, Mitsch et al. 1988, Mitsch 1994) have reported on the state of the art of simulation modelling in wetland ecology, but this powerful "systems" tool has rarely been used to predict mitigation success. Stochastic inputs, adaptive model structure (Jørgensen 1994), higher-order modelling languages (e.g., STELLA) and spatially dynamic models are useful advances in ecological modelling, but simple-structure models that aggregate components into overall variables such as "vegetation" or "nutrients" can be just as effective (Mitsch et al. 1995). In an application of modelling for a mitigation project in central Ohio, Niswander and Mitsch (1995) used simulation models both to "fill in" information to make calculations about ecosystem function (phosphorus retention) of a created freshwater marsh and to "enhance the time horizon" by predicting one structural aspect of this project well into the future—the survival of planted wetland trees over the next 50 yr. Modelling, of course, will not provide an exact prediction of conditions well into the future but, when used with good wetland ecology and sufficient field monitoring, it can provide another tool for those interested in predicting the future of created and restored wetlands.

## Conclusions

There is optimism that wetlands can be created and restored and that wetland function can be replaced, despite a recent spotty record in the United States with the mitigation of wetland loss. The spotty record is due, in our opinion, to little understanding of wetland function by those constructing the wetlands, insufficient time for the wetlands to develop, and a lack of recognition or underestimation of the self-design capacity of nature. Understanding wetlands enough to be able to create and restore them requires a substantial training in plants, soils, wildlife, hydrology, water quality, and engineering. We should give mitigation projects involving freshwater marshes enough time, closer to 15–20 yr rather than 5 yr, before judging their success. Restoration and creation of forested wetlands, coastal wetlands, or peatlands may require even more time. For example, the restoration of certain coastal salt marshes has been suggested to require at least 50 yr (Frenkel and Morlan 1991). Finally, we should recognize that Nature remains the chief agent of both self-design and ecosystem development; humans are not the only participants in the design process.

Science will need to make significant contributions to the process of reducing our uncertainty about predicting wetland success. Wetland mitigation needs to become part of an applied ecological science, not a technique that is relearned each time without theoretical underpinnings. Scientists need to make the connections between structural measures (e.g., vegetation density, diversity, productivity) and functions such as wildlife use, organic sediment accretion, or nutrient retention in quantitative and carefully designed experiments. Simply having a list of plant species is inadequate for regulators or managers to estimate ecosystem function. Simulation models and experimentation at the proper spatial and temporal scales should be able to help us predict the behavior of these wetlands and estimate proper designs.

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# Rapid decline of California's native inland fishes: A status assessment

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ABSTRACT

A quantitative protocol was developed to determine conservation status of all 129 freshwater fishes native to California. Seven (5%) were extinct; 33 (26%) were found to be in danger of extinction in the near future (endangered); 33 (26%) were rated as sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable); 34 (26%) were rated as declining species but not in immediate danger of extinction. Only 22 (17%) species were found to be of least concern. Of 31 species officially listed under federal and state endangered species acts (ESAs), 17 (55%) were rated as endangered by our criteria, while 12 (39%) were rated vulnerable. Conversely, of the 33 species that received our endangered rating, only 17 (51%) were officially listed under the ESAs. Among the seven metrics used to assess extinction threat, climate change, area occupied and anthropogenic threats had the largest negative impacts on status. Of 15 categories of causes of decline, those most likely to diminish status were alien species, agriculture, and dams. Overall, 83% of California's freshwater fishes are extinct or at risk of becoming so, a 16% increase since 1995 and a 21% increase since 1989. The rapid decline of California's inland fishes is probably typical of declines in other regions that are less well documented, indicating a strong need for improved conservation of freshwater ecosystems.

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## 1. Introduction

Extinction in freshwater environments is a world-wide crisis (Moyle and Williams, 1990; Saunders et al., 2002; Dudgeon et al., 2006) which is poorly documented (Strayer and Dudgeon, 2010; Vörösmarty et al., 2010). Loss of biodiversity seems to be occurring more rapidly from fresh water than from any other broad habitat type (Jenkins, 2003; Dudgeon et al., 2006). Driven by recent global assessments of mollusks (Bogan, 2008), crabs (Cumberlidge et al., 2009), amphibians (Stuart et al., 2004), and dragonflies (Clausnitzer et al., 2009), the number of freshwater species listed on International Union for the Conservation of Nature (IUCN) Red Lists has more than tripled since 2003 (Darwall et al., 2008). Nevertheless, the best-studied indicators of the problem remain freshwater fishes (Magurran, 2009) which account for about one-third of all described vertebrates, with roughly 13,000 species (Helfman, 2007; Lèvêque et al., 2008). In 1992, 20% of the world's freshwater fish fauna was estimated to be extinct or in serious decline (Moyle and Leidy, 1992). Less than 20 years later, 37% of the 3481 freshwater fish species evaluated globally by IUCN were regarded as extinct or imperiled (declining towards, or threatened, with extinction, Vié et al., 2009), although the IUCN database is likely biased towards including declining species. At the continental scale, 46% of 1187 described freshwater and diadromous fish species native to North America are extinct, imperiled, or have one subspecies or distinct population that is imperiled (Jelks et al., 2008) with the rate of extinction steadily increasing (Ricciardi and Rasmussen, 1999). Not surprisingly, the number of imperiled fish species is highly correlated with human population and economic growth (Limburg et al., 2011).

While large-scale assessments spotlight the global extent of the crisis, severity and causes are best understood through intensive studies of regional fish faunas because status can be repeatedly, systematically, and quantitatively documented over relatively short time periods. In this paper, we analyze the status of California's 129 native freshwater fishes. This regional fauna is reasonably well documented, occupies a wide variety of habitats, and exhibits a wide range of life history patterns including anadromy (Moyle, 2002; Moyle et al., 2008, 2010). Their status was previously analyzed in 1989 (Moyle and Williams, 1990) and 1995 (Moyle et al., 1995). Here, we use a new quantitative protocol to determine conservation status of each species. This protocol allows us to make status determinations independent of official agency designations and to find species needing protection that have been overlooked so far by state and federal agencies. Comparisons with official status designations also serve as a check on the usefulness of our protocol. In this paper, we answer the following questions:

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1. What is the status of California's inland fish fauna?
2. Are the fishes continuing to decline?
3. What factors are most strongly associated with declining status?
4. How do our results fit with official status designations?

### 1.1. The inland fishes of California

California's large size (411,000 km$^2$), length (1400 km and 10° latitude) and complex topography result in diverse habitats, including 50 isolated watersheds in which fish have evolved independently (Moyle, 2002, Moyle and Marchetti, 2006). For most of the state, the climate is Mediterranean; most precipitation falls in winter and spring, followed by long dry summers. This results in rivers that have high annual and seasonal variability in flows (Mount, 1995) and native fishes adapted to hydrologic extremes. There are 129 native inland fishes (defined as those breeding in fresh water) currently recognized (Appendix 1, which includes scientific names of fishes mentioned). Of these, 63% are endemic to the state and an additional 19% are also found in one adjacent state. Thus California's fishes fall within political and zoogeographic boundaries that largely coincide, important for a bioregional assessment (Moyle, 2002).

Conditions in California have produced an unusual number of anadromous fishes (24%) as well as fishes that thrive in isolated environments such as desert springs, intermittent streams, and alkaline lakes. Most fishes live in rivers of the Central Valley and North Coast, areas having the most water and most diverse aquatic habitats. Recent genetic and taxonomic studies have underscored the distinctiveness of California fishes and increased the number of taxa from 113 in 1989 (Moyle and Williams, 1990) to 129 in the present study.

Most California rivers have been dammed and diverted to move water from places of abundance to places of scarcity, where most Californians live (Hundley, 2001). Not surprisingly, native fishes have been in steady decline since the mid-19th century, although the first formal evaluation of their status was not conducted until 1989. At that time, 7 species (5%) were extinct, 15 (13%) were formally listed as Threatened or Endangered under the state or federal ESAs, and 51 (43%) were designated as Species of Special Concern by the State of California, indicating they were in decline or had small, vulnerable populations but were not yet threatened with immediate extinction (Moyle and Williams, 1990). The number of declining species has steadily increased so that in 1995, there were 18 (16%) listed and 51 (44%) in decline (Moyle et al., 1995). Today, the numbers are 30 (23%) listed and 70 (54%) in decline, meaning that 83% of California's native fishes have the potential to go extinct in coming decades or are already extinct (Appendix 1) (Fig. 1).

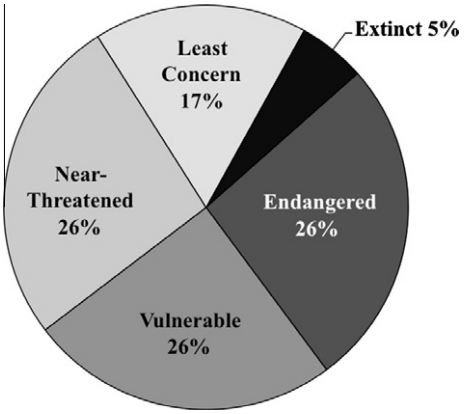


**Fig. 1.** Status of fishes ($N$ = 129) native to inland waters of California in 2010. All threat categories are approximately equivalent to IUCN threat levels of the same name. Extinct = globally extinct or extirpated in the inland waters of California. Endangered = highly vulnerable to extinction in its native range, approximately equivalent to IUCN threat level of *endangered* or *critically endangered*. Vulnerable = could easily become threatened or endangered if current trends continue. Near threatened = populations in decline or highly fragmented. Least concern = no extinction threat for California populations.

## 2. Methods

### 2.1. Sources of information

Taxa used were those that qualified as species under the federal Endangered Species Act of 1973, so include species, subspecies, Evolutionarily Significant Units, and Distinct Population Segments recognized by one or more agencies. The biology and status of each species was determined from information in Moyle (2002), Moyle et al. (1995, 2008, 2010), additional reports and papers from intensive literature searches, and by personal communications with biologists working with each taxon. The information was summarized in standardized species accounts which included evaluation of status. All accounts were reviewed by experts on each species. In a few cases, information was updated by field investigations by the authors. The status of each species is as of December 31, 2010.

### 2.2. Quantitative evaluation of status

Species status was determined using seven metrics scored on a 1–5 scale (Table 1) where 1 was a low score indicating major negative impact on status and 5 was a high score, indicating either no or a positive impact on status. Scores were assigned according to a rubric which was standardized to each threat category (Table 2). Metrics were designed to capture all significant risk factors faced by freshwater fishes while keeping redundancy among metrics to a minimum. Principal component analysis revealed relatively equal weighting of all seven metrics on the final status scores (eigenvectors for principal component one: area occupied, 0.322; adult population, 0.398; intervention dependence, 0.405: tolerance 0.341: genetic risk 0.406; climate change 0.381: anthropogenic threats 0.382). For each species, the seven criteria were averaged to produce a single score for which the threat of near-term extinc-

**Table 1**
Metrics for determining the status of California fishes, with Sacramento splittail as example. Each metric is scored on a 1–5 scale where 1 is a major negative factor contributing to status, 5 is a factor with no or positive effects on status, and 2–4 are intermediate values. Scoring is described in Table 2.

| Metric | Score | Justification |
|---|---|---|
| Area occupied | 2 | Two distinct populations in San Francisco Estuary, using different rivers for spawning |
| Estimated adult abundance | 4 | Large in upper estuary, likely small in lower |
| Intervention dependence | 3 | Floodplain areas need special management for spawning during droughts |
| Tolerance | 5 | One of the most physiologically tolerant native fishes |
| Genetic risk | 3 | Two populations; genetically fairly diverse |
| Climate change | 1 | Extremely vulnerable to droughts and sea level rise reducing habitat |
| Anthropogenic causes of decline | 2 | Multiple, see Table 3 |
| Average | 2.9 | 20/7 |
| Certainty (1–4) | 3 | Well studied |

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tion increased as the score decreased. The scores were placed in categories following the IUCN categories for imperiled species (Vié et al., 2009). Fishes with scores between 1.0 and 1.9 were rated *endangered* and regarded as being in serious danger of extinction, while those scoring 4.0–5.0 were regarded as *least concern*. Species with scores of 2.0–2.9 were rated *vulnerable* and regarded as likely to become threatened or endangered in the near future, while those scoring between 3.0 and 3.9 were in decline but not yet in immediate danger of extinction and so were rated *near-threatened*. In order to simplify discussion, all species scoring between 1.0 and 3.9, were collectively referred to as "imperiled" because they either had declining populations or had small, isolated populations that increased their risk of extinction. The scores only apply within California, so rare species with wide distributions and high abundance outside the state (e.g., chum and pink salmon) might receive low scores within the state even if there is no danger of extinction as species.

### 2.3. Metrics used to score taxon status

#### 2.3.1. Area occupied

We assumed that extinction threat was lower for species spread over many watersheds than for those with limited distributions. Inland fishes were scored by number and interconnectedness of large watersheds occupied. Anadromous fishes were scored on number of watersheds occupied (i.e., Functionally Independent Populations, Lindley et al., 2004, 2006).

#### 2.3.2. Estimated adult abundance

In general, the more adult individuals in a population, the more likely it is to persist through time. However, quantitative population estimates are rare, especially for non-game fishes (Jelks et al., 2008). We therefore used order-of-magnitude estimates of average annual numbers of mature individuals at the time of the study as a proxy for population size (Table 2). While we recognized

**Table 2**
Scoring rubric for seven metrics used to evaluate status of native freshwater fishes of California. Final status score is the average score of all seven metrics.

*1A. Area occupied: resident fish*
1. 1 watershed/stream system in California only based on watershed designations in Moyle and Marchetti (2006)
2. 2–3 watersheds/stream systems without fluvial connections to each other
3. 3–5 watersheds/stream systems with or without fluvial connections
4. 6–10 watersheds/stream systems
5. More than 10 watersheds/stream systems

1B. Area occupied: anadromous fish
1. 0–1 apparent self-sustaining populations
2. 2–4 apparent self-sustaining populations
3. 5–7 apparent self-sustaining populations
4. 8–10 apparent self-sustaining populations
5. More than 10 apparent self-sustaining populations

*2. Estimated adult abundance*
1. ⩽500
2. 501–5000
3. 5001–50,000
4. 50,001–500,000
5. 500,000+

*3. Dependence on human intervention for persistence*
1. Captive broodstock program or similar extreme measures required to prevent extinction
2. Continuous active management of habitats (e.g., water addition to streams, establishment of refuge populations, or similar measures) required
3. Frequent (usually annual) management actions needed (e.g., management of barriers, special flows, removal of alien species)
4. Long-term habitat protection or improvements (e.g., habitat restoration) needed but no immediate threats need to be dealt with
5. Species has self-sustaining populations that require minimal intervention

*4. Environmental tolerance under natural conditions*
1. Extremely narrow physiological tolerance in all habitats
2. Narrow physiological tolerance to conditions in all existing habitats or broad physiological limits but species may exist at extreme edge of tolerances
3. Moderate physiological tolerance in all existing habitats
4. Broad physiological tolerance under most conditions likely to be encountered
5. Physiological tolerance rarely an issue for persistence

*5. Genetic risks/problems*
1. Genetic viability reduced by fragmentation, genetic drift, and isolation by distance, owing to very low levels of migration, and/or frequent hybridization with related fish
2. As above, but limited gene flow among populations, although hybridization can be a threat
3. Moderately diverse genetically, some gene flow among populations; hybridization risks low but present
4. Genetically diverse but limited gene flow to other populations, often due to recent reductions in connectivity
5. Genetically diverse with gene flow to other populations (good metapopulation structure)

*6. Vulnerability to climate change*
1. Vulnerable to extinction in all watersheds inhabited
2. Vulnerable in most watersheds inhabited (possible refuges present)
3. Vulnerable in portions of watersheds inhabited (e.g., headwaters, lowermost reaches of coastal streams)
4. Low vulnerability due to location, cold water sources and/or active management
5. Not vulnerable, most habitats will remain within tolerance ranges

*7. Anthropogenic causes of decline*
1. 1 or more causes rated critical or 3 or more threats rated high–indicating species could be pushed to extinction by one or more threats in the immediate future (within 10–25 years)
2. 1 or 2 causes rated high; species could be pushed to extinction in the foreseeable future (within 50 years)
3. No causes rated high but 5 or more threats rated medium; no single threat likely to cause extinction but all threats in aggregate could push species to extinction in the next century
4. 1–4 causes rated medium; no immediate extinction risk but taken in aggregate causes reduce population viability
5. 1 medium, all others low; known causes do not imperil the species

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that the effect of adult population size upon persistence differs for large, long-lived species in contrast to small, short lived species (Flather et al., 2011), we rarely found this to be an issue for California fishes.

*2.3.3. Dependence on human intervention for persistence*

This metric scored how dependent a species was on direct human intervention for its continued survival. Thus, Eagle Lake rainbow trout received a score of '1' because it is completely dependent on artificial propagation for its persistence, while rough sculpin (a state listed species) scored a '4', because it needs only continued protection of its spring-fed streams (managed for trout fisheries) to maintain abundance.

*2.3.4. Environmental tolerance under natural conditions*

This metric measures overall physiological tolerance in relation to existing conditions in a species' range. Where possible this was based on results of laboratory or field studies of responses to ranges of temperature, salinity, dissolved oxygen and similar variables. However, if a species had fairly broad physiological tolerances in the laboratory but lived in waters (e.g., streams in southern California) where habitat conditions naturally approached the species limits of tolerance to temperature and other factors, its environmental tolerance was scored lower than that of a species likely to rarely encounter such conditions.

*2.3.5. Genetic risks*

This metric incorporates two concepts, hybridization and genetic bottlenecks. Hybridization with a related species, especially an introduced species, can result in sterility, reduced fitness and swamping of native genomes (Perry et al., 2002). Similarly, interbreeding between artificially propagated (hatchery) and wild individuals can reduce fitness of offspring (Araki et al., 2009).

In order to avoid over-weighting the impact of small population size on status, genetic impacts of small population size were not considered here. However, low genetic variation from hatchery management and/or other past reductions of effective population size may increase extinction threat (e.g., reduce the ability of species to adapt to environmental change) irrespective of current population size and so was included under this metric.

*2.3.6. Vulnerability to climate change*

Climate change is already having effects, as reflected in rising water temperatures and more variable stream flow; such effects are only likely to increase (Hayhoe et al., 2004; Anderson et al., 2008; Cayan et al., 2009). Vulnerability to future climate change was determined by examining geographic range of each species, its isolation (potential for finding refuges), and the types of habitat it inhabits. Species considered to have low vulnerability included those with broad thermal tolerances and those living in aquatic environments shielded (at least for now) from climate-driven change, such as spring-fed systems with constant sources of water (e.g., bigeye marbled sculpin and Saratoga Springs pupfish).

*2.3.7. Anthropogenic causes of decline*

We rated fifteen major categories of landscape-level factors likely to increase extinction risk as having no, low, medium, high or critical effect on species status, based on available information for each species summarized in Moyle (2002), and Moyle et al. (2008) (Table 3). A cause rated "critical" could push the species to extinction in three generations or 10 years which ever is less. A cause rated "high" could push the species to extinction in 10 generations or 11–50 years which ever is less. A cause rated "medium" was unlikely to drive a species to extinction by itself but contributed to increased extinction risk over the next century. A cause rated "low" could reduce populations but extinction was considered unlikely as a result. A cause rated "no" (no effect) has no known negative impact to the taxon under consideration.

For some species, a single threat was considered grave enough to cause extinction (e.g., hybridization for California golden trout), but for most species, number as well as severity of potential causes contributed to our final score (Table 2). We judged any species with even one critical rating as being in danger of extinction in the near future. The 15 causes of decline are summarized below.

*2.4. Anthropogenic causes of decline*

*2.4.1. Large dams*

Dams and their reservoirs had high impacts on status if they blocked access to much of the species range, caused major changes to physical habitat, or changed water quality and quantity. We regarded dams as having a low impact if they were present within the range of the species but their effects were small or beneficial.

*2.4.2. Agriculture*

Effects of agriculture were rated high if agricultural effluent polluted waterways of major importance to the species, if diversions severely reduced flow, if large amounts of silt flowed into streams from farmland, if pesticides had significant effects, and if other agricultural factors directly affected waters in which a species lives. We regarded agriculture as having a low impact if it was not pervasive in the species' range or was not known to be causing significant changes to a species' habitats.

**Table 3**
Ratings of major anthropogenic factors causing declines of freshwater fishes of California, using Sacramento splittail as an example. See text for definitions of ratings of causes.

| Status metric | Rating | Explanation |
|---|---|---|
| Major dams | High | All waters have flows regulated by dams and diversions; frequency of flooding of spawning areas reduced |
| Agriculture | Medium | Pollution, channel modification, entrainment in major diversions |
| Grazing | Low | Little known impact but occurs in spawning areas |
| Rural residential | Low | Residences on the edges of rearing marshes |
| Urbanization | Medium | Most habitat is on urban fringes; sewage; water diversion and entrainment |
| Instream mining | Low | Some gravel mining in floodplain areas |
| Mining | Low | Legacy effects of gold mining, e.g. mercury |
| Transportation | Medium | Migratory corridors lined with roads and railroads, |
| Logging | No | No known impact |
| Fire | Low | Indirect impacts from marsh/floodplain fires possible |
| Estuarine alteration | High | Major habitat areas highly altered |
| Recreation | Low | Recreational boating etc. may affect habitat |
| Harvest | Medium | Some harvest for bait and of migrating adults for food |
| Hatcheries | No | No known impact |
| Alien species | Medium | Effects of new invaders unpredictable; predation and competition possible |

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*2.4.3. Grazing*

We separated livestock grazing from other agriculture because its effects are widespread on range and forest lands throughout California. Impacts were rated high where stream banks were trampled and riparian vegetation was removed, resulting in incised streams, drying of adjacent wetlands, and lowering of water tables. Removal of vegetation can also result in increased siltation, higher water temperatures, and decreased summer flows. Impacts were rated low where grazing was present but had minimal negative effects.

*2.4.4. Rural residential*

As California's human population grows, people spread across the landscape, often settling in diffuse patterns along or near streams. Rural development results in water removal, streambed alteration (to protect houses, create swimming holes, construct road crossings, etc.), and pollution (especially from septic systems). We rated such housing as having high effect on fishes where it was abundant and unregulated and caused major changes to streams. Where such housing was present but scattered, the effects were usually rated as low.

*2.4.5. Urbanization*

Streams that flow mostly through cities are generally highly altered to reduce flooding and remove water, while pollution is pervasive, from sewage, runoff, and storm drain discharges. Generally, the more the important waters for a species were encompassed by urban development, the higher we rated the effects of urbanization on the species.

*2.4.6. Instream mining*

The most severe instream mining in California took place during the 19th and early 20th centuries when miners buried (through hydraulic mining), excavated, and dredged riverbeds for gold. We often gave the legacy effects on fishes of mining medium or high ratings. Similar scores were given to species affected by legacy effects of instream gravel mining, which creates large pits in streambeds and alters stream banks. Such mining is largely banned (in favor of mining off-channel areas) today. Impacts of contemporary recreational and professional suction dredge mining resulted in some intermediate ratings.

*2.4.7. Mining*

The effects of hard-rock mining (mostly for gold and mercury) were rated according to how much of a species' habitat was affected by tailings and acidic mine drainage. We gave high ratings where major mines, even if abandoned, had toxic tailings poised on edges of waterways (e.g., Iron Mountain Mine near Redding, on the Sacramento River). Our low threat scores usually came from situations where old mines were present but effects on biota of nearby streams were not evident.

*2.4.8. Transportation*

Many rivers and creeks have roads and railroads running along one or both sides, confining stream channels and causing pollution from siltation, vehicle emissions, waste disposal, and accidents. In addition, culverts and other hydrologic modifications associated with transportation often restrict fish movements. Our ratings here were based on how much a species depended on streams altered by roads and railways and how severe the alterations were.

*2.4.9. Logging*

Timber harvest is a major use of forested California watersheds which support many native fishes, including anadromous salmonids. Logging was relatively unregulated until mid-20th century, resulting in major alteration and degradation of stream habitats. Although better regulated today, logging is still a pervasive activity resulting in siltation of streams and reduced habitat complexity. We gave high threat ratings to species dependent on streams degraded by either legacy or contemporary effects of logging. Low threat ratings were given where such effects are of small significance.

*2.4.10. Fire*

Wildfires are part of California's natural landscape but human activities have increased their intensity and frequency. High ratings were given where fish habitat was, or has the potential to be, seriously degraded by catastrophic wildfire, via post-fire erosion, loss of riparian canopy, increased temperature and spilled fire-fighting chemicals. We assigned low ratings to fishes that live in areas where wildfires occur but for various reasons, such as low fuel load, have minimal impact on streams.

*2.4.11. Estuary alteration*

Many California fishes depend on estuaries for at least part of their life cycle. All California estuaries are highly altered by human activity, including siltation, pollution, diking and draining, bridge construction, and removal of sandbars between the estuary and ocean. Thus, the more estuarine-dependent a fish species is, the more likely we were to assign a high rating to estuary alteration as a cause of decline.

*2.4.12. Recreation*

Recreational use of streams has greatly increased with the human population. We found recreational effects usually to be low, although they were often concentrated when stream flows were low. We rated recreation effects as high when a taxon depended on streams that are heavily disturbed (e.g., by off-road vehicles) or contains enough boaters and swimmers to disturb spawning or holding (e.g., salmon and steelhead).

*2.4.13. Harvest*

We rated harvest effects as high for fishes known to be subject to overharvest, especially large species (e.g., sturgeons) or species that become isolated and are therefore vulnerable to poaching (e.g., summer steelhead). We rated both legal and illegal harvest, although for most native resident fishes, legal fishing was rarely an issue.

*2.4.14. Hatcheries*

Most fishes are not supported by fish hatcheries but for those that are, hatchery fish often have negative effects on wild populations through competition for habitat and food, direct predation, and interbreeding which results in loss of genetic diversity (Moyle, 2002). We rated severity of these effects based in part on hatchery dependence and/or known interbreeding between wild and hatchery populations. We regarded conservation hatcheries that focus on rare species as having relatively low impacts because of their efforts to reduce negative hatchery effects as much as possible.

*2.4.15. Alien species*

Non-native species are present in every California watershed and their impacts on native species through hybridization, predation, competition, and disease are often severe (Moyle and Marchetti, 2006). We rated this category as high for a species if there were major direct or indirect impacts of alien invaders. We rated it as low if contact with alien species was infrequent or not known to be negative.

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### 2.5. Certainty index

Because quality, amount and reliability of information varied among species, we developed a certainty index for our scores, on a 1–4 scale, where we scored status evaluations as follows:

1. Based on expert opinion (including our own) with little hard data.
2. Based on expert opinion supplemented with limited data and reports.
3. Based on extensive information found mainly in agency reports.
4. Based on reports from multiple sources including peer-reviewed literature.

This index lets managers know the risks involved in basing management decisions on our results.

## 3. Results

Of 129 freshwater fishes native to California, four are globally extinct (3%) and three (2%) are extirpated from the state (scores of 0). Another 33 (26%) are in danger of extinction in the near future if present trends continue (endangered, scores of 1.0–1.9) while 33 (26%) are sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable, scores of 2.0–2.9). Thirty-four (26%) are in long-term decline or have small isolated populations but do not face extinction in the foreseeable future, unless conditions change (near-threatened, scores of 3.0–3.9). The remaining 22 species (17%) are of least concern (4.0–5.0) (Fig. 1). The average status score of all extant taxa was 2.7. The certainty ratings of our status evaluations averaged 2.7 out of 4.0 (SD 1.2), with 66% of accounts based on extensive literature (4.0) and only 5% based mainly on our professional judgment (1.0).

Of the 31 species currently listed as Endangered or Threatened under federal and/or state endangered species acts, 17 had status scores of 1.0–1.9 and 12 had scores of 2.0–2.9 by our rating system (Appendix Table 1). Listed species made up half of the 33 species to which we gave status scores of 1.0–1.9 and 44% of extant species with scores <2.9. The number of listed species increased from 14 in 1989 to 18 in 1990 to 31 in 2010, a listing rate of about 0.8 species per year (Fig. 2). The total number of imperiled species increased from 55 to 100 in this same period (2.1 species per year) (Fig. 2). While the increase was partly the result of 14 taxa being added to the fauna, most of the increase reflects real declines in species status. Previous status determinations (Moyle and Williams, 1990; Moyle et al., 1995) were made without benefit of our systematic approach and were constrained by prior agency designations. However, because the senior author was in charge of all three assessments, the evaluations are fairly consistent.

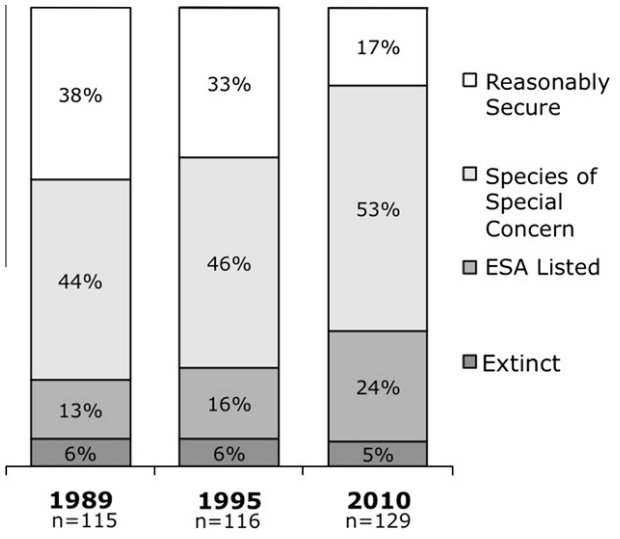


**Fig. 2.** Status of the native fishes of California from three surveys over 21 years, as shown by percentages of known species in conservation categories used by the state of California. Listed species are those listed under the state and federal endangered species acts as either Threatened or Endangered. Special Concern species are those in decline or in small isolated populations that are likely to be eligible for listing in the near future. For 2010, some Special Concern status determinations have not yet been officially recognized.

**Table 4**
Percentages of 122 extant California freshwater fishes assigned ratings of severity for 15 causes of fish declines. A cause rated 'critical' had the most severely negative effect on a species. See text for descriptions of causes and for definitions of critical, high, medium, and low rating levels.

| Cause | Critical | High | Medium | Low | No effect |
|---|---|---|---|---|---|
| *Percent of fish taxa with rating* | | | | | |
| Major dams | 3 | 21 | 32 | 27 | 17 |
| Agriculture | 1 | 17 | 50 | 25 | 7 |
| Grazing | 0 | 9 | 48 | 41 | 2 |
| Rural residential | 2 | 1 | 28 | 65 | 5 |
| Urbanization | 0 | 9 | 30 | 39 | 22 |
| Instream mining | 0 | 3 | 28 | 44 | 5 |
| Mining | 0 | 3 | 8 | 84 | 6 |
| Transportation | 0 | 4 | 46 | 48 | 3 |
| Logging | 2 | 4 | 27 | 55 | 12 |
| Fire | 0 | 4 | 42 | 50 | 4 |
| Estuary alteration | 2 | 10 | 22 | 7 | 61 |
| Recreation | 0 | 2 | 16 | 77 | 6 |
| Harvest | 1 | 8 | 13 | 29 | 49 |
| Hatcheries | 3 | 11 | 7 | 14 | 66 |
| Alien species | 11 | 23 | 35 | 30 | 1 |

In this status review, the metrics contributing most often to overall status scores of 1.0–2.9 were climate change (62% of species with such scores), anthropogenic threats (56%) and area occupied (55%). In contrast, fishes with scores of 4.0 and above had large populations, wide distributions, and high tolerance of environmental change. The anthropogenic threats that led to the most species with "critical" or "high" ratings were alien species (34%), dams (24%) and agriculture (18%) (Table 4). Twenty-five species (19%) had at least one "critical" rating, indicating high likelihood of extinction in the near future, while 63 species (49%) received at least one "high" rating. The largest number of "high" ratings awarded to a single species was six. All species had different combinations of causes of decline by kind and severity.

## 4. Discussion

### 4.1. What is the status of California's freshwater fish fauna?

In 1989, only 14 species were formally ESA listed as Threatened or Endangered (Moyle and Williams, 1990). Today, 31 species are formally listed and about one additional species is being listed every two years, despite a general slow-down in the listing process (Greenwald et al., 2006). In addition, seven species have gone extinct in the past 50 years. Clearly, the native fish fauna of California is in serious decline by official standards. However, our analysis indicates that the decline is more severe than recognized, with 107 (83%) of the native fishes prone to extinction. The major cause of decline is a growing human population that enjoys living in a mild Mediterranean climate where water is in short supply, especially in the dry summer season or during periods of drought. This shortage results in most waterways being dammed, diverted, polluted, or otherwise altered, with the additional threat of frequent invasions of alien fishes (Moyle, 2002; Moyle and Marchetti,

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2006). The highly endemic fishes of the region are vulnerable to change because many are confined to limited geographic areas or to habitats where conditions are naturally stressful. However, even many wide-ranging species (e.g., all salmon species and steelhead rainbow trout) are imperiled (Moyle, 2002; Moyle et al., 2008). Native species that have managed to thrive under altered conditions are those that have naturally large ranges, broad habitat requirements, high tolerance of adverse conditions, and an ability to become part of new fish assemblages that include alien species (e.g., Tahoe sucker, Sacramento pikeminnow).

### 4.2. Are the fishes continuing to decline?

Today, 83% of California's freshwater fishes are imperiled or extinct, a 16% increase since the last assessment in 1995 and a 21% increase since 1989. The increase is partly the result of improved information, but declines of most species are also real, as illustrated below by coho salmon, Central Valley fall Chinook salmon, delta smelt, Clear Lake hitch, and Sacramento perch.

*Coho salmon* (Salmonidae) are native to hundreds of coastal streams from Monterey Bay north to the Oregon border and once supported sport and commercial fisheries (Moyle, 2002). In the 1940s, estimated numbers of adults spawning in California streams were 200,000–400,000 (Moyle et al., 2008). They were regarded by Moyle and Williams (1990) as being in sharp decline but still common. Subsequent studies documented their rapid disappearance from their native streams throughout the state and by 1996 the two Evolutionary Significant Units (ESUs) of coho salmon present in California had been listed as federal Threatened or Endangered species. Our analysis scored status of the Central Coast ESU as 1.1 and the Southern Oregon Northern California Coast ESU as 1.7. The 2010 federal ESA recovery plan for California coho salmon is consequently regarded as more an extinction prevention plan than a real plan for recovery (NMFS, 2010).

*Central Valley fall Chinook salmon* ESU once historically made up the largest run of salmon in the Sacramento and San Joaquin River basins, with runs once estimated to be around a million fish annually; adult populations through most of the 20th century were 200,000–400,000 fish. Moyle and Williams (1990) considered it to be abundant and perhaps even increasing in abundance. However, its status score here is 2.0, because of a recent precipitous population crash (Moyle et al., 2008) which is apparently the indirect result of the population being almost entirely composed of fish of hatchery origin (Barnett-Johnson et al., 2007).

*Delta smelt* (Osmeridae) are endemic to the San Francisco Estuary and require fresh water for spawning (Moyle, 2002). In the 1970s, they were still one of the most abundant fish in the upper estuary but declined rapidly so that Moyle and Williams (1990) indicated they merited listing as a threatened species. They were listed as Threatened by both state and federal governments in 1993. Nevertheless, their decline has continued as the result of major environmental changes to the upper estuary related to increasing water exports and other factors (Bennett, 2005), despite major efforts to curtail mortalities in recent years. With a 1-year life cycle, they may be on verge of extinction and accordingly were given a score of 1.4.

*Clear Lake hitch* (Cyprinidae) is endemic to Clear Lake, a large natural lake in the Coast Range of California (Moyle, 2002). Although the lake has been highly altered for human use and has been heavily invaded by alien species, hitch are one of the few native species that have persisted; Moyle and Williams (1990) found them to be abundant but possibly declining. However, dramatic reduction in numbers of individuals in spawning streams, presumably related to the expanding population of piscivorous Florida largemouth bass (*Micropterus floridae*) in the lake as well as continued environmental degradation, resulted in a status score of 1.9.

*Sacramento perch* (Centrarchidae) were once one of the most abundant fish in the Central Valley and subject to commercial fisheries in the 19th century (Moyle, 2002). Today they are extirpated from their native range largely from competition and predation by introduced centrarchids (Crain and Moyle, 2011). They have persisted only because they have been introduced into scattered reservoirs and lakes in other parts of California and the western USA. However, many introduced populations are now gone and most others are located in waters that are not secure (Crain and Moyle, 2011). Moyle and Williams (1990) indicated concern about its decline but thought it did not merit listing as a threatened species. Because so many populations have disappeared or declined since then, it scored 1.6 in our evaluation.

### 4.3. What factors are most strongly associated with conservation status?

The causes of the declines have their roots in the 19th and early 20th centuries when unrestricted mining, logging, and wetland conversion, combined with wide-scale dam building, severely altered most rivers, lakes, and estuaries. In addition, approximately 50 species of alien fishes were successfully introduced, many of them better suited to altered environments than native species (Moyle and Marchetti, 2006). Nevertheless, each native species has its own idiosyncratic response to this changing environment, as a result of its natural characteristics interacting with changes occurring in its particular habitats. Our analyses showed that each imperiled species has its own combination of causes of decline but most common were factors reflecting large-scale landscape changes (dams, agriculture, logging, urbanization, Table 4). An issue common to all species is climate change, which was often an important factor affecting our final status score for each species. Increases in water temperatures and variability in stream flows are becoming an increasingly important limiting factor for most species, but especially those relying on streams with perennial flows of cool (<20–22 °C) water. Thus a systematic conservation approach has to deal both with broad issues and those particular to each species.

### 4.4. How do our results fit with official status designations?

Of the 31 California fish species listed under the ESA, 94% fell into our two most at-risk status categories, indicating that our scoring system approximates the criteria used in official ESA listing determinations. However, only 51% of 33 species that we rated as endangered (scores <2.0) were officially listed under the ESA, indicating that official protection is not keeping pace with the rapid decline of California's inland fishes. That ESA designations are not concordant with current status is also born out by the fact that 12 (36%) of the 33 species we rated as vulnerable (scores of 2.0–2.9) and two (6%) of the species we rated as near-threatened (scores of 3.0–3.9) were listed as threatened or endangered under the ESA. The reasons for the discrepancies between our ratings and official status are complex but largely stem from better information being available now than at the time of listing. For example, the rough sculpin (score of 3.4) was one of the first fishes listed under state law, when little was known about its distribution and biology. Subsequent studies have indicated it is fairly widespread in spring streams of the Pit River watershed and is even expanding its range in reservoirs (Moyle, 2002). However, recent genetic studies suggest rough sculpin is actually two disjunct populations (A. Kinziger, pers. comm. 2010), perhaps species, which might qualify for listing if treated independently.

Rating the quality (certainty) of the information on which each species status score was based enables managers to determine which species need more study. Most of our species status

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determinations are based on strong published evidence. However, species with low certainty scores should be re-evaluated for status frequently.

## 5. Conclusions

The native inland fish fauna of California is in rapid decline and many species are likely to disappear from the state within the next century if present trends continue. Unfortunately, global climate change and human population growth are likely to increase fish extinction rates as competition with humans for increasingly scarce water intensifies, stream flows become more variable, and water quality, especially temperature, changes. For coldwater fishes, thermal refuges may disappear from streams in many areas, leaving no place to escape unfavorable conditions. The patterns of decline we see in California have been documented in freshwater fishes in other arid climates (Moyle and Leidy, 1992; Aparicio et al., 2000; Maceda-Veiga et al., 2010). However, the decline of California's inland fishes is likely characteristic of freshwater fishes and their ecosystems worldwide. As better information and similar systematic approaches are employed in other regions, we predict more imminent extinctions will be detected than are presently appreciated. Given trends of rapid decline that we have documented it is likely that many species will be lost before effective conservation plans can be implemented. There is, therefore, no time to be lost in designing and implementing conservation efforts for freshwater species in California and worldwide.

## Acknowledgements

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## Appendix

Table 1. List of all native fishes known to breed in the inland waters of California, ranked by level of extinction threat. Asterisks denotes taxon listed by federal or state Endangered Species Acts. Extinct= globally extinct or extirpated from the inland waters of California. Status scores of 1.0-1.9 are roughly equivalent to IUCN threat level of *endangered* or *critically endangered*; 2.0-2.9, IUCN threat level of *vulnerable*; 3.0-3.9, IUCN threat level of *Near Threatened;* 4.0-5.0, IUCN threat level of *Least Concern*.

| Species | Status Score |
|---|---|
| Thicktail chub, Siphatales crassicauda | Extinct |
| High Rock Springs tui chub, *S. b. subsp.* | Extinct |
| Bonytail, *Gila elegans* | Extinct |
| Clear Lake splittail, *P. ciscoides* | Extinct |
| Colorado pikeminnow, *P. lucius* | Extinct |
| Bull trout, *Salvelinus confluentus* | Extinct |
| Tecopa pupfish, *C. n. calidae* | Extinct |

**Appendix** (*continued*)

| Species | Status Score |
|---|---|
| Long Valley speckled dace, *R. o. subsp.* | 1.0 |
| Central coast coho salmon, *O. kisutch* | 1.1* |
| Shoshone pupfish, *C. n. shoshone* | 1.1 |
| Razorback sucker, *Xyrauchen texanus* | 1.3* |
| Pink salmon, *O. gorbuscha* | 1.3 |
| Shay Creek stickleback, *G. a. subsp.* | 1.3 |
| Owens tui chub, *S. b. snyderi* | 1.4* |
| Mojave tui chub, *S. mohavensis* | 1.4* |
| Delta smelt, *Hypomesus pacificus* | 1.4* |
| Owens pupfish, *C. radiosus* | 1.4* |
| Southern green sturgeon, *A. medirostris* | 1.6* |
| Amargosa Canyon speckled dace, *R. o. nevadensis* | 1.6 |
| Santa Ana speckled dace, *R. o. subsp.* | 1.6 |
| Modoc sucker, *Catostomus microps* | 1.6* |
| Flannelmouth sucker, *C. latipinnis* | 1.6 |
| Eulachon, *Thaleichthys pacificus* | 1.6* |
| Upper Klamath-Trinity spring Chinook salmon, *O. tshawytscha* | 1.6 |
| Southern Oregon Northern California coast coho salmon, *O. kisutch* | 1.6* |
| Chum salmon, *O. keta* | 1.6 |
| Sacramento perch, *Archoplites interruptus* | 1.6 |
| Lost River sucker, *C. luxatus* | 1.7* |
| Santa Ana sucker, *C. santaanae* | 1.7* |
| Central Valley late fall Chinook salmon, *O. tshawytscha* | 1.7 |
| Klamath Mountains Province summer steelhead, *O. mykiss* | 1.7 |
| Southern California steelhead, *O. mykiss* | 1.7* |
| Paiute cutthroat trout, *O. c. seleneris* | 1.7* |
| Clear Lake hitch, *L. e. chi* | 1.9 |
| Owens speckled dace, *R. o. subsp.* | 1.9 |
| Northern California coast summer steelhead, *O. mykiss* | 1.9* |
| McCloud River redband trout, *O. m. stonei* | 1.9 |
| Kern River rainbow trout, *O. m. gilberti* | 1.9 |
| Desert pupfish, *Cyprinodon macularius* | 1.9* |
| Unarmored threespine stickleback, *G. a. williamsoni* | 1.9* |
| Kern brook lamprey, *L. hubbsi* | 2.0 |
| White sturgeon, *A. transmontanus* | 2.0 |
| Red Hills roach, *L. s. subsp.* | 2.0 |
| Klamath largescale sucker, *C. snyderi* | 2.0 |
| Shortnose sucker, *Chasmistes brevirostris* | 2.0* |
| Longfin smelt, *Spirinchus thaleichthys* | 2.0* |
| Central Valley winter Chinook salmon, *O. tshawytscha* | 2.0* |
| Central Valley spring Chinook salmon, *O. tshawytscha* | 2.0* |
| Central Valley fall Chinook salmon, *O. tshawytscha* | 2.0 |
| California golden trout, *O. m. aguabonita* | 2.0 |
| Little Kern golden trout, *O. m. whitei* | 2.0* |
| Eagle Lake rainbow trout, *O. m. aquilarum* | 2.1 |
| Lahontan cutthroat trout, *O. c. henshawi* | 2.1* |
| Cow Head tui chub, *S. t. vaccaceps* | 2.1 |
| Goose Lake sucker, *C. o. lacusanserinus* | 2.1 |
| Saratoga Springs pupfish, *C. n. nevadensis* | 2.1 |
| Arroyo chub, *Gila orcutti* | 2.3 |
| Amargosa River pupfish, *C. n. amargosae* | 2.3 |
| Lahontan Lake tui chub, *S. b. pectinifer* | 2.4 |

(*continued on next page*)

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**Appendix** (*continued*)

| Species | Status Score |
|---|---|
| Cottonball Marsh pupfish, *C. s. milleri* | 2.4* |
| Northern green sturgeon, *Acipenser medirostris* | 2.4 |
| Upper Klamath-Trinity fall Chinook salmon, *O. tshawytscha* | 2.4 |
| California Coast fall Chinook salmon, *O. tshawytscha* | 2.4* |
| Central Valley steelhead, *O. mykiss* | 2.4* |
| South Central California coast steelhead, *O. mykiss* | 2.4* |
| Salt Creek pupfish, *C. s. salinus* | 2.6 |
| Goose Lake lamprey, *Entosphenus sp.* | 2.6 |
| Monterey hitch, *L. e. harengeus* | 2.7 |
| Central California coast winter steelhead, *O. mykiss* | 2.7* |
| Bigeye marbled sculpin, *C. klamathensis macrops* | 2.7 |
| Sacramento splittail, *Pogonichthys macrolepidotus* | 2.9 |
| Tidewater goby, *Eucyclogobius newberryi* | 2.9* |
| Northern Roach, *L. mitrulus* | 2.9 |
| Russian River roach, *L. s. subsp* | 3.0 |
| Navarro Roach, *L. s. navarroensis* | 3.0 |
| Gualala roach, *L. parvipinnus* | 3.0 |
| Tomales Roach, *L. s. subspecies* | 3.0 |
| Upper Klamath marbled sculpin, *C. k. klamathensis* | 3.0 |
| Clear Lake tule perch, *H. t. lagunae* | 3.0 |
| Western brook lamprey, *L. richardsoni* | 3.1 |
| Clear Lake roach, *L s. subsp.* | 3.1 |
| Clear Lake prickly sculpin, *C. a. subsp.* | 3.1 |
| Russian River tule perch, *H. t. pomo* | 3.1 |
| Eagle Lake tui chub, *S. b. subsp.* | 3.3 |
| Sacramento hitch, *Lavinia e. exilicauda* | 3.3 |
| Monterey roach, *L. s. subditus* | 3.3 |
| Mountain sucker, *C. platyrhynchus* | 3.3 |
| Northern California coast winter steelhead, *O. mykiss* | 3.3 |
| Goose Lake redband trout, *O. m. subsp.* | 3.3 |
| Lower Klamath marbled sculpin, *C.k. polyporus* | 3.3 |
| Blue chub, Gila coerulea | 3.4 |
| Central California roach, *L. s. symmetricus* | 3.4 |
| Pacific lamprey, *Entosphenus tridentata* | 3.4 |
| Goose Lake tui chub, *S. t. thalassinus* | 3.4 |
| Hardhead, *Mylopharodon conocephalus* | 3.4 |
| Coastal cutthroat trout, *O. clarki clarki* | 3.4 |
| Rough sculpin, *Cottus asperrimus* | 3.4* |
| Riffle sculpin, *C. gulosus* | 3.4 |
| Sacramento tule perch, *Hysterocarpus t. traski* | 3.4 |
| River lamprey, *Lampetra ayersi* | 3.6 |
| Pit-Klamath brook lamprey, *L. lethophaga* | 3.6 |
| Southern Oregon Northern California coast fall Chinook salmon, *O. tshawytscha* | 3.7 |
| Klamath River lamprey, *E. similis* | 3.9 |
| Reticulate sculpin, *C. perplexus* | 3.9 |
| Owens sucker, *C. fumeiventris* | 3.9 |
| Mountain whitefish, *Prosopium williamsoni* | 3.9 |
| Klamath Mountains Province winter steelhead, *O. mykiss* | 3.9 |
| Pit River tui chub, *S. thalassinus subsp.* | 4.0 |
| Klamath tui chub, *S. b. bicolor* | 4.1 |
| Sacramento speckled dace, *Rhinichthys osculus subp.* | 4.1 |
| Monterey sucker, *C. o. mnioltiltus* | 4.1 |
| Klamath smallscale sucker, *C. rimiculus* | 4.1 |
| California killifish, *Fundulus parvipinnis* | 4.1 |

**Appendix** (*continued*)

| Species | Status Score |
|---|---|
| Inland threespine stickleback, *G. a. microcephalus* | 4.1 |
| Humboldt sucker, *C. o. humboldtianus* | 4.3 |
| Pit sculpin, *C. pitensis* | 4.3 |
| Coastrange sculpin, *C. aleuticus* | 4.4 |
| Sacramento blackfish, *Orthodon microlepidotus* | 4.4 |
| Paiute sculpin, *C. beldingi* | 4.4 |
| Coastal threespine stickleback, *Gasterosteus a. aculeatus* | 4.6 |
| Lahontan stream tui chub, *S. b. obesus* | 4.7 |
| Sacramento pikeminow, *Ptychocheilus grandis* | 4.7 |
| Coastal rainbow trout, *O. m. irideus* | 4.7 |
| Coastal Prickly sculpin, *C. asper subsp.* | 4.7 |
| Lahontan redside, *Richardsonius egregius* | 4.8 |
| Lahontan speckled dace, *R. o. robustus* | 4.8 |
| Klamath speckled dace, *R. o. klamathensis* | 4.8 |
| Tahoe sucker, *Catostomus tahoensis* | 5.0 |
| Sacramento sucker, *C. o. occidentalis* | 5.0 |

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# Geometry of Forest Landscape Connectivity: Pathways for Persistence

Deanna H. Olson and Kelly M. Burnett

## Abstract

Streamside areas may be dispersal funnels or runways for a variety of species. For over-ridge dispersal, headwaters offer the shortest distance links among riparian zones in adjacent drainages. We summarize landscape designs for connectivity of habitats using headwater riparian linkage areas as the foundation for a web of landscape-scale links. We developed management considerations for placement of headwater linkage areas including: 1) providing connections between larger basins; 2) maintaining habitat connectivity in the face of climate change; 3) incorporating place-based disturbance regimes such as headwater debris-flow-prone areas; 4) targeting connectivity areas to address sensitive species conservation strongholds; and 5) accounting for geometry at the forest-stand scale of a single project or proposed timber sale, including managing habitats to connect lands on adjacent federal ownerships, by means of connecting corners of checkerboard landscape blocks along diagonals. Although our proposed linkage areas are designed to target headwater species, the resulting web of connections across the landscape is expected to benefit many forest-dependent species.

**Keywords:** watersheds, forest, headwaters, biodiversity, linkage areas, dispersal.

## Introduction

Biodiversity retention and restoration is an emerging priority for global ecosystems. Astounding losses within major taxonomic groups have been reported nationally and internationally (41 percent of amphibians, 25 percent of mammals, 15 percent of bony fishes, 13 percent of birds: Hoffmann et al. 2010; 50–60 percent of turtles: Kiester and Olson 2011). In particular, protection and restoration of forests and forest biodiversity has become a paramount concern worldwide (e.g., Convention on Biological Diversity: *www.cbd.int/forest/*). A toolbox of management approaches has been developed to conserve forest biodiversity, largely through a mixture of fine- and coarse-grained habitat protections (e.g., United States Northwest Forest Plan: USDA and USDI 1993, 1994; Cissel et al. 1998; Lindenmayer and Franklin 2002; Raphael and Molina 2007; Lindenmayer et al. 2007) and site-specific designs to maintain or restore forest structural heterogeneity (McComb 2001; Lindenmayer and Franklin 2002; Brockerhoff et al. 2008).

Development of landscape designs to manage habitat connectivity for multiple species is an especially active research topic in forest biodiversity conservation, due to continuing trends of forest fragmentation and to an upswing

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in world reforestation efforts. Managing forested landscapes for connectivity functions benefiting biodiversity requires incorporating several fundamental conservation concepts. These basic conservation tenets include identifying the critical habitats used throughout species' life histories (breeding, foraging, overwintering, and dispersal habitats), and commensurate habitat protections to ensure that these biotic functions are retained. If an organism uses different habitats through its life cycle, then maintaining connectivity among these habitats is essential to ensure its persistence. Of particular relevance is the characterization and retention or restoration of dispersal habitat. This includes the home ranges of individuals and the broader dispersal of offspring or individuals that tie sub-populations and populations together over larger areas. This broader-scale dispersal function maintains genetic variation within natural populations, which may foster resiliency needed to adapt to changing environmental conditions. The future of species may rely on our careful attention to managing for connectivity now.

Defining the adequacy of dispersal habitat in forests is a complex topic (Noss et al. 1997) and may address a variety of elements, including habitat condition, corridor sizes (length, width), and corridor redundancy (Pinto and Keitt 2008). Redundancy is especially relevant because multiple connectivity pathways can assist dispersal across landscapes by organisms in different locations and increase the probability of movement in the face of many interacting site-specific factors (microsite features, disturbances). Redundancy of habitat connectivity hedges against catastrophe, uncertainty, and stochastic processes that can affect individuals and sub-populations that vary in their movement propensities, possibly related to patch size, habitat quality, and population demography.

Low-mobility species may merit special attention devoted to the placement and redundancy of connectivity corridors, because barriers to dispersal may arise as a result of their basic biology and ecology (Raphael and Molina 2007). These species may move slowly and require refugia along corridors because it may take them years to move between optimum habitat patches. Due to a potentially longer residency time within connectivity corridors, low-mobility species may be particularly vulnerable to sub-optimal corridor conditions and stochastic processes. Hence, redundancy of connections may be critically important to increase their likelihood of successful movement across landscapes for such low-mobility species. Patches of higher-quality habitat within dispersal corridors may be used as stepping stones for such species and may be an essential aspect of their long-term persistence (e.g., Grant et al. 2010). Such stepping stones may function as habitat refugia or "stopover reserves" (Dobson et al. 1999), which promote survival of individual organisms as they move through the environment. Stepping stones may have more suitable physical habitat conditions than the surrounding area, or may allow individuals to forage to replenish energy reserves or survive harsh seasons (summer, winter) in localized refugia, from which they may disperse again later.

Herein, we synthesize our ongoing studies of the utility of headwater riparian areas as proposed connectivity corridors, or linkage areas, for dispersal of riparian-associated and low-mobility species in Pacific Northwest forests. Once designed, such headwater linkage areas may benefit many taxa. Our studies also conceptually integrate aquatic network and upland-forest habitats, functions, and processes. The combination of protections for aquatic and upland systems is providing new insights into forest ecosystem management approaches. We summarize the key considerations for the geometric orientation of connectivity pathways to assist migration of species across watersheds and across webs of connections, to maintain linked aquatic-terrestrial populations at landscape scales. Our goal here is to provide

a summary of these conceptual designs, while research continues to address these issues and advance design effectiveness.

## Utility of Watersheds as Redundant Landscape-scale Linkage Units

Watersheds are widely accepted units for monitoring and evaluating the effects of land use on aquatic resources (Omernik and Bailey 1997). Where their boundaries can be clearly mapped, watersheds are increasingly common units for forest management planning and conservation designs. For example, in the U.S., the Aquatic Conservation Objectives of the federal Northwest Forest Plan (USDA and USDI 1994: p. B-11), address connectivity among watersheds:

> *"Maintain and restore spatial and temporal connectivity within and between watersheds. Lateral, longitudinal, and drainage network connections include floodplains, wetlands, upslope areas, headwater tributaries, and intact refugia. These network connections must provide chemically and physically unobstructed routes to areas critical for fulfilling life history requirements of aquatic and riparian-dependent species."*

Hydrologic units (HUs), delineated by the U.S. Geological Survey (Seaber et al. 1987), are also a convenient and widely used basis for forest assessment and planning (e.g., Maxwell et al. 1995; Suring et al. 2011). The HU coding describes a hierarchical system of units nested by drainage area; larger code numbers designate smaller drainage areas. Watersheds or segments of watersheds comprise HUs. Even though the majority of HUs at each level of the hierarchy are not true topographic watersheds, such a perspective can aid biodiversity conservation designs, especially as smaller headwater basins are delineated and used for replicating protected areas (e.g., 6t$^{h}$-code HUs: Suzuki et al. 2008) and creation of redundant connections across landscapes (via 6$^{th}$- and 7$^{th}$-code HUs: Olson and Burnett 2009).

The value of using headwater basins as the premise for establishing connectivity corridors across forested landscapes is due to their habitat conditions, potential use by a variety of organisms, frequency of occurrence on the landscape, and minimization of dispersal distances (fig. 1). Olson et al. (2007) summarized some of the merits of headwater riparian habitats for species in the northwest, including providing cool, moist microclimates for interior-forest dependent organisms and aquatic-riparian associated species such as amphibians. Some taxa may use these areas due to their habitat suitability; others may respond to streams as movement barriers, and then move along banks parallel to such barriers. Streamside areas may be dispersal funnels or runways for a variety of species. For example, we have seen terrestrial salamanders (species that do not use stream or pond habitats for breeding or other life-history functions) moving predominantly through near-stream areas (D. Olson and M. Kluber, unpubl. data). Additional taxa that use riparian corridors in northwestern forests include a variety of lichens, bryophytes, fungi, vascular plants, mollusks, mammals (e.g., ground-dwelling mammals: Wilk et al. 2010), birds, and general forest-obligates that may occur in legacy forest attributes such as wolf trees along riparian buffer zones. As a minimum estimate across taxonomic groups, over 100 species were identified as likely to benefit by habitat protections of combined intermittent and perennial streams provided by riparian reserves in federal forest lands in the range of the Northern Spotted Owl (*Strix occidentalis caurina*) (table 1) (USDA and USDI 1997). Species with restricted dispersal abilities were identified for special consideration relative to utility of riparian reserves during watershed analyses under the Northwest Forest Plan (USDA and USDI 1997).

Furthermore, the high density of small streams in upland northwest forests has been widely recognized over the last 20 years, as our basic

**Table 1—**Species benefitting from interim riparian reserves developed for the federal Northwest Forest Plan (from table B1 in USDA and USDI 1997). Riparian reserve protection includes a one site-potential tree-height or 30.5 m (100 ft) buffer, whichever is greater, as an interim measure along all intermittent streams, and a two site-potential tree-height buffer as an interim measure along perennial streams (see USDA and USDI 1993, page III-9).

| Taxonomic group | Species |
|---|---|
| **Bryophytes** | *Antitrichia curtipendula, Douinia ovata, Kurzia makinoana, Scouleria marginata, Tritomaria exectiformis* |
| **Fungi** | |
| Rare chanterelles | *Polyozellous multiplex* |
| Rare gilled mushrooms | *Clitocybesubditopoda, C. senilis, Neolentinus adherens, Rhodocybe nitida, Rhodocybe speciosa, Tricholomposis fulvenscens* |
| Rare cup fungi | *Helvella compressa, H. crassitunicata, H. elastica, H. maculata* |
| Jelly mushroom | *Phlogiotis helvelloides* |
| Moss-dwelling mushrooms | *Cyphellostereum leave, Galerina atkinsoniana, G. cerina, G. hetrocysis, G. sphagnicola, G. vittaeformis, Rickenella setipes* |
| **Lichens** | |
| Riparian lichens | *Certelia cetrarioides, Collema nigrescens, Leptogium burnetiae var. hirsutum, L. cyanescens, L. saturninum, L. teretiusculum, Platismatia lacunose, Ramalina thrausta, Usnea longissima* |
| Aquatic lichens | *Dermatocarpon luridum, Hydrothyria venosa, Leptogium rivale* |
| **Vascular plants** | *Bensoniella oregano, Botrychium minganense, B. montanum, Coptis trifolia* |
| **Mollusks** | *Ancotrema voyanum, Crypotmastix devia, C. henersoni, Monadenia fidelis salmonensis, Verspericola depressa, V. sierranus, Fluminicola* spp. nov. 1-20, *F. seminalis, Helisoma newberryi newberryi, Juga (C.) acutifilosa, J. (C.) occata, J (O.)* spp. nov. 2-3, *J. (Oreobasis) orickensis, Lanx alta, Lyogyrus* sp. nov. 1, 3, *Pyrgulopsis intermedia, Vorticifex klamathensis sintsini, V.* sp. nov. 1 |
| **Amphibians** | |
| Riparian | *Aneides flavipunctatus, Rhyacotriton cascadae, R. kezeri, R. variegatus, Dicamptodon copei, Plethodon vandykei, Ascaphus truei* |
| **Fish** | Coho Salmon (*Oncorhynchus kisutch*), fall and spring Chinook Salmon (*O. tshawytscha*), resident and sea-run Cutthroat Trout (*O. clarkii clarkii*), resident Rainbow Trout (*O. mykiss*), summer and winter Steelhead (anadromous *O. mykiss*) |
| **Birds** | Common Merganser (*Mergus merganser*)<br>[Marbled Murrelet, *Brachyramphus marmoratus*; Northern Spotted Owl, *Strix occidentalis caurina*] |
| **Bats** | Fringed, Long-eared, and Long-legged Myotis (*Myotis thysanodes, M. evotis, M. volans*), Hoary Bat (*Lasiurus cinereus*), Pallid Bat (*Antrozous pallidus*), Silver-haired Bat (*Lasionycteris noctivagans*) |
| **Other mammals** | Fisher (*Martes pennanti*), Marten (*Martes americana*), Red Tree Vole (*Arborimus longicaudus*) |

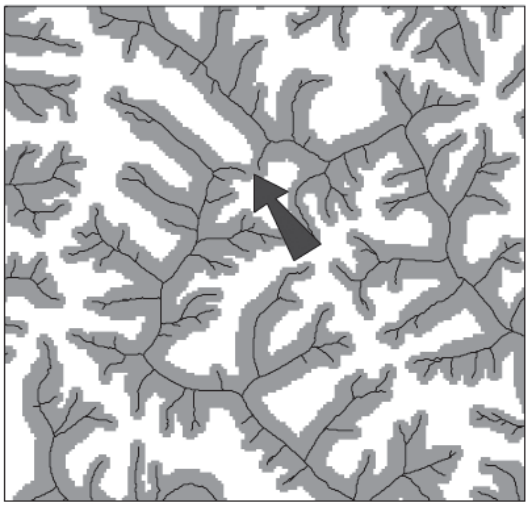

**Figure 1—**Example interim riparian reserve network from the US federal Northwest Forest Plan implemented in the Pacific Northwest, showing frequency of headwater streams on the landscape and the resulting one and two site-potential tree-height buffers along streams (upper left quadrant). Arrow indicates example over-ridge area where the distance between headwater riparian reserves in different watersheds is small and over-ridge connectivity may be more easily achieved. These headwater riparian areas can be used to facilitate landscape linkage area designs for organism dispersal and aquatic-terrestrial habitat connectivity functions.

knowledge of stream and forest ecology has expanded. In some areas, headwaters comprise 80 percent of a stream network (Gomi et al. 2002). This realization intersected with forest management practices when mapping of Northwest Forest Plan scenarios revealed that large percentages of watersheds were being incorporated into interim riparian reserves due to the high density of headwater stream networks (fig. 1). An additional value of using headwater drainages to plan landscape connectivity designs is that the distance from headwater streams to ridgelines is the shortest within a watershed, hence reducing travel distances for overland dispersal to neighboring stream-riparian areas or forest reserve blocks. Distance analysis tools, such as for "least-cost path" in landscape modeling (e.g., ArcGIS, Environmental Systems Research Institute, Inc., Redlands, CA), have been developed to assess distances between habitat patches. These tools would be useful for designing least-distance headwater linkage areas. Least "cost" path is a relevant term applied to the economics of animal movements, to minimize the distance moved—especially for mobility-restricted organisms. This term may also apply to the economics of forest management if identification of a dispersal corridor results in a financial cost for on-the-ground implementation or affects revenue from resource extraction in a managed forest context.

Northwest Forest Plan riparian reserves were intended as major contributors to the maintenance and restoration of aquatic conservation objectives, including aquatic network connectivity (USDA and USDI 1994). The importance of linking headwater stream functions and processes to those of downstream stream networks has been a focus of much work in the last two decades. Welsh (2011) captured many elements of the developing history of stream network theory and the role of aquatic connectivity in summarizing the conceptual frameworks of geomorphic channel processes (transfer and depositional zones), nutrient cycling (upstream marine influence via salmonid migration, downstream nutrient spiraling via down wood movements), aquatic-riparian linkages via reciprocal subsidies, and the intersection of herpetofaunal distributions with the classic stream continuum concept of taxonomic patterns that vary with stream order. As we look up the aquatic network into headwater streams and beyond, we summarize how extending riparian buffers up drainages and connecting them over ridgelines can both maintain terrestrial connectivity and functionally link aquatic-terrestrial systems.

Several conceptual designs of riparian buffer widths and patch reserves have been proposed to assist over-ridge migration of organisms within forests (fig. 2; Olson et al. 2007). Over-ridge connectivity considerations were further developed by Olson and Burnett (2009), and modeled for the Oregon Coastal Province. This model of connectivity linked every 6$^{th}$- and 7$^{th}$-code HU to each neighboring HU. Focusing on the Siuslaw River basin, a 4$^{th}$-code HU within

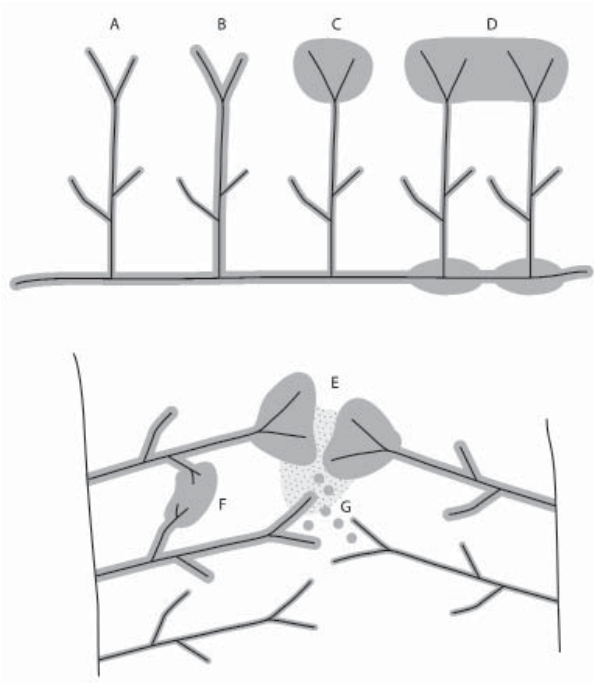


**Figure 2—**Headwater management considerations to retain aquatic-riparian biodiversity by stream buffers of different widths (A, B) and provide linkage areas between adjacent basins (C-G) using alternative forest management practices including uncut blocks (C, D, F), thinning (E), and leave islands (E, G) (from Olson et al. 2007).

that area, the linkage design illustrated where one over-ridge link could connect each adjacent HU (fig. 3). At the 7th-code HU scale, one link between each adjacent 7th-code watershed resulted in roughly 15 percent of headwater streams being extended and connected For the Oregon Coastal Province, this resulted in over 5,000 links, with about one link per 4.6 km$^2$. This is an example of redundant connectivity, essentially creating a web of connections across the landscape. Using the 6th-code HU scale, the amount of connectivity created is approximately halved, with one link per 9.3 km$^2$ for the Oregon Coastal Province.

There are no defined guidelines for how many links or how much habitat connectivity is necessary to maintain populations. The amount of dispersal habitat that might be needed to sustain even highly researched species, such as

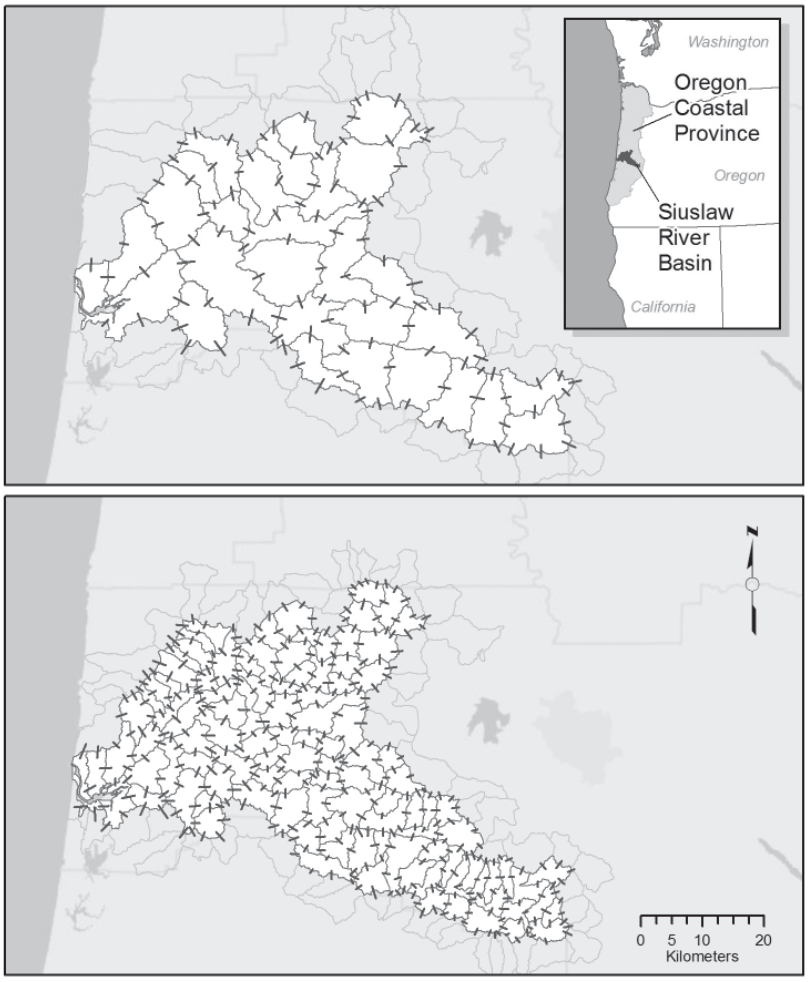


**Figure 3**—Linkage areas between watersheds can provide connectivity of headwater habitats across landscapes. In the Oregon Coast Range Province, the Siuslaw River basin, a 4th-code Hydrologic Unit (HU), is used to illustrate: A) a single connection between adjacent 6th-code HUs; and B) a single connection between adjacent 7th-code HUs, which results in 376 connections across the basin and if expanded to the entire province, about 5000 links within 23 000 km$^2$ (from Olson and Burnett 2009).

the northern spotted owl, is unknown; a "more is better" attitude prevails in the face of this uncertainty. Nevertheless, research is accruing about how much dispersal may be needed to maintain genetic diversity within and among populations. The "one migrant per generation" rule has been offered as a minimum level to reduce genetic isolation, inbreeding, and bottlenecks (e.g., Mills and Allendorf 1996). However, such a rule has many underlying assumptions that may not be supported when the complexities of natural systems are considered (e.g., Wang 2004).

Furthermore, relating effective migration rates to habitat protections in managed systems is not a straightforward exercise: if we build corridors, will they be used? Ongoing mark-recapture, radio tracking, and genetic studies are helping us to answer this question. For example, genetic connectivity analyses of stream-associated Rocky Mountain Tailed Frogs (*Ascaphus montanus*) in Idaho supported this species' affiliation with intact forested habitats: their path of connectivity followed riparian corridors in managed forests (Spear and Storfer 2010). This pattern supports the "riparian corridors as funnels" concept, but it contrasted with Coastal Tailed Frog (*A. truei*) genetic connectivity pathways in the Olympic Peninsula, Washington, which were primarily overland in areas that had timber harvest activities (Spear and Storfer 2008). Precipitation and population differences between these areas were hypothesized as accounting for these differences, as the more mesic conditions that prevail in northwestern Washington may facilitate the upland dispersal of moisture-reliant tailed frogs. Other studies (Wahbe et al. 2004; Johnston and Frid 2002; Dupuis and Steventon 1999; Nauman and Olson 2004) also found differences in riparian-corridor associations of various amphibian species in response to climate and forest conditions, generally supporting their ability to respond to microsite gradients with an apparent affiliation to cool, moist local conditions (e.g., riparian "funnels") (Olson et al. 2007). Furthermore, Spear et al. (2012) reported that Coastal Tailed Frogs track remnant tree patches in their migration pathways after the volcanic blast at Mount St. Helens, Washington. So, if we build it, will they come? The early answer is "yes, but…" —meaning that a variety of organisms appear to be occurring in or moving along pathways of retained habitats, but with geographic, taxonomic, and population-specific contexts being important considerations. A similar conclusion has recently been supported for hedgerows as corridors between woodland fragments (Davies and Pullin 2007). More research on the design of effective linkage areas will be needed. In the interim, conceptual priorities for landscape connectivity designs can be identified, and these relate directly to emerging research priorities.

## Priority Areas for Habitat Connectivity

Prioritizing linkage area placement may be important to address connectivity objectives under economic constraints, and to advance research into the effective design of linkage areas. Because linking all adjoining watersheds at small HU scales may be difficult for land managers to plan and implement in the face of myriad conflicting resource objectives, priorities may guide the first steps in connecting habitats. Olson and Burnett (2009) itemized linkage area considerations at two spatial scales, landscape and drainage area (table 2). Here, we further develop five of these priority considerations:

1. "Triads," where three large basins, with limited or no aquatic connectivity, converge at their headwaters;
2. Climate change considerations including north-south, east-west, and altitudinal linkages;
3. Landslide-prone areas;
4. Species conservation strongholds; and
5. Diagonal considerations.

**Table 2—**Design considerations for placement of headwater linkage areas to assist migration of forest-dependent species in the Pacific Northwest (Olson and Burnett 2009). **Bold-face type** indicates new concepts discussed further in text.

| Linkage Area Design Considerations | Priorities |
|---|---|
| ***Landscape scale*** | |
| 1. Connections across large basins | **"Triads"** – headwater locations that link three adjoining basins having no aquatic connectivity. |
| 2. Climate change migration corridors | North-south (latitudinal) dispersal routes.<br>Altitudinal dispersal routes.<br>Migration across ecoregion boundaries.<br>**East-west dispersal routes.** |
| 3. Linking landscape fragments | Connecting remnant late-successional and old-growth (LSOG) forest patches to other patches or restored habitats may aid dispersal of LSOG-associated species, especially those with dispersal limitations such as lichens, bryophytes, and mollusks; creation of connected archipelagos of patches. |
| 4. Disturbance frequency | Correlating frequency of connections with rates of landscape-scale disturbances, natural or anthropogenic; i.e., more linkage areas in more-disturbed places. |
| 5. **Redundancy** | Planning for multiple paths across landscapes will improve dispersal probabilities. |
| ***Drainage-basin scale*** | |
| 6. Known sites for target species | Low-mobility species.<br>LSOG-associated species.<br>Species with status of concern.<br>**Biodiversity hotspots** – communities.<br>**Species "strongholds"** – priority species management areas such as key watersheds |
| 7. Existing protections | Co-location of linkages on current set-asides (e.g., federal late-successional reserves, owl "cores", Survey and Manage species sites, botanical set asides, landslide-prone areas included in riparian reserves) |
| 8. Short connections | For economy of space, with economic and ecological benefits, shorter connectivity corridors are preferred; ecologically, shorter distances for dispersal may reduce energetic costs for individual movements and time needed for propagules to disperse. |
| 9. Paths of least resistance | Easier dispersal routes may be lower-gradient or lower-elevation "saddles" across ridgelines.<br>Wind-dispersers may have least resistance in paths that follow wind directions during seasons of dispersal. |
| 10. Risk of disturbance | Use hazard models for disturbances such as landslides, debris flows, ice/wind damage, and fire in placement of linkage areas, or in decisions about the need for redundant linkages. For example, debris-flow-prone areas may be headwater set-asides during riparian reserve delineation, and such areas may be co-located with dispersal corridors; redundant links may be considered in fire-prone areas. Mapped overlays of roads, recreation areas, human development, and mining might be avoided during linkage area delineation, when alternative locations exist. |
| 11. Land ownership patterns | Co-location of links on federal and state lands, where possible.<br>**Diagonal linkage areas across checkerboard ownerships.** |

Each of these five considerations results in a geometric view of how connectivity webs may be arranged across landscapes.

These five considerations are not mutually exclusive; how they may interact during prioritization exercises also is developed briefly here. Although they were derived for northwest forest landscapes, these concepts may have broader utility worldwide.

## 1. "Triads"

In the Oregon Coastal Province, Olson and Burnett (2009) highlighted the potential importance of linking larger river basins, which have no freshwater connectivity, through existing riparian buffer networks. Over-ridge forest habitat linkages may be absent unless reserves are placed in the area. Streams in such basins may flow directly to the Pacific Ocean or into a much larger river without a forested riparian area, and so have headwaters that are functionally disconnected. Here, we examined 4th-code HUs for the Oregon Coastal province, the scale of the Siuslaw River basin highlighted above. We then looked for locations where three of these 4th-code HUs joined at their headwaters: we call this a "triad" location. For example, headwaters of the Siuslaw River, Yaquina River, and Marys River converge at Marys Peak (between Corvallis, Newport, and Waldport, OR), which would be one such triad. Only 18 of these headwater triads exist for the Oregon Coastal Province (fig. 4). We suggest that such triads be considered priorities for habitat linkage areas because these would be spatially economical for land managers to implement and potentially ecologically efficient as connections across three watershed boundaries simultaneously.

A current research priority is to empirically assess the proposed linkage-area function of landscape locations such as headwater triads. Using a genetic approach, we have sampled northwestern amphibians from headwater streams of adjacent drainages that are potentially connected across ridgelines in the Oregon Coast Range, including three adjoining headwaters in triads (such as Marys Peak). Preliminary genetic analyses of the Coastal Giant Salamander, *Dicamptodon tenebrosus*, generally support our contention of over-ridge connectivity among drainages (L. Knowles and M.R. Marchán-Rivadeneira, Univ. Michigan, unpubl. data). Previous studies have supported overland connectivity of stream-breeding amphibians (e.g., Spear and Storfer 2008, 2010), and such animals have been found up to 400 m from streams (Olson et al. 2007), but no previous published study has designed

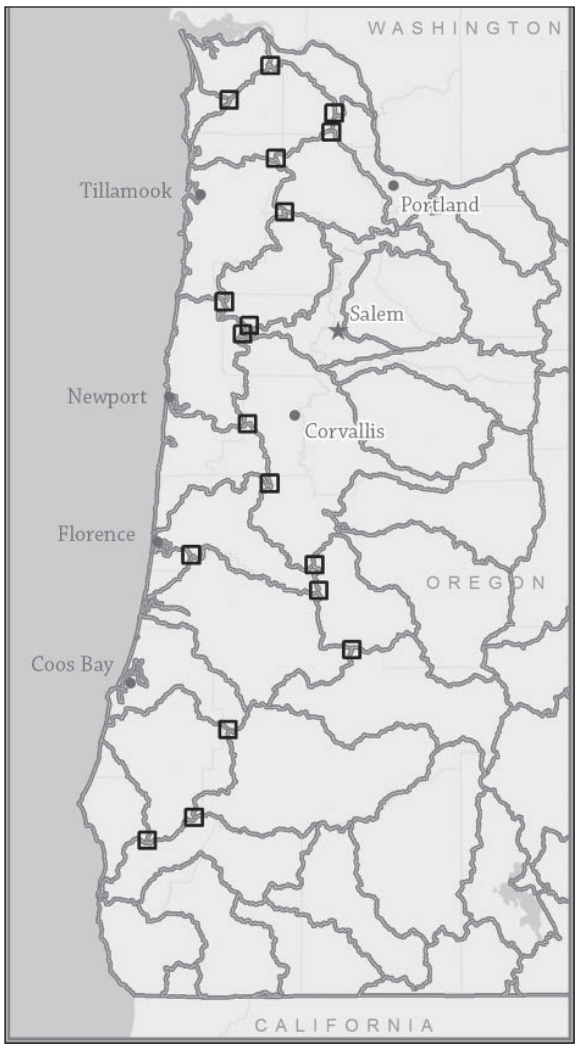


**Figure 4—**"Triads" are indicated (squares) where three 4th-code Hydrologic Units in the Oregon Coast Range Province meet at their headwaters. Triads are priority locations for linkage area or 'species stronghold' placement to effectively manage for species dispersal simultaneously across three distinct watershed boundaries.

sampling to specifically address headwater over-ridge connectivity among discrete drainages. This remains an information gap that could be addressed for all forest taxonomic groups, and would aid the adaptive management of the triad connectivity concept.

## 2. Climate Change

A second priority consideration for northwest forest connectivity is assisting migration in the face of climate change (Olson and Burnett 2009). Predicted climate change effects on northwest forest habitats include drought, insect, and fire effects on forest stands, with large conifers and high-elevation trees being vulnerable to losses (Spies et al. 2010). Aquatic habitat changes in forested landscapes are anticipated in cold-water mountain streams (Spies et al. 2010) and in headwaters (Olson and Burnett 2009). Increasing stream temperatures, with negative implications for cold-water fauna, are already apparent across the northwest (Isaak et al. 2011). Given uncertainty in the geographic specificity of climate change trajectories due to complex El Niño and Pacific Decadal Oscillation cycles, "dynamic and adaptive thinking" (Spies et al. 2010) is needed. A prudent course for linkage area placement may be to consider connected routes in north-south, east-west, and altitudinal directions within and among watersheds (fig. 5). Such consideration may allow multiple potential pathways of movement for species facing changing conditions. Pockets of suitable microhabitats for species persistence may be related to local conditions, and may occur as "stepping stones" along these linear trajectories, like beads along a string. Providing connectivity paths adjoining both riparian areas and north-facing slopes is one such example, with both near-stream areas and hill shading resulting from topographic relief providing cool, moist conditions for target species such as some late-successional and old-growth (LSOG)-associated salamanders (e.g., Suzuki et al. 2008). Landscape-scale monitoring of forest conditions and species distributions may inform adaptive management of likely climate change refugia for different taxa.

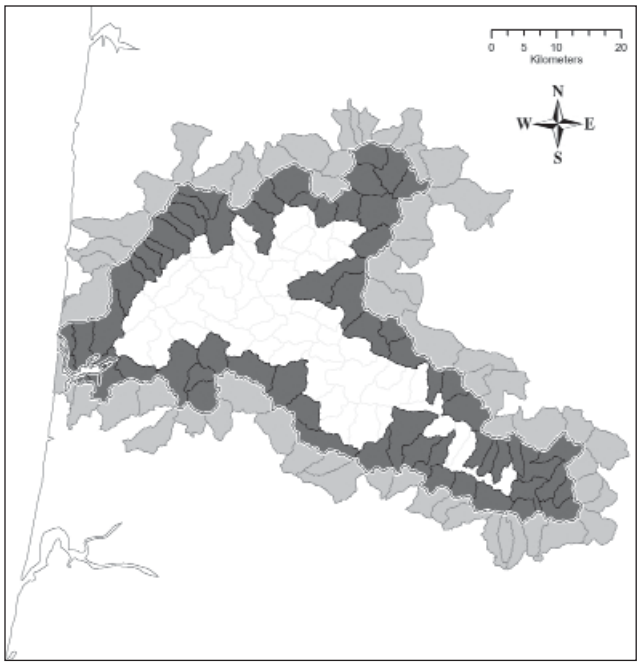


**Figure 5—**Designs for assisted migration of species in the face of climate change might include prioritizing headwater linkage area placement across north-south and east-west watershed boundaries. The Siuslaw River basin, a 4th-code Hydrologic Unit in the Oregon Coast Range Province, is shown highlighting perimeter sub-drainages (dark grey) where linkage areas could be made to discrete drainages to the north, south, and east.

## 3. Managing Disturbances: Landslide-Prone Areas

A third priority consideration for the design of linkage areas is to integrate their placement with local disturbance regimes. Landslides and debris flows can be dominant disturbance processes affecting headwater streams in forested, mountainous regions (e.g., Benda 1990; Iverson et al. 1997). The Northwest Forest Plan directs that riparian reserves incorporate landslide-prone areas to reduce the probability that activities associated with timber harvest will alter wood and sediment inputs to streams by changing the rate, magnitude, composition, or timing of debris flows. Co-locating linkage areas with existing riparian reserves, where these include steep areas prone to landsliding, can provide

economic efficiency and conservation synergy for land and resource managers. Burnett and Miller (2007) modeled differences among hill slopes and headwater channels in probabilities of initiating and transporting debris flows that deliver to fish-bearing channels for the Oregon Coastal Province (fig. 6). Those headwaters with the highest likelihood of affecting downstream areas important for fish might be high priorities for extending riparian reserves over ridgelines. Because debris flows can be important sources of large wood (May and Gresswell 2003; Hassan et al. 2005), a fundamental component of stream habitat complexity (Bilby and Bisson 1998; Gregory et al. 2003), managing these expanded riparian reserve areas to accelerate tree growth could be an additional consideration. Redundancy of connections would be important when planning ground-disturbing activities for linkage areas with a high probability of landsliding. To aid identification and adaptive management of landslide-prone areas, these areas have been mapped for many northwest forests by the NetMap interactive web-tool developed by Earth Systems Institute (*http://netmaptools.org/*).

## 4. Species Strongholds

"Species strongholds" are areas where biodiversity conservation is a priority, and where thriving populations can occur to anchor species persistence in the region. Retaining connectivity among species strongholds enhances the likelihood of persistence under the uncertainty of stochastic events (catastrophic fire, disease outbreaks) or emerging patterns of disturbance (climate change) that may affect any particular stronghold. Managing stronghold-to-stronghold connectivity is a fourth priority to consider in developing linkage area designs across forest landscapes. Species strongholds may be created for communities of diverse taxa at larger spatial scales by land-use allocations such as

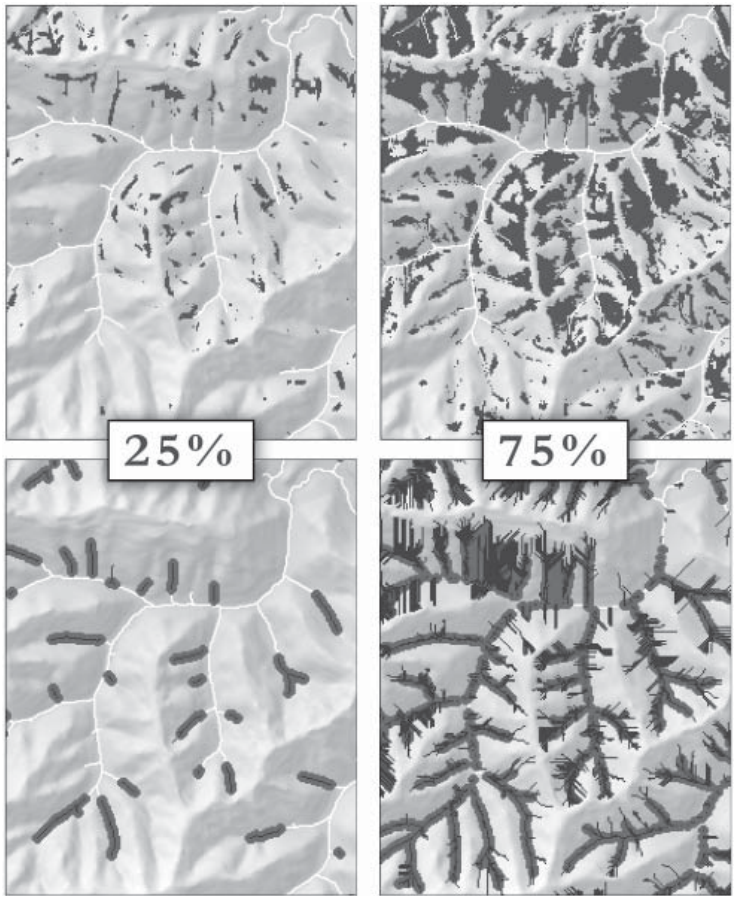


**Figure 6—**Placement of between-drainage links might consider other landscape-scale provisions such as management scenarios to retain the natural disturbance regime, including landslide-prone areas managed to deliver wood and sediment to streams. Top figures show models of 25 percent and 75 percent of the landslide-prone hillslopes in an example forest landscape, and bottom figures show their likely traversal paths to streams (Burnett and Miller 2007). Headwater riparian buffers of these areas provide long-term wood and sediment inputs for stream biota. From Olson and Burnett 2009.

Congressionally reserved lands (wilderness areas, national parks), or the Northwest Forest Plan late-successional reserves or key watersheds (USDA and USDI 1993, 1994). At smaller spatial scales, strongholds for a targeted species of concern may be critical habitat areas, such as caves, ponds, meadows, botanical set-asides, or areas managed for Survey and Manage species under the federal Northwest Forest Plan (USDA and USDI 1993, 1994). Riparian buffers themselves might be considered as strongholds, but here, we expand that perspective to other areas.

Developing new species strongholds is particularly important when considering connectivity issues. Three examples follow. First, areas with high "intrinsic potential," the capacity to support high-quality habitats for salmon (Burnett et al. 2007), may serve as nuclei for designing linkage areas. Intrinsic potential models have been developed and broadly applied for salmonids in the Pacific Northwest and elsewhere (e.g., Mollot and Bilby 2008; Sheer et al. 2009; Busch et al. 2011; Barnett and Spence 2011). Streams with high intrinsic potential can be identified and then targeted, as appropriate, for salmon conservation across a landscape. Such areas of high intrinsic potential are essentially "species strongholds" from which aquatic-terrestrial linkage areas can originate. Areas of high intrinsic potential for some salmonid species may occur in larger streams, but tools exist to easily identify headwater streams that feed into these both laterally and from upstream (Clarke et al. 2008).

Second, criteria for Priority Amphibian and Reptile Conservation Areas (PARCAs) are under development for nationwide application (Riley et al. 2011). PARCAs are being discussed for integration into the landscape planning processes of other entities, such as the U.S. Department of Interior Landscape Conservation Cooperatives (*http://www.doi.gov/lcc/index.cfm*), which is a partnership network to sustain America's land, water, wildlife, and cultural resources. Once established, PARCAs would function as species strongholds. Similarly, the International Union for the Conservation of Nature (IUCN) is developing criteria to identify sites of global significance for biodiversity conservation, called Key Biodiversity Areas. Such areas are synonymous with the concept of species strongholds. The additional element that we suggest is to provide connectivity among such areas.

Third, triads, as we previously described, could be ideal locations for species strongholds, as these occur at the ridgeline junction of three large basins. However, we note that triads are not established biodiversity hotspots, and are proposed here as a conceptual design.

Development of landscape-scale linkage webs from either new or existing species strongholds is needed to reduce isolation of those areas, and as possible to allow them to function as potential "source" habitats with optimal conditions that can anchor species over time and also connect to adjoining areas, in a metapopulation context. Linking dispersal pathways from strongholds up and over ridgelines to adjacent watersheds and neighboring strongholds is a direct approach that may offer a least-cost path. Relevant to our proposed headwater linkage areas concept, connecting such species strongholds to headwaters which then extend and connect over ridgelines is another consideration. Additionally, strongholds may be linked to protected riparian areas along larger streams that are subsequently extended upstream into headwaters and connected over ridgelines. Multiple connectivity pathways may be conceived. As a web of connections is considered relative to species stronghold connectivity, the previous priorities discussed above and outlined in table 2 can be overlain, including large basins and triads, linear trajectories to address for climate change gradients, and occurrence of landslide-prone areas.

Adaptive management of strongholds may need to be addressed over the long term as future conditions unfold. As applied here, the concept of a stronghold evokes less of an immovable fortress than an anchor. A species stronghold intended

to anchor habitat may need to function as do real anchors on occasion, and be repositioned or "drag" across landscapes in response to changing conditions or management priorities (Olson et al. 2007). The temporal scale of strongholds can be addressed at the time of their development, and interact with the spatial scale of stronghold designs and the frequency of strongholds. For example, habitat anchors designed to drag across landscapes may be implemented more easily if they are smaller and more numerous. Olson et al. (2007) suggested considering 6th-code watersheds (HUs) as a spatial scale for amphibian habitat anchors. The anchor concept warrants testing, with a sufficient timeframe to weigh success at the landscape scale, in addition to replication. It may have greater success if it were to be implemented in areas with more resilient ecosystems.

## 5. Thinking Diagonally: Funnels and Chains

The geometry and land-management context of land-use and land-ownership parcels on the landscape is a final set of priority considerations for linkage-area placements that we will develop briefly here. The northwest forest landscape is a patchwork of land ownerships and land-use allocations, each with differing management priorities, which creates a complex challenge for biodiversity conservation (Suzuki and Olson 2007). During planning for large blocks of forest land, and during planning of individual projects at smaller spatial scales, managing for connectivity within and among ownership areas can be difficult due to differing priorities across boundaries. To diminish the dilemma of achieving effective biodiversity conservation in such a multi-ownership landscape, it may help to think of streams as dispersal "funnels" that serve to channel organisms along protected riparian areas, and connectivity corridors or linkage areas as "chains" functionally moving animals up and over ridgelines (Olson and Kluber, unpubl. data). Overlaying many of the previously discussed priorities can provide an integrated perspective for addressing the challenges of land-ownership/allocation geometries.

Diagonal linkage areas are of specific relevance in a landscape with a checkerboard ownership pattern (fig. 7), and in other landscape geometries that abut at corners or other edge types (Olson and Kluber, unpubl. data). Species dispersal along such diagonals might be promoted by forest management actions that retain habitat elements toward the corners of such lands. For example, weighted green-tree retention, leave islands, and directional felling of down wood (recruitment of large logs, in particular) from corners may assist migration of species along the diagonal by providing chains or stepping stones of suitable microhabitats for species refugia. Linking chains of habitat elements from corners to stream- and riparian-protected areas, especially headwaters (fig. 7B), may functionally extend and connect riparian buffers. Organisms that are funneled along riparian areas may venture through corners via these habitat chains. A chain of habitat need not extend from headwaters, but could extend from any part of a riparian buffer, or from a species stronghold, as discussed above.

It may be neither feasible nor desirable to address habitat connectivity at all corners of adjacent lands within an ownership. Similarly, when land parcels are in close proximity but do not adjoin, it may not be possible to consider linkage areas along their entire boundaries. Several additional design concepts arise and interface with ideas presented above.

First, linkage areas among land parcels might be "stream-lined" if streams align through corners (fig. 8), or connect nearby land blocks. When streams follow diagonals in a checkerboard landscape, riparian protection may more effectively promote multi-species diagonal dispersal: funnels without the added chains linking across diagonals. Streams that loosely follow diagonals, not intersecting exactly at corners, could be quite functional to assist species

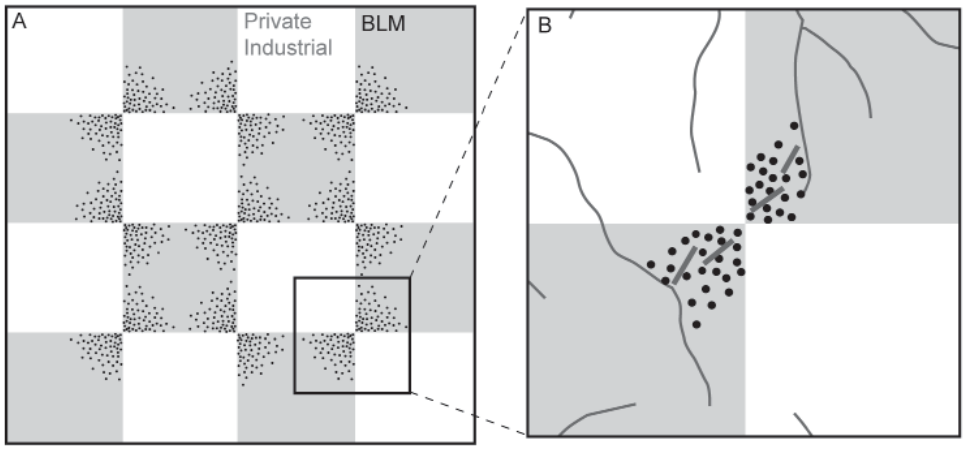


**Figure 7**—In a checkerboard ownership pattern, such as that created by the Oregon and California Lands Act (1937) where US Bureau of Land Management (BLM) and private industrial forestlands are intermixed, management for connectivity along diagonals may improve likelihood of species dispersal within ownerships. A: Corners are shaded to show linkage area considerations. However, routes along selected diagonals to species strongholds, reserves, or triads might be used to prioritize which corners are chosen for connectivity emphasis. B: Forest management options to facilitate species dispersal from stream corridors (which may serve to funnel species movements) to corners might include chains of habitat structures provided by green tree retention, directional log placement from corners to streams, or both. Concepts could be applied to other ownership geometries with corners or edges in proximity.

**Figure 8**—Connectivity designs to aid species dispersal among ownership blocks may overlay on streamside riparian management zones. This US Bureau of Land Management study site for the Density Management and Riparian Buffer Study of western Oregon (Cissel et al. 2006) shows riparian buffers extending along the full diagonal (A) as well as laterally toward an opposing corner (B), with leave islands and dispersed tree retention aiding habitat connectivity, and to a neighboring private land block (C). "Stream-lined" connectivity (A) may aid within-watershed dispersal, but overland connectivity designs (B and C) may warrant consideration to link or "chain" habitats overland between watersheds. Photo provided by Oregon Bureau of Land Management.

migration, in this regard. Streams that link disconnected parcels may similarly function to funnel organisms' movements. The context of the adjoining lands may need to be assessed, however. Managing such a stream-line to promote its potential connectivity function is a consideration, but such stream-lined connectivity does not address overland dispersal. Chains from streams to ridgelines are needed to fully integrate aquatic and terrestrial landscape connectivity functions. Collaborative management of such stream-lines and overland chains among ownerships and

across land-use allocations within ownerships, remains a challenge.

Second, in multi-ownership landscapes, road densities may be higher than in single owner landscapes. An assessment of the effects of roads on species connectivity designs may be particularly important in these landscapes. In particular, paved roads or high-use unpaved roads may be barriers to low-mobility species. As roads intersect streams, aquatic organism passage may be affected, with consequences for overland connectivity. Site-specific designs can include these considerations.

Third, as hazard models of disturbances are developed for a landscape, it may be helpful to ask how hazards align with land-ownership boundaries, land-use allocations, and existing connectivity webs. For example, how are landslide-prone areas arranged relative to the geometry of lands by ownership and land-use allocation? As discussed above, can priority linkage areas be designed to overlay on landslide-prone areas that are already set-asides for riparian reserve management, and now also serve "to chain" habitats to adjoin land-ownership blocks?

Fourth, in a larger landscape context, it may be useful to know how larger basins, climate change projections, and species strongholds are arranged and whether these be used to prioritize connectivity area pathways. Can dispersal routes be conceived from streams and then through land-ownership diagonals or between ownership blocks to foster connections relative to these issues?

Multiple overlapping considerations are emerging, and a stepwise process may be needed to integrate them. Limitations may emerge due to topography, geometry of land configurations at local scales, or pre-existing conditions. For example, a dispersal barrier such as a road may need to be considered first. The existence of under-road culverts may create spatially explicit bottlenecks for connectivity planning. Routing linkage area pathways to those stream corridors and culverts may be needed to increase the odds of dispersal across the road. Culverts that act as dispersal nodes in this way could be prioritized for enhancement to provide passage for non-aquatic species. Similarly, triads and species strongholds, as discussed above, are essentially dispersal nodes. Routing dispersal routes via headwater linkage area pathways to triads and strongholds could increase the overall effectiveness of these conservation measures.

## Conclusions

Forest biodiversity conservation is an ecosystem service that will continue to be addressed at local-to-landscape scales in the coming century. Retaining organisms across managed forest landscapes requires a toolbox of approaches including fine- and coarse-scale habitat protections and restoration practices, retaining or creating structural elements that are critical habitats for species, and development and management of connectivity pathways to allow gene flow. Renewed efforts to address communities of organisms as well as species of concern are called for as emerging stressors need evaluation, new knowledge is accrued, and adaptive management of existing forest plans are needed.

We review the numerous benefits of forest connectivity designs that rely on headwater linkage areas, and emphasize priorities for their placement at landscape scales. The benefits of headwater linkage areas include their likely functional role in integrating aquatic and terrestrial systems, their potential use by multiple taxonomic groups, their utility for creating webs of connections across forested lands to increase their effectiveness for biodiversity conservation, and their efficiency in minimizing both the distances that animals must move overland and the financial burdens of forest manager.

Placement of headwater linkage areas may include consideration of a variety of factors (table 2). Prioritizing linkage areas can provide a starting point for managing connectivity among

critical habitat areas, suggest directional routes for dispersal among areas, or identify dispersal nodes as anchors for connectivity webs. The five priority considerations that we developed include triads that effectively link three larger basins, north-south and east-west directional routes to address climate change scenarios, linkages overlaid on management of disturbances such as landslide-prone areas, links among species strongholds, and diagonal links that route dispersal across management boundaries. These five concepts can be integrated into an overall geometry of landscape connectivity designs. Our conceptualization of headwater linkage area utility and these priority considerations are posed as hypotheses warranting further study and development. We offer these ideas with the caveat that they will not benefit all taxa in forested landscapes. Extremely rare or patchily distributed organisms with low mobility may need a finer-grained, site-by-site conservation approach (Raphael and Molina 2007).

## Acknowledgments

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LETTERS

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# Species' traits influenced their response to recent climate change

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**Although it is widely accepted that future climatic change—if unabated—is likely to have major impacts on biodiversity[1,2], few studies have attempted to quantify the number of species whose populations have already been impacted by climate change[3,4]. Using a systematic review of published literature, we identified mammals and birds for which there is evidence that they have already been impacted by climate change. We modelled the relationships between observed responses and intrinsic (for example, body mass) and spatial traits (for example, temperature seasonality within the geographic range). Using this model, we estimated that 47% of terrestrial non-volant threatened mammals (out of 873 species) and 23.4% of threatened birds (out of 1,272 species) may have already been negatively impacted by climate change in at least part of their distribution. Our results suggest that populations of large numbers of threatened species are likely to be already affected by climate change, and that conservation managers, planners and policy makers must take this into account in efforts to safeguard the future of biodiversity.**

The rate of warming over the past 50 years (0.13 °C ± 0.03 °C per decade) is nearly twice that for the previous 50 years[5], and the global temperature by 2100 is likely to be 5–12 standard deviations above the Holocene mean[6]. The effects of climate change on some species are already being witnessed, with changes documented in spatial distribution, abundance, demography, phenology and morphology[7,8]. However, to date, no quantification of the number of species for which at least one population has been currently impacted by climate change, and the extent of these impacts, has been conducted, even for the better-studied taxa such as birds and mammals. The predominant focus of climate change assessments for species has been that of bioclimatic niche modelling, which focuses on correlative analyses between species' geographic ranges and bioclimatic variables[9,10], but these studies ignore observed changes in distribution, phenology and abundance of species in response to contemporary climate change[10]. Species' life-history traits, such as dispersal and generation length, have been hypothesized to be important in determining species' sensitivity to climate change and their capacity to adapt to it[11], but only a limited number of studies[12,13] have so far provided evidence that animal species with certain traits are more likely than others to be adversely affected by changes in climate[12–15].

In this study we first aimed at performing a meta-analysis to identify the life-history traits that confer vulnerability to climate change in birds and mammals (Supplementary Table 1). From a literature search, we identified 70 studies covering 120 mammal species and 66 studies relating to 569 bird species whose populations had (or sought evidence for) a response to climate change in recent decades. We divided this response into four categories: negative, if >50% of the populations experienced reductions in one or more of the following parameters: population size, geographic range size, reproductive rate, survival rate, body mass; positive, if the species experienced increases in one or more of the parameters and/or adaptability to new climatic conditions; unchanged, if no response was observed despite the recorded change in climate; and mixed, if the species showed opposite responses of one or more of the parameters across its geographic range (Supplementary Table 2; see Methods). For all mammals and birds covered by the studies, we compiled data on selected intrinsic traits and spatial traits to assess quantitatively which of these are associated with negative responses to climate change. To control for the magnitude of climate change experienced, we also computed the mean difference in temperature between the present and the recent past within the geographic range of each species, treating breeding and non-breeding ranges separately for migratory birds.

By using information on the impacts of climate change in the study areas and life-history traits, we were able to identify the species whose populations are more likely to have experienced negative impacts in the regions affected by climatic changes as those described in the analysed papers. We estimated the likelihood of a species' population to have exhibited any of the four categories of responses to climate change with a multinomial regression model. This allowed us to test our hypotheses about the relationship between intrinsic and spatial traits and the responses of mammals and birds to climate change. Since we believe that these factors mediate the response to climate change similarly worldwide, although future studies will be crucial to test this assumption, we then predicted the likely past responses of all birds and terrestrial non-volant mammals listed as threatened in the IUCN Red List of Threatened species[16]. By making predictions on the species for which the levels of climatic hazard experienced are known, we provide the first quantification of the number of taxa that may have already been impacted, although further data need to be collected to say with certainty that there has been an effect on the whole species' persistence. We focused on threatened species because the vast majority are known or inferred to have declined; therefore, if they are at risk from climate change there is a real chance that it

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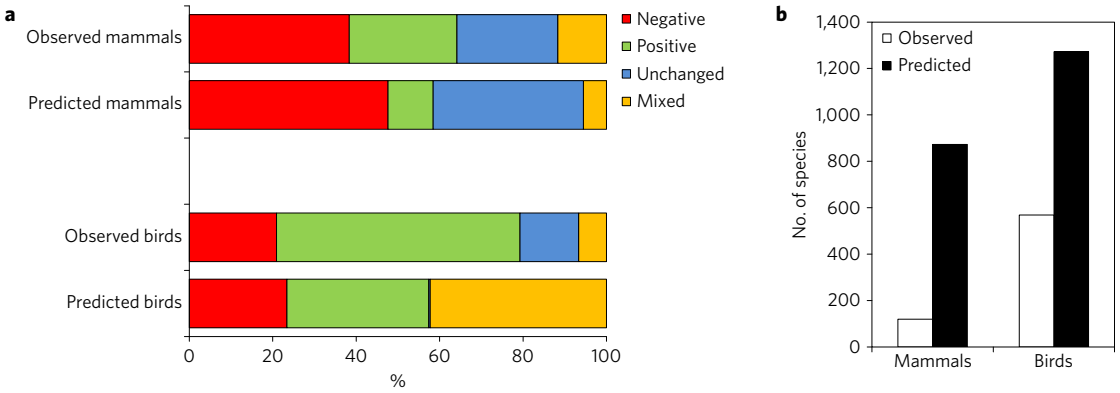


**Figure 1 | Observed and predicted response of mammals and birds to climate change. a**, Red bars show the percentage of species whose populations were documented to have had, or are predicted to have had, a negative response to climate change in the study period (studies spanned from 1858 to 2010); green bars represent the percentage of species with a positive response; blue bars indicate the percentage of species with no response; yellow bars show the percentage of species with mixed responses. **b**, Bars with the number of species whose populations had an observed response to climate change are coloured in white, whereas those used for predictions are shown in black.

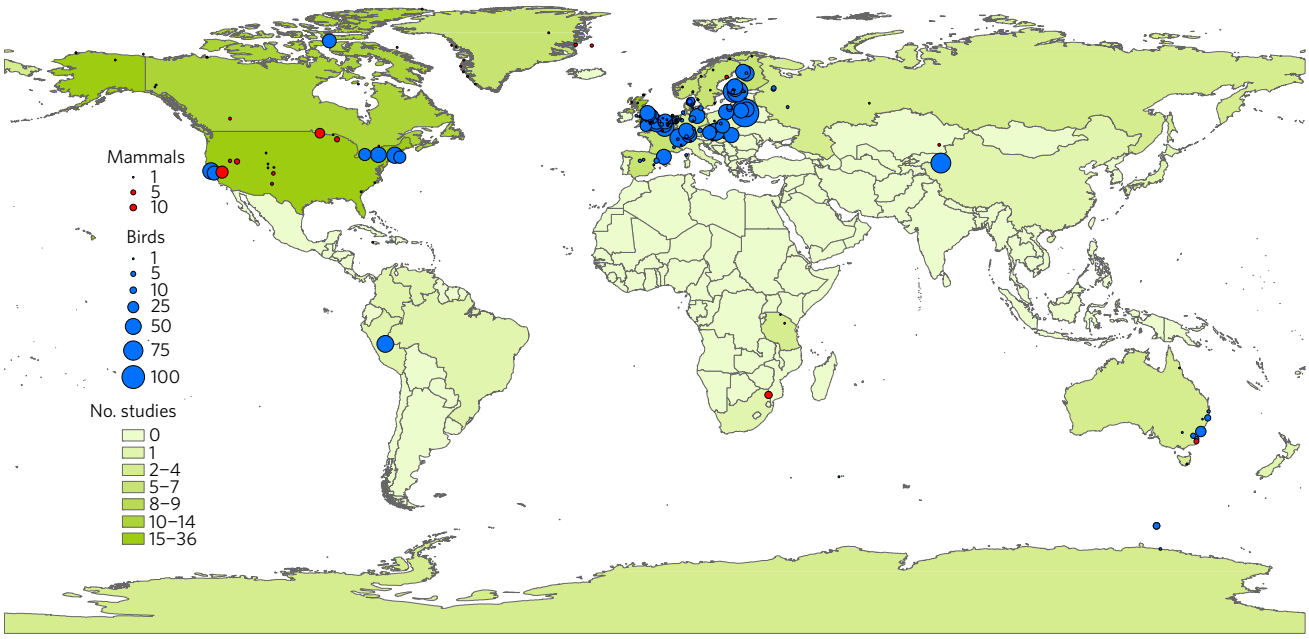


**Figure 2 | Map of the study sites.** Circle size represents the number of bird (blue) and mammal (red) species studied in each site. Colour of countries (shade of green) represents the number of studies per country.

has played a role in these declines, even if it was not recorded in the assessments.

For the first time we identified a relationship between a set of several variables, both intrinsic and spatial, and the response of mammals and birds to climate change, whereas previous studies mostly focused on a few biological traits and their relation with the type of impact[3,4,17,18]. In addition, we were able to provide insights into the estimation of climate change threat for poorly studied species.

## Characteristics of impacted species

The observed response to recent climate change was negative for 38.3% of mammals and 20.9% of birds in our data set (Fig. 1a). Birds and mammals in Europe and North America were the subjects of considerably more studies (54% and 38%, respectively) than were taxa in South America (4%) and Oceania (2%), and less than 1% of species in our data set were in Africa, Asia and Antarctica (Fig. 2). This spatial bias implies that, for species with particular traits living in less studied continents, our findings might be less generalizable.

Mammals most at risk from climate change are those not fossorial, that experienced large changes in temperature in the past 60 years and have low precipitation seasonality within their distributional ranges (Supplementary Table 3). In areas with reduced precipitation and/or temperature seasonality, it is likely that plant species may have narrower climatic tolerances, and therefore that these areas may have already experienced vegetation changes with consequential loss of habitat for animals living there[19]. A more specialized diet was also associated with greater probability of negative responses in mammals. Our findings are in agreement with previous studies on the predictors of general extinction risk[20], in which species with narrower diet breadths were associated with lower ability to exploit resources and adapt to new environmental conditions and selective pressures.

For birds, negative responses in both breeding and non-breeding areas were generally observed in species that experienced large changes in temperatures in the past 60 years, live at high altitudes, and have low temperature seasonality within their distributions. Negative impacts were also associated with relatively high maximum



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temperature recorded within breeding areas, and low dispersal distances, longer generation lengths, reduced precipitation seasonality and restricted altitudinal ranges in non-breeding distributions (Supplementary Tables 4 and 5). Populations of species living at high altitudes and in colder places have fewer opportunities to move towards cooler areas or upslope to avoid increasing temperatures, and hence may have increased extinction risk. Modest shifts to higher or lower altitudes are associated with large changes in ambient temperature[21], thus facilitating potential adaptive flexibility. In addition, temperature is an important determinant of laying dates of birds because higher temperatures may induce earlier laying[22], and so for animals living in these environments the effects of temperature changes may have been exacerbated, potentially leading to disruption in synchronization between the timing of chick-feeding and peak food availability[23]. Interestingly, we found that birds with longer generation times have responded less to warming. In long-lived species, the effects of climate change have probably been less evident because adaptation and range shifts occur over a longer time span[24]; therefore, we would need to monitor the populations of these species for an extended period to observe any changes.

On average, it is likely that at least one population of 414 threatened mammals out of 873 species (47%), and 298 threatened birds out of 1,272 (23.4%) has responded negatively to climate change (Fig. 1 and Supplementary Tables 6 and 7), because they have the same combinations of traits as those species documented to have declined owing to climate change. This implies that, in the presence of adverse environmental conditions, populations of these species had a high probability of being negatively impacted by recent climatic changes.

Mammals had only 2 orders out of 11 (that is, rodents and insectivores) that mostly benefited from recent climatic changes. Both of these orders are generally characterized by fast reproductive rates and low habitat specialization[25]. Moreover, most of the species in these orders are fossorial, and they may be less exposed to climate change owing to buffering of temperatures in burrows. Primates, Proboscidea and marsupials are the mammals with the highest percentage of threatened species predicted to have been negatively impacted by climate change (Table 1), and for which we are more confident about our predictions (Supplementary Table 10). Primates and marsupials are mostly concentrated in tropical areas[26], most of which have had climatically stable environments during the Holocene. Therefore, many of these taxa have evolved to live within restricted environmental tolerances and are likely to be most affected by rapid changes and extreme events[27]. In addition, primates and elephants are characterized by very slow reproductive rates that reduce their ability to adapt to rapid changes in environmental conditions[15].

Birds showed the opposite trend, with only 3 orders out of 19 (that is, Anseriformes, Charadriiformes and Cuculiformes) having more species with a predicted negative impact than not (Table 1). Most of the species included in the first two orders inhabit aquatic environments, which are considered among the most vulnerable to temperature increase due to habitat loss, fragmentation[28] and harmful algal bloom expansions[29]. In addition, changes in climate in tropical and subtropical forest areas, already exacerbated by habitat degradation[2], may threaten forest-dependent species (for example, Cuculiformes).

**Table 1 | Predicted responses of threatened species in different taxonomic orders to climate change.**

| Taxonomic order | Negative | Positive |
|---|---|---|
| Mammals | | |
| Carnivora | 18 (29.51%) | 35 (57.38%) |
| Cetartiodactyla | 56 (59.57%) | 2 (2.13%) |
| Dasyuromorphia | 12 (100%) | 0 |
| Didelphimorphia | 0 | 9 (100%) |
| Diprotodontia | 44 (100%) | 0 |
| Eulipotyphla | 0 | 4 (4.82%) |
| Lagomorpha | 10 (55.56%) | 0 |
| Perissodactyla | 8 (61.54%) | 0 |
| Primates | 199 (100%) | 0 |
| Proboscidea | 2 (100%) | 0 |
| Rodentia | 65 (19.23%) | 44 (13.02%) |
| Birds | | |
| Accipitriformes | 8 (16%) | 34 (68%) |
| Anseriformes | 10 (40%) | 8 (32%) |
| Bucerotiformes | 0 | 0 |
| Caprimulgiformes | 8 (13.11%) | 21 (34.43%) |
| Charadriiformes | 26 (57.78%) | 3 (6.67%) |
| Ciconiiformes | 3 (50%) | 3 (50%) |
| Columbiformes | 16 (25%) | 47 (73.44%) |
| Coraciiformes | 0 | 17 (89.47%) |
| Cuculiformes | 6 (66.67%) | 2 (22.22%) |
| Falconiformes | 2 (33.33%) | 0 |
| Galliformes | 22 (29.33%) | 3 (4%) |
| Gruiformes | 13 (29.55%) | 29 (65.91%) |
| Passeriformes | 171 (30%) | 112 (19.65%) |
| Pelecaniformes | 6 (31.58%) | 8 (42.11%) |
| Piciformes | 5 (14.71%) | 17 (50%) |
| Podicipediformes | 1 (25%) | 1 (25%) |
| Procellariiformes | 0 | 8 (13.56%) |
| Psittaciformes | 0 | 103 (99.04%) |
| Sphenisciformes | 1 (10%) | 0 |
| Strigiformes | 0 | 6 (13.95%) |
| Suliformes | 0 | 10 (100%) |

Positive responses were assigned to species that benefited from recent climatic changes. Percentages indicate the proportion of threatened species for each type of response.

## Conclusions

The vast majority of assessments of species' risk from climate change have focused on future projections (for example, refs 30,31), while analyses of observed impacts to date have focused on detecting a signal of climate change rather than quantifying the number of species whose populations are likely to have been impacted. By undertaking a systematic review, we found evidence of observed responses to recent changes in climate for almost 700 species of mammals and birds. We note that only 7% of mammals and 4% of birds for which we found evidence of a negative response are coded on the IUCN Red List of Threatened Species as threatened by 'climate change and severe weather' under the 'threats classification scheme' (Supplementary Tables 8 and 9). Although this can partly be explained by the fact that species classified as 'Least Concern' on the Red List generally have few or no threats coded, the figures we found were 11% and 31%, respectively for threatened mammals and birds. This apparent mismatch is probably due to the severity of decline driven by climate change being uncertain for most species. Reasons for this include: information from other parts of their distribution is not available; other threats (for example, habitat loss from agricultural expansion, overexploitation and so on.) may have had a greater impact, thus masking the effects of climate; and/or data on climatic trends at a local scale are difficult to obtain, making it difficult to make inferences about the threat severity. Furthermore, threats to several species remain poorly understood because the majority of threatened species live in tropical areas which are generally poorly studied and monitored[32].

Although our predictions for individual species may be subject to varying degrees of uncertainty, depending on the taxonomic order and the spatial or intrinsic trait considered, the confidence intervals around the number of species whose populations may have



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been negatively impacted suggest that our extrapolation is robust, especially for mammals. Improved monitoring of the abundance and distribution of those taxa identified as most vulnerable (Supplementary Figs 1–6), and targeting such monitoring in areas where the effects of climate change are likely to occur soonest—particularly in the tropics—are crucial to increase empirical knowledge about climate change impacts on species, and to validate and improve projections of future impacts.

Despite these uncertainties, our results suggest that the impact of climate change on mammals and birds in the recent past is currently greatly underappreciated: large numbers of threatened species have already been impacted in at least part of their range. Given that scientific efforts in this field have largely focused on predicting the impact of future climate change on species and ecosystems[33], we recommend that research and conservation efforts give greater attention to the 'here and now' of climate change impacts on life on Earth. This also has significant implications for intergovernmental policy fora such as the Convention on Biological Diversity and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, and the revision of the strategic plan of the United Nation Framework Convention on Climate Change.

## Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the online version of this paper.

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## Author contributions

M.P., P.V., C.R. and J.E.M.W. designed the framework for the meta-analysis. M.P. conducted the analyses and collected the data for mammals. P.V. contributed to the analyses. S.H.M.B. provided data and examined the results for birds. F.M.C. collected data for birds. All authors contributed to the writing, discussed the results and commented on the manuscript.

## Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.P.

## Competing financial interests

The authors declare no competing financial interests.



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## Methods

Using ISI Web of Knowledge we conducted a systematic literature search of all relevant articles—published between 1990 and 2015—that reported an observed change in climate in the study area; indicated that birds and/or mammals have undergone a change (for example, in distribution, population size, phenology, behaviour, genotype, phenotype) attributable to climate in the past 100 years; and/or suggested that populations of a species were not affected by recent climate change. For each study and each species considered (70 studies and 120 species for mammals, 66 studies and 569 species for birds), we identified the type of impact experienced.

A negative response was assigned to a species if all (at least one) or >50% of its populations (if the species had both negative and no responses in different portions of its range) were reported to have undergone declines in population size, geographic range size, survival or reproductive rate, and body mass, thus reducing the risk of false attributions. These responses were confidently attributable to recent climate change by the authors of the studies, for instance due to the fact that the most significant change in environmental and biotic conditions reported in the area in which the population of the species was impacted was related to climatic variables. Although we acknowledge that some of the studies may have been more rigorous than others, with such variation in the methods used and the effect size themselves it would have been difficult to adjudicate the level of confidence around the claimed relationship, although we believe that evaluating the strength of attribution is a priority for future work.

A positive response was assigned if the majority of the populations of a species experienced geographic range expansions, increase in population size, survival rate and/or reproductive rate, body mass, and/or changes in phenology. An unchanged response was attributed if no response was observed despite the recorded change in climate. Finally, species that exhibited a combination of the negative and positive (not necessarily in the same proportion) responses in different parts of their range were classified as mixed.

**Statistical analysis.** To identify the relationships between the observed response of mammals and birds to climate change and a set of intrinsic and spatial variables (see Supplementary Methods for description of these predictors and a priori hypotheses), we performed a multinomial logistic regression using the 'nnet' package in *R*. This model uses maximum likelihood estimation to evaluate the probability of the different possible outcomes of a categorical dependent variable with more than two classes. To reduce the overdispersion in models and avoid collinearity, we performed Spearman's correlation tests between the predictors and removed those that were highly correlated ($R^2 > 0.75$) and led to the minimum loss in model performance.

We included taxonomic order as fixed variable of our models, for a total of 11 orders of mammals and 22 of birds. By including taxonomy as a fixed effect, we aimed to control for the non-independence of observed responses across species, and for the latent variables that may affect the responses to climate change that are phylogenetically conserved. We did not include taxonomic family or genus because it resulted in strong underdispersion, as observed data on the response to climate change (which we used as a base for our predictions on threatened species) were often available only for the populations of one species per family/genus. Since we are not aware of frequentist methods to implement phylogenetically corrected models with a multinomial distribution, and concerned that phylogenetic non-independence in the species in our data set could nevertheless be important, we tested for the existence of phylogenetic signal in the residuals of our models. We used phylogenetic trees for mammals and birds[34,35] to estimate Pagel's lambda, assuming a star-shaped phylogeny and the actual phylogeny (Brownian motion models). We tested whether the value of lambda differed significantly from 0 (no phylogenetic signal) and 1 (trait distribution matches a Brownian model of evolution), by computing the likelihood ratio, and then comparing it to a Chi-squared distribution with one degree of freedom. If the test is significant there is phylogenetic signal in the residuals. However, we found lambda values of 6.73e-05, 5.56e-04 and 2.68e-04, and *p*-values of 0.51, 0.47 and 0.62 for mammals, birds in breeding ranges and birds in non-breeding ranges, respectively. Therefore we conclude that there is no phylogenetic signal in the residuals of the models and a phylogenetically informed model is not justified.

We performed a model selection using the Akaike Information Criterion (AIC) to find the set of predictors to include in the final model that minimize the Kullback–Leibler distance between the model and the observed values. We applied logarithmic and quadratic transformations to the predictors and included variable interactions in the models, but most of them did not lead to a decrease in AIC or increase in model performance calculated by using the Area Under the Curve (AUC). Finally, to test our models for overdispersion, we calculated the sum of squared Pearson residuals and compared it to the residual degrees of freedom by using a Chi-squared test. *P*-values close to 1 indicate that the probability of the model being overdispersed approaches 0 (Supplementary Table 13).

On the basis of the relationship between the observed response of species and our independent variables found with the best multinomial models, we predicted the probabilities of the four classes of response to climate change by using the function predict in *R*. For predictions we considered all threatened birds (1,272 species, as listed on the 2014 IUCN Red List) and terrestrial non-volant mammals (873 species) with available data. We excluded sea mammals from our analysis because the environmental variables that influence the persistence of marine and terrestrial species are different, and most of the variables important for marine species (for example, sea temperature, salinity) were not available for the study period. Chiroptera could not be considered in this study because of the paucity of data available on their life history.

Our model is at the species level, but our data (observed responses to climate change) is at the population level. Because the spatial extent of the study area was not available for the vast majority of studies, we were forced to average the annual temperature change experienced by the species across all of its range. However, the average climatic change might not be representative of the change experienced by the populations we used to train the model, especially with species with large range size. By resampling the response category assigned to each species from the multinomial distribution 100 times and deriving coefficient intervals and mean values of the richness of species with negative responses, we tried to reduce the uncertainty around our predictions. In addition, to identify the taxonomic orders for which our predictions were most reliable, we used a Kolmogorov–Smirnov nonparametric test which quantifies the distance between the empirical continuous distribution functions of two samples, and the null hypothesis is that the samples are drawn from the same distribution. By comparing the distribution of the same numeric trait in both the observed and the predicted sample, if the *p*-value of the test is above the $\alpha$ threshold, that is, 0.05, we can assume that threatened species in the considered taxonomic order are well represented in the sample of observed data. This means that, for this order, our predictions are more robust.

**Data availability.** The authors declare that (the/all other) data supporting the findings of this study are available within the article and its Supplementary Information files.

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# A globally coherent fingerprint of climate change impacts across natural systems

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**Causal attribution of recent biological trends to climate change is complicated because non-climatic influences dominate local, short-term biological changes. Any underlying signal from climate change is likely to be revealed by analyses that seek systematic trends across diverse species and geographic regions; however, debates within the Intergovernmental Panel on Climate Change (IPCC) reveal several definitions of a 'systematic trend'. Here, we explore these differences, apply diverse analyses to more than 1,700 species, and show that recent biological trends match climate change predictions. Global meta-analyses documented significant range shifts averaging 6.1 km per decade towards the poles (or metres per decade upward), and significant mean advancement of spring events by 2.3 days per decade. We define a diagnostic fingerprint of temporal and spatial 'sign-switching' responses uniquely predicted by twentieth century climate trends. Among appropriate long-term/large-scale/multi-species data sets, this diagnostic fingerprint was found for 279 species. This suite of analyses generates 'very high confidence' (as laid down by the IPCC) that climate change is already affecting living systems.**

The Intergovernmental Panel on Climate Change[1] (IPCC) assessed the extent to which recent observed changes in natural biological systems have been caused by climate change. This was a difficult task despite documented statistical correlations between changes in climate and biological changes[2–5]. With hindsight, the difficulties encountered by the IPCC can be attributed to the differences in approach between biologists and other disciplines, particularly economists. Studies in this area are, of necessity, correlational rather than experimental, and as a result, assignment of causation is inferential. This inference often comes from experimental studies of the effects of temperature and precipitation on the target species or on a related species with similar habitats. Confidence in this inferential process is subjective, and differs among disciplines, thus resulting in the first divergence of opinion within the IPCC.

The second impasse came from differences in perspective on what constitutes an 'important' factor. Anyone would consider a currently strong driver to be important, but biologists also attach importance to forces that are currently weak but are likely to persist. In contrast, economic approaches tend to discount events that will occur in the future, assigning little weight to weak but persistent forces. Differences of opinion among disciplines can therefore stem naturally from whether the principal motivation is to assess the magnitude of immediate impacts or of long-term trajectories. Most field biologists are convinced that they are already seeing important biological impacts of climate change[1–4,6–9]; however, they have encountered difficulty in convincing other academic disciplines, policy-makers and the general public. Here, we seek to improve communication, provide common ground for discussion, and give a comprehensive summary of the evidence.

How should a 'climate fingerprint' be defined? A straightforward view typical of an economist would be to conclude that climate change was important if it were principally responsible for a high proportion of current biotic changes. By this criterion a climate fingerprint appears weak. Most short-term local changes are not caused by climate change but by land-use change and by natural fluctuations in the abundance and distribution of species. This fact has been used by non-biologists to argue that climate change is of little importance to wild systems[10]. This approach, however, effectively ignores small, systematic trends that may become important in the longer term. Such underlying trends would be confounded (and often swamped) by strong forces such as habitat loss. Biologists have tended to concentrate on studies that minimize confounding factors, searching for trends in relatively undisturbed systems and then testing for significant associations with climate change. Economists have viewed this as biased (nonrandom exclusion of data) whereas biologists view this as reducing non-climatic noise. Thus, economists focus on total direct evidence and apply heavy time discounting; biologists apply a 'quality control' filter to available data, accept indirect (inferential) evidence and don't apply time discounting.

The test for a globally coherent climate fingerprint does not require that any single species show a climate change impact with 100% certitude. Rather, it seeks some defined level of confidence in a climate change signal on a global scale. Adopting the IPCC 'levels of confidence'[11] and applying the economists' view of a fingerprint, we would have "very high confidence" in a fingerprint if we estimated that more than 95% of observed changes were principally caused by climate change, "high confidence" between 95% and 67%, "medium confidence" between 33% and 67%, and "low confidence" below 33%. In contrast, the biologists' confidence level comes from the statistical probability that global biotic trends would match climate change predictions purely by chance, coupled with supporting experimental results showing causal relationships between climate and particular biological traits.

Here, we present quantitative estimates of the global biological impacts of climate change. We search for a climate fingerprint in the overall patterns, rather than critiquing each study individually. Using the biologists' approach, we synthesize a suite of correlational studies on diverse taxa over many regions to ask whether natural systems, in general, have responded to recent climate change. Furthermore, we attempt a cross-fertilization by applying an economists' measure—the estimated proportion of observed changes for which climate trends are the principal drivers—to data sets chosen using biologists' criteria. We call this a 'global coherence' approach to the detection of climate change impacts.

First, we explore a biologists' confidence assessment with two types of analyses of observed change: statistical meta-analyses of effect size in restricted data sets and more comprehensive categorical analyses of the full literature. Second, we present a probabilistic model that considers three variables: proportion of observations matching climate change predictions, numbers of competing explanations for each of those observations, and confidence in causal


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attribution of each observation to climate change. These three variables feature equally in a model that explores an economists' 'confidence' assessment. Finally, we explore diagnostic 'sign-switching' patterns that are predicted uniquely by climate change.

## The evidence

A few studies indicate evolutionary responses of particular species to climate change[12–14], but the generality of evolutionary response remains unknown. Here, we focus on phenological (timing) shifts, range boundary shifts, and community studies on species abundances (Table 1).

### Meta-analyses

We developed databases suitable for meta-analysis[15] on two phenomena: range-boundary changes and phenological shifts. To control for positive publishing bias, we used only multi-species studies that reported neutral and negative results as well as positive (see Methods).

For range boundaries, suitable data spanned 99 species of birds[16], butterflies[17] and alpine herbs[18,19] (see Methods). The meta-analysis showed that the range limits of species have moved on average 6.1 ($\pm$2.4) km per decade northward or m per decade upward, significantly in the direction predicted by climate change (bootstrapped 95% confidence interval of the mean ($CI_{mean}$) = 1.3–10.9 km $m^{-1}$ per decade; one-sample *t*-test, degrees of freedom (d.f.) = 98, $t = 2.52$, $P = 0.013$; Table 2).

For phenologies, suitable data were reported for herbs[20–23], shrubs[20–25], trees[20,23–25], birds[20,21], butterflies[26] and amphibians[27,28], a total of 172 species (see Methods). There was a mean shift towards earlier spring timing of 2.3 days per decade, with a bootstrapped 95% CI of 1.7–3.2 days advancement per decade (significant at $P < 0.05$).

### Categorical analyses

The remaining studies were not included in the meta-analyses, either because they were on single species or because they did not present data in the raw form of *x* unit change per *y* time units per species. These less-detailed data were simplified into four categories: changed in accord with or opposite to climate change predictions, changed in some other fashion or stable (see Methods).

As with previous studies[17], analyses ignore species classified as 'stable'. This category does not represent a single result, as apparent stability could arise from a diversity of situations[17] such as: 1) the phenology, abundance or distribution of the species is not driven by climatic factors; 2) the species is actually changing, but poor data resolution could not detect small changes; and 3) the phenology, abundance or distribution of the species is driven by climatic factors, but fails to respond to current climate change. Such failure could stem from anthropogenic barriers to dispersal (habitat fragmentation) or from a lag in response time. Lags are expected when limited dispersal capabilities retard poleward/upward colonization[29], or when a necessary resource has slower response time than the focal species[17].

**Phenological shifts.** We quantitatively assessed 677 species reported in the literature (Table 1). Over a time period range of 16–132 years (median 45 yrs), 27% showed no trends in phenologies, 9% showed trends towards delayed spring events, whereas the remaining 62% showed trends towards spring advancement. Observed trends include earlier frog breeding[27,28], bird nesting[30–32], first flowering[20–25], tree budburst[23–25], and arrival of migrant birds and butterflies[20,21,26,33] (Table 1). Shifts in phenologies that have occurred are overwhelmingly (87%) in the direction expected from climate change ($P < 0.1 \times 10^{-12}$; Table 2).

**Distribution/abundance shifts.** In a quantitative assessment covering >1,046 species, we were able to categorize 893 species, functional

Table 1 **Summary of data studying phenological and distributional changes of wild species**

| Taxon | Ref. number | Total no. of species (or species groups) | Spatial scale | | | Time scale (range years) | Change in direction predicted (*n*) | Change opposite to prediction (*n*) | Stable (*n*) | No prediction (*n*) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | L | R | C | | | | | |
| Phenological changes | | | | | | | | | | |
| Woody plants | 20,23,24*,25* | *n* = 38 sp | | 2 | 1 | 35–132 | 30 | 1 | 7 | – |
| Herbaceous plants | 20,21* | *n* = 38 sp | 1 | 1 | | 63–132 | 12 | – | 26 | – |
| Mixed plants | 22* | *n* = 385 sp | 1 | | | 46 | 279 | 46 | 60 | – |
| Birds | 20,21*,30,31,32,33 | *n* = 168 sp | 2 | 3 | 1 | 21–132 | 78 | 14 | 76 | – |
| Insects | 26 | *n* = 35 sp | | 1 | | 23 | 13 | – | 22 | – |
| Amphibians | 27,28 | *n* = 12 sp | 2 | | | 16–99 | 9 | – | 3 | – |
| Fish | 20 | *n* = 2 sp | | 1 | | 132 | 2 | – | – | – |
| Distribution/abundance changes | | | | | | | | | | |
| Tree lines | 54,55,56* | *n* = 4 sp + 5 grps | 2 | 1 | | 70–1,000 | 3 sp + 5 grps | – | 1 | – |
| Herbs and shrubs | 18,19,41*,42* | *n* > 66 sp, 15 detailed | | 3 | | 28–80 | 13 | 2 | – | – |
| Lichens | 36 | 4 biogeographic grps (*n* = 329 sp) | 1 | | | 22 | 43 | 9 | 113 | 164 |
| Birds | 8* | *n* = 3 sp | | 1 | | 50 | 3 | – | – | – |
| | 16,57* | N sp (*n* = 46 sp) | | 2 | | 20–36 | 13 | 15 | 18 | |
| | | S sp (*n* = 73 sp) | | 2 | | 20–36 | 36 | 16 | 21 | 6 |
| | 43* | Low elevation (>91 sp) | 1 | | | 20 | 71 | 11 | 9 | – |
| | | High elevation (>96 sp) | 1 | | | 20 | 37 | 27 | 32 | – |
| Mammals | 37 | *n* = 2 sp | | 1 | | 52 | 2 | – | – | – |
| Insects | 17,49* | *n* = 36 sp | | 1 | 1 | 98–137 | 23 | 2 | 10 | 1 |
| | 17 | N boundaries (*n* = 52 sp) | | 1 | | 98 | 34 | 1 | 17 | – |
| | | S boundaries (*n* = 40 sp) | | 1 | | 98 | 10 | 2 | 28 | – |
| Reptiles and amphibians | 43* | *n* = 7 sp | 1 | | | 17 | 6 | – | 1 | – |
| Fish | 39 | *4* biogeographic grps (*n* = 83 sp) | 1 | | | – | 2 grps | – | 1 grp | 1 grp |
| | 40* | N sp (*n* > 1 sp) | | 1 | | 70 | >1 | – | – | – |
| | | S sp (*n* > 1 sp) | | 1 | | 70 | >1 | – | – | – |
| Marine invertebrates | 34*,40* | N sp (*n* > 21) | 1 | 1 | | 66–70 | >19 | 2 | – | >1 sp not classified |
| | | S sp (*n* > 21) | 1 | 1 | | 66–70 | >20 | 1 | – | |
| | | Cosmopolitan sp (*n* = 28 sp) | 1 | | | 66 | – | – | – | 28 |
| Marine zooplankton | 40* | Cold water (*n* > 10 sp) | | 1 | | 70 | >10 | – | – | >8 sp not classified |
| | | Warm water (*n* > 14 sp) | | 1 | | 70 | >14 | – | – | |
| | 35 | 6 biogeographic grps (*n* ≥ 36 sp) | | | 1 | 39 | 6 grps | – | – | – |

N, species with generally northerly distributions (boreal/arctic); S, species with generally southerly distributions (temperate); L, local; R, regional (a substantial part of a species distribution; usually along a single range edge); C, continental (most or the whole of a species distribution). No prediction indicates that a change may have been detected, but the change was orthogonal to global warming predictions, was confounded by non-climatic factors, or there is insufficient theoretical basis for predicting how species or system would change with climate change.

*Study partially controlled for non-climatic human influences (for example, land-use change). Studies that were highly confounded with non-climatic factors were excluded. (See Supplementary Information for details of species classification.)


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groups or biogeographic groups (Table 1). Less than one-third (27%) of these have exhibited stable distributions during the twentieth century. Others (24%) show changes that are impossible to relate to climate change predictions. These two types of result neither support nor refute a climate change signal, although it will be important for predictive biological models to eventually determine what proportion of these are truly stable systems.

Some range shifts have been measured directly at range boundaries, whereas others have been inferred from abundance changes within local communities. Over all of the range and abundance shift data, 434 species were categorized as changing over time periods of 17–1,000 years (median 66 years) (Table 1). Of these, 80% have shifted in accord with climate change predictions (see Methods) ($P < 0.1 \times 10^{-12}$; Table 2). New species have colonized previously 'cool' regions, including sea anemones in Monterey Bay[34] and lichens and butterflies in Europe[17,36], whereas some Arctic species have contracted in range size[35,37]. Over the past 40 years, maximum range shifts vary from 200 km (butterflies[17]) to 1,000 km (marine copepods[34]).

## Probabilistic coherence

How strong is the climate change signal in the light of confounding factors and lack of experimentation? We investigate this argument in a probabilistic context. We formulated a probabilistic model to ask whether a climate change fingerprint exists in a disparate set of $n$ observed biological changes. Let $n'/n$ indicate the proportion of observations counter to climate change predictions and $p$ indicate the probability that climate change is the only possible causal agent of the observed biological change in any of the $n - n'$ species that do conform to climate change predictions. In practice, this can be estimated across a set of species by assigning each species a 0 or a 1, depending on whether or not competing explanations exist; $p$ then is the proportion of species that have no competing explanations.

Competing (non-climatic) explanations can, therefore, be expected in $\{(1 - p)(n - n')\}$ of the reported analyses. Finally, for any of the $n - n'$ climate-conforming species, let $\pi$ indicate the probability, determined from previous empirical study, that climate change is the principal causal agent of a particular biological change (independent of $p$).

These three variables, each varying from 0 to 1, are inputs to a binomial probability model whose output estimates the proportion of all species that are, in truth, being impacted by climate change. In practice, confounding factors can never be eliminated completely from observational studies; therefore, $p$ would normally have a low value. Here, we consider only the conservative case where $p = 0$; that is, we assume that non-climatic alternative explanations exist for every species. In the Supplementary Information, we present modelling schemes where $p$ varies from 0 to 1.0.

The importance of non-climatic explanations should decrease with increasing scale. Most local changes are idiosyncratic and consist of noise when scaled up; however, atmospheric carbon dioxide levels have risen nearly uniformly across the globe. Increased $CO_2$ can directly cause earlier flowering[38], as does increased temperature, making these effects difficult to separate. However, these two effects can be viewed as different aspects of global warming, legitimizing discussion of their joint impacts.

The variable $\pi$ reflects the extent to which previous study and experimentation provides clear mechanistic understanding of the links between climate variables and a species' behaviour and ecology. To understand the importance of $\pi$, consider the case of the silver-spotted skipper butterfly (*Hesperia comma*) that has expanded its distribution close to its northern boundary in England over the past 20 years. Possible ecological explanations for this expansion are regional warming and changes in land use. Comparing the magnitudes and directions of these two factors suggests that climate change is more likely than land-use change to be the cause of expansion[29]. Deeper support was provided by previous empirical studies documenting strong thermal limitation. At the northern boundary, development of offspring was restricted to the hottest microclimates (south-facing chalk slopes). Range expansion coincided with colonization of non-southern slopes. Simulation models based solely on previously measured thermal tolerances (that is, without land-use change) closely matched the observed expansion of 16.4 km (model prediction 14.4 km)[12]. Thus, mechanistic understanding of the system generates a high estimate for $\pi$.

Figure 1 shows relationships between the $n'/n$ proportions and the minimum value of $\pi$ that would be required to sustain different degrees of confidence for $p = 0$. For example, the medium confidence region shows minimum values of $\pi$ that would be required across the displayed range of $n'/n$ proportions to guarantee that about half of the observed species impacts were in truth being driven principally by climate change. Claiming a climate fingerprint with high confidence would require high minimum values for $\pi$ ($>0.67$) regardless of $n'/n$.

## Applying the probabilistic model

Using all of the data from Table 2 to parameterize the model, $n' = 147$ and $n = 770$, making $n'/n = 0.16$ (16% of species changing opposite to climate change predictions). We now consider $\pi$. The extent to which climate change can be isolated as the predominant driving force is extremely variable among species and systems. Such attribution results from a subjective synthesis of experimental and observational research, often conducted well before and independently of any study of long-term trends. The species for which $\pi$ is high are those with a history of basic biological research, especially where research has been conducted along several axes (controlled laboratory/greenhouse experiments, field manipulations and observations).

Table 2 **Summary statistics and synthetic analyses derived from Table 1**

| Type of change | Changed as predicted | Changed opposite to prediction | *P*-value |
|---|---|---|---|
| Phenological ($N = 484/(678)$) | 87% ($n = 423$) | 13% ($n = 61$) | $<0.1 \times 10^{-12}$ |
| Distributional changes | | | |
| At poleward/upper range boundaries | 81% | 19% | – |
| At equatorial/lower range boundaries | 75% | 25% | – |
| Community (abundance) changes | | | |
| Cold-adapted species | 74% | 26% | – |
| Warm-adapted species | 91% | 9% | – |
| $N = 460/(920)$ | 81% ($n = 372$) | 19% ($n = 88$) | $<0.1 \times 10^{-12}$ |
| Meta-analyses | | | |
| Range-boundaries ($N = 99$) | 6.1 km m$^{-1}$ per decade northward/upward shift* | | 0.013 |
| Phenologies ($N = 172$) | 2.3 days per decade advancement* | | $<0.05$ |

Data points represent species, functional groups or biogeographic groups. *N*, number of statistically or biologically significant changes/(total number species with data reported for boundary, timing, or abundance processes). The no prediction category is not included here.
*Bootstrap 95% confidence limits for mean range boundary change are 1.26, 10.87; for mean phenological shift the limits are −1.74, −3.23.


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This sort of biological detail reveals that climate and extreme weather events are mechanistically linked to body size, individual fitness and population dynamics for diverse species[3–9] (but not for all). Species for which confidence in climate as the primary driving mechanism is low are those for which long-term observational records exist, but not detailed empirical research on target species or on ecologically similar species. The black line in Fig. 1 suggests that medium confidence can be claimed for $n'/n = 0.16$ if $0.35 < \pi < 0.7$. Other contingencies, such as complications from a positive publishing bias or non-independence among confounding factors, can be considered through variations of the model (see Supplementary Information).

## Differentiating diagnostic patterns

Predictions of the impacts of climate change are not unidirectional, but may show opposite trends within communities and across long time spans or large spatial scales. Alternative causal agents would therefore have to be able to switch the sign of their impacts within a study if they were to form credible competing explanations. Such differentiating patterns greatly reduce the likelihood of hidden, non-climate competing explanations, thereby increasing $P$ and decreasing the value of $\pi$ necessary to achieve a given confidence level (see Supplementary Information). High confidence could be obtained under this scheme with existing patterns ($n'/n \leq 0.33$) and poor mechanistic understanding (low $\pi$). Sufficient data to quantify the differential impacts on species' distributions or phenologies across time periods or geographic regions were available for 334 species, among which 84% showed a sign-switching diagnostic of climate change response ($P < 0.1 \times 10^{-12}$; Table 3).

### Community representation sign switching

Community studies in regions of overlapping 'polar' and 'temperate' species base their climate change attribution on differential responses of these two categories. Among marine fish and intertidal invertebrates (for example, snails, barnacles, anemones, copepods and limpets) off the Californian coast[34,39] and in the North Atlantic[35,40], lichens in the Netherlands[36], foxes in Canada[37] and birds in Great Britain[16], polar species have tended to be stable or decline in abundance, whereas temperate species at the same site have increased in abundance and/or expanded their distributions. Analogous shifts are occurring even within the Arctic and Antarctic among penguins[8], woody plants[41] and vascular plants[42]. Similar patterns exist for lowland compared with highland birds in the tropics[43]. Most of these studies are local, with high variability of individual species' population dynamics. Even so, 80% of changes in community representation are in accord with climate change predictions (Tables 2 and 3).

### Temporal sign switching

Long-term studies encompass periods of climate cooling as well as warming. If the distributions of species are truly driven by climate trends, these species should show opposite responses to cooling and warming periods. Such sign switching has been documented in the United Kingdom for marine fish, limpets, barnacles and zooplankton[40], in the United Kingdom and Estonia for birds[20,31,44,45], and in the United Kingdom, Finland and Sweden for butterflies[17,46–48] (see also Table 3 legend). A typical pattern includes northward range shifts during the two twentieth-century warming periods (1930–45 and 1975–99), and southward shifts during the intervening cooling period (1950–70). No species showed opposing temporal trends (Table 3).

### Spatial sign switching

Whole-range, continental-scale studies, by encompassing the extremes of a species' distribution, allow testing for differential spatial impacts. In North America and Europe, detailed temporal data spanning the twentieth century were compiled for 36 butterfly species at both northern and southern range extremes[17,49]. Eight species (22%) exhibited a diagnostic pattern of northward expansion (new colonizations) and southern contraction (population extinctions). No species showed opposing range shift trends (northward contraction and southward expansion) (Table 3).

## Discussion

The logic of a global focus on biological change is analogous to that for climate change itself. With climate change, attribution of recent warming trends to changes in atmospheric gases comes from analysis of global patterns, not from detailed data from individual meteorological stations. Similarly, when assessing biological

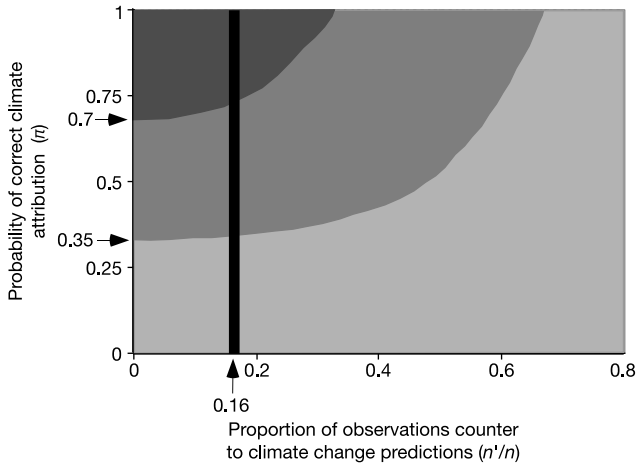


**Figure 1** Probabilistic model based on parameter estimates from a review of the literature. Levels of confidence in the linkage of biological changes to global climate change are: high (dark grey), medium (mid-grey) and low (light grey). Confidence regions assume $p = 0$ (competing explanations exist for all studies). The black line indicates the region of confidence possible using the probabilistic model on the basis of the parameter estimate of $n'/n$ from the literature review, and allowing $\pi$ to vary freely.

Table 3 **Biological fingerprint of climate change impacts**

| Sign-switching pattern | Percentage of species showing diagnostic pattern |
|---|---|
| Community | |
| Abundance changes have gone in opposite directions for cold-adapted compared with warm-adapted species. Usually local, but many species in each category. Diverse taxa, $n = 282$*. | 80% |
| Temporal | |
| Advancement of timing of northward expansion in warm decades (1930s/40s and 1980s/90s); delay of timing or southward contraction in cool decades (1950s/60s), 30–132 years per species. Diverse taxa, $n = 44$*. | 100% |
| Spatial | |
| Species exhibit different responses at extremes of range boundary during a particular climate phase. Data are from substantial parts of both northern and southern range boundaries for each species. All species are northern hemisphere butterflies, $n = 8$*. | 100% |

Differential sign-switching patterns diagnostic of climate change as the underlying driver.
*Numbers of species represent minimum estimates, as not all species were described in sufficient detail in each study to classify. A few species showed two types of sign switching, and so are included in more than one cell. Data are from references in text and from raw data provided by L. Kaila, J. Kullberg, J. J. Lennon, N. Ryrholm, C. D. Thomas, J. A. Thomas and M. Warren.


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impacts, the global pattern of change is far more important than any individual study.

The approach of biologists selects study systems to minimize confounding factors and deduces a strong climate signal both from systematic trends across studies and from empirically derived links between climate and biological systems. This deduction is made even if climate explains only a small part of the observed biological change. The meta-analyses of 334 species and the global analyses of 1,570 species (or functional/biogeographic groups) show highly significant, nonrandom patterns of change in accord with observed climate warming in the twentieth century, indicating a very high confidence (>95%) in a global climate change fingerprint (Table 2).

The approach of economists takes a broader view. In its purest form, applied to all existing data and incorporating time discounting, this approach would conclude that climate change has little total impact on wild species. We argue that this approach misses biologically important phenomena. Here we hybridize the two approaches by applying an economists' model to data that biologists would consider reasonable, and forego time discounting. A total of 74–91% of species that have changed have done so in accord with climate change predictions (Table 2) giving an estimate of $n'/n = 0.16$ for the hybrid model. Assessment of $\pi$, the probability of correct attribution to climate, is subjective and relies on the level of confidence in inferential evidence. Such evidence comes from empirical analyses and experimental manipulations, which have documented the importance of climatic variables to the dynamics, distributions and behaviour of species[3,5,8,9]. From these studies, biologists infer that expected values of $\pi$ are often high. We show that moderate values of $\pi$ (0.35–0.70) are consistent with medium confidence in a global climate change fingerprint.

The different approaches raise two distinct questions of the data and result in different levels of confidence in a climate change fingerprint. The questions are: (1) whether climate change can be shown to be an over-riding factor currently driving natural systems; and (2) whether there is sufficient evidence to implicate climate change as a common force impacting natural systems on a global scale. In an absolute sense, land-use change has probably been a stronger driver of twentieth century changes in wild plants and animals than has climate change (question 1). From a biological view, however, finding any significant climate signal amidst noisy biological data is unexpected in the absence of real climate drivers (question 2). Such small, persistent forces are inherently important in that they can alter species interactions, de-stabilize communities and drive major biome shifts.

A review of the literature reveals that the patterns that are being documented in natural systems are surprisingly simple, despite the real and potential complexity of biotic change. Change in any individual species, taxon or geographic region may have a number of possible explanations, but the overall effects of most confounding factors decline with increasing numbers of species/systems studied. Similarly, uncertainty in climate attribution for any particular study does not prevent the development of a global conclusion on the basis of a cumulative synthesis. In particular, a clear pattern emerges of temporal and spatial sign switches in biotic trends uniquely predicted as responses to climate change. With 279 species (84%) showing predicted sign switches, this diagnostic indicator increases confidence in a climate change fingerprint from either viewpoint.

The published IPCC conclusion stated high confidence ($P > 0.67$) in a climate signal across observed biotic and abiotic changes. Analyses presented here support that conclusion. Furthermore, a driver of small magnitude but consistent impact is important in that it systematically affects century-scale biological trajectories and ultimately the persistence of species. The climate fingerprint found here implicates climate change as an important driving force on natural systems. □

## Methods

### Climate change predictions

Expected phenological shifts for regions experiencing warming trends are for earlier spring events (for example, migrant arrival times, peak flight date, budburst, nesting, egg-laying, and flowering) and for later autumn events (for example, leaf fall, migrant departure times, and hibernation)[50,51]. Response to climate warming predicts a preponderance of polward/upward shifts[50,51]. Dynamics at the range boundaries are expected to be more influenced by climate than are dynamics within the interior of a species range. Thus, community level studies of abundance changes are used best to infer range shifts when they are located at ecotones involving species having fundamentally different geographic ranges: higher compared with lower latitudes, or upper compared with lower altitudes. Response to climate warming predicts that southerly species should outperform northerly species at the same site[50,51].

### Selection of studies for review

This was not an exhaustive review. The studies listed in Table 1 comprise the bulk of wild species studied with respect to climate change hypotheses. Selection of papers was aimed at those with one or more of the following attributes: long temporal span (>20 years), data covering a large geographic region, and/or data gathered in an unbiased manner for a multi-species assemblage (typically species abundance data of locally well-documented communities). We excluded several high-quality studies of single species performed at local scale or highly confounded by non-climatic global change factors. The stable category represents species for which any observed changes are indistinguishable from year to year fluctuations, either from a statistical test for trend using very long time series data or from comparing net long-term movement to expected yearly variation on the basis of basic biological knowledge of dispersal/colonization abilities.

### Meta-analyses

To create databases, studies were combined that made similar types of measurements and that reported quantitative estimates of change over a specified time period. All species were used; that is, even species that are categorized as stable in Table 1 were included in the meta-analysis. We treated phenological and distributional changes separately. To minimize positive publishing bias, only multi-species studies were included.

We considered each species as an independent data point, rather than each study. Only data reported in terms of change per individual species were included. This precluded use of studies that only report mean change across a set of species.

We used only distributional studies at range boundaries. We excluded equatorial and lower elevational boundaries because of a paucity of data combined with theoretical reasons for treating these boundaries separately from poleward/upper elevational boundaries[52]. Three studies met the criteria for data detail, covering 9 alpine herbs[18,19], 59 birds[16] and 31 butterflies[17]. The geographic locations of these boundaries were non-overlapping, reducing the likelihood of correlated confounding variables. Altitude was converted to latitudinal equivalent (for temperature clines, 1 km northward = 1 m upward). The United Kingdom bird data compared mean northern boundary in 1999 to that in 1972 using the ten northernmost occupied grid cells (on 10 $km^2$ grids) from published atlases. The Swedish butterfly data compared mean northern boundary in the period 1971–97 to mean northern boundary in 1900–20 using the five northernmost records per year. The Swiss herb data showed changes in species assemblages over the twentieth century in fixed plots up altitudinal gradients on 26 mountains.

The effect size per species was the absolute magnitude of range boundary shift, standardized across species to be in units of km $m^{-1}$ per decade, with northward/upslope shifts positive and southward/downslope shifts negative. Data were not skewed, and $n$ was large. Therefore, a one-sample $t$-test was used to evaluate the null hypothesis of no overall trends (that is, $H_ø$: mean boundary change across all species is zero). Variances were not available for all species, so we used an unweighted analysis. We performed an additional bootstrap analysis of 95% confidence limits on the mean boundary shift (10,000 iterations)[53].

The phenological meta-analysis was on spring timing events—there were insufficient studies on autumn phenology to warrant analysis. Nine studies published magnitudes of shift over a given time period (17–61 years). They included 11 trees[20,23–25], 6 shrubs[20,21,23–25], 85 herbs[20–23], 35 butterflies[26], 21 birds[21], 12 amphibians[27,28] and 2 fish[20]. This data set was inappropriate for the $t$-test owing to skew, but bootstrapped confidence limits provided an estimate of the probability that the true mean shift includes zero.

For both analyses, geography and taxa are confounded. For the range boundary analysis, all bird data are from the United Kingdom, all butterfly data from Sweden, and all herb data from Switzerland. For the phenological analysis, most shrub and bird data are from the United States, butterfly data from Great Britain, and trees from Europe. Therefore, it is not meaningful to split the analyses further.

### Categorical analyses

Reported data from all studies listed in Tables 1 and 3 were included in the categorical analyses. The predicted direction is a change predicted by global warming scenarios[50,51]. All studies were conducted in temperate Northern Hemisphere, except for 194 species in Costa Rica[43] and 5 species in Antarctica[8,42]. Two categories showing changes either predicted by or opposite to predictions of climate change theory were tested against the random expectation of an equal probability of observing changes in either direction. Analyses were by binomial test with $H_ø$: $P = 0.5$.

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# Ecological and Evolutionary Responses to Recent Climate Change

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## Key Words

aquatic, global warming, phenology, range shift, terrestrial, trophic asynchrony

## Abstract

Ecological changes in the phenology and distribution of plants and animals are occurring in all well-studied marine, freshwater, and terrestrial groups. These observed changes are heavily biased in the directions predicted from global warming and have been linked to local or regional climate change through correlations between climate and biological variation, field and laboratory experiments, and physiological research. Range-restricted species, particularly polar and mountaintop species, show severe range contractions and have been the first groups in which entire species have gone extinct due to recent climate change. Tropical coral reefs and amphibians have been most negatively affected. Predator-prey and plant-insect interactions have been disrupted when interacting species have responded differently to warming. Evolutionary adaptations to warmer conditions have occurred in the interiors of species' ranges, and resource use and dispersal have evolved rapidly at expanding range margins. Observed genetic shifts modulate local effects of climate change, but there is little evidence that they will mitigate negative effects at the species level.

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# INTRODUCTION

## Historical Perspective

Climate change is not a new topic in biology. The study of biological impacts of climate change has a rich history in the scientific literature, since long before there were political ramifications. Grinnell (1917) first elucidated the role of climatic thresholds in constraining the geographic boundaries of many species, followed by major works by Andrewartha & Birch (1954) and MacArthur (1972). Observations of range shifts in parallel with climate change have been particularly rich in northern European countries, where observational records for many birds, butterflies, herbs, and trees date back to the mid-1700s. Since the early part of the twentieth century, researchers have documented the sensitivity of insects to spring and summer temperatures (Bale et al. 2002, Dennis 1993, Uvarov 1931). Ford (1945) described northward range shifts of several butterflies in England, attributing these shifts to a summer warming trend that began around 1915 in Britain. Ford noted that one of these species, *Limenitis camilla*, expanded to occupy an area where attempted introductions prior to the warming had failed. Kaisila (1962) independently documented range shifts of Lepidoptera (primarily moths) in Finland, using historical data on range boundaries dating back to 1760. He showed repeated instances of southward contractions during decades of "harsh" climatic conditions (cold wet summers), followed by northward range expansion during decades with climate "amelioration" (warm summers and lack of extreme cold in winter). Further corroboration came from the strong correlations between summer temperatures and the northern range boundaries for many butterflies (Dennis 1993).

Similar databases exist for northern European birds. A burst of papers documented changed abundances and northerly range shifts of birds in Iceland, Finland, and Britain associated with the 1930s–1940s warming period (Gudmundsson 1951; Harris 1964; Kalela 1949, 1952; Salomonsen 1948). A second wave of papers in the 1970s described the subsequent retreats of many of these temperate bird and butterfly species following the cool, wet period of the 1950s–1960s (Burton 1975, Heath 1974, Sevenrty 1977, Williamson 1975).

Complementing this rich observational database is more than 100 years of basic research on the processes by which climate and extreme weather events affect plants and animals. As early as the 1890s, Bumpus (1899) noted the differential effects of an extreme winter storm on the introduced house sparrow (*Parus domesticus)*, resulting in stabilizing selection for intermediate body size in females and directional selection for large body size in males (Johnston et al. 1972). The first extensive studies of climate variability as a powerful driver of population evolution date back to the 1940s, when Dobzhansky (1943, 1947) discovered repeated cycles of seasonal evolution of temperature-associated chromosomal inversions within *Drosophila pseudoobscura* populations in response to temperature changes from spring through summer.

In summary, the history of biological research is rich in both mechanistic and observational studies of the impacts of extreme weather and climate change on wild species: Research encompasses impacts of single extreme weather events; experimental studies of physiological tolerances; snapshot correlations between

climatic variables and species' distributions; and correlations through time between climatic trends and changes in distributions, phenologies, genetics, and behaviors of wild plants and animals.

## Anthropogenic Climate Change

In spite of this wealth of literature on the fundamental importance of climate to wild biota, biologists have been reluctant to believe that modern (greenhouse gas-driven) climate change is a cause of concern for biodiversity. In his introduction to the 1992 *Annual Review of Ecology, Evolution, and Systematics* volume on "Global Environmental Change," Vitousek wrote, "ultimately, climate change probably has the greatest potential to alter the functioning of the Earth system . . . . nevertheless, the major effects of climate change are mostly in the future while most of the others are already with us." Individual authors in that volume tended to agree—papers were predominantly concerned with other global change factors: land use change, nitrogen fertilization, and the direct effects of increased atmospheric $CO_2$ on plant ecophysiology.

Just 14 years later, the direct impacts of anthropogenic climate change have been documented on every continent, in every ocean, and in most major taxonomic groups (reviewed in Badeck et al. 2004; Hoegh-Guldberg 1999, 2005b; Hughes 2000; IPCC 2001a; Parmesan 2005b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Sparks & Menzel 2002; Thomas 2005; Walther et al. 2002, 2005). The issue of whether observed biological changes can be conclusively linked to anthropogenic climate change has been analyzed and discussed at length in a plethora of syntheses, including those listed above. Similarly, complexity surrounding methodological issues of detection (correctly detecting a real trend) and attribution (assigning causation) has been explored in depth (Ahmad et al. 2001; Dose & Menzel 2004; Parmesan 2002, 2005a,b; Parmesan & Yohe 2003; Parmesan et al. 2000; Root et al. 2003, Root & Hughes 2005, Schwartz 1998, 1999; Shoo et al. 2006). The consensus is that, with proper attention to sampling and other statistical issues and through the use of scientific inference, studies of observed biological changes can provide rigorous tests of climate-change hypotheses. In particular, independent syntheses of studies worldwide have provided a clear, globally coherent conclusion: Twentieth-century anthropogenic global warming has already affected Earth's biota.

**Detection:** ability to discern long-term trends above yearly variability and real changes from apparent changes brought about by changes in sampling methodology and/or sampling intensity

**Attribution:** teasing out climate change as the causal driver of an observed biological change amid a backdrop of potential confounding factors

**Globally coherent:** a common term in economics, a process or event is globally coherent when it has similar effect across multiple systems spread across different locations throughout the world

## Scope of This Review

This review concentrates on studies of particularly long time series and/or particularly good mechanistic understanding of causes of observed changes. It deals exclusively with observed responses of wild biological species and systems to recent, anthropogenic climate change. In particular, agricultural impacts, human health, and ecosystem-level responses (e.g., carbon cycling) are not discussed. Because they have been extensively dealt with in previous publications, this review does not repeat discussions of detection and attribution, nor of the conservation implications of climate

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change. Rather, some of the best-understood cases are presented to illustrate the complex ways in which various facets of climatic change impact wild biota. The choice of studies for illustration attempts to draw attention to the taxonomic and geographic breadth of climate-change impacts and to the most-recent literature not already represented in prior reviews.

Researchers have frequently associated biological processes with indices of ocean-atmosphere dynamics, such as the El Niño Southern Oscillation and the North Atlantic Oscillation (Blenckner & Hillebrand 2002, Holmgren et al. 2001, Ottersen et al. 2001). However, the nature of the relationship between atmospheric dynamics, ocean circulation, and temperature is changing (Alley et al. 2003, IPCC 2001b, Karl & Trenberth 2003, Meehl et al. 2000). Therefore, there is large uncertainty as to how past relationships between biological systems and ocean indices reflect responses to ongoing anthropogenic climate change. Although I use individual examples where appropriate, this complex topic is not fully reviewed here.

## OVERVIEW OF IMPACTS LITERATURE

An extensive, but not exhaustive, literature search revealed 866 peer-reviewed papers that documented changes through time in species or systems that could, in whole or in part, be attributed to climate change. Some interesting broad patterns are revealed. Notably, the publication rate of climate-change responses increases sharply each year. The number of publications between 1899 and January 2003 (the date of two major syntheses) was 528. Therefore, approximately 40% of the 866 papers compiled for this review were published in the past three years (January 2003 to January 2006).

The studies are spread broadly across taxonomic groups. Whereas distributional studies concentrated on animals rather than plants, the reverse is true of phenological time series. This may simply be because historical data on species range boundaries have higher resolution for animals than for plants. Conversely, local records of spring events are much more numerous for plants (e.g., flowering and leaf out) than for animals (e.g., nesting).

Although there is still a terrestrial bias, studies in marine and freshwater environments are increasing in proportional representation. The largest gaps are geographic rather than taxonomic. In absolute numbers, most biological impact studies are from North America, northern Europe and Russia. Few biological studies have come from South America, and there are large holes in Africa and Asia, with most of the studies from these two continents coming from just two countries: South Africa and Japan. In past decades, Australia's impact studies have stemmed predominantly from the coral reef community, but in recent years scientists have dug deep to find historical data, and terrestrial impact studies are now emerging. Similarly, the Mediterranean/North African region (Spain, France, Italy, and Israel) has recently spawned a spate of studies. Antarctica stands out as a region where impacts (or lack of impacts) on most species and systems have been documented, even though data often have large geographic or temporal gaps.



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Few studies have been conducted at a scale that encompasses an entire species' range (i.e., a continental scale), with only a moderate number at the regional scale (e.g., the United Kingdom or Germany). Most have been conducted at local scales, typically at a research station or preserve. Continental-scale studies usually cover most or all of a species' range in terrestrial systems (Both et al. 2004, Burton 1998a,b, Dunn & Winkler 1999, Menzel & Fabian 1999, Parmesan 1996, Parmesan et al. 1999). However, even a continental scale cannot encompass the entire ranges of many oceanic species (Ainley & Divoky 1998, Ainley et al. 2003, Beaugrand et al. 2002, Croxall et al. 2002, Hoegh-Gulberg 1999, McGowan et al. 1998, Reid et al. 1998, Spear & Ainley 1999). Terrestrial endemics, in contrast, can have such small ranges that regional, or even local, studies may represent impacts on entire species (Pounds et al. 1999, 2006).

**Meta-analysis:** set of statistical techniques designed to synthesize quantitative results from similar and independent experiments

## Meta-Analyses and Syntheses: Globally Coherent Signals of Climate-Change Impacts

A handful of studies have conducted statistical meta-analyses of species' responses or have synthesized independent studies to reveal emergent patterns. The clear conclusion across global syntheses is that twentieth-century anthropogenic global warming has already affected the Earth's biota (IPCC 2001a; Parmesan 2005a,b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Thomas 2005; Walther et al. 2002, 2005).

One study estimated that more than half (59%) of 1598 species exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years (Parmesan & Yohe 2003). Analyses restricted to species that exhibited change documented that these changes were not random: They were systematically and predominantly in the direction expected from regional changes in the climate (Parmesan & Yohe 2003, Root et al. 2003). Responding species are spread across diverse ecosystems (from temperate grasslands to marine intertidal zones and tropical cloud forests) and come from a wide variety of taxonomic and functional groups, including birds, butterflies, alpine flowers, and coral reefs.

A meta-analysis of range boundary changes in the Northern Hemisphere estimated that northern and upper elevational boundaries had moved, on average, 6.1 km per decade northward or 6.1 m per decade upward ($P < 0.02$) (Parmesan & Yohe 2003). Quantitative analyses of phenological responses gave estimates of advancement of 2.3 days per decade across all species (Parmesan & Yohe 2003) and 5.1 days per decade for the subset of species showing substantive change (>1 day per decade) (Root et al. 2003).

A surprising result is the high proportion of species responding to recent, relatively mild climate change (global average warming of 0.6°C). The proportion of wild species impacted by climate change was estimated at 41% of all species (655 of 1598) (Parmesan & Yohe 2003). This estimate was derived by focusing on multispecies studies that reported stable as well as responding species. Because responders and

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stable species were often sympatric, variation of response is not merely a consequence of differential magnitudes of climate change experienced.

## PHENOLOGICAL CHANGES

By far, most observations of climate-change responses have involved alterations of species' phenologies. This is partly a result of the tight links between the seasons and agriculture: Planting and harvest dates (and associated climatic events such as day of last frost) have been well recorded, dating back hundreds of years for some crops. But the plethora of records also stems from the strong sociological significance of the change of the seasons, particularly in high-latitude countries. Peoples of Great Britain, the Netherlands, Sweden, and Finland have been keen on (some might say even obsessed with) recording the first signs of spring—the first leaf on an oak, the first peacock butterfly seen flying, the first crocus in bloom—as a mark that the long, dark winter is finally over. Fall has not captured as much enthusiasm as spring, but some good records exist, for example, for the turning of leaf color for trees.

The longest records of direct phenological observations are for flowering of cherry trees *Prunus jamasakura* and for grape harvests. Menzel & Dose (2005) show that timing of cherry blossom in Japan was highly variable among years, but no clear trends were discerned from 1400 to 1900. A statistically significant change point is first seen in the early 1900s, with steady advancement since 1952. Recent advancement exceeds observed variation of the previous 600 years. Menzel (2005) analyzed grape-harvest dates across Europe, for which April-August temperatures explain 84% of the variation. She found that the 2003 European heat wave stands out as an extreme early harvest (i.e., the warmest summer) going back 500 years. Although such lengthy observational records are extremely rare, these two unrelated plants on opposite sides of the world add an important historical perspective to results from shorter time series.

Several lines of evidence indicate a lengthening of vegetative growing season in the Northern Hemisphere, particularly at higher latitudes where temperature rise has been greatest. Summer photosynthetic activity (normalized difference vegetation index estimates from satellite data) increased from 1981–1991 (Myneni et al. 1997), concurrent with an advance and increase in amplitude of the annual $CO_2$ cycle (Keeling et al. 1996). White et al. (1999) modeled meteorological and satellite data to estimate actual growing season length each year from 1900–1987 in the United States. Growing season was unusually long during the warm period of the 1940s at all 12 sites. However, patterns have recently diverged. Since 1966, growing season length has increased only in four of the coldest, most-northerly zones (42°–45° latitude), not in the three warmest zones (32°–37° latitude). Across the European Phenological Gardens (experimental clones of 16 species of shrubs and trees at sites across Europe), a lengthening of the growing season by 10.8 days occurred from 1959–1993 (Menzel 2000, Menzel & Fabian 1999). Analysis of climatological variables (e.g., last frost date of spring and first frost date of fall) mirrors this finding, with an estimated lengthening of the growing season of 1.1–4.9 days per decade since 1951 (Menzel et al. 2003).



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Bradley et al. (1999) built on Aldo Leopold's observations from the 1930s and 1940s on the timing of spring events on a Wisconsin farm. Of 55 species resurveyed in the 1980s and 1990s, 18 (35%) showed advancement of spring events, whereas the rest showed no change in timing (with the exception of cowbirds arriving later). On average, spring events occurred 7.3 days earlier by the 1990s compared with 61 years before, coinciding with March temperatures being 2.8°C warmer.

Another long-term (100-year) study by Gibbs & Breisch (2001) compared recent records (1990–1999) of the calling phenology of six frog species in Ithaca, New York, with a turn-of-the-century study (1900–1912). They showed a 10–13-day advance associated with a 1.0–2.3°C rise in temperature during critical months. Amphibian breeding has also advanced in England, by 1–3 weeks per decade (Beebee 1995). Ecophysiological studies in frogs have shown that reproduction is closely linked to both nighttime and daytime temperatures (Beebee 1995).

In the United Kingdom, Crick et al. (1997), analyzing more than 74,000 nest records from 65 bird species between 1971 and 1995, found that the mean laying dates of first clutches for 20 species had advanced by an average 8.8 days. Brown et al. (1999) found a similar result for the Mexican jay (*Aphelocoma ultramarina*) in the mountains of southern Arizona. In the North Sea, migrant birds have advanced their passage dates by 0.5–2.8 days per decade since 1960, with no significant difference between short- and long-distance migrants (Hüppop & Hüppop 2003). In contrast, Gordo et al. (2005) found that three of six long-distance migrant birds had significantly delayed arrival to breeding grounds in Spain, with arrival date highly correlated with climatic conditions in their overwintering grounds in the southern Sahara.

Butterflies frequently show a high correlation between dates of first appearance and spring temperatures, so it is not surprising that their first appearance has advanced for 26 of 35 species in the United Kingdom (Roy & Sparks 2000) and for all 17 species analyzed in Spain (Stefanescu et al. 2003). Seventy percent of 23 species of butterfly in central California have advanced their first flight date over 31 years, by an average of 24 days (Forister & Shapiro 2003). Climate variables explained 85% of variation in flight date in the California study, with warmer, drier winters driving early flight.

There are only two continental-scale studies of bird phenology. Dunn & Winkler (1999) analyzed changes in breeding for tree swallows (*Tachycineta bicolor*) from 1959 to 1991 over the entire breeding range in the contiguous United States and Canada. Laying date was significantly correlated with mean May temperature and had advanced by an average of nine days over the 32-year period. In a complementary study, Both et al. (2004) analyzed the pied flycatcher (*Ficedula hypoleuca*) at 23 sites across Europe and found a significant advance in laying date for nine of the populations, which also tended to be those with the strongest warming trends. Continental-scale studies of both lilac (*Syringa vulgaris*) and honeysuckle (*Lonicera tatarica* and *L. korolkowii*) in the western United States have shown an advance in mean flowering dates of 2 and 3.8 days per decade, respectively (Cayan et al. 2001).

Aquatic systems exhibit similar trends to those of terrestrial systems. In a lake in the northwestern United States, phytoplankton bloom has advanced by 19 days from

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1962 to 2002, whereas zooplankton peak is more varied, with some species showing advance and others remaining stable (Winder & Schindler 2004). The Arctic seabird Brunnich's guillemot, *Uria lomvia*, has advanced its egg-laying date at its southern boundary (Hudson Bay) with no change at its northern boundary (Prince Leopold Island); both trends are closely correlated with changes in sea-ice cover (Gaston et al. 2005).

Roetzer et al. (2000) explicitly quantified the additional impacts of urban warming by comparing phenological trends between urban and rural sites from 1951 to 1995. Urban sites showed significantly stronger shifts toward earlier spring timing than nearby rural sites, by 2–4 days. An analysis of greening across the United States via satellite imagery also concluded that urban areas have experienced an earlier onset of spring compared with rural areas (White et al. 2002).

Researchers generally report phenological changes as a separate category from changes in species' distributions, but these two phenomena interplay with each other and with other factors, such as photoperiod, to ultimately determine how climate change affects each species (Bale et al. 2002, Chuine & Beaubien 2001).

## INTERACTIONS ACROSS TROPHIC LEVELS: MATCHES AND MISMATCHES

Species differ in their physiological tolerances, life-history strategies, probabilities of population extinctions and colonizations, and dispersal abilities. These individualistic traits likely underlie the high variability in strength of climate response across wild species, even among those subjected to similar climatic trends (Parmesan & Yohe 2003). For many species, the primary impact of climate change may be mediated through effects on synchrony with that species' food and habitat resources. More crucial than any absolute change in timing of a single species is the potential disruption of coordination in timing between the life cycles of predators and their prey, herbivorous insects and their host plants, parasitoids and their host insects, and insect pollinators with flowering plants (Harrington et al. 1999, Visser & Both 2005). In Britain, the butterfly *Anthocharis cardamines* has accurately tracked phenological shifts of its host plant, even when bud formation came two to three weeks early (Sparks & Yates 1997). However, this may be the exception rather than the rule.

Visser & Both (2005) reviewed the literature and found only 11 species' interactions in which sufficient information existed to address the question of altered synchrony. Nine of these were predator-prey interactions, and two were insect–host plant interactions. In spite of small sample size, an important trend emerged from this review: In the majority of cases (7 of 11), interacting species responded differently enough to climate warming that they are more out of synchrony now than at the start of the studies. In many cases, evidence for negative fitness consequences of the increasing asynchrony has been either observed directly or predicted from associated studies (Visser & Both 2005).

In one example, Inouye et al. (2000) reported results of monitoring between 1975 and 1999 at Rocky Mountain Biological Laboratory in Colorado, where there has been a 1.4°C rise in local temperature. The annual date of snowmelt and plant flowering did



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not change during the study period, but yellow-bellied marmots (*Marmota flaviventris*) advanced their emergence from hibernation by 23 days, changing the relative phenology of marmots and their food plants. In a similar vein, Winder & Schindler (2004) documented a growing asynchrony between peak phytoplankton bloom and peak zooplankton abundances in a freshwater lake.

More complex phenomena resulting from trophic mismatches have also been documented. For example, phenological asynchrony has been linked to a range shift in the butterfly *Euphydryas editha*. Warm and/or dry years alter insect emergence time relative to both the senescence times of annual hosts and the time of blooming of nectar sources (Singer 1972, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996, Weiss et al. 1988). Field studies have documented that butterfly-host asynchrony has resulted directly in population crashes and extinctions. Long-term censuses revealed that population extinctions occurred during extreme droughts and low snowpack years (Ehrlich et al. 1980, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996), and these extinctions have been highly skewed with respect to both latitude and elevation, shifting mean location of extant populations northward and upward (Parmesan 1996, 2003, 2005a).

Van Nouhuys & Lei (2004) showed that host-parasitoid synchrony was influenced signficantly by early spring temperatures. Warmer springs favored the parasitoid wasp *Cotesia melitaearum* by bringing it more in synchrony with its host, the butterfly *Melitaea cinxia*. Furthermore, they argue that because most butterfly populations are protandrous (i.e., males pupating earlier than females), temperature-driven shifts in synchrony with parasitoids may affect butterfly sex ratios.

**Intergovernmental Panel on Climate Change:** a scientific panel formed under the auspices of the United Nations and the World Meteorological Organization for the purpose of synthesizing literature and forming scientific consensus on climate change and its impacts

## OBSERVED RANGE SHIFTS AND TRENDS IN LOCAL ABUNDANCE

Expected distributional shifts in warming regions are poleward and upward range shifts. Studies on these shifts fall mainly into two types: (*a*) those that infer large-scale range shifts from small-scale observations across sections of a range boundary (with the total study area often determined by a political boundary such as state, province, or country lines) and (*b*) those that infer range shifts from changes in species' composition (abundances) in a local community. Studies encompassing the entire range of a species, or at least the northern and southern (or lower and upper) extremes, are few and have been concentrated on amphibians (Pounds et al. 1999, 2006), a mammal (Beever et al. 2003), and butterflies (Parmesan 1996, Parmesan et al. 1999). The paucity of whole-range studies likely stems from the difficulties of gathering data on the scale of a species' range—often covering much of a continent.

### Shifts at Polar Latitudes

Broad impacts of climate change in polar regions—from range shifts to community restructuring and ecosystem functioning—have been reviewed by the Intergovernmental Panel on Climate Change (Anisimov et al. 2001), the Arctic Climate Impact Assessment (2004) and the Millenium Ecosystem Assessment (Chapin et al. 2006).

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**SST:** sea surface temperature

**Antarctic.** Plant, bird, and marine life of Antarctica have exhibited pronounced responses to anthropogenic climate change. These responses have been largely attributed to extensive changes (mostly declines) in sea-ice extent, which in turn appears to have stimulated a trophic cascade effect in biological systems. Declines in sea-ice extent and duration since 1976 have apparently reduced abundances of ice algae, in turn leading to declines in krill (from 38%–75% per decade) in a large region where they have been historically concentrated, the southwest Atlantic (Atkinson et al. 2004). Krill (*Euphausia superba*) is a primary food resource for many fish, seabirds, and marine mammals. Interestingly, McMurdo Dry Valleys, which actually cooled between 1990 and 2000, also showed declines in lake phytoplankton abundances and in soil invertebrate abundances (Doran et al. 2002).

Penguins and other seabirds in Antarctica have shown dramatic responses to changes in sea-ice extent over the past century (Ainley et al. 2003, Croxall et al. 2002, Smith et al. 1999). The sea-ice dependent Adélie and emperor penguins (*Pygoscelis adeliae* and *Aptenodytes forsteri*, respectively) have nearly disappeared from their northernmost sites around Antarctica since 1970. Emperors have declined from 300 breeding pairs down to just 9 in the western Antarctic Peninsula (Gross 2005), with less severe declines at Terre Adélie (66° S), where they are now at 50% of pre-1970s abundances (Barbraud & Weimerskirch 2001). Adélies have declined by 70% on Anvers Island (64°–65° S along the Antarctic peninsula (Emslie et al. 1998, Fraser et al. 1992), whereas they are thriving at the more-southerly Ross Island at 77° S (Wilson et al. 2001)—effectively shifting this species poleward. In the long-term, sea-ice-dependent birds will suffer a general reduction of habitat as ice shelves contract [e.g., as has already occured in the Ross Sea (IPCC 2001b)] or collapse [e.g., as did the Larsen Ice Shelves along the Antarctic Peninsula in 2002 (Alley et al. 2005)].

In contrast, open-ocean feeding penguins—the chinstrap and gentoo—invaded southward along the Antarctic Peninsula between 20 and 50 years ago, with paleological evidence that gentoo had been absent from the Palmer region for 800 years previously (Emslie et al. 1998, Fraser et al. 1992). Plants have also benefited from warming conditions. Two Antarctic vascular plants (a grass, *Deschampsia antarctica*, and a cushion plant, *Colobanthus quitensis*) have increased in abundance and begun to colonize novel areas over a 27-year period (Smith 1994).

**Arctic.** Nearly every Arctic ecosystem shows marked shifts. Diatom and invertebrate assemblages in Arctic lakes have shown huge species' turnover, shifting away from benthic species toward more planktonic and warm-water-associated communities (Smol et al. 2005). Across northern Alaska, Canada, and parts of Russia, shrubs have been expanding into the tundra (Sturm et al. 2005). Field studies, experimentation, and modeling link this major community shift to warming air temperatures, increased snow cover, and increased soil microbial activity (Chapin et al. 1995; Sturm et al. 2001, 2005). Populations of a pole-pole migrant, the sooty shearwater (*Puffinus griseus*), have shifted their migration routes by hundreds of kilometers in concert with altered sea surface temperature (SST) in the Pacific (Spear & Ainley 1999).

Sea-ice decline in the Arctic has been more evenly distributed than in the Antarctic. Because of differing geology, with an ocean at the pole rather than land, Arctic species

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that are sea-ice dependent are effectively losing habitat at all range boundaries. Polar bears have suffered significant population declines at opposite geographic boundaries. At their southern range boundary (Hudson Bay), polar bears are declining both in numbers and in mean body weight (Stirling et al. 1999). Climate change has caused a lengthening of ice-free periods on Hudson Bay, periods during which the bears starve and live on their reserves because an ice shelf is necessary for feeding. Furthermore, researchers have also linked warming trends to reductions of the bears' main food, the ringed seal (Derocher et al. 2004, Ferguson et al. 2005). At the bears' northern range boundaries off Norway and Alaska, sea ice has also been reduced, but poorer records make it is less clear whether observed declines in body size and the number of cubs per female are linked to climate trends or to more basic density-dependent processes (Derocher 2005, Stirling 2002).

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## Shifts in Northern-Hemisphere Temperate Species

On a regional scale, a study of the 59 breeding bird species in Great Britain showed both expansions and contractions of northern range boundaries, but the average boundary change for 12 species that had not experienced overall changes in density was a mean northward shift of 18.9 km over a 20-year period (Thomas & Lennon 1999). For a few well-documented bird species, their northern U.K. boundaries have tracked winter temperatures for over 130 years (Williamson 1975). Physiological studies indicate that the northern boundaries of North American songbirds may generally be limited by winter nighttime temperatures (Burger 1998, Root 1988).

Analogous studies exist for Lepidoptera (butterflies and moths), which have undergone an expansion of northern boundaries situated in Finland (Marttila et al. 1990, Mikkola 1997), Great Britain (Hill et al. 2002, Pollard 1979, Pollard & Eversham 1995, Warren 1992), and across Europe (Parmesan et al. 1999). Depending on the study, some 30% to 75% of northern boundary sections had expanded north; a smaller portion (<20%) had contracted southward; and the remainder were classified as stable. In a study of 57 nonmigratory European butterflies, data were obtained from both northern and southern range boundaries for 35 species (Parmesan et al. 1999). Nearly two thirds (63%) had shifted their ranges to the north by 35–240 km, and only two species had shifted to the south (Parmesan et al. 1999). In the most-extreme cases, the southern edge contracted concurrent with northern edge expansion. For example, the sooty copper (*Heodes tityrus*) was common in the Montseny region of central Catalonia in the 1920s, but modern sightings are only from the Pyrenees, 50 km to the north. Symmetrically, *H. tityrus* entered Estonia for the first time in 1998, by 1999 had established several successful breeding populations, and by 2006 had reached the Baltic Sea (Parmesan et al. 1999; T. Tammaru, personal communication).

Another charismatic insect group with good historical records is Odonata (dragonflies and damselflies). In a study of all 37 species of resident odonates in the United Kingdom, Hickling et al. (2005) documented that 23 of the 24 temperate species had expanded their northern range limit between 1960–1995, with mean northward shift of 88 km.

Nondiapausing (i.e., active year-round) butterfly species are also moving northward with warmer winters. The northern boundary of the sachem skipper butterfly has expanded from California to Washington State (420 miles) in just 35 years (Crozier 2003, 2004). During a single year—the warmest on record (1998)—it moved 75 miles northward. Laboratory and field manipulations showed that individuals are killed by a single, short exposure to extreme low temperatures (–10°C) or repeated exposures to –4°C, indicating winter cold extremes dictate the northern range limit (Crozier 2003, 2004). The desert orange tip (*Colotis evagore*), which historically was confined to northern Africa, has established resident populations in Spain while maintaining the same ecological niche. Detailed ecological and physiological studies confirm that *C. evagore* has remained a specialist of hot microclimates, needing more than 164 days at greater than 12°C to mature. It has not undergone a host switch in its new habitat, and it has not evolved a diapause stage (Jordano et al. 1991).

In the Netherlands between 1979 and 2001, 77 new epiphytic lichens colonized from the south, nearly doubling the total number of species for that community (van Herk et al. 2002). Combined numbers of terrestrial and epiphytic lichen species increased from an average of 7.5 per site to 18.9 per site. An alternate approach to documenting colonizations is to document extinction patterns. Comparing recent censuses across North America (1993–1996) with historical records (1860–1986), Parmesan (1996) documented that high proportions of population extinctions along the southern range boundary of Edith's checkerspot butterfly (*E. editha*) had shifted the mean location of living populations 92 km farther north (Parmesan 1996, 2003, 2005a).

## Shifts of Tropical Species Ranges

Warming trends at lower latitudes are associated with movements of tropical species into more-temperate areas. The rufous hummingbird has undergone a dramatic shift in its winter range (Hill et al. 1998). Thirty years ago it wintered mainly in Mexico, and between 1900 and 1990, there were never more than 30 winter sightings per year along the Gulf Coast of the United States. In the early 1990s, sightings increased to more than 100 per year in the southern United States. The number of sightings has increased steadily since then—up to 1,643 by 1996, with evidence that, by 1998, resident populations had colonized 400 km inland (Howell 2002). Over this same period, winter temperatures rose by approximately 1°C (IPCC 2001b). In Florida, five new species of tropical dragonfly established themselves in 2000, an apparently natural invasion from Cuba and the Bahamas (Paulson 2001).

Similarly, North African species are moving into Spain and France, and Mediterranean species are moving up into the continental interior. The African plain tiger butterfly (*Danaus chrysippus*) established its first population in southern Spain in 1980 and by the 1990s had established multiple, large metapopulations (Haeger 1999).

## Elevational Shifts

Montane studies have generally been scarcer and less well documented (lower sampling resolution), but a few good data sets show a general movement of species upward



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in elevation. By comparing species compositions in fixed plots along an elevational gradient in Monteverde National Park, Costa Rica, Pounds et al. (1999, 2005) documented that lowland birds have begun breeding in montane cloud-forest habitat over the past 20 years. A similar study across 26 mountains in Switzerland documented that alpine flora have expanded toward the summits since the plots were first censused in the 1940s (Grabherr et al. 1994, Pauli et al. 1996). Upward movement of treelines has been observed in Siberia (Moiseev & Shiyatov 2003) and in the Canadian Rocky Mountains, where temperatures have risen by 1.5°C (Luckman & Kavanagh 2000).

The few studies of lower elevational limits show concurrent contractions upward of these warm range boundaries. Because warm boundaries generally have data gaps through time, these studies have conducted recensuses of historically recorded (sedentary) populations and looked for nonrandom patterns of long-term population extinctions.

A 1993–1996 recensus of Edith's checkerspot butterfly (*E. editha*) populations recorded 1860–1986 throughout its range (Mexico to Canada) documented that more than 40% of populations from 0–2400 m were extinct (in spite of having suitable habitat), whereas less than 15% were extinct at the highest elevations (2400–3500 m) (Parmesan 1996). Over the past 50–100 years, snowpack below 2400 m has become lighter by 14% and melts 7 days earlier, whereas higher elevations (2400–3500 m) have 8% heavier snowpack and no change in melt date (Johnson et al. 1999). In concert with altered snow dynamics, the mean location of *E. editha* populations has shifted upward by 105 m (Parmesan 1996, 2003, 2005a).

In southern France, metapopulations of the cool-adapted Apollo butterfly (*Parnassius apollo*) have gone extinct over the past 40 years on plateaus less than 850 m high but have remained healthy where plateaus were greater than 900 m high (Descimon et al. 2006). The data suggest that dispersal limitation was important, and this strong flyer can persist when nearby higher elevation habitats exist to colonize. In Spain, the lower elevational limits of 16 species of butterfly have risen an average of 212 m in 30 years, concurrent with a 1.3°C rise in mean annual temperatures (Wilson et al. 2005).

In the Great Basin of the western United States, 7 out of 25 recensused populations of the pika (*Ochotona princeps*, Lagomorpha) were extinct since being recorded in the 1930s (Beever et al. 2003). Human disturbance is minimal because pika habitat is high-elevation talus (scree) slopes, which are not suitable for ranching or recreational activities. Extinct populations were at significantly lower elevations than those still present (Parmesan & Galbraith 2004). Field observations by Smith (1974) documented that adult pika stopped foraging in the midday heat in August at low elevation sites. Subsequent experiments showed that adults were killed within a half hour at more than 31°C (Smith 1974).

## Marine Community Shifts

Decades of ecological and physiological research document that climatic variables are primary drivers of distributions and dynamics of marine plankton and fish (Hays et al. 2005, Roessig et al. 2004). Globally distributed planktonic records show strong shifts of phytoplankton and zooplankton communities in concert with regional oceanic

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climate regime shifts, as well as expected poleward range shifts and changes in timing of peak biomass (Beaugrand et al. 2002, deYoung et al. 2004, Hays et al. 2005, Richardson & Schoeman 2004). Some copepod communities have shifted as much as 1000 km northward (Beaugrand et al. 2002). Shifts in marine fish and invertebrate communities have been been particularly well documented off the coasts of western North America and the United Kingdom. These two systems make an interesting contrast (see below) because the west coast of North America has experienced a 60-year period of significant warming in nearshore sea temperatures, whereas much of the U.K. coast experienced substantial cooling in the 1950s and 1960s, with warming only beginning in the 1970s (Holbrook et al. 1997, Sagarin et al. 1999, Southward et al. 2005).

Sagarin et al. (1999) related a 2°C rise of SST in Monterey Bay, California, between 1931 and 1996 to a significant increase in southern-ranged species and decrease of northern-ranged species. Holbrook et al. (1997) found similar shifts over the past 25 years in fish communities in kelp habitat off California.

Much of the data from the North Atlantic, North Sea, and coastal United Kingdom have exceptionally high resolution and long time series, so they provide detailed information on annual variability, as well as long-term trends. Over 90 years, the timing of animal migration (e.g., veined squid, *Loligo forbesi*, and flounder *Platichthys flesus*) followed decadal trends in ocean temperature, being later in cool decades and up to 1–2 months earlier in warm years (Southward et al. 2005).

In the English Channel, cold-adapted fish (e.g., herring *Clupea harengus*) declined during both warming periods (1924 to the 1940s, and post-1979), whereas warm-adapted fish did the opposite (Southward et al. 1995, 2005). For example, pilchard *Sardina pilchardus* increased egg abundances by two to three orders of magnitude during recent warming. In the North Sea, warm-adapted species (e.g., anchovy *Engraulis encrasicolus* and pilchard) have increased in abundances since 1925 (Beare et al. 2004), and seven out of eight have shifted their ranges northward (e.g., bib, *Trisopterus luscus*) by as much as 100 km per decade (Perry et al. 2005). Records dating back to 1934 for intertidal invertebrates show equivalent shifts between warm- and cold-adapted species (e.g., the barnacles *Semibalanus balanoides* and *Chthamalus* spp., respectively), mirroring decadal shifts in coastal temperatures (Southward et al. 1995, 2005).

## Pest and Disease Shifts

Pest species are also moving poleward and upward. Over the past 32 years, the pine processionary moth (*Thaumetopoea pityocampa*) has expanded 87 km at its northern range boundary in France and 110–230 m at its upper altitudinal boundary in Italy (Battisti et al. 2005). Laboratory and field experiments have linked the feeding behavior and survival of this moth to minimum nighttime temperatures, and its expansion has been associated with warmer winters. In the Rocky Mountain range of the United States, mountain pine beetle (*Dendroctonus ponderosae*) has responded to warmer temperatures by altering its life cycle. It now only takes one year per generation rather than its previous two years, allowing large increases in population abundances, which, in turn, have increased incidences of a fungus they transmit (pine blister rust,



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*Cronartium ribicola*) (Logan et al. 2003). Increased abundance of a nemotode parasite has also occurred as its life cycle shortened in response to warming trends. This has had associated negative impacts on its wild musk oxen host, causing decreased survival and fecundity (Kutz et al. 2005).

In a single year (1991), the oyster parasite *Perkinsus marinus* extended its range northward from Chesapeake Bay to Maine—a 500 km shift. Censuses from 1949 to 1990 showed a stable distribution of the parasite from the Gulf of Mexico to its northern boundary at Chesapeake Bay. The rapid expansion in 1991 has been linked to above-average winter temperatures rather than human-driven introduction or genetic change (Ford 1996). A kidney disease has been implicated in low-elevation trout declines in Switzerland. High mortality from infection occurs above 15°–16°C, and water temperatures have risen in recent decades. High infection rates (27% of fish at 73% of sites) at sites below 400 m have been associated with a 67% decline in catch; mid-elevation sites had lower disease incidence and only moderate declines in catch; and the highest sites (800–3029 m) had no disease present and relatively stable catch rates (Hari et al. 2006).

Changes in the wild also affect human disease incidence and transmission through alterations in disease ecology and in distributions of their wild vectors (Parmesan & Martens 2006). For example, in Sweden, researchers have documented marked increases in abundances of the disease-transmitting tick *Ixodes ricinus* along its northernmost range limit (Lindgren & Gustafson 2001). Between the early 1980s and 1994, numbers of ticks found on domestic cats and dogs increased by 22%–44% along the tick's northern range boundary across central Sweden. In the same time period, this region had a marked decrease in the number of extremely cold days ($<-12$°C) in winter and a marked increase in warm days ($>10$°C) during the spring, summer, and fall. Previous studies on temperature developmental and activity thresholds indicated the observed warmer temperatures cause decreased tick mortality and longer growing seasons (Lindgren & Gustafson 2001).

## Trees and Treelines: Complex Responses

A complex of interacting factors determines treeline, often causing difficulties in interpretation of twentieth-century trends. Some species are "well behaved" in that they show similar patterns of increased growth at treeline during the early warming in the 1930s and 1940s as during the recent warming of the past 20 years. In recent decades, treelines have shifted northward in Sweden (Kullman 2001) and eastern Canada (Lescop-Sinclair & Payette 1995), and upward in Russia (Meshinev et al. 2000, Moiseev & Shiyatov 2003) and New Zealand (Wardle & Coleman 1992).

However, in other studies, researchers saw a strong response to warming in the late 1930s and 1940s but a weaker (or absent) response in recent warm decades (Innes 1991, Jacoby & D'Arrigo 1995, Lescop-Sinclair & Payette 1995, Briffa et al. 1998a,b), possibly resulting from differences in rainfall between the two warm periods. In Alaska, recent decades have been relatively dry, which may have prevented trees from responding to current warming as they did before (Barber et al. 2000, Briffa et al. 1998b). In contrast, treelines in the arid southwest United States, which has

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had increased rainfall, have shown unprecedented increased tree-ring growth at high elevations (Swetnam & Betancourt 1998).

An impressive study across all of northern Russia from 1953–2002 showed a shift in tree allometries. In areas where summer temperatures and precipitation have both increased, a general increase in biomass (up 9%) is primarily a result of increased greenery (33% more carbon in leaves and needles), rather than woody parts (roots and stem). In areas that have experienced warming and drying trends, greenery has decreased, and both roots and stems have increased (Lapenis et al. 2005).

## EXTINCTIONS

### Amphibians

Documented rapid loss of habitable climate space makes it no surprise that the first extinctions of entire species attributed to global warming are mountain-restricted species. Many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds et al. 1999, 2005). Among harlequin frogs in Central and South American tropics, an astounding 67% have disappeared over the past 20–30 years. Pounds et al. (2006) hypothesised that recent trends toward warmer nights and increased daytime cloud cover have shifted mid-elevation sites (1000–2400 m), where the preponderance of extinctions have occurred, into thermally optimum conditions for the chytrid fungus, *Batrachochytrium dendrobatidis*.

### Tropical Coral Reefs

Elevated sea temperatures as small as 1°C above long-term summer averages lead to bleaching (loss of coral algal symbiont), and global SST has risen an average of 0.1°–0.2°C since 1976 (Hoegh-Guldberg 1999, IPCC 2001b). A more acute problem for coral reefs is the increase in extreme temperature events. El Niño events have been increasing in frequency and severity since records began in the early 1900s, and researchers expect this trend to continue over coming decades (Easterling et al. 2000, IPCC 2001b, Meehl et al. 2000). A particularly strong El Niño in 1997–1998 caused bleaching in every ocean (up to 95% of corals bleached in the Indian Ocean), ultimately resulting in 16% of corals rendered extinct globally (Hoegh-Guldberg 1999, 2005b; Wilkinson 2000).

Recent evidence for genetic variation among the obligate algal symbiont in temperature thresholds suggests that some evolutionary response to higher water temperatures may be possible (Baker 2001, Rowan 2004). Changes in genotype frequencies toward increased frequency of high-temperature-tolerant symbiont appear to have occurred within some coral populations between the mass bleaching events of 1997–1998 and 2000–2001 (Baker et al. 2004). However, other studies indicate that many entire reefs are already at their thermal tolerance limits (Hoegh-Guldberg 1999). Coupled with poor dispersal of symbiont between reefs, this has led several researchers to conclude that local evolutionary responses are unlikely to mitigate the negative impacts of future temperature rises (Donner et al. 2005, Hoegh-Guldberg et al. 2002).



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One optimistic result suggests that corals, to some extent, may be able to mirror terrestrial range shifts. Two particularly cold-sensitive species (staghorn coral, *Acropora ceervicornis*, and elkhorn coral, *Acropora palmata*) have recently expanded their ranges into the northern Gulf of Mexico (first observation in 1998), concurrent with rising SST (Precht & Aronson 2004). Although continued poleward shift will be limited by light availability at some point (Hoegh-Guldberg 1999), small range shifts may aid in developing new refugia against extreme SST events in future.

Although impacts have not yet been observed, the fate of coral reefs may be as, or more, affected in coming decades by the direct effects of $CO_2$ rather than temperature rise. Increased atmospheric $CO_2$ since industrialization has significantly lowered ocean pH by 0.1. The more dire projections (a doubling to tripling of current $CO_2$ levels) suggest that, by 2050, oceans may be too acidic for corals to calcify (Caldeira & Wickett 2003, Hoegh-Guldberg 2005a, Orr et al. 2005).

### Population Extinctions Leading to Range Contractions

Many species have suffered reduced habitable area due to recent climate change. For those species that have already been driven extinct at their equatorial or lower range boundaries, some have either failed to expand poleward or are unable to expand due to geographic barriers. Such species have suffered absolute reductions in range size, putting them at greater risk of extinction in the near future.

This is particularly evident in polar species, as these are already pushed against a geographical limit. Researchers have seen large reductions in population abundances and general health along the extreme southern populations of Arctic polar bears (Derocher 2005, Derocher et al. 2004, Stirling et al. 1999) and the extreme northern populations of Antarctic Adélie and emperor penguins (Ainley et al. 2003, Croxall et al. 2002, Emslie et al. 1998, Fraser et al. 1992, Smith et al. 1999, Taylor & Wilson 1990, Wilson et al. 2001). In the United Kingdom, four boreal odonates have contracted northward by an average of 44 km over 40 years (Hickling et al. 2005).

Similarly, high numbers of population extinctions have occurred along the lower elevational boundaries of mountaintop species, such as pikas in the western United States (Beever et al. 2003) and the Apollo butterfly in France (Descimon et al. 2006). For 16 mountain-restricted butterflies in Spain, warming has already reduced their habitat by one third in just 30 years (Wilson et al. 2005). Warming and drying trends on Mt. Kiliminjaro have increased fire impacts, which have caused a 400-m downward contraction of closed (cloud) forest, now replaced by an open, dry alpine system (Hemp 2005). Temperate low-elevation species are not immune: Twenty-five percent of temperate butterflies in Europe contracted northward by 35–50 km over a 30–70-year period. For one of these, its northern range boundary had not expanded, so it suffered an overall contraction of range size (Parmesan et al. 1999).

## EVOLUTION AND PLASTICITY

Species ranges are dynamic. Historically, ecologists have viewed species' niches as static and range shifts over time as passive responses to major environmental changes (global climate shifts or geological changes in corridors and barriers).

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There is no doubt that climate plays a major role in limiting terrestrial species' ranges (Andrewartha & Birch 1954; Bale et al. 2002; Parmesan et al. 2000, 2005; Precht et al. 1973; Webb & Bartlein 1992; Weiser 1973; Woodward 1987). Recent physiological and biogeographic studies in marine systems also implicate temperature as a primary driver of species' ranges (Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg & Pearse 1995).

However, evolutionary processes clearly can substantially influence the patterns and rates of response to climate change. Theoretically, evolution can also drive range shifts in the absence of environmental change (Holt 2003). A prime example of this is the hybridization of two species of Australian fruit fly that led to novel adaptations, allowing range expansion with no concomitant environmental change (Lewontin & Birch 1966).

The problem of estimating the relative roles of evolution and plasticity is tractable with extensive, long-term ecological and genetic data. For example, genetic analysis of a population of red squirrels in the Arctic indicated that 62% of the change in breeding dates occurring over a 10-year period was a result of phenotypic plasticity, and 13% was a result of genetic change in the population (Berteaux et al. 2004, Réale et al. 2003).

Geneticists in the 1940s noticed that certain chromosomal inversions in fruit flies (*Drosophila*) were associated with heat tolerance (Dobzhansky 1943, 1947). These "hot" genotypes were more frequent in southern than in northern populations and increased within a population during each season, as temperatures rose from early spring through late summer. Increases in the frequencies of warm-adapted genotypes have occurred in wild populations of *Drosophila ssp* in Spain between 1976 and 1991 (Rodríguez-Trelles & Rodriguez 1998, Rodríguez-Trelles et al. 1996, 1998), as well as in the United States between 1946 and 2002 (Levitan 2003). The change in the United States was so great that populations in New York in 2002 were converging on genotype frequencies found in Missouri in 1946.

In contrast, red deer in Norway show completely plastic responses. Their body size responds rapidly to yearly variability of winter temperatures. Warmer winters cause developing males to become larger while females become smaller (Post et al. 1999). In consequence, the end result of a gradual winter warming trend has been an increase in sexual dimorphism.

A surprising twist is that species whose phenology is under photoperiodic control have also responded to temperature-driven selection for spring advancement or fall delay. Bradshaw & Holzapfel (2001) showed that the pitcher plant mosquito, *Wyeomyia smithii*, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

## The Role of Evolution in Shaping Species' Impacts

Increasing numbers of researchers use analyses of current intraspecific genetic variation for climate tolerance to argue for a substantive role of evolution in mitigating



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negative impacts of future climate change (Baker 2001, Baker et al. 2004, Davis & Shaw 2001, Rowan 2004). However, in spite of a plethora of data indicating local adaptation to climate change at specific sites, the fossil record shows little evidence for the evolution of novel phenotypes across a species as a whole. Pleistocene glaciations represent shifts 5–10 times the magnitude of twentieth-century global warming. These did not result in major evolution at the species level (i.e., appearance of new forms outside the bounds of known variation for that species), nor in major extinction or speciation events. Existing species appeared to shift their geographical distributions as though tracking the changing climate, rather than remaining stationary and evolving new forms (Coope 1994, Davis & Zabinski 1992, Huntley 1991).

Most of the empirical evidence for rapid adaptation to climate change comes from examples of evolution in the interiors of species' ranges toward higher frequencies of already existing heat-tolerant genotypes. In studies that focus on dynamics at the edge of a species' range or across an entire range, a different picture emerges. Several studies suggest that the effects of both genetic constraints and asymmetrical gene flow are intensified close to species' borders (Antonovics 1976, Garcia-Ramos & Kirkpatrick 1997, Hoffmann & Blows 1994). It is expected that a warming climate strengthens climate stress at equatorial range boundaries and reduces it at poleward boundaries. Equatorial boundary populations are often under natural selection for increased tolerance to extreme climate in the absence of climate change, but may be unable to respond due to lack of necessary genetic variance. Furthermore, gene flow from interior populations may stifle response to selection at the range limits, even when sufficient genetic variation exists (Kirkpatrick & Barton 1997).

Because of strong trade-offs between climate tolerance and resource/habitat preferences, a relaxation of selection on climate tolerance at northern boundaries may cause rapid evolution of these correlated traits. This process has been investigated in the European butterfly *Aricia agestis*, in which populations near the northern range boundary had previously adapted to cool conditions by specializing on the host genus, *Helianthemum*, which grows in hot microclimates and hence supports fast larval growth. Climate warming did not initially cause range expansion because *Helianthemum* was absent to the immediate north of the range limit. However, warming did permit rapid evolution of a broader diet at the range limit, to a host used in more southern populations, *Geranium*, which grows in cooler microclimates. Once this local diet evolution occurred, the boundary expanded northward across the band from which *Helianthemum* was absent but *Geranium* was present (Thomas et al. 2001).

This example shows how a complex interplay may occur between evolutionary processes and ecological responses to extreme climates and climate change. However, these evolutionary events did not constitute alternatives to ecological responses to climate change; they modulated those changes. Adaptive evolution of host preference occurred at the northern range boundary in response to temperature rise, but genetic variation for host use already existed within the *A. agestis* butterfly. In this case, evolutionary processes are not an alternative to range movement, but instead modulate the magnitude and dynamics of the range shift. This is not likely to be an isolated example because populations of other species near poleward boundaries

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are known to specialize on resources that mitigate the effects of cool climate. Such resources either support rapid growth or occur in the hottest available microclimates (Nylin 1988, Scriber & Lederhouse 1992, Thomas et al. 2001).

In addition to resource choice, dispersal tendency evolves at range margins in response to climate change. In nonmigratory species, the simplest explanation of northward range expansions is that individuals have always crossed the species' boundary, and with climate warming, some of these emigrants are successful at founding new populations outside the former range. When dispersal tendency is heritable, these new populations contain dispersive individuals and higher rates of dispersal will soon evolve at the expanding boundary.

Evolution toward greater dispersal has indeed been documented in several species of insect. Two species of wing-dimorphic bush crickets in the United Kingdom have evolved longer wings at their northern range boundary, as mostly long-winged forms participated in the range expansion and short-winged forms were left behind (Thomas et al. 2001). Adults of newly colonized populations of the speckled wood butterfly (*Pararge aegeria*) in the United Kingdom have larger thoraces and greater flight capability than historical populations just to the south (Hill et al. 1999). Variation in dispersal abilities can be cryptic. Newly founded populations of the butterfly *M. cinxia* contained females that were genetically superior dispersers due to increased production of ATP (Hanski et al. 2004).

Overall, empirical evidence suggests that evolution can complement, rather than supplant, projected ecological changes. However, there is little theoretical or experimental support to suggest that climate warming will cause absolute climatic tolerances of a species to evolve sufficiently to allow it to conserve its geographic distribution in the face of climate change and thereby inhabit previously unsuitable climatic regimes (Donner et al. 2005; Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg et al. 2002; Jump & Peñuelas 2005).

## CONCLUDING THOUGHTS ON EVOLUTION AND CLIMATE CHANGE

For species-level evolution to occur, either appropriate novel mutations or novel genetic architecture (new gene complexes) would have to emerge to allow a response to selection. Lynch & Lande (1993) used a genetic model to infer rates of environmental change that would allow populations to respond adaptively. However, Travis & Futuyma (1993)—discussing the same question from broad paleontological, population, genetic, and ecological perspectives—highlighted the complexity of predicting future responses from currently known processes. Fifteen years later, answers still lie very much in empirical observations. These observations indicate that, although local evolutionary responses to climate change have occurred with high frequency, there is no evidence for change in the absolute climate tolerances of a species. This view is supported by the disproportionate number of population extinctions documented along southern and low-elevation range edges in response to recent climate warming, resulting in contraction of species' ranges at these warm boundaries, as well as by extinctions of many species.



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## SUMMARY POINTS

1. The advance of spring events (bud burst, flowering, breaking hibernation, migrating, breeding) has been documented on all but one continent and in all major oceans for all well-studied marine, freshwater, and terrestrial groups.
2. Variation in phenological response between interacting species has already resulted in increasing asynchrony in predator-prey and insect-plant systems, with mostly negative consequences.
3. Poleward range shifts have been documented for individual species, as have expansions of warm-adapted communities, on all continents and in most of the major oceans for all well-studied plant and animal groups.
4. These observed changes have been mechanistically linked to local or regional climate change through long-term correlations between climate and biological variation, experimental manipulations in the field and laboratory, and basic physiological research.
5. Shifts in abundances and ranges of parasites and their vectors are beginning to influence human disease dynamics.
6. Range-restricted species, particularly polar and mountaintop species, show more-severe range contractions than other groups and have been the first groups in which whole species have gone extinct due to recent climate change. Tropical coral reefs and amphibians are the taxonomic groups most negatively impacted.
7. Although evolutionary responses have been documented (mainly in insects), there is little evidence that observed genetic shifts are of the type or magnitude to prevent predicted species extinctions.

## FUTURE ISSUES

1. Ocean-atmosphere processes are dynamically changing in response to anthropogenic forcings. Indices such as the El Niño Southern Oscillation and the North Atlantic Oscillation may be a poor basis for projecting future biological impacts.
2. Projections of impacts will be aided by a better mechanistic understanding of ecological, behavioral, and evolutionary responses to complex patterns of climate change, and in particular to impacts of extreme weather and climate events.

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# Air quality impacts of the October 2003 Southern California wildfires

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[1] In Southern California, dry summers followed by hot and dry westerly wind conditions contribute to the region's autumn fire season. In late October 2003, 13 large Southern California wildfires burned more than 750,000 acres of land, destroyed over 3500 structures, and displaced approximately 100,000 people. The fire episode was declared the deadliest and most devastating in more than a decade, and local media advised individuals to stay indoors to avoid exposure to excessive levels of PM, CO, VOCs, and ozone caused by the wildfires. This study examines the actual impact of these wildfires on air quality in urban Los Angeles (LA) using "opportunistic" data from other air pollution studies being conducted at the time of the fires. Measurements of pollutant gases (CO, $NO_x$, and ozone), particulate matter (PM), particle number (PN) concentrations, and particle size distributions at several sampling locations in the LA basin before, during, and after the fire episode are presented. In general, the wildfires caused the greatest increases in $PM_{10}$ levels (a factor of 3–4) and lesser increases in CO, NO, and PN (a factor of up to 2). $NO_2$ levels remained essentially unchanged, and ozone concentrations dropped during the fire episode. Particle size distributions of air sampled downwind of the fires showed number modes at diameters between 100 and 200 nm, significantly larger than that of typical urban air. The particles in this size range were shown to effectively penetrate indoors, raising questions about the effectiveness of staying indoors to avoid exposure to wildfire emissions.

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## 1. Introduction

[2] Wildfires can produce substantial increases in the concentration of gaseous pollutants such as carbon monoxide (CO), nitrogen oxides ($NO_x$), ozone ($O_3$), and volatile organic compounds (VOCs) [*Cheng et al.*, 1998; *Crutzen and Andreae*, 1990] as well as particulate matter (PM) [*Dennis et al.*, 2002; *Lighty et al.*, 2000]. In recent years, there has been much interest in studying the impact of wildfires in elevating the concentrations of pollutants in the atmosphere. For instance, high CO concentrations that occurred episodically in the southeastern United States during the summer of 1995 have been attributed to large forest fires in Canada [*Wotawa and Trainer*, 2000]. In addition to regional and local impacts [*Bravo et al.*, 2002] wildfires contribute significantly to global emissions of atmospheric trace gases including $NO_x$, CO, and $CO_2$ [*Crutzen et al.*, 1979]. Concerns arising from PM emissions from wildfires include acute health effects, direct and indirect climate forcing, and regional visibility [*Bravo et al.*, 2002; *LeCanut et al.*, 1996].

[3] Emission inventories by the U.S. Environmental Protection Agency (U.S. EPA) estimate that, for the calendar year 2001, wildfires in the U.S. emitted 7.1 million tons of CO, 0.98 million tons of VOCs, 0.60 million tons of $PM_{2.5}$, and 0.66 million tons of $PM_{10}$ to the atmosphere (National Emissions Inventory-Air Pollutant Emissions Trends, Current Emission Trends Summaries, August 2003, U.S. EPA), http://www.epa.gov/ttn/chief/trends/index.html). These amounts are significant, contributing 6%, 5%, 8% and 3% of the total CO, VOC, $PM_{2.5}$, and $PM_{10}$ emissions to the atmosphere in the United States in 2001, respectively. These figures obviously vary from year-to-year with the degree of wildfire activity, and in the severe fire season of 2000, 18% of the total $PM_{2.5}$ emissions in the U.S. were estimated to originate from wildfires. Other emission inventories in specific areas have calculated significant $NO_x$ emissions from wildfires as well [*Dennis et al.*, 2002]. Some systematic studies and source testing have been carried out for prescribed burns and controlled fires in North America [*Einfeld et al.*, 1991; *Radke et al.*, 1991;

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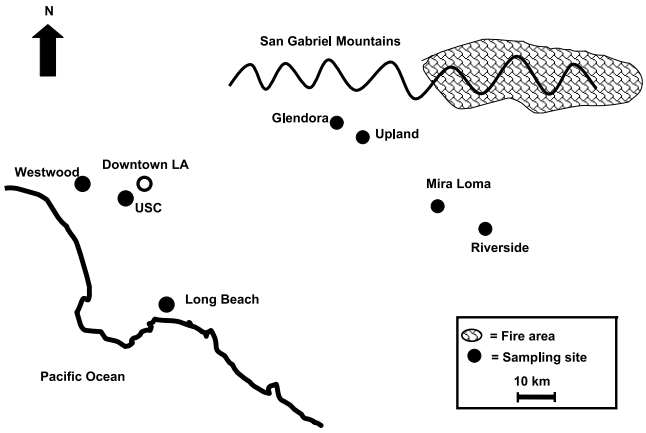


**Figure 1.** Map showing the fire area and the sampling sites in the Los Angeles basin.

*Woods et al.*, 1991]. Other studies on wildfire emissions have taken advantage of existing pollution monitoring networks and other focused air pollution studies which happen to be sampling when a wildfire event occurs [*Bravo et al.*, 2002; *Brunke et al.*, 2001; *Cheng et al.*, 1998; *Goode et al.*, 2000; *Nance et al.*, 1993]. Such "opportunistic" studies can provide valuable information on wildfire pollutant emission rates and the impacts on air quality levels.

[4] Dry summers, followed by conditions of hot and dry westerly winds (known as Santa Ana winds) contribute to Southern California's fire season in the autumn months. While the fire season usually starts around the middle of May, the exact date varies from year to year based on weather patterns and the moisture content, distribution, and amount of wild vegetation present. The fire season usually ends when cooler weather and precipitation conditions prevail. This usually occurs toward the end of October, but the fire season is occasionally extended well into January in some Southern California areas (California Department of Forestry and Fire Protection, Fire Statistics, http://www.fire.ca.gov/MiscDocuments/FAQs.asp#13). The presence of thick and dry foliage and bushy chaparral adds to the fire danger in the fire season in Southern California. In general, pollution levels are observed to be high during fire events [*Bravo et al.*, 2002]. The Los Angeles basin is surrounded by high mountains on three sides, opening to the Pacific Ocean to the west and southwest. The topography and frequent temperature inversions lead to the accumulation of airborne pollutants, particularly in the eastern portion of the basin, due to the prevailing westerly sea breeze [*Lu and Turco*, 1996].

[5] In late October 2003, 13 large Southern California wildfires, ranging from Simi Valley in the North to San Diego 150 miles to the south, burned more than 750,000 acres of land, destroyed over 3,500 structures, including 2,700 homes, and displaced 100,000 people. Twenty human deaths were attributed to the wildfires. The cost of the damage has been estimated to be $2 billion. The fires having the greatest effect on the air quality of the Los Angeles (LA) Basin included the Grand Prix and Old fires in San Bernardino County and the adjacent Padua fire in Los Angeles County. These fires were located to the northeast of central Los Angeles, with Santa Ana wind conditions, blowing toward the southwest, transporting emissions to the western portions of the Basin. The fuel was predominantly mixed chaparral, California sagebrush, annual grass and canyon live oak. Pine, perennial grass and other urban vegetation were also burned. The fires started around 23 October and had significant impacts on the air quality of the LA basin until 29 October, when the winds reversed direction and resumed their normal onshore pattern (National Interagency Coordination Centre, 2003, Statistics and Summary, http://www.nifc.gov/news/2003_statssumm/intro_summary.pdf). This fire episode was declared the deadliest and most devastating in more than a decade, and there was a significant level of worldwide press coverage. Local media advised individuals to stay indoors to avoid exposure to excessive levels of PM, CO, VOCs, and ozone caused by the wildfires. This motivated the following analysis that examines the actual impact of these wildfires on air quality and measured pollutant concentrations in urban Los Angeles. This paper presents measurements of pollutant gases (CO, $NO_x$, and ozone) as well as PM concentrations and characteristics at different sampling locations in the LA basin before, during, and after the October 2003 fire episode. In addition, the effect of fire on indoor particle concentrations and size distributions was also investigated. Since the fire episode could not be predicted, the current study took advantage of several preexisting air pollution studies that were being conducted at the time of the wildfires. Given the "opportunistic" nature of these samples, the measurement techniques were not necessarily targeted for fire emissions, and not all of the data is complete in all sampling sites.

## 2. Methods

[6] As part of the routine sampling of an ongoing study associated with the University of Southern California (USC) Children's Health Study (CHS), supported by the South Coast Air Quality Management District and the California Air Resources Board, concentrations of carbon monoxide (CO), ozone ($O_3$), nitrogen oxide (NO), nitrogen dioxide ($NO_2$,), particulate matter with aerodynamic diameters less than 10 $\mu$m ($PM_{10}$) and particle number (PN) are continuously measured in several locations in Southern California. Continuous data were collected concurrently throughout the calendar year 2003, and five sites within the LA Basin impacted by the wildfires were examined in this study: Long Beach, Glendora, Mira Loma, Upland and Riverside (see Figure 1). The choice of these sampling sites was based on their location within the Los Angeles Basin, the availability of the data for the desired period, and the observed impacts of the Grand Prix, Old and Padua fires. Generally, these urban sites are the most polluted among the monitoring sites of the CHS.

[7] Located near a busy surface street, the Long Beach station is about 1 km northeast of a major freeway. The Glendora station is located in a residential area nestled in the foothills of the San Gabriel Mountains. It is at least 1 km away from major roadways and 3 km from the nearest freeway. The Upland site is also located in a residential area about 6 km downwind of the Glendora site, but is located within 1 km of the I-210 freeway. The Mira Loma site is located in a building on the Jurupa Valley High School

campus. It is directly east of a major freeway interchange, is surrounded by several major warehouse facilities, and is located about 80 km east of downtown Los Angeles. The sampling location at Riverside is within the Citrus Research Center and Agricultural Experiment Station (CRCAES), a part of the University of California, Riverside. It is about 10 km southeast of the Mira Loma site and is situated upwind of surrounding freeways and major roads.

[8] The concentrations of CO were measured near-continuously by means of a Thermo Environmental Inc. Model 48C trace level CO monitor. Concentrations of NO and $NO_2$ were measured with a Continuous Chemiluminescence Analyzer (Monitor Labs Model 8840), and $O_3$ concentrations were monitored using a UV photometer (Dasibi Model 1003 AH). Total particle number concentrations (greater than about 10 nm in diameter) were measured continuously by a Condensation Particle Counter (CPC, Model 3022/A, TSI Incorporated, St. Paul, MN) set at a flow rate of 1.5 L $min^{-1}$. At the Upland site, the CPC was connected to a Scanning Mobility Particle Sizer (SMPS, Model 3936, TSI Incorporated, St. Paul, MN), to measure the size distribution of submicrometer aerosols (15–750 nm) using an electrical mobility detection technique. In this configuration, the CPC flow rate was maintained at 0.3 L $min^{-1}$ (with the sheath flow of the SMPS set at 3 L $min^{-1}$), and particle number counts were calculated from the SMPS size distributions. Unfortunately, due to a brief power outage and limited site access resulting from the nearby fires, SMPS data were lost from the morning of 24 October to noon of the 29 October (the peak of the fire impact). However, the other monitors at this site continued to function properly in this time window. Continuous particle number and gaseous copollutant concentrations were averaged to form 1-hour and 24-hour average values for the subsequent analysis.

[9] Hourly $PM_{10}$ mass concentrations in each site were measured by a low temperature Differential Tapered Element Oscillating Microbalance monitor (low temperature TEOM 1400A, R&P Inc., Albany, NY). The design and performance evaluation of this monitor is described in greater detail by *Jaques et al.* [2004]. Briefly, the system consists of a size-selective $PM_{10}$ inlet, followed by a Nafion® dryer that reduces the relative humidity of the sample aerosol to 50% or less. Downstream from the Nafion dryer and ahead of the TEOM sensor is an electrostatic precipitator (ESP) allowing for the removal of particles from the sample stream. The ESP is alternately switched on and off, for equal time periods of about 10 min. This dual sampling channel design makes it possible to account for effects such as volatilization of labile species, adsorption of organic vapors and changes in relative humidity and temperature, all of which affect the TEOM signal. The study by *Jaques et al.* [2004] showed that the time averaged TEOM $PM_{10}$ mass concentrations agreed within ±10% with those of collocated Federal Reference Methods (FRM).

[10] In addition to the data collected at the CHS sites, semicontinuous $PM_{2.5}$ (fine) and ultrafine PM mass concentrations were measured at the Southern California Supersite located near downtown Los Angeles at the University of Southern California (USC). Two-hour PM mass concentration data were collected with a Beta Attenuation Monitor (BAM, Model 1020, Met One instruments, Inc., OR) [*Chung et al.*, 2001]. The BAM consisted of a size-selective inlet (2.5 μm for fine and 0.15 μm for ultrafine) [*Chakrabarti et al.*, 2004], a filter tape, a beta radiation source, and a beta radiation detector. The difference in the transmission of beta radiation through the filter tape before and after a particulate sample has been collected, is measured and used to determine the mass of collected particulate matter. Continuous operation is achieved by automatic advancement of the filter tape between sampling periods.

[11] Finally, in a concurrent but unrelated study, particle size distributions were measured indoors and outdoors of a two-bedroom apartment in the Westwood Village area near the University of California, Los Angeles. The residence is located about 100 m mostly downwind (east) of the I-405 freeway, a very busy traffic source. A Scanning Mobility Particle Sizer (SMPS 3936, TSI Inc., St. Paul., MN) was set up in a bedroom and sampled alternating indoor and outdoor size distributions on a 24-hour basis. The aerosol sampling flow rate of the SMPS was set to 1.5 L $min^{-1}$ in order to measure particles as low as 6 nm as well as to minimize the diffusion losses of ultrafine particles during sampling. The maximum size detectable at these settings was 220 nm, and a scan time of 180 s was used. The sampling lines were kept the same length and as short as possible (1.5 m) for both indoor and outdoors samples. Measurements were made through a switching manifold that alternately sampled indoor and outdoor air, each for 9-min periods, in which three size distributions were taken in sequence. There were no known major indoor sources of aerosols in the residence for the period from 1000 to 1900 LT, when the residents were at work and from 2300 to 0700 LT when the residents were asleep in the other bedroom. The door of the sampling bedroom was always kept closed to minimize the influence of any other possible indoor activity. The residence was under natural ventilation with windows closed at all times during the sampling period. This study provided a unique opportunity to monitor infiltration of PM of outdoor origin into the indoor environment, and to estimate indoor exposures to PM from the wildfires.

## 3. Results and Discussion

[12] Figures 2a–2e present the 24-hour average concentrations of CO, NO, $NO_2$, $O_3$, $PM_{10}$ and particle number (PN) before, during and after the October fire period in Southern California at the five CHS sampling sites examined in this study. A summary of the average concentrations of the pollutants before, during and after the fire is given in Table 1. As surmised from the news reports and the data, the period of fire influence was from 23–29 October. Figure 2 clearly shows that the concentrations of all the pollutants drastically decreased on 30 October and then increased back to more typical levels by 4 or 5 November. The rapid decline is associated with the wind reversal on the afternoon of 29 October when an onshore wind pattern replaced the Santa Ana conditions, followed by rainfall on 30 and 31 October. Figure 3a displays a satellite photo from NASA Earth Observatory on 28 October 2003 showing the extent of the fires and the prevailing wind direction during the peak of the fire episode. On 29 October, the winds shifted to an onshore pattern (Figure 3b) blowing fresh fire emissions

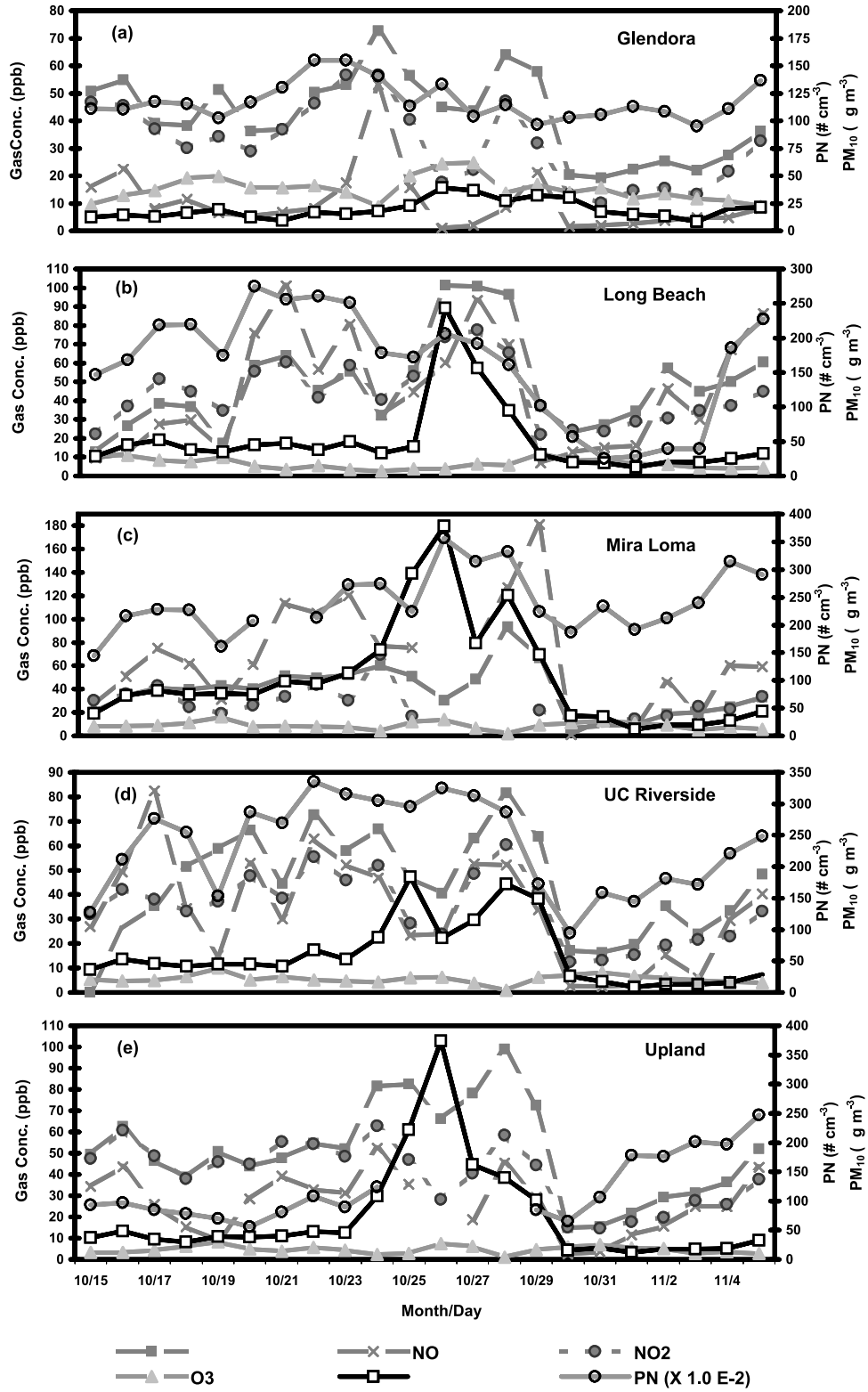


**Figure 2.** The 24-hour averaged PM and gaseous pollutant concentrations during the study at (a) Glendora, (b) Long Beach, (c) Mira Loma, (d) UC Riverside and (e) Upland. For comparison purposes, CO concentrations (in ppb) have been divided by 20, and PN concentrations (in $cm^{-3}$) have been divided by 100, as indicated in the legend.

**Table 1.** Average Hourly Concentrations of Pollutants With the Standard Deviation at the Five CHS Sites Before, During, and After the Fire[a]

| | | | Average Concentration, ± SD | | | |
|---|---|---|---|---|---|---|
| | CO, ppm | NO, ppb | $NO_2$, ppb | $O_3$, ppb | $PM_{10}$, μg $m^{-3}$ | PN, particles $cm^{-3}$ |
| | | | *Prefire* | | | |
| Glendora | 9 ± 3 | 11 ± 16 | 37 ± 16 | 37 ± 21 | 12 ± 14 | 10,400 ± 5500 |
| Long Beach | 6 ± 6 | 23 ± 49 | 47 ± 19 | 29 ± 18 | 33 ± 16 | 19,300 ± 12,400 |
| Mira Loma | 6 ± 4 | 45 ± 54 | 29 ± 14 | 25 ± 26 | 61 ± 35 | 16,200 ± 8200 |
| UC Riverside | 8 ± 6 | 40 ± 29 | 33 ± 19 | 29 ± 29 | 47 ± 23 | 16,200 ± 12,100 |
| Upland | 10 ± 4 | 24 ± 28 | 44 ± 16 | 21 ± 23 | 39 ± 18 | 9000 ± 3700 |
| | | | *During Fire* | | | |
| Glendora | 11 ± 5 | **25 ± 30** | 39 ± 28 | 44 ± 23 | **27 ± 25** | 12,200 ± 6200 |
| Long Beach | **14 ± 9** | **55 ± 68** | 56 ± 24 | **15 ± 16** | **93 ± 92** | 18,000 ± 8500 |
| Mira Loma | **12 ± 8** | **105 ± 85** | 39 ± 26 | **17 ± 18** | **215 ± 171** | **28,500 ± 14,600** |
| UC Riverside | **12 ± 7** | **46 ± 36** | 42 ± 22 | **18 ± 21** | **121 ± 112** | **28,800 ± 16,100** |
| Upland | **15 ± 7** | **43 ± 34** | 47 ± 24 | **15 ± 16** | **165 ± 138** | data not available |
| | | | *Postfire* | | | |
| Glendora | 5 ± 2 | 5 ± 5 | 17 ± 11 | 31 ± 11 | 18 ± 29 | 11,000 ± 6300 |
| Long Beach | 8 ± 6 | 39 ± 49 | 32 ± 11 | 16 ± 12 | 21 ± 10 | 8600 ± 9700 |
| Mira Loma | 4 ± 3 | 57 ± 45 | 20 ± 11 | 19 ± 15 | 28 ± 16 | 23,900 ± 10,700 |
| UC Riverside | 6 ± 4 | 14 ± 25 | 20 ± 10 | 23 ± 15 | 18 ± 10 | 1,7400 ± 11,000 |
| Upland | 6 ± 4 | 21 ± 25 | 23 ± 12 | 17 ± 13 | 19 ± 10 | 16,700 ± 8600 |

[a]Data in bold indicate statistically significant differences between the prefire and during-fire concentrations at p = 0.05.

toward the east away from the LA Basin. The fires continued to burn for many days after, but the cooler and wetter weather helped the firefighting effort and the fires were under control within another week.

[13] The data summary in Table 1 indicates that with the exceptions of $NO_2$ and $O_3$, the concentrations of CO, NO, $PM_{10}$ and PN during the fire event were significantly higher (at the p = 0.05 level) than their respective values preceding the fire event. Statistical comparisons between during and postfire concentrations was not conducted, because, as evident from the data in Table 1 and Figure 2, the unstable and wet weather conditions during the week of 30 October to 5 November resulted in lower than average air pollutant concentrations. It is of particular note, however, that the most dramatic increase in the concentrations of any pollutant during the fire events was observed for the $PM_{10}$ concentrations, which, with the exception of one site (Glendora), rose by almost three to four-fold in all sites during this period. While typical $PM_{10}$ concentrations in Los Angeles are on the order of 50 μg $m^{-3}$ or less [*Christoforou et al.*, 2000], levels rose to near or above 200 μg $m^{-3}$ at some sites during the fires. $PM_{10}$ levels at Glendora did not rise to the same degree, possibly due to the site's location at the base of a canyon in the San Gabriel Mountains. The Santa Ana winds tend to blow down the mountain canyons, and there was little or no fire activity in or upwind of this particular canyon. Upland, on the other hand, was within 2–3 km and directly downwind of extreme wildfire activity. The other three sites were all further downwind from the wildfires, but all sites experienced atypical $PM_{10}$ levels. It is possible that the higher wind speeds during Santa Ana conditions increased re-suspended dust emissions that contributed to the elevated $PM_{10}$ levels. This effect, if dominant, should be observed at all sites. However, the fact that Glendora $PM_{10}$ levels remained within the "typical" range indicates that the impact of fire smoke plumes is the main cause of the elevated $PM_{10}$ levels. Previously reported data during Santa Ana events without fires also demonstrate that such high levels of $PM_{10}$ are not typically observed on a 24-hour basis [*Geller et al.*, 2004].

[14] By contrast, the total particle number concentrations, also shown in Figure 2, did not exhibit the same extreme concentration increases during the fires. PN levels increased significantly only in Mira Loma and perhaps Riverside, and only by an approximate factor of two. Even these higher levels of PN have been observed on occasion under typical, nonfire influenced, conditions in the LA Basin [*Kim et al.*, 2002]. No significant increase in PN was observed at Long Beach, and Glendora, the latter being minimally affected by the fires as discussed above. Owing to the aforementioned power outage, PN data were not available at the closest site to the fires, Upland, during the wildfire period. Emissions testing of foliar fuels demonstrate that high particle number levels are emitted from these sources. However, given the observed high PM mass levels, and thus the increased PM surface area in the fire smoke plumes, it is conceivable that emitted smaller particles are scavenged by coagulation with larger particles in the smoke plume [*Formenti et al.*, 2003]. This process may occur over the few hours that it takes for the fire particles to reach our sampling sites. Many of the smaller particles, which make up the majority of particle number concentrations, may no longer exist as individual particles. Thus PM mass levels remain high while PN levels are diminished. This hypothesis may explain why the largest PN increase was seen at Mira Loma and Riverside, both of which are much closer to the fire areas than the sites further downwind such as Long Beach.

[15] Similar to particle number, CO concentrations at these sites were only modestly affected by the fires. With the exception of Glendora, the observed increases were statistically significant at the p = 0.05 level, but the degree of increase was much less than that observed for $PM_{10}$. Mira Loma, Upland and Long Beach experienced CO around twice normal levels during the fire. As in the case of PN, CO concentrations in the area of Glendora appear to be

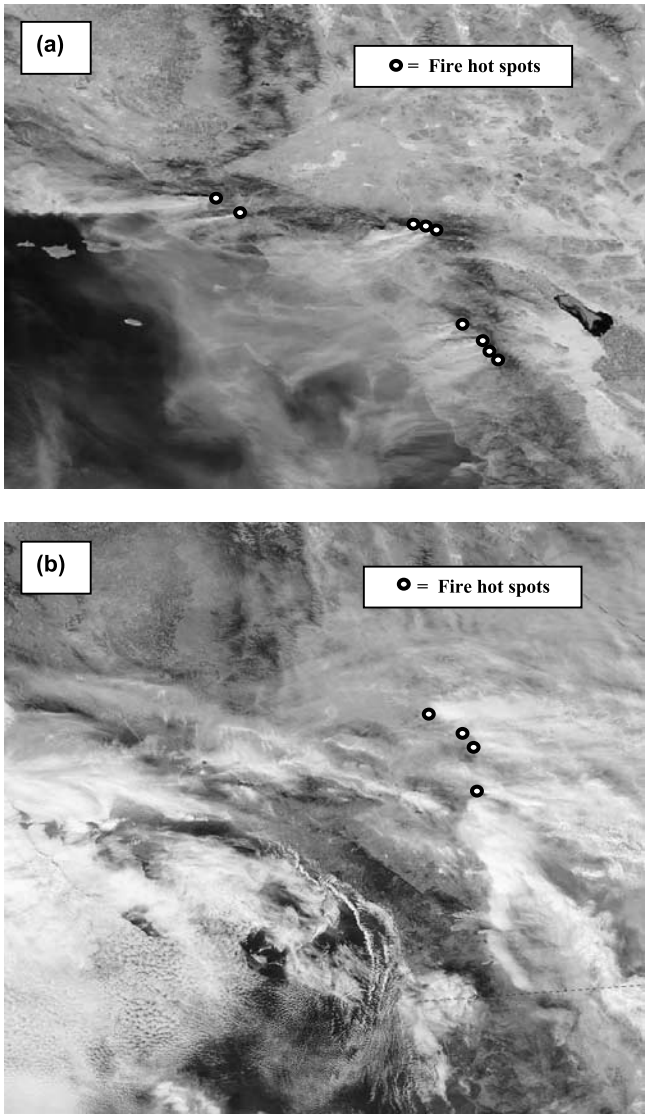


**Figure 3.** Satellite images from NASA earth observatory showing (a) Southern California during the peak of the fire episode on 28 October 2003, with the smoke plumes blowing west, and (b) the same area after the wind reversal with a visible marine layer and blowing the smoke plumes toward the northeast on the afternoon of 29 October 2003.

unaffected by the fire events. The relatively low increase in CO due to the fires can be explained by other, more significant sources of CO in Los Angeles. Emission factors from the U.S. EPA (AP-42, Fifth Edition, Volume I-Chapter 13.1: Wildfires and Prescribed Burning, U.S. EPA, October 1996) and other studies [*Barbosa et al.*, 1999; *Pereira et al.*, 1999; *Scholes et al.*, 1996] show that the ratio of CO mass to $PM_{10}$ mass in wildfire emissions lies typically between 8 and 16. The same ratio for various motor vehicles under varying driving conditions is much higher, ranging from about 200 to over 2000 [*Cadle et al.*, 2001; *Chase et al.*, 2000]. In urban areas dominated by vehicular sources, wildfires will thus affect ambient levels of CO to a lesser degree than the ambient levels of $PM_{10}$. A review of historical pollutant data during Santa Ana conditions without fire activity (9 February 2002 and 6 January 2003) shows that CO levels can diminish due to fewer CO sources upwind and increased basin ventilation. However, this effect is inconsistent, and varies greatly with sampling site and from event to event. Thus no true "Santa Ana baseline" can be established for comparison purposes. For this reason, comparisons are limited to the "typical" conditions before the fire episode.

[16] NO concentrations follow similar trends with those for CO and PN (i.e., they increase significantly in every location during the fire) but this increase is on the order of two-fold or less, hence smaller than the increase observed for $PM_{10}$. While the increase in NO concentrations during the fire event seems to be minor at the Riverside location, the nearby Mira Loma site shows more than double the NO levels relative to levels before the fire events. It is possible that Mira Loma may have been more directly downwind of fire areas than Riverside, which would explain this discrepancy. This is supported by the observed $PM_{10}$ levels at these two sites, which also increased more dramatically in Mira Loma than in Riverside. Relative to NO, PN, and $PM_{10}$, the effect of fires was negligible for $NO_2$ as the concentrations did not change significantly in any of the five sampling sites during the fire events. While some $NO_2$ is emitted directly from combustion processes, most of the $NO_2$ in urban air is formed in the atmosphere by the reaction of NO with ozone. Under normal conditions in Los Angeles, NO, and thus $NO_2$ levels are dominated by diesel vehicle emissions [*Fujita et al.*, 2003]. However, the NO increases observed during the fires were not accompanied by corresponding increases in $NO_2$ concentrations. Although no conclusive explanation can be determined from the current data, it is possible that the PM in the fire smoke blanketing the LA basin blocked incoming solar radiation and thus reduced photochemical activity in the atmosphere. This would result in lower ozone levels and thus lower observed levels of $NO_2$. Increased concentrations of organic gases (VOCs) emitted by the fires may also play a role in the complex atmospheric chemistry of NO, $NO_2$, and ozone [*Cheng et al.*, 1998]. Interestingly, with the exception of Glendora, which experienced marginally (but not significant) increased $O_3$ concentrations during the fire episode, the concentrations of $O_3$ decreased by about 25–50% at all the other sites during the fire period. As mentioned above, the fire smoke covering the basin and the corresponding reduction in photochemical activity may be a possible explanation for this decrease in concentration.

[17] The effect of the wind direction change can also be seen in the hourly concentrations of the measured pollutants in Upland as shown in Figures 4a and 4b. The high concentrations of $PM_{10}$ at Upland can be clearly seen during the entire fire period, with the highest hourly concentration measured at 769 $\mu g\ m^{-3}$. On 29 October, at 12:00 P.M., the $PM_{10}$ level was 153 $\mu g\ m^{-3}$ and within one hour it dropped to 65 $\mu g\ m^{-3}$. Within four hours, $PM_{10}$ concentrations dropped to below 20 $\mu g\ m^{-3}$. This marks the time of the wind reversal mentioned above. Unfortunately, hourly data of particle number concentrations in this time frame are not available due to the power outage. Similar to the 24-hour data, the hourly gaseous pollutant levels did not increase as much as the $PM_{10}$ levels during the period of wildfire influence. However, with the exception of ozone, concentrations of all the gaseous pollutants dropped precipitously when the wind reversal occurred.

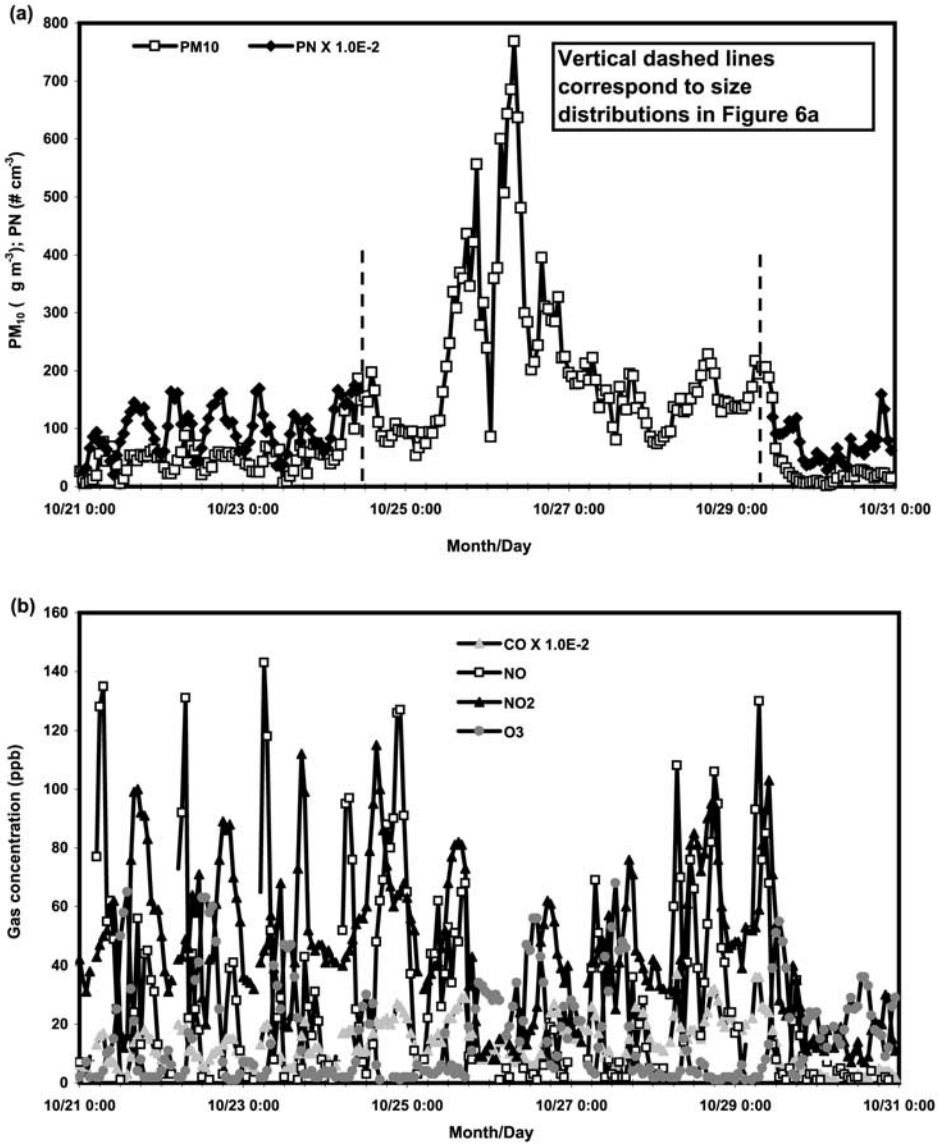


**Figure 4.** Hourly (a) PM and (b) gaseous pollutant concentrations at Upland.

[18] Semicontinuous ultrafine and fine ($PM_{2.5}$) particle mass concentration data support the argument that the atmospheric concentrations of smaller particles (measured above as PN), increased to a lesser extent than the larger particles. Figure 5 displays the 2-hour ultrafine and fine PM mass obtained from the BAM measurements at the USC site. The average ultrafine particle mass concentrations increased from an average value of 5.4 (±2.3) to 6.9 (±2.7) $\mu g\ m^{-3}$. While this increase is statistically significant ($p < 0.01$), it is still less dramatic than the obvious increase in $PM_{2.5}$ during the fire events. The average concentration of $PM_{2.5}$ more than doubled, from 19.1 (±5.2) to 51.3 (±26.1) $\mu g\ m^{-3}$. The highest fine particle mass measured during the fire episode at USC was 115 $\mu g\ m^{-3}$. The wind reversal was marked by a steep reduction in fine particle mass midday on 29 October when the fine PM dropped from 105 $\mu g\ m^{-3}$ in the morning to 25 $\mu g\ m^{-3}$ by 2:00 P.M.

[19] Figures 6a and 6b show the one-hour averaged particle size distribution at Upland corresponding to the times marked by vertical lines in Figure 4a. Because of the loss of SMPS data for almost entire fire period, we have selected times just before (Figure 6a) and just after (Figure 6b) the power outage. The particle size distribution at a given hour (1000 and 1200 LT) was averaged for different days before and after the fire, and compared to the same hour during the influence of the fires. It can be seen that the size distribution corresponding to the periods of fire influence significantly differs from those without the fire influence. The mode in the number-based particle size distribution spans from 100 to 300 nm and is indicative of the wildfire smoke. Previous emissions testing have shown similarly large number modes in the particle size distributions from the burning of foliar fuels [*Hays et al.*, 2002]. Such large diameter number modes are not normally seen in urban locations [*Kim et al.*, 2002] where particle number concentrations are dominated either by primary vehicular emissions or by nucleation processes [*Woo et al.*, 2001]. Since particle volume is proportional to the cube of the

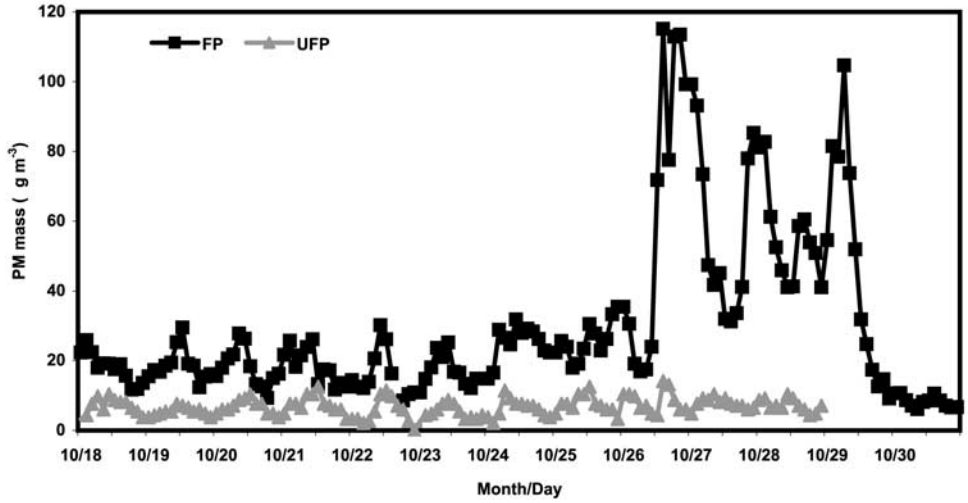


**Figure 5.** Two-hour averaged fine (FP) and ultrafine (UFP) particle mass concentrations at USC.

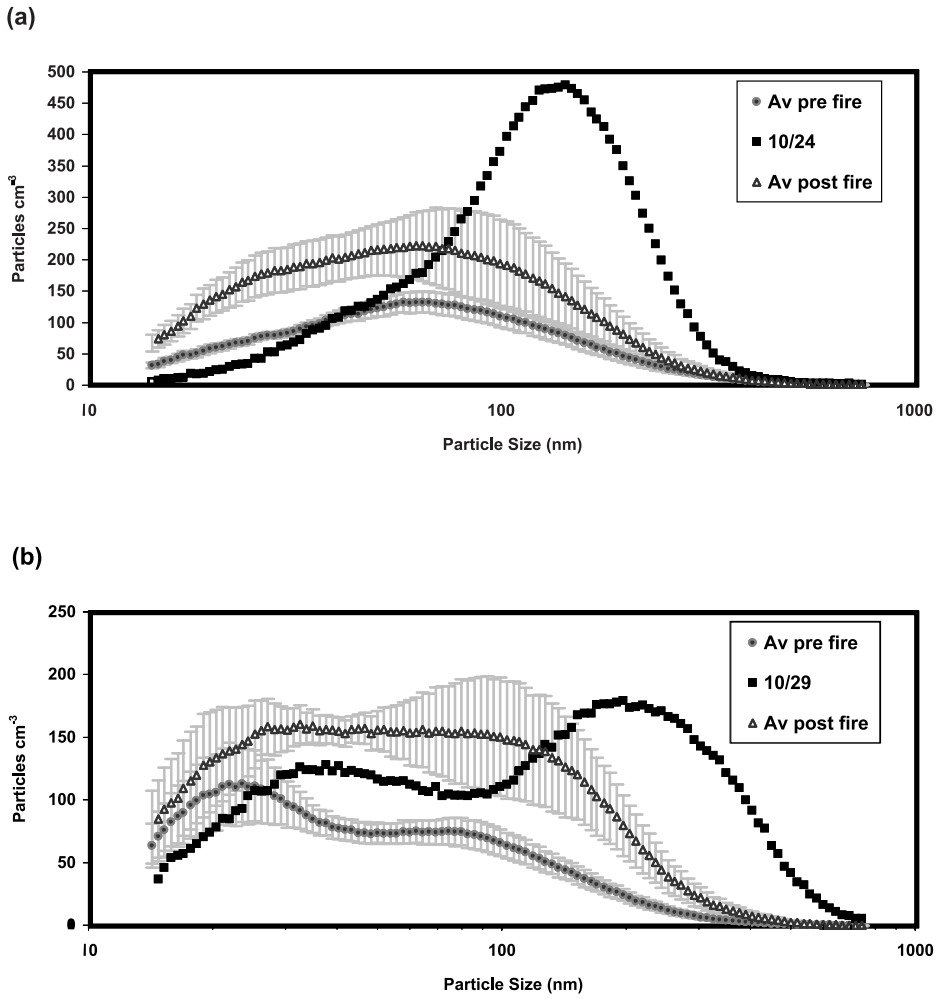


**Figure 6.** Particle size distributions at Upland (a) at 1000 LT before (24 October 2003) and after the fires and b) at 1200 LT before (29 October 2003) and after the fires.

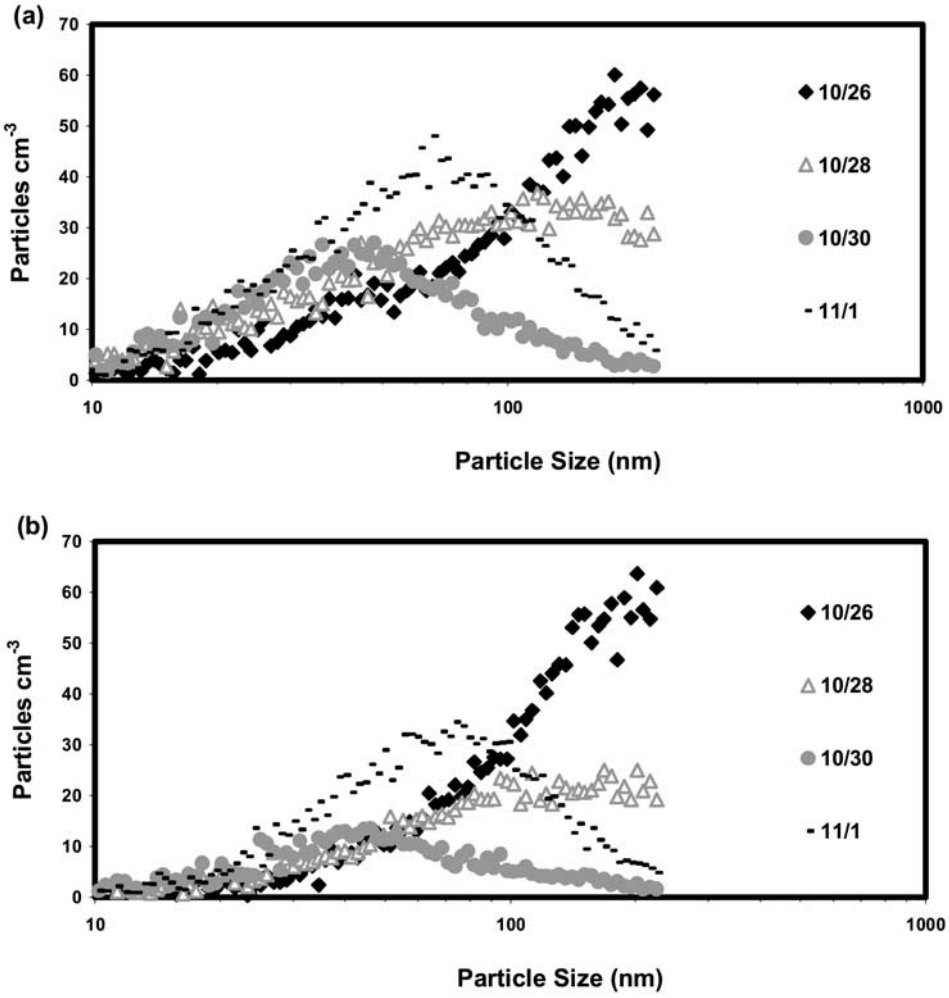


**Figure 7.** Particle size distributions on different days at 2300 LT in Westwood Village: (a) outdoor and (b) indoor.

diameter, a modest increase in particle number concentrations in these larger size modes is sufficient to account for the larger increases observed for PM mass.

[20] Indoor and outdoor particle number size distributions were also available from a concurrent study near UCLA in the western portion of the Los Angeles Basin. Figures 7a and 7b display ambient and corresponding indoor particle size distributions from 2300 to 2400 LT for different days during and after the fire events. This period was selected to minimize the influence of any possible indoor sources (i.e., cooking, cleaning) and outdoor traffic from the nearby freeway. The effect of the fires on indoor concentration is evident, with an aerosol mode diameter at about 200 nm on 26 and 28 October, and then a shift to a lower size range (between 50 to 70 nm) on 30 October and 1 November, respectively. Number concentrations both indoors and outdoors also decrease as we move away from the fire period. It is of interest to note that on 26 October (i.e., in the middle of the wildfire period), the indoor and outdoor size distributions are virtually identical in both number concentration and mode, which suggests that the majority of the outdoor aerosol infiltrated indoors with a penetration value close to 1. This is not a surprising result, considering that based on our measurements, the majority of the particles emitted from the fire are in the 100–300 nm range. This is also the range of maximum indoor penetration of outdoor aerosols and minimum indoor deposition rate [*Allen et al.*, 2003; *Long et al.*, 2001]. As the mode in aerosol size distributions shifts to smaller sizes, the indoor concentrations are approximately 50–75% lower than outdoors, which is also consistent with the penetration values determined by *Long et al.* [2001] and *Wallace and Howard-Reed* [2002] for the particles in the 40–80 nm range.

[21] To put the above results in perspective, Figures 8a and 8b show the measured indoor and outdoor particle size distributions during the morning traffic commute period, from 0600 to 0700 LT, while the wildfires were still active (27 October) and after the fire event (4 November). The outdoor size distribution on 27 October is characterized by one dominant mode at about 25 nm, which is associated with vehicular emissions [*Zhu et al.*, 2002a, 2002b], followed by a second mode at about 200 nm, which reflects the influence of the wildfires. The indoor size distribution for that date (Figure 8a) shows that the super-100 nm particles are virtually at identical concentrations with their corresponding outdoor levels, whereas the concentrations

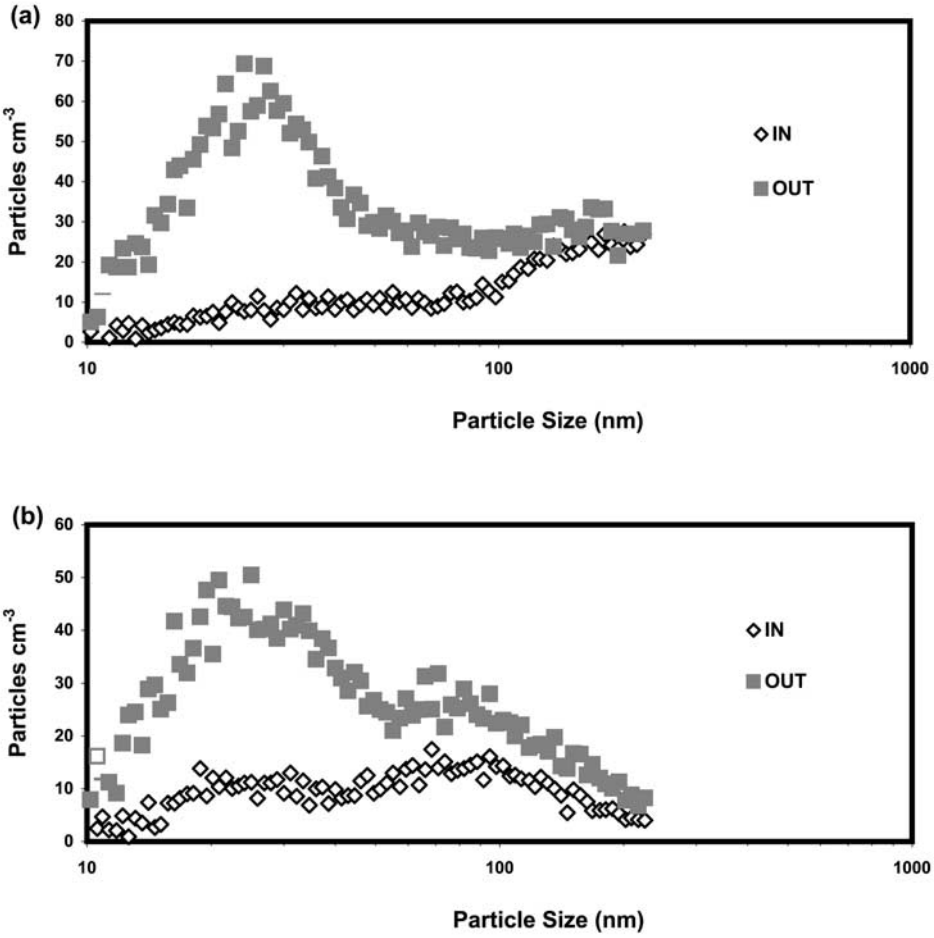


**Figure 8.** Indoor/outdoor particle size distributions at 0600 LT in Westwood Village on (a) 27 October 2003 and (b) 4 November 2003.

of smaller particles indoors are substantially lower than those outdoors. Similar trends are also shown in Figure 8b, with the exception that the second mode in the 200 nm range observed during the fire period no longer exists in either the indoor or outdoor environment.

[22] The data plotted in Figures 8a and 8b indicate an average outdoor-to-indoor penetration ratio of about 0.15 to 0.20 for particles in the 20–50 nm range, which, as stated above, originate from nearby traffic sources. This value is somewhat lower than the indoor penetration ratios reported by *Long et al.* [2001] and *Wallace and Howard-Reed* [2002] for that size range, which normally range between 0.3–0.7, depending on home characteristics and air exchange rates. One possible explanation for the lower values observed in our study may be that, as shown in recent reports in the literature [*Sakurai et al.*, 2003; *Tobias et al.*, 2001], sub-50 nm particles from vehicular emissions consist of semivolatile material, compared to the mostly nonvolatile particles in the 50–100 nm range. Thus, after penetrating indoors, they may have completely evaporated or shrunk to sizes below about 6 nm, the lower size detection limit of the SMPS. It is unknown what source, size or composition of ambient PM is responsible for the observed health effects. However, our results show that the prevailing advice during the fire episode for people to stay indoors may not be effective in reducing exposure to most of the particles emitted from wildfires.

## 4. Summary and Conclusions

[23] Coincidental air pollution sampling campaigns proved valuable in determining the impacts of the October 2003 wildfire episode on pollutant levels in the Los Angeles Basin. The greatest impact was observed on $PM_{10}$ concentrations which increased by factors of three or four depending on location. CO and NO levels increased to a lesser extent (a factor of approximately two), most likely due to the different relative emission rates of these pollutants from wildfires compared to typical urban sources such as traffic. Particle number concentrations and $NO_2$ were essentially unchanged, except at the sites nearest the fires where PN levels almost doubled. Ozone levels during the fires were observed to be lower during the fires at some sites, a possible result of light scattering by the smoke plume reducing photochemical activity levels. Particle number distributions downwind of the fires displayed number modes with diameters between 100 and 200 nm, larger than typical urban aerosol and explaining the larger increases in $PM_{10}$ and $PM_{2.5}$ mass concentrations than that for ultrafine particle mass and particle number. These particles were also

shown to penetrate effectively indoors, calling into question the prevailing advice to the public to remain inside to avoid exposure to harmful wildfire emissions.

[24] **Acknowledgments.** This work was supported by the California Air Resources Board and the South Coast Air Quality Management District through grants 53-4507-7822 and 53-4507-7823 to USC. Additional funding was provided by the Southern California Particle Center and Supersite (SCPCS), funded by the U.S. EPA (STAR award R82735201). This manuscript has not been subjected to the EPA and ARB's peer and policy review, and therefore does not necessarily reflect the views of the Agencies. No official endorsement should be inferred.

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RESEARCH ARTICLE

# Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach

**Naiara Pinto · Timothy H. Keitt**

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**Abstract** The impact of the landscape matrix on patterns of animal movement and population dynamics has been widely recognized by ecologists. However, few tools are available to model the matrix's influence on the length, relative quality, and redundancy of dispersal routes connecting habitat patches. Many GIS software packages can use land use/land cover maps to identify the route of least resistance between two points—the least-cost path. The limitation of this type of analysis is that only a single path is identified, even though alternative paths with comparable costs might exist. In this paper, we implemented two graph theory methods that extend the least-cost path approach: the Conditional Minimum Transit Cost (CMTC) tool and the Multiple Shortest Paths (MSPs) tool. Both methods enable the visualization of multiple dispersal routes that, together, are assumed to form a corridor. We show that corridors containing alternative dispersal routes emerge when favorable habitat is randomly distributed in space. As clusters of favorable habitat start forming, corridors become less redundant and dispersal bottlenecks become visible. Our approach is illustrated using data from a real landscape in the Brazilian Atlantic forest. We explored the effect of small, localized disturbance on dispersal routes linking conservation units. Simulated habitat destruction caused the appearance of alternative dispersal routes, or caused existing corridors to become narrower. These changes were observed even in the absence of significant differences in the length or cost of least-cost paths. Last, we discuss applications to animal movement studies and conservation initiatives.

**Keywords** Agroecosystems · Atlantic forest · Brazil · Functional connectivity · Corridors · Cost distance · Dispersal · Fragmentation · Graph theory · Matrix · Migration · Shortest path

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## Introduction

Animal movement can occur at a range of temporal scales, influencing foraging, migration, and gene flow (Crooks and Sanjayan 2006). The dispersal routes associated with these processes can be strongly constrained by the landscape matrix. Thus models specifying the effect of matrix heterogeneity on movement rates can more successfully predict patch occupancy (Ricketts 2001; Verbeylen et al. 2003), metapopulation dynamics (Vandermeer and Carvajal

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2001), genetic structure (Stevens et al. 2006), and persistence in fragmented landscapes (Laurance et al. 2002). The role of behavior and natural history in shaping species' responses to the matrix has recently motivated the concept of functional connectivity (Calabrese and Fagan 2004). While many connectivity studies have described the influence of different land cover types in channeling or repelling movement of particular species (e.g., Burel 1996; Lees and Peres 2008), few tools are available to integrate data on matrix heterogeneity and species' habitat preferences to model dispersal routes.

A challenge in modeling animal dispersal routes is that individuals rarely use a single optimum route (e.g., Driezen et al. 2007), and connectivity measures focusing on optimum routes fail to incorporate variation in individual behavior (Belisle 2005). In this paper, we model the location of multiple dispersal routes across a heterogeneous matrix. We employ a movement model that assumes successfully dispersing organisms are more likely to use the route of least resistance when moving between two points, or the least-cost path. Despite its simplifying assumptions, the least-cost path has been successfully used to predict patch occupancy (Chardon et al. 2003; Verbeylen et al. 2003) and inter-patch movement rates (Sutcliffe et al. 2003). The least-cost path is identified using a graph theory algorithm, Dijkstra's breadth-first search (Cormen et al. 2001). Many GIS software packages have functions to locate the least-cost path between two points. Although only one path is obtained, Dijkstra's algorithm can be easily modified to output multiple paths with similar costs. We describe this modification and its two outputs, the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs).

We propose that corridors are heterogeneous structures that may contain multiple dispersal routes. However, we do not advocate a method for designing corridors (including few or many dispersal routes), neither do we attempt to quantify corridors' role in conserving biodiversity. Rather, our goal is to integrate information on species' habitat preferences into regional-scale depictions of habitat connectivity. This paper has three parts. First, we applied our method to artificial landscapes in order to illustrate the effect of matrix heterogeneity on the cost and spatial distribution of dispersal routes. Second, we studied the effect of small, localized disturbance on large-scale dispersal routes. This was performed using data from the highly fragmented Brazilian Atlantic forest (Morellato and Haddad 2000). Last, we discussed how the approach proposed here can be refined and incorporated in animal movement studies and conservation initiatives.

## Methods

### The landscape graph

In this section, we describe the approach routinely employed to perform any type of distance calculations on grids. Most GIS software packages use graphs (Urban and Keitt 2001) to represent grid maps. Graphs are composed of vertices (V) placed on cell centers, and edges (E) that connect each vertex to its eight nearest neighbors (Fig. 1). Using this representation, we define two cost grids:

(a) Relative cost grid (Figs. 2a, 3a), also referred to as a friction layer (Verbeylen et al. 2003). Each vertex contains the relative cost to cross it in any direction.

(b) Cumulative cost grid (Figs. 2b, 3b). Consider a source (S) composed of one or more vertices. Each vertex in the cumulative cost grid contains the minimum cumulative cost to reach S. This is calculated in two steps: first, the cost to move between pairs of vertices is stored as edge weights. The weight *W* for an edge connecting vertices V1 and V2 is calculated as:

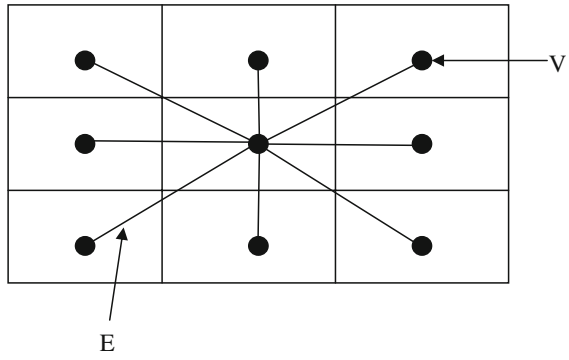


**Fig. 1** The landscape graph. In most software packages, grid maps are internally represented as a graph. Vertices (V) are located in cell centers. Each vertex is connected to its eight nearest neighbors by an edge (E). Edge weights (not shown) hold information on the cost to move between pairs of vertices

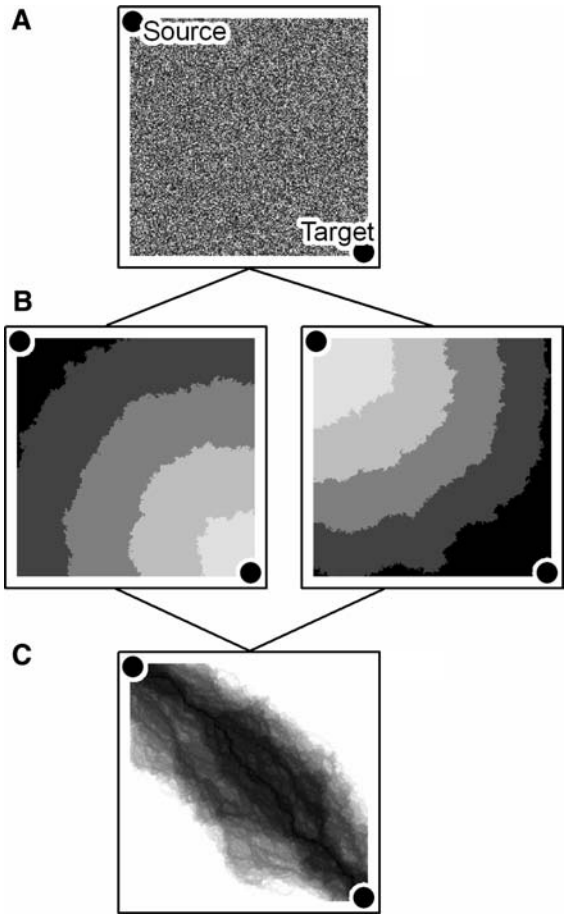


**Fig. 2** Illustration of the procedure for calculating the CMTC. **a** Relative cost grid. **b** The cumulative cost grid for the target (*left*) and the source (*right*). Lighter shades indicate lower cumulative cost. **c** The two grids from (**b**) are added to produce the CMTC grid

$$W = [\text{Relative Cost}\,(\text{V1}) + \text{Relative Cost}\,(\text{V2})]/2 \quad (1)$$

For diagonal edges, edge weights $W'$ are calculated as:

$$W\prime = W \times \sqrt{2} \quad (2)$$

Second, Dijkstra's breadth-first search algorithm (Cormen et al. 2001) is used to calculate the least-cost path between S and each vertex in the graph. The minimum cumulative cost between S and a given vertex (V) is the sum of all edge weights in the least-cost path connecting S and V. To calculate the

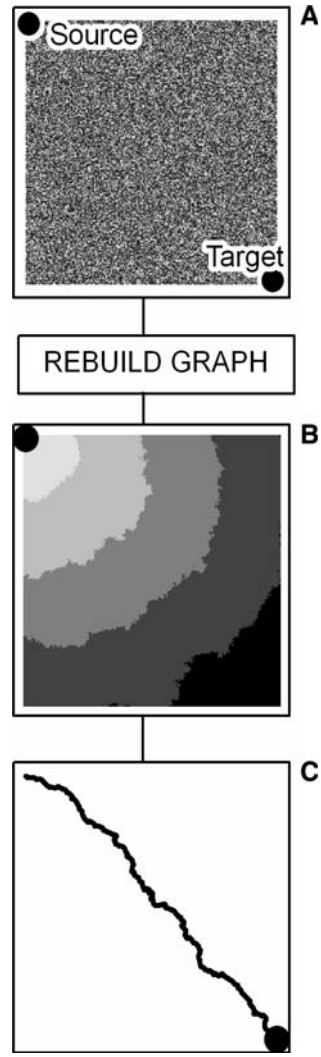


**Fig. 3** Illustration of the procedure for locating MSPs. **a** Relative cost grid, **b** cumulative cost grid for the source. *Lighter shades* indicate lower cumulative cost. This was calculated after rebuilding the graph that represents the landscape, **c** with the cumulative cost grid, we trace the least-cost path between source and target, **b** and **c** are repeated 100 times to produce 100 least-cost paths

least-cost path between two habitat patches P1 and P2 we define all vertices in P1 as sources and all vertices in P2 as targets. The least-cost path between patches P1 and P2 will most likely link the two patches' most external vertices.

In the next two sections, we build on the above representation and describe two methods that extend Dijkstra's breadth-first search algorithm.

### Conditional minimum transit cost (CMTC)

Consider a vertex (V) located between groups of source vertices (S) and target vertices (T). The Conditional Minimum Transit Cost (CMTC) for V is the cost-weighted distance to move from S to T, conditional on the route forming the shortest passage between S and T while passing through V. It is calculated as (Fig. 2):

$$\begin{aligned}\mathrm{CMTC}(\mathrm{V},\mathrm{S},\mathrm{T}) = {} & \text{Cumulative cost}(\mathrm{V},\mathrm{S}) \\ & + \text{Cumulative cost}(\mathrm{V},\mathrm{T}) \end{aligned} \quad (3)$$

The final CMTC grid was obtained by masking out all cells with CMTC values larger than the minimum CMTC value plus 10% (Fig. 2c). The remaining values were then divided by the grid's maximum CMTC. According to Forman (1995), a corridor is "a narrow strip of land that differs from the matrix on either side". We assume that areas within the 10% threshold form corridors, but emphasize that our choice of corridor width was arbitrary.

Our analysis generates corridors that are highly heterogeneous. Visually inspecting the CMTC grid (Fig. 2c) enables identification of contiguous cells with low CMTC value. We refer to these cell groups as "dispersal routes", while recognizing that distinction between routes that are close together is arbitrary. The least-cost path is invariably located within one dispersal route.

In practice, obtaining a CMTC grid is straightforward with modules such as spatial analyst within ArcGIS (Esri, California). Some conservation biologists strongly advocate the CMTC approach for designing wildlife corridors (Majka et al. 2007). But to our knowledge, the relationship between matrix heterogeneity and the distribution of dispersal routes as predicted by the CMTC has not yet been explored.

### Multiple shortest paths (MSPs)

We developed a stochastic version of Dijkstra's algorithm (Fig. 3) that outputs multiple realizations of the least-cost path, or Multiple Shortest Paths (MSPs). As described above, the least-cost path is obtained from a relative cost grid. Dijkstra's breadth-first search algorithm (Cormen et al. 2001) proceeds by iteratively marking vertices in the order of their cumulative distance from the source. At each step, the algorithm must identify the set of neighbors associated with the marked vertices. Standard algorithms use a static definition of the neighborhood, typically the nearest eight cells on a rectangular grid (Fig. 1). Our approach is to redefine the neighborhood as a stochastic function such that adjacency is non-deterministic and is instead determined randomly in proportion to edge weights. The algorithm proceeds as follows (Fig. 3):

1. Draw a number ($U$) between 0 and 1 from a random uniform distribution.
2. Delete edges in the graph. An edge with weight $W$ connecting two adjacent vertices V1 and V2 is deleted if $W > U$. That is, connections with lower costs are more likely to be maintained.

A program implementing Dijktra's algorithm (with the above modification) was run 100 times in order to produce 100 MSPs for each study case (Fig. 3c shows one path). The cumulative cost associated with each path is a measure of effective distance and is calculated by adding the weights of all edges in the path. The programs used to obtain both CMTCs and MSPs were written in the Java programing language.

### Applications to artificial landscapes

We generated artificial landscapes with different degrees of spatial autocorrelation using the method of wavelet synthesis (Keitt 2000). We started with a grid containing values between 0 and 1, drawn from a random uniform distribution. Using this grid, each landscape was created in four steps: (a) apply the discrete Haar wavelet transform; (b) obtain wavelet coefficients; (c) multiply coefficients by $2 \wedge (L \times \beta)$, where $L$ is the coefficient level (higher levels representing low-frequency variation); (d) apply the inverse Haar wavelet transform on the modified coefficients; (e) map results to a random uniform distribution ($\min = 0$; $\max = 1$). The last step is taken to ensure that the distribution of quality values is consistent across all landscapes. The values of the parameter $\beta$ were 0, 0.25, 0.50, 0.75, and 1. A $\beta$ value of zero generates a white noise landscape with no spatial autocorrelation. Increasing $\beta$ produces autocorrelated landscapes, where clusters of favorable habitat can be identified. Each artificial landscape represents one relative cost grid that served as input in calculations of CMTC and MSPs (Fig. 4a). We used ANOVA to test for differences among landscapes, in terms of

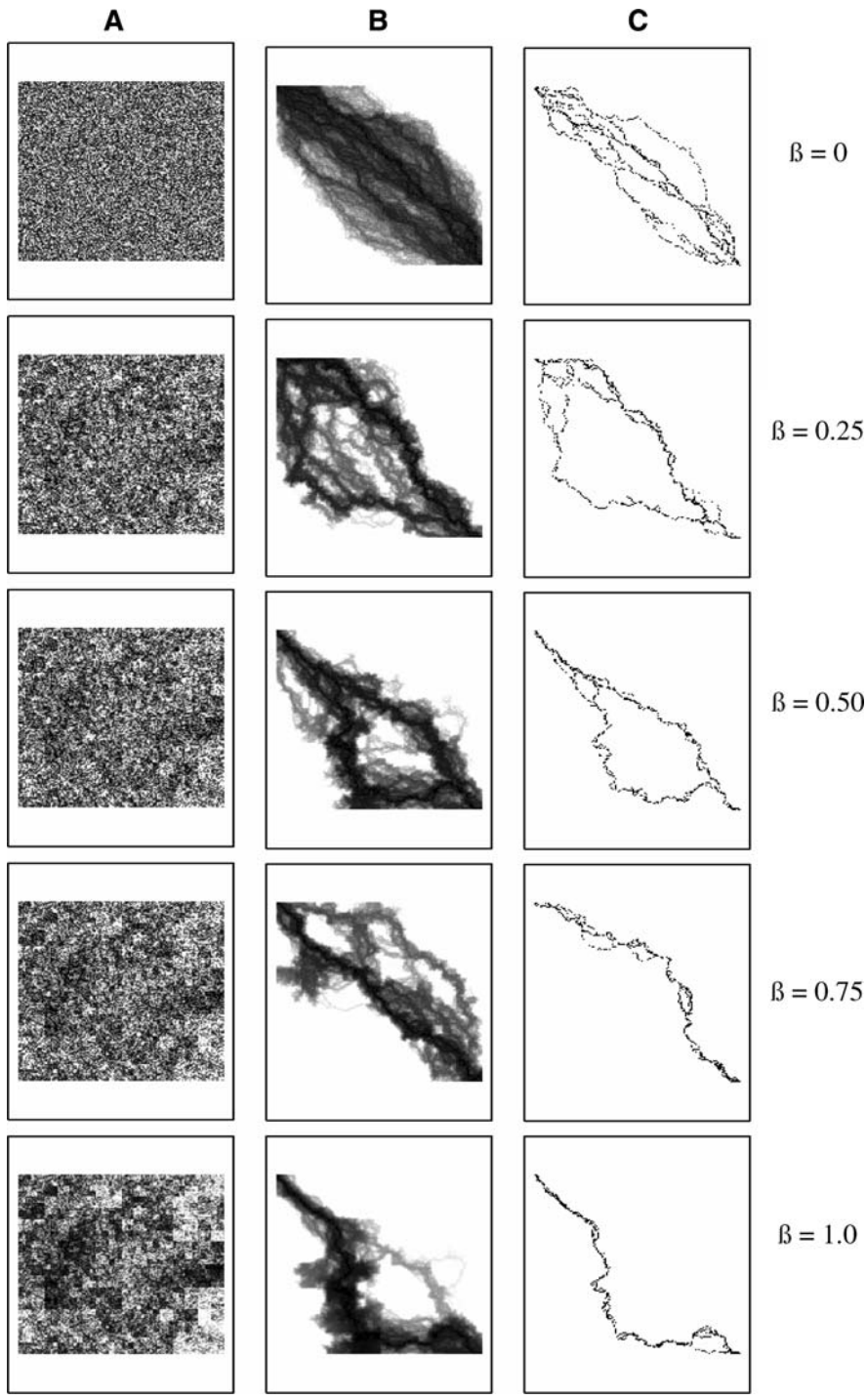


**Fig. 4** Relative cost grids generated with the use of wavelet transforms (**a**), and the values of CMTC (**b**) and location of MSPs (**c**) for each landscape. A $\beta$ value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as $\beta$ values increase

cumulative costs associated with MSPs and mean CMTC. The generation of artificial landscapes and ANOVA tests were performed using the R programing language (R Core Development Team 2008).

## Applications to real landscapes

We studied a real landscape (Fig. 5) that covers 111 km$^2$ of the Brazilian state of São Paulo (upper

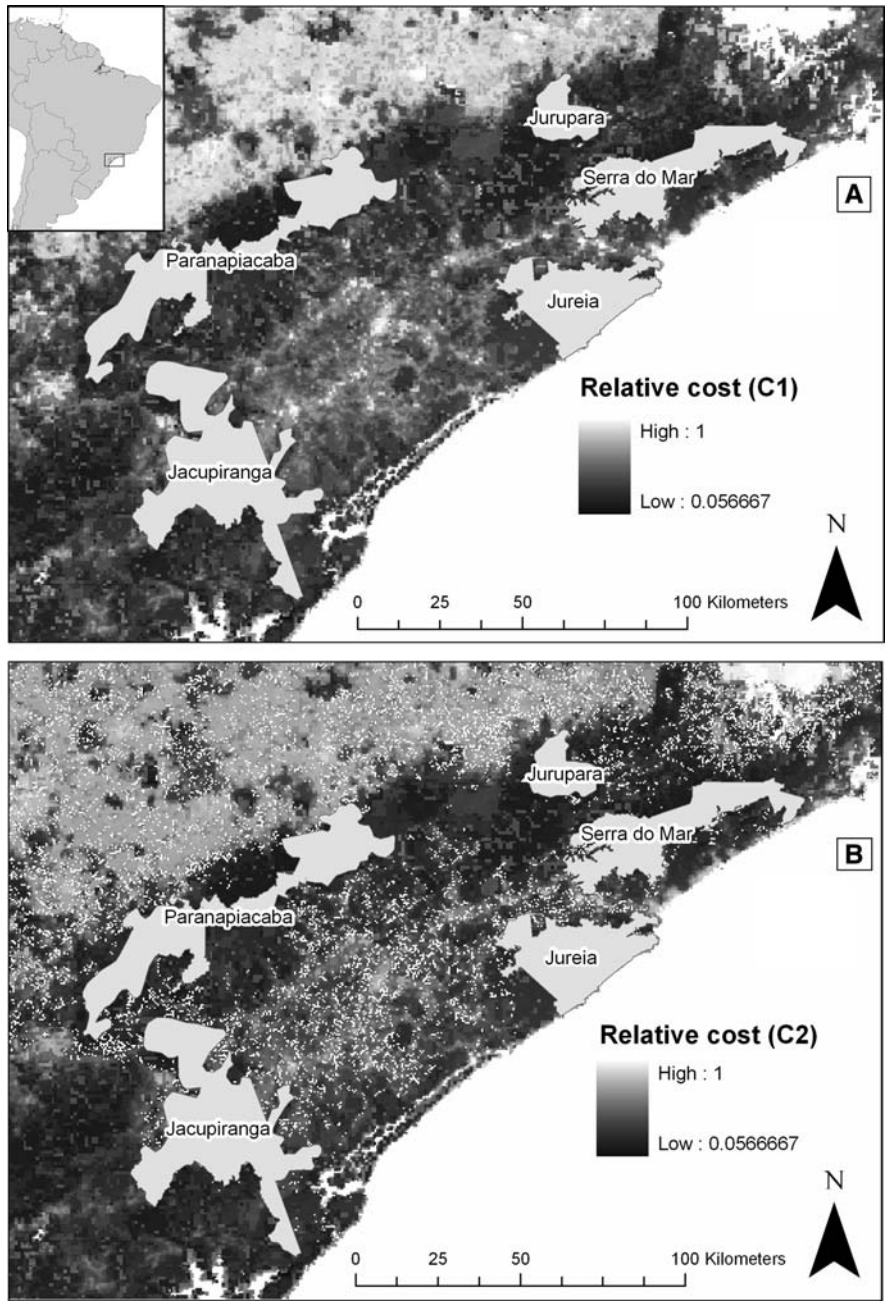


**Fig. 5** Study site in the Brazilian Atlantic forest, showing conservation units in Sao Paulo State. **a** Relative cost values for scenario C1. **b** Relative cost values for scenario C2 (after deletion of small forest fragments)

left coordinates: 23.60S, 49.00W; lower right coordinates: 25.40S, 46.20W). Remaining forests are part of the Atlantic forest biome (for a description, see Oliveira-Filho and Fontes 2000). Despite its location in highly industrialized São Paulo state, the study area still contains large forest tracts and rural properties. A recent vegetation map (Eva et al. 2002) estimates that 11.1% of the study area is devoted to intensive agriculture, 7% contains a mix of agriculture and degraded vegetation, 23% is a mix of agriculture and degraded forest, and 46% is covered with forest. Excluding São Paulo's metropolitan area, human populations per municipality range in size from 3,403 to 412,243 (mean = 60,410; IBGE 1991). Five conservation units are considered here: Pedro de Toledo Nucleus within Serra do Mar State Park (868 $km^2$), Juréia-Itatins Ecological Reserve (801 $km^2$), Jurupara State Park (259 $km^2$),

Jacupiranga State Park (1,552 km$^2$), and the contiguous units Intervales State Park, Carlos Botelho State Park, Ecological Station Xitué, and Alto do Ribeira Touristic State Park (1,282 km$^2$), referred together here as "Paranapiacaba" due to their location along the Paranapiacaba Valley.

Our analyses consisted of modeling dispersal routes between all pairs of conservation units. We have built a relative cost map in an attempt to capture the habitat preferences of species that move in forested areas and suffer higher mortality when crossing disturbed habitat. In the discussion, we describe how more detailed models can be built and refined to reflect the habitat preferences of a particular species. Three land use/land cover maps were the main input for our analyses (Table 1).

1. The Modis continous fields, (Hansen et al. 2003) contains estimates of percent tree cover. Values were manipulated (Table 1) in order to obtain a grid with values ranging between 0 (=100% tree cover) and 1 (=no tree cover).
2. The human footprint map (Sanderson et al. 2002) is a global dataset with estimates of anthropogenic impact ranging from 0 (pristine land) to 100 (most disturbed land), normalized per ecosystem. These estimates were based on patterns of human population density, land use, and transportation networks. We divided original values by 100 (Table 1) to obtain a grid with values ranging from 0 (=pristine land) to 1 (=most disturbed land).
3. The South American vegetation map (SAVM; Eva et al. 2002) contains information on forest distribution, degree of forest disturbance, and mixture with agricultural lands. We assigned each class in the SAVM grid (Table 1) a relative cost value ranging from 0 (=closed or dense forest) to 1 (intensive land use or non-forested ecosystems).

The Footprint and SAVM grids were rescaled so as to bring their spatial resolution to 500 m. The first relative cost map (C1; Fig. 5a) was obtained by averaging the values in the three grids described above (Table 1). As a result, we obtained a grid where cell values ranged from 0.057 (minimum relative cost to cross) to 1 (maximum relative cost to cross).

The second cost map (C2; Fig. 5b) simulated the removal of small forest fragments from C1, which could result from clear cutting, selective logging, or road construction. Results do not necessarily reflect actual land cover changes taking place in the Atlantic forest, but they enable us to explore the effect of small, localized disturbance on regional connectivity patterns. The C2 map was built in three steps. First, we produced a binary map with areas classified as "forest" or "non-forest" based on the SAVM map. This binary map was eroded and dilated (Serra 1982) by 0.5 pixel, resulting on the deletion of fragments with area <5 ha and linear elements (such as riparian corridors) <500 m wide. Last, C2 was obtained by assigning the maximum relative cost (1) to the deleted cells. All other cells contained the same values as C1, and the range of relative cost values for the entire grid remained unchanged (0.057–1). It was assumed that individuals could not move through water, thus a cost value of positive infinity was assigned to cells representing water bodies in both C1 and C2 scenarios. Finally, we calculated the CMTC and MSPs for both C1 and C2 scenarios. All GIS layers were processed using programs written in Java

**Table 1** Grids used to construct the relative cost maps used in the present study, their original spatial resolution (pixel size), period of data collection, and operations performed on original grid values

| Layer | Resolution (m) | Years | Operations performed on the original raster values |
|---|---|---|---|
| South America vegetation map | 1,000 | 1995–2000 | 0 = closed, dense, transitional forest |
| | | | 0.25 = open forest |
| | | | 0.5 = mosaic agriculture/degraded forest |
| | | | 0.75 = shrubland, savannah, grassland |
| | | | 1 = intensive agriculture, mosaic agriculture/degraded vegetation, desert, urban |
| Human footprint | 1,000 | 1960–2001 | Final value = (original value)/100 |
| Modis continuous fields, % tree | 500 | 2000–2001 | Final value = (100 − original value)/100 |

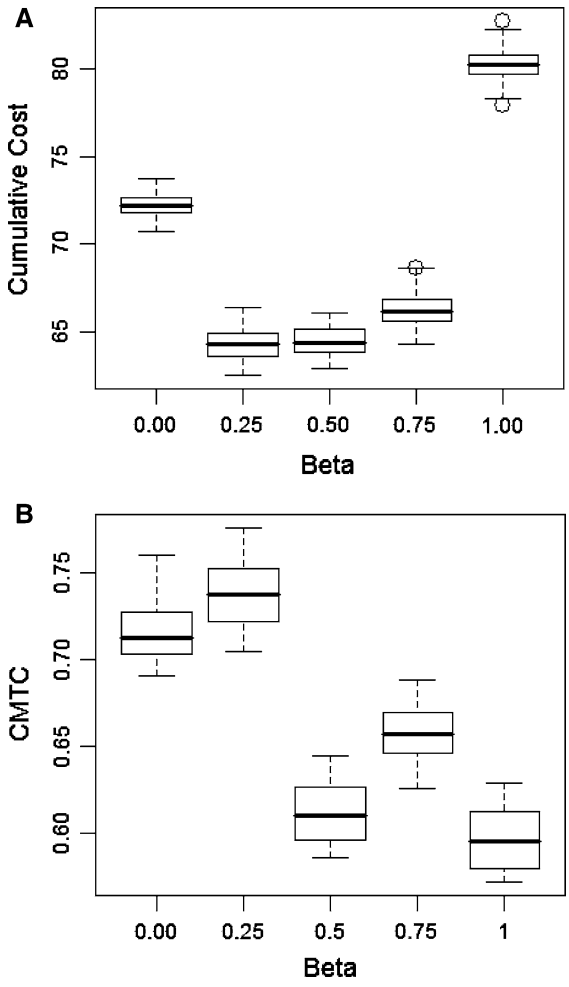


**Fig. 6** The distribution of values of **a** Multiple Shortest Paths **b** and Conditional Minimum Transit Costs. A $\beta$ value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as $\beta$ values increase

programing language, and illustrations were produced in ArcMap (Esri, California).

## Results

### Artificial landscapes

The two graph theory approaches proposed here outlined the influence of matrix heterogeneity on dispersal routes. We detected a significant difference in mean cumulative costs associated with Multiple Shortest Paths (MSPs) among the five artificial landscapes (ANOVA, $F = 6{,}934.5$; $P < 0.001$). MSPs with lowest costs were observed when landscapes had intermediate patchiness (Fig. 6a; Tukey multiple comparisons of means, 95% family-wise confidence level, $P < 0.001$). We also observed significant differences in mean Conditional Minimum Transit Cost (CMTC) values (ANOVA, $F = 474{,}104$; $P < 0.001$). The most autocorrelated landscapes produced the lowest CMTC values (Fig. 6b; Tukey multiple comparisons of means, 95% family-wise confidence level; $P < 0.001$). In addition, we observed differences in the spatial distribution of dispersal routes. Landscapes with little autocorrelation in relative habitat quality produced redundant corridors with more alternative dispersal routes (Fig. 4; $\beta$ closer to 0). As clusters of favorable habitat started to form, corridors became restricted to fewer routes (Fig. 4; $\beta$ closer to 1). This was evidenced in the outputs of both the CMTC and MSPs calculations.

### Real landscapes

We tested the influence of small, localized disturbance on corridors connecting five conservation units in the Brazilian Atlantic forest (Fig. 5). There were no significant differences in mean cumulative path costs calculated from MSPs, or in mean CMTC values ($t$-test, $P > 0.05$) between scenarios C1 and C2. But in most cases, simulated fragment removal influenced the spatial distribution of dispersal routes. Since small fragments were not homogeneously distributed in the study area, corridors obtained under scenario C1 were differentially affected by simulated fragment removal in scenario C2 (Table 2).

**Table 2** Conservation units included in the present study

| | Jacupiranga | Jurupará | Serra do Mar | Paranapiacaba |
|---|---|---|---|---|
| Juréia | 72.321 | 35.391 | 6.905 | 3.993 |
| | 5 | 3.6 | 10.4 | 5.5 |
| Jacupiranga | | 115.502 | 104.800 | 7.868 |
| | | 4.0 | 5.0 | 21.0 |
| Jurupará | | | 7.263 | 43.739 |
| | | | 2.0 | 1.2 |
| Serra do Mar | | | | 51.183 |
| | | | | 2.3 |

Each unit in a pair can serve as a source or a target for dispersing organisms. The first line contains the straight-line distance between units (in kilometers), and the second line shows the percentage of 500-$m^2$ cells deleted from the corridor as a result of simulating fragment removal

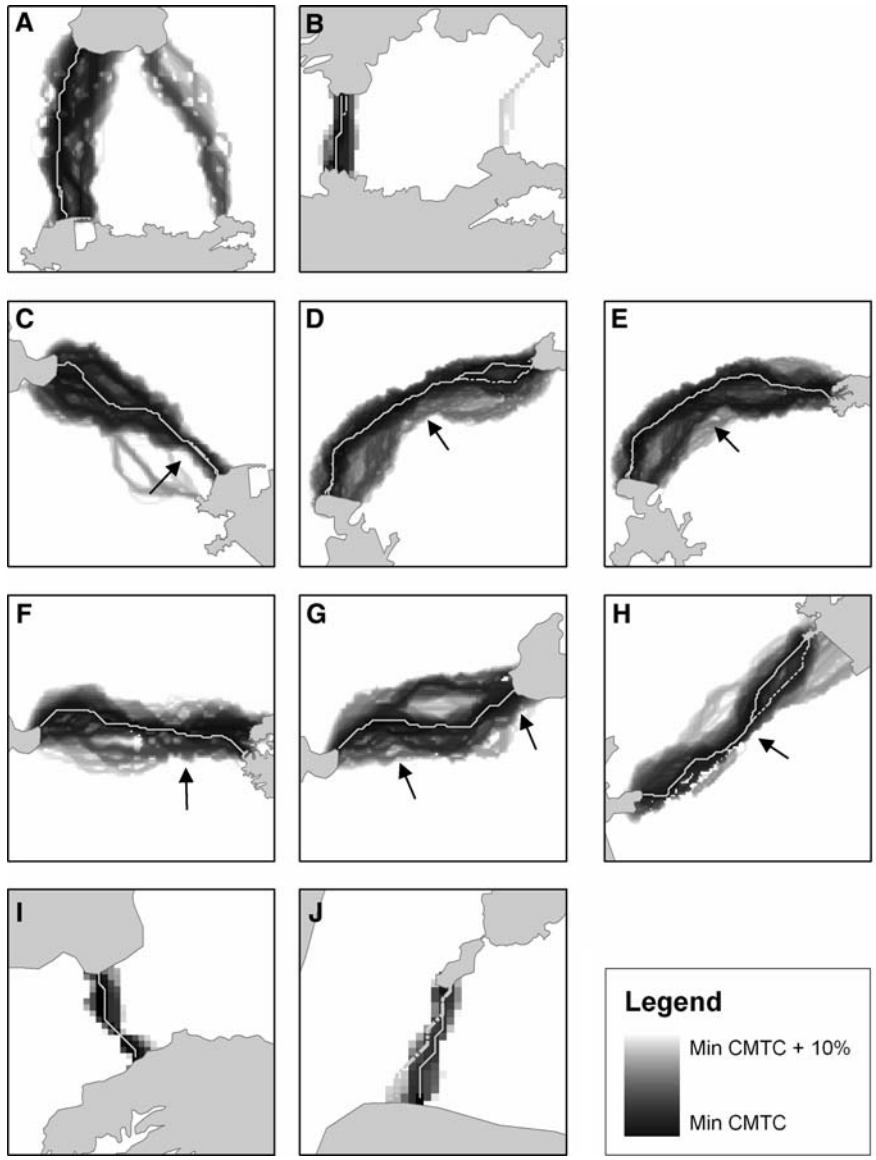


**Fig. 7** CMTC grids for the corridor connecting conservation units in São Paulo, Brazil. The pairs are: **a** Jurupará–Juréia, **b** Juréia–Serra do Mar, **c** Juréia–Paranapiacaba, **d** Jacupiranga–Jurupará, **e** Jacupiranga–Serra do Mar, **f** Paranapiacaba–Serra do Mar, **g** Paranapiacaba–Jurupará, **h** Juréia–Jacupiranga, **i** Serra do Mar–Jurupará, **j** Paranapiacaba–Jacupiranga. *Gray lines* show the least-cost path. *Solid lines* represent least-cost paths obtained for scenarios C1 and C2, whereas *interrupted lines* represent sections of the least-cost path obtained for scenario C2 only. *Arrows* indicate potential dispersal bottlenecks

In most cases, the CMTC grid displayed more than one alternative route between conservation units, one of them being the least-cost path (Fig. 7a–h). When conservation units were close, the distance between them was small with respect to the variation in their shape. In this case, the CMTC grid produced narrow corridors, coinciding with the links representing the shortest Euclidian distance (Fig. 7b, i, j). When corridors contained alternative routes, these were rarely disjoint (Fig. 7a, b). The constriction zones where dispersal routes merged represented potential dispersal bottlenecks (Fig. 7c–h). In most cases, the location of the least-cost path did not change substantially as a result of small fragment removal (Fig. 7a–c; e–g; i, j). But in two cases, the least-cost path for scenario C2 was displaced to an alternative route located a few kilometers away from the least-cost path for scenario C1 (Fig. 7d, h).

We also identified the MSPs between pairs of conservation units. Compared to the CMTC calculation, this tool provided a better assessment of the impact of fragment removal on corridor redundancy. Examining the MSPs produced for the scenarios C1 and C2, we observed two trends. In some cases,

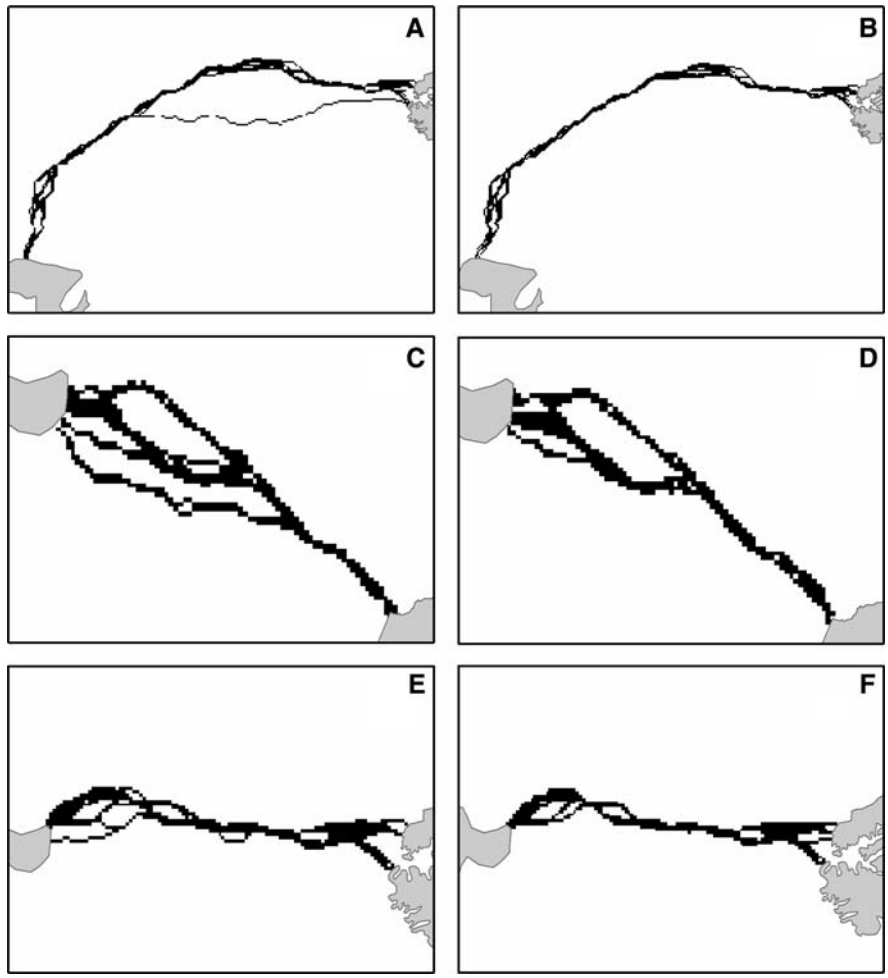


**Fig. 8** Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Jacupiranga–Serra do Mar, scenario C1; **b** Jacupiranga–Serra do Mar, scenario C2; **c** Juréia–Paranapiacaba, scenario C1; **d** Juréia–Paranapiacaba, scenario C2; **e** Serra do Mar–Paranapiacaba, scenario C1; **f** Serra do Mar–Paranapiacaba, scenario C2

fragment removal led to the disappearance of external dispersal routes; corridors became narrower and less redundant (Fig. 8). In other cases, new, more external routes emerged after fragment removal (Fig. 9).

## Discussion

Analyses of artificial landscapes show the influence of matrix heterogeneity on landscape connectivity. Redundant corridors with multiple alternative dispersal routes emerged in white noise landscapes, where favorable habitat is randomly distributed (Fig. 4, $\beta$ closer to 0). As patches of favorable habitat started forming, corridors became narrower and less redundant (Fig. 4, $\beta$ closer to 1). The cumulative cost of MSPs was on average lower in landscapes with intermediate degree of autocorrelation (Fig. 6a). This is because paths in white noise landscapes will often cross areas of high cost, whereas the presence of contiguous habitat patches in autocorrelated landscapes can lead to longer, more tortuous paths (Fig. 4c). The CMTC was on average lower in autocorrelated landscapes (Fig. 6b). This follows from our choice of CMTC value used to delimit corridors—under a 10% threshold, white noise landscapes produced wider corridors with higher CMTC values.

In addition to studying artificial landscapes, we illustrated our methods using data from a real landscape in the Brazilian Atlantic forest. In this region, a complex landscape matrix produced dispersal routes that were not apparent in land use/land cover maps (Fig. 7a–f, h–j), with the exception of the pair Paranapiacaba–Jurupará that is separated by an artificial dam (Fig. 7g). CMTC maps revealed highly

heterogeneous corridors displaying bottlenecks to animal movement (indicated by arrows in Fig. 7c–h). Removing small fragments did not produce a significant increase in the mean cumulative cost of MSPs but led to changes in their spatial distribution (Figs. 8, 9). Our work illustrates two possible large-scale effects of small, localized disturbance on the landscape matrix. Narrower corridors were produced (Fig. 8), and the importance of external dispersal routes increased (Fig. 9). The latter case included the two pairs of conservation units with the largest amount of deleted habitat in the scenario C2 (Table 2; Fig. 9c–f).

Results of least-cost path analyses are strongly dependent on the selection of relative cost grids (Adriaensen et al. 2003; Rae et al. 2007). Our choice of relative cost grids (Table 1) was made as an attempt to approximate the habitat preferences of a forest specialist. Relative cost grids can be further refined and validated for a particular species using patch occupancy data (Verbeylen et al. 2003) or from ecological niche modeling and tools such as the Mahalonobis distance (Farber and Kadmon 2003). In addition to habitat preference estimates, an important issue is the time scale over which individuals are expected to disperse. Here, we were not concerned with the time interval or number of generations that individuals (or populations) took to move between source and target fragments (conservation units). More realistic models can be obtained by adjusting the maximum Euclidian distance allowed between source and target fragments so as to match the maximum distance that can be crossed by a species given a particular time interval (Keitt et al. 1997). The issue of time scale is related to the question of whether corridors should function as habitat or as

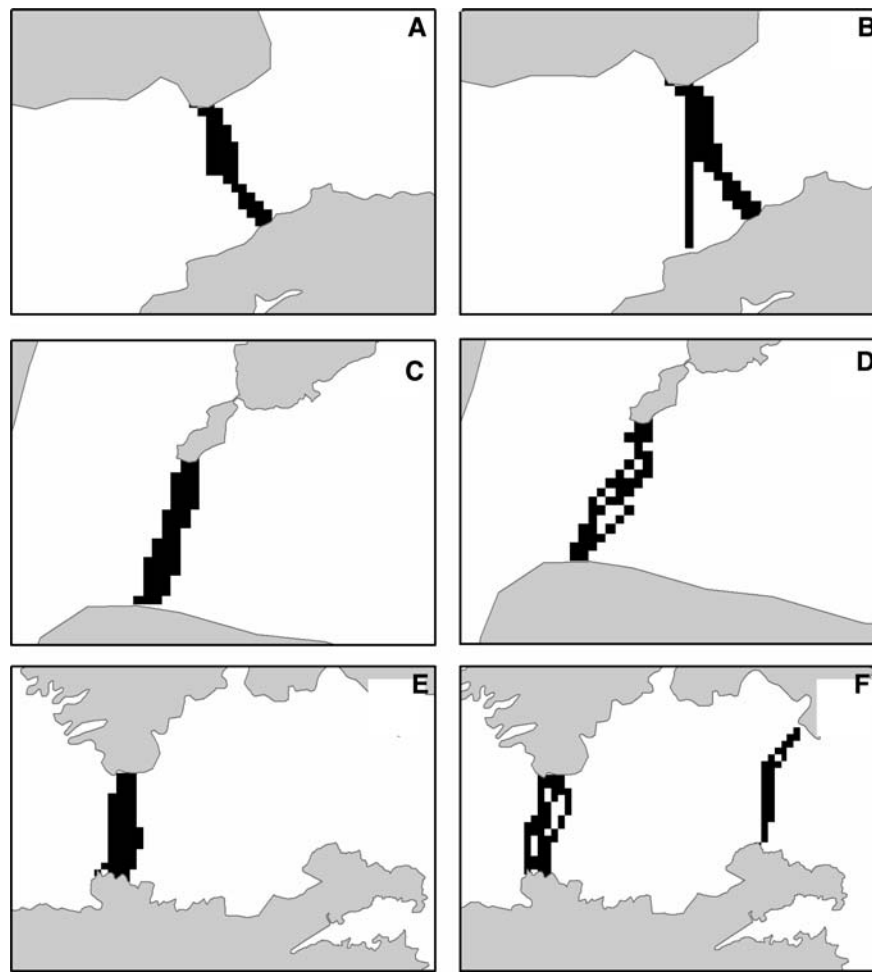


**Fig. 9** Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Serra do Mar–Jurupara, scenario C1; **b** Serra do Mar–Jurupará, scenario C2; **c** Paranapiacaba–Jacupiranga, scenario C1; **d** Paranapiacaba–Jacupiranga, scenario C2; **e** Juréia–Serra do Mar, scenario C1; **f** Juréia–Serra do Mar, scenario C2

conduits (Hess and Fischer 2001)—i.e., individuals are expected to spend more time in habitat corridors. Corridor width can be adjusted by increasing the CMTC threshold to ensure that corridors contain minimum habitat requirements.

The ability to identify multiple dispersal routes can be desirable in conservation studies, for three main reasons. First, least-cost paths have been employed in the design of linked reserve systems (Hoctor et al. 2000; Schadt et al. 2002; Larkin et al. 2004). This approach, however, can lead to very narrow linkages (Alagador and Cerdeira 2007) that might not be located in land tracts available for purchase. Second, dispersal routes that appear similar may differ in terms of their conservation value. For example, field studies in Canada (Clevenger et al. 2001) show that drainage culverts can act as habitat linkages for several mammal species, but culverts near roads with higher traffic volume and noise levels are less commonly used. Third, the approach shown here enable the visualization of functionally unique landscape structures (Manning et al. 2006): narrow corridors or dispersal bottlenecks within corridors (e.g., Fig. 7).

Considerable attention has been given to quantifying the role played by agroecosystems in conservation (i.e., Bestelmeyer and Wiens 1996; Reitsma et al. 2001; Mas and Dietsch 2003). Agricultural lands can help support wild populations by providing critical habitat (Moguel and Toledo 1999) and influencing neighboring fragments, in which case potential outcomes depend on the spatial configuration and degree of mixture with pristine habitat (Perfecto and Vandermeer 2002; Perfecto et al. 2003; Tscharntke et al. 2005). Our study of the Brazilian Atlantic forest shows that private lands can collectively influence ecological processes occurring at large spatial scales and supports the assertion that small fragments can potentially shape regional patterns of gene flow (Bodin et al. 2005). This raises the necessity to view agricultural lands' contribution to biodiversity in a larger context.

Movement behavior is a key aspect in functional connectivity studies, but detailed data on animal movement remains hard to collect, especially for large spatial scales. In fact, the ability to produce accurate movement models has long been recognized as one of the main challenges of population biology studies (Turchin 1998). There is no consensus on the amount of biological detail that should be used in functional connectivity studies. It has been suggested that movement models ought to increase in complexity in order to capture the behavior of particular species (Goodwin 2003). At the same time, conservation biologists have raised the need for rigorous methods that predict the location of dispersal routes for many species (Boitani et al. 2007). Clearly a compromise is needed, which requires determining how much simplification can be made before losing predictive power (Baguette and Van Dyck 2007). Least-cost path predictions can be derived for many species, given the ever growing maps of habitat quality produced by ecological niche modeling. Also, rigorous protocols already exist to compare least-cost predictions with field data (Driezen et al. 2007).

## Conclusions

In the present paper, we extended the graph theory algorithm that serves as the basis for least-cost path calculations. The two outputs are the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs). Our goal was to integrate information on habitat preferences to model dispersal patterns across a heterogeneous matrix. In addition to the path of least resistance between two points, the methods presented here outlined additional paths with similar length and relative cost. Results from artificial landscapes show that the location and relative cost of dispersal routes are strongly influenced by the spatial distribution of favorable habitat in the matrix. In addition, study of a real landscape shows that small, localized disturbance such as removal of small fragments can affect large-scale dispersal routes. Models producing multiple dispersal routes present a practical advantage over models assuming optimum behavior. Although the choice of number of dispersal routes or their location is application specific (and beyond the scope of this paper), our results suggest that the least-cost path is a flexible approach with a wide range of applications.

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# Rapid growth of the US wildland-urban interface raises wildfire risk

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**The wildland-urban interface (WUI) is the area where houses and wildland vegetation meet or intermingle, and where wildfire problems are most pronounced. Here we report that the WUI in the United States grew rapidly from 1990 to 2010 in terms of both number of new houses (from 30.8 to 43.4 million; 41% growth) and land area (from 581,000 to 770,000 km$^2$; 33% growth), making it the fastest-growing land use type in the conterminous United States. The vast majority of new WUI areas were the result of new housing (97%), not related to an increase in wildland vegetation. Within the perimeter of recent wildfires (1990–2015), there were 286,000 houses in 2010, compared with 177,000 in 1990. Furthermore, WUI growth often results in more wildfire ignitions, putting more lives and houses at risk. Wildfire problems will not abate if recent housing growth trends continue.**

wildfires | housing growth | sprawl | development | fragmentation

The wildland-urban interface (WUI), defined as the area where houses are in or near wildland vegetation, is the area where wildfires pose the greatest risk to people due to the proximity of flammable vegetation (1). Wildfires frequently burn houses in the WUI (2, 3), and are most difficult to fight there. Furthermore, the WUI is where people often ignite wildfires (4), and the vast majority of fires are human-caused (5). While fires are an integral part of many ecosystems and the Earth system as a whole (6), humans have changed fire regimes globally (7) and throughout the United States (5), and climate change will increase fire frequency in the future, including in the WUI (8).

The close proximity of houses and wildland vegetation does more than increase fire risk (9). As houses are built in the WUI, native vegetation is lost and fragmented (10); landscaping introduces nonnative species and soils are disturbed, causing nonnatives to spread (11); pets kill large quantities of wildlife (12); and zoonotic disease, such as Lyme disease, are transmitted (13). Thus, understanding WUI patterns and WUI growth is important with respect to wildfires and many other environmental problems.

The WUI is widespread in the United States (1, 14) and in many other parts of the world (15, 16), including Argentina (17), Australia (18), France (19), and South Africa (20). Furthermore, both the annual area burned (8, 21, 22) and fire suppression costs (23) have rapidly increased in the United States. The area burned annually nearly doubled, from an average of 18,000 km$^2$/y in 1985–94 to 33,000 km$^2$ in 2005–14 (22). Concomitantly, federal wildfire suppression expenditures tripled from $0.4 billion/y to $1.4 billion/y (23), and exceeded $2 billion in 2017.

While there is ample evidence that houses in the WUI pose problems, it is not clear how fast the WUI is growing. Overall, the US population grew by 60 million people and 29.2 million homes from 1990 to 2010, but how much of that growth occurred in the WUI is uncertain. Previous assessments of WUI growth (24, 25) analyzed only housing data up to 2000, and did not account for changes in wildland vegetation. Post-2000 housing data are important, because the United States entered a recession after 2008, accompanied by a strong downturn in the housing market. Similarly, without data on vegetation change, the major cause of WUI growth is unclear. Areas where forests are regrowing on abandoned farmland, such as in the New England states (26), could see WUI growth without any additional houses. Fundamentally, two processes can create new WUI: construction of new homes in or near existing wildland vegetation, and an increase in wildland vegetation within and near previously developed areas. The prevalence of each process is unclear.

Knowing how the WUI is growing, and why, is essential when evaluating management and policy responses (3, 8). In the United States, federal wildfire management policy prioritizes fuel treatments and the promotion of fire-adapted communities in the WUI. Local jurisdictions use a variety of land use planning tools to limit the environmental impacts of housing growth in the WUI. The importance of the WUI for the environment and for national policy, accompanied by the lack of information about WUI growth in the most recent decade, highlight the need to both assess WUI growth and identify its causes. Thus, we addressed three major questions: (*i*) how much has the WUI in the conterminous United States grown from 1990 to 2010; (*ii*) whether WUI growth is caused mainly by housing growth or by vegetation growth; and (*iii*) how much WUI growth has occurred within recent wildfire perimeters.

The lack of consistent, fine-resolution longitudinal housing data has been the biggest impediment to a nationwide assessment

## Significance

**When houses are built close to forests or other types of natural vegetation, they pose two problems related to wildfires. First, there will be more wildfires due to human ignitions. Second, wildfires that occur will pose a greater risk to lives and homes, they will be hard to fight, and letting natural fires burn becomes impossible. We examined the number of houses that have been built since 1990 in the United States in or near natural vegetation, in an area known as the wildland-urban interface (WUI), and found that a large number of houses have been built there. Approximately one in three houses and one in ten hectares are now in the WUI. These WUI growth trends will exacerbate wildfire problems in the future.**

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of WUI growth. The decennial US Census provides fine-resolution housing data for 1990, 2000, and 2010, but the boundaries of the smallest units for which housing units are reported (i.e., census blocks) often shift between decades, precluding direct change analyses (27). We have developed algorithms to convert the decennial Census data at census block resolution into a consistent dataset on housing growth across the conterminous United States (*Methods*), which we combined with 1992, 2001, and 2011 National Land Cover Data (NLCD) on wildland vegetation: forests (classes 41–43), shrublands (classes 51 and 52), grasslands (class 71), and woody wetlands (class 90). We mapped decadal WUI change from 1990 to 2010 within 2010 census block boundaries, based on the WUI definitions in the *Federal Register* and our previously developed WUI mapping algorithms (1, 14), and conducted several robustness checks of our new dataset (*Supporting Information*). Because of concerns about housing growth and wildfire management, we calculated housing growth for 1990–2010 within WUI burned areas identified in Landsat imagery between 1990 and 2015 (22).

We found that the WUI was widespread in 2010, covering 9.5% of the conterminous United States (Fig. 1), and that the WUI grew rapidly from 1990 to 2010 in all its aspects (Fig. 2).

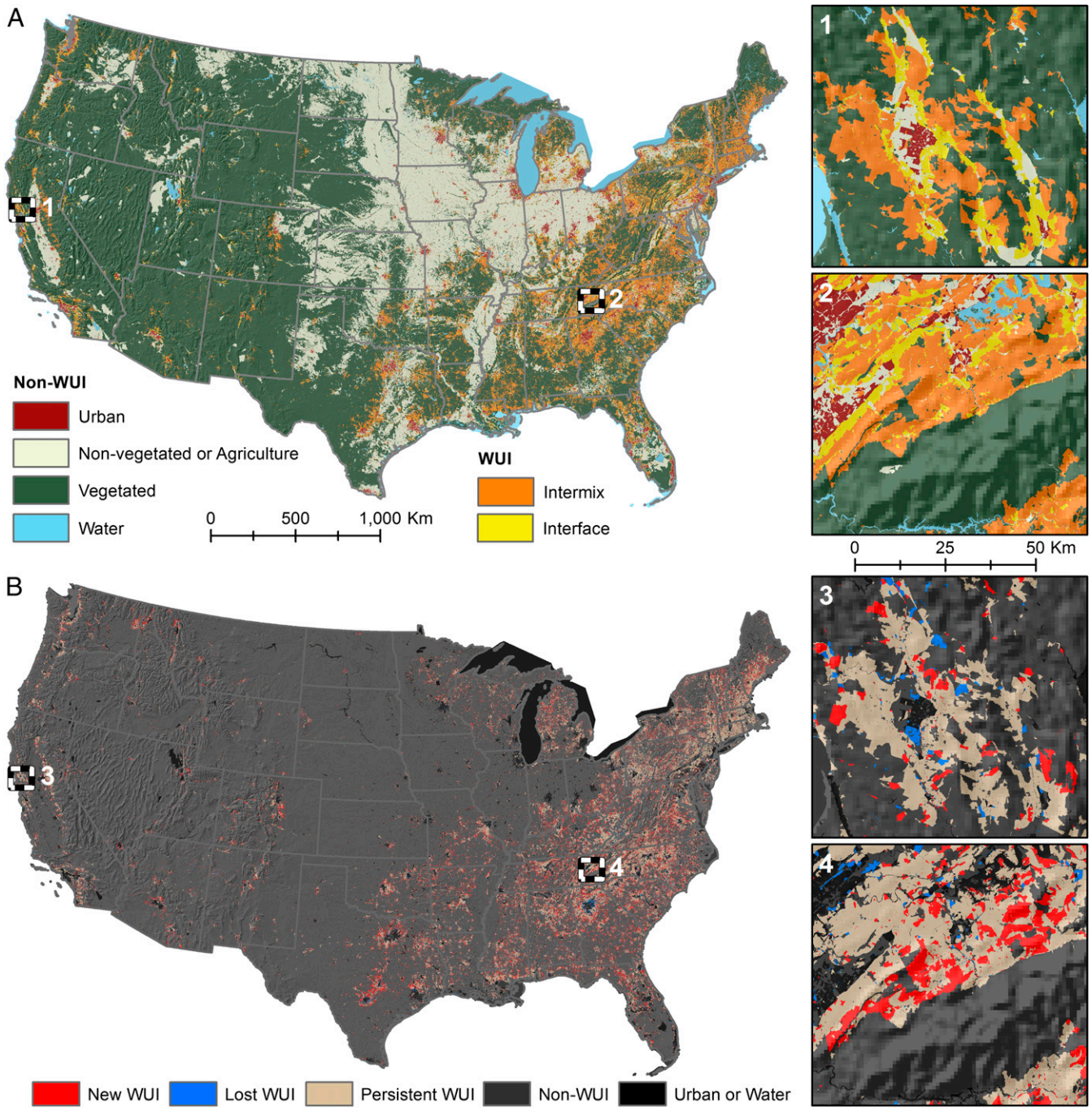


**Fig. 1.** The WUI in the United States was widespread in 2010 (*A*), as were changes in WUI area (*B*), for example, in and around Santa Rosa, California (1, 3), and Gatlinburg, Tennessee (2, 4), areas where wildfires destroyed many homes in 2017 and 2016, respectively.

The number of housing units ("houses" hereinafter) in the WUI grew fastest, followed by the number of people in the WUI and then WUI area (Fig. 2*B* and Table S1). New WUI area totaled 189,000 km$^2$, an area larger than Washington State. At 33%, WUI area growth is faster than that of any of the level I land cover categories included in the NLCD (28). Increases in houses and people were also strong, with 12.7 million more houses and 25 million more people in the WUI in 2010 compared with 1990. The overall combination of more WUI area (7.2% of the conterminous United States in 1990 vs. 9.5% in 2010; Fig. 2*C*) and higher growth rates for both houses and people in the WUI, compared with the nationwide averages (Table S1), increased the percentage of houses (from 30.3% to 33.2%) and people (from 29.4% to 31.9%) in the WUI from 1990 to 2010 (Fig. 2*C*). Even though the WUI occupies less than one tenth of the land area of the conterminous United States, 43% of all new houses were built there, and 61% of all new WUI homes were built in areas that were already in the WUI in 1990 (and remained in the WUI in 2010) (Tables S1 and S2).

There are two main types of WUI: intermix WUI, the area where houses and wildland vegetation directly intermingle, and interface WUI, where settled areas abut wildland vegetation (1). We found that intermix WUI was both more extensive and expanded much more rapidly in area (from 5.6% to 7.5% of the conterminous United States from 1990 to 2010) than interface WUI (from 1.6% to 2.0%). However, interface WUI had higher housing growth rates (43% from 1990 to 2010) than intermix WUI (38%) and non-WUI areas (23%; Table S1). In absolute numbers, there were 4.7 million more houses in the intermix WUI and 8.0 million more in the interface WUI in 2010 than in 1990.

Regional differences in WUI growth were striking (Fig. 3). The highest absolute gains in WUI area occurred in the East, whereas high gains in houses and people in the WUI were most common in the South and Southwest. Absolute gains are most relevant for management agencies, because they indicate how much area and how many people and houses may require management actions; however, rapid growth often garners the most attention. Across the United States there is an interesting dichotomy in that states in the East had large absolute gains, but relatively low WUI growth rates, largely because WUI was already so widespread in 1990. In contrast, states in the northern Rockies saw much smaller absolute gains in WUI area and houses, but rapid WUI growth rates.

New WUI areas arise either when new houses are built in or near wildland vegetation or when wildland vegetation regrows in or near settled areas. Between these two possible causes, housing growth was unambiguously the main cause for new WUI areas, with increases in vegetation contributing minimally. Of all new WUI areas, 97% were caused by housing growth in sparsely settled areas, pushing these areas over the threshold of 1 house per 40 acres (6.17 homes/km$^2$). Only 2% of new WUI area was due to vegetation growth alone, and 1% was due to the combination of both housing and vegetation growth (Table S2). Similarly, new houses were the cause of >80% of WUI growth in all states except Delaware, the District of Columbia, Maryland, and New Jersey (Fig. S1).

Among areas that were WUI in 1990, the vast majority were still WUI in 2010, and both homes and population increased in those areas over that time (Table S2). A small proportion (6%) of the 1990 WUI areas dropped out of the WUI by 2010. Among all WUI changes (i.e., gains and losses combined), 13% of the changes in WUI area and 23% of the changes in WUI houses from 1990 to 2010 were losses. In terms of the causes of WUI area loss, reduced housing density was the most important (65.0%), whereas the loss of vegetation accounted for 32.6%. Housing density may have declined due to actual removal of housing units, or possibly due to enumeration errors in the Census data. Loss of vegetation was the dominant driver of loss of homes from the WUI (65.0%), which occurred largely in densely settled areas where additional housing development, deforestation, or fuel management may have removed wildland vegetation.

The number of houses within burned areas in the different decades is a strong indication of how much WUI growth can exacerbate wildfire problems. In 1990, there were 177,000 houses within the perimeters of the fires that occurred in the subsequent 25 y. By 2010, there were 286,000 housing units in the same fire perimeters, i.e., 109,000 more, which corresponds to 62% growth (far outpacing the average US housing growth rate of 29%). Of these new houses, those built before the wildfires occurred complicated firefighting because more houses had to be protected and more residents had to be evacuated. Similarly, houses built after fires occurred are of concern because new development in areas that burned recently, and thus are known to have a high fire risk, suggests that there is little adaptation to fire risk (2).

Our results provide compelling evidence that the WUI in the United States has grown rapidly, despite the risks that wildfires pose to homes and lives (3) and despite the other environmental problems caused by housing development in or near wildland vegetation (9). Our findings are generally in alignment with previous studies that found rapid previous WUI growth (24) and widespread potential for future WUI growth (25, 29), even though absolute numbers are not comparable because of differences in WUI definitions, datasets, and time periods (30). Furthermore, the WUI is not unique to the United States, but is widespread in many other countries as well (15, 16, 18–20). Rampant WUI growth demonstrates that the social and economic factors that together propel WUI growth are strong. WUI areas are attractive places to live because of affordability and ready access to natural settings and recreation (31). As WUI areas attract new residents, the number of houses per capita often increases as well, due to increasing rates of seasonal homeownership and declining family size (32). Indeed, despite the economic downturn after 2008, the absolute number of

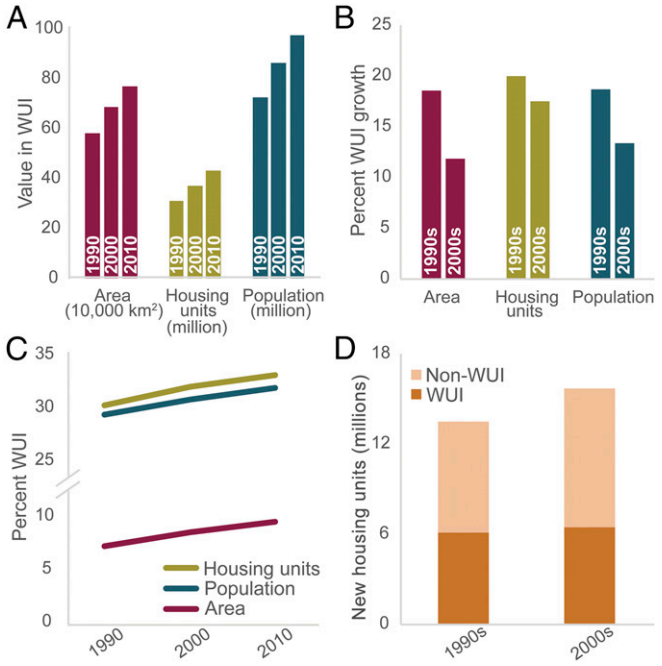


**Fig. 2.** WUI growth was rapid in terms of the absolute numbers of the area, houses, and people in the WUI in 1990, 2000, and 2010 (*A*); WUI growth rates during the 1990s and the 2000s (*B*); the proportion of all houses and people, as well as the land area in the WUI in 1990, 2000, and 2010 (*C*); and the absolute number of all new housing units within and outside the WUI during the 1990s and 2000s (*D*).

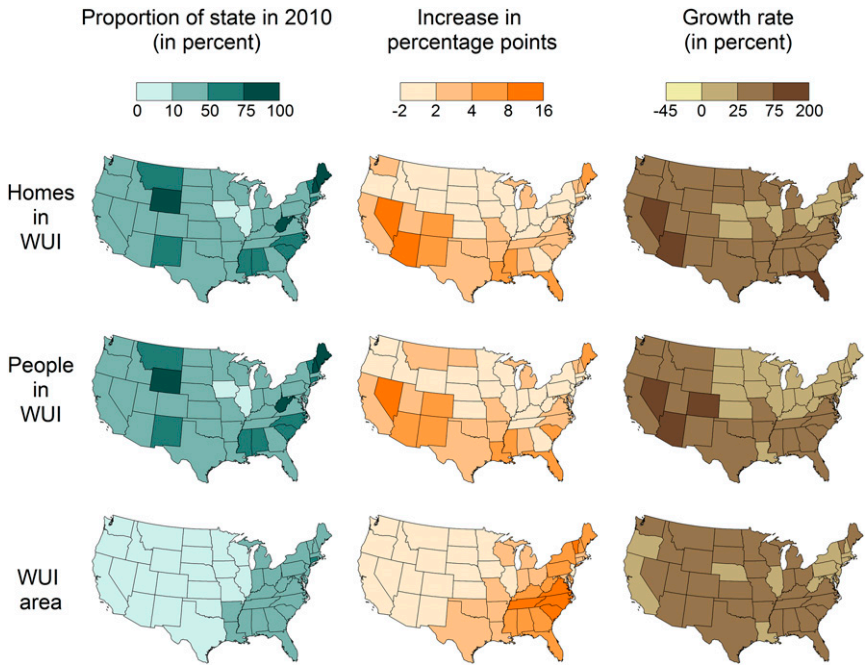


**Fig. 3.** WUI growth differed greatly among states, especially in the Southwest versus the Southeast, in terms of houses in the WUI, people in the WUI, and WUI area, calculated as the percentage of the state total in 2010, change in the WUI percentage from 1990 to 2010, and the growth rate (in percent) of the WUI from 1990 to 2010. Only the District of Columbia had negative absolute growth in the WUI (homes, people, and area). Fig. S2 summarizes these metrics at the county level.

houses built in the WUI, and in the United States as a whole, was higher between 2000 and 2010 than between 1990 and 2000 (Table S1). Demographic trends do not suggest slower future WUI growth. Furthermore, climate change projections indicate that conditions favorable for wildfires will occur more frequently in the future (8). Thus, increased wildfire ignition rates due to WUI expansion will initiate more wildfires in vegetation that is more susceptible to fire spread, leading to more widespread fires and possibly more severe fire behavior (33). This suggests that WUI growth and climate change together will compound the existing problems with wildfires in the WUI.

As WUI growth continues, there are many management options and policy tools to consider for addressing both wildfire and other environmental problems. Just as WUI-related problems involve actors (e.g., homeowners, community leaders) at many levels, so too must their solutions involve actors at multiple levels (i.e., local, regional, state, and national) (3, 8). Homeowners can reduce their individual fire risk by removing vegetation directly adjacent to their house (i.e., the home ignition zone; refs. 3 and 34), changing roofing and building materials, and following additional Firewise recommendations (35). To limit some of the other environmental problems associated with living in the WUI, homeowners can keep cats inside and dogs on a leash, limit fertilizer and pesticide use, and landscape with native plants (9). To reduce wildfire impacts, communities can coordinate fuel reduction efforts, educate homeowners, train firefighters, and establish wildfire management plans. Insurance companies can offer reduced premiums for communities taking mitigation action to incentivize community-level efforts to reduce wildfire losses. Communities and local jurisdictions could anticipate wildfires and environmental impacts more explicitly when planning future land use to avoid housing expansion in high-risk wildfire areas and other environmentally sensitive areas (36). State and federal agencies typically do not regulate development directly, but can allocate resources to areas experiencing rapid WUI growth, support local and regional planning efforts, and provide important research data and information to help communities adapt to fire-prone environments. Agencies managing public lands could consider targeted purchases of private inholdings to limit future housing growth within the administrative boundaries of public lands, which has been particularly rapid (37). In summary, there are many concrete management actions and policy responses that can limit the negative effects of WUI growth on wildfire risk and other environmental problems, but changes will require efforts at all levels by homeowners and community leaders, local and county governments, and state and federal agencies.

Housing development in the WUI greatly exacerbates wildfire problems and other environmental issues in the United States (1, 5, 8), and globally (16, 18–20). Our results highlight the magnitude and rapid rates of WUI growth in the US, underscoring the urgency of identifying what can be done to address WUI growth and its associated wildfire challenges (3). Past federal fire policy has focused largely on fighting and preventing wildfires and on fuel reduction, public outreach campaigns, and other actions (38). Although laudable, such efforts are unlikely to be successful by themselves, because housing growth is clearly the dominant cause of WUI growth, as well as a major factor contributing to wildfire occurrence and cost. As long as WUI growth is unchecked, wildfire problems will likely worsen. On a more hopeful note, to the extent that WUI growth reflects an affinity for nature, the evident consequences and costs of growth could prompt discussions on how to sustain those highly valued ecosystems in which so many people have chosen to live.

## Materials and Methods

Our WUI definition is based on the definition published by the US government in the *Federal Register* (39) and that has been widely used for WUI assessments in the past (1, 14, 40). It specifies two types of WUI, intermix and interface. Intermix WUI is where houses and wildland vegetation intermingle, with both a housing density of >1 house per 40 acres (6.17 houses/km$^2$) and >50% of the area in wildland vegetation. Interface WUI represents settled areas that have <50% vegetation, but lie within

1.5 miles (2.4 km) of a densely vegetated area (at least 75% wildland vegetation) that is at least 5 $km^2$ in size (so that settlements near small urban parks are not included in the WUI).

Our WUI assessment was based on two main datasets: US Census data, which provided housing data (TIGER shape files for block boundaries, plus Census summary files for attribute data), and the US Geologic Survey's NLCD, which provided information on wildland vegetation. We derived housing data from the US Decennial Censuses for 1990, 2000, and 2010 at its finest resolution, the census block level. However, a major obstacle to conducting change analyses is that census block boundaries frequently change from one decade to the next, preventing direct change analyses (27). Indeed, 62% of all blocks changed their boundaries from 1990 to 2000, and 56% changed from 2000 to 2010, invalidating any housing density change analysis that does not account for these boundary changes. We used additional information available from the US Census Bureau as relationship files that details for each decade which blocks of the starting date were at least partly contained by which block in the second decade, and vice versa, to calculate the number of 1990 and 2000 housing units for the boundaries for each 2010 census block.

Based on the Census Bureau relationship files, we first allocated 1990 housing units to 2000 block boundaries by identifying the type of relationship for each 1990 block to 2000 block(s), classifying the relationship as one-to-one, one-to-many, many-to-one, or many-to-many. For one-to-one and many-to-one relationships, 1990 housing units were allocated directly to corresponding 2000 blocks. For one-to-many relationships, 1990 housing units were allocated proportionally based on the number of housing units in the 2000 blocks. For many-to-many relationships, we identified the least common denominator of polygons that fully contained groups of both 1990 and 2000 blocks. For each least common denominator polygon, we then summed the 1990 housing units and allocated them based on the proportion of the 2000 housing units. To minimize instances of many-to-many relationships and maximize direct relationships, we removed blocks that were classified as water in 1990 and as vacant in 2000, as well as all 1990 and 2000 blocks that intersected by <1% of their area. Once 1990 housing units were allocated to 2000 census block geometry, we repeated the process using the 2000–2010 relationship files to allocate 2000 housing units to 2010 block boundaries. We then joined the 1990 housing units allocated to 2000 block boundaries with the 2000–2010 relationship files, and repeated the process to allocate 1990 housing units to 2010 block boundaries. The end result of our algorithms are 1990 and 2000 housing units allocated to the 2010 block geometry across the conterminous United States, i.e., a dataset that permits valid analyses of housing growth across the United States at fine spatial resolution and that minimizes erroneous changes due to changing census block boundaries.

We further refined census block boundaries by integrating them with information on the boundaries of protected areas. The boundaries of protected areas were provided by the Protected Area Database, version 2. Where protected areas intersected census block boundaries, we assumed that the houses in that block were located in nonprotected areas only. However, where census blocks with houses were entirely within a protected area, we made no changes, and assumed a uniform housing density throughout the block.

The 30-m resolution NLCD provided us with data on wildland vegetation. We analyzed both the 1992/93–2001 and the 2001–2011 land cover change products and calculated the percentage of each NLCD land cover class within each census block after refinement by the protected area boundaries. We included forest and grass/shrub land cover classes as wildland vegetation and excluded open water, urban, barren, wetlands, and ice/snow.

For each decade, we mapped the WUI separately, by combining 1990 Census data with 1992/93 data from the 1992/93–2001 land cover change product, and 2000 and 2010 Census data with 2001 and 2011 data from the 2001–2011 land cover change product. We first identified all intermix WUI areas based on the housing and vegetation thresholds. We then identified contiguous vegetation areas that were at least 5 $km^2$ in size and had >75% wildland vegetation, selecting areas within 2.4 km that were above the housing threshold (but below the 50% vegetation threshold), and labeling these as interface WUI. When census blocks were only partly within this distance, we split them.

The NLCD change products are not fully consistent, in that the 2001 land cover in the 1992/93–2001 change product differs from the 2001 land cover in the 2001–2011 change product. Thus, we conducted a sensitivity analysis and mapped the 2001 WUI twice, based on the two representations, and then compared the resulting WUI maps. The differences between the two WUI maps were very minor.

To calculate the number of homes within fire perimeters over time, we analyzed all fire perimeters of fires that burned between 1990 and 2015 according to the Monitoring Trends in Burn Severity (MTBS) dataset, which includes all fires >404 ha (1,000 ac) in the West and 202 ha (500 ac) in the East. We then assessed which census blocks were at least partially within these fire perimeters and calculated an area-weighted estimate of the number of housing units within the fire perimeters in 1990 (177,000), 2000 (210,000), and 2010 (286,000). We note that this is a conservative estimate of the number of houses affected by wildfires because the MTBS dataset does not include small fires.

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ENVIRONMENTAL HEALTH

RESEARCH Open Access

# Cardio-respiratory outcomes associated with exposure to wildfire smoke are modified by measures of community health

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## Abstract

**Background:** Characterizing factors which determine susceptibility to air pollution is an important step in understanding the distribution of risk in a population and is critical for setting appropriate policies. We evaluate general and specific measures of community health as modifiers of risk for asthma and congestive heart failure following an episode of acute exposure to wildfire smoke.

**Methods:** A population-based study of emergency department visits and daily concentrations of fine particulate matter during a wildfire in North Carolina was performed. Determinants of community health defined by County Health Rankings were evaluated as modifiers of the relative risk. A total of 40 mostly rural counties were included in the study. These rankings measure factors influencing health: health behaviors, access and quality of clinical care, social and economic factors, and physical environment, as well as, the outcomes of health: premature mortality and morbidity. Pollutant concentrations were obtained from a mathematically modeled smoke forecasting system. Estimates of relative risk for emergency department visits were based on Poisson mixed effects regression models applied to daily visit counts.

**Results:** For asthma, the strongest association was observed at lag day 0 with excess relative risk of 66%(28,117). For congestive heart failure the excess relative risk was 42%(5,93). The largest difference in risk was observed after stratifying on the basis of Socio-Economic Factors. Difference in risk between bottom and top ranked counties by Socio-Economic Factors was 85% and 124% for asthma and congestive heart failure respectively.

**Conclusions:** The results indicate that Socio-Economic Factors should be considered as modifying risk factors in air pollution studies and be evaluated in the assessment of air pollution impacts.

**Keywords:** Disparities and susceptibility, Air pollution, Climate change, Asthma, Congestive heart failure, Wildfires

## Background

Numerous studies have shown associations between air quality and cardio-respiratory morbidity and mortality. Particulate matter, particularly fine fraction ($PM_{2.5}$), can aggravate asthma and has been linked to irregular heartbeats, heart attacks, and premature death. However, it is clear that not all communities are affected equally. In particular, communities with lower socio-economic status (SES) typically measured by income, education, and racial composition, have consistently been shown to be at increased risk from air pollutants [1-4] but other health factors associated with low SES such as limited access to clinical care or an unhealthy diet may also play an important role in determining a community's health outcome to poor air quality [5-8]. Characterizing the relative importance of these health factors is an important step to understanding differences in community level risk and is critical to setting appropriate policy.

The most common difficulty encountered in evaluating community risk to air pollutants is that many health factors associated with poor health outcomes occur in

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communities where exposure to air pollutants is high. Several studies have shown that compared with those of higher SES, individuals in communities with low SES are more likely to be exposed to poorer air quality in ambient, residential and occupational environments [1,2]. Community risk studies are further complicated by the need to identify reliable health metrics that can be tracked consistently across communities [9]. Here, we sought to overcome these two obstacles and characterize community health factors indicative of acute health outcome risk by taking advantage of a natural phenomenon. We evaluated health responses following brief but acute wildfire smoke exposure in a region with low background pollution and utilized County Health Rankings (CHR) [10], based on a well established model of population health that characterize factors which determine community health. Concentrations of fine particulate matter ($PM_{2.5}$) from smoke forecasting models averaged to the county are taken as the exposure matrix.

In 2008, burning deposits of peat during a wildfire in the Pocosin Lakes National Wildlife refuge in North Carolina produced smoke and haze intermittently for a number of weeks. Previously, we evaluated health effects that occurred during a three day episode in which the smoke plume moved inland and dispersed hazardous concentrations of air pollutants over the eastern and central part of the state [11]. In contrast to the current analysis the episode of exposure was determined using satellite measured aerosol optical density rather than $PM_{2.5}$ concentrations. We found significant increases in emergency department (ED) visits for congestive heart failure (CHF), asthma, chronic obstructive pulmonary disease, pneumonia, and acute bronchitis in those counties which were most impacted by the wildfire. We hypothesized that the strong associations observed in the analysis may have been observed, in part, because the affected population was on average economically disadvantaged, rural, and with high prevalence of hypertension, diabetes, obesity, high blood pressure and other health conditions in comparison to the remainder of the state.

The use of 2010 County Health Rankings permits us to examine the modifying effect of health factors on ED visits for CHF and asthma at the community level. These rankings measure: health behaviors such as tobacco use, diet and exercise; access and quality of clinical care; social and economic factors such as education and income; and the physical environment. In addition, they provide a measure of the general health of the community by measuring two types of health outcomes (mortality, morbidity) at the county level. We focus on two clinical outcomes, CHF and asthma, that have distinct pathology but that have both been associated with susceptibility to the health effects of air pollution exposures [7,12,13]. We examine these indicators as modifiers of risk of adverse health outcomes following smoke exposure and show that the most important are socio-economic factors and measures of the overall health of counties.

## Methods

### Emergency department visits

Daily counts of ED visits were obtained from the NC Disease Event Tracking and Epidemiologic Collection Tool [14], a statewide, public health surveillance system. NCDETECT records daily ED visits from 111 of 114 civilian NC EDs with county of residence, gender, age, and discharge ICD-9-CM codes. In the study presented here we considered visits for two clinical outcomes: for asthma in patients over 18 years old (ICD-9-CM code 493); and for CHF patients over 44 years old (ICD-9-CM code 428). The study period was defined between the onset of the wildfire by lightening (June 1, 2008) and July 14th when the first rainfall, increased humidity, and controlled flooding contained the fire. During this period, average daily temperatures ranged from 69 to 86° F and no heat events were observed. More details are reported in [11]. The Human Subjects Institutional Review Board of the University of North Carolina at Chapel Hill, East Carolina University, and the Environmental Protection Agency approved the study.

### Exposure estimates

Concentrations of fine particulate matter dispersed from the Pocosin Lakes National Wildlife Refuge wildfire were obtained from the National Oceanic and Atmospheric Administration Smoke Forecasting System [15]. These estimates are based on smoke dispersion simulations from the Hybrid Single Particle Lagrangian Integrated Trajectory Model (HYSPLIT). The HYSPLIT model relies on satellite information of the wildfire location, U.S. Forest Service estimates for wildfire smoke emissions, and meteorological inputs from the North American Mesoscale mode. These are used as inputs to resolve vertical column integrated average concentrations hourly, at 0.15° latitude and longitude grid (~13.5 km). The estimated concentrations for the lowest 100 m surface layer were used and averaged over a 24 h period starting with midnight EST. We were unable to obtain a valid HYSPLIT simulation for June 4$^{th}$ GMT, the first day when the fire became an open flame wildfire, underestimating concentrations on June 4$^{th}$ and the night of June 3$^{rd}$. Daily averages at the county level were subsequently calculated by averaging the 24 h period over the county boundaries using Monte Carlo approximation. Daily concentrations were obtained for the duration of the study period June 1$^{st}$ – July 14$^{th}$ 2008.

### Effect modifiers

We used the 2010 County Health Rankings for North Carolina to characterize community health factors that could potentially influence health outcomes [10]. These were developed by the Robert Wood Johnson Foundation and the University of Wisconsin Population Health Institute. CHR groups determinants of community health into four types of Health Factors: Health Behaviors, factors measuring access and quality to Clinical Care, Socio-Economic Factors, and the Physical Environment. In addition to these factors, two types of health outcomes (mortality and morbidity) are used. These measure how long people live (mortality) and how healthy people feel while alive (morbidity) and are general indicators of community health. Health Factors and Health Outcomes thus measure two distinct aspects, determinants vs outcomes, of county health. The County Health Rankings use data from variety of national data sources including Behavioral Risk Factor Surveillance System survey data (BRFSS) of Centers for Disease Control and Prevention, American Community Survey, as well as Dartmouth Atlas of Healthcare.

Health Factors, Outcomes, and individual measures along with their relative weights are listed in Table 1. Among the counties of eastern North Carolina, Mortality and Morbidity Outcome Rankings and Socioeconomic Factor rankings are strongly inter-correlated and mildly correlated with Health Behavior Factors (Additional file 1). The remaining factors, Clinical Care and Physical Environment Factors, are only weakly correlated among themselves and with all other factors. We classified 40 counties into "top" and "bottom" ranked groups relative to the median rank of each outcome and factor. Top ranking by all measures is a more desired outcome, indicating communities with better health ranking.

**Table 1 Health Ranking Weights for the 2010 County Health Rankings (source www.countyhealthrankings.org accessed July 2010)**

| | Cumulative Weight | Measure | Weight |
|---|---|---|---|
| Health Outcomes | | | |
| Mortality | 50% | Years of potential life lost before age 75 | 50% |
| Morbidity | 50% | Quality of life | 50% |
| Health Factors | | | |
| Health Behavior | 30% | Tobacco use | 10% |
| | | Diet and exercise | 10% |
| | | Alcohol us | 5% |
| | | Unsafe sex | 5% |
| Clinical Care | 20% | Access to care | 10% |
| | | Quality of care | 10% |
| Socioeconomic Factors | 40% | Education | 10% |
| | | Employment | 10% |
| | | Income | 10% |
| | | Family and social support | 5% |
| | | Community safety | 5% |
| Physical Environment | 10% | Environmental quality | 5% |
| | | Built environment | 5% |

### Statistical approach

The goal of the analysis was to consider the modifying effect of community level determinants of health on the risk for CHF and asthma visits relative to the concentrations of $PM_{2.5}$. We applied a generalized linear mixed effects model with county specific intercept for Poisson count data to daily counts of ED visits (R version 2.11.1, lme4 package). Among the predictors, in the analysis we also included an indicator of daily concentration of $PM_{2.5}$ above the common detection limit (0.1 $\mu g/m^3$) to control for 0 inflated measurements arising from county-days without smoke. Log-transformed county population size estimates were used as the offset term in the analysis. A separate analysis was performed for two clinical outcomes by individual CHR outcome and factor. Relative risk of ED visits was examined with respect to the exposure concentrations on the day of the visit (lag 0), a day prior to the visit (lag 1), and the average of the two (average over lags 0 and 1) and compared with AIC/BIC criterions. In the case of asthma, exposure on the day of the visit was chosen as the best fitting model while in the case of CHF, the day prior to the visit was the main exposure variable. Results for health outcomes are summarized by excess relative risk or percent change ((RR-1)*100%) per 100 $\mu g/m^3$ increase in daily concentration of $PM_{2.5}$.

## Results

Counties experienced varying concentrations of smoke and length of time in the plume during the study period (Figure 1). Maximum daily smoke related $PM_{2.5}$ concentration ranged from 4 to 129 $\mu g/m^3$ (Figure 2). On average, during the study period, counties had 18 days of daily average concentrations above the detectable level and 3 days with average concentration higher than 20 $\mu g/m^3$. Average daily concentrations and average concentrations over the study period were comparable between top and bottom grouped counties for most rankings. The exception was found for Mortality Outcome and the Clinical Care Factor rankings. Worse ranked counties by Mortality had significantly lower particle concentrations than their better ranked counterparts. Opposite was true for Clinical Care Factor, where

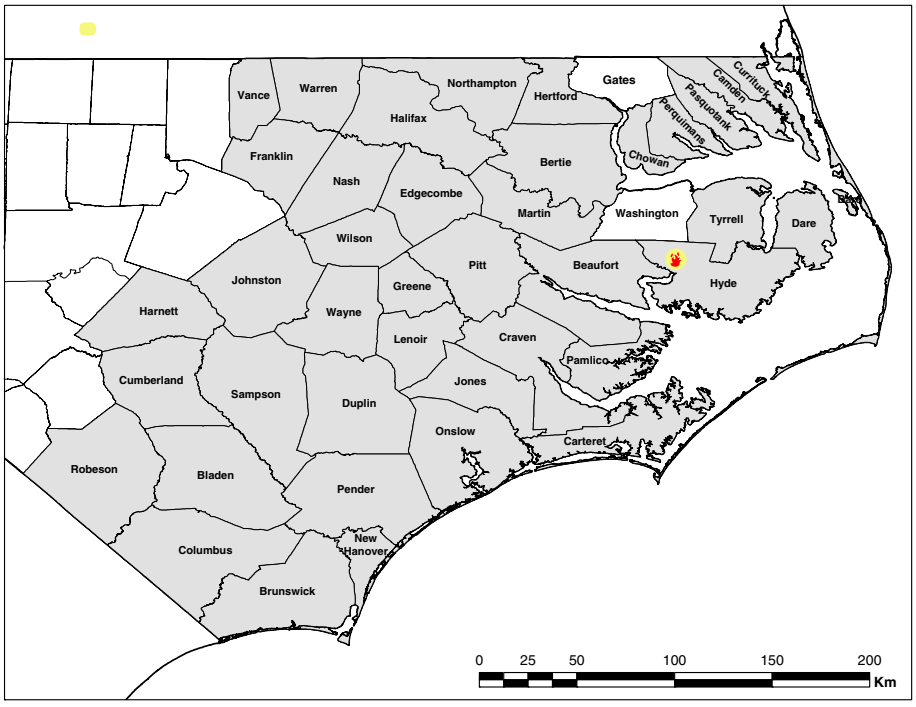


**Figure 1 An a real map of counties affected by the smoke.** Residents of two eastern counties, Washington and Gates, were excluded from the study; ED in Washington County did not participate in the surveillance program and Gates County was impacted by another fire.

worse ranked counties had significantly higher concentration of particles.

For asthma, the strongest association was observed on the day of the exposure (lag day 0) with 66 (28, 117)% increase in the rate of visits (per 100 μg/m3) while strongest association for CHF was observed with the day after the exposure (lag day 1) with 42 (5, 93)% increase in the rate of visits. The results for asthma are consistent with associations previously reported in the literature. The most common associations between exacerbations

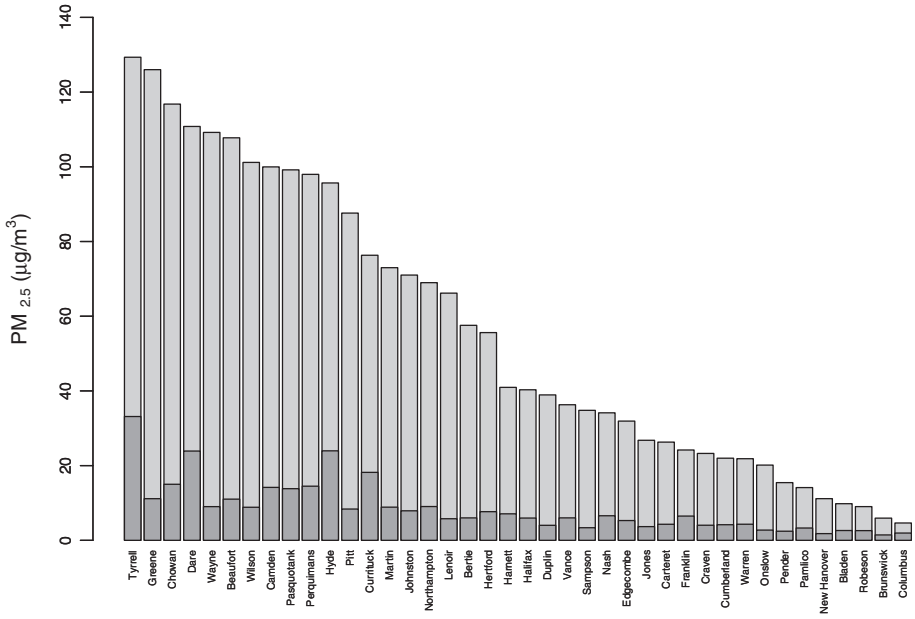


**Figure 2 Distribution of maximum daily concentrations (grey) and mean concentrations over the exposed (concentration > 1μg/m$^3$) days.**

of asthma and wildfire smoke have been reported at lag days 0 and 1 and the average of the two [16-18]. Studies of wildfire smoke report more mixed associations with cardio-vascular effects. However, urban air pollution studies consistently show effects at lag day 0 and 1 following exposure. The lag structure in respiratory and particularly, cardiovascular outcomes, is likely determined not only by the time course of the physiological and biological health effect but cultural, social and environmental conditions that determine one's use of the health care system.

Relative Risk (RR) in asthma, associated with the day of exposure (lag 0), was highly elevated or statistically significant in 'top' and 'bottom' ranked groups of counties across all factors and outcomes (Figure 3A). The largest difference however, between bottom and top ranked counties among the individual factors and outcomes was observed for Socio-Economic Factors and Mortality Outcomes. Bottom ranked counties had 85% and 67% percent points higher risk than top ranked counties for these two measures respectively. Stratification by the aggregate measures, Health Factors and Health Outcomes, similarly showed sizeable differences in risk of 76% and 45% respectively. For all other measures, RR was comparable in magnitude between counties when similarly dichotomized.

We observed significantly increased risk in the counties ranked at the bottom by Socio-Economic Factors, Physical Environment Factors and both outcome measures, one day following the exposures (lag 1) (Figure 3B). By contrast, no changes were observed for the top ranked counties at this time. Difference in relative risk between top and bottom ranked counties by these two measures were 65% and 51% respectively. Stratification by both aggregate measures, Health Factors and Health Outcomes, similarly showed sizeable differences in risk of 68% and 92% respectively. Additionally, differences between top and bottom grouped counties were statistically significant when counties were stratified by Mortality and by Health Outcomes. No changes in RR were observed for either group of county as defined by Health Behaviors and Clinical Care Factors. We did not observe any changes in RR at lag day 0 for congestive heart failure (Figure 4A).

However, associated with the day following the exposure (lag day 1), we observed significantly increased RR in bottom ranked counties by Socioeconomic Factors and Physical Environment, both outcome measures, as well as combined Health Factors and Health Outcomes (Figure 4B). In comparison, no changes in RR were observed for top ranked counties. Additionally, a statistically significant modifying effect was observed for counties grouped by Socio-Economic Factors, Health Behavior Factors and combined Health Factors.

The largest difference in risk between bottom and top ranked counties was again observed for Socio-Economic Factors with a difference of 124%. Mortality and Morbidity produced differences of 59% and 61% respectively. An opposite pattern was found for Health Behavior Factors where top ranked counties showed statistically significant risks while bottom ranked counties had no change.

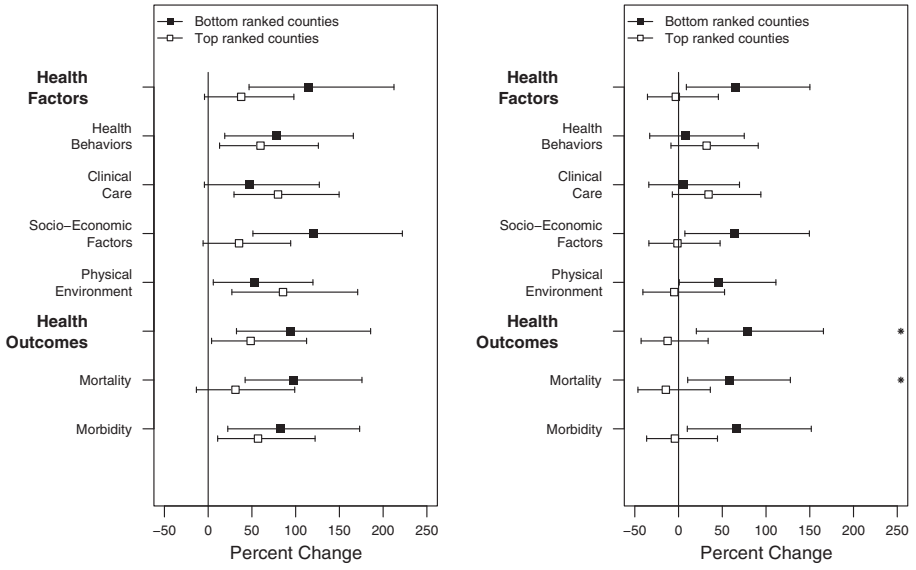


**Figure 3 Excess relative risk of emergency department visits for Asthma a) on the day of the exposure (at lag 0) and b) on the day following the exposure (lag 1).** Stars denote statistically significant difference in risk between two groups of counties. Estimates are reported per 100 μg/m$^3$ of $PM_{2.5}$.

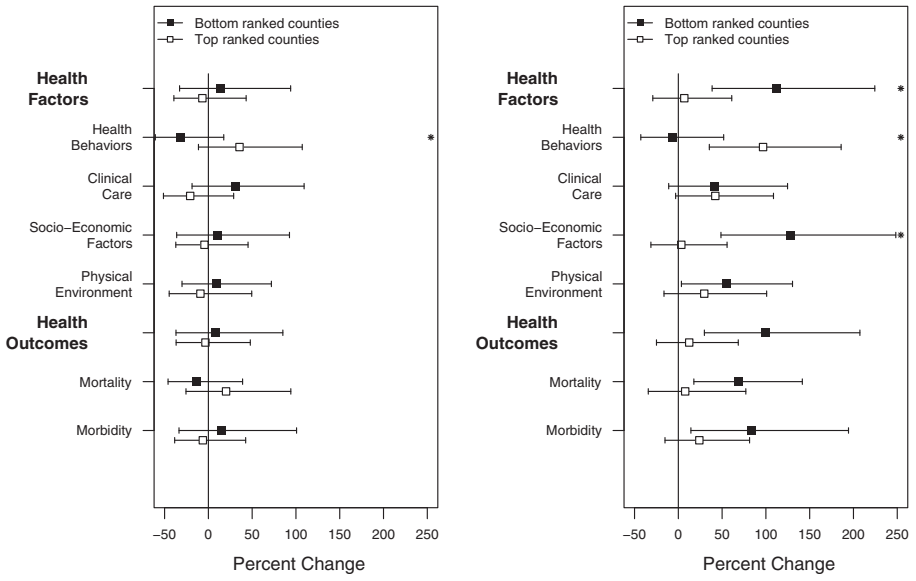


**Figure 4 Excess relative risk of emergency department visits for congestive heart failure a) on the day of the exposure (at lag 0), b) on the day following the exposure (lag1).** Stars denote statistically significant difference in risk between two groups of counties. Estimates are reported per 100 μg/m$^3$ of $PM_{2.5}$.

Among the individual measures of Socio-Economic Factor, 'Employment', 'Family and Social Support', and 'Community Safety' showed consistent differences between top and bottom ranked counties for both asthma and CHF. The most pronounced difference in RR for asthma was observed for 'Poverty' measured by children below poverty where bottom ranked counties had 2 times higher relative risk than top ranked counties (2.68 vs. 1.38) at lag 0, and 53% higher at lag 1. In the case of CHF, the largest differences were observed for 'income inequality' where 223% higher risk was observed in bottom ranked counties.

## Discussion

The results presented here support the hypothesis that general and specific determinants of community health may be used as indicators of susceptibility to adverse health effects following environmental exposures. Numerous studies have shown evidence of association between particulate matter and cardio-respiratory morbidity and many have addressed the biological and genetic factors that influence the association. However, relevant social factors are less well understood. With a nearly complete record of ED visits and detailed daily maps of smoke related $PM_{2.5}$ concentrations, we examined the impact of health factors on the risk of CHF and asthma in relation to the acute emissions of this pollutant. We demonstrate that among the different factors assessed, the strongest difference in relative risk for ED visits in both clinical outcomes was observed when counties were stratified on the basis of Socio-Economic Factors followed by indicators of community health Mortality and Morbidity Outcomes.

The category of Socio-Economic Factors measures 'Employment', 'Community Safety', 'Income', 'Education', and 'Family and Social Support'. Of these, 'Income' was the best indicator of risk. Although different strategies have been used to quantify income and financial resources of the community, CHR uses poverty and income inequality as basic indicators of the community's ability to meet the need for food, clothing, and shelter [10]. For asthma, poverty was the most important predictor while for CHF it was income inequality. Why these measures are better indicators than other factors more directly associated with clinical outcomes such as access to care or diet is unclear. There is a considerable literature on the detrimental health effects of poverty. A recent study [19], showed that poverty imposed the greatest burden of disease in the United States and is at least as important as smoking. Psychological and physical stress, highly present at conditions of severe poverty [20], and perceived inequalities by individuals have also been shown as important determinants of population health [21] explaining health inequalities at all social levels [22]. Stress impacts allostatic load in individuals, thus increasing the susceptibility to diseases. Populations with low SES share larger health burden as they have higher prevalence of chronic and under-treated medical conditions leading to an increased likelihood of adverse health effect in response to the exposures. Long-term exposure to psychological and social stress experienced in communities of low SES can also modify endocrine function and induce epigenetic

changes transferable to the children [23-25]. In addition to biological mechanisms, poverty impacts many of the other factors measured by the CHR through the ability to pay for medical care, access to healthy foods, community safety and social support; all factors we show are associated with risk from $PM_{2.5}$ exposure. The role of income inequality in defining health disparities has been long hypothesized and discussed area of research in social epidemiology. A traditional criticism has been the inability to separate individual and aggregate effects of income inequality in the society. However, more recent studies using multilevel data and multilevel statistical techniques suggest that evidence in support of association particularly at the aggregate levels such as counties and states [26].

The results for other Health Factors and specific measures were more complex. In particular, for asthma we observed an unexpected association between access to health care and ED visits on the day of the exposure. Those counties that ranked well in this category had higher rate of ED visits for asthma than the poorly ranked ones. Similarly, on the day following the exposure counties with higher primary care provider rate had increased risk of ED visits for CHF while poorly ranked counties did not. Access to health care is measured by the percentage of adults with no health insurance and the population per primary care provider in CHR. A possible explanation is that in the affected region, counties with a lower percentage of uninsured adults appear to have lower average income level and reflect communities comprised of many of the working poor. More specifically, using data from Census 2000 we have estimated a 1% (p value = 0.0063) increase in percent of uninsured adults for every $10 K increase in median household income at the county level. This is likely due to the large number of adults under the age of 65 that qualify for federal and state assistance and subsidized health plans in this region. While access and the quality of care may be important determinant of susceptibility at the individual level [8], at the community level we did not observe it to be a determinant of susceptibility.

A limitation of present study is in the ecological nature of the data on both exposures and effect modifiers, which are known only at the county level. For exposures, we have assumed that exposure to ambient air pollution are ubiquitous among the general population, that the mean personal exposures in a county are proportional to the county-wide concentration, and that personal exposures will be subject mainly to Berkson errors. Our analysis of HYSPLIT predictions against the satellite and monitoring data suggests that mis-specification of the magnitude of exposure as more likely source of error then mis-classification of day to day exposure status. For effect modifiers, the relationships at the county level examined in our study may not truly reflect relationships at the individual level due to an ecological bias. Our analysis shows that counties with higher poverty have stronger health associations with ambient smoke concentrations, suggestive that poor individuals may be more sensitive or vulnerable. However, an alternative explanation might be that all individuals in an impoverished county are equally sensitive regardless of individual level socioeconomic status, or even that wealthy individuals in impoverished counties are especially sensitive. Without individual level socioeconomic data on both cases and the referent population, one cannot distinguish between sensitivity or vulnerability conferred by individual or ecologic characteristics.

Environmental exposures often fall disproportionately on economically disadvantaged populations and minorities [3]. However, recent air pollution studies indicate that even after accounting for differences in exposure, the health risks are not equally distributed among populations. For example, urban studies where exposure to traffic pollution is positively associated with socioeconomic disparities [8,27] and those where negative association is observed [6], both report consistent results indicating enhanced health burden among socioeconomically disadvantaged communities. The results from the presented study suggest that, following an acute exposure, the same results may be transferable to the populations that experience generally low levels of background pollution and are unlikely to be due to levels or longevity of the exposure alone. This suggests that SES increase the susceptibility to health outcomes independently of the vulnerability to exposures.

## Conclusions

In the work presented here we evaluate general and specific measures of community health as indicators of susceptibility to adverse events following air pollution exposures. The results suggest that, among various measures of health, Socio-Economic Factors played the most important role in defining susceptibility at the community level. These factors are not commonly considered as modifiers of risk in pollution studies because they can be confounded with number of other susceptibility enhancing factors. For example, SES is typically confounded with short and long term exposures as well as the prevalence of existing medical conditions. Here, we use a wildfire episode during which smoke blanketed the region irrespective of the community health characteristics to evaluate differences in risk. The results, suggesting that SES characteristics should be considered as risk modifiers to the impacts of air pollution exposures, are important steps to understanding differences in community risk and for setting appropriate policies.

## Additional file

**Additional file 1: Table S1. Spearman Rank Correlation coefficient between Community Health Ranking indices over 40 counties.** Table S2. County Ranking Summaries for counties of eastern North Carolina and the remaining counties in the state.

### Abbreviations

$PM_{2.5}$, Particulate matter with and average aerodynamic diameter of less then 10 μm, fine particulate matter; CHF, Congestive heart failure; RR, Relative risk; SEF, Socio-economic factors; SES, Socio-economic status; CHR, County health ranking; ED, Emergency department; NC, North Carolina; NCDETECT, North Carolina disease event tracking and epidemiologic collection tool; ICD-9-CM, International classification of diseases, ninth revision, clinical modification; HYSPLIT, Hybrid single particle Lagrangian integrated trajectory model.

### Competing interests

Authors have no competing interests to declare.

### Authors' contributions

AGR has contributed substantially to the concept, design, analysis, interpretation of results and writing of the manuscript, WEC has contributed substantially to the concept and interpretation of results, VJK has contributed substantially to data collection and writing of the manuscript, SLS has contributed substantially to data collection and writing of the manuscript, LMN has contributed substantially to the concept, interpretation of results and writing of the manuscript, RBD has contributed substantially to the concept, interpretation of results and writing of the manuscript, DD-S has contributed substantially to the concept, interpretation of results and writing of the manuscript. All authors read and approved the final manuscript.

### Disclaimer

The research described in this article has been reviewed by the National Health and Environmental Effects Research Laboratory, U.S. EPA, and approved for publication. The contents of this article should not be construed to represent Agency policy nor does mention of trade names or commercial products constitute endorsement or recommendation for use. The NC DETECT Data Oversight Committee does not take responsibility for the scientific validity or accuracy of methodology, results, statistical analyses, or conclusions presented.

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# Critical Review of Health Impacts of Wildfire Smoke Exposure

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**Background:** Wildfire activity is predicted to increase in many parts of the world due to changes in temperature and precipitation patterns from global climate change. Wildfire smoke contains numerous hazardous air pollutants and many studies have documented population health effects from this exposure.

**Objectives:** We aimed to assess the evidence of health effects from exposure to wildfire smoke and to identify susceptible populations.

**Methods:** We reviewed the scientific literature for studies of wildfire smoke exposure on mortality and on respiratory, cardiovascular, mental, and perinatal health. Within those reviewed papers deemed to have minimal risk of bias, we assessed the coherence and consistency of findings.

**Discussion:** Consistent evidence documents associations between wildfire smoke exposure and general respiratory health effects, specifically exacerbations of asthma and chronic obstructive pulmonary disease. Growing evidence suggests associations with increased risk of respiratory infections and all-cause mortality. Evidence for cardiovascular effects is mixed, but a few recent studies have reported associations for specific cardiovascular end points. Insufficient research exists to identify specific population subgroups that are more susceptible to wildfire smoke exposure.

**Conclusions:** Consistent evidence from a large number of studies indicates that wildfire smoke exposure is associated with respiratory morbidity with growing evidence supporting an association with all-cause mortality. More research is needed to clarify which causes of mortality may be associated with wildfire smoke, whether cardiovascular outcomes are associated with wildfire smoke, and if certain populations are more susceptible.

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## Introduction

Wildfires are a global occurrence. Changes in temperature and precipitation patterns from climate change are increasing wildfire prevalence and severity (Westerling et al. 2006; Settele et al. 2014) resulting in longer fire seasons (Flannigan et al. 2013; Westerling et al. 2006) and larger geographic area burned (Gillett et al. 2004). Wildfire smoke contains many air pollutants of concern for public health, such as carbon monoxide (CO), nitrogen dioxide, ozone, particulate matter (PM), polycyclic aromatic hydrocarbons (PAHs), and volatile organic compounds (Naeher et al. 2007). Current estimated annual global premature mortality attributed to wildfire smoke is 339,000 (interquartile range of sensitivity analyses: 260,000–600,000) (Johnston et al. 2012), but the overall impact on public health in terms of respiratory, cardiovascular, and other morbidity effects is unknown. A better synthesis of current knowledge on the health effects of wildfire smoke is needed to guide public health responses.

Wildfire smoke epidemiology is an active area of research (Henderson and Johnston 2012) with new methods uncovering associations that were previously undetectable. Studies of health outcomes associated with wildfire smoke exposure tend to be retrospective and researchers have to rely on administrative health outcome data such as mortality or hospitalization records. Achieving adequate statistical power has been challenging because such severe outcomes are less common, fires tend to be episodic and short in duration, and exposed populations from individual events are often small. Many recent studies have increased statistical power by investigating very high exposure events that last for longer periods, large populations over many years in regions with frequent fires, more common health outcomes such as medication dispensations, or a combination of these methods.

Previous reviews of wildfire health impacts have either not included the full range of health end points associated with community exposure to wildfire smoke (Dennekamp and Abramson 2011; Henderson and Johnston 2012) or have summarized the literature without critical analysis of specific studies (Finlay et al. 2011; Liu et al. 2015; Youssouf et al. 2014). Our review follows a modified version of the systematic review methodology outlined in Woodruff and Sutton (2014) to analyze studies critically and to only evaluate the strongest evidence.

## Methods

We searched PubMed, Web of Science, and PsychInfo to identify scientific papers related to wildfire smoke exposure and relevant health outcomes. We conceptualized wildfires as those within the definition of landscape fires defined in Johnston et al. (2012). Our search strategy (Figure 1) yielded 778 journal articles in PubMed and 1,248 journal articles in Web of Science in November 2013. We then selected studies that potentially focused on human health effects related to wildfire smoke based on title and yielded 248 journal articles from PubMed and 217 from Web of Science. After discarding duplicates, 350 articles remained. PsychInfo did not yield any new peer-reviewed journal articles.

After reading abstracts, we removed articles if they assessed only exposure and not associated health effects, reported health surveillance outcomes without analysis of associations with exposure, did not analyze primary or secondary health data, did not adequately describe the exposure assessment or it was not clearly related to wildfire smoke, or were not published fully in English. This

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yielded 103 studies that we reviewed. We continually searched for new papers and subsequently added 12 more by August 2015. These papers included human experimental studies of woodsmoke, studies of effects on wildland firefighters, and studies whose outcomes were self-reported respiratory symptoms associated with wildfire smoke, but these are not included in this paper.

From the remaining epidemiological studies ($N$ = 53), we extracted information and made an expert judgment on the risk of bias for each study based on their sample size, exposure assessment methods, control for potential confounding factors, and use of objective outcome measures (see Table S1). We deemed studies to have a lower risk of bias if there were no concerns in any of these categories, moderate risk if there were minor concerns in one or more categories, and higher risk if either there were multiple concerns about bias or if one concern was sufficiently large based on our collective judgment.

All evaluation of results from these studies is based on the authors' interpretation of the reported findings in each paper. In this review "significant" means a 95% confidence interval (CI) that does not include the null, "suggestive" means a 95% CI that does include the null but would not with a slightly relaxed criterion such as a 90% CI, and "no association" means that the 95% CI includes the null with no indication of a relationship. We assumed that exposure to smoke from all types of landscape fires were comparable. We use the term wildfire to refer to all types of landscape fires.

Assessing human exposure to wildfire smoke is challenging for many reasons. Wildfires tend to occur in rural areas in which air pollution monitoring networks might be absent or less comprehensive than in cities. The studies we reviewed used various exposure assignment methods such as self-report, assignment to the nearest regulatory air pollution monitor, comparison of fire periods to non-fire periods, and use of satellite data or air quality modeling output. Heterogeneity of exposure assessment methods across studies (Table 1; see also Table S1) made a quantitative meta-analysis of effect estimates inappropriate. While publication bias could be present in this literature, we could not assess its extent due to the scarcity of studies for each health outcome.

## Results

Our review covers the following health outcomes: mortality, respiratory morbidity, cardiovascular morbidity, birth outcomes, and mental health. We further discuss the evidence from toxicological studies and for susceptible population subgroups. Table S1 provides more details on reviewed studies.

After review of 53 epidemiological papers, we evaluated 27 as having lower potential for bias, 17 as moderate potential for bias and 10 as higher potential for bias. Of the 10 deemed to have higher risk of bias, 4 did not adequately adjust for important covariates (Azevedo et al. 2011; Cooper et al. 1994; Prass et al. 2012; Resnick et al. 2015), 2 were likely underpowered due to small sample size (Cooper et al. 1994; Vedal and Dutton 2006), 3 used retrospective self-report for exposure assessment with high potential for bias (Ho et al. 2014; McDermott et al. 2005; Marshall et al. 2007), and the exposure assessment in 2 other studies was not clearly related to smoke from wildfires (Analitis et al. 2012, Caamano-Isorna et al. 2011). The remaining 43 studies deemed to have low to moderate risk of bias are discussed below. More detail

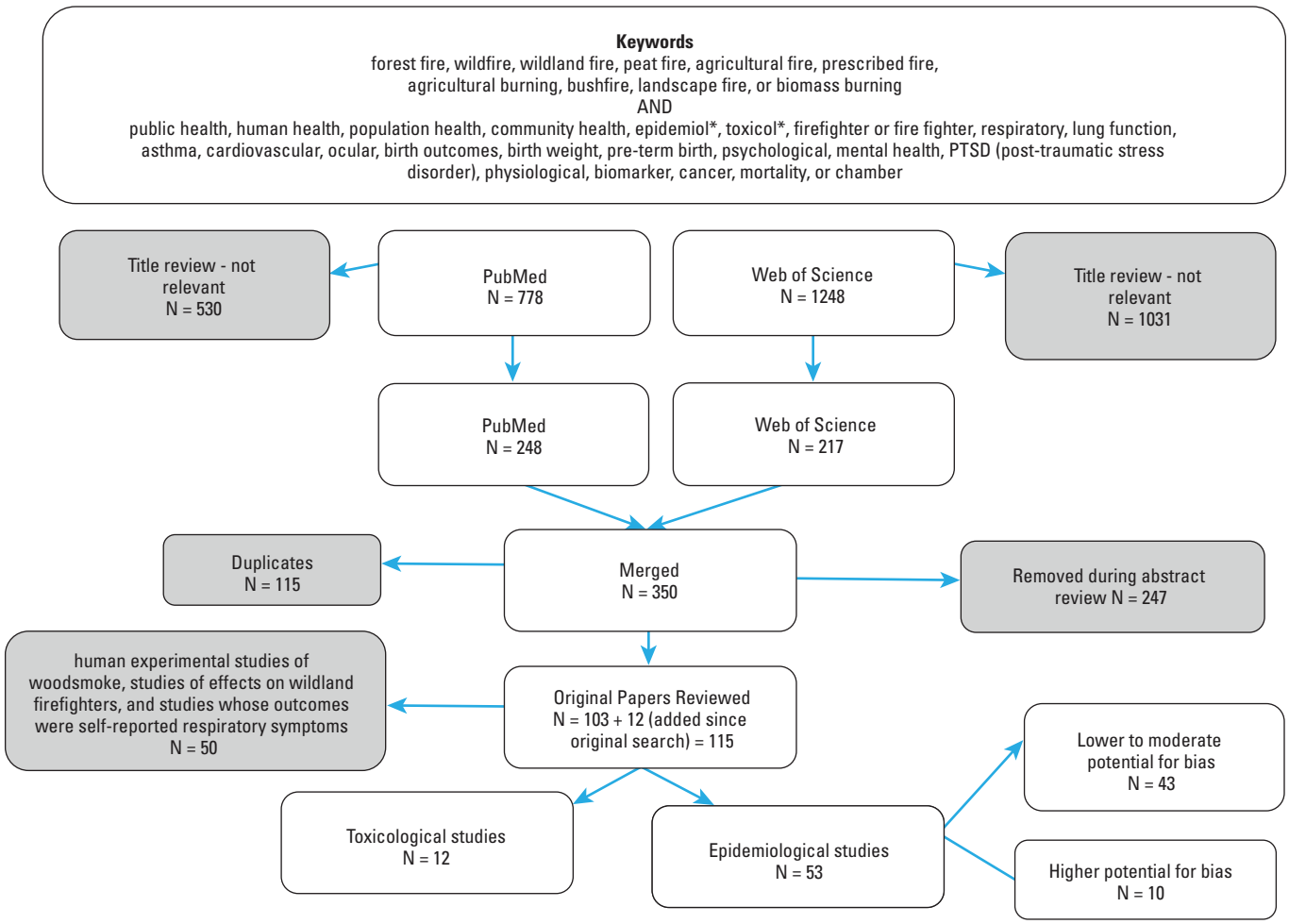


**Figure 1.** Review of studies flow chart.

on the findings from each study is provided in Table S2.

## Mortality

Growing evidence from the more recent, adequately statistically powered studies demonstrates associations between wildfire smoke exposure and all-cause mortality, but more studies are needed to determine whether specific causes of mortality are most affected.

A study of the 1997 southeast Asian wildfire found an increase in mortality in Malaysia associated with a measure of visibility and measured $PM_{10}$ ($PM \leq 10$ μm in aerodynamic diameter) both linearly and with various discrete levels of $PM_{10}$ (Sastry 2002). A study of the 2010 heat wave and wildfires in Moscow reported findings of an interaction between high temperatures and high $PM_{10}$ on deaths and that smoke exposure was responsible for about 29% of the 10,859 excess deaths during the 44-day heat wave (Shaposhnikov et al. 2014). A cross-sectional analysis of cardiovascular mortality among people older than 65 years in the Brazilian Amazon, where the predominant source of air pollution is from wildfires, found a significant association between the percentage of hours of $PM_{2.5}$ over 25 μg/m$^3$ and cardiovascular mortality (Nunes et al. 2013).

The most recent studies of wildfire smoke and mortality take advantage of long time series data and provide growing evidence of significant increases in mortality. A study of 13.5 years of data including 48 days affected by wildfire smoke in Sydney, Australia, demonstrated a significant increase in mortality associated with smoke-affected days (Johnston et al. 2011). An earlier study of mortality in Sydney, using 8 years of data, found a suggestive increase in mortality associated with wildfire-related $PM_{10}$ (Morgan et al. 2010). A meta-analysis of data from 2003 to 2010 in 10 cities in southern Europe found increases in cardiovascular mortality associated with $PM_{10}$ that were stronger on smoke-affected days than on non-affected days, but smoke was not significantly associated with respiratory mortality (Faustini et al. 2015). In Madrid, mortality, but not specifically respiratory or cardiovascular mortality, was associated with $PM_{10}$ on days with advection events associated with biomass burning (Linares et al. 2015). Further multi-year studies in regions regularly affected by wildfire smoke could help clarify if specific causes of mortality are associated with wildfire smoke exposure.

## Respiratory Morbidity

Epidemiological studies have demonstrated significant associations between wildfire smoke exposure and declines in lung function among non-asthmatic children (Jacobson et al. 2012, 2014), and increases in physician

**Table 1.** Findings from epidemiological research studies ($N = 43$) ordered by health outcome.

| Outcome | Article | Exposure assessment type | Direction of association |
|---|---|---|---|
| Mortality | | | |
| All | Sastry 2002 | Monitored PM | ↑↑ |
| | Morgan et al. 2010 | Monitored PM | ↑↑ |
| | Johnston et al. 2011 | Smoky versus non-smoky days | ↑↑ |
| | Faustini et al. 2015 | Smoky versus non-smoky days | ↑↑ |
| | Linares et al. 2015 | Monitored PM | ↑↑ |
| | Shaposhnikov et al. 2014 | Monitored PM | ↑↑ |
| Respiratory | Johnston et al. 2011 | Smoky versus non-smoky days | ↔ |
| | Morgan et al. 2010 | Monitored PM | ↔ |
| | Faustini et al. 2015 | Smoky versus non-smoky days | ↔ |
| | Linares et al. 2015 | Monitored PM | ↔ |
| Cardiovascular | Nunes et al. 2013 | Modeled PM and satellite data | ↑↑ |
| | Faustini et al. 2015 | Smoky versus non-smoky days | ↑↑ |
| | Johnston et al. 2011 | Smoky versus non-smoky days | ↑ |
| | Morgan et al. 2010 | Monitored PM | ↔ |
| | Linares et al. 2015 | Monitored PM | ↔ |
| Respiratory morbidity | | | |
| Lung function in people without asthma or bronchial hyperreactivity | Jacobson et al. 2012 | Monitored PM | ↓↓ |
| | Jacobson et al. 2014 | Monitored PM | ↓↓ |
| | Jalaludin et al. 2000 | Monitored PM | ↓↓ |
| Physician visits | Lee et al. 2009 | Monitored PM | ↑↑ |
| | Henderson et al. 2011 | Monitored PM | ↑↑ |
| | | Modeled PM | ↑ |
| | | Binary satellite indicator of smoke | ↑ |
| | Moore et al. 2006 | Temporal comparison | ↑↑ |
| | Mott et al. 2002 | Temporal comparison | ↑↑ |
| | Lee et al. 2009 | Monitored PM | ↑↑ |
| ED visits | Rappold et al. 2011 | Temporal and spatial comparisons | ↑↑ |
| | Tham et al. 2009 | Monitored PM | ↑↑ |
| | Thelen et al. 2013 | Modeled PM | ↑↑ |
| | Johnston et al. 2014 | Smoky versus non-smoky days | ↑↑ |
| Hospitalizations | Morgan et al. 2010 | Monitored PM | ↑↑ |
| | Henderson et al. 2011 | Monitored PM | ↑↑ |
| | | Modeled PM | ↑ |
| | | Binary satellite indicator of smoke | ↑ |
| | Johnston et al. 2007 | Monitored PM | ↑ |
| | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↑↑ |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↑↑ |
| | Chen et al. 2006 | PM monitoring for categorical exposures | ↑↑ |
| | Cançado et al. 2006 | PM monitoring | ↑↑ |
| | Mott et al. 2005 | Temporal comparison | ↑↑ |
| | Ignotti et al. 2010 | % annual hours > 80 μg/m$^3$ | ↑↑ |
| | Tham et al. 2009 | Monitored PM | ↔ |
| Asthma | | | |
| Lung function among people with asthma | Jacobson et al. 2012 | Monitored PM | ↔ |
| | Jalaludin et al. 2000 | Monitored PM | ↔ |
| | Vora et al. 2011 | Temporal comparison | ↔ |
| | Wiwatanadate and Liwsrisakun 2011 | Monitored PM | ↔ |
| Medications | Elliott et al. 2013 | PM monitoring, statistical modeling, and satellite information | ↑↑ |
| | Yao et al. 2016 | Modeled PM | ↑↑ |
| | Tse et al. 2015 | Temporal and spatial comparisons | ↑↑ |
| | Vora et al. 2011 | Temporal comparison | ↑↑ |
| | Johnston et al. 2006 | Monitored PM | ↑↑ |
| | Arbex et al. 2000 | Measurement of PM | ↑ |
| Physician visits | Henderson et al. 2011 | Monitored PM | ↑↑ |
| | | Modeled PM | ↑↑ |
| | | Binary satellite indicator | ↑ |
| | Yao et al. 2014 2016 | Monitored PM | ↑↑ |
| | | Modeled PM | ↑↑ |
| ED visits | Johnston et al. 2002 | Monitored PM | ↑↑ |
| | Rappold et al. 2011 | Temporal and spatial comparisons | ↑↑ |
| | Duclos et al. 1990 | Temporal comparison | ↑↑ |
| | Johnston et al. 2014 | Smoky versus non-smoky days | ↑↑ |
| | Smith et al. 1996 | Temporal comparison | ↑ |
| | Tse et al. 2015 | Temporal and spatial comparisons | ↔ |

*Table continued*

visits for respiratory problems (Henderson et al. 2011; Lee et al. 2009; Moore et al. 2006; Mott et al. 2002), respiratory emergency department (ED) visits (Johnston et al. 2014; Rappold et al. 2011; Tham et al. 2009; Thelen et al. 2013) and respiratory hospitalizations (Cançado et al. 2006; Chen et al. 2006; Delfino et al. 2009; Henderson et al. 2011; Ignotti et al. 2010; Martin et al. 2013; Morgan et al. 2010; Mott et al. 2005). Findings for specific respiratory end points are reviewed below.

***Asthma.*** Evidence from multiple epidemiological studies demonstrates that wildfire smoke exposure contributes to exacerbations of asthma. Studies have documented increased physician visits (Henderson et al. 2011; Yao et al. 2016), ED visits (Duclos et al. 1990; Johnston et al. 2002, 2014; Rappold et al. 2011) and hospitalizations (Arbex et al. 2007; Delfino et al. 2009; Martin et al. 2013; Morgan et al. 2010; Mott et al. 2005) for asthma associated with wildfire smoke exposure. Some studies found suggestive increases in asthma ED visits (Smith et al. 1996) and asthma hospital admissions (Johnston et al. 2007); these studies may have lacked statistical power due to short time periods (Smith et al. 1996) or small affected populations (Johnston et al. 2007). Another study did not find a significant increase in ED visits or hospitalizations among a cohort of asthmatic children in the year after large wildfires in San Diego, California, compared to the year prior to those fires (Tse et al. 2015).

Four studies demonstrated no significant acute changes in lung function among people with asthma related to PM from wildfires (Jacobson et al. 2012; Jalaludin et al. 2000; Vora et al. 2011; Wiwatanadate and Liwsrisakun 2011), although significant declines in lung function were found among those without asthma (Jacobson et al. 2012) and children without bronchial hyperreactivity (Jalaludin et al. 2000). One possible explanation for these counter-intuitive findings is increased use of rescue medication in response to elevated levels of smoke among those diagnosed with asthma as was found in one (Vora et al. 2011) of two studies (Vora et al. 2011; Jacobson et al. 2012) that investigated this mechanism.

Other studies documented associations between medication usage for obstructive lung disease and wildfire smoke exposure. Both usage of reliever medication and initiation of oral steroid use were associated with wildfire smoke in a panel study of adults and children in Australia (Johnston et al. 2006). People with asthma reported elevated levels of rescue medication usage during a wildfire in Southern California (Vora et al. 2011). Dispensations of reliever medications were related to metrics of wildfire smoke exposure

**Table 1.** *Continued.*

| Outcome | Article | Exposure assessment type | Direction of association |
|---|---|---|---|
| Hospitalizations | Morgan et al. 2010 | Monitored PM | ↑↑ |
| | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↑↑ |
| | Arbex et al. 2007 | PM monitoring | ↑↑ |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↑↑ |
| | Johnston et al. 2007 | Monitored PM | ↑ |
| | Tse et al. 2015 | Temporal and spatial comparisons | ↔ |
| COPD | | | |
| Physician visits | Yao et al. 2016 | Monitored PM | ↑↑ |
| | | Modeled PM | ↑↑ |
| ED visits | Rappold et al. 2011 | Temporal and spatial comparisons | ↑↑ |
| | Duclos et al. 1990 | Temporal comparison | ↑↑ |
| | Johnston et al. 2014 | Smoky versus non-smoky days | ↑↑ |
| Hospitalizations | Morgan et al. 2010 | Monitored PM | ↑↑ |
| | Johnston et al. 2007 | Monitored PM | ↑↑ |
| | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↑↑ |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↑↑ |
| | Mott et al. 2005 | Temporal comparison[a] | ↑↑ |
| Respiratory infections | | | |
| Physician visits | Yao et al. 2016 | Monitored PM[b] | ↑↑ |
| | | Modeled PM[b] | ↔ |
| | | Monitored PM[c] | ↑↑ |
| | | Modeled PM[c] | ↑↑ |
| | Henderson et al. 2011 | Monitored PM[d] | ↔ |
| ED visits | Duclos et al. 1990 | Temporal comparison[b] | ↑↑ |
| | Rappold et al. 2011 | Temporal and spatial comparisons[b] | ↑ |
| Hospitalizations | Johnston et al. 2007 | Monitored PM | ↔ |
| Pneumonia and bronchitis | | | |
| ED visits | Rappold et al. 2011 | Temporal and spatial comparisons | ↑↑ |
| | Johnston et al. 2014 | Smoky versus non-smoky days | ↔ |
| Hospitalizations | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↑↑ |
| | Morgan et al. 2010 | Monitored PM | ↑↑ |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↑ |
| | Duclos et al. 1990 | Temporal comparison[e] | ↑↑ |
| Cardiovascular morbidity | | | |
| Physician visits | Henderson et al. 2011 | Monitored PM | ↔ |
| | | Modeled PM | ↔ |
| | | Binary satellite indicator | ↔ |
| | Moore et al. 2006 | Temporal comparison | ↔ |
| | Lee et al. 2009 | Monitored PM | ↔ |
| | Yao et al. 2016 | Monitored PM | ↓↓ |
| | | Modeled PM | ↔ |
| ED visits | Rappold et al. 2011 | Temporal and spatial comparisons | ↔ |
| | Johnston et al. 2014 | Smoky versus non-smoky days | ↔ |
| Hospitalizations | Morgan et al. 2010 | Monitored PM | ↔ |
| | Hanigan et al. 2008 | PM estimated from visibility data | ↔ |
| | Henderson et al. 2011 | Monitored PM | ↔ |
| | | Modeled PM | ↔ |
| | | Binary satellite indicator | ↔ |
| | Johnston et al. 2007 | Monitored PM | ↔ |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↔ |
| CHF | | | |
| ED visits | Rappold et al. 2011 | Temporal and spatial comparisons | ↑↑ |
| Hospitalizations | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↑ |
| | Morgan et al. 2010 | Monitored PM | ↔ |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↔ |
| Cardiac arrest | | | |
| Out-of-hospital | Dennekamp et al. 2015 | PM monitoring | ↑↑ |
| | Haikerwal et al. 2015 | Modeled PM | ↑↑ |
| ED visits | Johnston et al. 2014 | Smoky versus non-smoky days | ↔ |
| Acute MI | | | |
| ED visits | Haikerwal et al. 2015 | Modeled PM | ↔ |
| Hospitalizations | Haikerwal et al. 2015 | Modeled PM | ↑↑ |

*Table continued*

in British Columbia (Elliott et al. 2013; Yao et al. 2016). Researchers found increases in physician-dispensed short-acting beta-agonists but not physician-prescribed oral corticosteroids for children with asthma in years after two catastrophic wildfires in southern California compared to the year prior to each wildfire (Tse et al. 2015). An association between visits to hospitals for inhalation therapy and daily mass of air particle sediment collected in four nearby water containers was found during one sugarcane-burning season in Brazil (Arbex et al. 2000).

All previously mentioned studies examined exacerbations of asthma, whereas only one study investigated incident asthma related to wildfire smoke. Methodological concerns in that portion of the study suggest a high potential for bias as new diagnoses occurring after, but not during, two large wildfire episodes were included (Tse et al. 2015).

***Chronic obstructive pulmonary disease (COPD).*** Epidemiological evidence of associations between wildfire smoke exposure and exacerbation of COPD is mounting. Elevated rates of hospitalizations (Delfino et al. 2009; Johnston et al. 2007; Martin et al. 2013; Morgan et al. 2010; Mott et al. 2005), ED visits (Duclos et al. 1990; Johnston et al. 2014; Rappold et al. 2011), and physician visits for COPD (Yao et al. 2016) have been associated with wildfire smoke exposure. Additionally, the findings of increased reliever medication dispensing during wildfire smoke exposure in British Columbia may indicate increases in COPD or asthma exacerbations (Elliott et al. 2013; Yao et al. 2016).

***Respiratory infections.*** The evidence for associations between wildfire smoke exposure and respiratory infections is inconsistent. Duclos et al. (1990) found a higher rate of ED visits for respiratory infections during major wildfires in California compared to a reference period. Rappold et al. (2011) found a suggestive increase in ED visits for upper respiratory infections in smoke-affected counties in North Carolina during peat fires compared to a reference period and this temporal increase was not found in non-smoke-affected counties. Henderson et al. (2011) and Yao et al. (2016), however, found no association between wildfire smoke exposure and physician visits for upper respiratory infections in British Columbia. Johnston et al. (2007) reported no association between PM predominantly from wildfires and hospitalizations for respiratory infections in Australia.

The evidence does suggest an association between wildfire smoke and acute bronchitis and pneumonia, however. Although Johnston et al. (2014) did not find an association between ED visits for pneumonia and bronchitis associated with wildfire smoke in Australia, most other studies did. Yao et al. (2016) found significant increases in physician visits for lower respiratory infections associated with $PM_{2.5}$ over 10 fire seasons in British Columbia. Rappold et al. (2011) documented increased ED visits for pneumonia and acute bronchitis associated with exposure to smoke from a peat fire. Duclos et al. (1990) found higher rates of hospitalization for bronchitis during a wildfire compared to a reference period. Moreover, Martin et al. (2013) reported associations between days with high levels of bushfire smoke and hospitalizations for pneumonia and acute bronchitis in Newcastle, Australia, although this association was not found in the larger city of Sydney; the authors attribute this to lack of precision in estimates of specific respiratory outcomes. Two studies have documented similar associations between wildfire smoke and background PM with bronchitis and pneumonia (Delfino et al. 2009; Morgan et al. 2010), suggesting that effects of wildfire and urban PM on these outcomes are similar.

### Cardiovascular Morbidity

Results from studies of associations between cardiovascular outcomes and wildfire smoke exposure are inconsistent. Many studies of wildfire smoke exposure have found no associations with grouped cardiovascular disease outcomes (Hanigan et al. 2008; Henderson et al. 2011; Johnston et al. 2007, 2014; Lee et al. 2009; Martin et al. 2013; Moore et al. 2006; Morgan et al. 2010; Rappold et al. 2011; Yao et al. 2016), although a few have documented evidence for specific end points. Rates of out-of-hospital cardiac arrests were associated with wildfire-related $PM_{2.5}$ in Australia (Dennekamp et al. 2015; Haikerwal et al. 2015). Hospitalizations but not ED visits for acute myocardial infarctions (MI) were associated with wildfire-related $PM_{2.5}$ during the same fires (Haikerwal

**Table 1.** *Continued.*

| Outcome | Article | Exposure assessment type | Direction of association |
|---|---|---|---|
| IHD | | | |
| Physician visits | Lee et al. 2009 | Monitored PM | ↑↑ |
| ED visits | Johnston et al. 2014 | Smoky versus non-smoky days | ↑ |
| | Haikerwal et al. 2015 | Modeled PM | ↑ |
| Hospitalizations | Mott et al. 2005 | Temporal comparison | ↑ |
| | Haikerwal et al. 2015 | Modeled PM | ↑ |
| | Morgan et al. 2010 | Monitored PM | ↔ |
| | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↔ |
| | Johnston et al. 2007 | Monitored PM | ↓↓ and ↑↑[f] |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↔ |
| Hypertension | | | |
| Physician visits | Henderson et al. 2011 | Monitored PM | ↔ |
| Hospitalizations | Arbex et al. 2010 | PM monitoring | ↑↑ |
| Cardiac dysrhythmias/arrhythmias | | | |
| ED visits | Johnston et al. 2014 | Smoky versus non-smoky days | ↔ |
| Hospitalizations | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↔ |
| | Martin et al. 2013 | Smoky versus non-smoky days | ↔ |
| Cerebrovascular disease | | | |
| ED visits | Johnston et al. 2014 | Smoky versus non-smoky days | ↔ |
| Hospitalizations | Delfino et al. 2009 | PM monitoring, statistical modeling, and satellite information | ↑ |
| | Morgan et al. 2010 | Monitored PM | ↔ |
| Angina | | | |
| Dispensations of fast-acting nitroglycerin | Yao et al. 2016 | Monitored PM | ↑↑ |
| ED visits | Haikerwal et al. 2015 | Modeled PM | ↑ |
| Hospitalizations | Haikerwal et al. 2015 | Modeled PM | ↔ |
| Birth outcomes | | | |
| Birth weight | Holstius et al. 2012 | Temporal comparison | ↓↓ |
| Proportion of cohort surviving | Jayachandran 2009 | Satellite data | ↓↓ |
| Low birth weight | Cândido da Silva et al. 2014 | Monitored PM | ↑↑ |
| Mental health | | | |
| Physician visits | Moore et al. 2006 | Temporal comparison | ↔ |
| Hospitalizations | Duclos et al. 1990 | Temporal comparison | ↔ |

[a]Asthma and COPD combined.
[b]Upper respiratory infections.
[c]Lower respiratory infections.
[d]Upper respiratory infections and acute bronchitis combined.
[e]Bronchitis alone.
[f]Significantly elevated for indigenous population, but significantly lower risk for whole population.
↔ No association. ↑ Suggestive increase. ↑↑ Significant increase. ↓↓ Significant decrease.

et al. 2015). ED visits for congestive heart failure (CHF) were associated with wildfire smoke exposure from a peat fire in North Carolina (Rappold et al. 2011), but only a suggestive association was found for CHF hospitalizations and $PM_{2.5}$ during a wildfire in southern California (Delfino et al. 2009). Johnston et al. (2014) did not find any association between wildfire smoke and ED cardiac failure. Other studies have found no associations between wildfire smoke exposure and CHF (Martin et al. 2013; Morgan et al. 2010) or cardiac dysrhythmias (Delfino et al. 2009; Johnston et al. 2014; Martin et al. 2013). And no associations were found in the one study that investigated angina in relation to wildfire $PM_{2.5}$ (Haikerwal et al. 2015).

Study results are also mixed for ischemic heart disease (IHD). Higher counts of hospitalizations for IHD than expected based on historical data were found in Sarawak, Malaysia, during the prolonged very high PM levels of the 1997 Southeast Asian wildfires (Mott et al. 2005). ED visits for IHD were higher on smoke-affected days in Sydney, Australia (Johnston et al. 2014), but two other studies in Australia (Martin et al. 2013; Morgan et al. 2010) and one in California (Delfino et al. 2009) reported no associations for IHD hospital admissions. A study in Darwin, Australia, found increased risk of IHD hospitalizations only among the indigenous population, whereas the results suggested an inverse association among the whole population (Johnston et al. 2007). Researchers also found a positive association between $PM_{10}$ during a wildfire and clinic visits for IHD in a Native American reservation in California (Lee et al. 2009).

Very few studies have investigated other cardiovascular outcomes, making definitive conclusions difficult. Arbex et al. (2010) found increases in hospitalizations for hypertension associated with exposure to total suspended particles over 2 years within a community seasonally exposed to smoke from burning sugarcane, but there was no clear difference in this finding between burning and non-burning periods, which implies that the relationship may not be due to the source of the particles. Henderson et al. (2011) did not find any relationship between $PM_{10}$ during a wildfire and physician visits for hypertension. One (Delfino et al. 2009) of three (Delfino et al. 2009; Morgan et al. 2010; Johnston et al. 2014) studies to investigate cerebrovascular disease or stroke found a suggestive association with wildfire smoke exposure.

Too few studies and too many inconsistencies in findings exist to determine whether wildfire smoke exposure is associated with specific cardiovascular outcomes, despite evidence that exposure to ambient PM is associated with increased risk of cardiovascular morbidity (Brook et al. 2010).

### Birth Outcomes

Corroborative evidence suggests that wildfire smoke exposure effects on birth outcomes are plausible. For example, a growing literature exists on associations between adverse birth outcomes and exposure to ambient air pollution (Woodruff et al. 2010), to wood smoke from household cooking and heating in developing countries (e.g., Lakshmi et al. 2013) and to household heating in developed countries (Gehring et al. 2014). While these exposures are chronic compared to the more acute nature of exposure to smoke from some wildfires, some studies have demonstrated links between wildfire smoke exposure and birth outcomes. Holstius et al. (2012) found lower birth weights, overall and for the second and third trimesters specifically, for babies that gestated during the 2003 southern California wildfires compared to babies from the same region born before or more than 9 months after the fires. Jayachandran (2009) found that prenatal smoke exposure from the 1997 Southeast Asian wildfire in the third trimester was the most important predictor of 'missing' children from the Indonesian 2000 Census, the only way to estimate early life deaths from the scant data in Indonesia. Pregnant women exposed to very high levels of $PM_{2.5}$ from agricultural burning in the Brazilian Amazon had higher rates of low birthweight babies compared to those exposed to lower levels (Cândido da Silva et al. 2014).

### Mental Health Outcomes

Although many studies have documented evidence of psychological impairment related to wildfires (e.g. Papanikolaou et al. 2011), few have investigated smoke exposure as a cause. We found six studies that investigated the association between objective mental health impacts and wildfire smoke exposure; however, four of those were deemed to have higher potential for bias (Ho et al. 2014; McDermott et al. 2005; Marshall et al. 2007; Caamano-Isorna et al. 2011). In the two studies that remain, one found no increase in physician visits for mental illness associated with PM during the 2003 wildfire season in British Columbia (Moore et al. 2006) and the other found no increase in mental health hospitalizations during the 1987 California fires compared to a reference period (Duclos et al. 1990).

### Toxicological Studies

A major pathway by which PM causes respiratory effects is through pulmonary oxidative stress and inflammation (Nakayama Wong et al. 2011). Systemic responses are the main pathways through which PM is thought to influence cardiovascular health. These are hypothesized to be induced either directly by the movement of pro-inflammatory, pro-coagulation, and pro-oxidant components of PM to the circulation, indirectly as a consequence of the pulmonary changes induced by PM, or through PM-mediated changes in the autonomic nervous system (Brook et al. 2010; Delfino et al. 2010).

*In vivo* animal studies of wildfire-derived PM exposure compared to controls have demonstrated increased oxidative stress and cell death in mice (Williams et al. 2013), and lower counts of lung macrophages, higher levels of inflammatory cells and cytokines, and greater antioxidant depletion in a study of smoke from a California wildfire in a mouse model (Wegesser et al. 2009, 2010). Similarly, increased respiratory inflammation and reduced lung mechanics compared with controls was documented from a mouse study of biomass smoke from burning sugarcane in Brazil (Mazzoli-Rocha et al. 2008). *In vivo* studies in humans have also demonstrated increased inflammatory responses, specifically elevated band neutrophil counts in peripheral blood (Tan et al. 2000) and elevated cytokines (van Eeden et al. 2001) associated with air pollution levels during the 1997 Southeast Asian wildfires.

*In vitro* studies have documented increased inflammation in rat alveolar macrophages exposed to $PM_{2.5}$ from prescribed fires (Myatt et al. 2011) and in human bronchial epithelial cells exposed to wildfire-derived $PM_{2.5}$ compared to cells exposed to ambient PM (Nakayama Wong et al. 2011). After exposure to wildfire-derived PM, human lung epithelial cells showed declines in glutathione, an important antioxidant (Pavagadhi et al. 2013); mouse peritoneal monocytes showed increased hydrogen peroxide production and oxygen radical generation (Leonard et al. 2007); and mouse macrophages (Franzi et al. 2011), rat macrophages (Myatt et al. 2011), and human lung epithelial cells (Pavagadhi et al. 2013) had increased cell death.

Oxidative stress can also lead to DNA damage. All size fractions of PM extracted from wildfire smoke caused DNA damage in mouse peritoneal monocytes (Leonard et al. 2007). Studies in regions near sugarcane burning in the Brazilian Amazon observed higher numbers of micronucleated cells, a measure of genotoxicity, in buccal cells from children in highly smoke-affected areas compared to children in a control community (Sisenando et al. 2012); however, it is unclear if the higher pollution in the study communities was solely due to agricultural burning because two factories are located in the exposed but not in the control region. Another study found more micronucleated buccal cells in sugarcane workers compared to nearby hospital administrative workers (Silveira et al. 2013), but the authors do not mention any control for other differences in these two populations that could explain this finding.

A recent study demonstrated the potential for early life exposure to wildfire smoke to confer immune effects, measured as reduced cytokine synthesis in peripheral blood cells, lasting into adolescence in Rhesus macaque monkeys (Miller et al. 2013). Short-term inhalation of wood smoke in general and not specifically from a wildfire can compromise lung immune responses, which may be one reason for the observed increased likelihood of lung infections in children exposed to wood smoke (Zelikoff et al. 2002). There is therefore growing evidence to support the theory that incidence of respiratory infections can be increased by exposure to wildfire smoke.

In summary, existing toxicological evidence supports potential respiratory and cardiovascular health effects of wildfire smoke exposure. The body of evidence, however, is relatively small compared to toxicological studies of general PM.

### *Vulnerable Populations*

Few epidemiological studies have investigated whether specific populations are more susceptible to wildfire smoke exposure than the general population. Susceptibility factors investigated include those related to lifestage, pre-existing disease, socioeconomic status (SES), and ethnicity. Unless otherwise stated, all subgroup differences are based on observed changes in the magnitudes of point estimates, not on significance tests.

The findings for differential effects by age are inconclusive. A study of $PM_{10}$ exposure in Malaysia from the 1997 Southeast Asian wildfires found higher rates of mortality among people 65–74 years old compared to others; a smaller suggestive effect was found among those ≥ 75 years old (Sastry 2002). People ≥ 65 years old had higher rates of respiratory hospitalizations compared to younger adults exposed to biomass burning in the Brazilian Amazon (Ignotti et al. 2010) and wildfire smoke in Australia (Morgan et al. 2010). Such older adults were also found to have higher rates of hospitalization for asthma than their younger counterparts during California wildfires (Delfino et al. 2009), and higher rates of out-of-hospital cardiac arrests and hospitalizations for IHD in Victoria, Australia (Haikerwal et al. 2015).

Other studies, however, have found higher effects for younger adults than for older adults. Wildfire PM-related respiratory admissions during Indonesian wildfires exceeded predictions for 40- to 64-year-olds but not for those ≥ 65 years (Mott et al. 2005). Similarly, ED visits for COPD, and pneumonia and acute bronchitis were more strongly associated with peat fire smoke among people < 65 years old compared to people ≥ 65 in North Carolina (Rappold et al. 2011). Although respiratory physician visits were associated with $PM_{10}$ among people 60–70 years old and among those ≥ 80 in a British Columbia wildfire, younger adults exhibited stronger associations (Henderson et al. 2011). No differences were found in either of the two studies that investigated differential effects by age for cardiovascular outcomes (Morgan et al. 2010, Henderson et al. 2011).

Children with asthma did not experience increased respiratory symptoms or medication use during Australian wildfires, whereas adults did (Johnston et al. 2006). Similarly, the highest PM-related increase in physician visits for asthma during a wildfire in British Columbia was found for adults (Henderson et al. 2011), as was true for ED visits for asthma on smoke-affected days in Australia (Johnston et al. 2014). Asthma hospitalizations among children ages 0–5 years were more strongly associated with wildfire $PM_{2.5}$ exposure than were asthma hospitalizations for both older children and adults < 65 years old during a California wildfire; but the greatest association was found for people ≥ 65 years (Delfino et al. 2009).

Some studies have used previous health care utilization as a measure of pre-existing health conditions. One study found no effect modification by number of physician visits in the previous year (Henderson et al. 2011). In contrast, people ≥ 65 years old who were hospitalized for any cardiorespiratory outcome in the first half of the year were at increased risk of being hospitalized during the 1997 Southeast Asian fires compared with similar temporal comparisons in previous years without fires (Mott et al. 2005). Pre-existing cardiac or respiratory conditions may plausibly increase vulnerability to wildfire smoke exposure; however, the available evidence is currently inconclusive.

A recent study found that body mass index modified the association of wildfire smoke exposure on exacerbations of asthma, as measured by prevalence of physician-dispensed short-acting beta-agonists for children with asthma in southern California (Tse et al. 2015).

Few studies have investigated how socioeconomic status (SES) influences responses to wildfire smoke exposure. Henderson et al. (2011) noted findings of no effect modification by neighborhood SES on associations between wildfire smoke exposure and physician visits in British Columbia, Canada, but detailed results were not presented. In contrast, during a North Carolina peat fire, North Carolina counties with lower SES had higher rates of ED visits for asthma and CHF compared to counties with higher SES (Rappold et al. 2012). Similarly, in Indonesia, districts with lower food consumption demonstrated larger adverse associations between smoke exposure and survival of birth cohorts than those with higher household food consumption (Jayachandran 2009).

To our knowledge only one ethnic subgroup has been studied in relation to differential health outcomes associated with wildfire smoke exposure. Indigenous people in Australia experienced higher rates of hospitalization for respiratory infections (Hanigan et al. 2008), and IHD (Johnston et al. 2007) associated with exposure to bushfire smoke than non-indigenous people. This effect may be explained by underlying health status, access to medical services, or other social characteristics in this group (Martin et al. 2013).

## Discussion

Our critical review demonstrated consistent evidence of associations between wildfire smoke exposure with general respiratory morbidity and with exacerbations of asthma and COPD (Table 1). Mounting epidemiological evidence and plausible toxicological mechanisms suggest an association between wildfire smoke exposure and respiratory infections, but inconsistencies remain. Increasing evidence suggests an association between wildfire smoke exposure and all-cause mortality, especially from more recent, higher-powered studies (e.g., Johnston et al. 2011; Morgan et al. 2010; Faustini et al. 2015). The current evidence for cardiovascular morbidity from wildfire smoke exposure remains mixed; many studies are inconclusive or negative, but some have demonstrated significant increases for specific cardiovascular outcomes, such as cardiac arrests. Toxicological findings are consistent with cardiac effects through evidence of systemic inflammation and increased coagulability. Most of the other end points of interest, including birth outcomes, mental health, and cancer have not been sufficiently studied.

Our review highlights the lack of information about which populations are most susceptible to wildfire smoke exposure. People already diagnosed with asthma or COPD are more susceptible. We found inconsistent evidence of differential effects by age or SES. Two studies have suggested differential effects by Australian indigenous status with no investigation of other ethnic groups.

Many gaps exist in understanding the public health implications of exposure to wildfire smoke. Larger studies with greater statistical power and more spatially refined exposure assessments are needed to better characterize impacts on mortality, cardiovascular disease, birth outcomes, and mental health effects. Currently, evidence exists of exacerbation, but not incidence, of asthma and COPD from wildfire smoke exposure. In temperate parts of the world, where wildfire smoke exposure is episodic, it is unlikely that changes in asthma incidence would be observed. Studies have not been conducted in populations more chronically exposed to wildfire smoke. Additionally, other health outcomes associated

with wildfire smoke exposure have not yet been sufficiently studied, such as otitis media, which has been associated with exposure to second-hand tobacco smoke (Kong and Coates 2009), air pollution from woodsmoke (MacIntyre et al. 2011) and recently wildfire smoke (Yao et al. 2016). Human experimental studies of exposures to wildfire smoke could help clarify biological mechanisms. Very little information exists on health effects associated with measures of pollutants in wildfire smoke other than PM, such as ozone or PAHs. Although this review combined results from studies of various types of fires, it is possible that smoke originating from peat fires, forest fires, grassland fires, and agricultural burning could lead to differential health effects due to different constituents in the smoke. To our knowledge, no studies have yet investigated chronic exposure to wildfire smoke, but many populations in Southeast Asia, Africa, and Latin America are exposed regularly for extended periods (Johnston et al. 2012).

Characterization of the exposure–response function is critical for setting smoke levels for public health warnings or interventions, and it is not yet known whether current levels based on undifferentiated PM sufficiently characterize the effects of wildfire smoke. Four studies (Arbex et al. 2010; Chen et al. 2006; Johnston et al. 2002; Sastry 2002) have attempted to identify effects at different exposure levels, but these studies are hard to compare because of differences in exposure assessment methods, health outcomes, types of fires, and population susceptibilities.

## Conclusions

We found consistent evidence of associations between wildfire smoke exposure and respiratory morbidity in general, and specifically for exacerbations of asthma and COPD. Growing evidence suggests associations with respiratory infections and all-cause mortality. More research is needed to determine whether wildfire smoke exposure is consistently associated with cardiovascular effects, specific causes of mortality, birth outcomes, and mental health outcomes. Research into which populations are most susceptible to health effects from wildfire smoke exposure is also needed to inform public health planning for future wildfires.

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FAST-TRACK

# A southern California freeway is a physical and social barrier to gene flow in carnivores

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## Abstract

**Roads present formidable barriers to dispersal. We examine movements of two highly mobile carnivores across the Ventura Freeway near Los Angeles, one of the busiest highways in the United States. The two species, bobcats and coyotes, can disappear from habitats isolated and fragmented by roads, and their ability to disperse across the Ventura Freeway tests the limits of vertebrates to overcome anthropogenic obstacles. We combine radio-telemetry data and genetically based assignments to identify individuals that have crossed the freeway. Although the freeway is a significant barrier to dispersal, we find that carnivores can cross the freeway and that 5–32% of sampled carnivores crossed over a 7-year period. However, despite moderate levels of migration, populations on either side of the freeway are genetically differentiated, and coalescent modelling shows their genetic isolation is consistent with a migration fraction less than 0.5% per generation. These results imply that individuals that cross the freeway rarely reproduce. Highways and development impose artificial home range boundaries on territorial and reproductive individuals and hence decrease genetically effective migration. Further, territory pile-up at freeway boundaries may decrease reproductive opportunities for dispersing individuals that do manage to cross. Consequently, freeways are filters favouring dispersing individuals that add to the migration rate but little to gene flow. Our results demonstrate that freeways can restrict gene flow even in wide-ranging species and suggest that for territorial animals, migration levels across anthropogenic barriers need to be an order of magnitude larger than commonly assumed to counteract genetic differentiation.**

*Keywords*: carnivores, conservation genetics, gene flow, habitat fragmentation, road and anthropogenic barriers, territoriality

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## Introduction

Roads are the primary threat to dispersal between habitat patches in urban landscapes (Forman & Alexander 1998) and, without dispersal, isolated populations may be doomed to extinction (Brown & Kodric-Brown 1977; Hanski *et al*. 1996). Roads can also isolate populations previously in genetic communication, and the resulting genetic erosion may contribute to population decline (Saccheri *et al*. 1998; Westemeier *et al*. 1998). Empirical data on the frequency of dispersal across roads and its effect on genetic variation and population persistence are few and limited to small and relatively abundant species with low vagility (e.g. frogs, Reh & Seiz 1990; voles, Gerlach & Musolf 2000; beetles, Keller & Largiadér 2003). In contrast, the ability of large carnivores to disperse long distances could mitigate the effects of genetic isolation. However, for carnivores, population densities are low and home range

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sizes and dispersal distances are large (Sunquist & Sunquist 2001), so their persistence should be strongly influenced by the isolating effects of roads and development. Additionally, carnivores are susceptible to the deleterious genetic effects of inbreeding in small populations (O'Brien *et al.* 1985; Roelke *et al.* 1993; Vila *et al.* 2003; Liberg *et al.* 2005). Although conservation biologists have focused on the importance of connectivity for carnivores, actual demonstrations of the genetic consequences of roads for such long-lived and mobile species have been lacking.

We studied dispersal and genetic differentiation in coyote (*Canis latrans*) and bobcat (*Lynx rufus*) populations separated by a wide and heavily travelled freeway in the highly urbanized landscape of southern California. To obtain a direct estimate of dispersal, we radio-tracked animals on both sides of the freeway over seven years, from 1996 to 2003. To obtain a genetic estimate of dispersal, we genotyped individuals using highly variable microsatellite loci and then used genetic assignment tests based on the composite genotypes to assign animals genetically to each side of the freeway. We then assessed levels of genetic differentiation between populations on the same and different sides of the freeway to measure the effect of the road on gene flow (genetically effective migration). Finally, we determined whether levels of observed migration were consistent with levels of gene flow estimated by a coalescent model based on the number of generations since the freeway was established. The use of both radio-tracking information and genetic data to monitor migration and gene flow allows an assessment of the long-term genetic consequences of roads and other anthropogenic barriers on genetic diversity and can lead to the development of plans to mitigate their effects.

## Materials and methods

We studied coyote and bobcat populations separated by the Ventura Freeway (US101), a congested 10–12 lane road in the San Fernando Valley 40 km from downtown Los Angeles. More than 150 000 vehicles use the road daily and the presence of a meridian fence largely restricts dispersal to underpasses and culverts (Fig. 1A) (Ng *et al.* 2004). The freeway was established in 1949 from a relatively undeveloped secondary road with minimal traffic (B. Marquez, personal communication), and there are no other natural barriers such as rivers or topographic features following the freeway that would have historically restricted gene flow. The study area consisted of 358 km$^2$ of chaparral, grassland, and oak woodland habitat (Table S1, Supplementary material) interspersed with secondary roads and housing developments. The 28.4-km length of the freeway connects the towns of Agoura Hills and Thousand Oaks that have a combined population of 200 000. The area is considered a critical habitat corridor connecting the Santa Monica Mountains with extensive natural habitat to the north (Penrod *et al.* 2001).

### *Animal capture and radiotelemetry*

Bobcats and coyotes were captured with padded foothold traps in 1996–1998 and with box traps (bobcats) and neck snares (coyotes) in 2000–2003. We also genotyped a population of bobcats from northern California where bobcats were captured with box traps from 1992 to 1995 (Riley *et al.* 2004). Captured animals were aged, sexed, weighed, measured, ear-tagged, radio-collared, and released at the capture site. Blood, hair, scat, and in some cases tissue samples were taken for genetic analyses.

Animals were radio-located by triangulation using three consecutive or two simultaneous compass directions obtained with a peak directional antenna. Locations were obtained throughout the 24-h daily cycle. We computed 95% minimum convex polygon home ranges for animals with at least 20 locations. Home range overlap was computed for animals that were radio-tracked concurrently. We computed overlap as the total percentage of the home range that intersected with any other animals of the same sex.

### *Genetic sampling*

All bobcat and coyote DNA samples were extracted from blood or tissue (ear punch) samples taken at time of capture. Standard phenol–chloroform extraction methods were utilized. Seven dinucleotide microsatellite loci developed for the domestic cat (Menotti-Raymond *et al.* 1999) and validated for polymorphism in the bobcat (Ernest *et al.* 2000) were used to genotype all bobcat specimens (FCA026, FCA043, FCA045, FCA077, FCA090, FCA096, and FCA132). Seven tetranucleotide microsatellite loci developed for the domestic dog (Breen *et al.* 2001) and validated as polymorphic for the coyote by the authors were used to type all coyote specimens (FH2001, FH2137, FH2422, FH2062, FH2226, FH2293, and PEZ19). Polymerase chain reactions (PCR) utilized either (i) a fluorescent dye-labelled forward primer, or (ii) a hybrid combination of forward primers consisting of the published forward primer with the M13F (–20) sequence (16 bp) added to the 5′ end and a fluorescent dye labelled M13F (–20) primer. The unlabelled reverse primer was used in both cases. We used the PCR conditions for the hybrid combination primer (a two-step cycle) (Boutin-Ganache *et al.* 2001). Primer dye labelling utilized BeckmanCoulter dye D4 and PCR products were sized on the BeckmanCoulter CEQ2000XL DNA Analysis System.

### *Genetic analysis*

Observed and expected heterozygosities, allelic diversity, and deviation from Hardy–Weinberg equilibrium were assessed with GENEPOP (Raymond & Rousset 1995; Table S2, Supplementary material). Bonferroni corrections to significance levels were applied to account for multiple

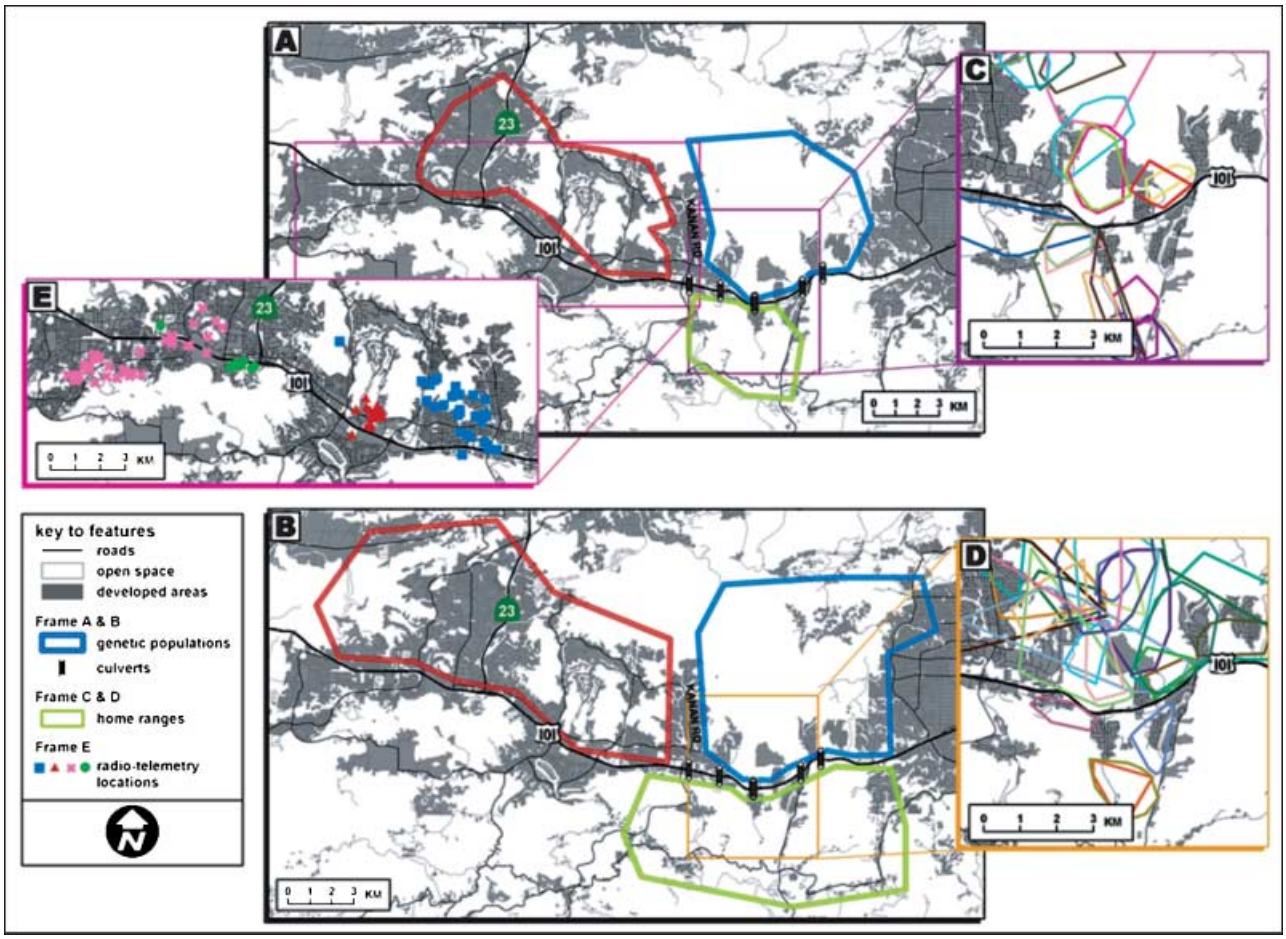


**Fig. 1** Study populations, home ranges and radio-locations of bobcats and coyotes near the Ventura Freeway in southern California. Bobcat (A) and coyote (B) study populations are located north and south of the Ventura Freeway. The north side populations are further divided by Kanan road into northeast and northwest populations. 95% minimum convex polygon (MCP) home ranges are shown for all radio-tracked bobcats (C) and coyotes (D) near the freeway between the south and northeast populations. In (E), radio-telemetry locations are shown for four bobcats with locations north and south of the freeway that were captured north of the freeway but assigned genetically to the population south of it (see Fig. 2).

tests in the determination of heterozygote deficiency/excess (Rice 1989). Coyote samples were grouped into two populations north and south of the freeway, whereas bobcats were divided into three populations, two north and one south of the freeway according to STRUCTURE results (see Results and discussion).

To obtain a genetic estimate of dispersal, we used assignment tests based on the composite microsatellite genotypes. Assignment tests identify the population of origin for each individual, and thus individuals assigned to a population other than the one in which they were caught can be considered migrants (Berry *et al*. 2004). We used the program STRUCTURE (Pritchard *et al*. 2000) to assign individuals to populations. STRUCTURE is a Bayesian clustering algorithm that uses multilocus genotypes to infer population structure and assign individuals to populations. All individuals were combined into one data set for analysis, without any a priori population assignments. We utilized a burn-in of 50 000 iterations, followed by 500 000 iterations of the Gibbs sampler. Admixture was allowed. We evaluated $K$ values, the number of assumed populations, from 1 to 6. Each value of $K$ was run a minimum of three times to evaluate stability. For the highest likelihood $K$ value, we then evaluated the cluster assignment results for each individual with respect to its capture location.

For potential migrants identified in the initial STRUCTURE analysis, we modified the STRUCTURE input data file to reassign them to their putative population of genetic origin based on the cluster assignment results. We then calculated the posterior probability of correct population assignment with this revised data set in STRUCTURE using the ancestry model with admixture, incorporating population information with the migration parameter set to $v = 0.1$ (Table S5, Supplementary material).

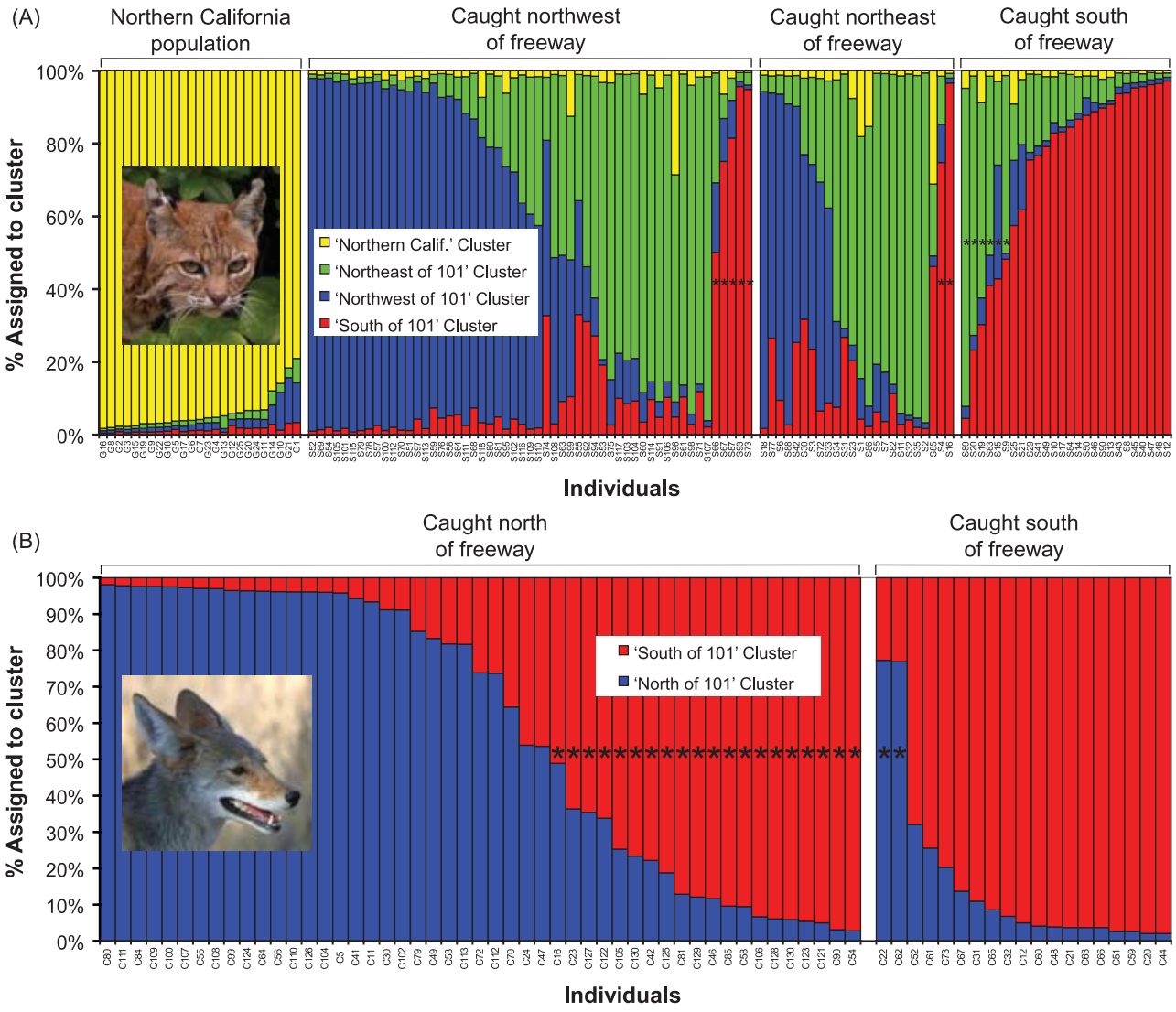


**Fig. 2** Genetic assignment results from the program STRUCTURE for bobcat (top) and coyote (bottom) populations. Individuals are grouped according to capture location. Genetic population clusters are coded with different colours and the fraction of colour for each individual represents the probability of assignment to the cluster with that colour. Four clusters were found in bobcats, corresponding to a northern California group (yellow), two groups on the north side of the freeway (blue and green) and one group on the south side of the freeway (red). In coyotes, two clusters are supported by STRUCTURE, corresponding to a north (blue) and south (red) cluster. Asterisks denote misassigned individuals (individuals with greater than 50% assignment to a cluster different from the capture location) that are potential migrants.

We measured population differentiation by calculating population pairwise $F_{ST}$ values and significance ($g$-test) using the program FSTAT (Goudet 2002). We estimated gene flow as the number of genetic migrants ($Nm$) between populations from $F_{ST}$ values [$F_{ST} \approx 1/(1 + 4Nm)$; Wright 1921]. Population membership was based on the capture location north or south of the Ventura Freeway. The northern population was additionally split into northwest and northeast populations to measure differentiation between populations on the same side of the freeway. Computing $F_{ST}$ between these two populations north of the freeway allows us to compare the amount of genetic differentiation across the freeway with that over the same or greater distance without the barrier. The east and west populations were divided by Kanan Road, a secondary road, and surrounding development (Fig. 1A,B).

We also computed the pairwise relatedness coefficient, $R$ between individuals, (Queller & Goodnight 1989) using the program KINSHIP (Goodnight 2005). We identified pairs of individuals significantly related ($\alpha = 0.05$) at the $R \geq 0.25$ level by first performing a simulation in KINSHIP using the complete population data set at $R = 0.25$, followed

by log-likelihood calculations for all possible pairs. Based on the three defined populations, two north and one south of the freeway, for both bobcats and coyotes, we then determined the percentage of number of close relatives ($R \geq 0.25$) across the freeway, across a similar distance on the same side of the freeway, and within each population (Fig. S1, Supplementary material).

We used coalescent simulation to generate predicted levels of genetic differentiation based on a population isolation event with the program SIMCOAL (version 1.0) (Excoffier 2004). SIMCOAL is a computer program for the simulation of molecular genetic diversity in an arbitrary number of diploid populations based on a retrospective coalescent approach. SIMCOAL was utilized to estimate expected population pairwise $F_{ST}$ values for both bobcat and coyote microsatellite results, based on the time since the freeway was built. A sensitivity analysis was performed on the parameter space of inference for the simulations by varying population effective sizes, sample sizes, migration rates, number of generations since a historical event (population separation), and microsatellite mutation rate. The microsatellite mutation rate was varied from $10^{-3}$ to $10^{-2}$ based on observed mutation rates for dinucleotide and tetranucleotide microsatellites for the domestic dog (Francisco *et al*. 1996). Effective population sizes ($N_e$) were estimated as the number of territorial adults in the study area based on telemetry observations. This calculation assumes that all territorial individuals reproduce equivalently; however, sensitivity analysis showed that results were not sensitive to small changes in $N_e$ or sample size. One thousand analysis iterations were performed for each combination of input parameters. SIMCOAL output results were then analysed using ARLEQUIN (Schneider *et al*. 2000) for pairwise population $F_{ST}$ estimation. $F_{ST}$ values were determined by averaging the $F_{ST}$ values of all 1000 iterations. Because sensitivity analysis showed that population effective size and sample size had minimal effect on $F_{ST}$ within the range of our study values, they were held constant at 200/50 (population effective size/sample size) for bobcats and 75/25 for coyotes. The number of generations since separation was varied from 25 to 100, and migration rate was varied from 0 to 10% of source population. We assume a 2-year generation time for coyotes and bobcats (Knick *et al*. 1985; Bekoff & Wells 1986).

## Results and discussion

We captured bobcats and coyotes on the north and south sides of the freeway and placed radio-telemetry collars on 110 (92 north side, 18 south side) coyotes and 87 (64 north side, 23 south side) bobcats. Using radio-telemetry, from 1996 to 2003 five (4.5%) radio-collared coyotes and 10 (11.5%) radio-collared bobcats were observed to cross the freeway, whereas 58 (52%) coyotes and 40 (45%) bobcats crossed major secondary roads. Because a principal study objective was to understand the effects of roads, and in particular the freeway, on carnivore movement, all radio-collared animals were captured within dispersal distance, and many within an average home range diameter, of both the freeway and secondary roads. However, only 213 (2.3%) of 9311 bobcat locations and 19 (0.4%) of 4565 coyote locations were on the opposite side of the freeway from the capture location of the individual.

Home range perimeters followed but did not cross roads such as the freeway, implying that they functioned as artificial territorial boundaries (Fig. 1C, D). For both male and female bobcats, home ranges that bordered on hard boundaries such as the freeway or development were significantly smaller than those that did not (males: $t = -1.919$, one-sided $P = 0.033$; females: $t = -2.186$, one-sided $P = 0.018$). Also, for adult female bobcats, the age class most important for reproduction, home range overlap was three times higher among individuals with home ranges adjacent to development and the freeway than in those with nonadjacent home ranges (38.8% vs. 12.4% overlap; $t = -1.77$, one-sided $P = 0.045$). For coyotes, we did not radio-track a sufficient proportion of territorial individuals throughout the study area to reliably measure territory overlap. Overall, the freeway was a significant barrier to movement as only about 5–10% of individuals crossed in the 7 years of observation, and home range boundaries, overlap, and size were affected by its proximity.

We genotyped 68 (49 north side, 19 south side) coyotes and 108 (82 north side, 26 south side) bobcats for variation in seven microsatellite loci. Microsatellite loci were highly polymorphic for both species (Table S2, Supplementary material). We also typed a population of 25 bobcats from Golden Gate National Recreation Area in the San Francisco Bay Area, a geographically remote and genetically distinct population (Riley *et al*. 2004). For bobcats, the STRUCTURE assignment test results determined that four populations best fit the data (Table S3, Supplementary material), with the northern California population clearly separated from those in southern California and two populations located north and one south of the freeway (Fig. 2A). All bobcats from northern California were assigned correctly to that population. However, seven bobcats caught north of the freeway, five to the west and two to the east, were assigned genetically to the south side population with assignment probabilities and posterior probabilities of greater than 50% (Fig. 2A; Table S5, Supplementary material). We had radio-telemetry observations on six of these seven bobcats, and four of the six were located south of the freeway at least once (Fig. 1E), corroborating their status as migrants. Six bobcats assigned north of the freeway were captured to the south (Fig. 2A). None of these bobcats were found north of the freeway based on

radio-telemetry observations, although three were located within 500 m of it, and two within 100 m. Therefore, based on genetic assignment and in part supported by telemetry observations, 9% (7 of 80) of the bobcats sampled from the north side of the freeway and 23% (6 of 26) of the bobcats sampled from the south side are putative migrants (see Fig. 2A). Considering the limited sampling of activity provided by radio-telemetry, the genetically derived estimate of migration (13 of 106 individuals or 12.3%) and that based on telemetry (10 of 87 individuals or 11.5%) are remarkably similar and suggest that about 12% of the sampled bobcat population crossed the freeway over the 7-year study period, or 3.4% per generation.

For coyotes, the assignment test determined that two populations best fit the observed data, one north and one south of the freeway (Fig. 2B; Table S3, Supplementary material). Two of 19 individuals (11%) captured south of the freeway were assigned to the north side population with assignment probabilities and posterior probabilities of greater than 50% (Fig. 2B; Table S5). Radio-telemetry observations were available for one of these two coyotes, and none of the 107 locations were north of the freeway, although six of the first seven locations were within 1.5 km of it, indicating that this coyote may have dispersed from the north. Twenty of the 49 coyotes (41%) captured on the north side of the freeway were assigned to the south side. We had radio-telemetry observation on 18 of these coyotes, and none showed evidence of crossing the freeway, although 11 of 18 were observed within 1 km of it. Consequently, the genetic results suggest that 10% of the South side population and as much as 41% of the north side population may be migrants. This implied migration fraction of 32% (22 of 68 individuals) or 9.1% per generation is much larger than the value of 4.5% or 1.3% per generation based on telemetry observations. Considering higher assignment thresholds of 80% and 90%, 21% (14 of 68) or 5.9% per generation and 10% (7 of 68) or 2.9% per generation, respectively, are still misassigned and likely to be migrants. The discrepancy between genetic- and telemetry-based estimates may reflect the unlikely probability of observing dispersal with limited radio-telemetry observations or the difficulty of classifying migrants in genetically similar populations. The use of assignment tests to measure dispersal requires a modest degree of genetic differentiation between populations, otherwise historical gene flow will confound the assessment of recent dispersal events (Berry *et al*. 2004). However, two observations argue for a higher dispersal rate than suggested by telemetry observations. First, coyotes generally disperse farther than bobcats (Van Vuren 1998), which had higher observed and implied rates of migration (see above). Second, of the 22 coyotes that were genetically misclassified, 14, or 64%, were juveniles or yearlings, the ages when coyotes typically disperse (Gese *et al*. 1989). This compares to 39% juveniles or yearlings in the population of coyotes that were not misclassified.

Although the freeway is a barrier to movement, rates of migration of 3.4% per generation for bobcats and from 1.3% to 9.1% per generation for coyotes as suggested by telemetry or genetic data imply high rates of gene flow sufficient to counteract drift (Mills & Allendorf 1996; Vucetich & Waite 2000). To assess levels of differentiation, we measured $F_{ST}$, the fixation index, for the seven microsatellite loci. For both species, we found that $F_{ST}$ values between populations on different sides of the freeway were two to nine times larger (and *Nm* 2–9 times smaller) than those between populations on the same side, although the latter populations were separated by greater distances (Figs 1A, B and 3). Additionally, 39.2% of alleles for coyotes and 23.6% of alleles for bobcats were unique to one side of the freeway (Table S4, Supplementary material). For coyotes, both pairwise $F_{ST}$ values across the freeway ($F_{ST}$ = 0.030 northwest-south, $F_{ST}$ = 0.037 northeast-south) were significantly different from zero ($P < 0.003$), whereas the $F_{ST}$ values between the two subpopulations on the same side of the freeway (0.004, northwest-northeast) was not ($P = 0.134$). For bobcats all three pairwise $F_{ST}$ values were significantly different from zero ($F_{ST}$ = 0.064 northwest-south, $F_{ST}$ = 0.039 northeast-south, $F_{ST}$ = 0.018 northwest-northeast) ($P < 0.003$), suggesting that Kanan Road, a busy secondary road, and the wide development corridor flanking it, may also be a significant barrier to gene flow for bobcats

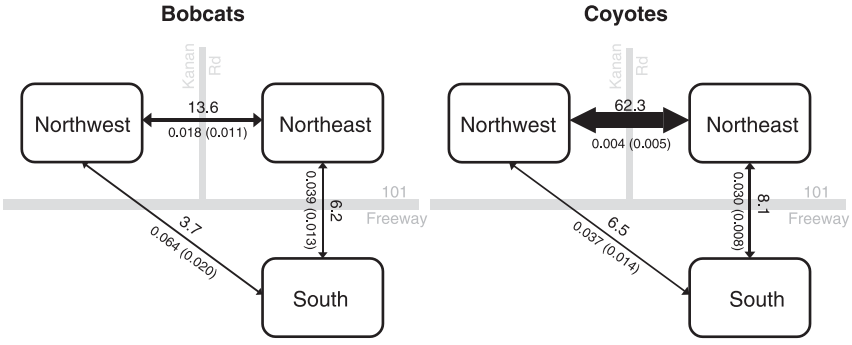


**Fig. 3** The number of genetic migrants (*Nm*, above line) and levels of genetic differentiation ($F_{ST}$, below line, standard error in parentheses) between populations across the freeway (northwest vs. south and northeast vs. south) and on the same side of the freeway (northeast vs. northwest) for bobcats and coyotes. Arrow widths are proportional to *Nm* values.

(Fig. 3). Relatedness values also indicated substantially more closely related pairs of animals ($R \geq 0.25$) between populations on the same side of the freeway (northeast vs. northwest) than across it (northeast vs. south) (Fig. S1, Supplementary material). Overall, these results clearly show that the Ventura Freeway is an imposing barrier to gene flow for both species.

To assess if these levels of genetic differentiation were consistent with population history and the observed and implied migration rates, we used coalescent simulation modelling to estimate north side–south side pairwise $F_{ST}$ indices resulting from the division of a single population by the creation of the freeway in 1949. The simulation results (Fig. 4) showed that a genetically effective migration rate of approximately 0.5% per generation or less is required to explain the observed level of population differentiation for both carnivore species. Consequently, given

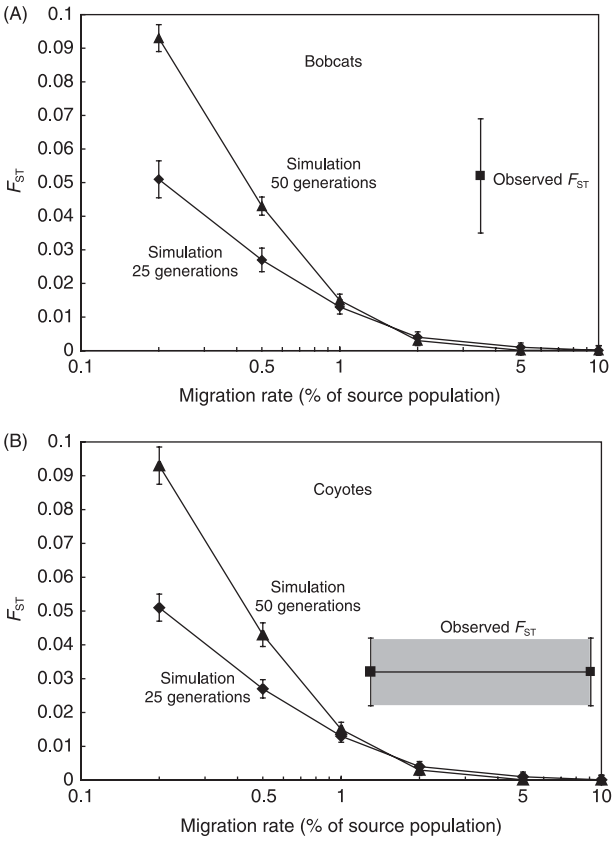


**Fig. 4** Comparison of predicted genetic divergence ($F_{ST}$) using coalescence simulations (*Y*-axis) with observed $F_{ST}$ values as a function of migration rate (*X*-axis) between bobcat (A) and coyote (B) populations north and south of the freeway. Migration rates for observed $F_{ST}$ values are based on radio-tracking observations and genetic assignment tests (see text). Error bars for $F_{ST}$ values represent one standard error. Observed genetic differentiation is consistent with a migration rate of 0.5% or less for both species given 25 or 50 generations since isolation.

that our observations span a period of about three generations (Knick *et al*. 1985; Bekoff & Wells 1986), the genetically effective migration rates estimated by the coalescent simulation are approximately 3–18 times lower than migration rates between populations separated by the freeway based on direct observation or genetic population assignment.

The disparity between observed migration rates and inferred gene flow likely reflects the lack of reproductive success of migrants. For example, 6 of the 10 bobcats that were found on both sides of the freeway were located across it less than four times, and of the four that stayed across, the two females were known not to have produced kittens the following spring. Of the five coyotes radio-tracked across the freeway, four did not reproduce since they were located six or fewer times across the road and over only a short period of time outside the reproductive season. Further, of the potential migrants observed by telemetry and implied by genetic results, 54% were classified as less than 2 years old. In undisturbed populations, young dispersers enter a matrix of occupied and unoccupied territories, reflecting natural mortality of territorial adults. However, in our study area, home ranges follow the freeway boundary (Fig. 1C, D) and consequently, territorial and reproductive individuals contribute genes to the population on one side of the freeway only. Additionally, in our urban study area, mortality from hunting and trapping is low or nonexistent, and carnivore survival rates were high (Riley *et al*. 2003). High survival rates, small home ranges, high home range overlap, and the barrier effect of roads and development all resulted in territory packing along hard boundaries such as the freeway. This territory pile-up likely produced a formidable social and behavioural barrier to genetically effective dispersal because dispersers are unlikely to obtain and hold territories near the freeway. This unique genetic-isolating effect of roads and other artificial boundaries likely applies to other territorial species.

Conceivably, genetic differences may also correspond to changes in habitat composition across the freeway. For example, continent-wide climate and habitat changes have been associated with genetic structure in grey wolves (*Canis lupus*; Geffen *et al*. 2004), and regional-scale biome changes, e.g. between mountainous regions and flat valley expanses, were associated with genetic structure in coyotes (Sacks *et al*. 2004). However, both the geographic scale and diversity in habitats sampled by these studies far exceed the habitat differences observed throughout the area that we studied. Both sides of the freeway consist of a similar mix of the three dominant types of vegetation in the Santa Monica Mountains and Simi Hills including mixed scrub (64–85%), grassland (8–26%) and riparian and oak woodland (2–11%; Table S1, Supplementary material). There is variation in the amounts of specific

types of scrub communities (e.g. coastal sage scrub, dominated by *Salvia* spp. and *Artemisia californica*, and chaparral, dominated by *Adenostoma fasciculatum* or *Ceanothus* spp.) across the entire study area, but coyotes and bobcats on both sides of the freeway used both of these scrub communities, indicating a lack of ecological specialization. Coyotes and bobcats are generalist carnivores, and we feel such small-scale ecological differences are an unlikely explanation of our results. Unfortunately, there are too few historical specimens from our study area in museum collections to directly assess genetic differentiation prior to the construction of the freeway.

Roads are a primary threat to the persistence of animal populations in urban landscapes. This threat is caused directly through vehicle mortality or indirectly by increasing the probability that isolated populations will become extinct through random demographic processes (Forman 2003). Our results show that the genetic effects of roads can also be substantial even for large, highly mobile species. Levels of differentiation between coyote and bobcat populations isolated for about 50 years are as large as those between coyote populations separated by several hundred kilometres (Roy *et al*. 1994). These levels of differentiation were found even between high-density populations of bobcats and coyotes. The isolating effects of roads would likely be even more severe for very small populations and rare species (Spielman *et al*. 2004). An additional insidious factor is the effect of roads in decreasing gene flow well below that expected from migration rates or existing between similarly spaced populations on the same side of the freeway. We suggest this decrease may be caused by: (i) roads acting as home range boundaries for terrestrial and reproductive individuals, and thus decreasing the migration rate of genes, and (ii) home range pile-up near roads that make it less likely that dispersing individuals can find territories. To counteract such genetic isolation, corridors across freeways could conceivably include more natural habitat so that home ranges could extend across the freeway and rates of genetic exchange might be increased. Five of the six potential crossing points in our study (Fig. 1A, B) were unvegetated culverts or paved underpasses. Finally, our results imply that observed migration rates across anthropogenic barriers may be poor surrogates for gene flow, and that molecular genetic studies of even recently isolated populations may provide new insights for conservation.

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## Supplementary material

The supplementary material is available from http://www.blackwellpublishing.com/products/journals/suppmat/MEC/MEC2907/MEC2907sm.htm

**Table S1** Percentage of different habitat types in the sampled areas, determined by overlaying the polygons for each population (Fig. 1) on a vegetation map of the Santa Monica Mountains and Simi Hills (Franklin 1997). Chaparral consists of scrub habitat dominated by chamise (*Adenostoma fasciculatum*) and ceanothus (*Ceanothus* spp.); coastal sage scrub consists of scrub habitat dominated by sage (*Salvia* spp.) and California sagebrush (*Artemisia tridentata*); grassland is mostly introduced annual grasses; woodland consists of oak and riparian woodlands and some walnut woodlands.

**Table S2** Observed and expected heterozygosities, allelic diversity and deviations from Hardy–Weinberg equilibrium (significant deviations indicated by ±).

**Table S3** Likelihood values for inferred number of genetic clusters (*K*) from STRUCTURE (3 iterations per value of *K*).

**Table S4** Private alleles as percentage of total alleles per locus in each population.

**Table S5** Cluster assignment and posterior probability of correct genetic population assignment of potential migrants.

**Fig. S1** Comparison of the percentage bobcat and coyote pairs that were closely related genetically, as defined by having an *R* value of 0.25 or greater between populations across the freeway (south vs. northwest and northeast) and on the same side of the freeway (across Kanan road, northwest vs. northeast). Bar widths are proportional to percentage values.

**Fig. S2** Sensitivity of the SIMCOAL simulation algorithm for $F_{ST}$ as a function of microsatellite mutation rate (μ), migration rate, and number of generations since population separation (since construction of the freeway).

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Report

# Individual Behaviors Dominate the Dynamics of an Urban Mountain Lion Population Isolated by Roads

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## Summary

**Large carnivores can be particularly sensitive to the effects of habitat fragmentation on genetic diversity [1, 2]. The Santa Monica Mountains (SMMs), a large natural area within Greater Los Angeles, is completely isolated by urban development and the 101 freeway to the north. Yet the SMMs support a population of mountain lions (*Puma concolor*), a very rare example of a large carnivore persisting within the boundaries of a megacity. GPS locations of radio-collared lions indicate that freeways are a near-absolute barrier to movement. We genotyped 42 lions using 54 microsatellite loci and found that genetic diversity in SMM lions, prior to 2009, was lower than that for any population in North America except in southern Florida, where inbreeding depression led to reproductive failure [3–5]. We document multiple instances of father-daughter inbreeding and high levels of intraspecific strife, including the unexpected behavior of a male killing two of his offspring and a mate and his son killing two of his brothers. Overall, no individuals from the SMMs have successfully dispersed. Gene flow is critical for this population, and we show that a single male immigrated in 2009, successfully mated, and substantially enhanced genetic diversity. Our results imply that individual behaviors, most likely caused by limited area and reduced opportunities to disperse, may dominate the fate of small, isolated populations of large carnivores. Consequently, comprehensive behavioral monitoring can suggest novel solutions for the persistence of small populations, such as the transfer of individuals across dispersal barriers.**

## Results

### Movements, Mortality, and Dispersal in an Urban Landscape

We captured, genotyped, and radio-tracked 26 mountain lions in the Santa Monica Mountains (SMMs; n = 21) and Santa Susana Mountains (including the Simi Hills; n = 5) from July 2002 through July 2012 (Figure 1). We also genotyped 17 other mountain lions from opportunistically collected samples, including from Angeles National Forest and the Verdugo Hills. Large freeways, including the 101 freeway (Figure 2A), the 5 freeway (Figure 2B), and the 405 freeway (Figure 2A), were significant barriers to movement (i.e., were almost never crossed by mountain lions) and often acted as home-range boundaries. One smaller freeway, the 118 freeway between the Simi Hills and the Santa Susana Mountains (Figure 1), was crossed at least 23 times by two radio-collared mountain lions in an area with a large tunnel and natural habitat on both sides [6]. In February 2009, subadult male P12 crossed the 101 freeway into the SMMs, the only time that a radio-collared mountain lion crossed 101, which separates the SMMs from all areas to the north.

Fourteen radio-collared lions died during the study period: six from intraspecific strife, two from vehicles, two of anticoagulant toxicosis from ingesting rodenticides, one from poaching, one from starvation as a young kitten, and two from unknown causes. Overall, 50% of mortalities of known cause were from intraspecific strife. An uncollared young male was also killed by another lion, for a total of seven instances of intraspecific killing. In five of these cases we were able to identify the surviving individual, and in all five we found that an adult male killed his offspring, his brother, or a previous mate (Table S1 available online).

We tracked the fate of young mountain lions, especially males, to assess dispersal. In the SMMs, we radio-tracked ten subadult male mountain lions and sampled five others that originated there (Table S1). Not one of these 15 young males was known to disperse from the SMMs to a home range with mating opportunities. Of the 12 young males from the SMMs whose ultimate fates are known, 11 died before or during dispersal from intraspecific strife (n = 5), vehicle strikes (n = 4), control action by police (n = 1), and unknown causes (n = 1). The only young male to successfully disperse from the SMMs, P22, settled in Griffith Park, requiring the crossing of two freeways (405 and 101; Figure 1). For more than 2 years, this male inhabited a home range of 26 $km^2$, as compared to 500 $km^2$ for adult male P1 (Figure 1). P22's home range was entirely bounded by freeways and urbanization, and he was its sole occupant.

North of 101, we radio-tracked three subadult males and sampled three others that were killed on roads (Table S1). All three collared animals successfully crossed roads and established home ranges as adults. P3 moved regularly between the Simi Hills and the Santa Susana Mountains across the 118 freeway. P12 crossed 101 and subsequently established himself as a dominant male in the SMMs. Perhaps most instructive, young male P16, who shared the eastern Santa Susana Mountains with his father, P21, dispersed north across highway 126 and established a home range (Figure 1). Among radio-collared animals of known fate, the least biased sample for mortality and dispersal, none of the seven subadult males from the SMMs successfully dispersed and established viable home ranges, while all three from the Santa Susana Mountains did.

### Population Genetics of a Small, Isolated Population

We found very low genetic diversity compared to large, contiguous populations in California and in other parts of the west

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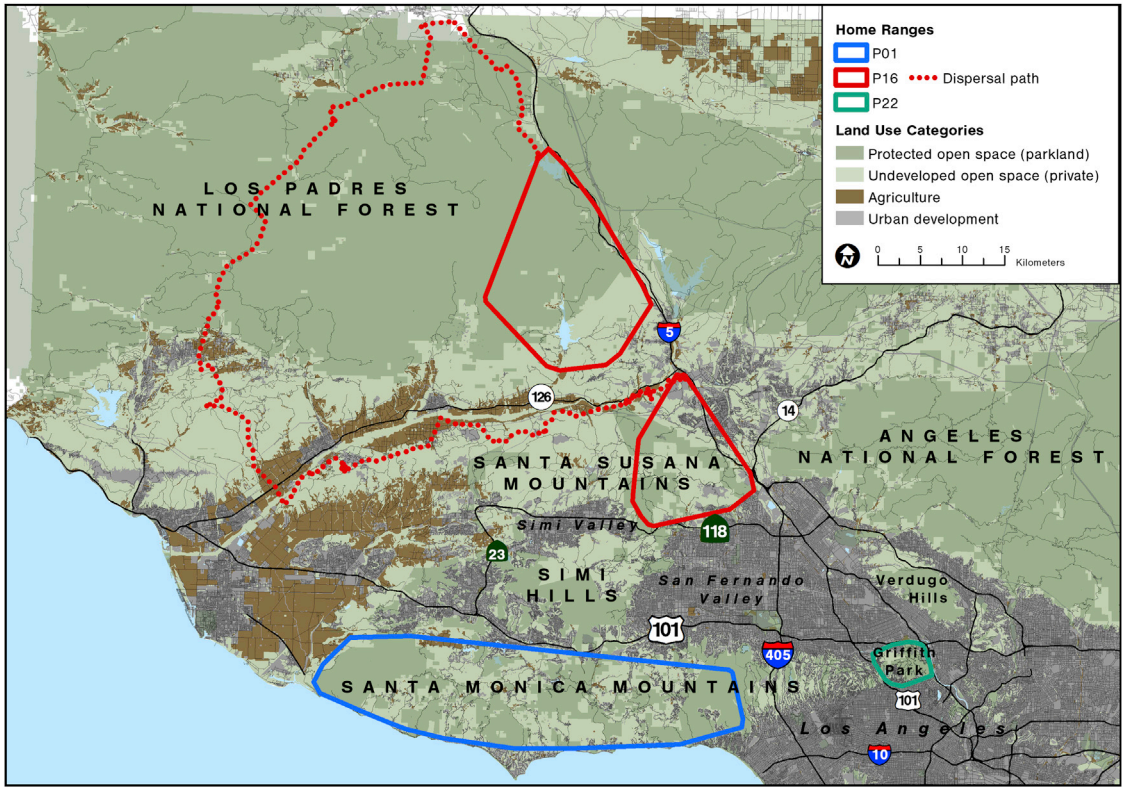


Figure 1. Study Area for Mountain Lion Movements and Population Genetics in and around Santa Monica Mountains National Recreation Area Northwest of Los Angeles

Large natural areas and major freeways are labeled. Home ranges are 100% minimum convex polygons for male P22 in Griffith Park, male P01 in the SMMs, and male P16 that dispersed from the eastern Santa Susana Mountains, across highway 126 to Los Padres National Forest. See also Table S1.

(Tables 1 and S2). Genetic diversity was particularly low in the SMMs south of the 101 freeway, which is the largest and busiest road to the north (175,000 vehicles/day versus 115,000 for the 118 freeway and 22,000 for highway 126; [7]). This population is also farthest away from the putative source populations in Los Padres and Angeles National Forests. The expected heterozygosity ($H_E$), total number of alleles ($N_A$), and number of effective alleles ($N_E$) were all significantly lower in the SMMs than north of the 101 freeway (Table 1). For private alleles (defined here as those present only in one study population), 67 of 172 discovered alleles were absent from the SMM population, and 78% of loci (42 of 54) had at least one private allele north of 101.

Genetic differences between local populations were also apparent from Bayesian cluster analyses (Figure 3A). Despite the small sample sizes, the program STRUCTURE [8] indicated strong clustering into three groups (K = 3 by the Evanno ΔK method [9]; Figure S1). The $F_{ST}$ value between populations north and south of the 101 freeway was 0.12 ($p < 0.05$), three times larger than that previously found for other carnivores in the area [10]. The SMM mountain lion population showed evidence of having experienced a genetic bottleneck based both on significant heterozygote excess (program Bottleneck [11]; single-step mutation probabilities of 90%, $p = 0.00044$ and 78%, $p = 0.00004$) and Garza and Williamson's M ratio test ([12]; average M = 0.75; for single-step mutation proportion, 90%, $p < 0.0001$). The current effective population size, $N_E$, for mountain lions south of 101 was just six individuals.

## The Influence of Specific Behavioral Events on Population Demography and Genetics

Our analysis of a genetically based pedigree showed that specific behavioral events greatly affected population dynamics and genetic composition (Figure 3B). For example, the migration into the SMMs of P12, who was genetically assigned to the population north of 101 (Figure 3A, blue cluster) and had private northern alleles at 33% of microsatellite loci, demonstrated that the 101 freeway can be traversed. Critically, P12 then survived in the SMMs and bred with resident females, including female P13 twice and his daughter, P19 (Figure 3B). This was the second instance of father-daughter mating, as P13 was the result of male P01 mating with his daughter, female P06 (Figure 3B) [13].

The immigration and subsequent matings of male P12 increased the genetic diversity and decreased the internal relatedness (IR) of the SMM population (Table 1) and thus is an example of a genetic rescue. P12 possessed 20 private alleles from north of the freeway, 19 of which he passed on to his offspring, such that private alleles absent from the SMMs decreased from 67 to 47, loci with private alleles to the north decreased from 42 to 32, and monomorphic loci in the SMMs decreased from 13 to 9. Bayesian clustering analysis also clearly showed the impact of P12's immigration (Figure 3A). Ninety-seven percent of P12's genome was assigned to the Santa Susanna Mountain population, and he fathered eight offspring based on our pedigree (Figure 3B). Six of these, including the five with P13 (99% assigned to the SMMs) exhibited a near equal mix of the

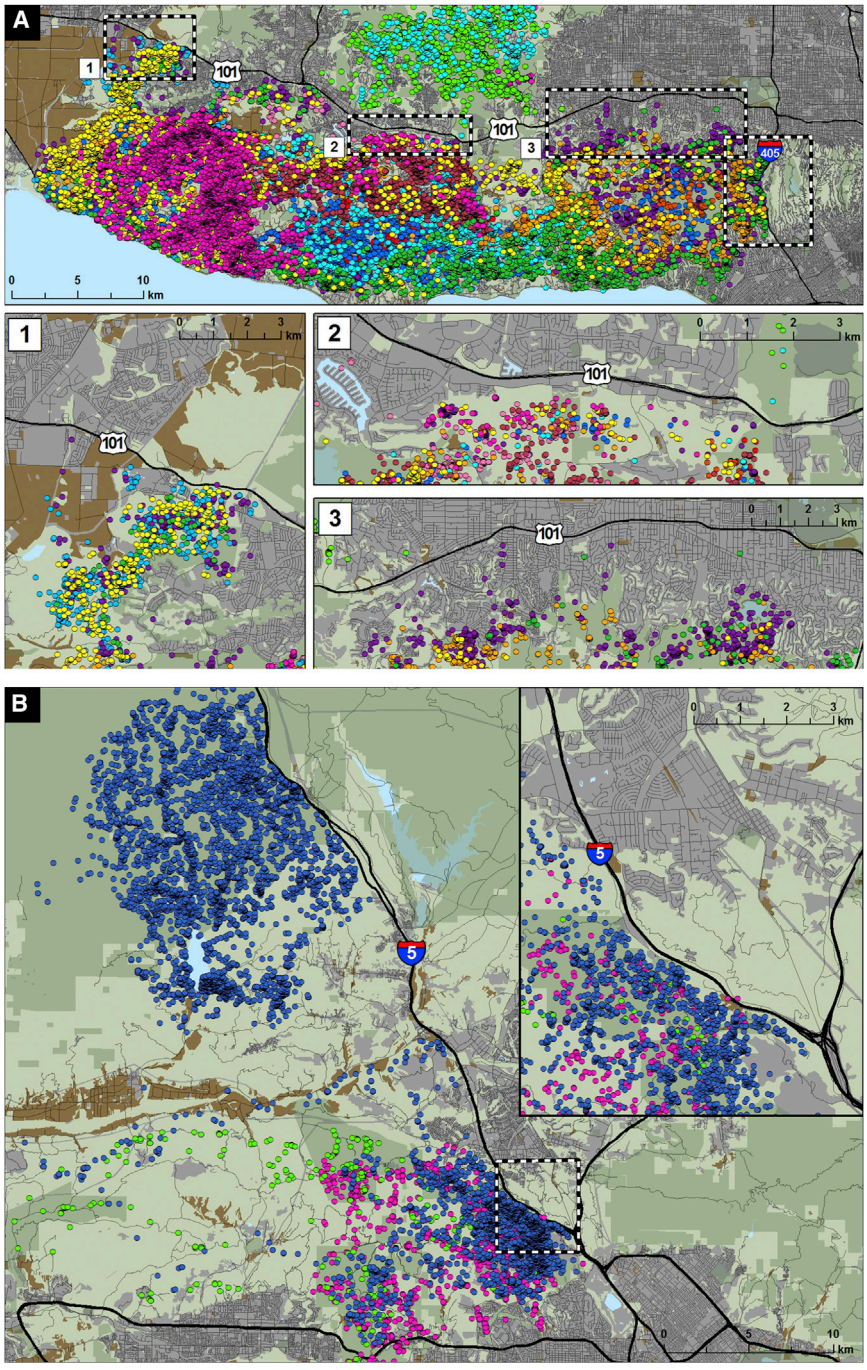


Figure 2. Locations of Mountain Lions along Freeways in Southern California from GPS Radio Collars, 2002–2012

(A) Locations near the 101 freeway, which runs east-west north of the Santa Monica Mountains. Because there is urban development along most of this freeway, in many areas (insets 2 and 3) animals do not approach the freeway. Toward the east end of the SMMs, the 405 freeway passes north-south through the mountains. This freeway is also a major barrier to mountain lion movement.

(B) Locations north of 101 in the Santa Susana Mountains and Los Padres National Forest near the 5 freeway, which runs north-south through the region.

SMM (green) and Santa Susanna Mountain (blue) clusters (Figure 3A). Interestingly, P23 and P24, the offspring of P12 and his daughter, P19, each had about three-quarter assignment to the Santa Susana Mountains, as expected (Figures 3A and 3B).

The effects of individual mating events on population genetic measures were also evident as quantified with our pedigree by gene-drop analysis (program PMx [14]) applied for the first time to a wild population. Both the mean inbreeding coefficient (F) and mean kinship increased in 2007 after male P1 bred with his daughter, decreased in 2010 after migrant P12 began to produce offspring in the SMMs, and then rose again in 2013 after P12 bred with his daughter. Similarly, gene diversity showed the opposite pattern, decreasing after the first close inbreeding event, rising in 2010 after P12 bred, and then decreasing with the second inbreeding event (Table S3). The dramatic shifting values of these coefficients over short time periods demonstrate how important individual matings are to the levels of inbreeding and relatedness in the population (Figure S2).

Finally, the IR, a measure that has the potential to provide novel insight about inbreeding and genetic health [15], reflected both the initial bottleneck and the effects of the inbreeding and genetic rescue events. The mean IR for SMM animals dropped from 0.09 (SE = 0.014) to 0.03 (SE = 0.036) when P12 and his offspring were included, as IR values for the initial offspring of the genetic rescue event were low and averaged −0.16 (range −0.10 to −0.35). For P23 and P24, the incestuous offspring of P12 and his daughter, IR values rose again to 0.10 and 0.09, indicating that one close inbreeding event may have reversed much of the value of the genetic rescue.

Our results from this small, isolated population also indicate how individual male mountain lions can monopolize breeding opportunities and genetically dominate future generations. Two males, first P01 and later P12, had very high reproductive success based on the pedigree (Figure 3B). Specifically, P01 fathered ≥15 offspring, P12 fathered ≥8 offspring, and no individual in the SMM population was fathered by any other male. The pedigree and PMx analyses indicated that P01 had 22 descendants, including six of the seven animals known in the population in 2013, and that P12 had eight descendants, including four of the seven current animals; 33.9% of the copies of the genome in the current population are derived from P01 and 35.7% from P12 (see Table S4).

Table 1. Genetic Diversity Based on 54 Microsatellite Loci for Mountain Lions in and around the Santa Monica Mountains, California, 2002–2012

| Population | $N_A$ | $N_E$ | Poly (%) | $H_E$ | $H_O$ | IR |
|---|---|---|---|---|---|---|
| Santa Monica Mountains only, south of the 101 freeway before P12 crossing (n = 17) | 1.9 ± 0.2 | 1.6 ± 0.1 | 76% | 0.31 ± 0.03 | 0.38 ± 0.04 | 0.09 ± 0.04 |
| North and east of the Santa Monica Mountains, north of the 101 freeway (n = 15) | 3.1 ± 0.1 | 2.1 ± 0.1 | 100% | 0.48 ± 0.02 | 0.42 ± 0.02 | 0.17 ± 0.05 |
| Santa Monica Mountains only, south of the 101 freeway after P12 crossing (n = 26) | 2.3 ± 0.1 | 1.8 ± 0.1 | 83% | 0.36 ± 0.03 | 0.36 ± 0.03 | 0.03 ± 0.04 |

Populations are from the SMMs before the genetic rescue event (the dispersal of subadult male P12 from north to south), from north of 101 in the Santa Susana Mountains and San Gabriel Mountains, and from in the SMMs after the genetic rescue event. $N_A$ is the total number of alleles, $N_E$ is the number of effective alleles, poly (%) is the percentage of loci that are polymorphic, $H_E$ is expected heterzygosity, $H_O$ is observed heterozygosity, and IR is individual heterozygosity or internal relatedness (see the Supplemental Experimental Procedures for details). $N_A$, $N_E$, and $H_E$ are significantly lower (nonoverlapping 95% confidence intervals) for the SMMs before P12 crossed than for north of the 101 freeway. Mean ± SE is shown. See also Table S2.

## Discussion

### Individual Effects on Population Dynamics and Genetic Diversity

Urban environments are generally inhospitable for large carnivores. Therefore, it is remarkable that a population of a large carnivore extends into the metropolitan area of Los Angeles, one of 30 world megacities (metropolitan areas of >10,000,000 people). However, the challenges for the long-term persistence of this population are substantial. Freeways in the area are almost complete barriers to mountain lion movement (Figure 2). This severe isolation most likely caused a striking assignment of lions to a single genetic cluster in the SMMs (Figure 3A). SMM lions were also clearly differentiated from those east of the 5 freeway (red cluster in Figure 3A), which separates the Angeles National Forest from the Santa Susana Mountains and Los Padres National Forest (Figure 1). The $F_{ST}$ value of 0.12 across the 101 freeway is high given its relatively recent age (1949) and given that other studies of *Puma concolor* microsatellite loci have found $F_{ST} < 0.10$ among 15 subpopulations across the state of Idaho (distances of $\geq$500 km; [16]) and an average $F_{ST}$ of 0.041 among 20 subpopulations from four southwestern states (700 by 700 km; [17]).

Genetic diversity in SMM mountain lions also is very low relative to populations north of the 101 freeway and elsewhere in California and the western US (Table S2). A measure that is less affected by sample size, the expected heterozygosity, is 0.31 for the SMMs before the immigration event, a value that is the lowest ever reported for western mountain lions, with the exception of another isolated population in the Santa Ana Mountains of Southern California that has comparable variability (H.B.E., unpublished data). The average number of alleles per locus ($N_A$) was also lower in the SMMs than north of 101 and was one-half to two-thirds of the average value from other populations across the western range (Table S2). The sole population with lower genetic diversity than the SMM population across all of these measures is the Florida panther, *Puma concolor coryi*, a federally endangered subspecies that suffered from substantial inbreeding depression and had been isolated for more than a century before lions from Texas were introduced to alleviate inbreeding depression (Table S2) [4, 5].

In the small, isolated SMM population, individual behavioral events can have a significant impact on population dynamics and genetics. We documented only one movement across the 101 freeway, by subadult male P12. But after his establishment as a dominant breeding male, new alleles entered the population, and, particularly for his mixed offspring, genetic diversity increased and measures of inbreeding decreased. However, first-order inbreeding events (father-daughter matings) by males P1 and P12 had the opposite effect, increasing inbreeding and reducing diversity. This kind of close inbreeding has only rarely been documented in mountain lions, specifically in the small and isolated southern Florida population [3, 4].

We also found significant effects of individual behavior on two other critical aspects of population dynamics, dispersal and mortality. Although typically every young male and half of young females disperse out of their natal range [18], not a single subadult mountain lion has successfully dispersed out of the SMMs. Instead, young males have died, principally from intraspecific strife and vehicles. In the one dramatic case, male P22 dispersed from the SMMs into the Hollywood Hills and has lived for 2 years in a home range of 26 $km^2$, the smallest annual range ever reported for an adult male. In this range, P22 was surrounded by roads and development (Figure 1) and had no opportunity to mate. Male mountain lion home ranges are typically an order of magnitude larger, at 300–400 $km^2$ or more [18, 19], and overlap with those of multiple females. By contrast, all three of the young males that we radio-tracked in the Santa Susanna Mountains successfully dispersed and established home ranges.

Intraspecific strife, the most common cause of mortality, can also be important in other populations, particularly those that are not hunted [20, 21]. However, in the SMMs, we documented repeated cases of males killing their offspring, their brothers, and previous mates. Little has been reported about paternity or kin recognition in mountain lions [18, 22], but clearly this is rarely a sound evolutionary strategy as the survivorship of offspring or siblings is traded against the probability of future reproduction [23]. It is particularly hard to imagine an advantage from killing potential mates or female offspring (Table S1). In fact, in the Santa Susanna Mountains, we observed the opposite pattern. Male P21 was the father of subadult males P12 and P16 (Figure 3B), both of which successfully emigrated and established long-term home ranges: P12 south into the SMMs and P16 north across highway 126 (Figure 1). None of the young males originating in the SMMs, dominated by adult males P1 and P12, have lived beyond age 2, so with respect to male mountain lions, the SMMs are a population sink. In other aspects of ecology and behavior, including home-range size (males, 300–500 $km^2$; females, 100–200 $km^2$), diet ($\geq$90% deer), annual adult survival ($\geq$75%), and litter size (two to four) [6], the SMM lion population is similar to those throughout the southwest [20].

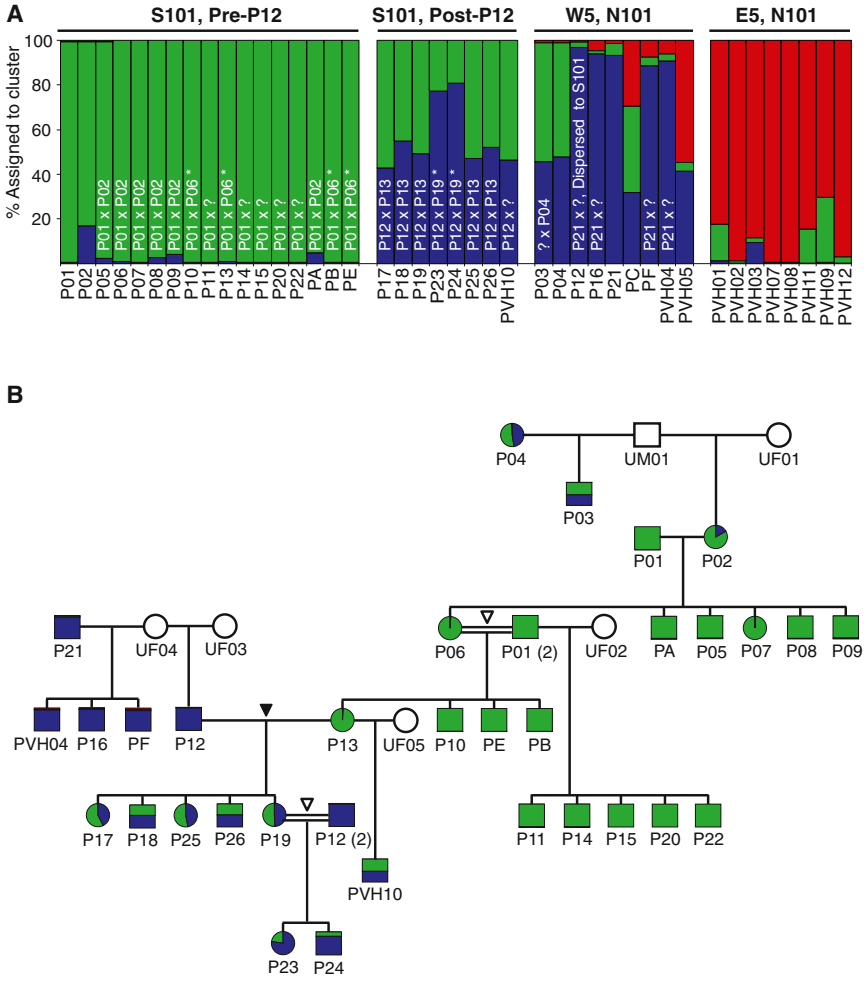


Figure 3. Genetic-Based Cluster Assignments and Recreated Pedigree Based on 54 Microsatellite Loci

(A) Results of program STRUCTURE for 42 mountain lions in the SMM region in Southern California, 2002–2012. The "S101, pre-P12" group is mountain lions from the SMMs, south of the 101 freeway (see Figure 1), before male P12 crossed the 101 freeway from the Simi Hills to the SMMs. The "S101, post-P12" group includes animals sampled in the SMMs that are the offspring of male P12 after he crossed the 101 freeway. "W5, N101" includes animals from the Simi Hills and Santa Susana Mountains, north of the 101 freeway. "E5, N101" includes mountain lions east of the 5 freeway in the San Gabriel Mountains and Verdugo Hills. White lettering for the first three groups indicates the known parentage based on the recreated pedigree. See also Figure S1.

(B) Pedigree for mountain lions in and around the SMMs, 2002–2012. The pedigree was constructed using the programs CERVUS and Colony (see the Supplemental Experimental Procedures). Colors for individual animals correspond to the genetic cluster assignments determined using STRUCTURE: green is the SMM cluster, and blue is the "W5, N101" or Santa Susana Mountains cluster. Symbols with two colors indicate animals with assignment to both clusters. Animals that were not sampled but whose presence is presumed are labeled "UF" for unknown females or "UM" for unknown males. Double lines and open triangles between animals indicate close inbreeding events, specifically father-daughter mating. The black triangle indicates the outbreeding event when P12, from north of the 101 freeway, bred with P13, from the SMMs. See also Figure S2 and Tables S3 and S4.

Very small populations are subject to Allee effects in which low growth rates result from low density, often caused by social disruption as individuals are too sparse to form social groups or find mates [24]. In the SMMs, the inverse has occurred as a small mountain lion population is at high density but lives in a spatially constrained area, resulting in social disruption through negative interactions between close relatives that normally would be rare or nonexistent. The result is reduced population health as indicated by low genetic diversity and increased inbreeding. Such "inverse Allee effects" leading to social disruption could be an important but largely unrecognized problem in isolated and densely packed urban environments.

### Implications for Management and Conservation of Large Carnivores in Urban Landscapes

The importance of specific behavioral events such as dispersal, inbreeding, and killing of close relatives in this small, isolated mountain lion population has implications for conservation in fragmented landscapes. First, detailed behavioral and genetic monitoring may be critical for understanding the factors that threaten population persistence. Only through the collection of extensive demographic and behavioral data on most of the population were we able to identify the most important behaviors affecting population dynamics and genetic diversity.

Second, the maintenance and restoration of habitat connectivity is vital for small populations of large carnivores. Migration events between populations may not have to be frequent to maintain genetic diversity [25], and we have observed that one successful migrant can have a significant impact, especially in mountain lions, where individual males can have high reproductive success. However, the skewed reproduction in small mountain lion populations [26] can result in dominance of the gene pool by individual males, especially when close inbreeding is also occurring, which may be detrimental to population persistence. In the wolves at Isle Royale National Park, although a single male wolf immigrated into the population and increased genetic diversity, the effects were reversed by reproductive dominance of this individual and associated inbreeding [27, 28]. Connectivity is also important because stochastic effects, such as the loss of one dominant male through a vehicle collision, are more extreme and can result in extinction. Previous research on mountain lions in the Santa Ana Mountains suggested that an area of less than 1,100 $km^2$ was unlikely to support mountain lions without some immigration [29], and the SMMs are only about 660 $km^2$. In highly developed areas, the conservation of natural habitat on both sides of freeways and effective corridors across them [30] or translocations may be necessary if large carnivores are to persist in proximity to the megacities of the future.

### Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and four tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.07.029.

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# Effects of urbanization on cougar foraging ecology along the wildland–urban gradient of western Washington

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**Abstract.** Humans have dramatically altered ecosystem structure through landscape manipulation, often leaving refuge patches of suitable habitat for wildlife amidst inhospitable terrain. Large carnivores are especially vulnerable to such habitat modification because they tend to have low population densities and wide-ranging movements necessitated by their food requirements. Cougars (*Puma concolor*), unlike many other large carnivores, have demonstrated an ability to exploit resources in fragmented and managed landscapes. The influence of increasing landscape development on cougar foraging behavior, however, has yet to be fully elucidated. Accordingly, we investigated variation in cougar use of three prey types (synanthropes, ungulates, and rodents) along a wildland–urban gradient in western Washington to determine how urbanization affects the foraging ecology of this apex predator. We predicted that cougar diets would comprise more synanthropic prey (e.g., prolific urban species) and fewer deer as a function of increasing residential development. Generalized linear mixed model results showed that the odds of cougar predation on synanthropic prey did increase with urbanization. The odds of ungulate predation, however, remained relatively consistent across the wildland–urban gradient despite cougar use of black-tailed deer (*Odocoileus hemionus columbianus*) and elk (*Cervus canadensis*) increasing over time. These results suggest that cougar–ungulate predator–prey systems can persist in landscapes with substantial human presence. The odds of forest-associated rodent (*Castor* sp., *Aplodontia* sp.) predation decreased with increasing development, suggesting that urbanization may coincide with more intensive beaver management near residences and thereby reduce beaver and mountain beaver presence in exurban landscapes in western Washington. Most cougars exhibited similar diets, but certain individuals deviated significantly from the population averages characterizing use of all three major prey categories. This variation suggests that cougar population responses to urbanization are unlikely to be uniform and that cases of human–cougar conflict may be linked to individual cats, rather than the population as a whole.

**Key words:** building density; development; exurban; *Odocoileus hemionus; Puma concolor;* rodents; specialization; synanthropes.

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## INTRODUCTION

Since the onset of plant and animal domestication ~12,000 yr ago (Diamond 2002, Price and Bar-Yosef 2011), humans have been reshaping ecosystems through landscape modification (Ellis et al. 2010, Moss et al. 2016*a*). Today, landscape development in the form of agriculture

and urbanization are among the greatest drivers of species extinction and biodiversity decline worldwide (Pimm and Raven 2000, Maxwell et al. 2016). Urbanization, and the development of wild landscapes specifically, often happens in the form of residential sprawl, which creates a gradient of human disturbance at the interface of built and natural ecosystems (Radeloff et al. 2005, Conedera et al. 2015). Recent studies have shown that human activities can alter patterns of disturbance and resource availability along such gradients and that these effects may extend well into rural and even wildland areas (Palkovacs et al. 2012, McDonnell and Hahs 2015, Alberti et al. 2017). There remains a need, however, for a better understanding of how species and ecological communities respond to the varying amounts of development that characterize wildland–urban gradients.

Community assemblages along wildland–urban gradients are often shaped by differences in species' capacity to exploit anthropogenic resource subsidies and their tolerance for human proximity and disturbed landscapes (Markovchick-Nicholls et al. 2008, Ordeñana et al. 2010, Newsome et al. 2015*b*). In northeastern Illinois, USA, for example, urbanization has translated into changes to mesopredator community structure, as certain species, like raccoons (*Procyon lotor*), continue to increase in abundance, limiting resources for Virginia opossums (*Didelphis virginiana*) and striped skunks (*Mephitis mephitis*; Prange and Gehrt 2004). Large mammalian carnivores are especially vulnerable to human development as these species tend to have low reproductive rates, must roam widely in search of prey, and often come into conflict with humans over livestock depredation and personal safety (Cardillo et al. 2005, Ripple et al. 2014). Consequently, many large carnivores have experienced substantial population declines and range contractions in the face of ongoing anthropogenic landscape development (Laliberte and Ripple 2004, Newsome et al. 2016). Some carnivores, however, have shown the ability to adapt to living in human-dominated environments (Tigas et al. 2002, Newsome et al. 2015*a*). In Luxembourg, for example, the socio-spatial organization of stone marten (*Martes foina*) populations is largely unaffected by urbanization (Herr et al. 2009). In urban Chicago, USA, Newsome et al. (2015*a*) showed that individual variation in movement and diet facilitated the successful establishment of coyotes (*Canis latrans*) throughout the Chicago metropolitan area. Additional studies exploring carnivore use of human-modified landscapes could help to build a general framework for predicting which species are likely (and not likely) to exhibit population-level resilience to ecosystem disturbances (Weaver et al. 1996) and potentially aid wildlife managers in mitigating conflicts between humans and wildlife (Lowry et al. 2013, Moss et al. 2016*a*).

Cougars (*Puma concolor*) are solitary, far-ranging felids that are capable of occupying a broad range of habitat types in both temperate and tropical environments (Sunquist and Sunquist 2002). Historically, cougars were associated with wildland environments, but recent studies have revealed that cougars are capable of utilizing areas with an extensive human presence (Beier et al. 2010, Kertson et al. 2013, Wilmers et al. 2013). Though some studies across the western United States and southern Canada have indicated that cougar presence decreases as urbanization intensifies (Kertson et al. 2011*b*, Lewis et al. 2015*a*, Gray et al. 2016), cougars in urban environments have also demonstrated the capacity to adapt by changing their foraging behavior and temporal activity patterns (Knopff et al. 2014, Wang et al. 2015, Blecha et al. 2018). Cougars in urbanized ecosystems have also been found to increase their consumption of non-ungulate prey, which is presumably a by-product of increased availability due to landscape development (Smith et al. 2015, Moss et al. 2016*a*, *b*). As urbanization intensifies, overlap between cougar and human populations will increase, especially in areas where residential development extends into cougar activity spaces and wild landscapes. Thus far, however, only two studies from the same ecosystem in northern Colorado have addressed changes in cougar foraging behavior over time along a wildland–urban gradient (Moss et al. 2016*a*, *b*). No study has yet considered changes in the probability of particular prey species being killed by cougars as they exploit increasingly urbanized portions of the landscape. Additional longitudinal studies of this nature are crucial to broadening our understanding of how the intensity of urbanization functionally changes cougar ecology and for

predicting how cougar populations will fare as urbanization continues to increase. Accordingly, we examined changes to cougar foraging behavior over time along an urbanizing wildland–urban gradient in western Washington.

In the state of Washington, many cougar populations overlap with exurban and suburban environments, making them ideal for long-term research on predator responses to anthropogenic disturbance. In western Washington at the foothills of the Cascade Mountains, cougars occur throughout a well-defined wildland–urban gradient (0–>10 residences/ha; Robinson et al. 2005, Kertson et al. 2013). Examination of cougar space use along this gradient revealed that resident cougars exhibited similar movement patterns in wildland and residential environments (Kertson et al. 2011*b*) but varied markedly in their space use. By inference, cougars in this system have been able to find suitable habitats and resources within a matrix of residential development while keeping interaction rates with humans low (1.6 interactions/1000 radio days; Kertson et al. 2013). Moreover, Kertson et al. (2011*a*) documented differential prey use across the gradient, suggesting that urbanization and corresponding residential development have shaped cougar diets in western Washington. The spatiotemporal relationship between building density and cougar diets in this system has not been investigated, however. Accordingly, we evaluated changes to cougar diets spatially across a wildland–urban gradient using kill site data collected during two study periods, the years 2004–2008 (termed hereafter as "study period 1") and 2013–2016 (termed "study period 2" hereafter), in a region where we were also able to quantify building density (per ha). Under the hypothesis that cougars adjust their foraging behavior to take advantage of widely available prey (Kertson et al. 2011*a*, Moss et al. 2016*a*), we predicted that increasing building density would be associated with an elevated presence of synanthropic species (e.g., prolific urban species; McKinney 2006, Moss et al. 2016, Alberti et al. 2017) in cougar diets, and a commensurate decrease in forest-associated ungulates and rodents that are generally taken in wildland portions of the study area (Kertson et al. 2011*a*). We also included a study period variable in our analysis to determine if any temporal changes to cougar diets occurred between the two data collection phases. Lastly, we hypothesized that while cougars would forage opportunistically, individuals would be likely to vary in their foraging responses to urbanization, mirroring the individual variation exhibited in their space use (Kertson et al. 2013).

## Methods

### *Study site*

We examined cougar kill site locations in a 4450-km$^2$ study site encompassing portions of King, Snohomish, and Pierce counties in Washington, USA (590,000 E, 5,260,000 N; Fig. 1). Landownership within the study site was an amalgamation of state, federal, municipal, and private property. Major landowners included the Washington Department of Natural Resources, the United States Forest Service, City of Seattle, King County, Campbell Global, Hancock Forest Management, and Fruit Growers Supply Incorporated (King County GIS Center, 2016). Major cities and towns within the study area include Bellevue (population 139,820), Redmond (60,598), Issaquah (36,081), Snoqualmie (13,169), Duvall (7674), and North Bend (6679; US Census Bureau 2015).

The study site is topographically complex and characterized by a gradual east–west gradient spanning wildland, exurban (<2.5 residences/ha), suburban (2.5–10 residences/ha), and urban (>10 residences/ha) environments (Robinson et al. 2005, Kertson et al. 2011*b*). Private timberland, Washington Department of Natural Resources forest, and United States Forest Service holdings comprise the majority of the eastern portion of the study site. The majority of wildland spaces within the study area consist of temperate coniferous forests typical of the North Cascades ecoregion (Franklin and Dyrness 1973). The topographic, physiographic, and developmental characteristics of the study site are described at greater length in Kertson et al. (2011*b*, 2013).

### *Radio-tagging and GPS cluster analysis*

We used trained dogs and cage traps to capture and radio-tag cougars throughout the study site from 2004 to 2008, and again from 2013 to 2016. Once captured, cougars were immobilized, given a physical examination, and outfitted with

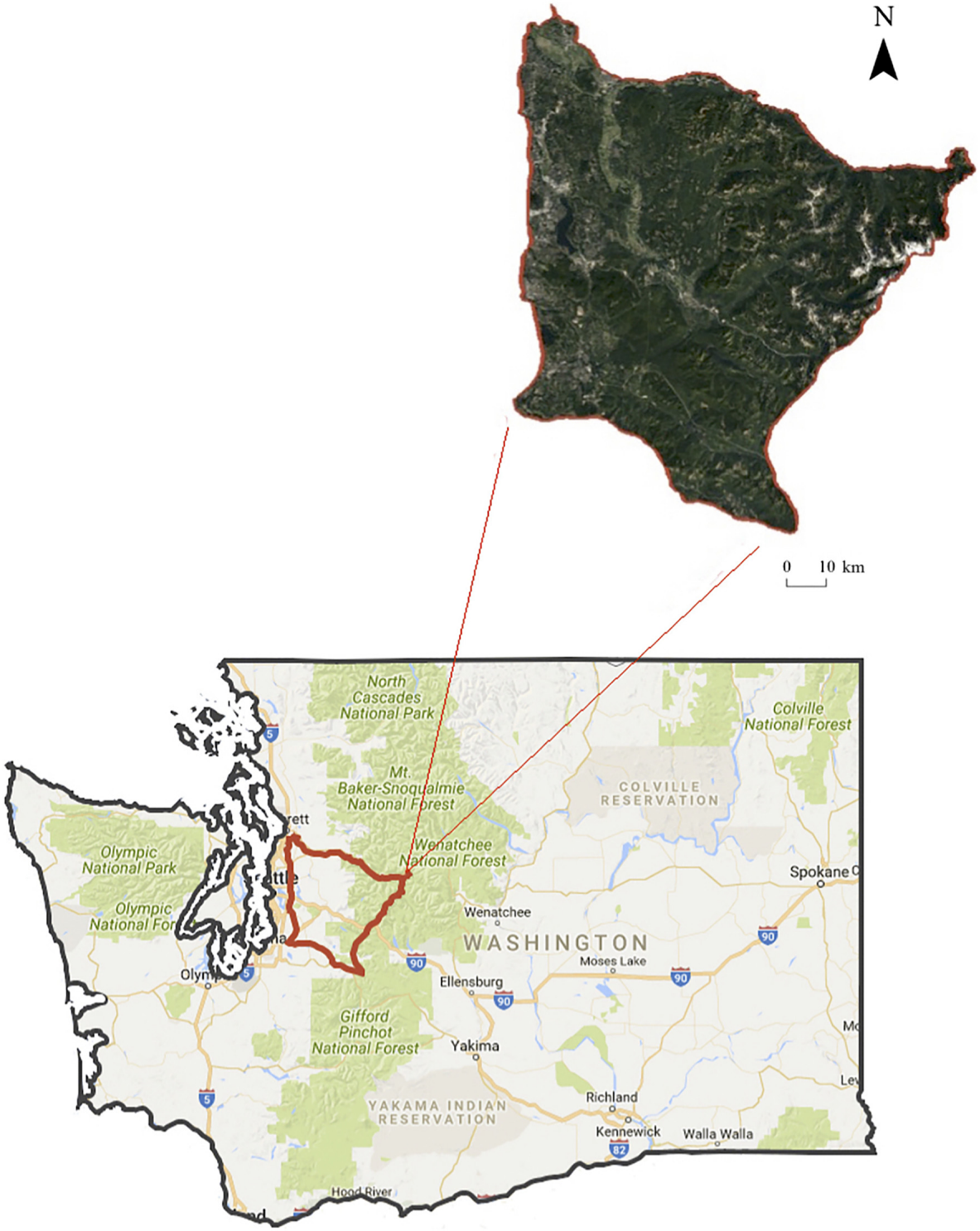


Fig. 1. Location of the 4450-km$^2$ cougar (*Puma concolor*) study site encompassing portions of King County, Snohomish County, and a small section of wildland in Pierce County (<75 km$^2$). The study site used by Washington's

(Fig. 1. *Continued*)
Department of Fish and Wildlife during period 1 was smaller (3500 $km^2$), although King County portions of the study site were identical. Residential and suburban development was concentrated in the western third of the study area with development densities generally decreasing from west to east.

a global positioning system (GPS) radio collar equipped with Vhf/Uhf download or Globalstar satellite uplinks (Models GPS-Simplex; Televilt, Lindesberg, Sweden, and GPS Plus-2; Vectronic Aerospace, Berlin, Germany). All captured cougars were anesthetized using a 10:1 mixture of ketamine hydrochloride and xylazine hydrochloride (Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) at a dosage of 8.8 mg/kg ketamine and 0.88 mg/kg xylazine and handled in accordance with University of Washington Institutional Animal Care and Use Committee (IACUC) protocol No. 3077-07. All capture methods have been vetted previously and described in detail elsewhere (Kertson and Marzluff 2010, Kertson et al. 2011*a*, *b*, 2013).

We programmed GPS radio collars to attempt a satellite fix for 180 s every four hours at 2:00, 6:00, 10:00, 14:00, 18:00, and 22:00 hours. The 4-h fix interval was chosen to maximize data acquisition and battery life (Cain et al. 2005, Kertson et al. 2011*b*). We identified potential kill site locations during study period 2 in accordance with the methodology used by Kertson et al. (2011*a*) during study period 1. Namely, we first plotted cougar relocations in ArcMap 10.3 and 10.4 (Environmental Systems Research Institute 2016) and Google Earth (Google, Mountain View, California, USA) and then defined location clusters as ≥3 GPS fixes occurring within an area ≤100 $m^2$ (methods by Anderson and Lindzey 2003 adapted to account for small prey items). We used a handheld GPS receiver (Model Etrex 20; Garmin, Schaffhausen, Switzerland) to navigate to the geometric center of the cluster, and we searched in concentric circles varying between 5 and 10 m apart (depending on visibility) out to the extent of the cluster radius (up to 100 m) or until prey remains were discovered. We recorded a GPS location at the kill site if prey remains were found that closely matched the dates during which the cluster was created and if we also found definitive evidence of cougar feeding behavior (e.g., carcass caching behavior, drag marks, hemorrhaging, skeletal remains, and cougar scat; Knopff et al. 2009, Kertson et al. 2011*a*, Wilckens et al. 2016).

### *Kill site assessment*

Kill site assessment followed the same methodology during study period 2 as in study period 1. Namely, after confirming each kill site location, we adjusted kill site coordinates on-site to correspond to the location of the rumen. Cougars may cache a carcass 0–80 m from the initial kill location during subsequent feeding bouts (Beier et al. 1995), so designating the position of the rumen as the kill location allowed for more consistent assessment of kill site features. Whenever possible, we documented prey species, sex, age, condition, and relative carcass consumption (Kertson et al. 2011*a*). We determined prey sex in ungulates based on antler presence or absence, and prey age using dentition and patterns of tooth wear and replacement (Severinghaus 1949).

### *Statistical analysis*

We used generalized linear mixed models (GLMMs) to test whether building density, a proxy for urbanization intensity (Theobald 2005, 2010), had an effect on the occurrence of certain prey items at cougar kill sites across the wildland–urban gradient. To create a building density predictor variable, we quantified urbanization within the study site using ArcMap 10.4 (Silverman 1986) and GIS parcel data from King and Snohomish counties, Washington, USA. We acquired parcel data for years 2007 and 2015 (King County) and 2004 and 2016 (Snohomish County) through the University of Washington Libraries media archive, along with the associated assessor's tables containing parcel attribute data, and created landscape categories based on Robinson et al. (2005) and Alberti et al. (2007), and urbanization was quantified as the density of built structures per hectare. We used the 2004 and 2007 shapefiles to approximate the extent of landscape development at kill site locations in both Snohomish and King counties during study period 1, whereas the 2015 and 2016 shapefiles

were used to approximate landscape development at kill sites during study period 2. Parcels with forms of development such as parking lots, residences, office spaces, shopping centers, major roads, schools, hospitals, and government institutions were used to generate building density raster layers. In other words, the measure of urbanization in this study can be considered the density of actual physical obstructions to cougar movement across the landscape. Regression models used by Alberti et al. (2007) indicated that land-use and housing density data along Washington's wildland–urban gradient are good predictors of land cover composition and configuration.

To quantify building density at each cougar kill location throughout the study site, we determined the year in which each kill was made and then calculated building density at that location from the most temporally relevant parcel layer (e.g., the King County 2004 parcel layer was used to measure building density at a kill in King County from 2005). Once all kills had a temporally appropriate representation of building density, we extracted raster cell values for all kill site locations. The resulting values represented a continuous building density variable per hectare. Average building density at kill site locations was 0.05 structures/ha. All kills that occurred in the Pierce County portion of the study area occurred in wildland areas, obviating the need to quantify building density for Pierce County kill sites. To address the hypothesis that building density would affect the occurrence of different prey species in cougar diets, we modeled the type of species killed using logistic regressions with building density, cougar sex, and study period as independent variables, and cougar ID included as a random effect. To achieve sample sizes necessary for modeling of cougar diets, we grouped prey species into three ecologically relevant categories: ungulates, synanthropes, and rodents. These prey categories closely mirror those used by Moss et al. (2016*b*), who grouped prey into meaningful categories based on isotopic signatures. The ungulate group in this study consisted of species heavily preyed upon by cougars in western Washington: namely, black-tailed deer (*Odocoileus hemionus columbianus*), elk (*Cervus canadensis*), and mountain goat (*Oreamnos americanus*). Rodents (i.e., beaver, *Castor canadensis*; mountain beaver, *Aplodontia rufa*) are largely wildland obligates in our system. Synanthropic species included coyotes, raccoons, opossums, and domestic species. Whereas coyotes are capable of occupying all land cover types in the study area, coyote predation by cougars often occurred along the urban fringe in western Washington, supporting the inclusion of this species in the synanthrope group. Null models contained only a single fixed intercept. We considered all possible interaction effects among fixed predictor variables in candidate models for each response.

We built candidate model sets (i.e., various predictor variable combinations) for each of the three prey categories, with a binary response of either 1 for the prey type of interest (e.g., synanthropes) or 0 for the other two prey categories combined (e.g., ungulates, rodents). We then ranked candidate models based on differences in the Akaike information criterion (AIC) in accordance with Burnham and Anderson (2002). Differences in AIC ($\Delta$AIC) were calculated relative to the best model, and we only considered models with $\Delta AIC \leq 2$ relative to the best model to be competitive (Burnham and Anderson 2002). We considered fixed and random effects significant if 95% confidence intervals (CIs) for their respective coefficient estimates did not overlap 0. Profile CIs were used to evaluate the standard deviation of the cougar ID random effect in each top model, and standard Wald CIs were used to quantify the uncertainty of fixed effect estimates. Odds ratios and their associated 95% CIs were used to evaluate the effect magnitude of the fixed and random effects in each of the top models and were considered significant if they did not overlap 1.0. We built all models using the glmer and glm functions in the lme4 package (Bates et al. 2016) in the R statistical package (R Core Team 2016).

## Results

### *Cougar foraging behavior*

We evaluated diets from 20 individual cougars to determine whether cougar diets varied spatially (i.e., across the urban gradient), and whether cougar diets changed over time (i.e., between study periods). Overall, cougar diets included 15 different prey species (Fig. 2), with

black-tailed deer ($n$ = 407 kills) and American beaver ($n$ = 70 kills) accounting for the majority of cougar kills based on investigation of GPS clusters (Table 1). Spatially, synanthropic species tended to occur in areas with greater building density than areas associated with rodent and ungulate kills (Appendix S1: Fig. S1). The study period fixed effect was only included in the ungulate and rodent top models (Table 2), indicating little temporal change in cougar predation on synanthropes. The distributions of kill site locations from study period 1 and study period 2 were roughly equivalent across the wildland–urban gradient, minimizing the likelihood that differences in cougar diets between study periods were a function of differences in sampling effort in residential areas (Fig. 3; Appendix S1: Table S1). Despite synanthropic species occurring in areas with greater building density, building density changed little among prey groups across time, and the average residential density at which kill site locations occurred did not vary markedly across all years of the investigation (Fig. 4).

The occurrence of synanthropic species in cougar diets was strongly tied to individual cougar identity, as well as the extent of urbanization (Fig. 5). Namely, the top synanthrope model included building density as the sole fixed effect (Table 2) and indicated that there was a multiplicative increase of 4.92 (95% CI: 1.09, 22.23) in the odds of cougar predation on synanthropic species with each additional building per hectare. The cougar random effect in this model accounted for a considerable amount of variability in synanthrope usage, where the estimated standard deviation of the random effects was $\hat{\sigma} = 1.26$ (95% CI: 0.68, 2.26). Predicted probabilities of synanthrope kills calculated at average building density were similar across the majority of cougars in this study (Fig. 6). Three individuals (F30, M324, and F325), however, differed significantly from the study average in their predicted probability of predation on synanthropic prey.

There was a high probability of ungulate predation across the wildland–urban gradient (Fig. 5), and individual cougar identity was also the dominant driver of cougar predation on ungulates. Specifically, the top ungulate model included fixed effects for sex and study period and the random cougar effect with no interaction

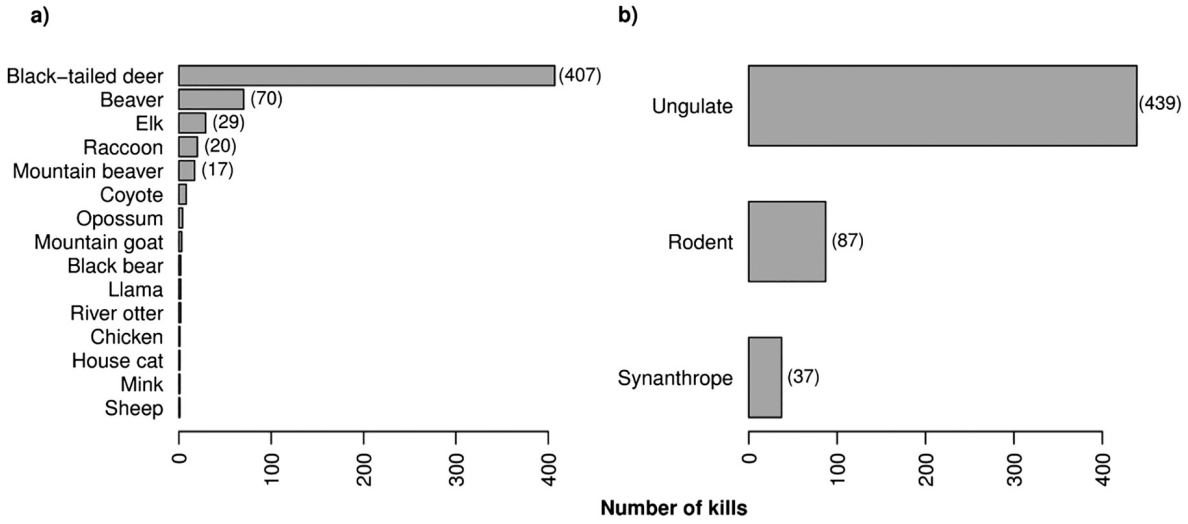


Fig. 2. (a) Numbers of prey individuals killed by cougars ($n$ = 568) across all study years, grouped by species; and (b) the numbers of cougar kills included in each of the three prey categories: ungulates (black-tailed deer, elk, mountain goat); rodents (beaver, mountain beaver); and synanthropes (raccoon, coyote, opossum). Two black bear kills, two river otter kills, and one mink kill were removed when grouping prey because these species, though considered wildland mammals, are not rodents or ungulates. Kill numbers for species and prey groups with ≥20 kills are indicated in parentheses.

Table 1. Percentage of kills by prey type (ungulate, rodent, or synanthrope) for each individual cougar.

| Cat ID | Sex | Period | Kills | Building density | | | Percentage of kills | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Mean | Min. | Max. | Ung. | Rod. | Syn. |
| 136 | F | 1 | 64 | 0.0 | 0.0 | 0.1 | 75 | 22 | 3 |
| 137 | F | 1 | 18 | 27.7 | 0.0 | 126.9 | 89 | 11 | 0 |
| 325 | F | 1 | 8 | 3.0 | 0.0 | 13.2 | 62 | 0 | 38 |
| 327 | F | 1 | 18 | 0.0 | 0.0 | 0.0 | 89 | 11 | 0 |
| 331 | F | 1 | 7 | 0.0 | 0.0 | 0.0 | 100 | 0 | 0 |
| 131 | M | 1 | 21 | 11.1 | 0.0 | 70.5 | 95 | 0 | 5 |
| 309 | M | 1 | 10 | 2.7 | 0.0 | 13.4 | 50 | 40 | 10 |
| 323 | M | 1 | 78 | 2.5 | 0.0 | 38.8 | 50 | 45 | 5 |
| 324 | M | 1 | 43 | 10.9 | 0.0 | 80.6 | 49 | 23 | 28 |
| 326 | M | 1 | 7 | 49.9 | 0.0 | 208.2 | 71 | 14 | 14 |
| 6 | F | 2 | 35 | 0.0 | 0.0 | 0.0 | 97 | 3 | 0 |
| 8 | F | 2 | 34 | 0.0 | 0.0 | 0.0 | 94 | 6 | 0 |
| 12 | F | 2 | 21 | 11.7 | 0.0 | 32.5 | 81 | 5 | 14 |
| 14 | F | 2 | 39 | 2.2 | 0.0 | 26.1 | 97 | 3 | 0 |
| 17 | F | 2 | 49 | 0.0 | 0.0 | 0.0 | 86 | 12 | 2 |
| 30 | F | 2 | 12 | 7.1 | 0.0 | 21.5 | 67 | 0 | 33 |
| 34 | F | 2 | 16 | 30.7 | 11.9 | 57.1 | 88 | 0 | 12 |
| 35 | F | 2 | 26 | 1.6 | 0.0 | 14.6 | 85 | 8 | 8 |
| 137 | F | 2 | 33 | 0.0 | 0.0 | 0.2 | 88 | 12 | 0 |
| 5 | M | 2 | 10 | 3.6 | 0.0 | 36.0 | 100 | 0 | 0 |
| 37 | M | 2 | 14 | 12.4 | 0.0 | 117.1 | 79 | 14 | 7 |

*Notes:* Also shown are sex, study period, number of kills, and building density (mean, minimum, and maximum) across all kill sites for each cougar. Building density is expressed as number of buildings per 100 ha for visualization purposes.

Table 2. All candidate models with a ΔAIC ≤ 2 when compared to the top model for each prey type.

| Response variable | Predictor variables | AIC | ΔAIC | Model likelihood | AIC weight |
|---|---|---|---|---|---|
| Synanthrope | Building density, r. effect | 251.0 | 0.0 | 1.00 | 0.24 |
| | Sex, building density, r. effect | 252.4 | 1.4 | 0.50 | 0.12 |
| | Study period, building density, r. effect | 252.4 | 1.4 | 0.50 | 0.12 |
| | R. effect only | 252.9 | 1.9 | 0.40 | 0.09 |
| | None (null model) | 275.0 | 24.0 | 0.00 | 0.00 |
| Ungulate | Sex, study period, r. effect | 537.0 | 0.0 | 1.00 | 0.16 |
| | Sex, study period, sex–study period interaction, r. effect | 537.6 | 0.6 | 0.76 | 0.12 |
| | Study period, r. effect | 537.6 | 0.6 | 0.74 | 0.12 |
| | Sex, r. effect | 537.7 | 0.7 | 0.71 | 0.12 |
| | Sex, study period, building density, r. effect | 538.6 | 1.6 | 0.45 | 0.07 |
| | R. effect only | 539.7 | 2.7 | 0.26 | 0.04 |
| | None (null model) | 595.7 | 58.7 | 0.00 | 0.00 |
| Rodent | Sex, study period, building density, r. effect | 426.6 | 0.0 | 1.00 | 0.26 |
| | Sex, study period, building density, sex–study period interaction, r. effect | 428.1 | 1.5 | 0.48 | 0.12 |
| | Study period, building density, r. effect | 428.5 | 1.8 | 0.40 | 0.10 |
| | Sex, study period, building density, study period–building density interaction, r. effect | 428.5 | 1.9 | 0.39 | 0.10 |
| | Sex, study period, building density, sex–building density interaction, r. effect | 428.6 | 2.0 | 0.37 | 0.09 |
| | R. effect only | 440.9 | 14.3 | 0.00 | 0.00 |
| | None (null model) | 486.7 | 60.1 | 0.00 | 0.00 |

*Notes:* Null models (intercept only) and models only including random cougar effects are shown for reference. Random effect indicated with r. effect. AIC, Akaike information criterion.

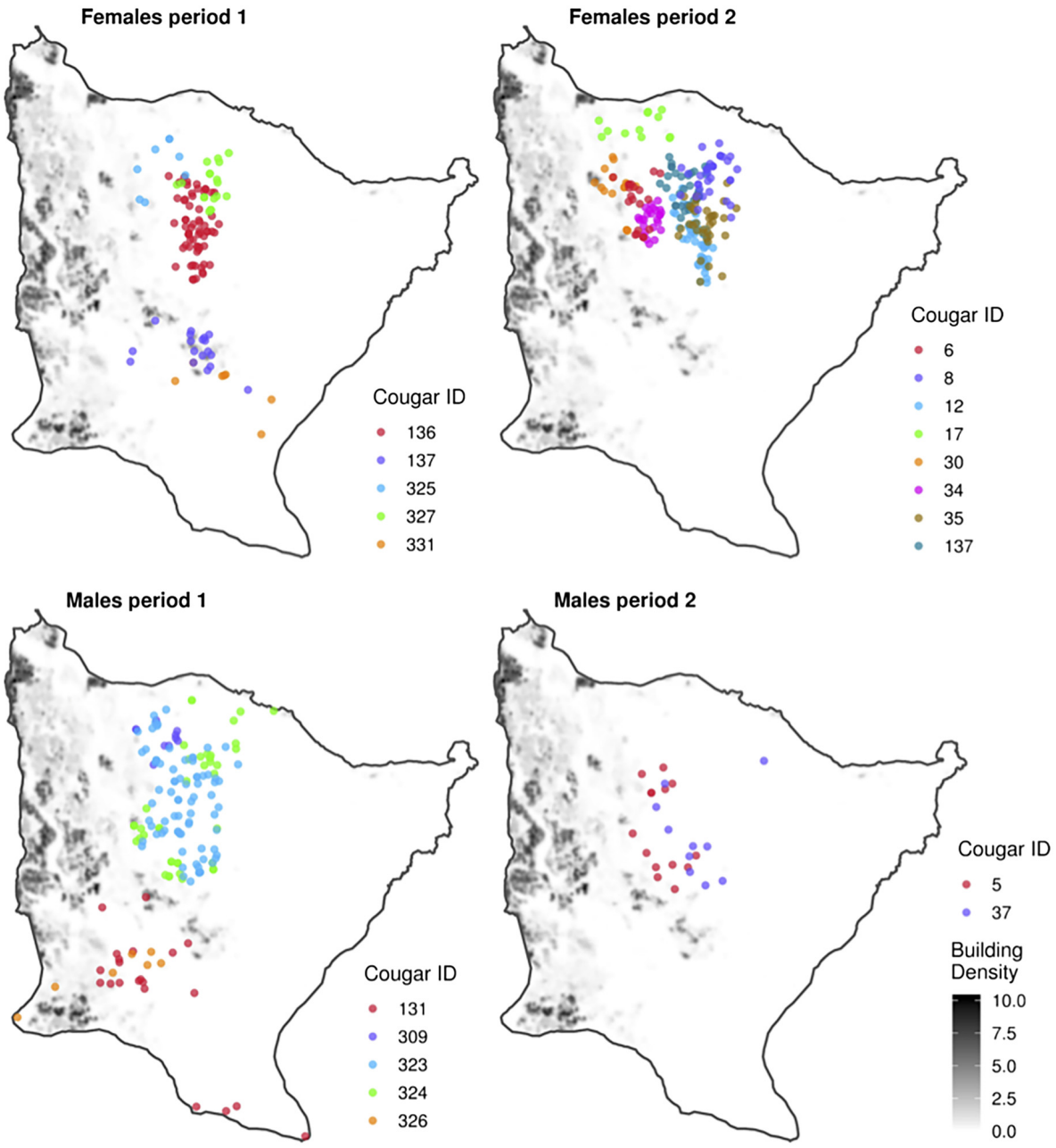


Fig. 3. Cougar kill site distribution across the study area, with panels distinguished by sex and study period (cougar ID indicated). Urbanization across the study area is indicated by the gray scale of 0–10 buildings per hectare.

effects (Table 2). This model suggested that the odds of preying on an ungulate were 2.16 times greater for females compared to males (95% CI: 0.91, 5.15) and were 2.06 times greater in period 2 compared to period 1 (95% CI: 0.92, 4.57), but the 95% CIs for these odds ratios both included 1.0. The estimated standard deviation of the cougar random effect, on the other hand, had a 95% CI that did not overlap zero ($\hat{\sigma} = 0.62$, CI = 0.23, 1.17) indicating significant differences in the use

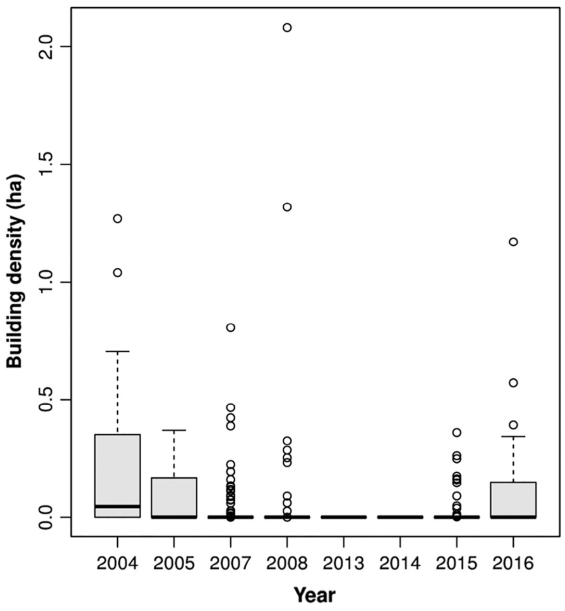


Fig. 4. Average building density at all cougar kill locations during every study year since 2004. Despite a few outlying kills occurring in high-density areas in 2004, 2008, and 2016, kills across years occurred on average in areas with <0.5 built parcels per hectare.

of ungulates among individuals in this study. Specifically, the predicted probabilities of ungulate kills were similar for the majority of cougars; however, three individuals (M309, M323, and M324) exhibited ungulate predation probabilities that were significantly lower than the average study animal (Fig. 6).

The intensity of urbanization (Fig. 5) and individual cougar identity were both important drivers of cougar predation on rodents. Namely, the top rodent model included the fixed effects of sex, study period, and building density, along with the random effect for individual cougars, with no interactions among predictors (Table 2). Additionally, the odds of a rodent kill were estimated to decrease by a multiplicative factor of 1.94 (95% CI: 1.16–3.23) for every increase of just 0.1 buildings per hectare. The odds of a rodent kill for males were 2.49 times greater than those for females (95% CI: 1.07–5.77), and 2.61 times greater in study period 1 than in study period 2 (95% CI: 1.15–5.96). The random effect for cougars had a marginal contribution to the top rodent model after accounting for the other variables ($\hat{\sigma} = 0.49$, 95% CI: 0.00, 1.08). When the

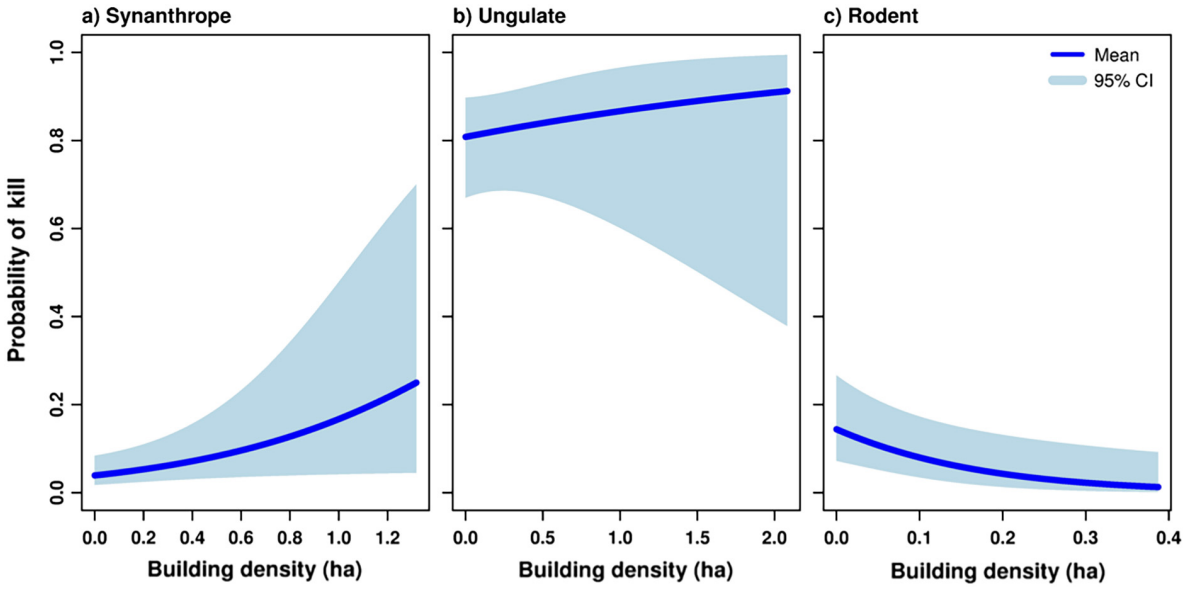


Fig. 5. The probabilities of a cougar kill by prey type (synanthrope (a), ungulate (b), rodent (c)) as a function of increasing building density. Dark blue lines indicate probability estimates and shaded regions indicate 95% confidence intervals. Both ungulate and rodent plots are based on females from study period 1 as probability estimates under both models differed by sex and study period.

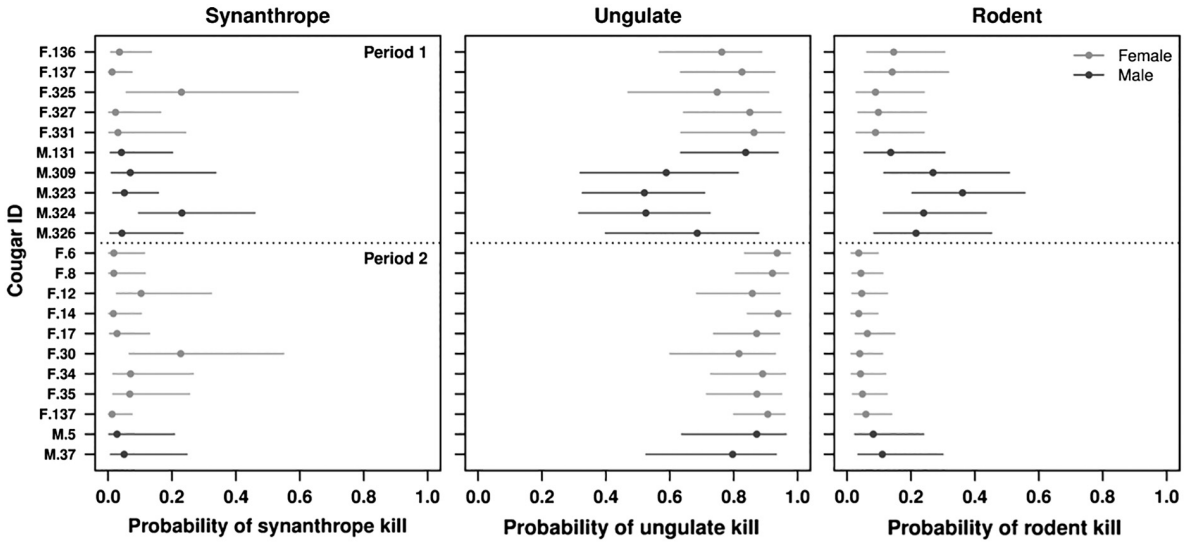


Fig. 6. Predicted probabilities of kills by prey type with associated 95% confidence intervals for each individual cougar. Predictions are from top models, and predictions for the synanthrope and rodent models are calculated at the average building density across all kill sites.

random effect was dropped from the top model, the change in AIC was only 1.57, indicating that the other variables accounted for much of the variability among individual cougars. However, one cougar (M323) had a significantly higher predicted probability of rodent kills at average housing density when compared to the average cougar in this study (Fig. 6).

## Discussion

Conflicts with humans remain the key threat to carnivore persistence globally (Chapron et al. 2003, Ripple et al. 2014), and as human populations increase, it is likely that a growing number of species will come into contact with people and anthropogenically altered landscapes (Bateman and Fleming 2012). Urbanization, ranging from low- to high-density residential development, continues to be a principal cause of broad-scale landscape change and can alter animal behavior (Lewis et al. 2015*b*) as well as ecological processes and community structure (Shochat et al. 2006, McKinney 2008, Ordeñana et al. 2010). Based on the findings of Kertson et al. (2011*a*), Smith et al. (2016), Moss et al. (2016*a*), and Blecha et al. (2018), we predicted that cougars foraging along a wildland–urban gradient in western Washington would increase their reliance on synanthropic prey species as a positive function of building density. Consistent with this prediction, building density was a significant predictor of synanthrope predation. The study period variable was not a significant predictor of predation on synanthropic species, suggesting that the study period 1 cougar cohort was similar to the cohort from study period 2 in their predation on synanthropes. As predicted, rodent predation was negatively associated with building density, and rodent predation significantly decreased between the study periods. The change in rodent predation between the study periods may simply be a function of differences in cougar cohorts, as male M323 (study period 1) accounted for 50% of rodent predation during this investigation. Ungulates were consistently the top prey item over the course of the study, and the degree of urban development was not a significant predictor of the use of these prey species, suggesting that under certain conditions, cougars may be able to continually rely on their primary prey even when their environment is subject to anthropogenic changes. Notably, individual differences accounted for a significant amount of variation in the use of all three prey groups. By implication, understanding patterns

of individual variability may be key to predicting how adaptable large carnivores respond to urbanization.

The odds of synanthrope predation by cougars increased as a function of building density, confirming our expectation that individuals exposed to increased opportunity to exploit urban prey would do so. Hence, our findings build on several previous studies (Kertson et al. 2011*a*, Moss et al. 2016*a*, Smith et al. 2016, Blecha et al. 2018) that underscore the dietary flexibility of cougars and suggest that individuals in urbanized environments may be able to persist and perhaps mitigate intra-specific competition for traditional prey by exploiting human-associated food. We also observed significant individual variation in synanthrope usage. It is possible that these differences among cougars owed to home range arrangement on the landscape, whereby individual cougar diets differed simply because of variation in the availability of prey items within their respective home ranges (i.e., because of differences in ecological opportunity; Araújo et al. 2011). The kill site locations for cougars in this study overlapped, however, and therefore do not strongly support this idea. We nevertheless acknowledge that the differences in predation on any of the prey types we documented could have stemmed at least in part from intra-specific variation in access to prey but were unable to address this possibility because no prey data were available in our study system. Individual specialization is an alternative explanation for the observed variability in the use of synanthropes, with a recent review of predator selectivity indicating that many generalist predator populations consist of individual dietary specialists, with part of the specialization associated with their phenotype (Pettorelli et al. 2011). Accordingly, the responses of particular cougars to varying degrees of urbanization may depend on divergent prey preferences possibly stemming from inheritance, learning, and/or competition (Araújo et al. 2011).

Contrary to our expectation, the odds of ungulate predation by cougars remained relatively stable across the wildland–urban gradient, suggesting that cougars were able to consistently rely on wild ungulates, particularly black-tailed deer, despite potential differences in ungulate availability as a function of urbanization. Indeed, the three cougars (M309, M323, M324) that deviated significantly from other study animals in their predation on ungulate prey had the majority of their kill site locations in wildland portions of the study area. The availability of black-tailed deer throughout the wildland–urban gradient might be tied to urbanization (Bender et al. 2004*a*, *b*), but contrary to our expectation of an inverse relationship, low-density development may actually augment ungulate use of residential landscapes and these individuals may be particularly susceptible to predation by cougars (Blecha et al. 2018). More importantly, our observations of the continued reliance on black-tailed deer and limited use of livestock by cougars suggest that some predator–prey systems can be maintained at the wildland–urban interface over an extended period of human population growth.

In accordance with our expectation, the odds of rodent predation decreased significantly as building density increased across the wildland–urban gradient. Previous cougar research in western Washington revealed that the majority of beaver and mountain beaver kills occurred within 100m of water and that cougars frequently foraged along hard habitat edges (Kertson et al. 2011*a*). Accordingly, our results suggest that these areas where cougars target beavers and mountain beavers may disappear with urban development and are therefore consistent with the idea that increasing urbanization in western Washington reduces the quality and availability of riparian habitats for cougars. Individual cougars differed in their use of rodents, with males exhibiting significantly greater use of rodents than females. M323 was responsible for a substantial portion of beaver kills during this investigation and may be the primary reason for this demographic disparity in rodent predation. By inference, any dietary shift at the population level induced by diminishing rodent habitat through urbanization is likely to be modest relative to those produced by changes to synanthrope and ungulate availability.

The changes to cougar diets in response to urbanization reported in this study are similar to previous studies elsewhere and suggest widespread applicability of our findings. For example, housing density influenced cougar consumption of small prey (<20 kg) in central California (Smith et al. 2016) and prey switching behavior

among cougars in northern Colorado (Moss et al. 2016*b*). Although Kertson et al. (2011*a*) noted individual patterns in foraging behavior among cougars, to our knowledge no study to date has modeled individual differences in the use of particular prey types along a wildland–urban gradient. In the present study, individual differences among cougars were a significant predictor of predation on all three prey groups, and the dominant driver of cougar use of synanthrope and ungulate prey. This pattern of individual variation in cougar diets mirrors the individual differences in space use documented by Kertson et al. (2011*b*) in the same system. It also suggests that cougar population responses to urbanization, and other forms of human disturbance, are unlikely to be uniform, and therefore that understanding the drivers that cause individuals to specialize on certain prey types is key to predicting how cougar populations will be shaped by anthropogenic landscape modification.

Investigation of cougar predation patterns in western Washington using cluster methodology allowed for the detection of non-ungulate prey items but was not without its limitations (Kertson et al. 2011*a*). For example, kill site examination through GPS cluster analysis has been shown to skew detection rates of predation events toward larger-bodied prey in other large carnivores (e.g., gray wolves, *Canis lupus*; Webb et al. 2008). Additionally, despite similar fix rates among GPS collars in study period 1 and study period 2 (80–95%), data transmission rates differed between collar types. The Vectronic GPS Plus GPS collars used during study period 1 achieved 100% data retrieval through the download on demand capability. Full data retrieval during study period 1 provided adequate opportunities for the detection of predation events spanning <24 h (Kertson et al. 2011*a*). The GPS Plus GlobalStar collars used during study period 2, however, frequently had data transmission rates of 60–70%, providing only a subset of the GPS location data and potentially weakening detection of clusters spanning <24 h. It is therefore possible, owing to lower detection probability for small prey, that differences in data transmission between the study periods contributed to a greater proportion of black-tailed deer predation events in study period 2. The individual variation in cougar diets revealed here occurred both during and across the two study periods, however, suggesting that the results of this investigation were not simply a function of methodological variation.

Large carnivores are controversial species whose management and conservation are complicated by broader psychological, political, and socioeconomic issues (Treves and Karnath 2003, Chapron et al. 2014, Ripple et al. 2014). Like many other large carnivores, cougars are periodically involved in conflicts with livestock producers and rural residents (Gilbert et al. 2016). Wildlife professionals also frequently feel considerable pressure to reduce large carnivore populations in an effort to bolster ungulate populations (Todd 2002, Hurley et al. 2011). Experimental efforts to reduce depredations and change ungulate demography through broad-scale predator removal have proven to have minimal effect on prey populations (Hurley et al. 2011), with studies on coyote (Austin et al. 1977, Trainer et al. 1981) and cougar (Robinette et al. 1977, Logan and Sweanor 2001) removal exhibiting variable results on mule deer survival. Alternatively, targeted predator management has proven useful in minimizing livestock depredations by wolves in Montana, Idaho, and Wyoming (Poudyal et al. 2016). Though we focused on a relatively small sample of cougars, our results reveal that certain individuals deviated markedly from the average usage of three prey categories. Thus, they provide additional evidence that management actions targeting individual animals are likely to be more effective in reducing human conflict with cougars, and potentially other large predators, than indiscriminate population reduction.

Cougars in Washington, as well as other predators globally, present unique conservation challenges because of human safety concerns and predation on domestic species (Campbell and Lancaster 2010, Campbell 2013). Yet, our results indicate that despite individual dietary differences, most cougars exhibited similar diets that were dominated by wild ungulates across the wildland–urban gradient and in both study periods. This pattern has implications for wildlife management and human–cougar coexistence. First, cougars in our system relied heavily on black-tailed deer, so promoting healthy native ungulate populations in wildland–urban areas may be a feasible approach to minimizing cougar

use of domestic species along urban gradients. By the same token, minimizing anthropogenic subsidies for deer and other food resources for deer near homes could be an effective approach for keeping both deer and foraging cougars away from residences.

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## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2605/full

behaviour of the various complexes is the same, but they exhibit profoundly different emission properties, we conclude that the specific nature of the bridge is the key to the colour switching phenomenon. It is well known that electron conduction, stabilization and delocalization on such bridging ligands depend on the geometry, energetics and structural features of the molecules[19–21]. Furthermore, use of different polymers with a higher-energy LUMO level (the HOMO level is chosen to be the same)—so that electron transfer mediated by the Ru complex cannot populate their excited state—did not result in green emission at reverse bias.

Symmetric devices with Au as anode and cathode have symmetric emission properties (that is, they show red emission at both forward and reverse bias), clearly indicating that an asymmetry in the device's charge injection behaviour is needed for the differentiation of the two possible mechanisms of light emission in the $[Ru(ph)_4\text{-}Ru]^{4+}$ PPV system. As the work functions of the ITO and Au contacts are energetically comparable, and the red/green switching behaviour is also seen when Au is replaced by Al, influences other than simple energetics must also have a role in allowing the stepwise electron transfer at reverse bias; we intend to study these influences in greater detail in the near future. □

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# Fingerprints of global warming on wild animals and plants

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**Over the past 100 years, the global average temperature has increased by approximately 0.6 °C and is projected to continue to rise at a rapid rate[1]. Although species have responded to climatic changes throughout their evolutionary history[2], a primary concern for wild species and their ecosystems is this rapid rate of change[3]. We gathered information on species and global warming from 143 studies for our meta-analyses. These analyses reveal a consistent temperature-related shift, or 'fingerprint', in species ranging from molluscs to mammals and from grasses to trees. Indeed, more than 80% of the species that show changes are shifting in the direction expected on the basis of known physiological constraints of species. Consequently, the balance of evidence from these studies strongly suggests that a significant impact of global warming is already discernible in animal and plant populations. The synergism of rapid temperature rise and other stresses, in particular habitat destruction, could easily disrupt the connectedness among species and lead to a reformulation of species communities, reflecting differential changes in species, and to numerous extirpations and possibly extinctions.**

Many studies have examined biological changes in relation to climatic change[4,5], but generally they are concentrated in particular regions or examine a limited set of taxa. To test whether or not a coherent pattern exists across regions and taxa that is consistent with predictions of expected change, we used two types of meta-analyses on these studies: vote counting and the regression-slope model (see Methods). One advantage of meta-analyses is that a broad spectrum of findings can be combined, including those for which statistical significance has not been shown. We examined thousands of articles, including those assembled by Working Group II of the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC TAR WGII)[6]. Of these, we included in our analyses only those that (1) examined a span of at least 10 years, (2) found that a trait of at least one species shows change over time, and (3) found either a temporal change in temperature at the study site or a strong association between the species trait and site-specific temperature. Because we were looking for trends, we also excluded studies examining climatic cycles, such as North Atlantic Oscillation and El Niño/Southern Oscillation. We divided 143 studies that met our criteria into two 'tiers': those demonstrating a statistically significant trend for at least one species examined (tier 1, most of which were used as the methodological basis for conclusions in the IPCC TAR WGII[6,7]) and those in which statistical significance was not shown by the study's authors (tier 2), usually because no statistical tests were applied. We performed our analyses for each tier taken separately and for the two combined. Appendices 1 and 2 of the Supplementary Information provide the data and citations


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Table 1 **Summary statistics for meta-analyses**

| | Significant species | Nonsignificant species | Combined species |
|---|---|---|---|
| Number of species changing | 586 | 882 | 1,468 |
| Number changing in expected direction | 482 | 708 | 1,190 |
| Percentage in expected direction | 82.3% | 80.4% | 81.1% |
| 90% confidence interval for percentage in expected direction | 73.4–88.6% | 70.5–87.4% | 74.2–86.5% |
| Effect size ($\delta$) | −0.09 | −0.23 | −0.23 |
| 90% confidence interval for $\delta$ | −0.12 to −0.06 | −0.30 to −0.14 | −0.29 to −0.17 |
| Standard error for $\delta$ | 0.0004 | 0.0023 | 0.0014 |
| Correlation coefficient ($r$) | −0.05 | −0.12 | −0.12 |
| 90% confidence interval for $r$ | −0.06 to −0.03 | −0.16 to −0.07 | −0.15 to −0.09 |
| Standard error for $r$ | 0.0002 | 0.0012 | 0.0007 |

A breakdown of values for those species or groups of species that were found, in the studies examined, to have statistically significant trends for various traits and for those that were not statistically significant. In addition, values are listed for the combination of these two categories of species or species groups.

for all of the studies used in our meta-analyses.

We focused on temperature change and ignored other climatic changes, such as precipitation, because the biological effects of temperature are often better understood for most of the organisms examined. Explicitly considering drought in our analyses would have allowed us to include many more studies, particularly from the Southern Hemisphere, but attributing local droughts to globally coherent patterns of climatic changes can often be difficult. We do, however, recognize that factors influencing populations interact in complex ways: temperature can exert its influence, for example, by affecting moisture availability.

Four types of change in species' traits due to warming may be possible. First, the density of species may change at given locations, and the ranges of species may shift either poleward or up in elevation as species move to occupy areas within their metabolic temperature tolerances. Second, because many natural history traits of species are triggered by temperature-related cues, changes could occur in the timing of events (phenology), such as migration, flowering or egg laying. Third, changes in morphology, such as body size, and behaviour may occur. Fourth, genetic frequencies may shift.

Attributing observed changes in populations of plants and animals to climatic change, specifically temperature increases, is possible because we expect the trends created by the large-scale pressure of global warming to show widespread, predictable and concordant patterns of change. In addition, we expect these changes to be concentrated in areas where temperature changes are largest (that is, at higher latitudes and altitudes) and for changes to be less evident elsewhere. Climate change is only one of a long list of pressures that influence the distributions and health of populations, as well as traits such as timing of activities and processes. These other pressures (for example, habitat modification, pollinator loss and exotic species introductions) often result in localized (often around centres of human populations) or multidirectional patterns of alterations to populations of species. To document a strong role for climate change in explaining many of the observed changes in animal and plant populations, we looked for repeated examples occurring over long temporal and broad spatial scales that showed unidirectional changes predicted by our understanding of the physiological tolerances of species to temperature. The predicted result, or fingerprint, of an underlying consistent shift in a large-scale pattern shown by many species around the globe, coupled with an understanding of the possible causal mechanisms, provides confidence in attributing observed species changes to climatic change. The 85 tier 1 studies and 58 tier 2 studies found strong changes occurring around the globe in various types (taxa) of animals and plants (see Supplementary Information). The meta-analyses we used to analyse the findings of these studies were the vote-counting method[8] and the regression-slope model[9]. We applied the vote-counting method to three different categories of data: 1) the 587+ species or groups of species ('+' because some studies do not provide numbers) in tier 1 (see Methods) that show statistically significant change; 2 the 886+ species or groups of species in both tier 1 and tier 2 that show statistically nonsignificant change or where the significance was unknown; and 3) the combined species (1,473+) showing change. For all three categories, the percentage of species changing in the expected direction was around 81% with a 90% confidence interval ranging from 71% to 89% (Table 1). The meta-analysis results of effect sizes and correlation coefficients were statistically different from zero ($P < 0.05$), which means that we can reject the null hypothesis of equal change in both the expected and opposite directions. Consequently, even this fairly low-powered vote-counting meta-analysis indicates that most changes are consistent with our understanding of how temperature change influences various traits of a variety of species and populations from around the globe. Hence, we can safely state that there has probably been a discernible impact of recent global warming on animals and plants.

The actual amount of change shown can be determined for those studies that examined shifts in spring phenologies. The 61 studies that investigated the change in timing of events occurring within the

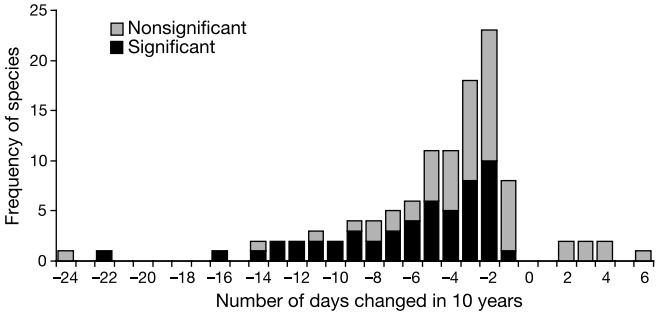


**Figure 1** Frequency distribution of species and groups of species (see text) with a temperature-related trait changing by number of days in 10 years. No data were tabulated for species showing zero days changing in ten years (see Methods).

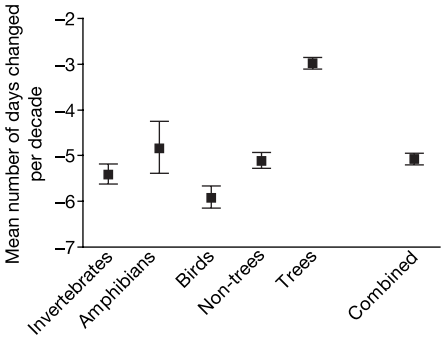


**Figure 2** Means ± s.e.m. of days changed for the given groups of species. The 'Combined' category includes only those species tallied in the groups of species (that is, data for the one mammal, two fish and zooplankton are not included).


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past 50 years examined a total of 694 species or groups of species. Our meta-analyses of these species indicate that over an average decade within the past 50 years, a statistically significant change towards earlier timing of spring events has occurred. The number of days changed per decade for a given species or species group ranges from 24 days earlier per decade for the breeding of North American common murre (*Uria aalge*) to 6.3 days per decade later for the breeding of North American Fowler's toad (*Bufo fowlen*) (Fig. 1). Using the regression-slope model[9] (see Methods), we found that the estimated mean number of days changed per decade for all species showing change in spring phenology is 5.1 days earlier (s.e.m. $\pm$ 0.1; Fig. 1). When the data are grouped by statistical significance, the estimated mean of the species with nonsignificant findings is closer to zero than that for species with significant findings ($-3.4 \pm 0.1$; $-6.9 \pm 0.1$, respectively; negative numbers indicate an earlier shift). The latter mean is understandably earlier than the former, given that regression analysis is more powerful at discriminating steeper slopes than shallower ones. However, all three estimated averages are statistically significantly different from zero, which means that these species are all showing a marked shift towards earlier spring events.

Given that higher latitudes have warmed more than the lower latitudes in the past half century (see Fig. 3d of ref. 1), we expect phenological responses to be larger nearer the poles and not as pronounced closer to the equator. (Unfortunately, our pool of literature did not allow us to test elevational changes.) The latitudes of the spring phenology studies in the Northern Hemisphere extend from 32° N to 72° N, with one study in the Southern Hemisphere at 39°. Because of the unevenness of the location of the data (for example, a preponderance of studies in the United Kingdom), we were able to have large enough sample sizes in each group only by dividing them into two groups along 50° latitude circles. The sample size from 32° to 49.9° was 24 +, which includes the one Southern Hemisphere study. From 50° to 72° N latitude, 85+ species or species groups were examined. As expected, the estimated mean and s.e.m. of the phenological shifts (see Methods) from 32° to 49.9° latitude is smaller ($-4.2 \pm 0.2$) than that between 50° and 72° N latitude band ($-5.5 \pm 0.1$). These two means are statistically significantly different from each other (Kruskal–Wallis test, ($P < 0.0001$), which strongly suggests that species at higher latitudes are indeed reacting more strongly to the more intense change in temperature.

Our spring phenology data set consists of species and populations from major taxa from molluscs to mammals. We had large enough sample sizes to examine the estimated means of the phenological shifts separately for invertebrates, amphibians and birds, and for trees and other plants (Fig. 2). Four of the five means cluster around an earlier shift of 5 days, which is the estimated mean for all taxa combined. Trees, however, show an estimated mean that is later than the cluster ($-3.0 \pm 0.1$). This estimated mean is statistically different from the other means (Kruskal–Wallis test), and the other four means are not statistically different from one another.

Our study shows that recent temperature change has apparently already had a marked influence on many species. Meta-analyses provide a way to combine results, whether significant or not, from various studies, and to find an underlying consistent shift, or fingerprint, among species from different taxa examined at disparate locations. The findings for the nonsignificant species, when aggregated, show nearly as much significant change as the group of species showing statistical significance (Table 1 and Fig. 1). Hence, for the studies we examined, the balance of evidence suggests that a significant impact of recent climatic warming is discernible in the form of long-term, large-scale alterations of animal and plant populations. For example, the average shift in spring phenology (timing) of events, such as breeding or blooming, for temperate-zone species is 5.1 $\pm$ 0.1 days earlier in a decade. The observed consistent broad-scale patterns of changes in the expected directions (80% of species showing change) strongly suggest that recent temperature trends are the most likely explanation for these observed phenomena. Clearly, if such climatic and ecological changes are now being detected when the globe has warmed by an estimated average of only 0.6 °C, many more far-reaching effects on species and ecosystems will probably occur in response to changes in temperature to levels predicted by IPCC[1], which run as high as 6 °C by 2100.

Projected future rapid climate change could soon become a more looming concern, especially when occurring together with other already well-established stressors, particularly habitat destruction. During rapid climatic changes in the past, species showed differential movements[10], rather than shifting together as suggested by many authors, including Darwin[11]. Such differential movement could result in a disruption of the connectedness among many species in current ecosystems (for example, a tearing apart of communities[7]). Research and conservation attention needs to be focused not only on global warming and each of the other stressors by themselves, but also on the synergism of several pressures that together are likely to prove to be the greatest challenge to animal and plant conservation in the twenty-first century[3,12]. Because anticipation of changes improves the capacity to manage—by acting proactively rather than reactively—it behoves us to increase our understanding about the responses of plants and animals to a changing climate. This understanding, coupled with further documentation of change, may well indicate a need for actions to modify conservation efforts and future planning to account for climate change, and to slow the projected rate of warming. □

## Methods

We used results from 143 studies, each of which found some trait of a species showing a trend over a span of at least 10 years. The geometric mean of the time span for all studies was 30.3 years and the average was 34.5 years. Gaps between years were allowed. Several studies investigated more than one species and some species showed no change. The relative number of species exhibiting change compared with all species reported in the literature sources we examined is not the relevant metric we consider, because we are not trying to determine what percentage of species is responding to current climatic changes. Given that all species examined in this study (and indeed by the entire scientific community) represents only a small proportion of the total number of species that exist in the world (itself unknown), such percentage claims are untenable by any analysis. Rather, a relevant metric to detect a discernible influence of global warming on plants and animals is the fraction of those species exhibiting change that have changed in the direction expected given a temperature trend at their location. For those studies finding change in more than one species and reporting the change as an average for several species, only one entry is used in the various tests performed. For example, Fleming and Tatchell[13] reported the change in flight period of five aphids as 2.6 days earlier per decade. To be conservative, for all our analyses, this group of aphids (and all similarly grouped species) is considered as one entry, rather than as five.

### Meta-analyses used

We used two types of meta-analysis, vote counting and regression slope, to determine whether changes observed are consistent with the possibility that one force, global warming, is instigating a noticeable change in species. The vote-counting method is explained in detail in ref. 8. This method is biased towards finding zero or no effect[14]—of global warming, in our case. The various studies have different sampling lengths ($K_i$) and so we use a geometric mean of these numbers to determine $K$, the mean length of years the studies examined traits of species or populations. In all three vote-counting analyses that we used—species showing statistically significant change, species showing nonsignificant change, and the combined species that showed change—the value of $K$ is 30.

The regression-slope meta-analysis provides a way to examine directly the shift in spring phenological changes. For this method to work, the various studies examined must have used the same measurement of change, which in these meta-analyses is the number of days changed per decade. We included only those studies that examined more recent spring shifts, from 1951 to 2001. Details of the methods we used here to derive estimated slopes are given in ref. 9. Our only deviation from this formulation is that we did not include the sampling variance term in the calculation of the variance of the slope parameter. This is because most studies examined do not report some of the data necessary to derive the sampling variance. This term acts to reduce the size of the variance of the regression slope. Consequently, the variances presented here are slight overestimates, making our inferences more conservative.

### Potential biases

Apart from the problems inherent in summarizing information from diverse studies of numerous subjects and methods, potential biases in the data are also of concern in analyses like ours. We do not claim that all authors of studies in the literature we cite report all


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species they observe, and there may be a bias to report primarily those species that show change. Even if there were such a bias, however, it would have no influence on our claim of a discernible impact of warming on plants and animals, because our metric of investigation is what fraction of those species that exhibit change has changed in the direction expected with local temperature trends, not what fraction of all species has exhibited change. The only way that observer bias could influence our metric would be if there were a systematic bias among the scores of studies we examine for researchers to select as study subjects only species showing changes in the direction preconceived by the authors to reflect temperature change. In addition, these many authors would have to have deliberately and systematically suppressed reporting on those species that changed in directions opposite to that expected. We find this possibility of widespread and systematic biases far-fetched, and thus believe that the metric we use is adequate for examining in an unbiased manner the existence of a discernible climatic signal in the traits of many plants and animals.

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**Supplementary Information** accompanies the paper on *Nature*'s website (http://www.nature.com/nature).

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# True navigation and magnetic maps in spiny lobsters

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**Animals are capable of true navigation if, after displacement to a location where they have never been, they can determine their position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey[1,2]. So far, only a few animals, all vertebrates, have been shown to possess true navigation[3]. Those few invertebrates that have been carefully studied return to target areas using path integration, landmark recognition, compass orientation and other mechanisms that cannot compensate for displacements into unfamiliar territory[4,5]. Here we report, however, that the spiny lobster *Panulirus argus* oriented reliably towards a capture site when displaced 12–37 km to unfamiliar locations, even when deprived of all known orientation cues *en route*. Little is known about how lobsters and other animals determine position during true navigation. To test the hypothesis that lobsters derive positional information from the Earth's magnetic field, lobsters were exposed to fields replicating those that exist at specific locations in their environment. Lobsters tested in a field north of the capture site oriented themselves southwards, whereas those tested in a field south of the capture site oriented themselves northwards. These results imply that true navigation in spiny lobsters, and perhaps in other animals, is based on a magnetic map sense.**

In the context of homing behaviour, an animal capable of true navigation must possess both a positional sense to determine its location and a directional or compass sense to orient in the appropriate homeward direction[6,7]. Many animals, both vertebrate and invertebrate, possess diverse compasses based on the Earth's magnetic field, the position of the Sun, patterns of skylight polarization and the positions of stars[4,8]. In contrast, few animals are known to possess the ability to determine position relative to a goal after being displaced to unfamiliar areas under conditions in which

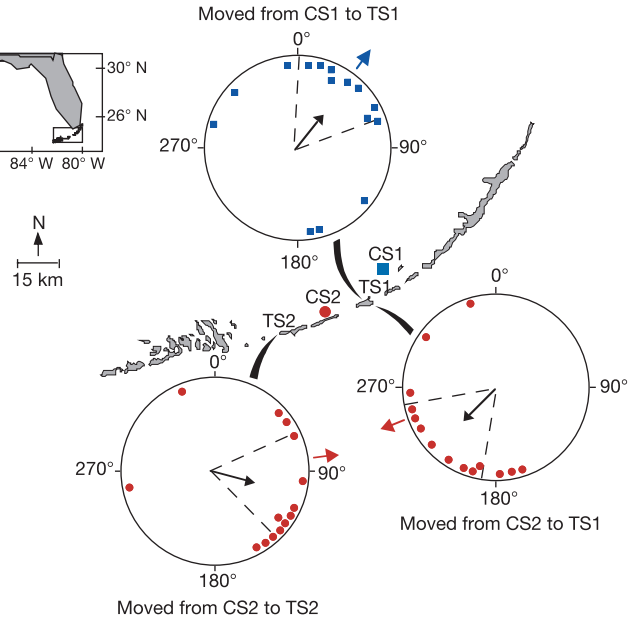


**Figure 1** Orientation of displaced lobsters. Lobsters were transported by boat from two capture sites (CS1, CS2) via circuitous routes (see the text) to one of two test sites (TS1, TS2). In the orientation diagrams, each small symbol represents the mean angle of a single lobster. Blue squares indicate lobsters captured at CS1, whereas red circles indicate lobsters captured at CS2. The arrow in the centre of each orientation diagram indicates the mean angle of each group; the arrow length is proportional to the mean vector **r**, with the radius of the circle corresponding to $r = 1$. Lobsters transported from CS1 to TS1 were significantly oriented ($r = 0.51$, $Z = 3.92$, $P < 0.02$, Rayleigh test) with a mean angle of 38°. Lobsters transported from CS2 to TS1 were significantly oriented ($r = 0.65$, $Z = 5.96$, $P < 0.01$) with a mean angle of 222°. Lobsters displaced from CS2 to TS2 were also significantly oriented ($r = 0.51$, $Z = 3.89$, $P < 0.02$) with a mean angle of 105°. In all orientation diagrams, the dashed lines represent the 95% confidence interval for the mean angle. Data are plotted relative to magnetic north. The blue or red arrow outside each orientation diagram indicates the direction from the test site to the capture site. In each case, the mean angle of orientation coincided closely with the direction towards the capture site (see the text) and the 95% confidence interval encompassed this 'homeward' direction.


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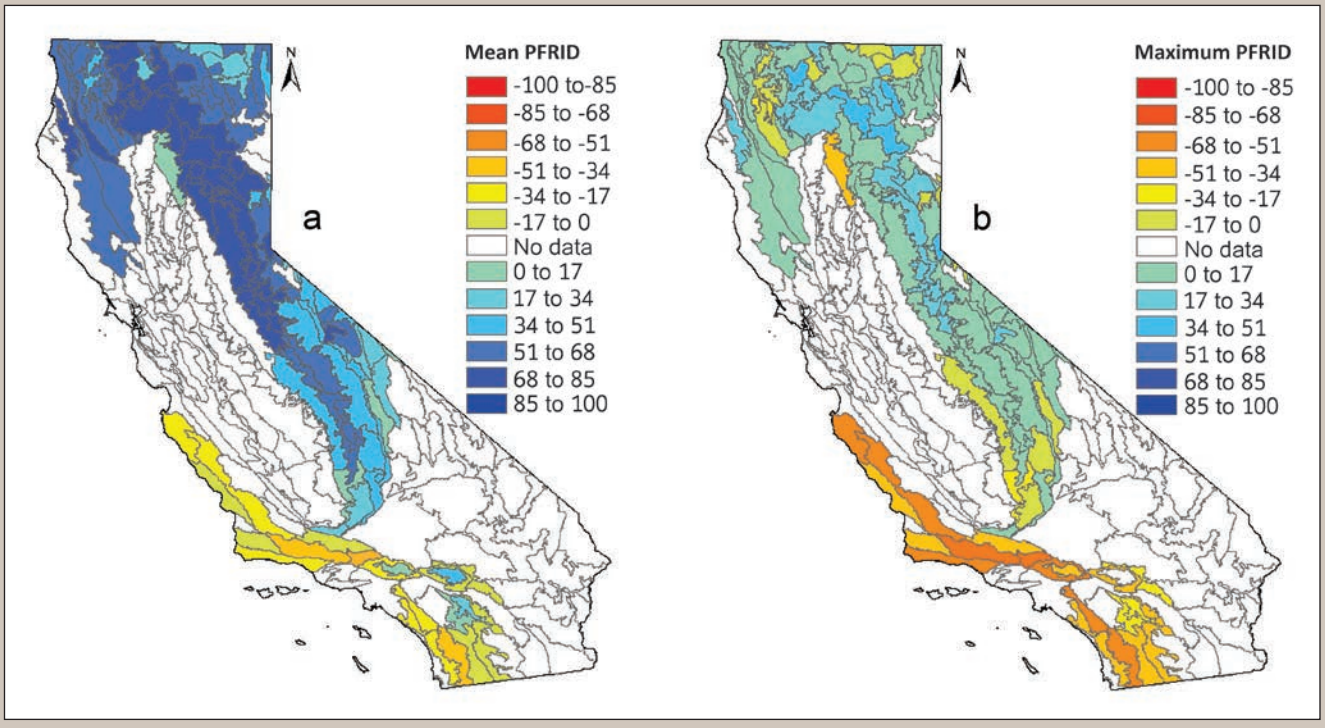
# Using Fire Return Interval Departure (FRID) Analysis to Map Spatial and Temporal Changes in Fire Frequency on National Forest Lands in California

Hugh D. Safford and Kip M. Van de Water



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## Summary

In the state of California, fire regimes and related ecosystem processes have been altered by land use practices associated with Euro-American settlement, and climate warming is exacerbating the magnitude and effects of these changes. Because of changing environmental baselines, restoration of narrowly defined historical conditions may no longer be an attainable or sustainable long-term management goal, but comparisons between historical and current fire regimes can assist managers in prioritizing areas for ecological restoration and other management actions. Fire return interval departure (FRID) analysis quantifies the difference between current and presettlement fire frequencies, allowing managers to target areas at high risk of threshold-type responses owing to altered fire regimes and interactions with other factors. We assessed FRID variability along geographic, climatic, and vegetation gradients in California on lands managed by the U.S. Department of Agriculture Forest Service and three forest-dominated national parks, using two types of FRID metrics: percent FRID, and the NPS-FRID index. Percent FRID (PFRID) quantifies the extent in percentage to which contemporary fires (i.e., since 1908) are burning at frequencies similar to those that occurred prior to Euro-American settlement. The NPS-FRID index represents the number of intervals missed since the last fire relative to the central tendency of presettlement fire return interval (FRI) distributions. Much of northwestern (NW) California and the Sierra Nevada sensu lato (including the southern Cascades, Modoc Plateau, and White and Inyo Mountains) has missed multiple fire cycles owing to fire suppression, while southern California is characterized by large areas burning at higher frequencies than under presettlement conditions. Ecologically speaking, fire suppression is a management necessity in much of southern California, but it is a major contributor to the growing forest fuels problem in NW California and the Sierra Nevada region. The PFRID exhibited a unimodal (hump-shaped) relationship to elevation in all three regions. The PFRID showed little relationship to precipitation in NW California or the Sierra Nevada region, but it decreased with precipitation in southern California. PFRID trends with temperature were unimodal, reaching a maximum at temperatures that approximate the elevation of the mean freezing line in winter storms, which is also

the transition between moist mixed conifer and red fir in most of northern California. Low- and middle-elevation vegetation types supported the greatest departures from presettlement fire frequencies, with oak woodlands, yellow pine, and mixed-conifer forests missing the most fire cycles, and coastal fir, coastal sage scrub, and chaparral tending to experience shorter FRIs than under presettlement conditions. We provide examples of how FRID data may be used in resource management in an age of global change. Our results help refine our understanding of departures from presettlement fire regimes across California, and provide a spatial basis for resource management and planning focused on ecological restoration and adaptation to climate change in a fire-prone region.

## Abstract

**Safford, Hugh D.; Van de Water, Kip M. 2014.** Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California. Res. Pap. PSW-RP-266. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 59 p.

In California, fire regimes and related ecosystem processes have been altered by land use practices associated with Euro-American settlement, and climate warming is exacerbating the magnitude and effects of these changes. Because of changing environmental baselines, restoration of narrowly defined historical conditions may no longer be an attainable or sustainable long-term management goal, but comparisons between historical and current fire regimes can assist managers in prioritizing areas for ecological restoration and other management actions. Fire return interval departure (FRID) analysis quantifies the difference between current and presettlement fire frequencies. We assessed FRID variability along geographic, climatic, and vegetation gradients in California on lands managed by the U.S. Department of Agriculture Forest Service and three forest-dominated national parks, using two types of FRID metrics: percent FRID (PFRID), and the NPS-FRID index. Much of northern California north of the Tehachapi Mountains has missed multiple fire cycles owing to fire suppression, while southern California is characterized by large areas burning at higher frequencies than under presettlement conditions. PFRID exhibited a unimodal (hump-shaped) relationship to elevation across our study area. PFRID showed little relationship to precipitation in northwest California or the Sierra Nevada region, but it decreased with precipitation in southern California. PFRID trends with temperature were unimodal, reaching a maximum at temperatures that approximate the elevation of the mean freezing line in winter storms, which also marks the transition between moist mixed conifer and red fir in most of northern California. Low- and middle-elevation vegetation types supported the greatest departures from presettlement fire frequencies, with oak woodlands, yellow pine, and mixed-conifer forests missing the most fire cycles, and coastal fir, coastal sage scrub, and chaparral tending to experience shorter FRIs than under presettlement conditions. Our results help refine our understanding of departures from presettlement fire regimes across California, and provide a spatial basis for resource management and planning focused on ecological restoration and adaptation to climate change in a fire-prone region.

Keywords: Ecological restoration, fire history, presettlement fire regime, Sierra Nevada, time since last fire.

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## Introduction

Fire is a keystone ecological process in most of the world's Mediterranean-climate regions (Keeley et al. 2011). In the state of California, which comprises most of the North American Mediterranean-climate region, fire regimes (including fire frequency, severity, extent, spatial patterning, etc.) and related ecosystem processes have been profoundly altered by land use practices associated with Euro-American settlement, especially since American settlement began in earnest after 1849. These changes have in turn led to major modifications in vegetation distribution, structure, and composition (Agee 1993, Barbour et al. 2007, Skinner and Chang 1996, Sugihara et al. 2006). Climate variability at different temporal scales has also been shown to be associated with past, current, and projected changes in fire regimes, vegetation, and other ecosystem properties across California (Lenihan et al. 2003; Miller et al. 2009, 2012; National Research Council 2011; Swetnam 1993; Westerling et al. 2006, 2011). In a drought- and fire-prone region like California, ecological restoration efforts intended to increase ecosystem resilience to global change should consider fire and climate as central organizing principles (Keeley et al. 2011, North et al. 2009).

Practices of ecological restoration traditionally depend on the characterization of reference conditions, which can provide management targets and a means to measure management success (Egan and Howell 2001). Because modern human alteration of many ecosystems has been so profound, reference states must often be derived from historical information from before the onset of anthropogenic change. Maintaining managed ecosystems within the bounds of the "historical range of variation" (HRV) for key ecosystem patterns or processes has traditionally been seen as the best hope for preserving species and landscapes and ensuring long-term ecological sustainability (Egan and Howell 2001, Landres et al. 1999). Our trust in history as a dependable guide to the future has been tempered, however, by the revelation that many key ecosystem processes are not stationary, and that historical environmental baselines may or may not represent conditions that are particularly germane to either contemporary or future circumstances (Millar et al. 2007, Safford et al. 2012, Stephenson et al. 2010). At the same time, there is widespread recognition that the real problem lies not in history itself, which provides our only window into ecological processes operating at longer temporal scales, but rather in how historical information is applied to resource management (Stephenson et al. 2010, Wiens et al. 2012).

Because of the uncertainty surrounding future effects of climate and land use change on ecological processes such as fire, myopic focus on restoration of narrowly defined and static snapshots of historical conditions is probably not a

sustainable management option in most California ecosystems (Millar et al. 2007, Safford et al. 2012). Nevertheless, information on fire regimes and ecosystem response to fire before Euro-American settlement is of elementary importance to current and future resource management (Fulé 2008, Millar et al. 2007, North et al. 2009, Van de Water and Safford 2011, Wiens et al. 2012). Such historical information can provide a foundation for understanding status of and trends in fire activity and its ecological effects over time; improve our understanding of the mechanisms that drive ecosystem response to climate and fire, their variability and their interactions with the landscape; furnish data upon which models of "properly functioning" or "resilient" ecosystems might be built; and determine to what extent current conditions may be historically anomalous and worthy of management intervention (Safford et al. 2012, Wiens et al. 2012).

The most commonly used fire regime attribute in reconstructions of historical fire regimes is fire frequency (Agee 1993, Johnson and Gutsell 1994). Disturbance frequency is a major driver of ecological and evolutionary response (Connell 1978, Huston 1994, Pickett and White 1985), and although frequency is only one component of the fire regime, the dependence of fire occurrence and behavior on the growth of vegetation produces a broadly inverse relationship between fire frequency and intensity (within a given ecosystem type, and assuming a constant climate) (Huston 2003, Turner et al. 1989). This relationship has permitted the development of simplistic but useful frequency-based and severity-based (a measure of the effect of fire intensity on the ecosystem) fire regime classifications that underlie mapping and management of wildland fire and fuels in the United States (e.g., Hardy et al. 1998, Heinselman 1978, Kilgore 1981). Within ecosystem types, this relationship also allows some (cautious) inference to be made about the effects of changing fire frequency on other fire regime attributes.

Drawing comparisons between past and current fire frequencies can assist resource managers in prioritizing areas for ecological restoration, fuels reduction, certain fire or habitat management practices, and other activities. Fire return interval departure (FRID) analysis is a method for quantifying the difference between current and presettlement fire frequencies on a management landscape (Caprio et al. 1997, Caprio and Graber 2000, van Wagtendonk et al. 2002). By comparing current fire return intervals (FRIs) with the range of reported pre-Euro-American settlement FRIs from the literature, a sort of rudimentary HRV analysis can be conducted. In such an analysis, quantified current departures from the reference conditions provide a basis to identify areas on the management landscape that are at high risk of type conversion or threshold-type responses owing to either greatly accelerated or greatly decelerated fire frequencies; areas that are within HRV can also be identified and targeted for maintenance management or study.

Several FRID assessments have been conducted in California, focused on individual national parks in the Sierra Nevada (Caprio et al. 1997, Caprio and Graber 2000, van Wagtendonk et al. 2002). These studies are enlightening, but they are of limited use in regional-scale restoration planning applications. In addition, the national park FRID analyses have been focused only on the time since the most recent fire, rather than on the complete record of fire location and size that has been collected since the early 20$^{th}$ century. Restoration of fire as an ecological process, and restoration of other ecosystem properties dependent on fire, will require more than a single application of prescribed fire or the occurrence of a single wildland fire. We therefore developed a complementary set of different FRID measures based on spatial fire records from throughout the last century. These percentage-based measures are less sensitive to the incidence of a single fire, and are more suitable to comparisons of fire frequencies over time between the current and pre-Euro-American settlement periods.

In this study, we determined time since last fire (TSLF) and calculated two sets of FRID measures (percent-based and National Park Service [NPS] calculations) for the approximately 8.1 million ha of land managed by the U.S. Forest Service in California. Except in some wilderness areas, most fires on Forest Service lands in California are subject to fire-suppression efforts, although indirect attack techniques can allow for significant fire spread under some circumstances. For comparison, we also include analyses of three of the largest national parks in California (Sequoia, Kings Canyon, and Yosemite national parks (NPs), 1.6 million ha in total), which encompass large areas where naturally ignited fires are allowed to burn under certain conditions for ecological benefit (van Wagtendonk 2007). In our analysis, we divided the state into three large geographic regions, which exhibit notable differences in climate, geography, and human land use that we expected to affect FRID: northwestern (NW) California; the Sierra Nevada, southern Cascades, Modoc Plateau, and White and Inyo Mountains (the combination of which we refer to as the "Sierra Nevada"); and southern California. Our focus was on identifying and interpreting major patterns in FRID across gradients of geography, climate, vegetation, and management, so as to provide a basis for broad-scale decisionmaking in resource management and planning on Forest Service and neighboring lands across California.

## Methods

### Study Area

The analysis area for this study, which consisted of the 19 national forests (NFs) and three NPs in California, was divided into three geographic regions: (1) NW

California (Klamath, Mendocino, Shasta-Trinity, and Six Rivers NFs); (2) the Sierra Nevada, including the southern Cascades, Modoc Plateau, and White and Inyo Mountains (El Dorado, Humboldt-Toiyabe [California portion only], Inyo, Lassen, Modoc, Plumas, Sequoia, Sierra, Tahoe, and Stanislaus NFs); the Lake Tahoe Basin Management Unit; and Yosemite, Sequoia, and Kings Canyon NPs; and (3) Southern California (Angeles, Cleveland, Los Padres, and San Bernardino NFs) (fig. 1). Most of California and almost all Forest Service lands in the state (except the eastern Inyo and Modoc NFs) are found in the Mediterranean-climate zone. In this paper, we refer collectively to the NW California and Sierra Nevada regions as "northern California." In northern California, winters are cool and wet, and summers are warm and dry. In most of southern California, winters are cool but not as wet (except for the northern and central maritime portions of ecological section 261A (Miles and Goudey 1997) (fig. 1), and summers are warmer and drier than in the north. See Major (1988) and Minnich (2007) for information on temperature and precipitation in each region. Elevations in the NW California region range from near sea level to 4320 m; in the Sierra Nevada region, elevations range from 50 to

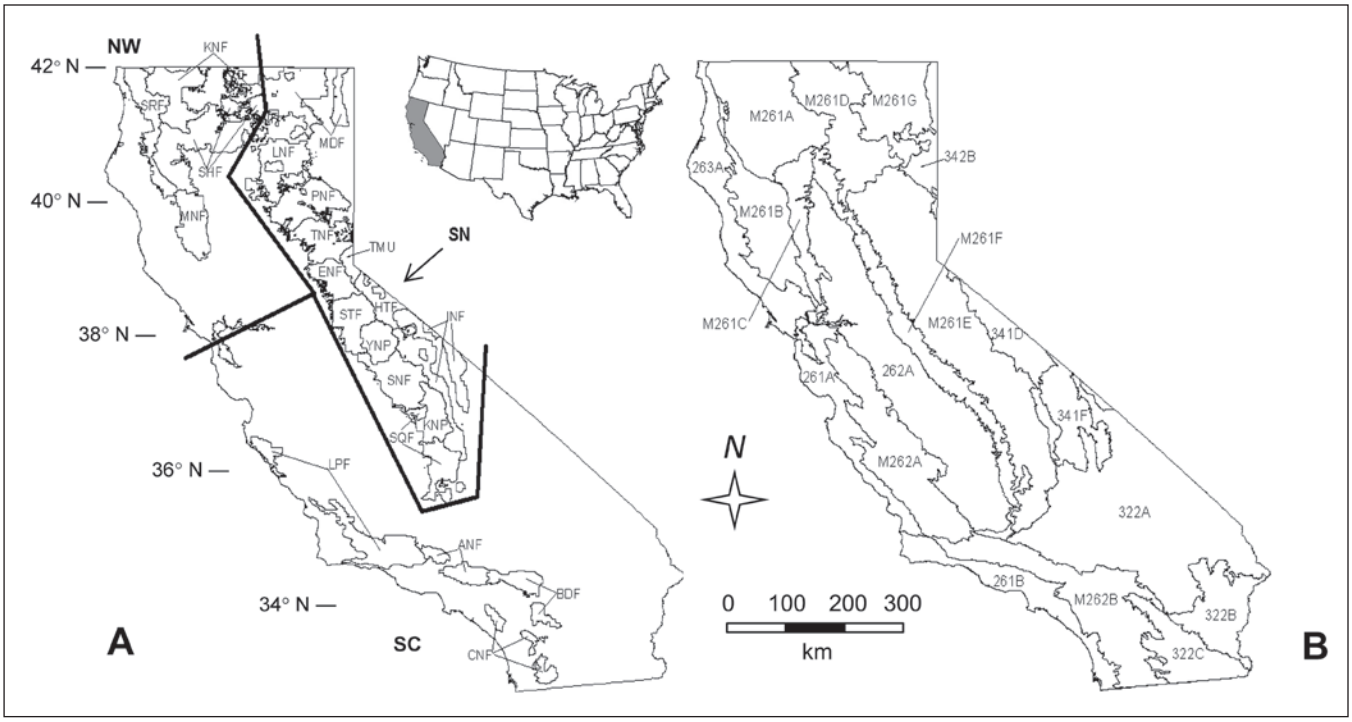


Figure 1—The study area. (A) Federal land management units included in the study area, segregated by geographic region (see text): NW = northwest California region; SN = Sierra Nevada region; SC = southern California region. National forests, clockwise from NW to SC: MNF = Mendocino, SRF = Six Rivers, SHF = Shasta-Trinity, KNF = Klamath; MDF = Modoc, LNF = Lassen, PNF = Plumas, TNF = Tahoe, TMU = Lake Tahoe Basin Management Unit, ENF = Eldorado, STF = Stanislaus, HTF = Humboldt-Toiyabe, SNF = Sierra, INF = Inyo, SQF = Sequoia; BDF = San Bernardino, CNF = Cleveland, ANF = Angeles, LPF = Los Padres. National Parks, in the Sierra Nevada: YNP = Yosemite, KNP = Sequoia-Kings Canyon. (B) Ecological sections in California, from Miles and Goudey (1997), and defined in table 2 on p. 12.

4420 m; in the southern California region, elevations range from near sea level to 3500 m. Vegetation in the analysis area in northern California is dominated by conifer forest, with substantial hardwood presence in lower and middle elevation areas with sufficient precipitation. Vegetation in the analysis area in southern California is dominated by hardwood forests/woodlands and shrublands (Barbour et al. 2007) with conifer forests of relatively small areal extent at high elevations.

## Fire Regime Typing

Current existing vegetation types within the analysis area (as identified by the Forest Service's CALVEG classification) (Franklin et al. 2000; see http://www.fs.usda.gov/detail/r5/landmanagement/resourcemanagement/?cid=stelprdb5347192) were organized into 28 presettlement fire regime (PFR) groups according to the similarity of their historical relationships with fire (Van de Water and Safford 2011). The PFRs were developed only for vegetation types dominated by woody plants, as our understanding of historical fire regimes in herbaceous vegetation is poor. For each PFR, we conducted an exhaustive review of the published and unpublished literature pertaining to mean, median, minimum, and maximum FRIs that occurred prior to significant Euro-American settlement (i.e., the middle of the 19$^{th}$ century), and the average was taken of all mean, median, minimum, and maximum FRI values to yield a single mean, median, mean minimum, and mean maximum FRI estimate for each PFR (Van de Water and Safford 2011) (table 1). Most of the data used came from composite dendrochronological fire histories including records from multiple trees in a defined area. Our reference period is thus primarily the c. 200 to 500 years before 1850, although some of the records we accessed go back over 2000 years (Van de Water and Safford 2011).

Polygons were created for each area dominated by a given PFR and its associated presettlement mean, median, minimum, and maximum FRIs using ArcGIS 9.3[1] (ESRI 2008). The mapping base was the Forest Service existing vegetation (EVEG) geodatabase (available at http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327836), which uses the CALVEG classification. We chose to use existing-vegetation polygons instead of potential natural vegetation (PNV) types because Forest Service PNV mapping was never completed in California and completed PNV mapping (mostly) disregarded disturbances like fire. The LANDFIRE Biophysical Settings (BpS) data are PNV types that incorporate disturbance (Rollins 2009), but the mapped accuracy of this modeled data layer varies across

[1] Use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

**Table 1—Mean, mean minimum (min) and mean maximum (max) pre-Euro-American settlement fire return intervals (FRIs) for the presettlement fire regime (PFR) groups, and the current FRIs associated with the boundaries between condition classes (CCs)**

| PFR | Mean min FRI | CCs-2 and-3 | CCs-1 and-2 | Mean FRI | CCs 1 and 2 | CCs 2 and 3 | Mean max FRI |
|---|---|---|---|---|---|---|---|
| | | | | *Years* | | | |
| Aspen | 10 | 6.3 | 12.7 | 19 | 28.4 | 57.6 | 90 |
| Big sagebrush | 15 | 11.6 | 23.5 | 35 | 52.2 | 106.1 | 85 |
| Bigcone Douglas-fir | 5 | 10.2 | 20.8 | 31 | 46.3 | 93.9 | 95 |
| Black and low sagebrush | 35 | 21.8 | 44.2 | 66 | 98.5 | 200.0 | 115 |
| California juniper | 5 | 27.4 | 55.6 | 83 | 123.9 | 251.5 | 335 |
| Chaparral and serotinous conifers | 30 | 18.2 | 36.9 | 55 | 82.1 | 166.7 | 90 |
| Coastal fir | 90 | 32.7 | 66.3 | 99 | 147.8 | 300.0 | 435 |
| Coastal sage scrub | 20 | 25.1 | 50.9 | 76 | 113.4 | 230.3 | 120 |
| Curl-leaf mountain mahogany | 30 | 17.2 | 34.8 | 52 | 77.6 | 157.6 | 130 |
| Desert mixed shrub | 120 | 201.3 | 408.7 | 610 | 910.4 | 1,848.5 | 1,440 |
| Dry mixed conifer | 5 | 3.6 | 7.4 | 11 | 16.4 | 33.3 | 50 |
| Fire-sensitive spruce or fir | 90 | 38.6 | 78.4 | 117 | 174.6 | 354.5 | 250 |
| Lodgepole pine | 15 | 12.2 | 24.8 | 37 | 55.2 | 112.1 | 290 |
| Mixed evergreen | 15 | 9.6 | 19.4 | 29 | 43.3 | 87.9 | 80 |
| Moist mixed conifer | 5 | 5.3 | 10.7 | 16 | 23.9 | 48.5 | 80 |
| Montane chaparral | 15 | 8.9 | 18.1 | 27 | 40.3 | 81.8 | 50 |
| Oak woodland | 5 | 4.0 | 8.0 | 12 | 17.9 | 36.4 | 45 |
| Pinyon-juniper | 50 | 49.8 | 101.2 | 151 | 225.4 | 457.6 | 250 |
| Port Orford cedar | 10 | 9.9 | 20.1 | 30 | 44.8 | 90.9 | 160 |
| Red fir | 15 | 13.2 | 26.8 | 40 | 59.7 | 121.2 | 130 |
| Redwood | 10 | 7.6 | 15.4 | 23 | 34.3 | 69.7 | 170 |
| Semidesert chaparral | 50 | 21.5 | 43.6 | 65 | 97.0 | 197.0 | 115 |
| Shore pine | 190 | 82.5 | 167.5 | 250 | 373.1 | 757.6 | 1,025 |
| Silver sagebrush | 15 | 11.6 | 23.5 | 35 | 52.2 | 106.1 | 65 |
| Spruce-hemlock | 180 | 90.8 | 184.3 | 275 | 410.4 | 833.3 | 550 |
| Subalpine forest | 100 | 43.9 | 89.1 | 133 | 198.5 | 403.0 | 420 |
| Western white pine | 15 | 16.5 | 33.5 | 50 | 74.6 | 151.5 | 370 |
| Yellow pine | 5 | 3.6 | 7.4 | 11 | 16.4 | 33.3 | 40 |

Note: Mean, mean minimum, and mean maximum FRIs are from Van de Water and Safford (2011).

Forest Service lands in California. We believe the BpS maps are of reasonable accuracy at the regional (e.g., NW California, Sierra Nevada, southern California) or statewide scale, especially when similar vegetation types are pooled (see, e.g., Miller and Safford 2012), but our FRID geodatabase is intended to support planning and management at all spatial scales. Local inaccuracies in the BpS maps make use at or below the scale of a national forest or national park unit challenging. Note that our use of an existing-vegetation map from the 2000s as our base layer means that

major changes in vegetation that have occurred since Euro-American settlement will affect the accuracy of our results. We elaborate on this issue in the "Discussion" section.

We carried out a union between the PFR geodatabase and CalFire's Fire Perimeters database (FRAP 2011), which tracks California fire history. The Fire Perimeters database is considered more or less complete for fires larger than 40 ha after 1908, and over 4 ha after 1950 (Miller et al. 2009); many smaller fires are also reported. The resulting geodatabase split the PFR polygons into smaller polygons based on the number of fires that had occurred in each PFR polygon since 1908.

## FRID Mapping

Time since last fire was calculated by subtracting the year of the last fire in each polygon from 2010 (the most recent year included in the Fire Perimeters database when we conducted our analysis). Any polygon that had not had a fire since prior to 1908 was assigned a default TSLF value of 103 years; in many cases, TSLF will thus be a conservative measure of the time since last burn. Current FRI was calculated by dividing the number of years in the fire record (i.e., 2010–1908 = 103 years inclusive) by the number of fires occurring in each polygon (according to the Fire Perimeters database) plus one (current FRI = 103/number of times burned + 1). This calculation of current FRI is generally conservative because small fires (<40 ha prior to 1950, <4 ha after 1950) are not included in the Fire Perimeters database (FRAP 2011), prescribed fires are rarely included, and some parts of California have poor fire records for the period before World War II.

Five FRID metrics were calculated for each polygon. Four of them—mean, median, mininum, and maximum percent FRID (PFRID)—were calculated using the following equation when current FRI is longer than presettlement FRI (Hann and Strohm 2003):

$$PFRID = [1 - (\text{presettlement FRI}/\text{purrent FRI})] \times 100,$$

or, when current FRI is shorter than presettlement FRI:

$$PFRID = -[1 - (\text{current FRI}/\text{presettlement FRI})] \times 100$$

where presettlement mean, median, mean minimum, and mean maximum FRI are each substituted for their respective PFRID metrics. These PFRID metrics quantify the extent in percent to which contemporary fires (i.e., since 1908) are burning at frequencies similar to the frequencies that occurred prior to Euro-American settlement. To use an example: assuming a presettlement mean FRI of 10 years for some theoretical PFR, a current FRI of 30 years would be a +67 percent departure ([1 – (10/30)] × 100); for the same PFR, a current FRI of 5 years would be a -50 percent departure (-[1 – (5/10)] × 100). PFRID considers the cumulative fire

history of each polygon since 1908 and does not return to zero when a fire occurs. For areas dominated by PFRs with a presettlement FRI greater than 103 years and that have not burned in the period of historical record considered in this analysis (i.e., since 1908), PFRID is assumed to equal zero.

Plotted against current FRI, the underlying distribution of the PFRID metric appears approximately linear between -99.9 percent and about +40 percent departure, but above +40 percent departure, increasingly larger leaps in current FRI are required to move the departure statistic (fig. 2), This is because the metric is actually asymptotic (see plot of PFRID against a logarithmic scale of current FRI, fig. 2 inset), owing to the behavior of the PFRID formulas, which divide presettlement FRI by current FRI in cases of positive PFRID and divide current FRI by presettlement FRI in cases of negative PFRID (Hann 2004, Hann and Strohm 2003). This property of the PFRID equations makes them particularly well suited to the analysis of fire frequency distributions where the mean and median FRIs are similar but a small number of high values results in a long tail to the right. This is not an uncommon situation with discrete data sets (Von Hippel 2005) and is the case with many of our nonmaritime forested PFRs (see fig. 1 in Van de Water and Safford 2011).

Mean and median PFRID measure the departure of current FRIs from the central tendency of presettlement FRIs, with median PFRID perhaps better representing the skewed nature of FRI distributions in some vegetation types (i.e., more short or long intervals, depending on the fire regime). Mean PFRID is the standard measure used by the Forest Service in California to spatially map contemporary departure from presettlement fire frequencies (Safford et al. 2011). Mean minimum and mean maximum (hereafter min and max) PFRIDs represent liberal and conservative estimates, respectively, of the departure of current from presettlement FRIs. Min and max PFRIDs are important variables, as they (hypothetically) provide us with approximate lower and upper bounds of sustainability/resilience for the ecosystems represented by our PFRs. Landscapes that are characterized by negative min PFRID values are burning much more frequently today than under presettlement conditions; these landscapes may have undergone or may be undergoing vegetation type conversion and should be focus areas for enhanced fire suppression and public education efforts. In contrast, landscapes that are characterized by positive max PFRID values are usually those that were historically characterized by frequent fire but have not experienced fire for a half century or more. These areas may have experienced major changes in vegetation composition and fuels and should be focus areas for fuel reduction by fire restoration or fire surrogates.

We categorized mean PFRID values into “condition classes” (CCs) (see Safford et al. 2011), where values from 0 to 33 percent and 0 to -33 percent are classified as

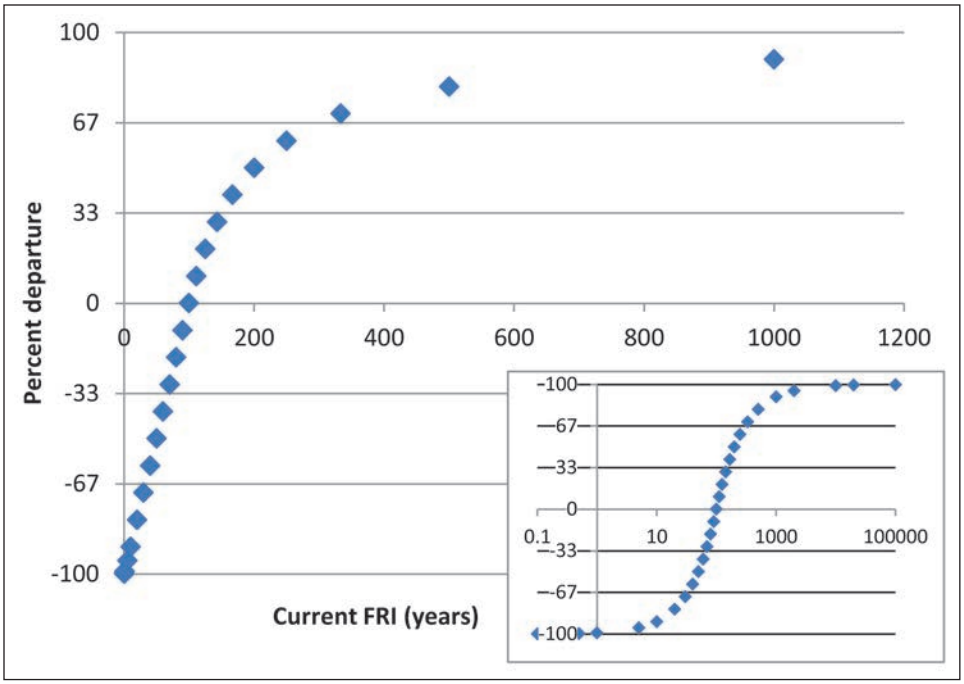


Figure 2—Percent departure versus current fire return interval (FRI) for a presettlement fire regime with a mean presettlement reference FRI of 100 years. The inset plots the departure from -99.9 percent to +99.9 percent against a Log FRI scale.

CC 1 and CC -1 ("low departure"), respectively, while values from 33 to 67 percent and -33 to -67 percent are CC 2 and CC -2 ("moderate departure"), and values greater than 67 percent and more negative than -67 percent are CC 3 and CC -3 ("high departure"). This CC categorization, which simply divides the 0 to 100-percent departure scale into thirds, was developed by the interagency Fire Regime Condition Class (FRCC) program (Hann 2004, Hann and Strom 2003). Positive CCs apply where contemporary fire frequencies are less than presettlement frequencies (Hann and Strohm 2003); negative CCs apply where contemporary fire frequencies are greater than presettlement frequencies (Safford et al. 2011).

Table 1 provides background information to help in the interpretation of the PFRID statistics. Table 1 expands on Van de Water and Safford (2011) to provide the current FRIs associated with the boundaries between the CCs for each PFR. It can be appreciated from table 1 that CC 1 and CC -1 occupy the area between current FRIs that are one-half the frequency of the presettlement FRI and 1.5 times the presettlement FRI. Condition class 2 is found in the area where current FRI is between 1.5 and three times the presettlement FRI; CC 3 is thus defined as any current FRI that is more than three times the presettlement FRI. The boundary between CCs -2 and -3 is found where current FRIs are one-third the presettlement FRIs (i.e., current fires are three times as frequent as the presettlement mean).

The fifth FRID metric we calculated was the NPS FRID index, which represents the number of intervals missed since the last fire relative to the central tendency of presettlement FRI distributions. The NPS-FRID index was calculated using the following equation:

NPS-FRID index = -[(presettlement mean FRI-TSLF)/presettlement mean FRI].

Note that the sign of the equation used in this analysis has been reversed from the original formula (see van Wagtendonk et al. 2002) to facilitate interpretation of FRID trends that is consistent with the sign of our other PFRID metrics. The NPS-FRID metrics were developed by the NPS for the southern Sierra Nevada and do not consider the cumulative fire history of each polygon, but only the time since the last fire (Caprio et al. 1997, Caprio and Graber 2000, Keifer et al. 2000, van Wagtendonk et al. 2002). The NPS-FRID metrics measure the number of presettlement FRIs missed since the first missed cycle, and are thus not helpful in identifying areas where current FRI is shorter than presettlement FRI. The NPS-FRID index values less than 0 are classified as low departure, while values from 0 to 2 are moderate, values from 2 to 5 are high, and values greater than 5 are extreme (van Wagtendonk et al. 2002). Note that the interpretive differences between the two metrics notwithstanding, the numerical boundary between moderate and high NPS-FRID (three missed fires) is equivalent to the boundary between moderate (CC 2) and high (CC 3) departure in the PFRID measure (current FRI = three times the reference FRI).

Fire return interval departure mapping products described above (including PFR, number of fires since 1908, TSLF, and all FRID values) were developed by the Forest Service's Pacific Southwest Region Ecology Program and Remote Sensing Lab (Safford et al. 2011) and are available online at http://www.fs.usda.gov/main/r5/landmanagement/gis.

To provide some geoecological context for our spatial patterns of departure, FRID GIS layers were intersected with a layer consisting of the ecological sections and subsections in California (figs. 1 and 3) (Miles and Goudey 1997). The subsection descriptions in Miles and Goudey (1997) provide information on prevalent environmental conditions in each subsection, including elevations, temperature and precipitation, soils, geology, vegetation, and human uses. The area-weighted average of TSLF and FRID values within each subsection was calculated, using only those Forest Service or analyzed NPS lands that occurred within each subsection, and then TSLF and FRID values were mapped by subsection; the section summaries in table 2 are the summed results from the subsection area-weighting and likewise represent only analyzed federal lands. We report results only for subsections that contained at least 5 percent Forest Service or NPS lands. Figure 3

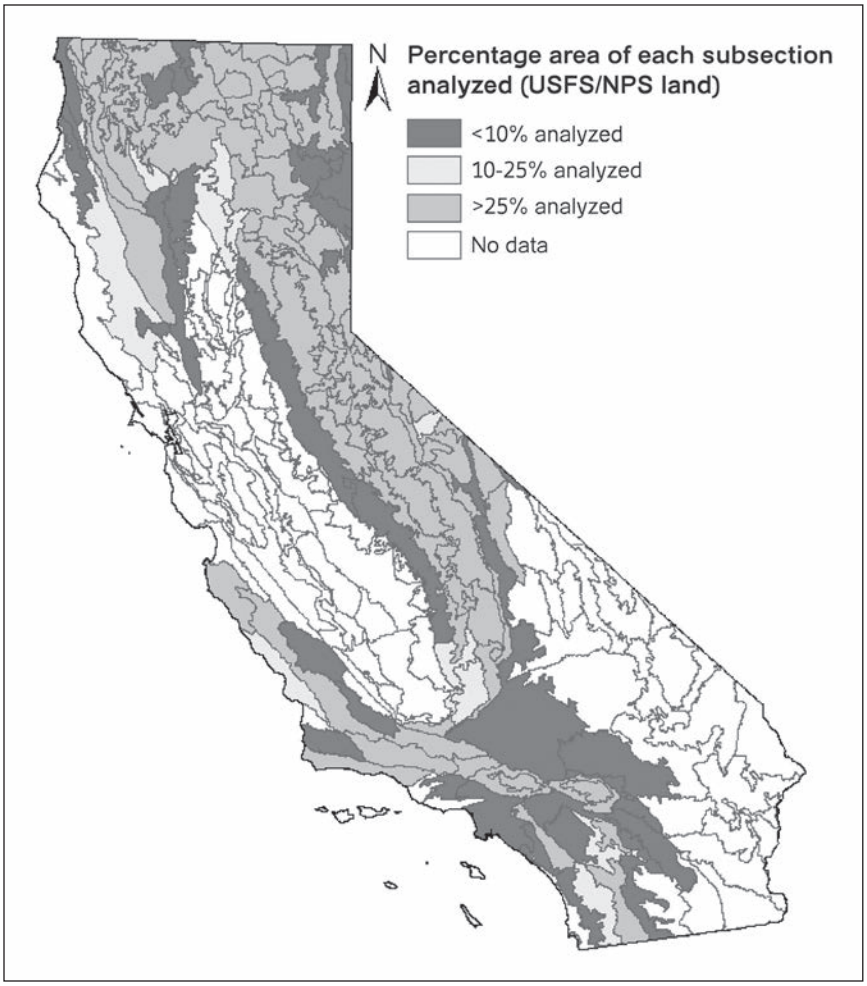


Figure 3—Ecological subsections intersecting with the national forests and national parks analyzed in this study. Dark gray subsections are those where >25 percent of the land base is found within analyzed management units; light gray = 10 to 25 percent of the land base is within analyzed management units; black = ≤ 10 percent of the land base is within analyzed management units. USFS = United States Forest Service, NPS = Natioinal Park Service.

**Table 2—Differences in time since last fire (TSLF) and fire return interval departure (FRID)[a] among ecological sections[a], averaged from subsections within the section that contains lands under Forest Service or National Park Service (NPS) (Yosemite or Sequoia-Kings Canyon National Parks) administration**

| Ecological section | Code | n | Analyzed area | Section area | Percentage of section analyzed | TSLF | Min. PFRID | Mean-PFRID | Median PFRID | Max. PFRID | NPS-FRID Index[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Hectares* | | | *Years* | | | | | |
| Central Coast | 261A | 2 | 137 055 | 1 375 722 | 10.0 | 16 | 25 | -19 | -7 | -57 | -0.6 |
| Southern Coast | 261B | 5 | 75 765 | 1 449 424 | 5.2 | 33 | 30 | -20 | -25 | -49 | -0.4 |
| Northern Coast | 263A | 3 | 11 637 | 1 722 125 | 0.7 | 101 | 85 | 71 | 83 | 18 | 3.3 |
| Mojave Desert | 322A | 3 | 26 074 | 6 683 237 | 0.4 | 79 | 16 | -1 | -4 | -17 | -0.3 |
| Colorado Desert | 322C | 1 | 229 | 1 185 242 | 0.0 | 19 | -65 | -91 | -92 | -95 | -1.0 |
| Mono | 341D | 14 | 402 040 | 798 345 | 50.4 | 98 | 65 | 39 | 39 | 8 | 1.0 |
| Southeastern Great Basin | 341F | 4 | 83 116 | 1 103 764 | 7.5 | 103 | 38 | 21 | 21 | 5 | 0.2 |
| Northwestern Basin and Range | 342B | 5 | 3 776 | 522 403 | 0.7 | 94 | 78 | 53 | 51 | 6 | 1.8 |
| Klamath Mountains | M261A | 16 | 1 755 085 | 2 256 796 | 77.8 | 77 | 84 | 67 | 79 | 10 | 3.3 |
| Northern Coast Ranges | M261B | 3 | 614 783 | 1 552 449 | 39.6 | 77 | 82 | 64 | 70 | 9 | 3.3 |
| Northern Interior Coast Ranges | M261C | 2 | 4267 | 749 443 | 0.6 | 69 | 74 | 52 | 60 | 3 | 2.3 |
| Southern Cascades | M261D | 9 | 958 842 | 1 702 525 | 56.3 | 90 | 86 | 70 | 73 | 18 | 4.6 |
| Sierra Nevada | M261E | 21 | 4 116 267 | 5 159 316 | 79.8 | 84 | 78 | 61 | 66 | 11 | 3.3 |
| Sierra Nevada Foothills | M261F | 5 | 152 857 | 1 819 108 | 8.4 | 58 | 62 | 31 | 39 | -18 | 1.8 |
| Modoc Plateau | M261G | 11 | 711 801 | 1 430 882 | 49.8 | 90 | 75 | 51 | 56 | 13 | 2.9 |
| Central Coast Ranges | M262A | 3 | 190 822 | 2 485 244 | 7.7 | 22 | 0 | -41 | -45 | -63 | -0.6 |
| Southern Mountains and Valleys | M262B | 16 | 1 193 734 | 2 755 093 | 43.3 | 43 | 34 | -6 | -5 | -40 | 0.3 |

n = Number of analyzed ecological subsections within each section.

[a] Percentage fire return interval departure (PFRID) data are read as percentage departure.

[b] Sign of NPS-FRID Index values reversed to allow consistent interpretation with other FRID measures.

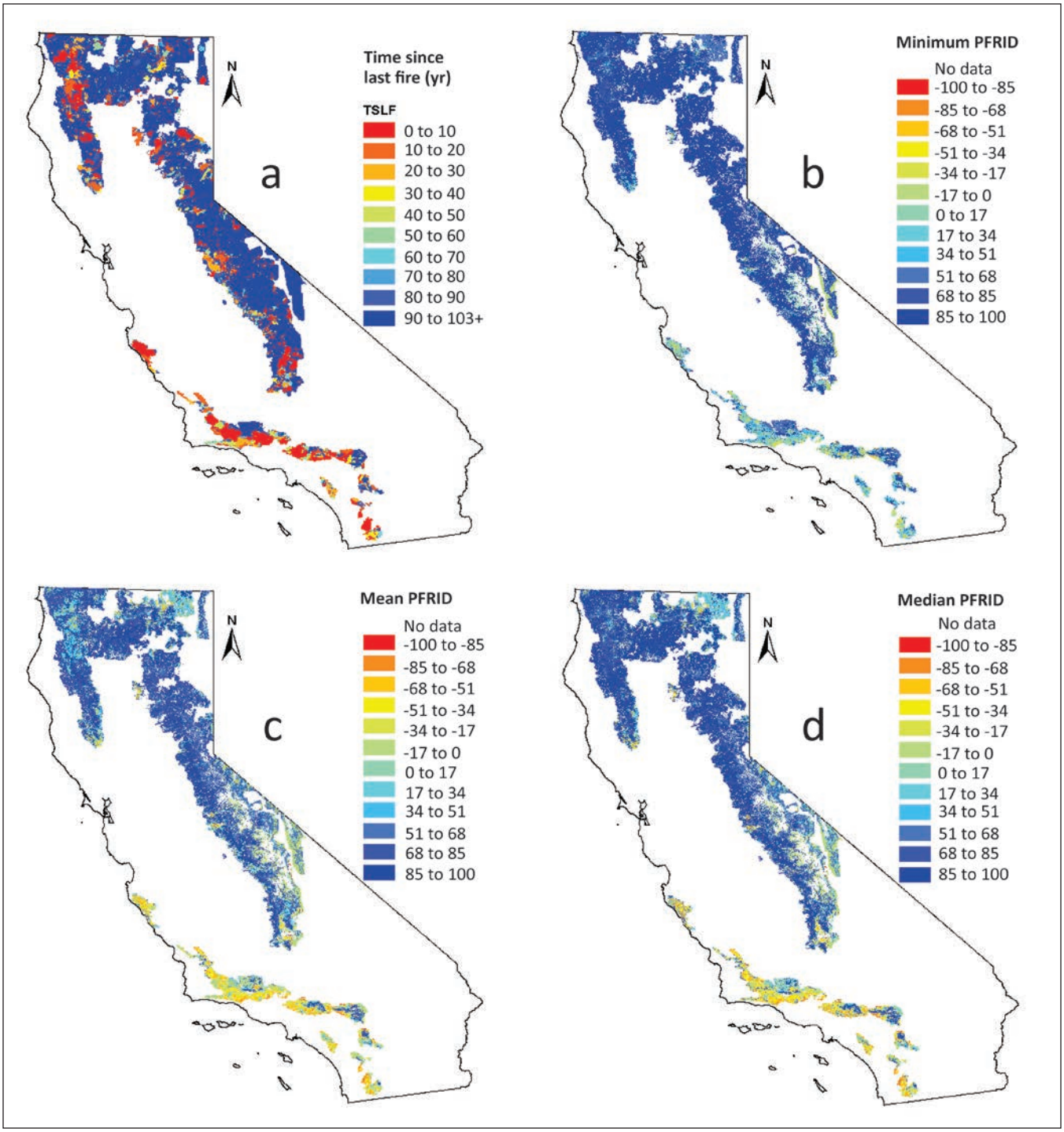


Figure 4—Time since last fire and the five fire return interval departure metrics for federal lands analyzed in this study. Negative percent FRID (PFRID) measures (warm colors) identifies places where current fire return interval (FRI) is shorter than the presettlement FRI; positive PFRID (cool colors) identifies places where current FRI is longer than the presettlement FRI. The PFRID measures are grouped into categories that approximately correspond to the standard condition classes from Hann and Strohm (2003) (see "Methods"). For the National Park Service FRID Index, see "Methods" for interpretation of the index values.

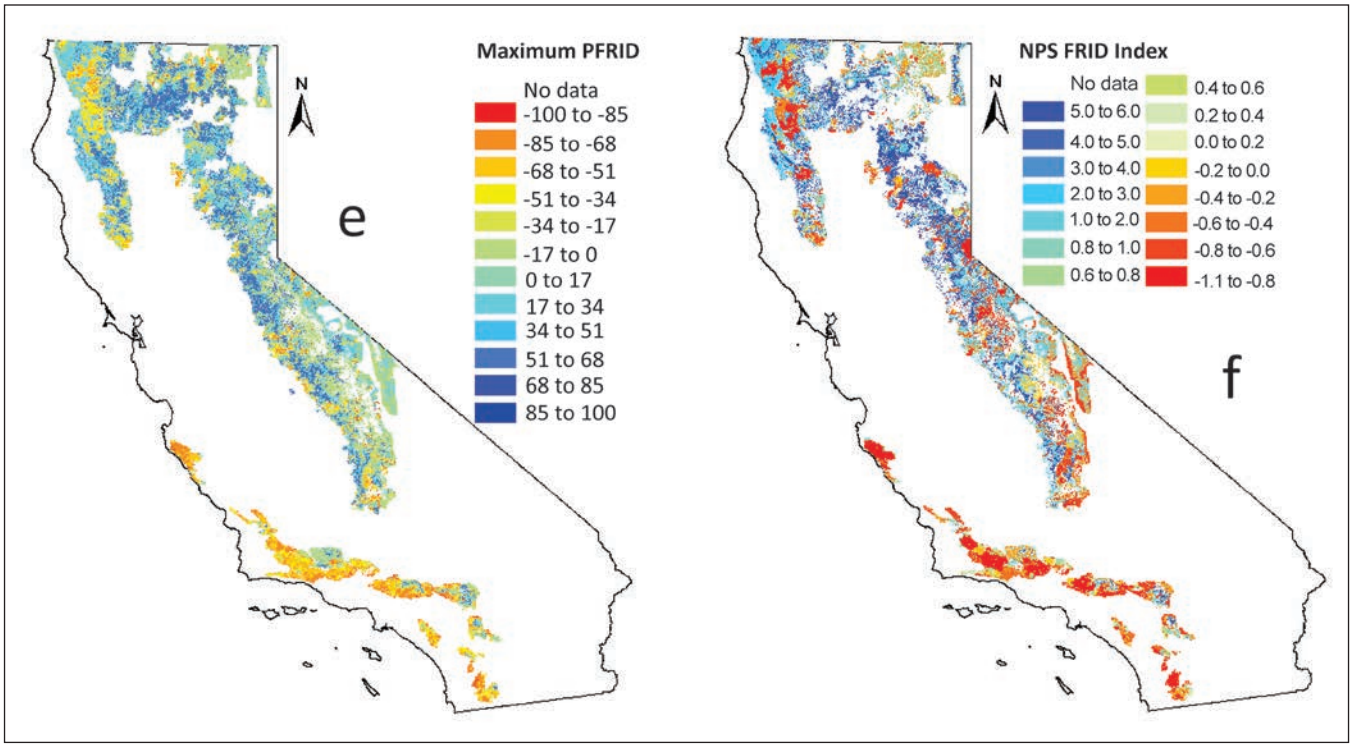


Figure 4—Continued.

identifies those ecological subsections where these federal lands account for < 25 percent and < 10 percent of subsection area. Be careful to avoid overinterpretation of our results in these subsections.

We selected those ecological subsections with the highest positive departure (greater than 17 percent departure, n = 25; the "P" group) as determined by max PFRID (see fig. 4), and those subsections with the most negative departure (more than 33 percent negative departure, n = 17; the "N" group), and used data from Miles and Goudey (1997) to characterize each of the 42 subsections with respect to lowest elevation, mean annual precipitation (from the range given); low mean annual temperature; high mean annual temperature; mean annual frost-free period in days (from the range given); dominant precipitation type (rain = 1, snow = 2, mix = 1.5); soil temperature (thermic = 4, mesic = 3, frigid = 2, cryic = 1; intermediate values given for mixes); and soil moisture (udic = 3, xeric = 2, aridic = 1; intermediate values given for mixes). Each of the 42 subsections was assigned a predominant pre-Euro-American settlement FRI using the predominant vegetation types described by Miles and Goudey (1997) and crosswalking these to the PFRs in Van de Water and Safford (2011). We also assigned each subsection a human

population density from the California county that the subsection was found in; in cases of multiple counties, we averaged the densities (data from http://www.csac.counties.org/). The above data were entered into a Principal Components Analysis (PCA) ordination using PC-ORD v. 5 (McCune and Mefford 2006). Before analysis, the input data were relativized by their maximum values. Monte Carlo permutations of the data were carried out 1,000 times in order to calculate correlations of the environmental data with the ordination axes. We also statistically compared the P and N group means for the environmental and population data listed above using the univariate nonparametric Mann-Whitney U test.

In the southern Sierra Nevada, we compared differences in FRID between three large national parks (Yosemite, Sequoia, and Kings Canyon, all of which include large areas where naturally ignited fires are allowed to burn for ecological benefit) and the five adjacent national forests by calculating the area-weighted average of TSLF and FRID values in the two jurisdictions.

Elevational trends in departure were explored using the zonal statistics function of ArcGIS 9.3 (ESRI 2008), which averaged the TSLF and FRID values of all cells of identical elevation in a 100-m digital elevation model. Trends in departure along precipitation, mean, minimum, and maximum temperature gradients were also explored using zonal statistics on averaged annual PRISM climate normal grids, 1971–2000 (PRISM Group 2004).

## Results

### Geographic Patterns

Geographic patterns of FRI departure on the analyzed Forest Service and NPS lands generally showed positive FRID and longer TSLF in NW California and Sierra Nevada, and negative FRID and shorter TSLF in southern California; trends were relatively consistent across all metrics (table 2, figs. 3 through 6). TSLF strongly reflected the fire seasons of 2003 and 2005–2008 and resulted in very low departure according to the NPS-FRID Index (which is based only on the most recent fire) for much of southern California and scattered portions of the North Coast Ranges, Klamath Mountains, and Sierra Nevada (figs. 4a–4f).

The PFRID measures, which consider fire history across the entire 103-year study period, were much less affected by recent fire seasons (figs. 4b–4e). Min PFRID, which is based on the mean minimum presettlement FRI for the mapped PFRs (Van de Water and Safford 2011), classified most of the study area at high positive departure (fig. 4b). Lower elevation PFRs in the southern California national forests were an exception: some areas in the southern California foothills

mapped as high negative departure even using the min PFRID measure, which means they have burned much more frequently over the last century than during any comparable (average) presettlement period in our reference period. Mean and median PFRID were nearly indistinguishable: both showed very high positive departure from presettlement fire frequencies throughout most of NW California and the Sierra Nevada (with some exceptions of low to moderate departure in the central Klamath Mountains, parts of the Modoc Plateau, and the southeastern Sierra Nevada), and a belt of moderate to high negative departures through most of lower and middle elevation southern California (figs. 4c–4d). Max PFRID, based on the mean maximum presettlement FRI, is a more conservative measure of departure for places that are lacking fire and a more liberal measure for places that are seeing much more fire (fig. 4e). Places identified as high positive departure using max PFRID have missed a greater than average number of fire cycles; these tended to be centered in the eastern Klamath Mountains, the southern Cascades, and middle elevations in the main Sierra Nevada. As would be expected, most of southern California is mapped as very large negative departure using the max PFRID measure (fig. 4e).

Figure 5 compares the three major geographic regions by the proportion of area in Forest Service and (in the Sierra Nevada) NPS jurisdiction that falls in each of the CCs, based on the standard mean PFRID measure. It can be readily seen how different southern California is from the northern California regions. Forty-three percent of Forest Service lands in southern California are burning more (CC -2) or much more (CC -3) frequently currently than under the pre-Euro-American settlement fire regime; only 2 percent of the Sierra Nevada and 1 percent of NW California lands fall into this category (fig. 5). About one-third of southern California falls into CCs 1 and -1, within +/- 33 percent of the presettlement mean fire frequency, versus 16 percent in the Sierra Nevada and 9 percent in NW California. More than 85 percent of Forest Service lands in NW California is burning either less frequently (CC 2) or much less frequently (CC 3) currently than under presettlement conditions, compared with 67 percent of Forest Service and NPS lands in the Sierra Nevada and 19 percent in southern California.

Table 2 averages results of the area-weighting procedure among the ecological sections (see fig. 1 for map); figure 6 portrays the geographic results by ecological subsection for mean and max PFRID. After rounding, only seven ecological sections contained more than 40 percent Forest Service or NPS lands (table 2). It is important to remember that our results summarized by ecological units (sections and subsections) are only valid for the Forest Service and NPS lands within those units. As noted above, the highest positive FRID values were consistently on Forest

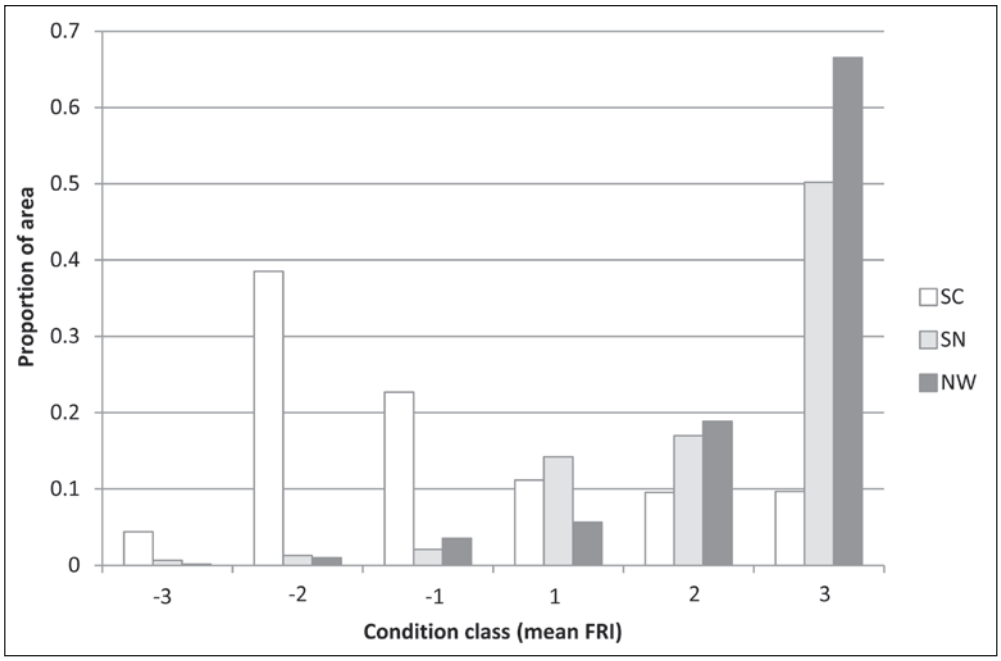


Figure 5—Proportion of total analyzed area in the three geographic regions falling into each of the six condition classes (CCs). Negative CCs represent places where the current fire return interval (FRI) is shorter than the presettlement FRI; positive CCs identify places where current FRI is longer than the presettlement FRI. SC = Southern California, SN = Sierra Nevada, NW = Northwestern California.

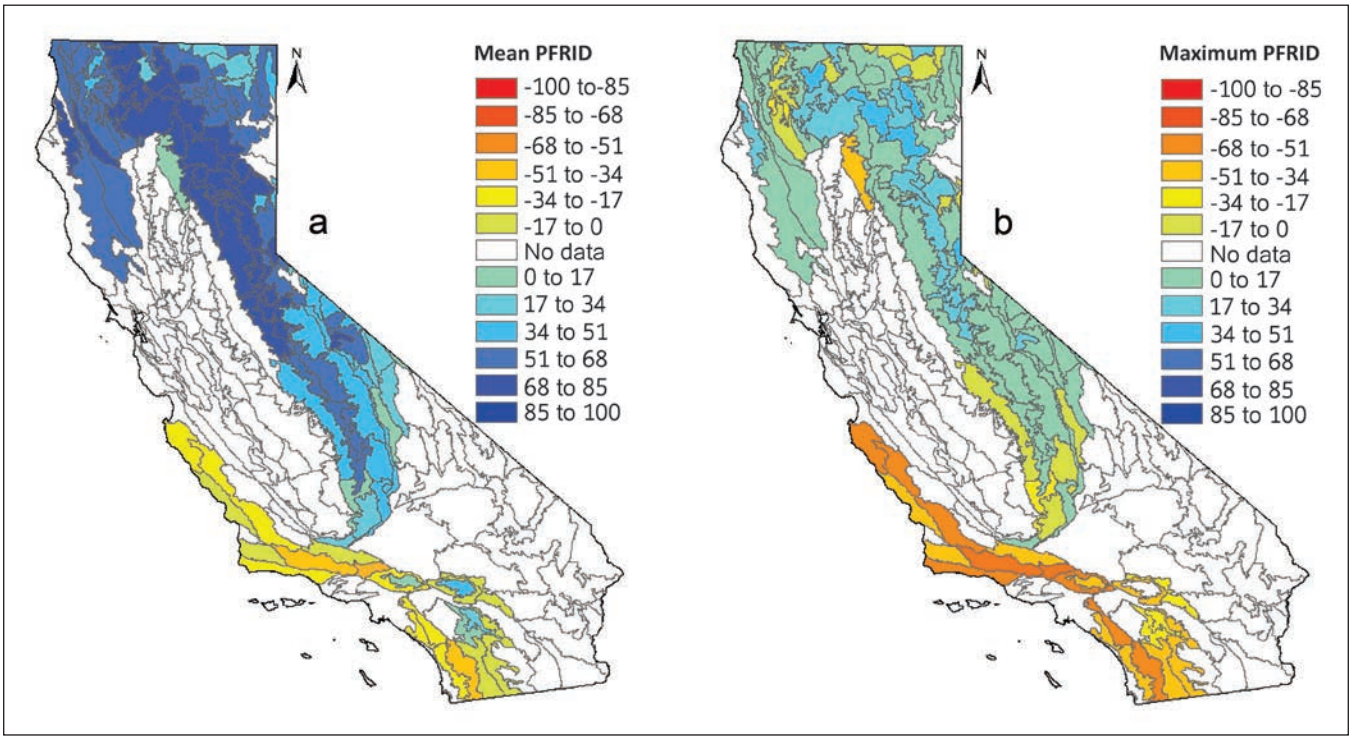


Figure 6—Mean and max percent fire return interval departure (PFRID), with the results of figure 4 extrapolated to the ecological subsection boundaries (Miles and Goudey 1997). See figure 3 for percentages of subsections analyzed; in this figure, subsections with < 5 percent analyzed land have been removed.

Service lands in the eastern Klamath Mountains and the southern Cascades (fig. 6). Mean TSLF averaged 68 years, ranging from 16 years in the Central Coast Ecological Section to 103+ years in the Southeastern Great Basin Section (table 2). The min PFRID measure averaged 50 and ranged from -65 in the very small area of Forest Service land in the Colorado Desert Section to 86 in the Southern Cascades Section (table 2). Mean PFRID averaged 24 across the analyzed subsections, which is high CC 1. Mean PFRID varied from -91 in the Colorado Desert Section to 70 in the Southern Cascades and 71 in the North Coast Section (table 2, fig. 6a). The median PFRID measure averaged 27 and varied from -92 in the Colorado Desert Section to 83 in the North Coast Section (table 2). Max PFRID averaged -14, and ranged from -95 in the Colorado Desert Section to 18 in the Northern Coast and Southern Cascades Sections (table 2, fig. 6b). The NPS-FRID index averaged 1 (moderate departure), ranging from -1.0 in the Colorado Desert Section to 4.6 in the Southern Cascades Section; many northern California Sections fell between 2.9 and 3.3, which fall in the "high" departure category (table 2).

The results of the Principal Components Analysis (PCA) on the subsection environmental data are shown in figure 7. Axis 1 explained 51.3 percent of the variance in the data matrix, axis 2 explained 17.8 percent, and axis 3 explained 11 percent. The subsections supporting strongly positive FRIDs (as determined using max PFRID) were clearly segregated from the subsections supporting strongly negative FRIDs. Of the 25 subsections in the positive FRID (P) group, all but three were from NW California and the Sierra Nevada (the exceptions being P23–25, which are the Upper San Gabriel, Upper San Gorgonio, and San Jacinto Mountains in southern California). Of the 17 subsections in the negative FRID (N) group, all but one (N17—Tuscan Flows [Miles and Goudey 1997]) were from southern California. Along axis 1, all but one of the subsections in the N group were clustered to the right of the ordination center; all but three of the subsections in the P group were grouped to the left of center (fig. 7). Axis 1 was most strongly correlated with environmental variables related to temperature and elevation, with the warmest and lowest subsections (excepting P6) all in the N group. The most strongly correlated variables with axis 1 were: high mean temperature ($r = 0.924$); lowest elevation ($r = -0.919$); and mean frost-free period ($r = 0.894$). Soil temperature was a categorical variable and an $r$ value could not be determined, but it was the most closely associated variable with axis 1. Axis 2 was most closely correlated with moisture (mean annual precipitation [$r = -0.745$] and soil moisture [categorical variable]) and presettlement FRI ($r = 0.542$). Along axis 2, the P subsections were evenly distributed above and below the ordination center, but most of the N sites were near or below the center (i.e., N sites tend to be drier and support longer presettlement

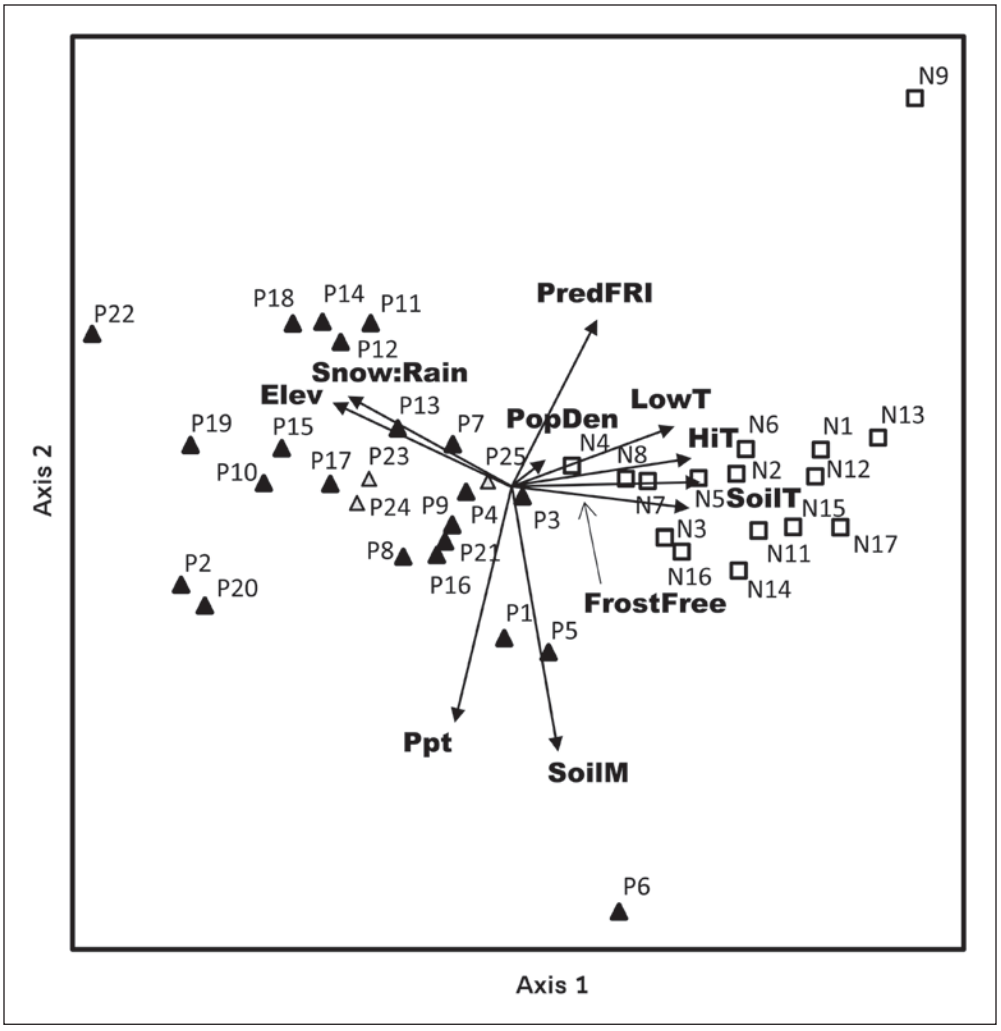


Figure 7—Principal Components Analysis ordination of highly positively ("P," triangles) and highly negatively departed ("N," squares) subsections (see "Methods"). The gray triangles are three southern California sites belonging to the P group.

FRIs). Population density was correlated with axis 3 at $r = 0.960$, which was the strongest correlation overall between the environmental variables and any axis; the arrow representing population density in the ordination diagram seems very short because the effect of population density is nearly orthogonal to axes 1 and 2. Along axis 3, the N sites were characterized by high population densities (and are in the distance along axis 3) and the P sites (which are nearer to the observer along axis 3) by low population densities (fig. 7).

We compared the means for the environmental data entered into the PCA for the N and P groups using Mann-Whitney U tests. The results are shown in figure 8. Based on figures 7 and 8 and Miles and Goudey (1997), we can describe the P group as predominantly northern California (plus a few small areas

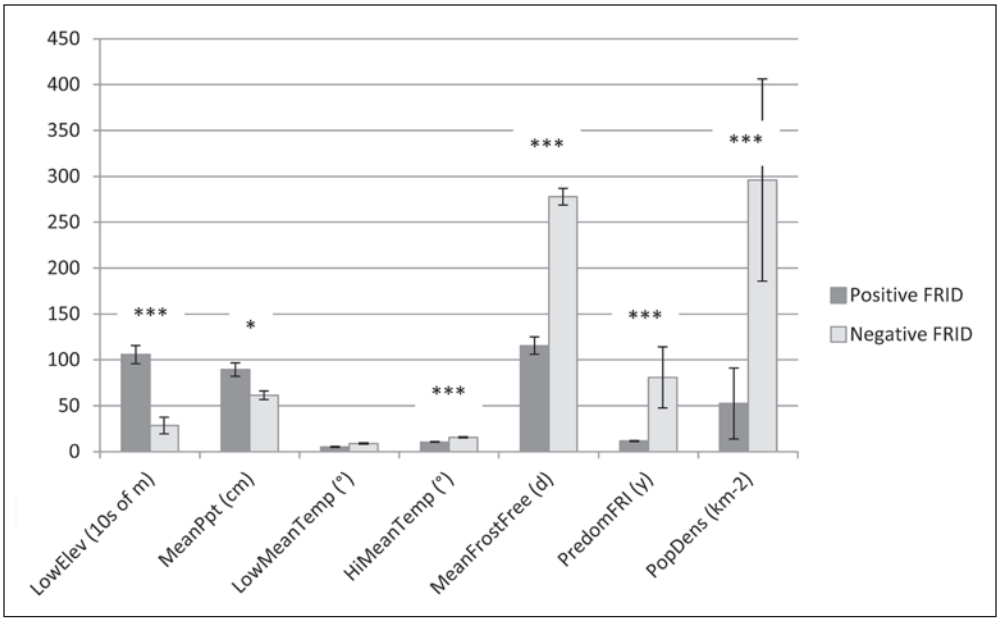


Figure 8—Means comparisons for six environmental variables and human population density between the positive (P) and negative (N) subsection groups from the Principal Components Analysis ordination. LowElev = lowest listed elevation; MeanPpt = mean annual precipitation; LowMeanTemp = lowest listed mean annual temperature; HiMeanTemp = highest listed mean annual temperature; MeanFrostFree = mean length of annual frost free period, in days; PredomFRI = mean presettlement fire return interval (FRI) for the predominant vegetation type in the subsection; PopDens = mean human population density. See "Methods" for data sources. Comparison made with nonparametric Mann-Whitney U-test; * = significantly different at $P < 0.05$; *** = significantly different at $P < 0.001$.

of high-elevation southern California); higher elevation, wetter and cooler, with most precipitation arriving as snow; growing season of 3 to 4 months; conifer forest-dominated vegetation with short presettlement FRIs; mesic to frigid soil temperature regime; and in areas of low population density. The N group can be characterized as predominantly southern California; lower elevation, warmer and drier, with precipitation arriving as rain; growing season of 8 to 10+ months; shrub-dominated vegetation with longer presettlement FRIs; thermic to mesic soil temperature regime; and in areas of high population density.

## Differences Among Management Units

Using mean PFRID and considering only those lands for which FRID was calculated (i.e., ignoring barren and rocky areas, lakes, herbaceous vegetation, etc.), the percentage of lands with negative FRI departures (CC -2 and -3) vs. lands within 33 percent of the mean presettlement FRI (CC -1 and 1) vs. lands with positive FRI departures (CC 2 and 3) is different in the three Sierra Nevada national parks (2, 30, and 68 percent) compared to Forest Service-managed lands in the Sierra Nevada (2, 18, and 80 percent). If only the five national forests adjacent to the parks

are compared, however (Humboldt-Toiyabe, Inyo, Stanislaus, Sierra, and Sequoia NFs), the national forest percentages are very similar to the national parks (3, 27, and, 70 percent). Most other measures of fire frequency departure in the neighboring national forests are also relatively similar (table 3). Average TSLF is lower in the national parks, although Sequoia NF has the lowest overall TSLF (table 3). The NPS-FRID index is in the "moderate" range (0-2) in the national parks, while the national forests average in the "high" range of departure. Two national forests with large areas of high-elevation wilderness (Inyo and Humboldt-Toiyabe) also fall in the low range (table 3).

Table 3 also highlights the strong differences between NW California plus Sierra Nevada and southern California. The average TSLF in southern California is less than half of the value in the other two regions, and the average PFRID values are all negative in southern California, compared to highly positive numbers in NW California and the Sierra Nevada. The extensive 2008 fires result in a lower TSLF in NW California than the Sierra Nevada, but Min, Mean, and Median PFRID and the NPS-FRID index are all lower in the Sierra Nevada. Averaged across all national forest land, NW California is the region with the greatest FRI departures, but the individual national forest units with the greatest departures are found in the central and northern Sierra Nevada (table 3).

We can also compare management units on the basis of the CC measures derived from mean PFRID. On three national forests in the Sierra Nevada (Lassen, Plumas, and Tahoe), over 70 percent of the landscape falls in CC 3, which is to say that on 7/10 of these lands there has been a greater than 67 percent decrease in fire frequency (i.e., at least three FRIs have been missed) over the last century as compared to the pre-Euro-American settlement period (fig. 9a). The Shasta-Trinity NF in NW California is nearly as extreme. In terms of overall area, the Shasta-Trinity is the only management unit with over 500 000 ha of CC 3 lands; the Klamath, Lassen, Plumas, and Six Rivers NFs all manage more than 300 000 ha of CC 3 lands (fig. 9b).

The lowest percentage and area of CC 3 lands are found in the shrub and hardwood-dominated southern California national forests. At the same time, these four national forests (Angeles, Cleveland, Los Padres, and San Bernardino) contain the only substantial areas of negative CCs (where fire frequencies are currently greater than in presettlement conditions) in California (figs. 4, 6, and 9). In management units dominated by conifer forests, only Yosemite and Sequoia-Kings Canyon National Parks and the Inyo NF have less than one-third of their area in CC 3. Three other national forests in the Sierra Nevada region (Sequoia, Sierra, and Modoc) are 40 to 44 percent CC 3 (fig. 9).

**Table 3—Differences in time since last fire (TSLF) and fire return interval departure (FRID) measures between national park (NP) and adjacent national forest (NF) lands in the southern Sierra Nevada, followed by TSLF and FRID measures for the remaining NFs analyzed**

| Unit | TSLF | Min PFRID | Mean PFRID | Median PFRID | Max PFRID | NPS-FRID Index[a] | Analyzed area[b] | |
|---|---|---|---|---|---|---|---|---|
| | *Years* | | | | | | *Hectares* | |
| National parks: | | | | | | | | |
| Sequoia-Kings Canyon NPs | 80 | 60 | 43 | 48 | -2 | 1.3 | 222 045 | |
| Yosemite NP | 77 | 70 | 51 | 57 | 1 | 1.7 | 237 318 | |
| National park mean | 78 | 65 | 47 | 52 | -1 | 1.5 | 459 363 | Total |
| Adjacent national forests: | | | | | | | | |
| Humboldt-Toiyabe NF | 91 | 73 | 50 | 50 | 7 | 1.9 | 339 646 | |
| Inyo NF | 98 | 55 | 35 | 35 | 7 | 1.0 | 766 030 | |
| Sequoia NF | 71 | 71 | 46 | 51 | -1 | 2.3 | 538 316 | |
| Sierra NF | 89 | 71 | 56 | 63 | 10 | 3.4 | 529 756 | |
| Stanislaus NF | 81 | 83 | 68 | 74 | 17 | 4.2 | 395 477 | |
| Adjacent national forest mean | 87 | 68 | 49 | 52 | 8 | 2.4 | 2 569 225 | Total |
| Northwest (NW) California: | | | | | | | | |
| Klamath NF | 82 | 83 | 65 | 74 | 11 | 3.6 | 803 959 | |
| Mendocino NF | 73 | 79 | 60 | 64 | 6 | 3.3 | 435 526 | |
| Shasta-Trinity NF | 81 | 87 | 73 | 80 | 17 | 4.3 | 1 219 109 | |
| Six Rivers NF | 79 | 82 | 63 | 79 | 4 | 2.4 | 546 924 | |
| NW California mean | 80 | 84 | 67 | 76 | 11 | 3.6 | 3 005 517 | Total |
| Southern California: | | | | | | | | |
| Angeles NF | 34 | 27 | -16 | -14 | -50 | 0.0 | 264 271 | |
| Cleveland NF | 31 | 23 | -21 | -22 | -52 | -0.2 | 221 536 | |
| Los Padres NF | 35 | 33 | -13 | -11 | -45 | -0.2 | 753 572 | |
| San Bernardino NF | 56 | 46 | 13 | 15 | -24 | 1.1 | 310 261 | |
| Southern California mean | 39 | 33 | -9 | -8 | -43 | 0.1 | 1 549 640 | Total |
| Sierra Nevada: | | | | | | | | |
| El Dorado NF | 91 | 90 | 76 | 82 | 22 | 4.8 | 325 558 | |
| Modoc NF | 89 | 75 | 50 | 55 | 11 | 2.9 | 835 343 | |
| Lassen NF | 86 | 87 | 72 | 76 | 17 | 4.4 | 609 661 | |
| Plumas NF | 79 | 91 | 77 | 82 | 16 | 4.4 | 559 398 | |
| Tahoe NF | 86 | 89 | 75 | 80 | 16 | 4.4 | 447 880 | |
| Lake Tahoe Basin management unit | 99 | 83 | 71 | 74 | 23 | 4.0 | 53 218 | |
| Sierra Nevada mean[c] | 87 | 77 | 59 | 63 | 12 | 3.2 | 5 400 282 | Total |

PFRID = percentage of FRID.

[a] Sign of NPS FRID values reversed for consistent interpretation.

[b] Areas refer only to lands for which FRID was calculated, i.e., they exclude rocky and barren areas, herbaceous vegetation, lakes, etc.

[c] Sierra Nevada means values and local area calculated from 11 Sierra Nevada region forests.

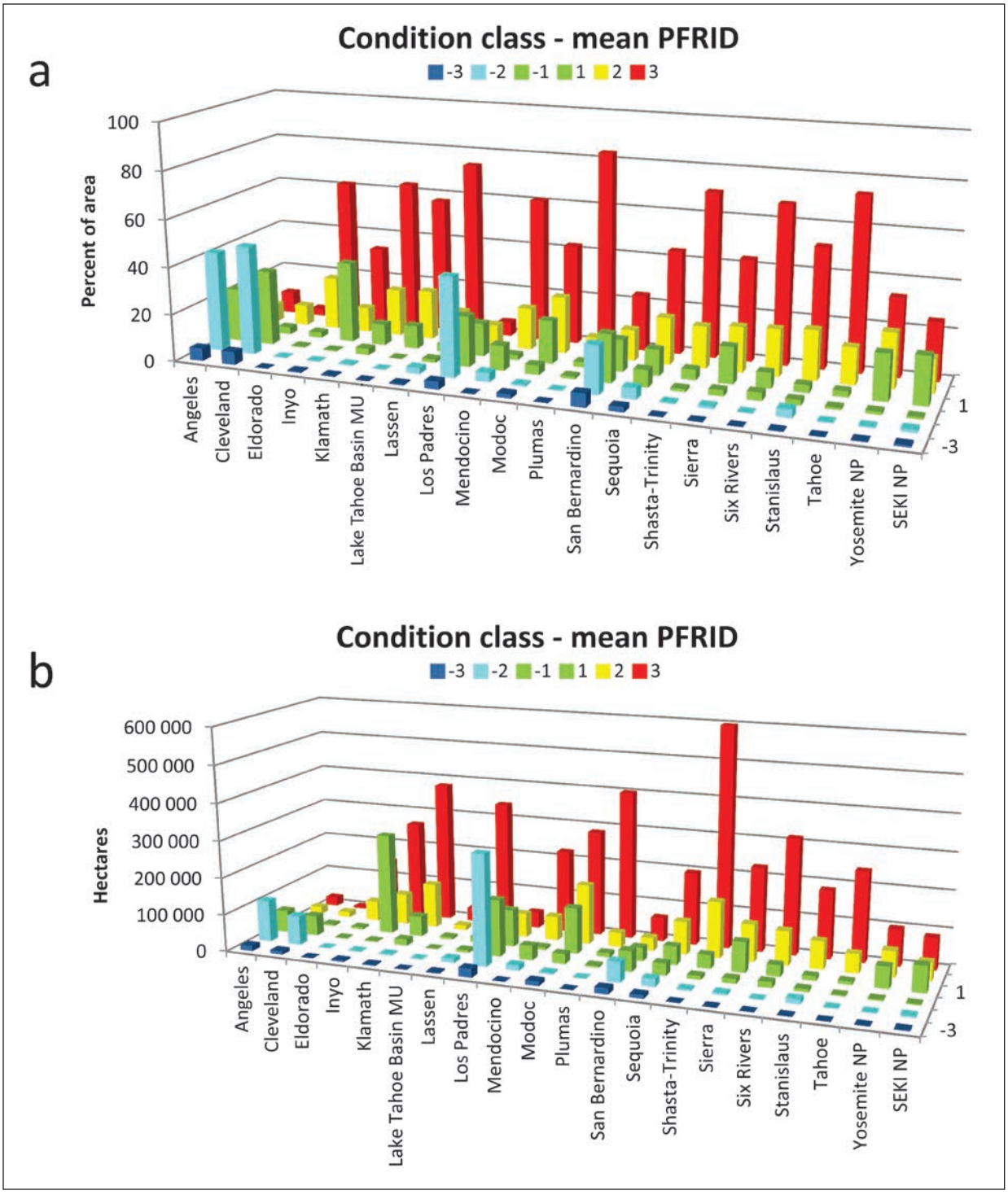


Figure 9—Comparison of condition class (CC) measures (from the mean percent fire return interval departure [PFRID] metric) for the 18 California national forests managed by the Pacific Southwest Region, and Yosemite and Sequoia-Kings Canyon National Parks (NPs); (a) percentage of area; (b) total area. Total area of each management unit includes lands not in woody vegetation (grassland and meadows, barren lands, rocks, etc.), so totals do not add up to 100 percent. Colors are reversed from figures 3 and 5 to correspond to the nationally standard color scheme for CCs 1 through 3 (green-yellow-red).

## Elevational Trends

Above 700 m, TSLF rose in all three regions when plotted against elevation (fig. 10). Fire return interval departure measures were mostly unimodally related to elevation, but they rose over most of the elevational gradient in southern California, and dropped over the upper half of the gradient in NW California and the Sierra Nevada. In NW California, the 100-m moving average of TSLF decreased as elevation increased from sea level to 400 m, then increased again at higher elevations (fig. 10a). The 100-m moving averages of mean, median, min, and max PFRID and the NPS-FRID index rose slightly between sea level and 1500–1700 m, then decreased to a minimum at 2900 m. Mean, median, and min PFRID, and NPS-FRID index remained largely positive over the entire elevational range, while max PFRID transitioned from positive to negative at approximately 2400 m. In the Sierra Nevada, TSLF decreased between sea level and 700 m, then increased again at higher elevations (fig. 10b). Mean, median, min, and max PFRID, and the NPS-FRID index decreased between sea level and 700 m, increased until 1750 m, then decreased to a minimum at 3700 m. Mean, median, and min PFRID remained positive over the entire elevation range, while max PFRID was negative from 450 m to 1000 m, and the NPS-FRID index was negative from 3050 m to 3700 m. As elevation increased in southern California, TSLF decreased from sea level to approximately 700 m, then increased again at higher elevations (fig. 10c). Mean, median, min, and max PFRID, and the NPS-FRID index also decreased between sea level and approximately 750 m, then increased to a maximum at around 2500 m before decreasing again. Mean and min PFRID remained largely positive over most of the elevational range. Median PFRID transitioned from negative to positive at approximately 1400 m, max PFRID transitioned at 1800 m, and the NPS-FRID index transitioned at 1600 m.

Using the standard mean PFRID measure as an index of central tendency, the southern California landscape is mostly in CC 2 from about 1500 m to 2900 m elevation (fig. 10c). Averaged across the NW California area, mean PFRID remained above CC 1 throughout the elevational profile until about 2200 m; mean PFRID was in CC 3 between 1200 and 1800 m elevation (fig. 10a). In the Sierra Nevada, mean PFRID showed similar patterns to NW California: it was greater than CC 1 throughout the elevational gradient and in CC 3 between 1600 and 2000 m. Mean PFRID fell to CC 1 values above about 2700 m (fig. 10b). The NPS-FRID index never reached “high” (>2) values in southern California, was >2 between 1000 and 1600 in NW California, and >2 between 900 and 2200 m in the Sierra Nevada.

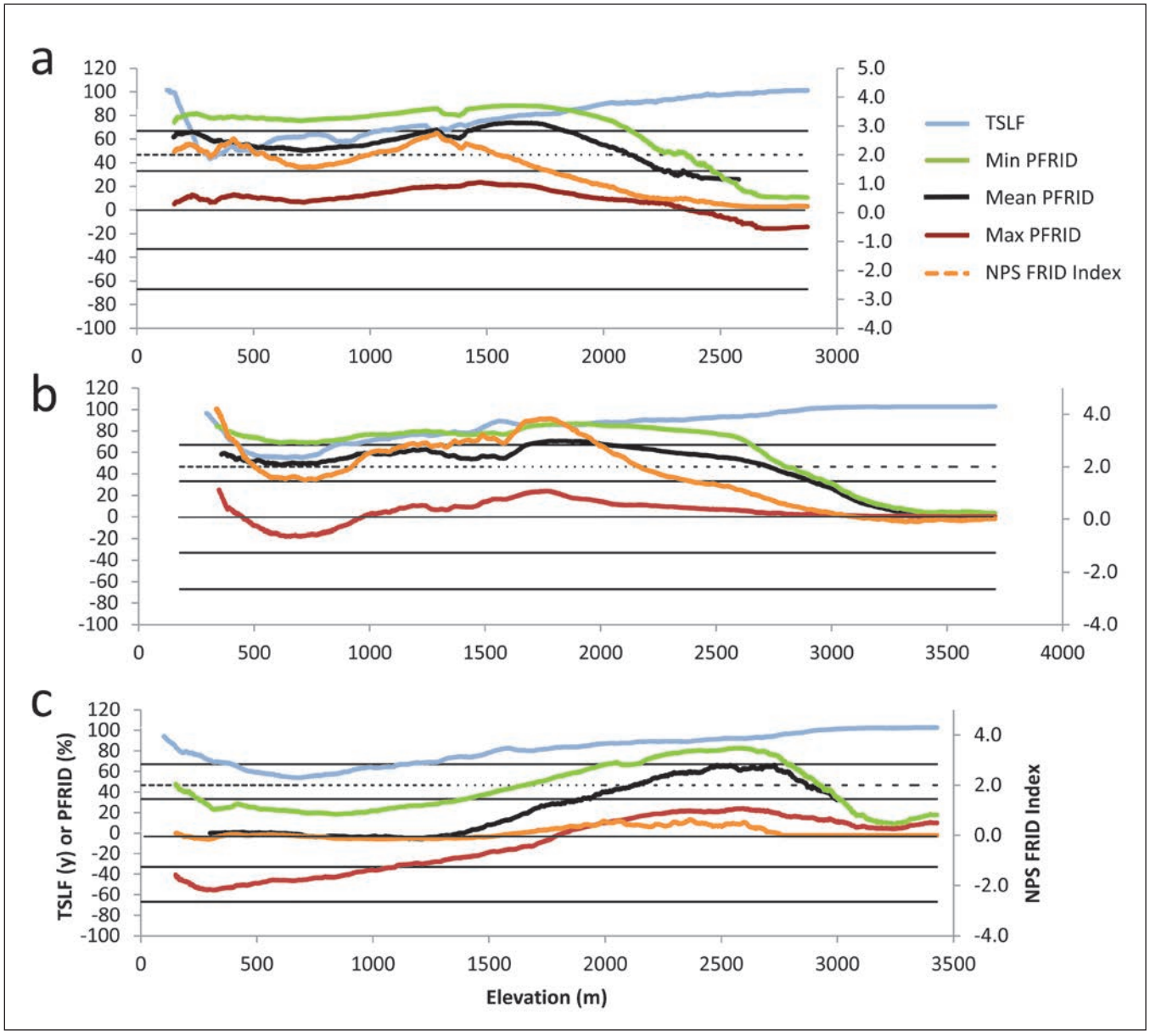


Figure 10—100-m moving averages of time since last fire (TSLF) and fire return interval departure (FRID) versus elevation in (A) northwest California region, (B) Sierra Nevada region, and (C) southern California region. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. For figures 10 through 14, solid horizontal reference lines are provided for PFRID values of -67 (transition from CC -2 to CC -3), -33 (CC -1 to CC -2), +33 (CC 1 to CC 2), and +67 (CC 2 to CC 3). Dotted reference line refers to the National Park Service (NPS) FRID Index value of 2, which is the transition from "moderate" departure to "high" departure.

## Precipitation Trends

The TSLF in NW California fluctuated considerably but generally increased with increasing annual precipitation, from 55 years at 25 cm to 103+ years at 420 cm (fig. 11a). As precipitation increased in the Sierra Nevada, TSLF decreased between 10 and 85 cm, increased until 130 cm, decreased until 250 cm, and then increased to a maximum at 300 cm (fig. 11b). Annual precipitation had little relationship to the different FRID measures in either NW California or the Sierra Nevada. In both regions, most FRID measures rose almost imperceptibly across the precipitation gradient (except below 50 cm), although max PFRID decreased gradually with precipitation in NW California. The TSLF and the FRID measures in southern California decreased with precipitation, except between 50 and 100 cm, where they leveled off (fig. 11c). Mean PFRID decreased as precipitation increased from 20 to 50 cm, rose slightly to 100 cm, and then dropped again; the NPS-FRID index stayed near zero, except at the highest precipitation values. Min PFRID remained positive over the entire precipitation gradient, whereas max PFRID remained negative.

In both NW California and the Sierra Nevada, mean PFRID tracked the boundary between CC 2 and 3 across most precipitation values. In southern California, areas with precipitation over 110 cm generally fell in the CC 1 to CC -1 belt (within +/-33 percent of presettlement fire frequency) (fig. 11).

## Temperature Trends

Fire return interval departure trends with temperature in NW California and the Sierra Nevada were broadly similar. In both regions, FRID measures were (generally) low at low temperatures, gradually rose to a maximum, then gently declined (figs. 12 and 13). In both regions, the maximum departure between contemporary and presettlement fire frequency was generally reached between -4 and -2 °C mean minimum temperatures, 9 to 11 °C mean temperatures, and 25 to 27 °C mean maximum temperatures. In the Sierra Nevada, a rise in all of the FRID values also occurred again at the highest temperatures (fig. 13). In NW California, mean PFRID exceeded CC 1 along most of the temperature gradient, beginning at about -7 °C mean minimum temperature, 4 °C mean temperature, and 19 °C mean maximum temperature (fig. 12). In the Sierra Nevada, mean PFRID exceeded CC 1 above -10 °C mean minimum temperature, 3 °C mean temperature, and 19° mean maximum temperature; it fell back within CC 1 above 4 °C mean minimum temperature.

In southern California, FRID measures rose with increasing temperature until approximately -6 °C mean minimum temperature, 7 °C mean temperature, and 25 °C mean maximum temperature (fig. 14). Thereafter all measures dropped strongly

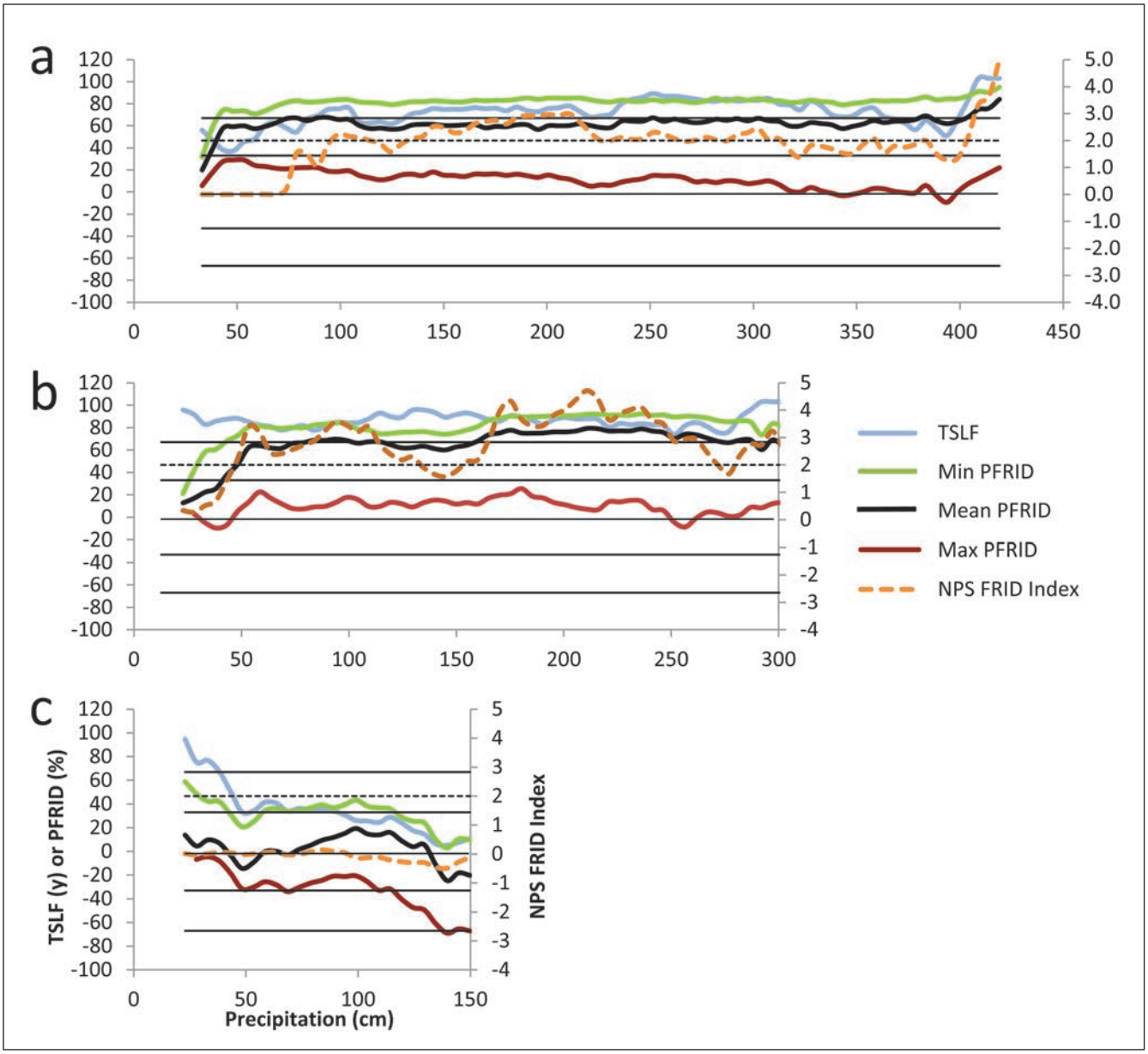


Figure 11—Time since last fire (TSLF) and fire return interval departure (FRID) versus precipitation in (A) northwest California region, (B) Sierra Nevada region, and (C) southern California region. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

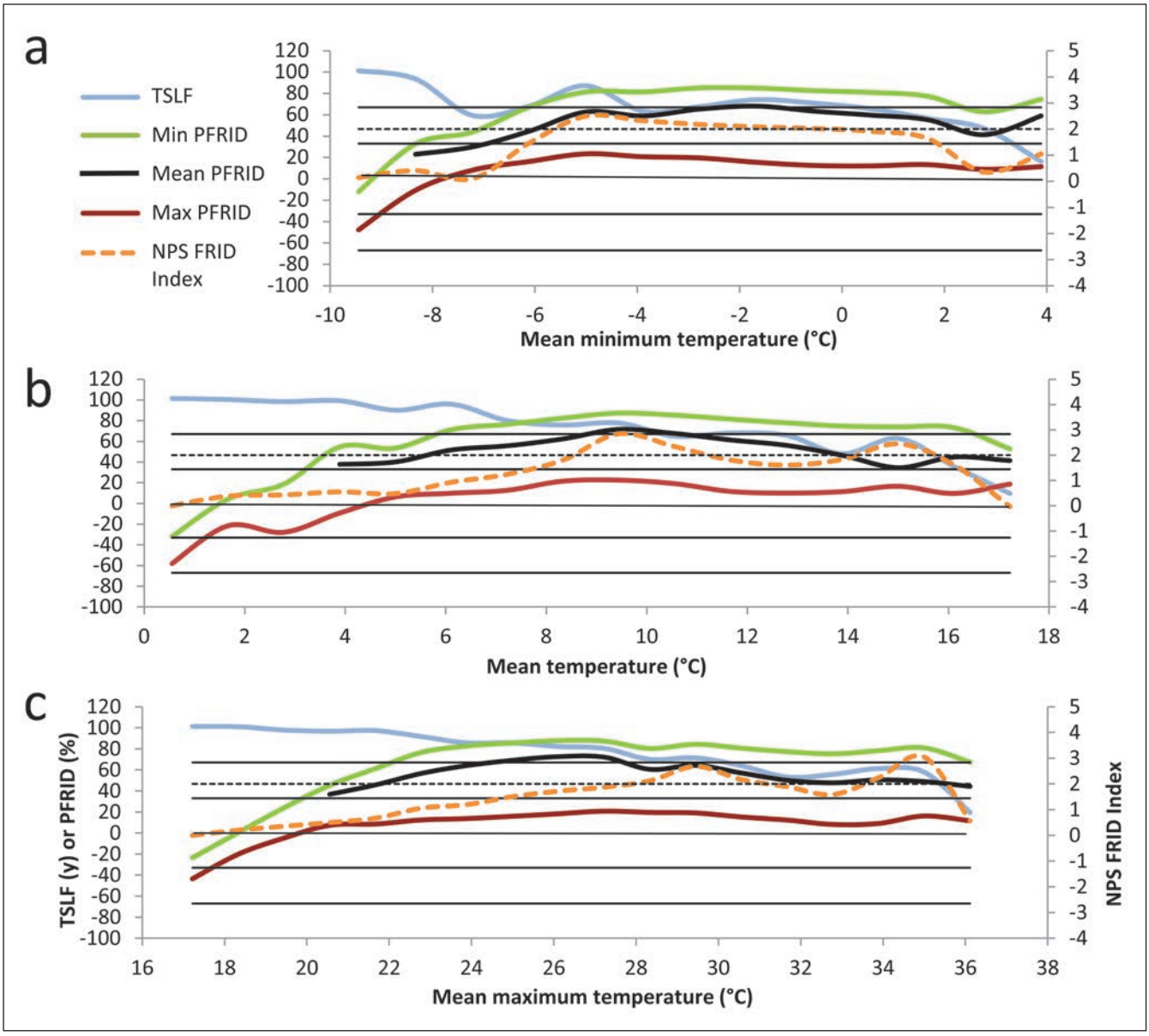


Figure 12—For the northwest California region, time since last fire (TSLF) and fire return interval departure (FRID) versus (A) mean minimum annual temperature, (B) mean annual temperature, and (C) mean maximum annual temperature. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

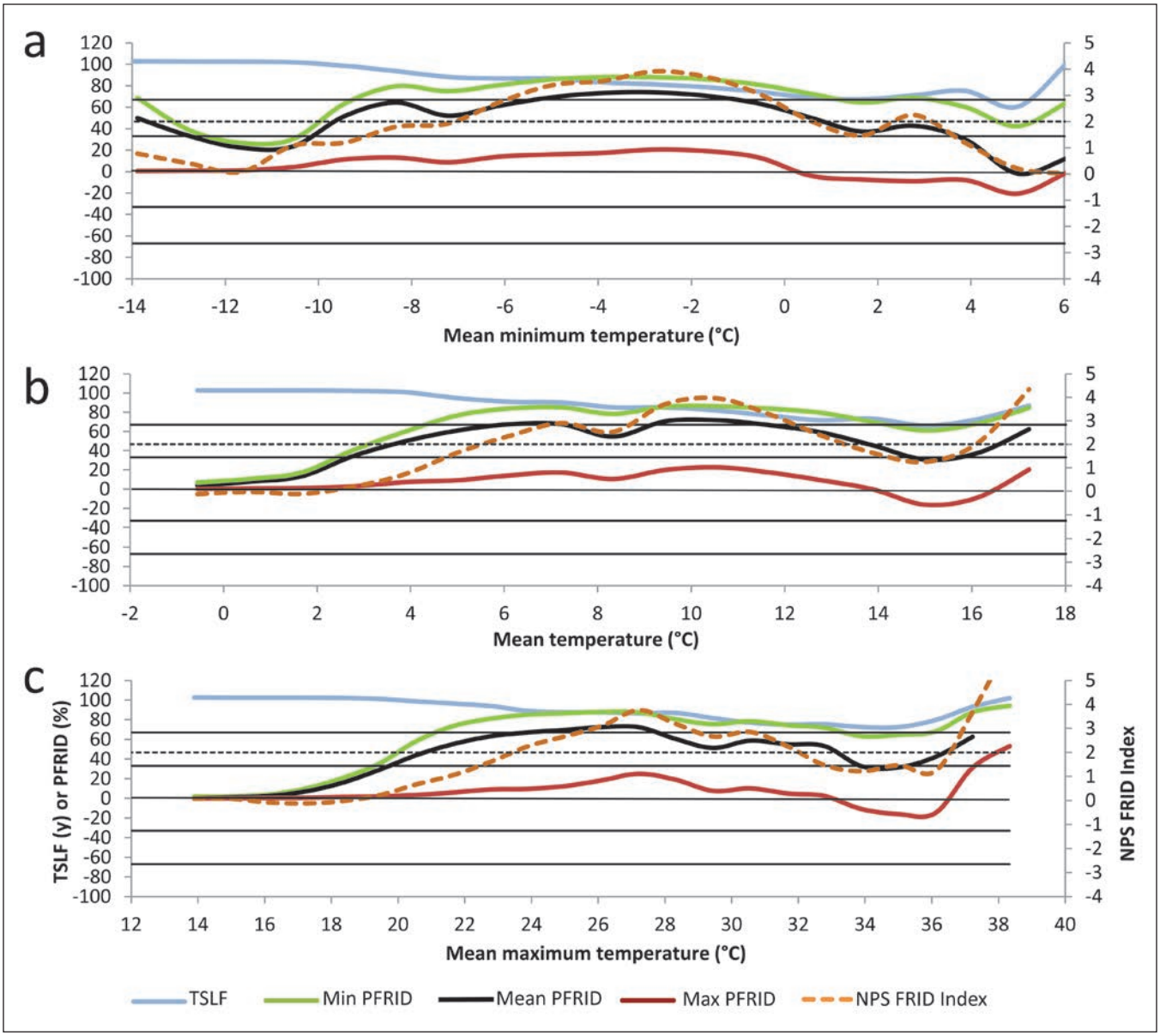


Figure 13—For the Sierra Nevada region, time since last fire (TSLF) and fire return interval departure (FRID) versus (A) mean minimum annual temperature, (B) mean annual temperature, and (C) mean maximum annual temperature. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

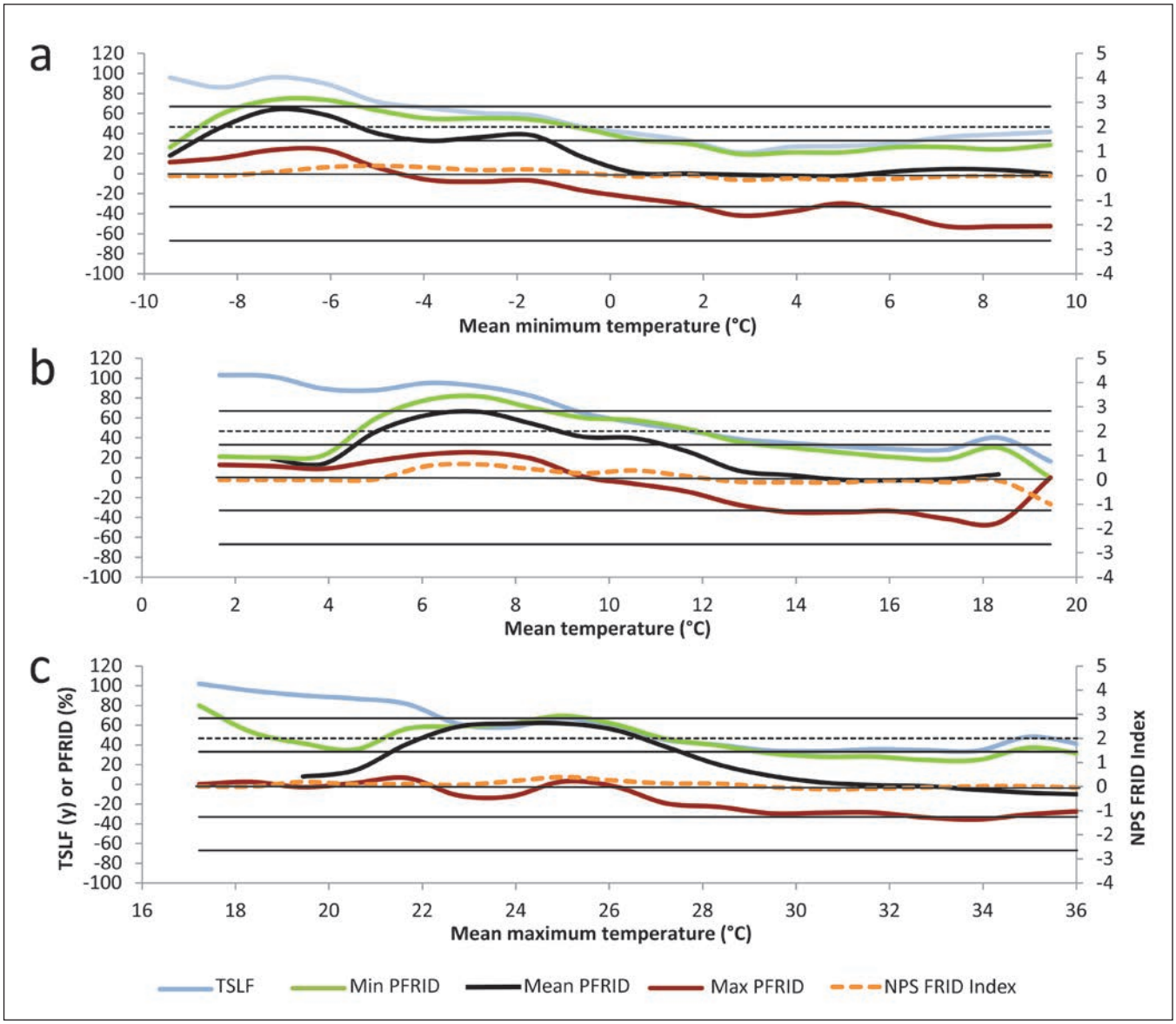


Figure 14—For the southern California region, time since last fire (TSLF) and fire return interval (FRID versus (A) mean minimum annual temperature, (B) mean annual temperature, and (C) mean maximum annual temperature. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

with increasing temperature. In southern California, mean PFRID (and most other indices) fell in the CC 1 to CC -1 belt above -1 °C mean minimum temperature, 11 °C mean temperature and 27 °C mean maximum temperature (fig. 14).

### Differences Among Presettlement Fire Regime (PFR) Types

There were notable differences in departure statistics among the 28 major PFR types (table 4). With respect to PFRs experiencing missed fire events, the most extreme departures (CC 3) were in lower montane and montane forest and woodland types, with the degree of departure decreasing broadly with increasing elevation, precipitation and the snow:rain ratio, and decreasing temperature: yellow pine (*Pinus ponderosa* Dougl. ex Loud. and *P. jeffreyi* Balf. ) and dry mixed conifer > moist mixed conifer (all CC 3) > lodgepole pine (*P contorta* Douglas ex Louden) > red fir (*Abies magnifica* A. Murry bis) > western white pine (*P. monticola* ex D. Don) (all CC 2) > subalpine (CC 1) (table 4). Aspen (*Populus tremuloides* Michx.) was another PFR type with mean PFRID in CC 3. With respect to PFRs experiencing enhanced fire activity, there were two groups with high departures: coastal fir and fire-sensitive spruce/fir (both CC -2), which are primarily ± maritime or in areas of higher precipitation; and coastal sage scrub (also CC -2 on average), a shrub type in coastal and near coastal southern California. Much chaparral in southern California is also in CC -2 or -3, but northern California stands are not as prone to anthropogenic fire, and statewide averaging results in an overall mean PFRID of only -19 (CC -1). With respect to Great Basin PFRs, the three sagebrush types were ranked thus: silver sagebrush (*Artemisia cana*; almost CC 3) > big sagebrush (*A. tridentata*; high CC 2) > black and low sagebrush (*A. nova, A. arbuscula*; CC 1). The pinyon-juniper PFR was ranked CC -1 (table 4). Both desert shrubland PFRs (desert mixed shrub and semidesert chaparral) were CC -1, with some geographic areas experiencing much higher current frequencies of fire than under presettlement conditions (e.g., the western Colorado desert), and others not.

## Discussion

Our analysis highlights some broad dichotomies and notable gradients in the contemporary occurrence of wildland fire when viewed in the context of the probable "natural" fire frequencies experienced by the ecosystems over the centuries preceding Euro-American settlement. Geographically speaking, there are major differences between northern California and southern California, continental-climate California (Great Basin and desert) and Mediterranean-climate California, and wildland and suburban California. Elevation is unimodally related to most FRID measures, as are mean minimum, mean, and mean maximum temperatures.

**Table 4—Total area and spatial averages of time since last fire (TSLF) and fire return interval departure (FRID) measures for the 28 presettlement fire regime (PFR)[a] groups analyzed in this study**

| PFR | Area | TSLF | Mean PFRID | Median PFRID | Min PFRID | Max PFRID | NPS-FRID Index |
|---|---|---|---|---|---|---|---|
| | *Hectares* | *Years* | | | | | |
| Aspen | 24 533 | 96 | 80 | 79 | 89 | 7 | 4.0 |
| Big sagebrush | 1 105 857 | 89 | 57 | 50 | 82 | 5 | 1.5 |
| Bigcone Douglas-fir | 31 939 | 31 | 20 | 23 | 87 | -51 | 0.0 |
| Black and low sagebrush | 336 888 | 99 | 32 | 45 | 63 | -4 | 0.5 |
| California juniper | 7084 | 71 | -4 | 1 | 93 | -32 | -0.2 |
| Chaparral and serotinous conifers | 1 575 973 | 38 | -19 | -23 | 24 | -47 | -0.3 |
| Coastal fir | 18 036 | 20 | -57 | -67 | 23 | -72 | -0.7 |
| Coastal sage scrub | 108 323 | 40 | -33 | -48 | 51 | -53 | -0.5 |
| Curl-leaf mountain mahogany | 64 907 | 96 | 43 | 32 | 67 | -8 | 0.9 |
| Desert mixed shrub | 308 386 | 99 | -4 | -4 | -3 | -4 | -0.9 |
| Dry mixed conifer | 1 398 610 | 85 | 85 | 88 | 93 | 35 | 6.7 |
| Fire-sensitive spruce or fir | 159 | 16 | -63 | -47 | -38 | -75 | -0.8 |
| Lodgepole pine | 186 298 | 99 | 62 | 63 | 84 | -5 | 1.7 |
| Mixed evergreen | 1 302 184 | 67 | 51 | 78 | 74 | -11 | 1.3 |
| Moist mixed conifer | 2 090 128 | 85 | 80 | 85 | 94 | 7 | 4.3 |
| Montane chaparral | 519 106 | 73 | 61 | 64 | 77 | 27 | 1.8 |
| Oak woodland | 184 673 | 73 | 79 | 79 | 91 | 25 | 5.1 |
| Pinyon juniper | 650 199 | 95 | -7 | 3 | 46 | -8 | -0.5 |
| Port Orford cedar | 8373 | 91 | 65 | 81 | 88 | -12 | 2.0 |
| Red fir | 522 511 | 93 | 55 | 63 | 83 | -8 | 1.4 |
| Redwood | 7585 | 60 | 51 | 68 | 78 | -38 | 1.6 |
| Semidesert chaparral | 56 233 | 58 | -2 | -2 | 15 | -35 | -0.1 |
| Silver sagebrush | 7921 | 98 | 64 | 69 | 84 | 33 | 1.8 |
| Spruce-hemlock | 636 | 103 | 0 | 0 | 0 | 0 | -0.6 |
| Subalpine forest | 335 339 | 100 | -2 | -2 | 1 | -3 | -0.5 |
| Western white pine | 35 066 | 99 | 48 | 57 | 84 | -5 | 1.0 |
| Yellow pine | 1 279 302 | 80 | 84 | 90 | 93 | 43 | 6.3 |

Note: Results for the shore pine PFR are not reported as it does not occur in the analysis area. Percent fire return interval departure PFRID data are read as percentage departure.

[a] From Van de Water and Safford (2011).

In southern California, precipitation is negatively related to FRID, but elsewhere (both NW California and the Sierra Nevada) it shows little relationship above 50 cm. There are differences among management units and vegetation types as well. We discuss these patterns below.

Vegetation in "northern California" (NW California and Sierra Nevada regions) is dominated primarily by conifer forest and woodland, while shrublands and hardwoods dominate coastal southern California with dryland and desert vegetation covering interior southern California. For any given longitude, precipitation

in northern California is generally higher than in southern California, and areas of similar elevation and topographic position are usually warmer and drier in southern California. The fire season in southern California is nearly year-round (compared to 4 to 6 months in most of northern California), and half of the year is characterized by periodic strong, dry easterly winds (e.g., "Santa Ana winds") that are rare north of latitude 35°. About two-thirds of California's human population lives in the southern one-fifth of the state, and fire ignition patterns strongly follow this pattern. The proportion of lightning to human ignitions (on Forest Service lands) is about 1:5 in southern California, but closer to 1:1 in the rest of the state (and 1.3:1 if the Lake Tahoe Basin is excluded) (Keeley 1982). These major ecogeographic differences between southern and "northern" California are key to understanding many of the geographic gradients we see in the FRID data.

## Patterns in Southern California

Forest Service lands in 6 of 18 of the ecological sections had average mean and median PFRID values less than 0, and all of these are in southern California. Most of these averaged in the CC -1 range (0 to 33 percent departure), with the exception of Forest Service lands in the Colorado Desert section (a very small area in only one subsection analyzed), which were CC -3 or borderline by all of the PFRID measures, and the central Coast Ranges section, which were CC -2 (almost all Forest Service land in the section is in one subsection, the southern part of the interior Santa Lucia Range). In our analysis, the Colorado Desert section was represented by 521 ha of Forest Service land in the Coachella Valley subsection. Much of the valley is populated or converted to agriculture, and human ignitions are affecting Forest Service lands in areas that are (or were) dominated by the desert mixed shrub PFR, which has the longest reference mean FRI (610 years) of the 28 PFR types in our study (Van de Water and Safford 2011). The Anza-Borrego desert to its south (the Borrego-West Mesa subsection, not in our study area) is also subject to a regime of numerous ignitions by humans. In both subsections, invasion of drylands by exotic grasses and forbs (e.g., red brome [*Bromus madritensis* L. ssp. *rubens*], Mediterranean grass [*Schismus* spp.], Sahara mustard [*Brassica tournefortii* Gouan]) is widespread and leads to fuel continuity that abets fire spread (Brooks and Minnich 2006). Similar invasion by highly flammable exotic species is also occurring in areas of the Mojave Desert Section (which is also mapped predominantly in the mixed desert shrub PFR), but Forest Service lands in the Mojave Desert are only a very small proportion of the section area (fig. 3, table 2) and they are dominated by stands of California juniper (*Juniperus californica*), whose mean presettlement FRI (77 years) is very close to the average TSLF for the section (table 3).

Many areas in the Southern Coast and Southern Mountains and Valleys ecological sections have seen fire frequencies rise dramatically over the last century. Most of this increase in fire activity has occurred since the end of World War II, and temporal and spatial patterns in increasing fire frequency in southern California are strongly correlated with human population growth (Keeley and Fotheringham 2001, Syphard et al. 2007). Interactions between human populations and highly flammable vegetation types like coastal sage scrub and chaparral have led to major changes in fire regimes in and around southern California's urban areas. The ecological subsections surrounding the San Diego, Los Angeles, and Santa Barbara metropolitan areas are among the most negatively departed in the state (figs. 4 and 6; because they did not include Forest Service lands, the coastal subsections including the San Diego and Los Angeles metropolitan areas, Oxnard, and the Santa Monica Mountains were not analyzed in our study, but they have some of the highest fire frequencies in California). In these areas, extensive landscapes characterized originally by dense native shrublands have been converted to degraded, open stands of native shrubs and exotic annual grasses and forbs, which are easily reignited. These fire-mediated changes in vegetation lead to higher rates of erosion, increased exotic species invasion, and higher fire hazard as grass fuels replace shrubs (Merriam et al. 2006, Wells 1987, Zedler et al. 1983).

For its size, southern California between Santa Barbara, San Diego, and San Bernardino is the national leader in average annual wildfire frequency and area, as well as fire-caused human mortality, home loss, and economic damages (Halsey 2004, Hammer et al. 2007, Safford 2007). Although the ecological consequences of the contemporary anthropogenic fire regime in southern California are significant, they receive comparatively little coverage in the popular press, and further degradation of the remaining natural landscapes in southern California will feed back into yet greater human exposure to natural hazards like debris flows, flash floods, and wildfires in suburban settings (Cannon and Gartner 2005, Halsey 2004). Continued high fire frequencies in southern California also threaten the viability of plant and animal species that require longer fire-free periods. High-profile examples of such species include the federally listed California gnatcatcher (*Polioptila californica*) and Tecate and Cuyamaca cypress (*Hesperocyparis forbesii, H. stephensonii*) (Bontrager et al. 1995, Gouvenain and Ansary 2006).

Three small areas of higher mountains (up to 3500 m) rise above southern California south of 35° N latitude. These are found within the Upper San Gabriel, Upper San Gorgonio, and San Jacinto Ecological Subsections. These three subsections can be clearly seen in the mean PFRID map in fig. 6a, where they appear as positive (blue) inclusions in the sea of negatively departed landscapes. These

mountain "sky islands" support coniferous PFRs like dry mixed conifer, yellow pine, and lodgepole pine, as well as mixed evergreen forest and montane chaparral. To a great extent, plant communities inhabiting these higher mountains are southern extensions of montane communities in the Sierra Nevada, and their historical relationship with fire is similar (Sugihara et al. 2006). Lightning-ignited fires once burned frequently in these high-elevation forests, but—unlike in lowland chaparral—fire suppression policies have been successful in nearly eliminating wildfire as an ecological force (Keeley et al. 2009). This has resulted in a curious elevational schizophrenia in contemporary southern California fire regimes, where high-elevation forests that once experienced frequent, low- to moderate-severity fire now rarely experience it (and when they do, it is often high severity), while many areas of lower elevation shrublands that experienced relatively infrequent fire before Euro-American settlement (on average maybe every 50 to 80 years) (Van de Water and Safford 2011) are now seeing fire return intervals of 10 to 20 years or less (Safford 2007).

Although it is also part of our southern California block, Forest Service lands in the Central Coast Section are mostly within the probable HRV for fire frequency or are only moderately departed (table 2, figs. 4 and 6) (Moritz 1997). Although a spate of recent large fires in the northern Santa Lucia Range has brought attention to the area, presettlement mean FRIs for the dominant vegetation types in the area were between 23 years (redwood; but this was strongly anthropogenic [Greenlee and Langenheim 1990]) and 76 years (coastal sage scrub) (Van de Water and Safford 2011). Most Forest Service lands in the north and south Santa Lucia Range subsections have burned between two and four times since 1908, so FRIs over the last century are mostly between 25 and 50 years.

## Great Basin

In similar fashion to the southern California deserts but to an even greater degree, the Great Basin is experiencing a rash of large fires in lower elevation ecosystems that are driven largely by invasive species (chief among them cheatgrass [*Bromus tectorum* L.] and red brome), which have altered fire regimes by increasing fine fuels, fuel connectivity, and the rate of fire spread (Link et al. 2006). Most PFRs mapped in the small portion of eastern California belonging to the Great Basin sensu lato (ecological sections include Mono, the Southeastern Great Basin, and the Northwestern Basin and Range) (table 2) had presettlement FRIs between 35 and 150+ years (Van de Water and Safford 2011). Some areas in the Great Basin of Nevada and southern Idaho are now burning at intervals of 3 to 5 years (Whisenant 1990). Such extremely high fire frequencies are not yet common in the Great Basin

portion of our study area, because the wave of cheatgrass invasion only recently arrived in eastern California, but also because Great Basin lands contained in the California national forests tend to be higher elevation and are less subject to invasion by annual grasses (D'Antonio et al. 2004). Fire frequencies are very high in the Nevada counties east of Lake Tahoe and northeast of Mono Lake (between 38 and 40° N latitude, in Washoe, Douglas, and Lyon Counties and Carson City, just to the east of our study area), and many former stands of single-leaf pinyon pine (*Pinus monophylla* Torr. & Frém. ), juniper (*Juniperus* spp.), sagebrush (especially subspecies of *Artemisia tridentate* Nutt.), and even Jeffrey pine have been eliminated and replaced by degraded landscapes of exotic grasses and scattered shrubs. Cheatgrass has recently become an issue in the Mediterranean part of California as well, and it is now a frequent invader of burned areas along the west slope of the Sierra Nevada, especially where the regenerating shrub layer is sparse (McGinnis et al. 2010).

## Northwestern California and Sierra Nevada Regions

Unlike most of southern California, the NW California and Sierra Nevada Regions ("northern California") are experiencing major ecosystem impacts from a century of fire suppression. The effects of fire exclusion on fire frequencies in northern California are the most obvious large-scale pattern in figures 4 to 6 and table 2. Densities of ignitions by humans are much lower in northern California; northern California is less subject to extreme thermal winds than southern California; the northern California fire season is shorter; and fires in contemporary forests in northern California burn largely through woody coniferous fuels, in which relatively low vertical and horizontal continuity in fuel structure makes the occurrence and sustenance of crown fire much less likely than in the more homogeneous and continuous fuels found in southern California chaparral. As a result, the fire suppression policy has been effective in much of northern California, although recent trends in fire activity, burned area, and fire severity suggest that the situation is rapidly changing as climate warms and fuels continue to accumulate (Miller and Safford 2012, Miller et al. 2009, Westerling et al. 2011).

The ecological sections with Forest Service lands having the greatest FRI departures in California are the Southern Cascades, the North Coast (but only a very small part of the section analyzed), the Klamath Mountains, the Northern Coast Ranges and the Sierra Nevada (table 2). The NPS-FRID index, which focuses on the time since last fire, identifies the Southern Cascades as the section with the greatest departure—its 4.6 score is almost in the "extreme" range—while the other sections listed above all scored as 3.3, or "high" departure. There have been very

few wildfires in the Southern Cascades section during the contemporary period, largely because—between the volcanoes—much of the landscape is comprised of forests on rolling lava beds and the road density is high, which combine to permit rapid firefighter access to and containment of fire starts (Skinner and Taylor 2006). Another factor contributing to high FRID in certain NW California and Sierra Nevada ecological sections is the high level of fragmentation of federal land ownership. The checkerboard ownership pattern across much of eastern NW California and the northern Sierra Nevada leaves little opportunity for creative fire management to serve ecological purposes, as private land is usually within a burning period of any ignition point.

The only large area of low CC 2 (in some cases CC 1) lands in the Sierra Nevada and NW California regions is found in the southern Sierra Nevada (fig. 6). Here, checkerboard ownership is rare, and Forest Service and NPS lands combine to form one of the largest contiguous blocks of federally managed forest lands in the lower 48 States. The core of this block is formed by Yosemite, Sequoia, and Kings Canyon NPs, all of which include large areas of wilderness managed to promote the occurrence of naturally ignited wildfires. Neighboring national forests (e.g., Sequoia, Sierra, Stanislaus, Inyo, and Humboldt-Toiyabe) also include large tracts of high-elevation wilderness, and wildfires are much more likely to be managed for ecological benefits here than on any other national forests in California. That said, it is noteworthy that the mean PFRID averaged across these southern Sierra Nevada management units still falls into CC 2 (in the case of the Stanislaus NF, CC 3) (table 3). The similarities in PFRID metrics between the adjacent national forest and NPS units are due to the fact that fire was suppressed in both land ownerships for the majority of the time period considered in our analysis (until the early 1970s, when the NPS embarked on a more aggressive wildland fire-use program [note that the term "wildland fire use" is no longer in use]), and relatively few areas have burned a sufficient number of times since 1908 to make up the long-term deficit in fire. If we had based our PFRID comparisons on current FRIs beginning in 1970 instead of 1908, the differences between the NPS units and the national forests would doubtless be much greater. A further consideration is that naturally ignited fires managed for ecological benefit tend to occur in higher elevation forests (e.g., high-elevation mixed-conifer, red fir, subalpine), where fire is more easily controlled owing to lower tree densities, low fuel loadings, and higher fuel moistures, but where FRIs are longer and FRID is generally lower than at lower elevations that are (or were once) dominated by yellow pine, oak, and dry mixed-conifer forests. Fire managers are much less comfortable allowing fires in lower elevation forests to burn, as high

fuel loads, drier conditions, and the presence of human communities magnify the consequences of a fire escape. Such lower elevation forests are the core of the fuels problem however, and—at the landscape scale—the use of managed fire in high-elevation forests, while commendable, does nothing to resolve the growing potential for high-severity fire in the yellow pine and mixed-conifer belt (Miller et al. 2009, Miller and Safford 2012). Even under a much expanded managed fire program, it will take many decades of progressive wildfire use in these landscapes to restore them to a compositional and structural state that is reasonably resilient to the probably accelerated disturbance regimes of a warmer future (Overpeck et al. 1990).

The only ecological subsections in NW California and the Sierra Nevada with contemporary fire frequencies approaching presettlement frequencies are in the northern and southern ends of the Sierra Nevada Foothills, the mountain ranges and dry valleys of the Mojave/Southeastern Great Basin, and portions of the Modoc Plateau in the northeastern corner of the state (fig. 6). In the case of the Sierra Nevada Foothills, these are largely landscapes of grasslands and oak woodlands, where contemporary fire frequencies are high owing to intensive human land use and relatively high population densities. The Great Basin and Modoc Plateau subsections support dryland ecosystems (sagebrush, pinyon-juniper, etc.) with longer natural FRIs (35 to 151+ years), and fire frequencies have been relatively low over the last century. The ongoing invasion of cheatgrass into the Great Basin borderlands seems likely to increase fire activity in these subsections as the climate continues to warm (Billings 1994, Brooks and Minnich 2006).

## FRID Trends Along Environmental Gradients

Fire return interval departure trends along the analyzed environmental gradients (elevation, precipitation, and temperature) underline the similarities between NW California and the Sierra Nevada, and the different nature of the fire situation in southern California. Along the west coast of North America at 90° W longitude and between 20° and 60° N latitude, the latitudinal gradient in monthly mean temperature averages about 5.6 °C per 1000 km (ranging from 8.7° January to 2.5° July; calculated from isotherms in FAA [1975]). Thus, on average, mean annual temperatures in interior NW California at latitude 41° N are about 1.8 °C cooler than at the same elevation in the central Sierra Nevada (latitude 38° N) and about 4.3 °C cooler than the same elevation in interior southern California (latitude 34° N). The latitudinal increase in warmth to the south results in an upward shift of the major forest types. The elevations and temperatures of the maximum mean PFRID values in NW California and the Sierra Nevada (elevations of 1500 to 1700 m in the former, 1700 to 1900 m in the latter; corresponding temperatures of -2 °C mean minimum,

10 °C mean, 27 °C mean maximum; figs. 10 through 13) correspond broadly to the average elevation of the transition from moist mixed-conifer ("lower montane") to red fir ("upper montane") forest. These elevations are slightly above the level of maximum annual precipitation (Armstrong and Stidd 1967, Barbour et al. 2007), and correspond approximately to the elevations at which the mean freezing level occurs during mid-winter storms (Barbour et al. 2002). Red fir-dominated forests above this transition receive the highest snowfall totals of any vegetation type in California, the growing season is short, and productivity is markedly lower than in lower montane forests (Barbour et al. 2002, 2007). This leads to lower levels of fuel accumulation, moister fuel beds in the early fire season, and lower fire hazard than in the mixed-conifer belt (Cope 1993, Kilgore 1981, Sugihara et al. 2006); the latter is also partly due to the enhanced component of fir needles in surface litter in red fir forest, as fir litter is substantially less flammable than pine litter (Fonda et al. 1998). Presettlement FRIs in the red fir belt averaged 40 years (range of means = 15 to 130), while moist mixed-conifer forests in the lower montane zone supported much more frequent fire (mean = 16 years, range = 5 to 80) (Van de Water and Safford 2011).

In southern California, the behavior of FRID metrics along the environmental gradients was substantially different than in the two northern California regions. The elevations of the maximum mean PFRID values were much higher than in northern California (2500 to 2700 m), and the temperatures much lower (-7 °C mean minimum, 7 °C mean, 25 °C mean maximum; these correspond to about 2600 m). Above these elevations, FRID dropped rapidly (fig. 10), suggesting a threshold type of response. We believe this is because there is no red fir in southern California, so there is no transitional fire regime between the mixed-conifer and subalpine forests, which begin above 2400 to 2700 m in southern California. According to Minnich (2007), the mixed-conifer/subalpine ecotone in southern California represents a shift from frequent surface burns to infrequent stand-replacing burns, and our data support this generalization. As in NW California and the Sierra Nevada, the elevation of the highest mean PFRID values in southern California corresponded broadly to the elevation of the mean freezing level during winter storms, which ranges from 2300 to 2500 m (Minnich 1986) in the San Bernardino Mountains.

The NPS-FRID index is almost invariant along the analyzed environmental gradients in southern California, remaining very near zero in almost all cases. The only slight rises in the NPS-FRID index in southern California are at about those temperatures or elevations that correspond to the maximum mean PFRID values. Because it was developed for assessing departure in fire-suppressed forests, the NPS-FRID index is insensitive to fire frequencies that are occurring at shorter

intervals than under reference conditions, which is the case in most of the southern California lowlands that we analyzed. The fact that the NPS-FRID index remains near zero even in fire-suppressed montane forests underlines the recent increase in fire activity that has characterized southern California in general. The PFRID metrics, which depend on FRI information from the entire 103-year record of fire perimeters, show major departures from presettlement conditions and dilute the signal of recent rises in burned area and the incidence of large fires in southern California, which have been ascribed to the effects of increasing drought severities on fuel conditions (Keeley and Zedler 2009).

On its own, precipitation shows no obvious relationship to any of the FRID metrics or TSLF in northern California, but most of the FRID metrics and TSLF appear to decline with rising precipitation in southern California. The range of precipitation in NW California and the Sierra Nevada is at least twice as broad as the range in southern California (fig. 11). All of the regions include some areas with annual precipitation < 50 cm, but none of our southern California analysis area receives more than 150 cm annually, while many areas in the Sierra Nevada and NW California do (fig. 11) (Minnich 2007, Potter 1998). Working in the Sierra Nevada and NW California, Miller et al. (2009, 2012) found that for the period 1908–1910 to 2006–2008 (depending on the region), annual precipitation had no relationship to annual fire number, mean or maximum fire size, or total annual burned area in either region (only forest fires analyzed). However, different seasonal precipitation totals explained substantial variation in the response variables, with the season in question changing over the course of the study period; summer (June through August) or spring (March through May) precipitation had the strongest relationship over the last 20 to 25 years (Miller et al. 2009, 2012). We did not relate seasonal precipitation totals to FRID or TSLF, but Miller et al.'s results, where no single season of precipitation was related to fire number, size, or area measures through the entire study period, make us confident that we would have found no simple relationship. The lower PFRID and NPS-FRID index measures below 50 cm precipitation in NW California and the Sierra Nevada are driven partly by the longer reference FRIs in sagebrush-dominated habitats in the northeastern and southeastern Sierra Nevada regions, and partly by recurrent fires in drier lowland habitats around the Central Valley and elsewhere (fig. 6).

In southern California, the strong drop in TSLF and the PFRID metrics (and the slight dip in the NPS-FRID index) above 100 cm precipitation (fig. 11) is due to the very large 2008 and 2009 southern and central California fires, which burned over 160 000 ha in areas of relatively high precipitation, including the Monterey District of the Los Padres NF (which includes the only part of southern California

with mean annual precipitation > 120 cm), and the San Gabriel Mountains around Mount Wilson. Higher PFRID values below 50 cm precipitation (fig. 11) are due primarily to the northeastern, transmontane part of the main body of the Los Padres NF (see figs. 1 and 4), which supports >100 000 ha of pinyon-juniper (presettlement FRI mean = 151 years, range 50 to 250), California juniper (mean = 83 years, range = 5 to 335), and related dryland vegetation and has largely escaped fire for the last century.

## Using FRID Data in Resource Management

Using historical data to inform resource management is not simple, and a number of critical limitations must be surmounted. Important limitations include how to account for the roles of humans in reference ecosystems, mismatches in scale within the data and between the data and their application, the quality and quantity of available data, and the lack of stationarity in environmental baselines (Wiens et al. 2012). We discuss these complications below, and then finish with a few examples of how our FRID data can be used in resource management and restoration.

**The role of human ignitions prior to Euro-American settlement**—
A question that always arises when restoration of fire is discussed is, What role did humans have in the pre-Euro-American settlement regime, and should we be targeting that regime or some version of a fire regime driven only by "natural" (lightning, etc.) ignition sources? The presettlement fire record is derived primarily from fire-caused injury lesions in tree stems or charcoal in layers of sediment or peat, and we are mostly unable to discern lightning-ignited fires from anthropogenic fires. Although lightning occurrence differs temporally at multiple scales, contemporary lightning strike densities (LSDs) can provide some idea as to where on the landscape the ratio of lightning to anthropogenic ignitions was skewed one way or another. California is one of the least lightning-prone states in the United States, with most of the Mediterranean part of the state averaging only 0 to 0.25 strikes per square kilometer per year (compare to the Gulf Coast, with over six strikes per square kilometer per year, or the southeastern and Midwestern United States, with more than three strikes per square kilometer per year [Orville 2008]). The highest LSDs in California are in the deserts of southeastern California and the eastern and higher western slopes of the Sierra Nevada, where average annual LSDs range from 0.3 to 0.55 strikes per square kilometer per year. Highlands in the eastern Klamath Mountains, the southern Cascades, and the interior ranges of southern California average about 0.25 to 0.3 strikes per square kilometer per year (van Wagtendonk and Cayan 2008). Pre-Euro-American settlement fire frequencies in the California Coast Ranges were clearly due primarily to human use of fire, with redwood and

coastal oak woodlands being two of the best examples of ecosystems strongly shaped by human fire management. The relative magnitude of human inputs to the fire regime in the Sierra Nevada before Euro-American settlement is much less certain, although anthropogenic fire was certainly a significant factor within some radius of many Native American cultural sites and as California probably supported more Native Americans than any other Western State (Anderson 2005, Starr 2005), giving consideration to their role in molding California ecosystems seems both wise and justified. (Anderson 2005, Sugihara et al. 2006). Depending on desired conditions and the results of collaborative planning, restoration target conditions in California landscapes might focus on the cultural presettlement landscape, or on some vision of an ecosystem resilient to warming temperatures and higher fire hazard in the future, or even on some conception of how the landscape might have looked in the absence of anthropogenic fire. Whatever the location and the management situation, humans have been in California for more than 10,000 years.

**Issues of scale**—
We conducted our assessment primarily at the state and regional level, which necessarily hides substantial variability at finer scales. For example, the Sierra Nevada sensu stricto is nearly 700 km long, and precipitation drops and temperature rises from north to south. Forest structure and composition also change. Tree densities and canopy cover decrease to the south, pine dominance increases, and shade tolerant tree species like Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), tanoak (*Notholithocarpus densiflorus* Hook. & Arn.) Manos, CH. Cannon & S. oh), and madrone (*Arbutus menziesii* Pursh) are rare or altogether absent south of 37° 30’ N latitude (Barbour et al. 2007). Other tree species, like giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Bucholz) and foxtail pine (*Pinus balfouriana* Balf.), are restricted primarily or completely to the southern Sierra Nevada. Such clinal changes can have major effects on the fire regime, even within a single vegetation or PFR type. As noted in Van de Water and Safford (2011), different FRI measures (mean, median, minimum, maximum) may be of more use in different parts of the PFR range. Where local data on pre-Euro-American settlement fire regimes are available, they should be consulted (see Van de Water and Safford [2011] for a comprehensive list of pre-2011 references). Spatial relationships between PFRs can also have a major impact on local fire regimes. For example, where vegetation types of very different flammabilities are juxtaposed, fire frequencies will be locally affected. Vegetation patch sizes are also important and can be an important determinant of the local fire regime (Agee 1998, Bond and van Wilgen 1996). Our FRID mapping products are available for all Forest Service units in California, so assessments at finer scales are possible.

Another scalar issue is related to the numerical resolution of the FRID data and the resolution at which they are applied. Condition classes based on some aspect of fire regime or its effects on ecosystem status (e.g., vegetation structure, such as in the FRCC program [Hann and Strohm 2003]) have become widely used measures of ecosystem status and management progress in reducing fuels or restoring forest structure. The green-yellow-red (good-poor-bad) color scheme of many condition class maps or graphics (e.g., fig. 9) is a useful and eye-catching method for highlighting areas in need of management intervention, but it can hide important variation in the analyzed ecosystems and landscapes, and it can suggest one-size-fits-all remedies for situations that require nuanced consideration. Our addition of the negative cc to the classic green-yellow-red (CC1-2-3) scheme for the mean PFRID metric (Safford et al. 2011) was an attempt to allow managers to recognize the very different ecological situations and management challenges created by departures caused by overly frequent fire. Broad categories like condition classes make wide generalizations possible, which may be useful for political, budgetary, and educational purposes. However, we recommend that the PFRID metrics be considered principally in their raw, unclassified form (e.g., 53 percent departure rather than "CC 2") and with a keen eye to local conditions and information that can provide a more reasoned and realistic assessment at scales that matter to on-the-ground management.

A third scalar issue pertains to the temporal scale of comparison between the reference FRI information and current FRIs. Our PFRID metrics are set up to compare two relatively long-term data sets: the current FRIs, which in this study are obtained from the 103 (inclusive) years between 1908 and 2010, and the pre-Euro-American settlement FRIs, which were primarily derived from the two to five centuries before 1850. Fire management in California has passed through a number of different philosophical and tactical phases (Stephens and Sugihara 2006), and the effects of these different management periods on fire occurrence are masked or diluted by a metric based on averages from 103 years of data. The best example of this effect is in the comparisons we made between Yosemite, Sequoia and Kings Canyon NPs and the adjacent Sierra Nevada national forests. Extensive management of natural ignited fires for resource benefits began in the national parks in the 1970s, and a PFRID comparison using only the current FRIs since that time would probably show much greater differences between the national parks and the national forests, which continue to suppress most wildfires.

**Data quality considerations**—
The PFR data provided in Van de Water and Safford (2011) are not infallible, and we know of a number of situations where future data collection and finer differentiation of fire regimes are recommendable. For example, Jeffrey pine was placed into the yellow pine PFR by Van de Water and Safford (2011), but it is very stress tolerant and often found in situations where low site productivity notably reduces growth and fuel accumulation. Such sites simply cannot support the very high fire frequencies associated with modal Jeffrey pine sites. Examples include ultramafic "serpentine" soils in NW California and the Sierra Nevada, where Jeffrey pine is often the dominant tree species (Safford and Mallek 2010). The high positive FRID found for the Upper and Lower Scott Mountains ecological subsections in the eastern Klamath Mountains, which are largely underlain by ultramafic substrates, is thus almost certainly an overestimate of departure. In the Sierra Nevada on nonserpentine sites, Jeffrey pine grows extensively on the east side of the range at moderate elevations and on the west side in upper montane forests, where it generally occupies rocky, exposed sites with California juniper and other stress tolerators. The reference FRI in these low-productivity west-side sites, nested in forest with mean presettlement FRIs $\geq$ 40 years, is likewise surely longer than the standard yellow pine PFR (Van de Water and Safford 2011). The many shrub and closed-cone conifer types grouped together under the huge PFR category "chaparral and serotinous conifers" by Van de Water and Safford (2011) also include variability in FRIs across climatic and edaphic clines that may be better incorporated into a number of groups.

The fire perimeter data upon which the FRID polygons are based are also far from perfect. Because the database focus is on the fire perimeter, many unburned inclusions within fires are missed. Older fire perimeters (pre-World War II) are notoriously inexact, and some fires are represented simply by circular polygons of the appropriate fire size centered on the approximate fire location. Some portions of California are missing records of most fires before 1950. Most prescribed fires are missing from the database, although we are currently working with the Forest Service and NPS to remedy this deficiency. With all of these problems, however, the California Fire Perimeters database (FRAP 2011) is the most extensive and complete data source for fire location, size, and shape in the world to our knowledge. It is considered approximately complete for fires over 4 ha in size back to 1950, and mostly comprehensive for Forest Service fires to about 1908, when the agency began to require the collection of data on fire location and size (see McKelvey and Busse 1996, Miller et al. 2009).

Optimally, we would base an assessment of current FRID from pre-Euro-American settlement conditions on a vegetation map of average presettlement conditions. Obviously such a map does not exist. We considered using potential vegetation maps such as the Küchler map of California from 1976 (Barbour and Major 1988) or the Biophysical Settings (BpS) map from the LANDFIRE project (Rollins 2009), but the former was drawn qualitatively on a very broad-scale map of the state before the advent of geographic information systems, and the latter has too many inaccuracies at the subregional scale. The Forest Service inventoried California's nondesert wildlands in the 1920s and 1930s, but this was 70 to 80 years after settlement (although only a few decades after the beginnings of federal fire suppression), and the project was halted after about 60 percent of the area had been mapped (Wieslander 1935). Our decision to go with the most accurate statewide map of existing vegetation means that any substantial changes in vegetation over the time since 1850 could have an impact on the accuracy of our metrics. One of the best documented widespread changes has been the decrease in pine dominance and the increase in fire-intolerant species in lower and middle elevation forests in northern California (and higher elevation southern California) owing to 19$^{th-}$ and 20$^{th}$-century timber harvest and 20$^{th}$ century fire suppression (Barbour et al. 2007, Minnich et al. 1995, Sugihara et al. 2006, Thorne et al. 2008). Many forest stands mapped today as mixed conifer would probably have been mapped as yellow pine in the mid-19$^{th}$ century. In these cases, our FRID measures of current departure from presettlement FRIs understate the actual magnitude of change, as the FRID measures are being calculated based on the mixed-conifer reference FRIs, which are up to 45 percent longer (in the case of moist mixed conifer) than the yellow pine reference FRIs (Van de Water and Safford 2011). In other cases, the reverse may be true. For example, comparison of the 1930s Forest Service maps of the Sierra Nevada (Wieslander 1935) with the current EVEG maps suggests that some areas originally mapped as subalpine forest are now dominated by red fir, which would reduce the presettlement baseline mean FRI from 133 years to 40 years. In this case, our FRID measures are somewhat more difficult to interpret, as the vegetation change is more likely due to climate warming than human management (Dolanc et al. 2012), and management attempts to reverse the trend may be counterproductive.

**Consideration of changing climate**—
Ecosystem transformations caused by directional climate change form the basis for a recent wave of concern regarding the usefulness and applicability of historical data to contemporary and, more importantly, future management problems (Millar et al. 2007, Stephenson et al. 2010, Wiens et al. 2012). The traditional assumption that ecosystem patterns and processes vary about some long-term mean (i.e., that

they exhibit stationarity) was always untenable, but it has become even more so in the "Anthropocene" Epoch (Steffen et al. 2007). Changes in the environmental baseline resulting from climate change, or human land use, or invasive species, etc., make the uncritical use of historical data as a management target less and less defensible, but this does not reduce the value of historical data; indeed, the less we know about the future, the more we will have to rely on insight gained from our experiences with the past (Wiens et al. 2012). In the case of fire-suppressed forest types that historically burned at high frequency, human management has pushed the range of variation for fire occurrence far below the HRV. Modeled or inferred considerations of fire frequency over the next 50 to 100 years nearly unanimously project increasing potential for wildfire, perhaps even above levels that reigned when Euro-Americans settled California (see below). In this case, restoration of HRV conditions is a logical first step and might be treated as a waypoint toward the ultimate goal of increasing resilience to a much warmer future (Safford et al. 2012).

**Management application of FRID data**—
Fire return interval departure data can provide a template for assessing ecosystem conditions and evaluating landscapes for restoration need. Yosemite, Sequoia, and Kings Canyon NPs have used the NPS-FRID index for such purposes for over two decades (Caprio et al. 1997, Keifer et al. 2000, van Wagtendonk et al. 2002). At the simplest level, relationships between FRID and ecosystem type (as represented by our PFRs) can help direct broad landscape-level strategies. In northern California, high-elevation forests (red fir, western white pine, subalpine) are only moderately departed from historical conditions and—ecologically speaking—tend not to be high-payoff landscapes for fuels reduction, wildland fire use for ecological benefit, or other types of restoration management (Agee 2005). However, these are often the safest and easiest places to carry out such management (and climate warming is increasing concern for lower elevation red fir forests, which are transitional from the mixed-conifer belt). Areas of extreme departure, especially when evaluated against min or max PFRID, are probably at or beyond the HRV for fire frequency. These landscapes, mostly shrublands in southern California and low to middle elevation forests in northern California, may seem like logical places to focus ecological restoration efforts, but in some cases, they may be too difficult, too remote, too expensive, or too controversial to actively manage. The projected future environment of the restoration landscape will need to be considered in restoration planning, and management targets may need to be adjusted. The FRIs documented in the database do not need to represent the long-term target condition for the restored landscape, but they provide an idea of the range of fire frequencies that might best promote sustainability of the reference ecosystem type.

Future projections suggest even more ecological potential for wildfire in most Western U.S. forests than was the case during our pre-Euro-American settlement reference period (Lenihan et al. 2003, National Research Council 2011, Westerling et al. 2011), when fire was much more common than today. Climate-driven projections also suggest higher levels of drought and stress-related susceptibility to insect attack and disease (Evangelista et al. 2011, Sturrock et al. 2011). These projections suggest that a serious management effort will be required to increase the resilience of fire- and drought-prone landscapes to future environmental stressors. Our mean PFRID metric can be used in conjunction with the NPS-FRID index to identify recently burned locations that have experienced fire frequencies in the 20$^{th}$ century that are within or near HRV. Lydersen and North (2012) recently used a similar protocol to identify frequently burned mixed-conifer stands in the Sierra Nevada and conducted ground sampling to develop a picture of forest structure in fire-resilient stands. These are places to begin use of prescribed or managed wildland fire to ensure long-term maintenance of fire-resilient composition and structure. Such places could also be used as core areas around which to expand restoration efforts into the surrounding landscape.

As restoration efforts proceed, FRID data can be used to track progress and measure management success. Miller and Davis (2009) carried out fire modeling in two watersheds of Sequoia-Kings Canyon and Yosemite NPs based on suppressed lightning ignitions that had occurred during a previous 20-year period. At the end of their study period, they assessed the outcome of their exercise by generating a hypothetical map of the NPS-FRID index and comparing it to the actual FRID map that existed without the modeled fires. Tracking of fire restoration efforts at the broader landscape scale could be accomplished with a similar comparative protocol. For short-term monitoring, the NPS-FRID index may be the most useful performance measure, as it considers only the time since the most recent fire. In the end, repeated fires at appropriate levels of severity will be required to sufficiently restore the fire regime, vegetation structure and composition, wildlife habitat, and other ecosystem patterns and processes in frequent-fire forest types. In southern California shrubland ecosystems, on the other hand, the focus should be on reducing fire frequencies. Measures like mean, min, and max PFRID, which are better at evaluating the frequency of fire in an ecosystem over time, will be more helpful in targeting and tracking a long-term strategy to promote resilience. The final goal should not be a slavish adherence to the mean pre-Euro-American settlement fire frequencies listed in Van de Water and Safford (2011) and elsewhere. However, these values and their ranges can be used profitably as short- or medium-term targets for restoration efforts, in the understanding that the long-term goal is not some

static picture postcard of a presettlement landscape, but a dynamic ecosystem that is more resilient to disturbance, a warming climate, and all of the other stressors that will come with global change.

When using the PFRID measures, managers may have the tendency to focus their restoration efforts on areas mapped as CCs 3 or -3, because current management policies are focused on highly departed lands. In most cases, this is probably a reasonable course of action, although—as noted above—for most situations we recommend use of the raw FRID data rather than the condition class categories. The extent to which the CC 2 and 3 or -2 and -3 boundaries might represent a reliable ecological warning bell can be gauged by the information provided in table 1. Table 1 compares the mean minimum and mean maximum pre-Euro-American settlement FRIs from Van de Water and Safford (2011) with the FRIs associated with the CC 2 and 3 (+67 percent departure) and CC -2 and -3 (-67 percent departure) boundaries. The 33 percent and 67 percent cutoffs used to identify CCs 1, 2, and 3 were based on simple division of the 100 percent maximum departure into thirds (Hann 2004, Hann and Strom 2003), thus there is no underlying statistical distribution of fire frequencies assumed. This leads to different relationships between the range of presettlement FRIs associated with each PFR and the FRIs represented by the CC 2 and 3 and CC -2 and -3 boundaries (table 1, fig. 15).

Looking at table 1, some generalizations can be made about these differences. For example, most tree-dominated PFRs show longer mean maximum FRIs than the FRIs associated with the CC 3 boundary (e.g., fig. 15), while shrub-dominated PFRs in table 1 universally show shorter mean maximum presettlement FRIs than the FRIs represented by the CC 3 boundary (table 1). These differences are probably due both to differences in sample size (there are many fewer studies of fire history in shrub vs. forest ecosystems) (Van de Water and Safford 2011), and inherent differences in the distributions of fire frequencies in the two ecosystem types (e.g., Grissino-Mayer 1999, Moritz 2003). For tree-dominated PFRs with longer mean maximum FRIs, managers might want to treat the mean maximum FRI as a higher class of departure ("extreme?"). For shrub PFRs with shorter mean maximum FRIs, CC 3 is a more conservative measure of departure than the mean maximum FRI. On the negative side of the PFRID scale, for most shrub PFRs the mean minimum presettlement FRI is longer than the FRI represented by the CC -3 boundary (table 1). In practical terms, this means that for PFRs like chaparral/serotinous conifers or semidesert chaparral, both with extensive distributions in southern California, use of the CC -3 category as an ecological alarm bell for overly frequent fire may actually underestimate the magnitude of the ecological departure.

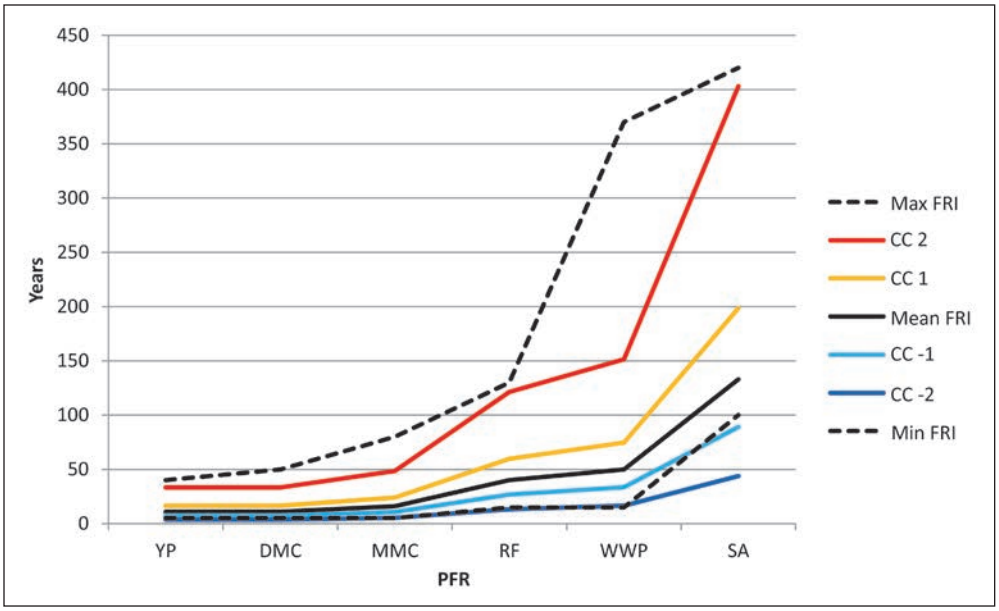


Figure. 15—Elevational gradient (left to right: low elevation to high) of six forest presettlement fire regimes (PFRs) on the west slope of the Sierra Nevada, comparing the condition class (CC) boundaries for each PFR with the approximate range of pre-Euro-American settlement fire return intervals (FRIs) (the area between mean maximum ["max FRI"] and mean minimum ["min FRI"]). Condition class color scheme corresponds to figure 9. YP = yellow pine, DMC = dry mixed conifer, MMC = moist mixed conifer, RF = red fir, WWP = western white pine, and SA = subalpine forest.

Fire return interval departure users should pay careful attention to the various limitations and caveats inherent to the tool. As discussed above, these include scalar issues, issues with data quality and extent, issues with the reference baseline, and issues with interpretation. We finish by reminding the reader that FRID analysis does not include information on aspects of the fire regime other than fire frequency calibrated by vegetation type. Fire occurrence and behavior are driven by such factors as topography, weather, and fuel conditions that were not directly considered in our analysis. FRID is a useful broad-scale planning tool, but proper interpretation at scales meaningful to resource managers will require concurrent consideration of other sources of information as well, such as site history, fuel loading and vegetation structure, topography, weather, and other components of the fire regime, including fire size, severity, and spatial pattern.

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## English Equivalents

| When you know: | Multiply by: | To find: |
|---|---|---|
| Millimeters (mm) | 0.0394 | Inches |
| Meters(m) | 0.394 | Feet |
| Kilometers (km) | 0.621 | Miles |
| Hectares (ha) | 2.47 | Acres |
| Square kilometers ($km^2$) | 0.386 | Square miles |
| Degrees Celsius (°C) | 1.8 °C + 32 | Degrees Fahrenheit |

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REVIEW SUMMARY

CLIMATE CHANGE

# The broad footprint of climate change from genes to biomes to people

**Brett R. Scheffers,* Luc De Meester, Tom C. L. Bridge, Ary A. Hoffmann, John M. Pandolfi, Richard T. Corlett, Stuart H. M. Butchart, Paul Pearce-Kelly, Kit M. Kovacs, David Dudgeon, Michela Pacifici, Carlo Rondinini, Wendy B. Foden, Tara G. Martin, Camilo Mora, David Bickford, James E. M. Watson**

**BACKGROUND:** Climate change impacts have now been documented across every ecosystem on Earth, despite an average warming of only ~1°C so far. Here, we describe the full range and scale of climate change effects on global biodiversity that have been observed in natural systems. To do this, we identify a set of core ecological processes (32 in terrestrial and 31 each in marine and freshwater ecosystems) that underpin ecosystem functioning and support services to people. Of the 94 processes considered, 82% show evidence of impact from climate change in the peer-reviewed literature. Examples of observed impacts from meta-analyses and case studies go beyond well-established shifts in species ranges and changes to phenology and population dynamics to include disruptions that scale from the gene to the ecosystem.

**ADVANCES:** Species are undergoing evolutionary adaptation to temperature extremes, and climate change has substantial impacts on species physiology that include changes in tolerances to high temperatures, shifts in sex ratios in species with temperature-dependent sex determination, and increased metabolic costs of living in a warmer world. These physiological adjustments have observable impacts on morphology, with many species in both aquatic and terrestrial systems shrinking in body size because large surface-to-volume ratios are generally favored under warmer conditions. Other morphological changes include reductions in melanism to improve thermoregulation, and altered wing and bill length in birds. Broader-scale responses to climate change include changes in the phenology, abundance, and distribution of species. Temperate plants are budding and flowering earlier in spring and later in autumn. Comparable adjustments have been observed in marine and freshwater fish spawning events and in the timing of seasonal migrations of animals worldwide. Changes in the abundance and age structure of populations have also been observed, with widespread evidence of range expansion in warm-adapted species and range contraction in cold-adapted species. As a by-product of species redistributions, novel community interactions have emerged. Tropical and boreal species are increasingly incorporated into temperate and polar communities, respectively, and when possible, lowland species are increasingly assimilating into mountain communities. Multiplicative impacts from gene to community levels scale up to produce ecological regime shifts, in which one ecosystem state shifts to an alternative state.

**OUTLOOK:** The many observed impacts of climate change at different levels of biological organization point toward an increasingly unpredictable future for humans. Reduced genetic diversity in crops, inconsistent crop yields, decreased productivity in fisheries from reduced body size, and decreased fruit yields from fewer winter chill events threaten food security. Changes in the distribution of disease vectors alongside the emergence of novel pathogens and pests are a direct threat to human health as well as to crops, timber, and livestock resources. Humanity depends on intact, functioning ecosystems for a range of goods and services. Enhanced understanding of the observed impacts of climate change on core ecological processes is an essential first step to adapting to them and mitigating their influence on biodiversity and ecosystem service provision. ■

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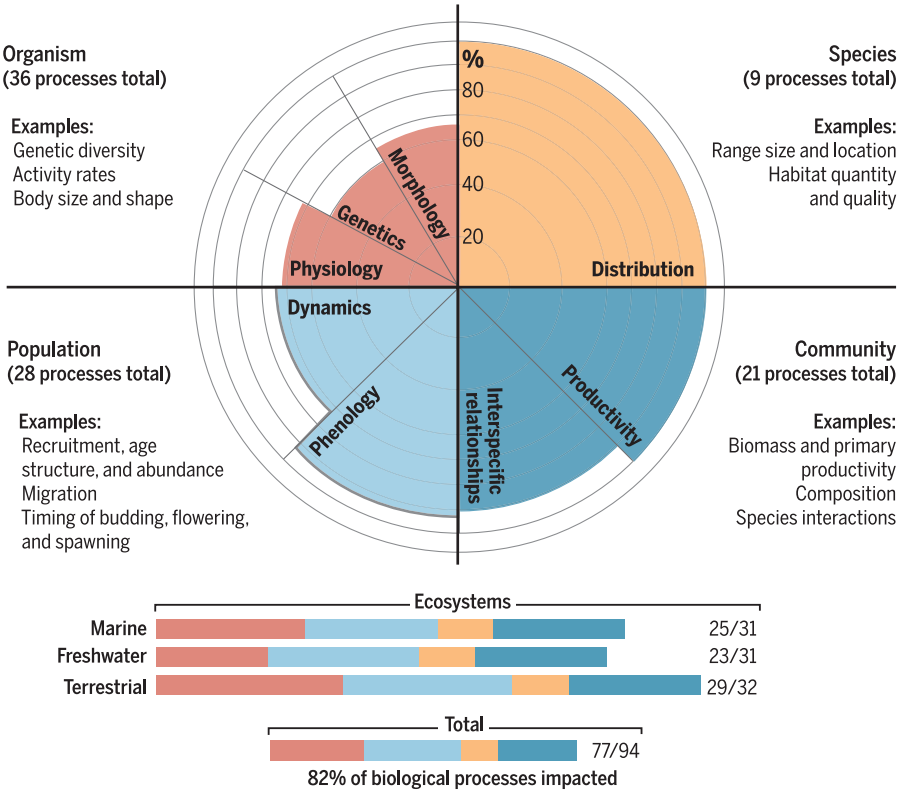


**Climate change impacts on ecological processes in marine, freshwater, and terrestrial ecosystems.** Impacts can be measured on multiple processes at different levels of biological organization within ecosystems. In total, 82% of 94 ecological processes show evidence of being affected by climate change. Within levels of organization, the percentage of processes impacted varies from 60% for genetics to 100% for species distribution.

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REVIEW

CLIMATE CHANGE

# The broad footprint of climate change from genes to biomes to people

**Brett R. Scheffers,[1]* Luc De Meester,[2] Tom C. L. Bridge,[3,4] Ary A. Hoffmann,[5] John M. Pandolfi,[6] Richard T. Corlett,[7] Stuart H. M. Butchart,[8,9] Paul Pearce-Kelly,[10] Kit M. Kovacs,[11] David Dudgeon,[12] Michela Pacifici,[13] Carlo Rondinini,[13] Wendy B. Foden,[14] Tara G. Martin,[15] Camilo Mora,[16] David Bickford,[17]† James E. M. Watson[18,19]**

**Most ecological processes now show responses to anthropogenic climate change. In terrestrial, freshwater, and marine ecosystems, species are changing genetically, physiologically, morphologically, and phenologically and are shifting their distributions, which affects food webs and results in new interactions. Disruptions scale from the gene to the ecosystem and have documented consequences for people, including unpredictable fisheries and crop yields, loss of genetic diversity in wild crop varieties, and increasing impacts of pests and diseases. In addition to the more easily observed changes, such as shifts in flowering phenology, we argue that many hidden dynamics, such as genetic changes, are also taking place. Understanding shifts in ecological processes can guide human adaptation strategies. In addition to reducing greenhouse gases, climate action and policy must therefore focus equally on strategies that safeguard biodiversity and ecosystems.**

Atmospheric concentrations of greenhouse gases from burning fossil fuels and deforestation are approaching levels that have not been detected in the past 20 million years (*1*). This has altered the chemical composition of the Earth's atmosphere, oceans, and fresh waters (*2*). As a result, temperatures in the upper ocean and on land are now ~1°C higher than in preindustrial times, and temperature, wind, and precipitation regimes have become more variable and extreme (*3*, *4*). These changes are having clear impacts on planetary biophysical processes, including desalinization and acidification of the world's oceans (*5*) and melting of permafrost, ice sheets, and glaciers (*6*, *7*). Lakes and rivers have increased in temperature, altering seasonal patterns of mixing and flows (*8*).

Changing climate regimes have been an important driver of natural selection in the past (*9*) and, as in the past, species are responding to the current human-induced climate event in various ways. Previous reviews have covered many of the more obvious changes in species ranges, phenologies, and population dynamics (*10*–*15*) but have usually focused on one ecological system at a time. Here, we discuss the full range and scale of climate change effects on biota, including some of the less obvious disruptions observed in natural systems. We present examples of case studies of observed impacts across terrestrial and aquatic biomes and find evidence that climate change is now affecting most biological and ecological processes on Earth—spanning genetics, organismal physiology and life-history, population distributions and dynamics, community structure, and ecosystem functioning (Fig. 1 and table S1). People depend on intact, functioning ecosystems for a range of goods and services, including those associated with climate adaptation (*16*). Understanding the observed impacts of current climate change on core ecological processes is therefore an essential first step in humans planning and adapting to changing ecosystem conditions.

Although inherently different, marine, freshwater, and terrestrial realms share a common hierarchy of levels of biological organization, ranging from genes to organisms, populations, species, communities, and ecosystems. Broadly adapting from Bellard *et al.* (*17*), we screened the literature (supplementary materials) to evaluate evidence that climate change is affecting ecological components across different levels of biological organization, each of which comprises a core set of ecological processes (Fig. 1, fig. S1, and table S1). We identify a set of core ecological processes on Earth (32 in terrestrial and 31 each in marine and freshwater), which together facilitate ecosystem functioning that supports services to people (*17*). These processes include changes in genetic diversity (genetics), metabolic rates (physiology), body size (morphology), timing of migration (phenology), recruitment (population dynamics), range size (distribution), loss of synchronization (interspecific relationships), and biomass (productivity) (*17*). Because our main goal is to assess what processes are affected by climate change, we define "impact" on each process as an observed change in that process linked to climate change. We do not differentiate between "positive" (adaptive, buffering, or mitigating) and "negative" (stress or damage) responses because responses may be positive at one level of biological organization (such as genetic adaptation to climate change) but negative at another (such as reduced genetic variation and capacity to deal with other stressors). We then consider the relevance of the affected ecological processes in human systems and illustrate observed impacts to ecosystem services such as food and resource security (fisheries, agriculture, forestry, and livestock production), human health, and hazard reduction.

## Ecological impacts of climate change

### *Organisms*

#### *Genetics*

There is now growing evidence that species are undergoing evolutionary adaptation to human-induced climate change. For example, between the 1960s and 2000s the water flea (*Daphnia magna*) evolved to cope with higher thermal extremes in the UK (*18*), and cornflower (*Centaurea cyanus*) life history traits have recently evolved in response to warmer springs across northern France (*19*). Other examples include the evolution of earlier migration timing in anadromous pink salmon (*Oncorhynchus gorbuscha*), with decreased frequency of incidence of a genetic marker that encodes for late migration (*20*). Time-series data that control for physiological acclimatization also show strong evidence for genetic responses to climate change. For example, Bradshaw and Holzapfel showed that genotypic values for the critical day length that induces diapause in the pitcher plant mosquito (*Wyeomyia smithii*) change with latitude, and that the latitudinal relationship has changed over the period from 1972 to 1996 (*21*). Onset of diapause now occurs later, which is consistent with a longer

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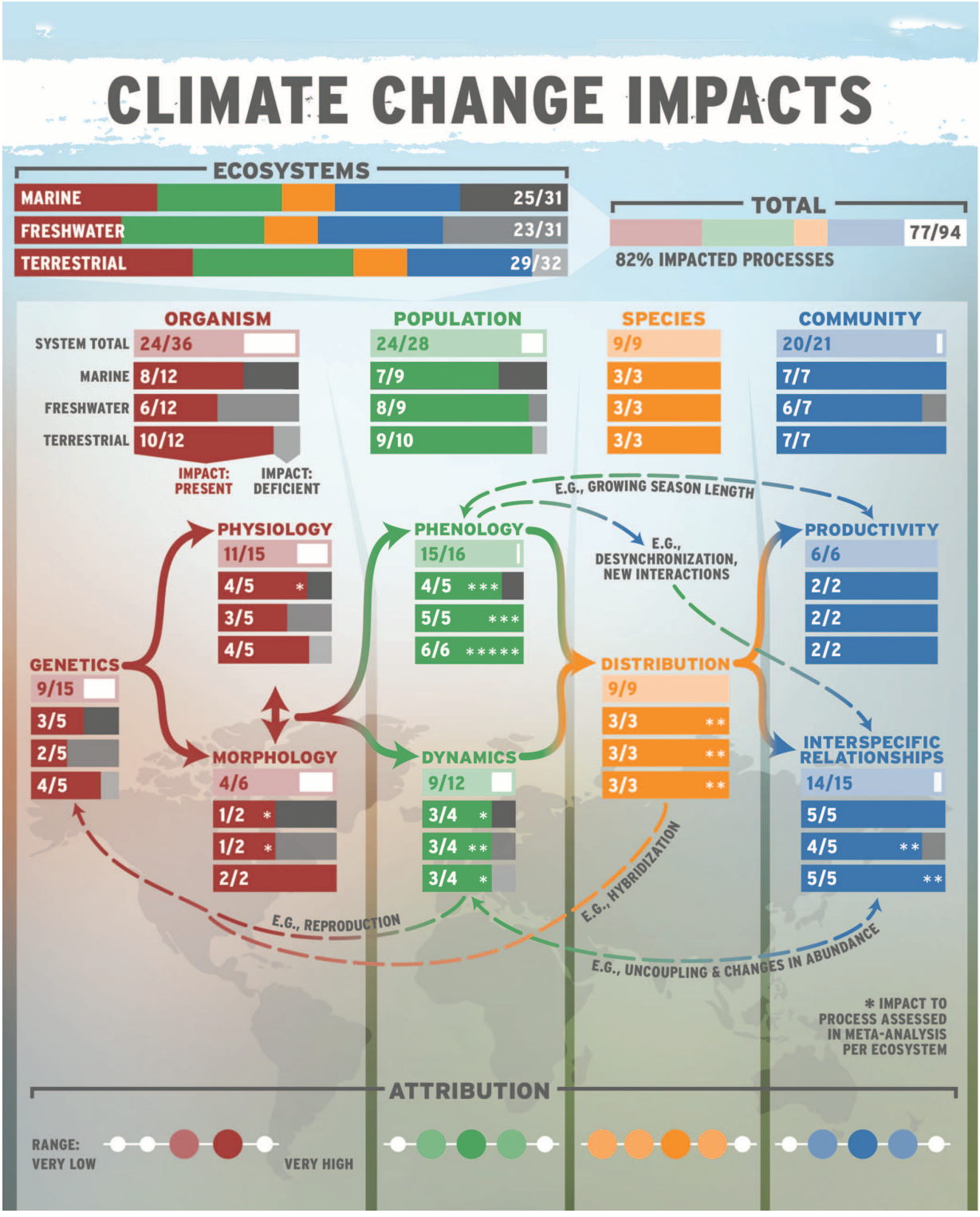


**Fig. 1. Climate change impacts on Earth's marine, terrestrial, and freshwater systems.** The presence of observed impacts on the different levels of biological organization and its inner components across the Earth's marine, terrestrial, and freshwater ecosystems. The denominator represents the total number of processes that we considered for each group, and the numerator is the number of these processes with evidence of impact (a complete list of processes is provided in fig. S1 and table S1). In total, 82% of all ($n$ = 94) ecological processes that were considered have observed evidence of impact by climate change. Each process has at least one supporting case study. The asterisk indicates whether the affected process was assessed in a meta-analysis in addition to case studies. Thus, double-asterisk indicates that two processes were assessed in at least one meta-analysis. Confidence that the observed impact can be attributed to climate change was assigned for each level of organization and ranges from very low, low, medium, high, to very high; this assessment is based on tables 18-7, 18-8, and 18-11 in (*13*). The darkest circle indicates confidence level with the most literature support.

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growing season under warmer conditions. Oceanic phytoplankton have adapted to a temperature change of +0.73°C associated with 15 years of climate warming in the Gulf of Cariaco, Venezuela, by adjusting their thermal niche by +0.45°C (*22*). Although such evidence from small organisms with short generation times is accumulating, we found little documented evidence of evolutionary change from species with longer generation times such as birds, mammals, and trees (*14*, *23*), although adaptation appears to be possible in some long-lived reef corals (*24*).

Changes in species ranges have altered or created new "hybridization zones" across the planet. For example, in North America, hybrid zones between black-capped (*Poecile atricapillus*) and Carolina chickadees (*P. carolinensis*) are shifting in response to warmer winter temperatures (*25*), and because the southern flying squirrel (*Glaucomys volans*) has expanded its range northward in eastern North America, it is now hybridizing with the northern flying squirrel (*G. sabrinus*) (*26*). In North American rivers and streams, hybridization between invasive rainbow trout (*Oncorhynchus mykiss*) and native cutthroat trout (*O. clarkia*) has increased in frequency as the former expand into warming waters (*27*). Such hybridization events have also been observed in some marine fishes, such as the coastal West Coast dusky cob (*Argyrosomus coronus*), and are expected to increase as species shift their ranges poleward in response to rapidly warming ocean conditions (*28*).

### Physiology

Many species display temperature-driven trait plasticity in physiological processes such as thermal optima (*29*). Whereas some responses, such as acclimation to high temperatures, maximize fitness, others can reflect failure to cope with temperature stress and other climate-mediated changes. These responses can occur within a generation or between generations through maternal or epigenetic effects (*30*).

There is some observational evidence that warming has affected temperature-dependent sex determination (TSD) of species in marine and terrestrial systems. Snake pipefish (*Entelurus aequoreus*) in the northeastern Atlantic have altered their operational sex ratios and reproductive rates as a consequence of warmer sea surface temperatures (*31*). Most evidence for impacts on TSD in marine systems, however, is derived from experimental studies, which provide strong support for TSD changes in sea turtles and various fish species (*32*, *33*). In terrestrial and freshwater systems, TSD has been implicated in masculinization and feminization, respectively, of lizard and turtle populations (*34*, *35*).

In marine systems, physiological responses to both climate warming and changing ocean conditions are widespread (*36*, *37*). Matching field and laboratory data for the eelpout (*Zoarces viviparus*) show increased metabolic costs associated with warming in the North and Baltic Seas (*38*). In aquatic systems, warming increases oxygen demand but decreases oxygen content of the water, resulting in substantial metabolic costs (*39*). Although climate change per se does not cause acidification of the oceans, both arise directly from higher atmospheric carbon dioxide, and experimental evidence has raised concerns regarding negative effects of ocean acidification on calcification, growth, development, and survival of calcifying organisms (*12*). For example, acidification has led to extensive shell dissolution in populations of the pteropod *Limacina helicina* in northwest North America and in the Southern Ocean off Antarctica (*40*, *41*).

### Morphology

Individuals in some species are becoming smaller with increasing warming because large surface-to-volume ratios are generally favored under warmer conditions (*42*)—a phenomenon that is linked to standard metabolic principles (*43*). In the Appalachian Mountains, six species of *Plethodon* woodland salamander have undergone, on average, an 8% reduction in body size over the past 50 years (*44*). Similarly, three species of passerine birds from the northeast United States show an average 4% decrease in wing length correlated with recent warming (*45*), and the long-distance migrant bird the red knot (*Calidris canutus*) is now producing smaller offspring with smaller bills, which reduces survival in juveniles because of altered foraging success on underground bivalves (*46*). In general, decreasing body size with warming is expected, but evidence from cold, high-altitude habitats suggests that increased primary productivity and longer growing seasons from warming have led to increased body size in some mammal species such as American marten (*Martes americana*) and yellow-bellied marmot (*Marmota flaviventris*) (*47*, *48*). In South Australia, leaf width in soapberry (*Dodonaea viscosa*) has decreased compared with the ancestral condition documented under cooler temperatures 127 years ago (*49*). Other climate change impacts on morphology include color changes in butterflies, dragonflies, and birds (*50*–*53*) and pronounced changes in skull shape in the alpine chipmunk (*Tamias alpinus*) (*54*).

## Population

### Phenology

For most species, migrations and life-history processes (such as budding and flowering in plants, hatching and fledging in birds, and hibernation in mammals) are closely tied to seasonal and interannual variation in climate, and there is now overwhelming evidence that both have been affected by climate change (*10*, *37*, *55*, *56*). Across marine, freshwater, and terrestrial ecosystems, spring phenologies have advanced by 2.3 to 5.1 days per decade (*10*, *57*). A combination of climate warming and higher atmospheric $CO_2$ concentrations has extended the growing period of many plant populations (*58*). In a large global analysis, which included 21 phenological metrics such as leaf-off and leaf-on dates and growing-season length, plant phenologies were found to have shifted by more than 2 standard deviations across 54% of Earth's land area during the past three decades (*59*).

In marine and freshwater systems, advances in the timing of annual phytoplankton blooms—the basis for many aquatic food webs—have occurred more rapidly than temporal shifts in terrestrial plants (*37*, *60*). Such changes in plankton phenology have been attributed to increases in water temperatures, reduction in the duration of ice cover, and the alteration of the seasonal duration of thermal stability or stratification of the water column.

Shifts in spawning times have been documented for 43 fish species in the northeast Pacific Ocean from 1951 to 2008, with earlier spawning associated with increased sea surface temperature and later spawning associated with delays in seasonal upwelling of nutrients toward the ocean surface (*61*). Similar impacts on breeding have been observed in terrestrial and marine bird species (*62*).

Changes in the timing of migration events have been extensively documented, including advances in spring arrival dates of long-distance migratory bird species in Europe, North America, and Australia (*63*–*65*). Similarly, long-term data on many amphibians and mammals have shown advancements in spring and delays in autumn migration (*66*–*68*) and altered peak calling periods of male amphibians (*67*–*69*). In the largest meta-analysis to date of phenological drivers and trends among species in the southern hemisphere, 82% of terrestrial data sets and 42% of marine data sets demonstrated an advance in phenology associated with rising temperature (*70*).

### Abundance and population dynamics

Acute temperature stress can have severe negative effects on population dynamics such as abundance, recruitment, age structure, and sex ratios. Meta-analyses across thousands of species report that ~80% of communities across terrestrial, freshwater, and marine ecosystems exhibited a response in abundance that was in accordance with climate change predictions (*10*, *70*). In a meta-analysis of marine species, 52% of warm-adapted species increased in abundance, whereas 52% of cold-adapted species decreased (*71*). Temperature spikes may cause mass mortality of key ecosystem engineers in both temperate and tropical oceans. Excessive heat kills canopy-forming macroalgae in temperate marine systems (*72*) and causes bleaching and mass mortality of corals in the tropics (*73*). Reductions in sea ice extent have caused declines in abundances of ice-affiliated species in the Arctic [for example, ivory gulls (*Pagophila eburnea*), ringed seals (*Pusa hispida*), and polar bears (*Ursus maritimus*) (*74*)] whereas in some cases, such as on Beaufort Island in the southern Ross Sea, the loss of ice from receding glaciers resulted in increased abundances of Adélie penguins (*Pygoscelis adeliae*) (*75*). In the United States, the bull trout (*Salvelinus confluentus*) has lost >10% of its spawning grounds in central Idaho over the past 13 years because of increased water temperatures (*76*), while the brown trout (*Salmo*

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*trutta*) has lost habitat in the Swiss Alps (*77*). In western Canada, reduced survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*) has been observed with increased water temperatures (*78*), and in eastern Canadian lakes, golden-brown algae dramatically increased in abundance as water temperature increased 1.5°C during the latter part of the 20th century (*79*). Some of the best evidence for climate-change impacts on the abundance of terrestrial species comes from analyses of bird population trends derived from systematic monitoring schemes in Europe, with warm-adapted species having increased in abundance on average since the 1980s and cold-adapted species having declined (*80*).

Climate change can increase the abundance of temperature-sensitive disease vectors, with subsequent effects on disease outbreaks. In the African Serengeti, there is some evidence that a combination of extreme weather, high abundances of ticks carrying *Babesia*-piroplasm, and suppressed immunity to canine distemper virus led to widespread mortality of lions (*Panthera leo*) (*81*). In marine systems, field evidence shows that corals are increasingly susceptible to white band disease at higher temperatures, leading to declines in two of the most important reef-building acroporid (branching) corals in the western Atlantic (*82*).

## Species

### Distribution

One of the most rapid responses observed for marine, freshwater, and terrestrial species is a shift in their distributions to track optimal habitat conditions (*71*, *83*, *84*). Across land and aquatic ecosystems, species have expanded their leading (cold limit) edge by 19.7 km per decade, with marine species expanding by 72 km per decade compared with 6 km per decade in terrestrial species (*37*). The distributions of many marine taxa have shifted at higher velocities than those of terrestrial taxa (*37*) because areas with rapid changes in climate extend across broader regions of the ocean than on land, and connectivity in marine environments tends to be high (*85*). To illustrate this point, corals around Japan have shifted their range by up to 14 km per year over the past 80 years (*86*), and in waters off the southeast coast of Australia, intertidal invertebrate species have shifted their geographic distributions polewards at an average rate of 29 km per decade (*87*). Where connectivity allows for dispersal, some freshwater fishes are capable of shifting at rates comparable with those of marine and terrestrial taxa (*88*), but mean shifts by river fishes in some regions have been insufficient to compensate for measured temperature rises (*89*).

There has been a consistent overall trend for tropical, warm-adapted species to expand their ranges into environments previously dominated by temperate cold-tolerant species ("tropicalization") (*90*). A similar phenomenon has been documented in the Arctic, where boreal fish communities have responded to warming in the Barents Sea by shifting northward, resulting in a high turnover in Arctic fish communities ("borealization") (*91*). Similarly, on land, increased minimum temperatures have driven rapid changes in the range size (as well as distribution) of Swedish birds, with northern species retracting and southern species expanding northward (*92*).

In addition to latitudinal changes, many observed shifts in species distributions have occured across elevation gradients. In the mountains of New Guinea, birds have shifted their distributions upslope by 95 to 152 m from 1965 to 2013 (*93*). A similar upslope shift was observed in recent decades in mountainous stream-dwelling fish in France (*89*), North American plants (*94*), and Bornean insects (*95*). An analogous response has been the shift to deeper, colder waters among some marine fishes (*91*).

In some cases, species have shown no response or even downhill shifts in their distributions (*96*) or increased frequency of range disjunction rather than poleward or upward range shifts (*97*). Savage and Vellend (*98*) found upward range shifts in North American plant species and an overall trend toward biotic homogenization from 1970 to 2010, but their study also documents considerable time lags between warming and plant responses (*99*, *100*). Delayed community responses to increasing temperature may be in part due to the buffering effects of microhabitats (*101*, *102*) and possibly moisture, which is a critical, but less often studied, driver in the redistribution of species (*103*). For example, Crimmins *et al.* observed downhill movements for North American plants under climate change over an 80-year period, which they attribute to changes in water balance rather than temperature (*104*).

## Community

### Interspecific relationships

As a by-product of the redistribution of species in response to changing climate, existing interactions among species are being disrupted, and new interactions are emerging (*105*, *106*). These novel biotic interactions can exacerbate the impacts of abiotic climate change (*107*, *108*). Woody plants are invading arctic and alpine herb-dominated communities in response to rapid warming in recent decades, leading to secondary shifts in distribution of other plants and animals (*92*). In the Sierra Nevada Mountains of California, Tingley and Beissinger found high levels of avian community turnover during the past 100 years at the lowest and highest elevations (*109*), and in Greece, Sgardeli *et al.* found similar patterns of temperature-driven turnover in butterfly communities (*110*). There are surprisingly few studies of observed impacts of climate change on competitive interactions (*108*). In one example from Sweden, Wittwer *et al.* found that among four bird species occupying the same ecological guild, resident birds were able to adapt to warmer temperatures and outcompete the sole long-distance migrant, *Ficedula hypoleuca* (*111*).

New interactions among species can also lead to trophic disruptions such as overgrazing. In western Australia, for example, overgrazing of subtropical reefs by the poleward spread of tropical browsing fish has suppressed recovery of seaweeds after temperature-induced mortality (*112*). These types of trophic disruptions are escalating, with range shifts by tropical herbivorous fishes increasing herbivory rates in subtropical and temperate coastal ecosystems where seaweeds are the dominant habitat-forming taxa (*90*).

Phenological mismatches have been observed between butterflies and their annual host plants, with the plants dying before the insect larvae were ready to enter diapause (*113*). Similarly, an analysis of 27 years of predator-prey data from the UK showed asynchronous shifts between the tawny owl (*Strix aluco*) and its principle prey, the field vole (*Microtus agrestis*), which led to reduced owl fledging success (*114*). In Lake Washington, United States, spring diatom blooms advanced by over 20 days since 1962, resulting in predator-prey mismatches with their main grazer, the water flea (*Daphnia pulicaria*), and population declines in the latter (*60*). In Canadian Arctic lakes, asynchronous shifts in diatom blooms resulted in generalist water fleas being replaced by more specialist species (*115*). At higher trophic levels, warming has affected the fry and the juvenile life-history stages of lake char (*Salvelinus umbla*) via direct impacts on their zooplankton and vendace (*Coregonus alba*) food sources (*116*).

### Productivity

Changes in productivity are one of the most critical impacts of climate change across aquatic and terrestrial ecosystems (*117*, *118*). In marine systems, climate-mediated changes in chlorophyll-a concentrations as a proxy of phytoplankton biomass have been highly variable (*119*). Depending on location, these include both dramatic increases and decreases in abundance as well as changes in phenology and distribution of phytoplankton over the past several decades. In a global study of phytoplankton since 1899, an ~1% decline in global median phytoplankton per year was strongly correlated with increases in sea surface temperature (*120*), whereas in the Antarctic Peninsula, phytoplankton increased by 66% in southern subregions and decreased by 12% in northern subregions over a 30-year period. These conflicting observations in the Antarctic are in part linked to changes in sea surface temperature but also changes in ice cover, cloudiness, and windiness, which effect water-column mixing (*121*).

In deep tropical freshwater lakes dominated by internal nutrient loading through regular mixing, warmer surface waters confer greater thermal stability, with reduced mixing and return of nutrients to the photic zone, substantially decreasing primary productivity (*122*), phytoplankton growth (*123*), and fish abundance (*122*). In contrast, eutrophication effects are exacerbated by higher temperatures in shallow lakes, resulting in increased productivity and phytoplankton and toxic cyanobacteria blooms (*124*).

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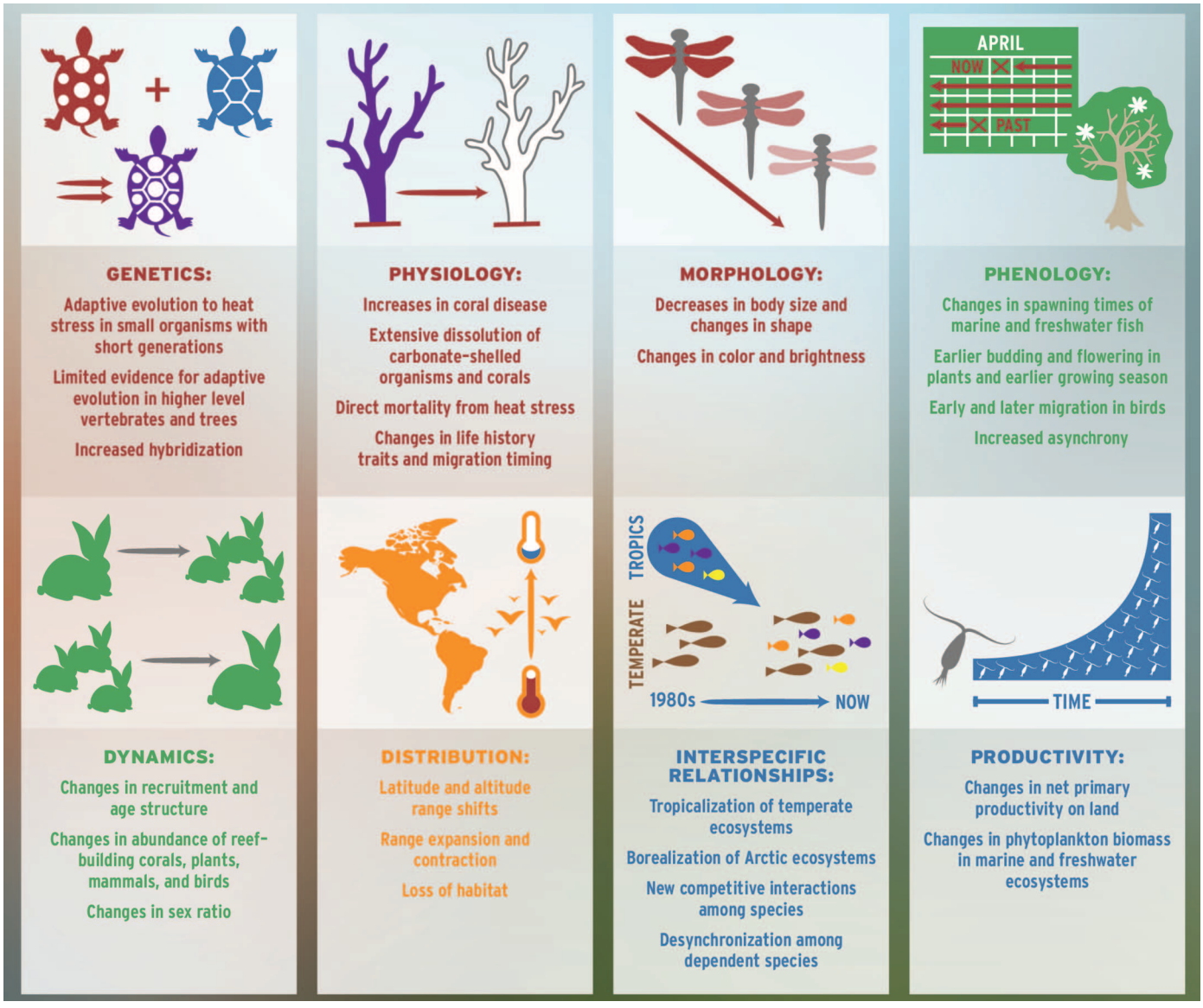


**Fig. 2. Climate impacts on ecological processes.** Examples of ecological components and processes affected by climate changes across marine, freshwater, and terrestrial ecosystems (fig. S1 and table S1).

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Globally, terrestrial plant growth has increased with increasing temperatures and $CO_2$ levels. This may in part explain the on average 6% increase in net primary productivity (NPP) from 1982 to 1999 (*125*), although these changes in NPP may also be related to natural variation in El Niño–La Niña cycles (*126*). However, responses are highly variable, and some terrestrial systems are not experiencing increased productivity owing to either extreme temperatures or lack of water. Severe short-term droughts in climatically stable rainforest environments are unusual but in recent years have increased in frequency. These events have led to changes in forest canopy structure in Amazonia (*127*) and decreases in aboveground woody and leaf biomass in the Congo basin (*128*). Across large expanses of the Amazon, there has been an overall reduction in aboveground biomass owing to increased climate variability over the past three decades (*129*).

### Impacts across ecosystems

All three biotic realms (terrestrial, freshwater, and marine) are being affected by climate change, and the evidence summarized here reveals that these impacts span the biological hierarchy from genes to communities. Of the 94 processes considered, we found that 82% have evidence of impact by climate change, and this has occurred with just 1°C of average warming globally (Fig. 1). Impacts range from genetic and physiological changes to responses in population abundance and distribution (Fig. 2).

The fact that evidence is missing for some processes is more likely to reflect data deficiencies than the absence of any response to climate change. We only considered field-based case studies that report changes in the processes through time. For many components, such as genetics (*23*) and physiology (*29*), there is strong evidence from experiments on a wide range of species that individuals and populations can and likely will respond to climate change. Thus, even though we found compelling evidence of widespread responses across the biological hierarchy, we still consider our discussion of impacted processes to be conservative. To illustrate this point, Box 1 shows the range of observed responses in the water flea *Daphnia*, which spans the entire hierarchy of biological organization.

#### Ecosystem state shifts

As ecological systems continue to accumulate stress through compromised ecological processes

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**Box 1. A complete hierarchy of climate change impact in one model system: the water flea *Daphnia*.** Combining time-series data with experimental approaches can lend insights to the breadth of climate change impacts. For water fleas of the genus *Daphnia*, for instance, there is evidence for responses to temperature at all levels of biological organization. *Daphnia* are important grazers in lakes and ponds (*180*). They adapt to temperature increase through genetic changes in thermal tolerance (*18*), body size, and life history traits (*181*, *182*). In the laboratory, *Daphnia* exhibit phenotypic plasticity in physiology to changing temperatures [for example, hemoglobin quality and quantity (*183*) or metabolic activity (*184*)], behavior [such as swimming activity (*184*)], life history traits (*185*), and body size (*182*). *Daphnia* adjust their phenology (*186*) and abundance (*187*) in response to increases in temperature, which results in mismatches with phytoplankton dynamics (*60*). Warmer, drier weather over two decades can lead to expanded distributions and increased colonization capacity (*188*). Temperature influences interactions of *Daphnia* with predators (*189*) and parasites (*190*), and adaptation to increased temperature influences competitive strength (*185*). In the absence of fish, high abundances of *Daphnia* in +4°C heated mesocosms exert strong top-down control on phytoplankton (*191*).

either directly from climate change or interactively with other forced disturbances (discussion is provided in the supplementary materials), diminished resilience may lead to ecological regime shifts—in which one ecosystem state shifts to an alternative and potentially undesirable stable state. For example, some reefs are transitioning from coral- to algal-dominated states as a consequence of mass coral mortality (*130*), whereas kelp forests are turning into rocky barrens in temperate seas (*90*, *131*, *132*). In lakes, climate change has increased the risk of regime shifts from clear-water to turbid states and increased the occurrence of cyanobacteria blooms (*124*). If sufficient community-based processes are affected at regional scales, wholesale biome shifts can occur such as has been observed in Alaska, where tundra is transitioning to boreal conditions (*133*). These are clear signs of large-scale ecosystem change and disruption, in which disequilibrium rapidly pushes the system into a new state (*134*).

## Using ecology to better understand climate change impacts on human well-being

### Threats to production

The impacts of climate change on marine fisheries have major consequences for human societies because these currently provide ~17% of the global protein for people (*135*). There is, however, no current consensus on the costs and benefits of the ongoing global redistribution of fisheries because trends are highly variable. In the Arctic, commercially important fish, such as Atlantic cod (*Gadus morhua*) and walleye pollock (*Theragra chalcogramma*), have increased in biomass primarily because of increases in plankton production from reduced sea ice (*136*, *137*), whereas changes in fish biomass in the Southern Ocean are less clear (*138*). In Switzerland, which has experienced twice the average global temperature increase, trout catches have been halved over two decades because of rising temperatures in Alpine streams (*77*).

Changes in total marine productivity are not just attributed to abundance shifts but also morphological shifts. Indeed, some fish species appear to be shrinking, but attributing this solely to ocean warming is difficult because size-dependent responses can be triggered by commercial fishing as well as long-term climate change (*139*). However, long-term trend analyses show convincingly that eight commercial fish species in the North Sea underwent simultaneous reductions in body size over a 40-year period because of ocean warming, resulting in 23% lower yields (*140*). Reduced body size in fish is also being recorded in lakes and rivers throughout Europe and has been linked to increased temperature and climate-induced shifts in nutrient inputs (*141*, *142*).

Impacts on plant genetics and physiology are influencing human agricultural systems. For example, yields in rice, maize, and coffee have declined in response to the combined effects of rising temperatures and increasing precipitation variability over past decades (*143*–*145*). Genetics is being used to counteract decreasing yields in some key crops such as wheat [for which, globally, yields have declined by 6% since the early 1980s (*146*)] through crossing domesticated crops with wild relatives to maintain the evolutionary potential of varieties (*147*). Yet, some important wild strains are also showing signs of impact from climate change. Nevo *et al*. documented high levels of genetic changes in the progenitors of cultivated wheat and barley in Israel over the past 28 years (*148*). These wild cereals exhibited landscape-level changes in flowering time and a loss of genetic diversity in response to increasing temperatures.

Losing genetic resources in nature may undermine future development of novel crop varieties (*149*) and compromise key strategies that humans use to adapt to climate change. One such strategy is to use assisted gene flow, the managed movement of individuals or gametes between populations to mitigate local maladaptation in the short and long term (*150*). Where genetic introgression—the movement of genetic material from one species into the genome of another—can occur from unexploited natural populations to managed or exploited populations that are poorly adapted to warmer or drier conditions, adaptive changes may be facilitated (*147*), as in white spruce (*Picea glauca*), a tree commonly harvested for timber (*151*). Human-assisted evolution may also be a key strategy in maintaining reef-dependent fisheries by accelerating and enhancing the stress tolerance of corals (*152*).

Phenological changes due to milder winters are influencing crop and fruit production (*153*). Climate change has reduced winter chill events in temperate agricultural areas (*154*), which can desynchronize male and female flowers and trigger delayed pollination, delayed foliation, and reduced fruit yield and quality. To counter this, tree crop industries have developed adaptation measures such as low-chill cultivars with dormancy-breaking chemicals. For example, the "UFBest" peach requires four times fewer chill days than cultivars from more temperate climates (*155*). Advances in the timing of budding, flowering, and fruiting of plant species has induced earlier harvesting periods in some countries [such as Japan (*156*)].

Pollination is a key process linked to yields for a large number of crops. The short-lived, highly mobile insect species that provide pollination services to numerous crops have responded rapidly to changing climates by shifting their ranges throughout North America and Europe (*157*). Additionally, over the past 120 years, many plant-pollinator networks have been lost with overall decline in pollination services, which is attributed to a combination of habitat loss, pollution, and climate warming (*158*). Yet, observed changes in the phenology, abundance, and distribution of common pollinators have not been directly linked to declines in yields of animal-pollinated crops. This is likely due to limited data that directly link pollination services to crop yield over time and may, in part, reflect resilience provided by the diversity of insect species that pollinate many crops (*159*, *160*). More specialized pollination systems are expected to be more vulnerable to climate change. Humans have adapted to the declines in native pollinators by transporting domesticated pollinators to crop locations.

### Pest and disease threats

Climate-induced ecosystem-level changes, such as forest die-offs, have an obvious impact on

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**Table 1. Climate change consequences for humans.** Affected ecological processes have direct consequences in food systems and human health.

| | Organism | Population | Species | Community |
|---|---|---|---|---|
| | **Genetics, physiology, morphology** | **Phenology, dynamics** | **Distribution** | **Interspecific relationships, productivity** |
| **Resource security** | Rapid genetic adaptation to climate change in timber species | Increased herbivory on crops and timber by pests | Overall distribution shifts in marine and freshwater fisheries | Decline in plant-pollinator networks and pollination services |
| | Decreased crop yields in hot climates and increases in cool climates | Decreased genetic diversity and altered flowering time in wild cereals and novel crop varieties | Reduced range size or changes in pollinator abundance | Novel pests and invasive species |
| | Increased weed-crop competition and parasite-livestock interactions | Reduced fruit yields from fewer winter chill events | | |
| | Decreased yield in fisheries from reduced body size | Reduced productivity in commercial fisheries | | |
| **Human health** | Decline in reef calcifiers threatens coastal communities; loss of protection from storm surges and loss of food/protein sources | Increased costs and risk to subsistence communities from loss of sea ice and permafrost | Expanding and/or new distributions of disease vectors | Increased human-wildlife conflicts |
| | Rapid adaptation of disease vectors to new climatic conditions | | Redistribution of arable land | Novel disease vectors |

people, with a reduction in timber supplies and carbon sequestration, and changes in water quality and watershed volume (*161*–*163*). Several native insect species from North America, with no prior records of severe infestation, have recently emerged as severe pathogens of forest resources because of changes in population dynamics. These include the Aspen leaf miner (*Phyllocnistis populiella*), the leafblotch miner (*Micrurapteryx salicifoliella*), and the Janet's looper (*Nepytia janetae*), which have decimated millions of hectares of aspen, willows, and spruce-fir forests since the early 1990s (*164*). Known pests such as mountain and southern pine beetles (*Dendroctonus frontalis* and *D. ponderosae*, respectively) and spruce beetles (*D. rufipennis*) have recently expanded their distribution and infestation intensity on commercially important pine and spruce trees (*161*, *164*). These outbreaks may increase in the future because hundreds of plant pest and pathogen species have shifted their distributions 2 to 3.5 km year$^{-1}$ poleward since the 1960s (*165*).

An emerging threat to human health under climate change is vector-borne disease (*166*). Vectors that have shifted their ranges and abundance can be found in marine, freshwater, and terrestrial systems. For example, in marine systems, unprecedented warming in the Baltic Sea led to emergence of *Vibrio* infections in Northern Europe (*167*, *168*), a geographic locality that had limited prior occurrence of this waterborne bacterial pathogen. Mosquitoes (e.g., *Aedes japonicus, A. aegypti, A. albopictus*) are extending their distribution into areas that are much warmer than their original habitats. As a result of ecological adaptation, mosquitos have become more competent vectors for spreading diseases such as chikungunya, dengue, and possibly the emerging Zika virus (*169*). Last, in terrestrial systems Levi *et al.* found that the nymph stage of the Lyme disease–carrying blacklegged tick (*Ixodes scapularis*) exhibited an overall advancement in nymph and larvae phenology since 1994, shifting the timing of greatest risk for pathogen transfer to humans to earlier in the year (*170*).

### *Losing intact ecosystems and their function*

Changes in ecological processes might compromise the functionality of ecosystems. This is an important consideration because healthy systems (both terrestrial and marine) sequester substantial amounts of carbon (*171*), regulate local climate regimes (*172*), and reduce risks associated with climate-related hazards such as floods, sea-level rise, and cyclones (*173*). In island and coastal communities, coral reefs can reduce wave energy by an average of 97% (*174*), and coastal ecosystems such as mangroves and tidal marshes buffer storms (*175*), while on land intact native forests are important in reducing the frequency and severity of floods (*176*). In many cases, maintaining functioning systems offers more sustainable, cost-effective, and ecologically sound alternatives than conventional engineering solutions (*16*).

## Science and action in a warmer world

The United Nations Framework Convention on Climate Change (UNFCCC) and the recent COP21 agreement in Paris presently offer the best opportunity for decisive action to reduce the current trajectory of climate change. This latter agreement set global warming targets of 1.5 to 2°C above preindustrial levels in order to avoid "dangerous climate change," yet the current 1°C average increase has already had broad and worrying impacts on natural systems, with accumulating consequences for people (Table 1). Minimizing the impacts of climate change on core ecological processes must now be a key policy priority for all nations, given the adoption of the UN Sustainable Development Goals aiming to increase human well-being. This will require continued funding of basic science focused on understanding how ecological processes are interacting with climate change, and of programs aimed at supporting ecosystem-based adaptations that enhance natural defences against climate hazards for people and nature and ensure ongoing provision of natural goods and services (*177*).

We must also recognize the role that intact natural ecosystems, particularly large areas, play in overcoming the challenges that climate change presents, not only as important repositories for carbon but also because of their ability to buffer and regulate local climate regimes and help human populations adapt to climate change (*16*, *173*). These systems are also critical for maintaining global biodiversity because the connectivity provided by large, contiguous areas spanning environmental gradients—such as altitude, depth, or salinity—will maximize the potential for gene flow and genetic adaptation while also allowing species to track shifting climate spatially (*178*).

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The overriding priority of the UNFCCC is to set in motion a sustained global reduction in greenhouse gas emissions. This must be achieved alongside an improvement in our understanding of key ecological processes that form the foundation of biological and human systems, and in tandem with efforts to conserve the natural habitats in which such ecological processes operate.

It is now up to national governments to make good on the promises they made in Paris through regular tightening of emission targets, and also to recognize the importance of healthy ecosystems in times of unprecedented change (*179*). Time is running out for a globally synchronized response to climate change that integrates adequate protection of biodiversity and ecosystem services.

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**SUPPLEMENTARY MATERIALS**

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**The broad footprint of climate change from genes to biomes to people**

Brett R. Scheffers, Luc De Meester, Tom C. L. Bridge, Ary A. Hoffmann, John M. Pandolfi, Richard T. Corlett, Stuart H. M. Butchart, Paul Pearce-Kelly, Kit M. Kovacs, David Dudgeon, Michela Pacifici, Carlo Rondinini, Wendy B. Foden, Tara G. Martin, Camilo Mora, David Bickford and James E. M. Watson

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Editor's Summary

**Accumulating impacts**

Anthropogenic climate change is now in full swing, our global average temperature already having increased by 1°C from preindustrial levels. Many studies have documented individual impacts of the changing climate that are particular to species or regions, but individual impacts are accumulating and being amplified more broadly. Scheffers *et al.* review the set of impacts that have been observed across genes, species, and ecosystems to reveal a world already undergoing substantial change. Understanding the causes, consequences, and potential mitigation of these changes will be essential as we move forward into a warming world.

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*Review*

# Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles

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**Abstract:** *Terrestrial habitats surrounding wetlands are critical to the management of natural resources. Although the protection of water resources from human activities such as agriculture, silviculture, and urban development is obvious, it is also apparent that terrestrial areas surrounding wetlands are core habitats for many semiaquatic species that depend on mesic ecotones to complete their life cycle. For purposes of conservation and management, it is important to define core habitats used by local breeding populations surrounding wetlands. Our objective was to provide an estimate of the biologically relevant size of core habitats surrounding wetlands for amphibians and reptiles. We summarize data from the literature on the use of terrestrial habitats by amphibians and reptiles associated with wetlands (19 frog and 13 salamander species representing 1363 individuals; 5 snake and 28 turtle species representing more than 2245 individuals). Core terrestrial habitat ranged from 159 to 290 m for amphibians and from 127 to 289 m for reptiles from the edge of the aquatic site. Data from these studies also indicated the importance of terrestrial habitats for feeding, overwintering, and nesting, and, thus, the biological interdependence between aquatic and terrestrial habitats that is essential for the persistence of populations. The minimum and maximum values for core habitats, depending on the level of protection needed, can be used to set biologically meaningful buffers for wetland and riparian habitats. These results indicate that large areas of terrestrial habitat surrounding wetlands are critical for maintaining biodiversity.*

Criterios Biológicos para Zonas de Amortiguamiento Alrededor de Hábitats de Humedales y Riparios para Anfibios y Reptiles

**Resumen:** *Los hábitats terrestres que rodean humedales son críticos para el manejo de recursos naturales. Aunque la protección de recursos acuáticos contra actividades humanas como agricultura, silvicultura y desarrollo urbano es obvia, también es aparente que las áreas terrestres que rodean a humedales son hábitat núcleo para muchas especies semiacuáticas que dependen de los ecotonos mésicos para completar sus ciclos de vida. Para propósitos de conservación y manejo, es importante definir los hábitats núcleo utilizados por las poblaciones reproductivas locales alrededor de humedales. Nuestro objetivo fue proporcionar una estimación del tamaño biológicamente relevante de los hábitats núcleo alrededor de humedales para anfibios y reptiles. Resumimos datos de la literatura sobre el uso de hábitats terrestres por anfibios y reptiles asociados con humedales (19 especies de ranas y 13 de salamandras, representando a 1363 individuos; 5 especies de serpientes y 28 de tortugas representando a más de 2245 individuos). Los hábitats núcleo terrestres variaron de 159 a 290 m para anfibios y de 127 a 289 para reptiles desde el borde del sitio acuático. Datos de estos estudios también indicaron la importancia de los hábitats terrestres para alimentación, hibernación y anidación, y, por lo tanto, que la interdependencia biológica entre hábitats acuáticos y terrestres es esencial para la persistencia de poblaciones. Dependiendo del nivel de protección requerida, se pueden utilizar los valores mínimos y máximos de hábitats núcleo para definir amortiguamientos biológicamente significativos para hábitats de humedales y riparios. Estos resultados indican que extensas áreas de hábitats terrestres que rodean humedales son críticas para el mantenimiento de la biodiversidad.*

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## Introduction

Terrestrial habitats surrounding wetlands are critical for the management of water and wildlife resources. It is well established that these terrestrial habitats are the sites of physical and chemical filtration processes that protect water resources (e.g., drinking water, fisheries) from siltation, chemical pollution, and increases in water temperature caused by human activities such as agriculture, silviculture, and urban development (e.g., Lowrance et al. 1984; Forsythe & Roelle 1990). It is generally acknowledged that terrestrial buffers or riparian strips 30–60 m wide will effectively protect water resources (e.g., Lee & Samuel 1976; Phillips 1989; Hartman & Scrivener 1990; Davies & Nelson 1994; Brosofske et al. 1997).

However, terrestrial habitats surrounding wetlands are important to more than just the protection of water resources. They are also essential to the conservation and management of semiaquatic species. In the last few years, a number of studies have documented the use of terrestrial habitats adjacent to wetlands by a broad range of taxa, including mammals, birds, reptiles, and amphibians (e.g., Rudolph & Dickson 1990; McComb et al. 1993; Darveau et al. 1995; Spackman & Hughes 1995; Hodges & Krementz 1996; Semlitsch 1998; Bodie 2001; Darveau et al. 2001). These studies have shown the close dependence of semiaquatic species, such as amphibians and reptiles, on terrestrial habitats for critical life-history functions. For example, amphibians, such as frogs and salamanders, breed and lay eggs in wetlands during short breeding seasons lasting only a few days or weeks and during the remainder of the year emigrate to terrestrial habitats to forage and overwinter (e.g., Madison 1997; Richter et al. 2001). Reptiles, such as turtles and snakes, often live and forage in aquatic habitats most of the year but emigrate to upland habitats to nest or overwinter (e.g., Gibbons et al. 1977; Semlitsch et al. 1988; Burke & Gibbons 1995; Bodie 2001).

The biological importance of these habitats in maintaining biodiversity is obvious, yet criteria by which to define habitats and regulations to protect them are ambiguous or lacking (Semlitsch & Bodie 1998; Semlitsch & Jensen 2001). More importantly, a serious gap is created in biodiversity protection when regulations or ordinances, especially those of local or state governments, have been set based on criteria to protect water resources alone, without considering habitats critical to wildlife species. Further, the aquatic and terrestrial habitats needed to carry out life-history functions are essential and are defined here as "core habitats." No summaries of habitat use by amphibians and reptiles exist to estimate the biologically relevant size of core habitats surrounding wetlands that are needed to protect biodiversity.

For conservation and management, it is important to define and distinguish core habitats used by local breeding populations surrounding wetlands. For example, adult frogs, salamanders, and turtles are generally philopatric to individual wetlands and migrate annually between aquatic and terrestrial habitats to forage, reproduce, and overwinter (e.g., Burke & Gibbons 1995; Semlitsch 1998). The amount of terrestrial habitats used during migrations to and from wetlands and for foraging defines the terrestrial core habitat of a population. This aggregation of breeding adults constitutes a local population centered on a single wetland or wetland complex. Local populations are connected by dispersal and are part of a larger metapopulation, which extends across the landscape (Pulliam 1988; Marsh & Trenham 2001).

Annual migrations centered on a single wetland or wetland complex are biologically different than dispersal to new breeding sites. It is thought that dispersal among populations is achieved primarily by juveniles for amphibians (e.g., Gill 1978; Breden 1987; Berven & Grudzien 1990) or by males for turtles (e.g., Morreale et al. 1984). Dispersal by juvenile amphibians tends to be unidirectional and longer in distance than the annual migratory movements of breeding adults (e.g., Breden 1987; Seburn et al. 1997). Thus, habitats adjacent to wetlands can serve as stopping points and corridors for dispersal to other nearby wetlands. Ultimately, conservation and management plans must consider both local and landscape dynamics (Semlitsch 2000), but core habitats for local populations need to be defined before issues of connectivity at the metapopulation level are considered.

## Literature Review

We summarize data from the literature on the use of terrestrial habitats by amphibians and reptiles associated with wetlands. We define wetlands as both lentic (pond) and lotic (stream) habitats that are either permanent or temporary (Cowardin et al. 1979). Also, we use the term riparian in the broadest sense of encompassing the shore, bank, or edge of any wetland. We used data from studies that define habitat use mainly by the adult population and report a mean, mode, or range of distance of migrations from the outer edge of wetlands (Appendices 1 & 2). We used these values to calculate a grand mean for major taxa (Table 1). Rather than calculating a 95% confidence limit, which depends on knowing the distribution of migration distances, and because some studies did not report means, we calculated a mean minimum and maximum distance for amphibians and reptiles from the distance values reported for species in each study (Table 1). These minimum and maximum values likely encompass a large portion of populations and adequately represent the majority of species. We did not use observations of individuals of unknown origin, especially juveniles, found at some distance from a wet-

**Table 1. Mean minimum and maximum core terrestrial habitat for amphibians and reptiles.***

| Group | Mean minimum (m) | Mean maximum (m) |
|---|---|---|
| Frogs | 205 | 368 |
| Salamanders | 117 | 218 |
| Amphibians | 159 | 290 |
| Snakes | 168 | 304 |
| Turtles | 123 | 287 |
| Reptiles | 127 | 289 |
| Herpetofauna | 142 | 289 |

**Values represent mean linear radii extending outward from the edge of aquatic habitats compiled from summary data in Appendices 1 and 2.*

land. Such anecdotal observations are relevant to maximum dispersal distances and the probability of recolonization and connectivity for species (Pulliam 1988) but are misleading for the calculation of core terrestrial habitat for the maintenance of local populations. The data we report reflect the size of terrestrial habitats that are biologically necessary for the conservation of amphibian and reptile diversity at individual wetlands. Further, we discuss the use of core habitat sizes in conjunction with a buffer zone and how land-use practices in the surrounding landscape matrix may modify the amount of habitat needed for adequate protection.

## Amphibian Core Habitat

Amphibians constitute an important and diverse fauna associated with both isolated wetlands (e.g., Texas, 15 species [Wiest 1982]; Florida, 16 species [Dodd 1992]; South Carolina, 27 species [Semlitsch et al. 1996]; Tennessee, 19 species [Scott & Bufalino 1997]) and stream or river floodplains (e.g., Virginia, 21 species [Buhlmann et al. 1993]; California, 4 species [Panik & Barrett 1994]; Illinois, 14 species [Burbrink et al. 1998]). The studies we reviewed indicate that amphibians use a wide range of terrestrial habitats adjacent to wetlands and streams. Most of these habitats are related to foraging, refuge, or overwintering sites and typically consist of leaf litter, coarse woody debris, boulders, small mammal burrows, cracks in rocks, spring-seeps, and rocky pools. Data on emigration distances from wetlands were found for 19 species of frogs and 13 species of salamanders representing 1363 individuals (Appendix 1).

Patterns of variation in distances traveled appear related to life-history differences between major taxonomic groups. In general, the plethodontid stream salamanders (e.g., *Desmognathus fuscus, Eurycea bislineata, Eurycea longicauda*), although migratory at some stage of their life cycle, remain close to the edges of ponds and streams and seldom move more than 20–30 m from aquatic habitats. Alternatively, some species of frogs, toads, and newts are highly vagile and move 1000–1600 m (e.g., *Bufo bufo, Rana catesbeiana, Notophthalmus viridescens*). The majority of the remaining species use intermediate distances, where they emigrate to find suitable terrestrial habitats. The overall core terrestrial habitat for amphibians ranged from 159 to 290 m from the edge of the aquatic site (Table 1).

## Reptile Core Habitat

We summarized data for five snake and 28 turtle species from 25 U.S. states and five countries (Appendix 2). We gathered migration distances from studies of known sample size (total $n = 2245$ individuals) and from those of unknown sample size. Relatively few studies have been conducted on terrestrial migrations of hydrophilic snakes. Snakes migrated into adjacent uplands for the purpose of aestivating, basking, hibernating, or nesting. Although most studies of terrestrial migrations by turtles have focused on nesting, turtles also migrated for the purposes of aestivating, feeding, and hibernating.

Similar to that of amphibians, variation in reptile migration distances appears related to taxon-specific differences in life-history patterns. Some colubrid snakes (e.g., *Nerodia* sp., *Opheodrys aestivus*), trionychid turtles (e.g., *Apalone* sp.), some emydid turtles (e.g., *Graptemys geographica*, *Sternotherus* sp.), and one chelydrid turtle (i.e., *Macroclemys temminckii*) rarely migrate >30 m from aquatic habitats. In contrast, one colubrid snake (i.e., *Coluber constrictor*), viperid snakes (e.g., *Crotalus horridus*, *Sistrurus catenatus*), many kinosternid turtles (e.g., *Kinosternum leucostomum*, *K. subrubrum*), and several emydid turtles (e.g., *Chrysemys picta*, *Clemmys* sp., *Emydoidea blandingi*, *Trachemys scripta*) routinely migrate >100 m. The length of time spent in the terrestrial habitat ranges from <1 hour (e.g., nesting *Chelydra serpentina*; Punzo 1975) to 88% of recorded activity (e.g., *Nerodia sipedon*; Tiebout & Cary 1987). Some migrations into terrestrial habitats occurred following significant rainfall or stream flooding when uplands were temporarily inundated with water (e.g., *Graptemys pseudogeographica* foraging in flooded forest; Bodie & Semlitsch 2000). The overall core terrestrial habitat for reptiles ranged from 127 to 289 m from the edge of the aquatic site (Table 1).

## Protection and Management of Terrestrial Habitat

It is not surprising that the terrestrial ecology of semiaquatic species is often underappreciated or overlooked by managers and conservation planners. Some semiaquatic reptiles make only brief visits to terrestrial habitats when nesting, and hibernacula are rarely observed. Additionally, many pond-breeding amphibians are fosso-

rial and are also rarely observed in terrestrial habitats. Surveys and studies of these animals are consequently concentrated within stream and wetland sites, where they are found seasonally, rather than in terrestrial habitats, where detection is extremely difficult but where much of their life history occurs. Aquatic habitats may not be used by semiaquatic species for extended periods of their lives, including between breeding seasons and during droughts. For example, a population of striped newts (*Notophthalmus perstriatus*) in northern Florida was relegated to predominantly terrestrial activity during a 5-year drought (Dodd 1993). Eastern mud turtles (*Kinosternon subrubrum*) in South Carolina often leave aquatic sites after mating in late spring and do not return until the following spring (Bennett et al. 1970). In both cases, the upland forest habitat had obvious importance as a reservoir for adults of these species until breeding and reproduction again occurred.

Although wetlands vary in many characteristics related to type, region, topography, climate, and land-use surrounding them, the data we compiled suggest that a single all-encompassing value for the size of core habitats can be used effectively. Maximum values generated from a taxon with the greatest need for terrestrial habitat—that is, the largest core area or home range (Table 1)—would likely encompass all other taxa and could be used more broadly. On public lands or reserve systems, where first priority is given to conserving biodiversity, this maximum value can facilitate management objectives. On private lands or areas, however, where sustainable land use is the priority, a stratified system of protection zones can minimize impacts on wildlife and support desired land uses. For example, for streams in managed forests in North America, it is recommended by deMaynadier and Hunter (1995) that criteria be adjusted for stream attributes such as width, intensity of logging, and slope adjacent to the stream. Further, the authors recommend a two-tiered approach in which the terrestrial habitat closest to the water is fully protected and a second, outer area provides limited protection (e.g., the forestry practice of light partial cutting and removal of no more than 25% of the basal area).

We propose that stratification should include three terrestrial zones adjacent to core aquatic and wetland habitats (Fig. 1): (1) a first terrestrial zone immediately adjacent to the aquatic habitat, which is restricted from use and designed to buffer the core aquatic habitat and protect water resources; (2) starting again from the wetland edge and overlapping with the first zone, a second terrestrial zone that encompasses the core terrestrial habitat defined by semiaquatic focal-group use (e.g., amphibians 159–290 m; Table 1); and (3) a third zone, outside the second zone, that serves to buffer the core terrestrial habitat from edge effects from surrounding land use (e.g., 50 m; Murcia 1995).

All things being equal, these zones of protection should extend outward from the edge of wetlands far

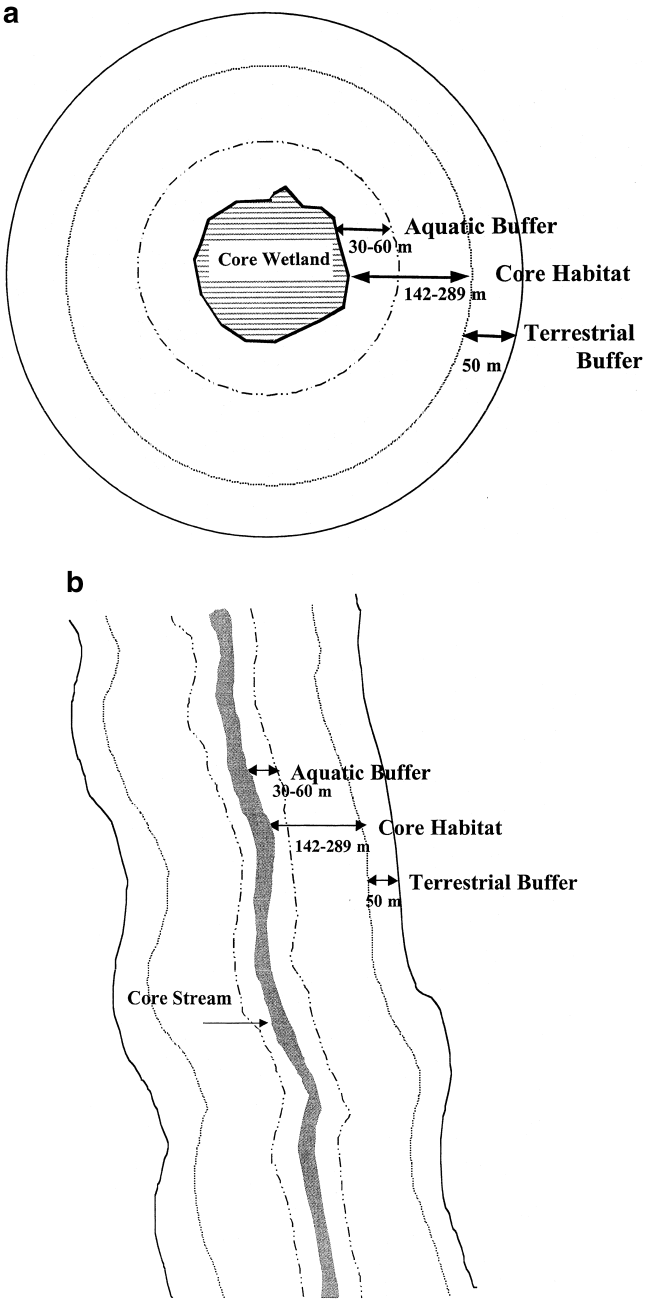


*Figure 1. Proposed zones of protection of (a) wetlands and (b) streams. Both core habitat and aquatic buffer requirements are met within the second zone, which may range from 142 to 289 m for amphibians and reptiles (see Table 1 for taxon-specific values). An additional 50-m buffer is recommended to protect core habitat from edge effects (Murcia 1995).*

enough to encompass all species populations. However, the habitats used by various species or at different life-history stages are probably not evenly distributed. To protect those habitats essential for species functions, we need to know more about species requirements at each

life-history stage and season of the year. We know that special habitats are required by some species, such as the presence of highly aerated pools along small streams or caves for thermal refuges (e.g., overwintering sites for green frogs [*Rana clamitans*; Lamoureux & Madison 1999; Birchfield & Semlitsch unpublished data], yellow-legged frogs [*Rana muscosa*; Matthews & Pope 1999], and pickerel frogs [*Rana palustris*; R.D.S., personal observation]) and mammal burrows for thermal and predatory refuges (e.g., gopher frog [*Rana sevosa*; Richter et al. 2001]), and must be included within protective zones. Habitat generalists probably use whatever habitat is available, and land use such as silviculture may be compatible with maintaining their populations. Little is known, however, about habitat requirements for even common species such as the American toad (*Bufo americanus*), often used as an example of a generalist but which may not be a generalist during all life stages. Newly metamorphosed *B. americanus* exhibit strong selection for forest habitat in the summer in Missouri (Rothermel & Semlitsch 2002). Adjusting the size of terrestrial zones, such as the core habitat, could be done on the basis of protecting different portions of the population (e.g., for turtles 50–90% [Burke & Gibbons 1995]; for ambystomatid salamanders 50–95% [Semlitsch 1998]). It is not known, however, how protecting different amounts of terrestrial habitat affects the population persistence of any species or how habitat quality (e.g., density of mammal burrows; Loredo et al. 1996) might influence that decision.

Decisions about how restrictive each zone might be to land-use practices would depend on management goals and species of concern. Although little data are available on how various amphibians and reptiles might respond to major land-use practices (e.g., logging, farming, residential development), it is reasonable to assume that some activities (e.g., hiking, bicycling), especially those not destroying essential habitats (e.g., for amphibians, vegetation canopy for shade, coarse woody debris and a litter layer used for refuge and food sources), could be conducted in this outer zone of protection and be compatible with the goal of protecting biodiversity. In applying these criteria and bolstering the biological values of core terrestrial habitats, policymakers could develop stratified habitat zones that guide associated protection or management intensity, resulting in more effective conservation of biodiversity along with sustainable land use.

## Conclusions

We provide biologically based estimates for the protection of terrestrial habitats surrounding wetlands. Our data clearly indicate that buffers of 15–30 m, used to protect wetland species in many states, are inadequate for amphibians and reptiles. Further, we emphasize that our estimates are derived from the core terrestrial habitats used by amphibians and reptiles and therefore are not buffers per se but necessary habitat. Additional area of terrestrial habitat is needed to fully protect core habitats and minimize edge effects (Fig. 1). For maximum protection, this may be more land than managers can provide, although we do not believe that our estimates are excessive biologically. And we are not naïve enough to believe that all terrestrial land-use activities around wetlands must be excluded. It is our intent, however, to ensure that managers and conservation biologists recognize that both aquatic and terrestrial habitats are essential for maintaining biodiversity and that they must be managed as an integral unit to protect biodiversity. Further, we want managers to know that little is known about the effects of land-use practices on amphibians and reptiles and that without further research it cannot be known whether any such practices used within the core habitat are potentially harmful to their long-term persistence. We hope this discussion generates more research on the effects of land-use practices on plants and animals and that biologists begin testing the effectiveness of various criteria for protecting the core habitats of species. A sustainable balance between continuing economic development and protecting natural resources depends on knowing and responding to species' biological requirements and knowing how tradeoffs affect the maintenance of biodiversity.

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**Appendix 1. Summary of terrestrial migration distances from aquatic breeding sites for amphibians.**

| *Species and location* | Distance in m (sample size) | *Data source* |
|---|---|---|
| Frogs | | |
| *Acris crepitans,* Illinois | range 8–22 (189) | O'Neil 2001[a] |
| *Bufo americanus,* Ontario | range 23–480 (176) | Oldham 1966[a] |
| *Bufo boreas,* Colorado | mode = 900 | Campbell 1970[b] |
| Wyoming | maximum = 101 | Carpenter 1954[a] |
| *Bufo bufo,* Germany | mode 70–760, maximum = 1600 | Sinsch 1988[a] |
| *Bufo hemiophrys,* Minnesota | range 23–35 (6) | Breckenridge & Tester 1961[b] |
| *Bufo japonicus formosus,* Japan | mean = 98.5, range 27–260 (19) | Kusano et al. 1995[c] |
| *Bufo marinus,* New Guinea | mean = 150 | Zug & Zug 1979[a] |
| *Bufo valliceps,* Texas | range 31–72 | Blair 1953[a] |
| *Hyla andersoni,* New Jersey | mean = 70, maximum = 106 (8) | Freda & Gonzalez 1986[b] |
| *Hyla regilla,* Oregon | mode = 92, maximum = 240 | Jameson 1956[a] |
| *Pseudacris ornata,* Florida | maximum = 55 | Ashton & Ashton 1977[b] |
| *Pseudacris triseriata,* Indiana | mean = 75, maximum = 213 (9) | Kramer 1973[b] |
| *Rana capito,* Florida | range 280–480 | Greenberg 2001[a] |
| *Rana catesbeiana,* New York | mean = 406, mode = 1046 (22) | Ingram & Raney 1943[a] |
| *Rana clamitans,* Ontario | mean = 137, maximum 457 | Oldham 1967[a] |
| New York | mean = 121, maximum = 360 | Lamoureux & Madison 1999[c] |
| Missouri | mean = 485, range 321–570 (6) | Birchfield & Semlitsch 2002[c] |
| *Rana muscosa,* California | range 66–142 (81) | Matthews & Pope 1999[a] |
| *Rana pretiosa,* Montana | range 41–443 | Hollenbeck 1976[a] |
| Wyoming | maximum = 46 | Carpenter 1954[a] |
| Wyoming | range 369–462 | Turner 1960[a] |
| *Rana sevosa* , Mississippi | mean = 173, range 49–299 (12) | Richter et al. 2001[c] |
| *Syrrhophus marnocki,* Texas | mean = 213, range 114–303 | Jameson 1955[a] |
| Salamanders | | |
| *Ambystoma californiense,* California | mean = 36, range 8–129 (59) | Loredo et al. 1996[a] |
| California | mean = 114, maximum = 248 (11) | Trenham 2001[c] |
| *Ambystoma jeffersonianum,* Michigan | mean = 39, range 22–108 (6) | Wacasey 1961[a] |
| Michigan | mean = 92, range 15–231 (45) | Wacasey 1961[d] |
| Indiana | mean = 252, range 20–625 (86) | Williams 1973[b] |
| Kentucky | mean = 250 (10) | Douglas & Monroe 1981[b] |
| *Ambystoma maculatum,* Michigan | mean = 67, range 26–108 (2) | Wacasey 1961[a] |
| Michigan | mean = 103, range 15–200 (14) | Wacasey 1961[d] |
| Indiana | mean = 64, range 0–125 (7) | Williams 1973[b] |
| Kentucky | mean = 150, range 6–220 (8) | Douglas & Monroe 1981[b] |
| Michigan | mean = 192, range 157–249 (6) | Kleeberger & Werner 1983[b] |
| New York | mean = 118, range 15–210 (8) | Madison 1997[c] |
| *Ambystoma opacum,* Indiana | mean = 194, range 0–450 (12) | Williams 1973[b] |
| Kentucky | mean = 30 (6) | Douglas & Monroe 1981[b] |
| *Ambystoma talpoideum,* South Carolina | mean = 178, range 13–287 (17) | Semlitsch 1981[b] |
| *Ambystoma texanum,* Indiana | mean = 52, range 0–125 (10) | Williams 1973[b] |
| *Ambystoma tigrinum,* South Carolina | 162 (1) | Semlitsch 1983[b] |
| South Carolina | mean = 215, range 112–450 (4) | Semlitsch et al., unpublished data[c] |
| New York | mean = 60, range 0–286 (27) | Madison & Farrand 1998[c] |
| *Desmognathus fuscus, Kentucky* | maximum = 17 (14) | Barbour et al. 1969[b] |
| Ohio | maximum = 20 (16) | Ashton 1975[b] |
| *Eurycea bislineata,* Ohio | maximum = 31 (20) | Ashton & Ashton 1978[b] |
| *Eurycea longicauda,* New Jersey | mode = 6, maximum = 31 | Anderson & Martino 1966[a] |
| *Hynobius nebulosus tokyoensis,* Japan | maximum = 100 (48) | Kusano & Miyashita 1984[a] |
| *Notophthalmus viridescens,* Massachusetts | mode = 800 (383) | Healy 1975[a] |
| *Taricha torosa granulosa,* Oregon | mode = 185 | Pimentel 1960[a] |

[a] *Uniquely marked individuals.*
[b] *Radioactive tags.*
[c] *Radiotransmitters.*
[d] *Unmarked individuals.*

**Appendix 2.** **Summary of terrestrial migration distances from aquatic sites for reptiles.**

| *Species and location* | *Distance in m (sample size)* | *Data source* |
|---|---|---|
| Snakes | | |
| *Crotalus horridus*, New Jersey | maximum = 700 (15) | Reinert & Zappalorti 1988[a] |
| *Nerodia harteri*, Texas | mean = 2.1, range 0–15 (8) | Whiting et al. 1997[a] |
| *Nerodia sipedon*, Wisconsin | maximum = 6 (10) | Tiebout & Cary 1987[a] |
| *Opheodrys aestivus*, Arkansas | mode = 3, range 0–5 (31) | Plummer 1981[b] |
| *Sistrurus catenatus*, Pennsylvania | mode = 200 (25) | Reinert & Kodrich 1982[a] |
| Turtles | | |
| *Apalone ferox*, Florida | 22.9 (1) | Goff & Goff 1935[c] |
| *Apalone mutica*, Iowa | range 3–18 | Muller 1921[c] |
| Iowa | range 2–8 | Goldsmith 1945[c] |
| Kansas | mean = 38.2, range 4–90 (104) | Fitch & Plummer 1975[c] |
| *Apalone spinifera*, Arkansas | mean = 2.5, range 2–3 (4) | Plummer et al. 1997[b] |
| Indiana | mode = 2 | Newman 1906[c] |
| Minnesota | 0.3 (1) | Hedrick & Holmes 1956[c] |
| Nebraska | 4.5 (1) | Gehlbach & Collette 1959[c] |
| *Chelydra serpentina*, Florida | mean = 93.7, range 38–141 (7) | Punzo 1975[c] |
| Michigan | mean = 37.2, range 1–183 (210) | Congdon et al. 1987[b] |
| Nebraska | mode = 25, maximum =100 | Iverson et al. 1997[b,c] |
| New York | mean = 27.4, range 1–89 | Petokas & Alexander 1980[b] |
| *Chrysemys picta*, Idaho | mode = 200, maximum = 600 | Lindeman 1992[b] |
| Michigan | mean = 60.4, range 1–164 (185) | Congdon & Gatten 1989[b] |
| Quebec, Canada | mean = 90.4, range 1–621 (51) | Christens & Bider 1986[a,b] |
| *Clemmys guttata*, Connecticut | range = 3–265 (9) | Perillo 1997[a] |
| Michigan | maximum = 150 | Harding & Bloomer 1979[b] |
| Pennsylvania | range 60–250 (207) | Ernst 1976[b] |
| *Clemmys insculpta*, Canada | mean = 27, range 0–500 (10) | Foscarini & Brooks 1993[b] |
| Pennsylvania | mode = 300, maximum = 600 (50) | Kaufmann 1992[a,b] |
| New Hampshire | mean = 60.3 (9) | Tuttle & Carroll 1997[a] |
| New York | maximum = 200 (189) | Carroll & Ehrenfeld 1978[b] |
| *Clemmys marmorata*, California | mean = 168, range 39–423 (19) | Reese 1996[a] |
| *Deirochelys reticularia*, Texas | 30 (1) | David 1975[c] |
| Virginia | mean = 95, range 32–192 (4) | Buhlmann 1995[a] |
| *Emydoidea blandingi*, Illinois | mean = 815, range 650–900 (3) | Rowe & Moll 1991[a] |
| Michigan | mean = 135, range 2–1115 (105) | Congdon et al. 1983[b] |
| Wisconsin | mean = 168 (16) | Ross & Anderson 1990[a,b] |
| *Graptemys barbouri*, Florida | 200 (1) | Ewert & Jackson 1994[c] |
| *Graptemys ernsti*, Alabama | range 3–15 | Shealy 1976[b] |
| *Graptemys flavimaculata*, Mississippi | mode = 100 (20) | Jones 1996[a] |
| *Graptemys geographica*, Quebec, Canada | mean = 2.3, range 2–3 (3) | Gordon & MacCulloch 1980[b] |
| *Graptemys oculifera*, Mississippi | range 7–17 | Jones 1991[c] |
| *Graptemys pseudogeographica*, Missouri | mean = 353, range 0–1133 (15) | Bodie & Semlitsch 2000[a] |
| *Kinosternon baurii*, Florida | mean = 15.6, range 1–49 (23) | Wygoda 1979[b] |
| *Kinosternon flavescens*, Iowa | range 100–450 | Christiansen et al. 1985[a] |
| Nebraska | range 21–191 (33) | Iverson 1990[a] |
| *Kinosternon leucostomum*, Mexico | mean = 275, range 0–600 (14) | Morales-Verdeja & Vogt 1997[a] |
| *Kinosternon subrubrum,* South Carolina | mean = 103.4, range 1–600 (20) | Bennett et al. 1970[d] |
| South Carolina | mean = 200, range 100–300 (2) | Bennett 1972[d] |
| South Carolina | mean = 49.3, range 17–90 (25) | Burke et al. 1994[a] |
| South Carolina | mean = 61.6, range 18–135 (115) | Burke 1995[a] |
| *Macroclemys temminicki*, Florida | mean = 12.2, range 3–22 (12) | Ewert 1976[c] |
| Florida | maximum = 200 (106) | Ewert & Jackson 1994[c] |
| *Malaclemys terrapin*, New Jersey | mode = 150 (40) | Burger & Montevecchi 1975[c] |
| *Podocnemis unifilis*, Venezuela | mean = 38.3, range 21–80 (422) | Escalona & Fa 1998[c] |
| *Pseudemys floridana*, South Carolina | mean = 106.7, range 62–286 (19) | Burke 1995[a] |
| *Pseudemys rubriventris*, Massachusetts | range 10-250 | Ernst et al. 1994[b] |
| *Sternotherus depressus*, Alabama | 6.5 (1) | Dodd 1988[c] |
| *Sternotherus odoratus*, Pennsylvania | mean = 6.6, range 3–11 (27) | Ernst 1986[c] |
| *Trachemys scripta*, Florida | mode = 180 | Carr 1952[c] |
| Louisiana | maximum = 1600 | Cagle 1950[c] |
| Missouri | mean = 348, range 0–1394 (11) | Bodie & Semlitsch 2000[a] |
| Panama | mean = 50, range 2–320 (139) | Moll & Legler 1971[b] |
| South Carolina | mean = 86.5, range 23–299 (11) | Burke 1995[a] |

[a] *Radiotransmitters.*
[b] *Uniquely marked individuals.*
[c] *Unmarked individuals.*
[d] *Radioactive tags.*

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# Constant Wildfires Leave California Firefighters Strained

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Heard on Weekend Edition Saturday

California hasn't had a month without a wildfire since 2012. NPR's Scott Simon speaks with Mike Feyh of the Sacramento Fire Department about the strain on firefighters.

SCOTT SIMON, HOST:

The Carr Fire rages in Northern California this weekend, but there's also the Ferguson Fire and the Butte Fire. State emergency management officials say there hasn't been a month without a wildfire in California since 2012. Many firefighters are working 16-hour shifts. Jason Campbell was fighting the Ferguson fire when he learned his house burned in the Carr Fire. He still reported to work.

(SOUNDBITE OF ARCHIVED RECORDING)

JASON CAMPBELL: The only way I felt that I was going to be able to deal with it is just to come out here and deal with the fire personally. You know, it might have taken everything that belongs to me, but it's taken everything from other people. So I made it my personal goal just to get out here and show the guys that, you know, this is what you do. The community comes together, and everybody come out here with a common goal. And that was to get this thing out, so it doesn't happen to other people.

SIMON: Firefighter Jason Campbell, who is a crew boss with the commercial disaster response firm GFP. We're going to turn now to Capt. Mike Feyh of the Sacramento Fire Department.

Captain, thanks so much for being with us.

MIKE FEYH: Sure, it's a pleasure.

SIMON: Help us understand what kind of strain all of these fires have caused firefighters in their departments.

FEYH: Well, it's been a huge strain. I mean, currently here in the city of Sacramento, we have two rigs that are currently deployed - as well as what we call overhead team members. So that's another four individuals. So currently that's just 12, which then impacts our staffing hugely when we're already stretched to the limits.

SIMON: You've been on the fire line yourself, haven't you?

FEYH: Yes, I have. I've been out on these wildland incidents. And typically for our department, which we refer to as local government, we'll go out for 14 to 16 days at a time. And we're out there - and we alternate with 24-hour shifts. But sometimes in the beginning, you'll end up being out on the line for up to 48 hours before you actually get back in and can get some rest and food.

SIMON: Which means, by the time you actually have to fight the fire, you might be - you will be sleep-deprived, exhausted, hungry. And months and months of this must - forgive the phrase - burn out people.

FEYH: And it is. And we're starting to see that among our members. We talk about fire season, but there truly isn't a fire season anymore. Traditionally, that would run from April to May through, you know, September to October here in the state of California. But last year, the Thomas Fire was burning into December. And actually I don't think it was officially put out until March.

SIMON: And is there - as there is in a group of soldiers or police officers, is there some ethic or code of conduct which seems to discourage firefighters from saying they're

injured or hungry or need help?

FEYH: And that's one of the other things that we've been battling. And we've tried to raise awareness to firefighters throughout the country - is on the behavioral health side of stuff. We have people who need help. They've got injured. They're suffering from maybe addiction - alcohol, drug. And we've found that if we can actually get out there, do a little bit of preventive education for our members, that we can actually maybe start to reduce the number of firefighter suicides, which has increased drastically over the last 10 to 15 years.

SIMON: I didn't know that. Firefighter suicides have been increasing?

FEYH: Yes. It's almost getting to epidemic proportion. I mean, it's starting to rival our other work-related injuries. And we're finding that a lot of it's due to chronic exposure to multiple trauma and emergency-type response incidents. And then you stack on increased hours, increased workload. And the strain just continues to grow and grow on firefighters to the point where - I mean, it's almost like a rubber band. They're stretched completely thin. Eventually, they're going to snap.

SIMON: If wildfires are going to become a way of life, what do you need?

FEYH: Well, I've been on the Sacramento Fire Department for 24 years. We still have the same number of engines and trucks as we did when I first came on this job. Since then, our call volume has more than tripled. So we need to add resources. We don't have the firefighters and the equipment that we need.

SIMON: We just had a clip from firefighter Jason Campbell, who's with a commercial disaster response company. Is there an increased role for companies like that?

FEYH: I'm sure there is. But some of the things that we're doing with the public agencies is the fact that they will always be there. Civilian agencies, private contractors - there's never that assurance that they're going to be there from the next day.

SIMON: Capt. Mike Feyh of the Sacramento Fire Department. Thanks so much, sir.

FEYH: You're welcome, Scott. Have a nice day.

(SOUNDBITE OF BRONTIDE'S "KNIVES")

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# Birdsong and anthropogenic noise: implications and applications for conservation

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**Abstract**

**The dramatic increase in human activities all over the world has caused, on an evolutionary time scale, a sudden rise in especially low-pitched noise levels. Ambient noise may be detrimental to birds through direct stress, masking of predator arrival or associated alarm calls, and by interference of acoustic signals in general. Two of the most important functions of avian acoustic signals are territory defence and mate attraction. Both of these functions are hampered when signal efficiency is reduced through rising noise levels, resulting in direct negative fitness consequences. Many bird species are less abundant near highways and studies are becoming available on reduced reproductive success in noisy territories. Urbanization typically leads to homogenization of bird communities over large geographical ranges. We review current evidence for whether and how anthropogenic noise plays a role in these patterns of decline in diversity and density. We also provide details of a case study on great tits (*Parus major*), a successful urban species. Great tits show features that other species may lack and make them unsuitable for city life. We hypothesize that behavioural plasticity in singing behaviour may allow species more time to adapt to human-altered environments and we address the potential for microevolutionary changes and urban speciation in European blackbirds (*Turdus merula*). We conclude by providing an overview of mitigating measures available to abate noise levels that are degrading bird breeding areas. Bird conservationists probably gain most by realizing that birds and humans often benefit from the same or only slightly modified measures.**

*Keywords*: adaptation, biodiversity, city life, conservation, ecological speciation, homogenization, traffic noise, urbanization

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## Introduction

Urbanization concerns all environmental changes associated with urban development and is a global phenomenon affecting animals, including humans, as well as plants (Vitousek et al. 1997; Western 2001). Expectations are that in the next two decades an additional two billion people will need a place to live, and they will not live in the current cities but in newly developed urban areas (Meyer & Turner 1992; World Resources Institute 2004). Urbanization usually has a negative effect on rare species and favours others that become more and more common, which can be native generalist species, but often means non-native urban colonizers (Bolger et al. 1997; Sewell & Catterall 1998; Lim & Sodhi 2004; Marzluff 2005). At a local scale, urbanization does not necessarily lead to a drop in species diversity because the heterogeneous urban habitat does provide quite a variety of niches. However, at a larger scale, urbanization leads to homogenization and a drop in diversity because the typical urban species turn out to be the same everywhere irrespective of the original fauna (Clergeau et al. 2006; McKinney 2006). For species that still occur within and outside of cities, it is known that urban challenges may be relatively stressful as reflected for example by a divergence in heterophil-leucocyte ratios (Ruiz et al. 2002) or increased baseline cortecosterone levels in male birds of city environments (Bonier et al. 2007). Nevertheless, although many species disappear from urban areas because they depend on habitat features that do not exist anymore, others find a new niche among bricks and concrete and adapt to a life in the city (Luniak 2004).

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Cities differ from rural or forested areas in a number of ways (Warren *et al*. 2006; Slabbekoorn *et al*. 2007). Urban areas are usually warmer, have artificial lighting regimes, more chemical pollution, and have relatively little and often exotic vegetation in a landscape dominated by street pavement and concrete buildings. Furthermore, cities harbour a different suit of parasites (Gregoire *et al*. 2002) and predators including domestic cats (Woods *et al*. 2003; Lepczyk *et al*. 2004), and a different set of food sources (Horak & Lebreton 1998). For example, urban house sparrows are reported to have higher cholesterol levels compared to rural ones, and food samples indeed reveal higher fat and protein content in urban diets (Gavett & Wakeley 1986). Consequently, food preferences also affect which species are more likely to do well under the urban food conditions; omnivorous and frugivorous birds are typically more successful than insectivorous and carnivorous species (Clergeau *et al*. 1998; Lim & Sodhi 2004).

One of the most prominent novel urban conditions concerns the ambient noise and the acoustic space available for animals to use acoustic signals (Slabbekoorn & Peet 2003; Katti & Warren 2004). All habitats are noisy to some extent, but the usual urban cacophony produced by cars, mopeds and all sorts of machinery is evolutionarily speaking novel and dramatically different from most natural habitats. Urban noise is typically loud and low in pitch which also applies to anthropogenic noise in areas around highways, railway lines and airports — which together form an ever denser network penetrating deeply into rural and forested areas (Forman & Alexander 1998; Reijnen & Foppen 2006). Anthropogenic noise could be an important factor driving bird species out of cities and away from highways, even when other habitat requirements are still sufficient.

Many studies have reported lower species diversity and lower breeding densities of birds along highways (Van der Zande *et al*. 1980; Reijnen & Foppen 1991, 1994; Illner 1992; Kuitunen *et al*. 1998, 2003). The negative impact of roads on birds has been linked repeatedly with traffic load (Reijnen *et al*. 1995, 1997; Forman *et al*. 2002; Peris & Pescador 2004), showing that the impact is not due to the mere presence of a road. However, direct evidence for traffic noise being the dominant detrimental factor is still lacking and other potential factors are visual disturbance, chemical pollution, road-kills and soil vibration. An interesting study concerns an impact assessment along a German motorway, which revealed a song-frequency-dependent pattern in breeding density in two transects parallel to the road (Rheindt 2003). Bird species with relatively low mean song frequencies were less abundant near the road, while species singing with higher frequencies occurred in higher numbers near the noisy road than in the more quiet transect. Although the lack of replication and statistical significance were limitations to this study, this is the first direct indication that low-frequency traffic noise may constrain breeding opportunities of birds.

Few studies have tried to assess a negative impact of anthropogenic noise on birds while excluding other possibly contributing factors. A study in natural habitat of the Rocky Mountains, USA, showed a negative correlation between the number of species and anthropogenic noise levels (Stone 2000). Another recent study reported the first data on a decline in reproductive success due to anthropogenic noise without confounding parameters typically associated with highway or urban studies (Habib *et al*. 2007). The authors compared ovenbirds (*Seiurus auropilla*) in Canada, in two sets of territories of equal quality, except for either being located next to noise-generating compressor stations or next to noiseless well pads. Significantly more inexperienced first-year breeders were found at the noisy locations, while the pairing success at noisy territories showed a considerable decline, independent of the individual quality. This study unequivocally confirms a negative impact of human-generated ambient noise, but how does the sound affect the birds?

In this paper, we will address in what way birds may be affected by anthropogenic noise as well as how birds may counteract artificially altered noise conditions in their territories. We will discuss a case study of great tits (*Parus major*) which provides insight into how a successful urban species gets at least partly around the noise problem in cities across Europe. Subsequently, we will address to what extent urban habitat may drive divergence of urban populations and how sensible it is to make a case for ecological speciation in this context. The potential emergence of new urban species takes place over an evolutionary time scale and does not relate to conservation of today's biodiversity. Therefore, we will conclude with considering the available options to abate the negative impact of anthropogenic noise on current species at an ecological time scale.

## *Noise annoys*

Extreme noise levels can result in temporary and permanent hearing loss (Ryals *et al*. 1999), but also the ubiquitous condition of more moderate noise levels may have adverse impacts. In humans, traffic noise at the front door of people's houses is a significant predictor of ischemic heart disease (a hospital-based case-control study with controls matched according to sex, age and hospital: Babisch *et al*. 2005), and repetitive exposure to aircraft noise has been shown to reduce performance at school (Stansfeld *et al*. 2005). Even relatively modest noise levels of train- and car traffic can already negatively affect cognitive development and reading skills (Lercher *et al*. 2003). Clearly, humans pay a price for

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living in noisy cities or along roads with heavy traffic loads with respect to physical and psychological welfare (Miedema & Vos 1998; Nilsson & Berglund 2006). This may also be true for animals, including birds.

Measurements to assess direct and detrimental physical effects of anthropogenic noise on birds, such as an increased heart-beat (Helb & Hüppop 1991), are rare or nonexistent. Nevertheless, a wide variety of animal species has been reported to be affected by anthropogenic noise as indicated by behavioural changes (e.g. birds: Slabbekoorn & Peet 2003; Brumm 2004; whales: Foote *et al*. 2004; Miller *et al*. 2000; frogs: Sun & Narins 2005; ground squirrels: Rabin *et al*. 2006). One of the behavioural changes concerns an increase in vigilance behaviour at the expense of time spent feeding (Rabin *et al*. 2006). For example, chaffinches (*Fringilla coelebs*) spend less time with their head down, pecking at food, during artificially increased noise levels (Quinn *et al*. 2006). The nature of the behavioural change in this experiment suggests that these birds did not change general alertness due to a novel stimulus but have to rely more on visual scanning for predators when the detection of auditory cues is limited by masking noise. Predation risk in noisy conditions may therefore have negative consequences for food-intake rates and ultimately lead to lower survival and lower reproductive success.

Anthropogenic noise may not only hamper the detection of heterospecific predators but also the detection of conspecifics. Many animal species, and especially birds, depend heavily on acoustic signals for intraspecific communication (Catchpole & Slater 1995; Marler & Slabbekoorn 2004). Typically, males defend a territory for access to food, hiding places and nest sites. Singing and song features such as repertoire size or spectral and temporal details may have a direct impact on how well they are able to do so. Encoded in acoustic variation, birds may convey a message about their species identity, fighting ability and motivation to defend a resource (e.g. Ten Cate *et al*. 2002; Ripmeester *et al*. in press). Successful transmission of such a message may prevent competitors from approaching and may save energy, time and risks of injury. In addition, females also pay attention to these messages and are known to select their mates based on male song features (Riebel 2003). Therefore, whether songs are heard properly or not may have serious consequences for territory tenure and mate attraction (Klump 1996), potentially affecting individual fitness and population viability.

However, there are many signalling strategies available to birds to avoid or reduce masking by ambient noise (Brumm & Slabbekoorn 2005). Species-specific abilities in this respect may explain why some species resist urban noise conditions and others do not. A widespread strategy, for example, concerns the Lombard effect: birds as well as humans raise their signal amplitude with noise level. Recently, urban nightingales (*Luscinia megarhynchos*) in the city of Berlin, Germany, were found to raise their song volume in response to traffic noise; as a result they appear to sing louder on weekday mornings than in weekends (Brumm 2004). Another way to adjust to fluctuating noise conditions concerns a temporal shift in singing activity. Several urban bird species are reported to start singing earlier during the day than their forest counterparts (Bergen & Abs 1997), but the potential relationship with avoiding traffic peaks has not been investigated in enough detail yet. However, European robins (*Erithacus rubecula*) sing both, during day and night time, and whether or not birds are active during the night was recently shown to be dependent on day-time noise levels in a study in the city of Sheffield, UK (Fuller *et al*. in press). There was less of an effect in this study of ambient light pollution, to which nocturnal singing in urban birds is frequently attributed. Although it is not clear yet whether nocturnally active robins reduce their day-time activity and whether they gain any fitness benefits by doing so, it seem plausible that this strategy may enable them to avoid masking noise and breed in noisy territories. In general, a division between species surviving in urban conditions and those fleeing the cities may very well depend on how effectively members of a species can adjust their signalling behaviour to the volume, temporal fluctuations or spectral characteristics of traffic noise.

### *Signalling flexibility in urban great tits*

Over the last five years, we have studied patterns of song variation among individual great tits (*Parus major*) within an urban population in Leiden, The Netherlands, and among 20 different urban and forest populations across Europe. We first found in the single-population study that individual variation in the frequency range correlated to local urban noise levels (Slabbekoorn & Peet 2003). Birds of noisier territories sang with higher minimum frequencies, thereby avoiding masking by low-pitched traffic noise (Fig. 1). We speculated at the time that these results could mean that urban birds could have diverged from forest birds, and that flexibility through learning may be the behavioural mechanism underlying the correlation. Subsequently, we confirmed that urban birds across Europe have diverged from nearby forest birds in several parameters, among which the minimum frequency. A surprising 10 out of 10 independent city–forest comparisons revealed a consistent shift (Slabbekoorn & den Boer-Visser 2006).

The habitat-dependent acoustic shift in great tits could be an evolutionary or ontogenetic shift, or it could be based on the ability to adjust at an even shorter temporal

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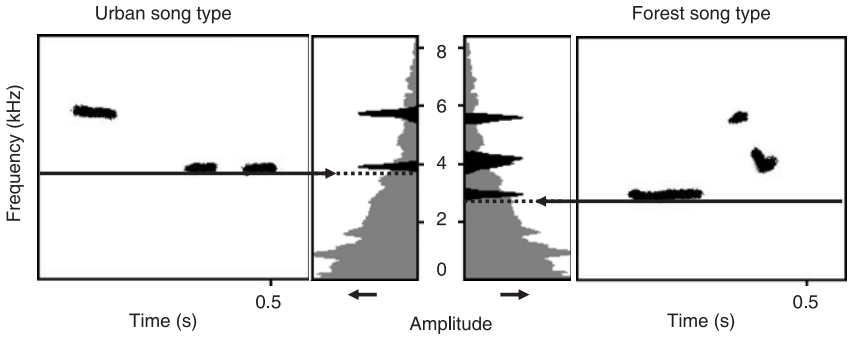


**Fig. 1** Sonograms of a three-note song type recorded in an urban habitat, with a relatively high minimum frequency (3.8 kHz, left graph) and of a three-note song type recorded in a forest habitat with a relatively low minimum frequency (2.7 kHz, right graph). The centre panels illustrate the energy concentration of each of the spectral components present in the song, normalized at an equal amplitude and contrasted, at an arbitrary level, against the energy distribution of a typical anthropogenic sound spectrum of urban traffic noise. Noise levels gradually increase towards lower frequencies, and the figure illustrates that critical signal-to-noise ratios leading to perceptual problems are more likely for notes of low frequency. As a consequence, song types without relatively low notes will on average be heard better in noisy cities.

scale (Patricelli & Blickley 2006). It is known from long-term field observations that great tits are probably capable of postdispersal adjustment of song-type repertoires guided by vocal interactions with neighbours (McGregor & Krebs 1989). Noisy conditions may affect such social influences through selective copying or selective reinforcement: song types of neighbours that are not heard well may not be copied, and song types sung but hardly eliciting a response from neighbours may be dropped. Recently, we found that adult males are even more flexible than previously thought. We played back unfamiliar song types and assessed the repertoire of a series of males before and after playback (Franco & Slabbekoorn, unpublished). The song-type repertoire size remained relatively constant over the season, but the rates at which different song types were sung varied and the repertoire composition was sometimes modified dramatically within a week. This shows that great tits have a larger repertoire memorized than they actually sing at a time or that they can make up new song types late in life. Most importantly, this means they have remarkably flexible singing behaviour. They are capable of mobilizing a large set of song types to adjust to new neighbours or possibly to new noise conditions.

The singing behaviour and repertoire flexibility of great tits has likely evolved to fit their social system in the context of the original forest habitat. They may be just lucky in the sense that these features turn out to be very suitable for coping with dramatic and, evolutionarily speaking, sudden rises in anthropogenic noise levels. The ability to spectrally adjust their song after dispersal to the local circumstances of a breeding territory, and this potentially throughout life, may be key to urban success. At the same time, despite the fact that they remain in cities breeding at relatively high densities, it is not certain that great tits are not at all negatively affected by anthropogenic noise (see Box 1). However, their acoustic counter-strategy seems at least sufficient for urban populations to survive under potentially suboptimal conditions (also see Junker-Bornholdt *et al.* 1998). Our results from the single-population study have now been independently replicated in two other North American bird species that are also very successful in urban environments (house finch, *Carpodacus mexicanus*: Fernández-Juricic *et al*. 2005; song sparrow, *Melospiza melodia*: Wood & Yezerinac 2006). An earlier study on chaffinches did not find a correlation between traffic noise levels and call characteristics (Skiba 2000). Nevertheless, this species, which can be very common in cities, does show the same increase in minimum frequency of their songs with varying levels of natural river noise (Brumm & Slater 2006). We are now waiting for data showing that bird species which are less successful in noisy areas are lacking the ability of spectral adjustment through repertoire changes.

### *Divergent phenotypes in great tits: a case for urban speciation?*

Behavioural plasticity may allow urban birds enough time to evolve and adapt to human-altered environments. Although it is possible, currently there is no evidence that the acoustic divergence between city and forest tits involves any microevolutionary changes and associated genetic differentiation. However, habitat-dependent divergence in a sexual trait like song in birds may play an important role in population divergence and ecological speciation (Slabbekoorn & Smith 2002a, b), and we may be able to consider urban speciation. Species with a distribution across ecological gradients may evolve different subpopulations in different habitats. These

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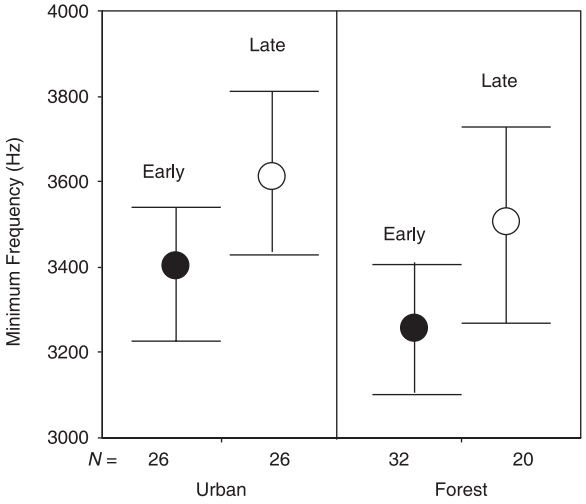
**Box 1 Is singing low important to great tits?**

There is a general relationship in birds between body size and frequency of pitch: larger species typically sing lower. Small birds with small vocal organs may be lacking the power, the essential size of the vibrating source, or the suitable resonance features of the vocal tract, that allow the production of low-pitched sounds. This creates the possibility of using low frequencies as a way to signal condition or size to competitors and potential mates (Ten Cate *et al*. 2002). However, we do not know whether intraspecific variation in male body measures is related to the minimum frequency in great tits, nor do we know if female great tits prefer males singing low-pitched songs. If it were hard for great tits with a territory to sing low, you may expect that they sing songs relatively high in pitch when the motivation to sing is low. Such a situation occurs at the end of the breeding season, in both urban and forest habitat. Males still sing their stereotypic song types but the resources at stake in their territory have decreased in value until the start of the next breeding season. A decline in motivation to sing is clear from a decline in number of repeated songs (phrases) in a strophe, independent of habitat: in the city of Rotterdam from six to three phrases, and in the forest called the Liesbos from six to four phrases on average (ANOVA: $F_{2,100} = 27.4$, $P < 0.001$). Interestingly, controlling for habitat differences, we found that the minimum frequency increases dramatically when recordings from relatively early in the season (early April: 'Early') are compared to recordings from late in the season (late May: 'Late', ANOVA: $F_{2,100} = 7.8$, $P < 0.01$). We therefore hypothesize that it may be an important signal of quality to have low-pitched notes in the song type repertoire, which may cause a trade-off especially for the urban birds in noisy territories. Low-frequency noise may constrain the capacity to signal individual qualities: urban birds may need to choose between being heard well or being rated high as a competitor or mate. High noise levels may increase the number of intruding competitors needing physical combat and may affect the number and quality of potential mates that are attracted. Consequently, although great tits are successful in cities, and even though they show a remarkable flexibility in spectral adjustment to local noise conditions, this does not mean that traffic noise interference is not harmful to individual birds.




subpopulations may show genetic divergence in fitness-related traits related to morphology, physiology, neurobiology or life-history. Congruent geographical patterns of variation in sexual and fitness-related traits may arise because varying environmental selection pressures in different habitats shape both types of traits. Congruent patterns may also emerge because acoustic changes are an inherent result of, for example, changes in bill morphology (Slabbekoorn & Smith 2000; Podos *et al*. 2004). As a consequence, under both conditions, songs may guide female birds to the locally adapted males, accelerating the process of reproductive divergence. The fact that many birds learn their songs from conspecifics adds a layer of complexity (Baker & Cunningham 1985; Slabbekoorn & Smith 2002b), as it will accelerate phenotypic divergence among populations but may actually constrain genetic differentiation (Ellers & Slabbekoorn 2003). Nevertheless, divergence in learned song will still increase the rate and chance of speciation for a subset of evolutionary scenarios (Lachlan & Servedio 2004; Ellers *et al*. unpublished).

In terms of gene flow, it may be improbable that urban habitat could generate phenotypically distinct and reproductively isolated subpopulations, as cities are typically scattered geographically and form a patchy network within a matrix of forested and agricultural area (Marzluff 2005). Habitat imprinting, on the other hand, may strongly influence dispersal patterns, and urban-borne birds may preferentially settle in urban territories (see e.g. Septon *et al*. 1995). In terms of consistent directional selection, despite considerable heterogeneity within urban habitat, some urban selection pressures are clearly distinct and dramatically different from those in more natural habitat. These consistent habitat-dependent selection pressures may have the potential for driving divergence of an urban phenotype despite ongoing gene flow.

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We are not aware of any publications on gene flow, or dispersal, between urban and nonurban populations of great tits, but there are some studies on urban-related phenotypic divergence. Plastic environmental responses were found for carotenoid-derived plumage coloration, with urban birds being less yellow compared to forest birds (Horak & Lebreton 1998) and also for timing of reproduction and clutch size, with later and smaller broods in (sub)urban great tits compared to their forest counterparts (Riddington & Gosler 1995). Another study, not involving urban habitat, addressed the balance between the response to divergent selection pressures and levels of gene flow over a very short distance. A partial cross-fostering experiment with great tits of two qualitatively different parts of Wytham Woods in Oxfordshire, UK, allowed the separation of genetic and environmental sources of variation (Shapiro *et al*. 2006). Nestlings in the high-quality part of the forest were larger, heavier and in better condition than in the low-quality part irrespective of the part from which they originated. Interestingly, in addition, significant differences in condition and shape could be attributed to area of origin, suggesting genetic differentiation. The areas of varying quality in this comparison were only a few kilometres apart and interconnected by forest, which reveals the evolutionary potential of divergent selection in ecologically distinct habitat for driving populations apart. Another recent and small-scale study on great-tit populations also reported interesting findings with respect to the balance between divergent selection and gene flow. A biased influx of birds from the mainland to only one side of the Dutch island of Vlieland created a local abundance of breeding birds that were not locally adapted (Postma & van Noordwijk 2005).

### *Evidence for microevolutionary changes in urban habitat*

The evidence for genetic differentiation related to anthropogenic selection pressures in cities is also still scarce when we look at bird species beyond great tits. A nice example of selection in an urban environment driving evolutionary change is found in an exceptional urban bird population on the campus of the University of California in San Diego, USA. Dark-eyed juncos (*Junco hyemalis*) have been breeding in this urban setting since the early 1980s (Yeh & Price 2004). The birds were presumably winter visitors that decided to stay instead of return to their natural breeding habitat: montane pine forest at least more than 70 km away (Nolan *et al*. 2002). Population comparisons and a common-garden experiment with hand-raised birds revealed that wing- and tail size, as well as a sexual trait (the amount of white in the tail) has diverged on campus beyond the extend attributable to phenotypic plasticity or drift (Rasner *et al*. 2004; Yeh 2004). However, there was only limited evidence for song divergence between this small urban population of about 70 pairs and four forest populations (Slabbekoorn *et al*. 2007). Although there were strong indications for divergent selection pressures on acoustic signals related to sound transmission, sexual selection based on song may be relaxed, as suggested by a reduced response to playback of junco songs in the urban population (Newman *et al*. 2006). The urban juncos make a strong case for microevolutionary changes related to anthropogenic selection pressures, but they require more study and better replication to increase our insight into the role of song in urban speciation.

Another bird species for which there is growing evidence for urban-related population divergence is the European blackbird (*Turdus merula*), a very common city bird in most parts of Europe (Luniak *et al*. 1990). Urban blackbirds breed in higher densities and start breeding earlier in the year than their forest counterparts (Partecke 2003). A common garden experiment, with nestlings collected in the city of Munich and the nearby Lichtenauer Forest, revealed phenotypically plastic divergence but also suggested that some of the variation reflects genetic differentiation (Partecke *et al*. 2004, 2005, 2006a). The habitat-dependent difference in timing of reproduction corresponds to an earlier initiation of the development of the reproductive system in male and female urban birds (Partecke & Gwinner 2007). The prolonged breeding season allows urban individuals to have more breeding attempts per year than individuals from forests, who on the other hand have a larger clutch size and more fledglings per successful nest (Gregoire 2003). Urban blackbirds also live longer than forest birds (Luniak *et al*. 1990), have a smaller tendency to migrate (Stephan 1999; Partecke & Gwinner 2007) and have a lower acute corticosterone stress response (Partecke *et al*. 2006b). Finally, a pattern of habitat-dependent divergence starts to emerge from several studies at different geographical locations, with blackbirds from cities and forests being distinct from each other in several morphological measures (Lippens & van Hengel 1962; Partecke 2003; Ripmeester & Slabbekoorn, unpublished).

European blackbirds may become the first bird species for which there is evidence for urban habitat-related divergence in both, fitness-related traits (as described above) and acoustic traits (Ripmeester & Slabbekoorn, unpublished). We are in the process of testing with playback recordings whether urban songs trigger stronger responses in city birds than in forest birds and vice versa. At the moment, we do not know yet whether congruent habitat-dependent divergence in song and morphology promotes the process of urban speciation. There is also no information available yet about habitat-guided dispersal, although a first study on divergence in neutral markers between the urban and forest birds of the common garden experiment in Germany could not confirm such a

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phenomenon (Partecke *et al*. 2006a). It is clear, however, that the aspects of coding and neutral genetic divergence between urban and forest blackbirds warrant further investigation and several complementary studies are on the way.

### *Considerations on making bird breeding habitat more quiet*

It is possible to make bird breeding habitat close to, or surrounded by, anthropogenic noise sources more quiet. We can build noise barriers, make depressed highways or underground tunnels (e.g. Maekawa 1977), or introduce porous road surfaces, speed limitations and restrictions on allowable noise emissions for road traffic related to engine features, break systems and tire types (e.g. Sandberg 1991). There are many examples of successful implementation of these techniques, typically to reduce noise exposure to humans. This means that the main threshold for applications to the benefit of wildlife will likely be the financial costs. However, when considering expensive mitigating measures, it is very important to realize that birds and humans often benefit from the same, or only slightly modified, measures. Urban birds live and breed near human residences, and birds of more natural areas inhabit space often used for recreational activities. The importance to human health and well-being can be used as additional arguments for installing measures to improve bird-breeding areas. In cases where noise barriers are already in place to the benefit of humans, small cost-effective modifications (e.g. increased height, added absorbent) could be a successful strategy (see Box 2).

Urban planners are increasingly aware of the need to consider noise pollution in constructing cities and residential neighbourhoods from a human perspective (Grimm *et al*. 2000; Yli-Pelkonen & Niemelä 2005; Bucur 2006; Nilsson & Berglund 2006). For example, the idea of urban canyons has received considerable attention: the use of relatively continuous rows of office buildings or apartment flats separating noisy human activities from living space in which noise is not appreciated (de Ruiter 2004). This living space may concern pedestrian areas, urban parks and private gardens, all areas in which urban birds would also benefit from reduced noise levels. The strategy of urban canyons also entails concentration of noise sources: canalization of traffic in a limited number of busy through-roads. This will limit the number of canyons to be constructed and make plans economically more feasible (Thorsson & Ögren 2005). Similarly, it is more realistic to concentrate on a restricted set of specified areas which are shielded from noise, instead of trying to reduce noise levels in all public areas (Kihlman & Kropp 2001; Thorsson *et al*. 2004). Urban canyons and 'quiet zones' provide people living in noisy cities with access to at least some quiet areas nearby, which may be a last resort for noise-sensitive bird species at the same time. In the best scenario, bird-breeding data and species-conservation values would be incorporated in the process of selecting the areas to be relieved from urban racket.

More and more tools have been developed to assist policy makers to predict and extrapolate noise levels spatially, based on traffic flow, vehicle types and distance to the road (e.g. Horoshenkov *et al*. 1999; Li *et al*. 2002; de Coensel *et al*. 2005). Spatial extrapolation has also been applied to reveal the impact of traffic noise on bird habitat by using road effect-distances based on general dB-threshold values that are just acceptable for birds, and which depend on habitat type and target species (Reijnen *et al*. 1997). For example, roads with 50 000 vehicles a day result in effect-distances from 75 to 930 meters for grassland species and from 60 to 810 meters for woodland species, as was shown by a meta-analysis combining nine studies (Reijnen & Foppen 2006). Highways may negatively affect bird-breeding habitat in a variety of ways, as stated earlier (e.g. collision, chemical pollution). However, visual disturbance and noise are the primary factors that reach furthest in open habitat, while noise is the single most important factor impacting forested habitat beyond 50 meters from the road (Reijnen & Foppen 2006).

### *The importance of temporal and spectral overlap*

Birds often have a diurnal cycle of vocal activity which matches periods of optimal sound transmission early in the day (Staicer *et al*. 1996; Brown & Handford 2003). Diurnal fluctuations in anthropogenic noise levels are also highly stereotypic with, not surprisingly, noise peaks during the morning and evening rush hour (Jabben *et al*. 2001). Interestingly, traffic jams during these periods may bring down noise levels because of lower driving speeds. Most importantly, however, this means that dawn chorus and rush hour can co-occur at optimal times for sound transmission depending on latitude and season (see Warren *et al*. 2006). Good signalling periods are thus disproportionally affected due to temporal overlap with traffic activity.

The fact that there are often periods during the day in which anthropogenic noise is most detrimental due to concentration of bird singing activity and optimal noise-transmission conditions seems 'bad luck' but also provides the opportunity to ecologically sensible noise control. Reducing traffic flow for short but crucial periods of time, for example, on roads through nature reserves, will raise habitat quality for breeding birds with limited impact on human activities. Similarly, on a slightly larger temporal scale, traffic limitations through sensitive areas during the critical period in spring, when males vocally attract females, could also significantly improve habitat

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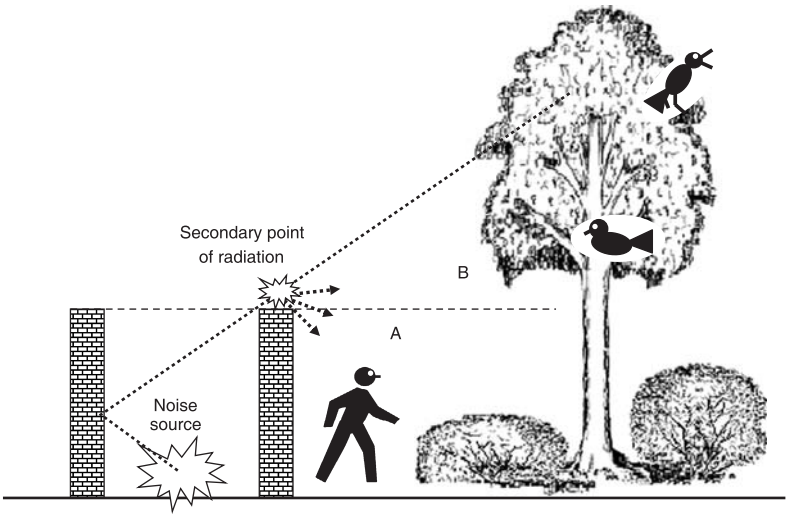
**Box 2 Noise barriers for birds**

Raising a barrier between the noise source and bird breeding habitat can lead to a significant reduction in detrimental noise levels. Vegetation is only of limited use, although the effectiveness will increase with stem and leaf density and width of the zone (e.g. Cook & van Haverbeke 1972; Bucur 2006). A solid barrier as close as possible to the noise source will be most effective (Maekawa 1977; Ishizuka & Fujiwara 2004). Adding an overhang on the road side or increasing the height of a barrier which is already in place to benefit pedestrians at ground level (A), could be a very cost-effective measure to the benefit of flying and tree-dwelling birds at a higher level (B). It is usually also easier to filter out the bird-relevant frequency components of traffic or industrial noise than to block the lower frequencies. Construction details and barrier shape especially can have a big impact in the frequency range between 2.0 and 8.0 kHz. For example, sound-pressure levels at the barrier's edge (= secondary point of radiation) can be significantly decreased by installing a soft, absorbent material on top. This will lead to a decrease in the noise level behind the barrier, especially in the field below the barrier height (A). Specific shapes of the barrier top with multiple diffracting edges may add to this effect. For example, T–shaped noise barriers with soft material on top only have to be three meters high to be as effective as a 10-metre high rigid–edged plain barrier (Ishizuka & Fujiwara 2004). This effect steadily gets stronger with frequencies above 250 Hz, also for the sound field above barrier height (B), which concerns the habitat layer typically most important for acoustic signalling in many bird species (Slabbekoorn 2004). Noise barriers at both sides of a road shield areas in both directions, but multiple reflections and scattering effects between the barriers will reduce the shielding capacity. Noise levels become higher especially above the barrier compared to a single barrier situation (Maekawa 1977). Buildings by the side of a busy road typically also increase noise levels within the street or urban canyon (Oldham & Radwan 1994; Heutschi 1995). Both inside and outside urban areas, the problem can be brought down by noise abatement schemes using a more absorbent ground surface and intermittent or continuous absorbers on the walls of buildings or noise barriers (Horoshenkov *et al*. 1999). Placing noise barriers at an angle will also reduce the impact of reflections by beaming them more upward into the sky or downward back towards the tarmac. Finally, the choice of construction material or absorbent matter may make noise barriers also bird-friendly in nonacoustic ways. Combination barriers incorporating trees or shrub layers can reduce the negative impact of an artificial, visual barrier in the landscape, and potentially provide nesting and foraging opportunities.




quality. These critical periods can be quite brief, as in some migratory species, for example, where males arrive at the breeding grounds just before the females. For such species, male singing effort peaks upon arrival and may already decline after one or two weeks.

In addition to seasonal and diurnal fluctuations in bird singing activity and noise levels, more short-term fluctuations may also warrant some attention. Fluctuating noise levels in terms of overall amplitude are usually more annoying to humans than relatively continuous noise levels,

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especially when areas are relatively quiet overall with sudden unpredictable noise peaks (de Coensel *et al*. 2005). For birds, mean noise levels may similarly not describe the potential for auditory masking or stress levels adequately. Therefore, analyses of sound-level fluctuations in time can add a relevant descriptor capturing more of the dynamics of noise interference.

Traffic-noise fluctuations in terms of frequency are chaotic, but most of the common anthropogenic noise sources show a general decrease in amplitude from low to high frequencies. Bird species in many taxa, such as doves, owls, corvids, woodpeckers, herons and rails use frequencies well below 1.0 kHz. Whether or not species in these groups occur in urban areas or along highways (and some are typically abundant within these habitat types) is probably largely determined by other factors than the impact of noise interference. However, declining signalling efficiency may influence the balance between costs and benefits of city life, especially for those species relying on vocalizations for long-distance communication. Not many noncorvid songbirds use frequencies below 2.0 kHz. The majority of these species uses a bandwidth of 3.0–6.0 kHz, starting at 2.0 or 3.0 kHz and often going up to around 8.0 kHz. The few songbirds that do use very low frequencies down to 1.0 kHz, typically use wideband songs with a bandwidth of about 6.0–9.0 kHz (examples are: European blackbird; nightingale; house sparrow, *Passer domesticus*; European starling, *Sturnus vulgaris*; house martin, *Delichon urbica*), and may therefore be less vulnerable to noise pollution (although we do not know yet whether this is true). Few songbird species rely just on relatively low frequencies, but species that do, like the oriole (*Oriolus oriolus*), the great reed warbler (*Acrocephalus arundinaceus*) and the mistle thrush (*Turdus viscivorus*), may for this reason be relatively sensitive to the masking effect of traffic noise.

A study on distribution and breeding success of great reed warblers in a wetland area in the central part of The Netherlands provides interesting support for the suspected sensitivity to noise in this species (Foppen & Deuzeman 2007). A reed bed in the Vossemeer was known to be inhabited by about 5–10 pairs of reed warblers up until the early 1990s. This reed bed has not changed much since, but it is now situated right beside a road (Vossemeerdijk) with a few thousand cars passing by per day. In the last 15 years, typically only one or two territories each spring have been occupied by singing reed warblers. However, in two years (2003 and 2004) the road was closed to traffic for a substantial time during spring due to road works. The absence of the usual traffic was correlated with an increase from two in 2002 to seven territories in 2003. The return of the noise source was correlated with a decline from five in 2004 back to one territory in 2005. These fluctuations over the course of four seasons constitute only anecdotal evidence, but they do suggest that the vulnerability to a masking of the low-pitched song by traffic noise may have contributed to the overall decline in reed warbler territories in this area since the early 1990s.

Although low-frequency bird songs are most affected by typical anthropogenic noise, it is not true that higher frequencies are free of the impact of anthropogenic noise interference. Masking depends on the amplitude of the acoustic signal relative to the amplitude of the ambient noise within the same frequency range (Lohr *et al*. 2003; Brumm & Slabbekoorn 2005), both measured at the receiver. So, the impact on detection and recognition of acoustic detail can still be serious and deleterious for faint high-pitched notes. Also, high-pitched songs heard at a large distance from the singer, with the receiver potentially being closer to the noise source, may be hampered by the high component of traffic noise which has most energy at low frequencies.

## Conclusions

It is becoming more and more clear that the omnipresence of anthropogenic sounds is not only detrimental to human health and well-being, but can also negatively affect birds. Efforts to bring down anthropogenic noise levels to the benefit of bird-breeding areas will almost certainly encounter financial trade-offs. Mitigating measures are typically expensive or counteract economic values, for instance by slowing down, or putting restrictions on, traffic flow. When considering or arguing for expensive noise-reducing actions, it is very important to realize that birds and humans often benefit from the same or only slightly modified measures.

It is obvious from the remarks above on song spectra that we need a thorough comparative study to assess noise sensitivity of bird communities, or at least of those species of high conservation value. Although it may be true in general that making habitat more quiet will improve breeding conditions for many species, we still lack much essential data to guide conservation efforts with adequate detail. Optimally, such data would come from a comparative study that includes experimental assessment of developmental flexibility, tolerance to spectral range reduction and an assessment of the fitness consequences of masking (cf. Habib *et al*. 2007). Data on urban survivors, such as the great tit (Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006), as well as urban 'losers' will be valuable to generate the insight needed to come up with ecologically solid recommendations.

Behavioural flexibility, such as song plasticity in postdispersal adjustment to neighbours under local noise conditions, may allow some species more time to adapt to human-altered environments. Consequently, thriving urban populations may be diverging from their

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forest counterparts in several traits and may be on a track towards becoming even more successful and potentially an independent urban species. However, this may be true for a 'lucky' few, since many species will not be able to go down this fortunate path. Hopefully in the near future, we will be able to explain which species are negatively affected by anthropogenic noise and why. For those situations for which there is the political will and the financial support to reduce detrimental noise exposure, we hope our considerations on making bird breeding habitat more quiet will prove to be useful.

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# Top carnivores increase their kill rates on prey as a response to human-induced fear

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The fear induced by predators on their prey is well known to cause behavioural adjustments by prey that can ripple through food webs. Little is known, however, about the analogous impacts of humans as perceived top predators on the foraging behaviour of carnivores. Here, we investigate the influence of human-induced fear on puma foraging behaviour using location and prey consumption data from 30 tagged individuals living along a gradient of human development. We observed strong behavioural responses by female pumas to human development, whereby their fidelity to kill sites and overall consumption time of prey declined with increasing housing density by 36 and 42%, respectively. Females responded to this decline in prey consumption time by increasing the number of deer they killed in high housing density areas by 36% over what they killed in areas with little residential development. The loss of food from declines in prey consumption time paired with increases in energetic costs associated with killing more prey may have consequences for puma populations, particularly with regard to reproductive success. In addition, greater carcass availability is likely to alter community dynamics by augmenting food resources for scavengers. In light of the extensive and growing impact of habitat modification, our study emphasizes that knowledge of the indirect effects of human activity on animal behaviour is a necessary component in understanding anthropogenic impacts on community dynamics and food web function.

## 1. Introduction

Anthropogenic disturbance can cause shifts in biotic community dynamics, generally through the loss of native species, introduction of novel species or artificially enhanced populations of native generalists [1]. These changes are characterized most often by quantifying the population size or presence of particular species. However, behaviour-mediated interactions are predicted to have equal or greater impacts on animal populations than purely numerical mechanisms [2–4]. Animal behavioural responses to anthropogenic disturbances have the potential to be cryptic but powerful drivers of ecological change in modified habitats [5].

Large carnivores are widely recognized to be sensitive to human disturbances owing to slow life cycles, large space requirements, direct persecution by humans and avoidance of human-dominated areas, often resulting in their decline or extirpation. Reduced large carnivore density and occupancy in some developed areas has resulted in both mesopredator release [6,7] and overpopulation of primary consumers [8,9]. Yet, some large carnivores do persist in modified landscapes, but alter their behaviour to reduce interactions with humans [10,11]. Owing to the strong regulatory influence large carnivores can exert on their competitors and prey, changes in their behaviour are likely to contribute to whole community responses to anthropogenic disturbances [12].

Hunting and foraging are costly behaviours for carnivores, but are often assumed to be optimized so that individuals gain the most energy (or other limiting nutrients) for the least effort [13]. Animals that choose to expend more energy than what is perceived to be optimal may be responding to risks that increase the long-term pay-off of certain energy-expensive behaviours through decreased chance of non-starvation mortality [14]. Hunting in high-risk habitats can therefore create a risk-foraging trade-off in which animals sacrifice efficient foraging to compensate

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for increased vigilance and risk avoidance. Giving-up density studies support that an animal's perceived risk is inversely correlated with food intake, suggesting that time spent consuming a food item reflects the fear experienced by forager [15].

Top carnivores generally kill large-bodied prey species, which require a high initial energetic cost during the hunting stage [16], but provide high energy gain during consumption. However, because carnivores are constrained by gut capacity, solitary carnivores can only maximize their caloric yield by repeatedly returning to feed on a prey carcass. In developed habitats, carnivores can be particularly vulnerable to risk-foraging trade-offs because disturbance-induced carcass abandonment can result in food loss owing to scavenging [17] or decomposition [18]. Prey consumption time can therefore be limited by external forces that reduce carnivore access to a carcass. Anthropogenic disturbances can ultimately reduce the net caloric gain carnivores receive from consuming large prey [19] by displacing carnivores from kill sites and decreasing their prey consumption time at kills. If perceived risk increases with human disturbance, the magnitude of human impact should be a predictor of foraging efficiency and consumption time.

We examined puma (*Puma concolor*) behavioural changes associated with perceived risk at kill sites with increasing housing density levels and investigated the relationship between risk-avoidance behaviours and kill rates in disturbed areas. We hypothesized that disturbance would displace pumas more often in highly developed areas, reducing overall prey consumption time and increasing kill rates. In the long term, we anticipate that more frequent risk-avoidance behaviours will increase puma kill rate and subsequently alter interactions with prey, competitors and scavengers.

## 2. Material and methods

Our research was conducted in the Santa Cruz Mountains, which lie in the Central Coast region of California. We captured 30 pumas from 2008 to 2013 and fitted them with GPS/radio telemetry collars (IACUC no. WILMC1011 Model GPS Plus 1 or 2 D, Vectronics Aerospace, Berlin, Germany). Collars were programmed to record locations every 4 h, and location data were downloaded remotely via UHF once a month. We used a custom cluster generation algorithm integrated in the Geographical Information Systems program ArcGIS (v. 10; ESRI, 2010) using the programming languages R (v. 2.1.3.1; R Development Core Team, 2010) and Python (v. 2.6; Python Software Foundation, 2010) to identify groups of locations in which each location was within 100 m of the cluster centre and 6 days of another location in the cluster (for full details on the algorithm, see [10]). We field-investigated clusters in reverse chronological order from their time of formation using the most recently downloaded GPS data. Clusters were investigated within 30 days of their first recorded locations. At investigated clusters, we recorded whether a kill was present, and if so, the species, age and sex of the kill (if identifiable).

We constructed a mixed-effects binomial logistic regression model to predict deer kill sites from all generated clusters. We chose to only use deer kills because deer are the preferred prey in our study area. In addition, small prey cannot be predicted accurately from location data in our study area owing to high variability in puma behaviours at small kill sites. The variables used to fit the model were behavioural characteristics associated with clusters, including number of night locations (NIGHT), a binary variable indicating greater than 1 day duration (BINARY), the harmonic mean distance of locations from the cluster centre within the cluster (HMDIST), the proportion of locations occurring at night (P.NIGHT), site fidelity measured by the proportion of points occurring within the cluster over the cluster duration (P.ACTIVE) and the farthest distance travelled during a cluster period (DIST). Total duration of a cluster (DUR) was excluded owing to high correlation ($r > 0.7$) with variables already used in the model. We allowed for random slopes and intercepts for individual pumas when fitting the best model. We also constructed a truncated model without behavioural variables that we expected to correlate with housing density in order to allow inference on behavioural influences on kill rates. This model excluded P.NIGHT, P.ACTIVE and DIST. We compared the truncated model and best-fit model to assess if we could confidently use the truncated model. We constructed receiver operating characteristic curves for both full and truncated models and calculated the area under the curve (AUC) to ensure that both models were similar in their predictive abilities. The AUC for the full model (AUC = 0.818) and the truncated model (AUC = 0.820) were nearly identical, and both support good discriminative ability [20]. We assigned each generated cluster as a deer kill or not a deer kill by applying the truncated model to all generated clusters.

We first investigated puma behavioural responses at the population level at four levels of housing density within 150 m of predicted kill sites: no housing, rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to 1.236 houses per hectare) and suburban (greater than 1.236 and up to 9.884 houses $ha^{-1}$; [21]). Owing to the discrete nature of housing count data, each housing class was rounded up to the nearest number of houses, resulting in housing classes within 150 m of a cluster to be defined as 0 houses for no housing, one house for rural, two to nine houses for exurban and greater than nine houses for suburban. We used the 150 m buffer because this is the scale of development found to most impact puma hunting in our study area [10]. We constrained the response variables to only include behaviours we expected to be associated with risk aversion, which were narrowed down to P.NIGHT, P.ACTIVE, DUR, DIST and a final measure of prey consumption time (P.C.TIME) which was calculated as P.ACTIVE × DUR. We added the prey consumption time measure because it best reflects the energetic gain an animal receives from a kill. We tested the differences in behaviours at all predicted kill sites in different housing density categories using an ANOVA test and examined pairwise comparisons with Tukey's HSD test for all behaviours found to vary significantly with housing density.

To determine kill rates, we calculated the total number of deer predicted to be killed by each puma from the output of the deer kill prediction model using all generated GPS clusters. We divided the predicted number of kills by the total time each puma was actively collecting GPS data to obtain annual deer kill rates. We investigated sex-specific relationships between kill rates and average values for P.NIGHT, P.ACTIVE, DIST, DUR and P.C.TIME for individual pumas using univariate linear regressions owing to high correlation values ($r > 0.7$) among variables.

In order to assess the impact of housing on individual pumas, we calculated housing density within each puma home range. Puma home ranges were obtained using a local convex hull (LOCOH) home range estimator, where the 95% isopleth represented the home range boundary [22,23]. All housing points in the Santa Cruz Mountains were manually digitized from high-resolution satellite imagery. We calculated puma home range housing density as the number of houses per $km^2$. We tested for the relationship between individual puma kill rates and home range housing densities using univariate linear regression.

## 3. Results

### (a) Behavioural shifts

Of 703 field-investigated clusters, 208 were classified as deer kill sites. The other remaining clusters included 66 non-deer

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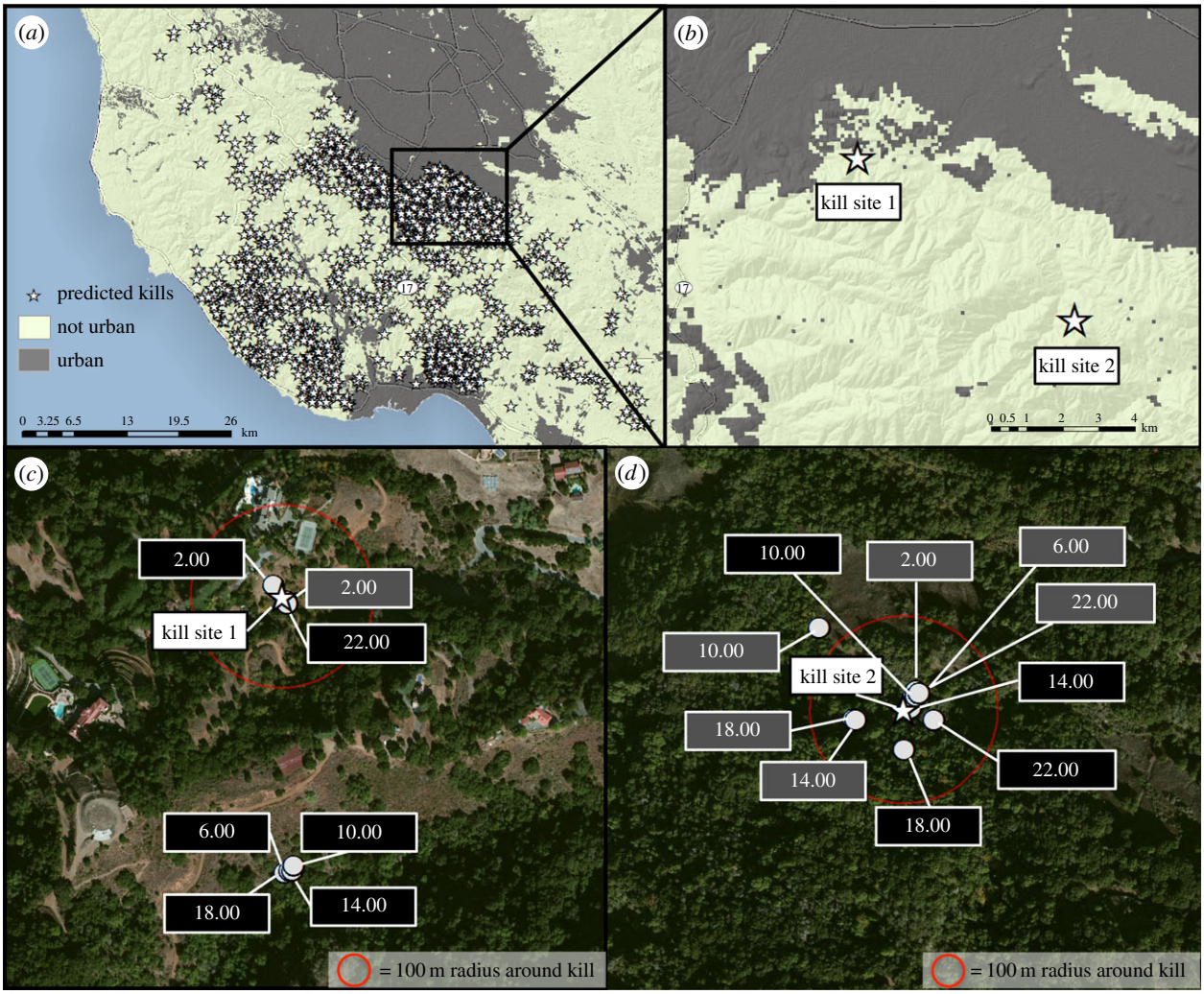


**Figure 1.** (*a*) Study area and predicted kill sites in relation to housing density. Box shows area (*b*) in which kill site examples (*c*,*d*) are shown. Kill site 1 (*c*) belongs to puma 13F, whose home range is in the top quartile of housing densities among female pumas. Kill site 2 (*d*) belongs to 28F, whose home range in the bottom quartile of housing densities among female pumas. Grey labels depict location times during the first day at the kill site and black labels depict location times during the second day. Note that at kill site 1, the puma has made a kill close to development but spends the majority of time away from the kill, whereas at kill site 2, which has no nearby development, the puma stays within the vicinity of the kill. (Online version in colour.)

kills (e.g. raccoons and house cats) and 429 non-kills (often bed sites). Our best-fit binomial logistic regression model to predict deer kills included NIGHT, BINARY, HMDIST, P.NIGHT and P.ACTIVE. The truncated model included NIGHT, BINARY and HMDIST. Neither the random intercept nor a random slope was included in the best-fit full model or the best-fit truncated model. We used the truncated model to predict 1537 deer kills from 8523 generated clusters (figure 1).

At predicted kill sites, females had lower P.ACTIVE ($F = 67.7$, $p \ll 0.001$), higher DIST ($F = 16.0$, $p < 0.001$) and shorter P.C.TIME ($F = 44.2$, $p \ll 0.001$) as housing density increased (figure 2; example shown in figure 1). In suburban habitat, female P.ACTIVE was 36% lower, DIST was 31% higher and P.C.TIME was 42% lower than in no housing areas. Both males ($F = 19.3$, $p < 0.001$) and females ($F = 144.4$, $p \ll 0.001$) were more nocturnal (higher P.NIGHT) with increasing housing density at kill sites. Males did not show any responses to housing density concerning time spent at kill sites. Identical analyses using only confirmed kills supported each of the reported trends for predicted kills.

## (b) Deer kill rates

Male average home range size was $163.0 \pm 7.7$ s.e. km$^2$ with $15.6 \pm 0.8$ s.e. houses km$^{-2}$. Female average home range size was $53.8 \pm 2.1$ s.e. km$^2$ with $25.5 \pm 1.3$ s.e. houses km$^{-2}$. Males had an average deer kill rate of 43.7 deer yr$^{-1}$, whereas females killed on average 67.3 deer yr$^{-1}$. Male deer kill rates were not correlated with any of our variables of interest (P.ACTIVE, P.NIGHT, DIST, DUR or P.C.TIME), nor with home range housing density ($p = 0.9$, $r^2 = 0.005$; figure 3). Conversely, female deer kill rates showed a strong positive and linear correlation with home range housing density within its observed range ($p = 0.0003$, $r^2 = 0.745$; figure 3). Females with home ranges in the top quartile of housing density killed 36% more deer per year (81.2) than females in the bottom quartile of housing density (59.7). Female kill rates were also negatively correlated with average fidelity to kill sites (P.ACTIVE; $p = 0.05$, $r^2 = 0.322$).

## 4. Discussion

Our estimate of average male kill rates (43.7 kills yr$^{-1}$) stayed constant across housing densities and was comparable to previously reported values described by Knopff *et al.* (35 ungulates yr$^{-1}$, [24]) and Anderson & Lindzey (47 kills yr$^{-1}$, [25]). However, female kill rates increased positively, strongly and linearly with housing density. Although female kill rates in lower housing density areas (59.7 kills yr$^{-1}$) were

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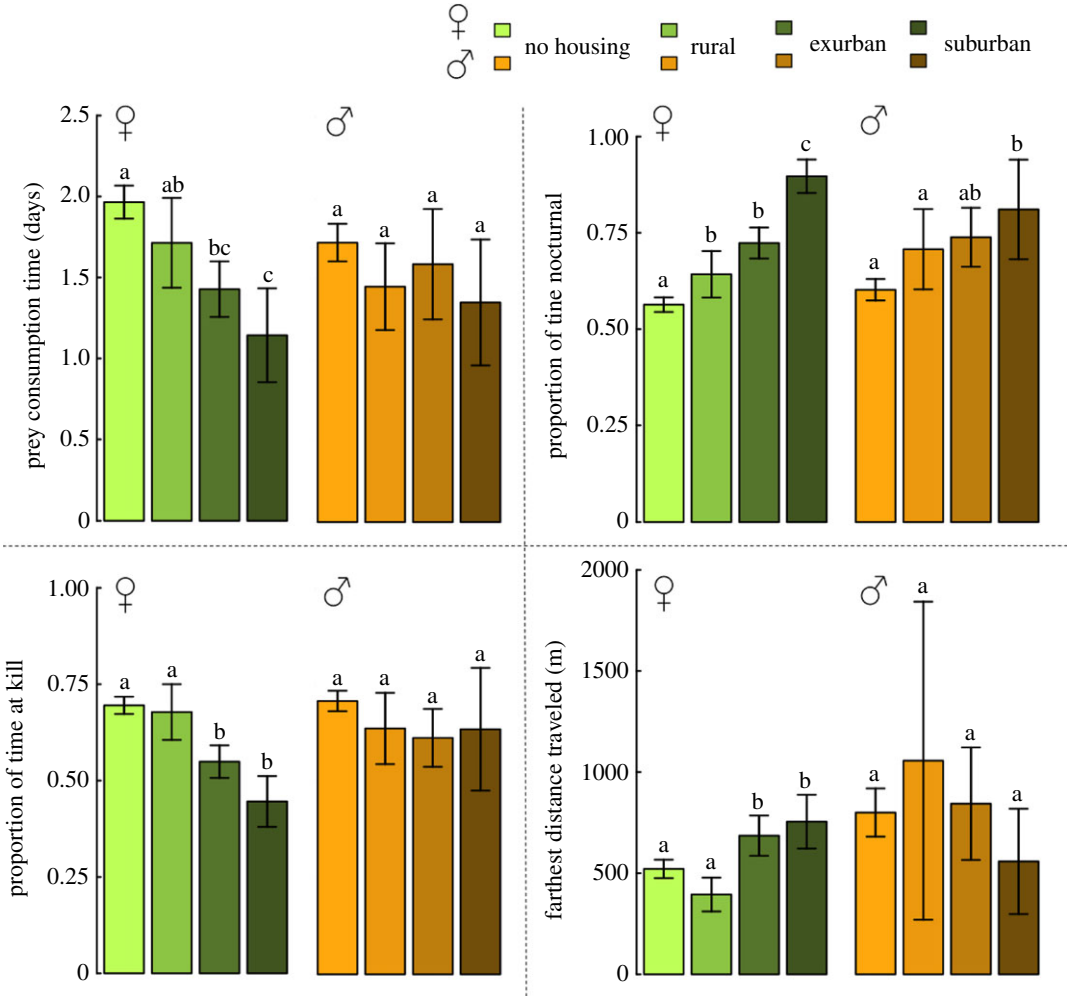


**Figure 2.** Behaviours that vary with housing density at predicted kill sites. Pairwise comparisons from Tukey's HSD tests reported in superscripts, where different letters represent a statistically significant difference. Error bars represent two standard errors from the mean. Sample sizes of housing classes at female kills are: no housing, 719; rural, 83; exurban, 186; suburban, 71. Sample sizes of housing classes at male kill sites are: no housing, 389; rural, 32; exurban, 42; suburban, 15. (Online version in colour.)

comparable to previously estimated mule deer kill rates for solitary adult females (52.5 kills $yr^{-1}$, [25]) and females with kittens (62.4 kills $yr^{-1}$, [26]; 68.1 kills $yr^{-1}$, [25]; 57.2 kills $yr^{-1}$, [24]), female kill rates in the highest quartile of home range housing densities were substantially higher (81.2 kills $yr^{-1}$). This 36% increase in kill rates between the top and bottom quartiles indicates that development may exert a significant energetic cost associated with hunting behaviour.

Hunting deer requires large energetic investments in the stalking, subduing and killing stages for pumas [16]. We have documented a sizable increase in female kill rates that we expect represents higher energetic costs for females in developed landscapes. Although these costs do not appear to influence adult survival (C. C. Wilmers 2014, unpublished data), impacts on reproductive success possibly make development-interface zones sinks for the puma population. Anecdotally, we have observed that the tagged female living in the most developed habitat in our study area has lost at least three litters in the last 3 years, one of which was confirmed as abandonment (C. C. Wilmers 2014, unpublished data). The three other females living in less developed portions of our study area for which we have also documented at least three dens have had the majority of their litters survive. Although there are many stressors in a developed landscape that might influence kitten survival, we expect that higher energetic costs from increased hunting may contribute to this pattern.

Males did not alter their kill rates or prey consumption time at kills with increasing housing density. Because male life histories are constrained by requirements to defend much larger territories [27], this is perhaps not surprising. We found that male pumas have home ranges that are approximately three times as large as female home ranges on average. Male pumas are also known to spend significantly more time performing scent-marking behaviours than females [28]. We found that males have lower DUR at kills than females by 7.2 h on average (males = 2.86 days $\pm$ 0.06 s.e., females = 2.56 days $\pm$ 0.05 s.e.; $t = 3.83$, d.f. = 1000, $p \ll 0.001$), probably owing to their need to patrol and defend their home range boundaries from encroaching males. Therefore, because males already tend to leave their kills early, they may be less influenced by chronic disturbance. In addition, male home ranges are characterized by much lower overall housing densities, indicating that males may exhibit risk-avoidance behaviours at the landscape scale rather than at the kill site scale.

Higher deer kill rates by females in response to increased housing density appear to be driven by a behavioural shift to a lower proportion of time spent at kill sites over the consumption period. Although females did not alter their total duration spent at clusters, their overall prey consumption times declined owing to a lower proportion of time spent at kills, indicating reduced utilization of carcasses at higher housing densities.

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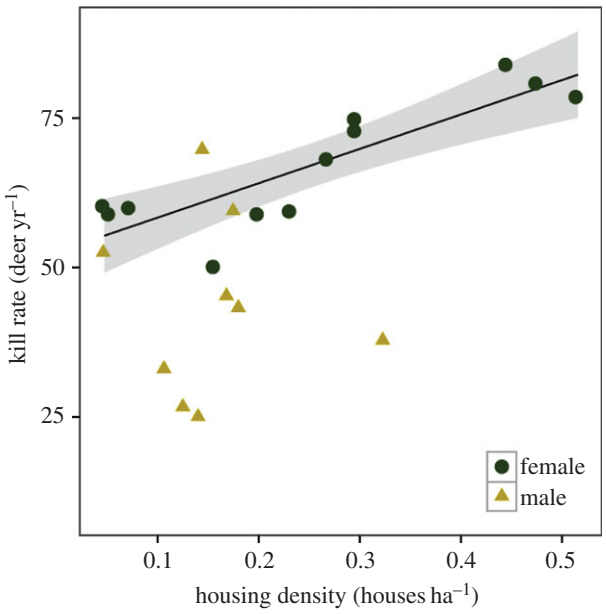


**Figure 3.** Kill rates of individual male and female pumas in response to housing density per hectare within their 95% LOCOH home range. Regression line and 95% CIs for female kill rates in relation to housing density are shown. Housing density coefficient $\beta_1 = 91.4$. (Online version in colour.)

Other possible explanations for female increase in deer kill rate are not supported by our understanding of puma energetics and reproduction. Deer in our study have lower detection rates in more developed habitats (C. C. Wilmers 2014, unpublished data), therefore variation in deer activity or abundance is unlikely to explain these patterns. In addition, it is unlikely that increased kill rate could be a result of greater reproductive activity in high housing density areas because females in our study area avoid anthropogenic development when denning [10]. We conclude that behavioural risk avoidance is a substantial contributor to female prey consumption time and hence hunting patterns, due to our observation that housing density is associated with decreased prey consumption time. Both food loss and increased movement as a result of these behavioural shifts may contribute to observed increased kill rate in human-modified habitats.

An increase in ungulate carcasses left by female pumas may impact the biotic community by providing additional carrion subsidies to scavengers. By leaving their kills for longer periods of time in more developed areas, female pumas might create greater opportunity for scavenging by mesopredators and birds. Subordinate predators often scavenge kills of apex predators when kills are abandoned or not guarded [29], and carrion can form a large proportion of their diets [30]. Pumas are known to be important sources of food subsidies to mesopredators through carcass abandonment [31]. Our results suggest that mesopredator release may occur not only through the well-documented pathway of apex predator extirpations, but also via behaviour changes in extant apex predators leading to increased food provisioning. The presence of scavengers can exacerbate this pattern by reducing apex predator prey consumption time via food loss [17].

## 5. Conclusion

The results presented here have bearing on human-modified systems globally. Behavioural responses are often overlooked as ecosystem drivers in modified systems, overshadowed by population declines and extirpations. However, many species are able to persist in developing landscapes, but in an altered behavioural state. Our findings suggest a strong, perceivable impact of observed human-induced behavioural change on species interactions instigated by the presence of development. Risk aversion behaviours that result from anthropogenic disturbances are likely to restructure predator–prey interactions in a variety of contexts, given the large effects risk has been shown to have on foraging across taxa. Behaviour-mediated interactions are powerful forces in biotic systems, often playing an even more impactful role than consumptive interactions. A greater focus on behaviour-mediated effects of habitat alteration can further expand our understanding of community-level processes in human-modified systems.

Ethics statement. The study was carried out under the IACUC approval no. WILMC1011.

Data accessibility. Because pumas are a specially protected species in California, the location data are sensitive and have not been made accessible. However, the data can be available on request by contacting Justine A. Smith at jsmith5@ucsc.edu.

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Author contributions. J.A.S. conceived the study, carried out the data analysis and drafted the manuscript. Y.W. assisted in project development and edited the manuscript. C.C.W. conceived and designed the overall study, supervised data collection, advised on data analysis and edited the manuscript.

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Conflict of interests. We have no competing interests.

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THE ROYAL SOCIETY PUBLISHING

# Fear of the human 'super predator' reduces feeding time in large carnivores

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Large carnivores' fear of the human 'super predator' has the potential to alter their feeding behaviour and result in human-induced trophic cascades. However, it has yet to be experimentally tested if large carnivores perceive humans as predators and react strongly enough to have cascading effects on their prey. We conducted a predator playback experiment exposing pumas to predator (human) and non-predator control (frog) sounds at puma feeding sites to measure immediate fear responses to humans and the subsequent impacts on feeding. We found that pumas fled more frequently, took longer to return, and reduced their overall feeding time by more than half in response to hearing the human 'super predator'. Combined with our previous work showing higher kill rates of deer in more urbanized landscapes, this study reveals that fear is the mechanism driving an ecological cascade from humans to increased puma predation on deer. By demonstrating that the fear of humans can cause a strong reduction in feeding by pumas, our results support that non-consumptive forms of human disturbance may alter the ecological role of large carnivores.

## 1. Introduction

Humans have assumed the role of 'super predator' in animal communities globally, killing terrestrial carnivores at rates as much as nine times higher than their natural predators [1]. In addition to directly killing large carnivores, humans might also elicit fear responses in these species as they do in other wildlife taxa that experience human-caused mortality [2,3]. Indeed, correlative evidence of human-induced changes in large carnivore space use and movement suggests that fear of humans is a common phenomenon among top predators [4–8]. However, it has yet to be experimentally tested if large carnivores perceive humans as predators and whether changes in large carnivore behaviour caused by fear of humans affects ecological communities.

It is increasingly recognized that, even in the absence of direct mortality, fear of predators can itself drive cascading changes across food webs [9,10]. Human-induced fear in large carnivores is likely to have similar cascading effects because of the well-documented top-down effects of large carnivores on their prey and competitors [11–13]. However, different outcomes of human-induced fear in carnivores on prey populations might be expected depending on the nature of the carnivore response. One potential outcome of large carnivore fear of humans is the human shield effect, whereby prey find refuge in human-dominated habitats and are released from top-down forces because carnivores spatially avoid human disturbance [14,15]. However, human disturbance could have the opposite effect on the regulatory role of large carnivores if carnivores persist in human-dominated habitat by instead avoiding humans temporally. This counterintuitive response may actually increase predation pressure on prey by altering carnivore hunting behaviour to accommodate an enhanced risk–foraging trade-off; temporal avoidance could lead to reduced total feeding

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time at a kill, which would require increased kill rates to compensate for lost energetic return from each kill. As land is increasingly transformed by anthropogenic development, quantifying how the fear of humans affects interactions between large carnivores and their prey is essential to understanding novel ecological dynamics emerging in human-dominated landscapes [7,11,16].

We previously reported that pumas (*Puma concolor*) in the Santa Cruz Mountains of Central California spent less time at kill sites in more residential areas and increased kill rates of prey [5]. This increased kill rate could potentially be explained by altered prey communities in human-dominated habitats (either from a perceived human shield or access to anthropogenic food subsidies) leading to more vulnerable [17] or available [18] prey. However, if reduced time at kill sites near residential development is fear-induced, it could also result in increased kill rates to compensate for reduced energy gained per individual predation event. Here, we experimentally test whether pumas exhibit fear responses to the human 'super predator' and whether changes in puma feeding behaviour in response to human-induced fear can explain our previously reported differences in puma feeding time and kill rate between areas of high and low human presence in the Santa Cruz Mountains [5]. To our knowledge this is the first direct experimental test of whether large carnivores respond fearfully to human presence, and whether this response has measurable ecological consequences.

To test the relationship between fear of humans and feeding behaviour, we executed a playback experiment on wild pumas. Predator playback experiments have been used to substantiate fundamental ecological relationships [19], including that the fear of predation reduces reproductive success in birds [20], that fear can have cascading impacts on animal communities [10], and that mesocarnivores exhibit heightened fear responses to human 'super predators' relative to non-human predators [3]. However, no study has linked the fear of humans to feeding behaviour in large carnivores. Our study builds on protocols used in over 200 predator playback experiments [19]. Hearing a predator vocalization signals to prey the direct presence of the predator in relatively close proximity, which is why simulating this using audio predator playbacks provides such a powerful means of directly testing fear responses [3,19,21]. Previous experiments have established that prey hunted by the human 'super predator' react to human vocalizations just as prey react to the vocalizations of any other predator [3], demonstrating that assessing responses to human vocalizations provides the means to directly test the prey's perception of humans *as* predators, rather than humans as simply a source of noise and disturbance (*sensu* [4]). Our experimental approach correspondingly allows us to make direct inferences concerning fear of the human 'super predator' and the resulting consequences of anthropogenic disturbance on risk–foraging trade-offs in a large carnivore. Combined with our previous work [5] our study reveals an ecological cascade from humans to increased predation on deer mediated by fear.

## 2. Methods

Our experiment was part of a long-term study on puma ecology in the Santa Cruz Mountains of Central California, USA [5,6]. The region has a Mediterranean climate characterized by a rainy season in winter and dry season in summer. Habitat types include mixed hardwood forest, redwood forest, chaparral and grassland. The Santa Cruz Mountains are heavily impacted by human use, particularly residential development and outdoor recreation. Puma exposure to humans here is thus commonplace; all pumas in this study have housing developments in their home range (mean: 21.7 houses $km^{-2}$) and kill and cache prey as close to 5 m from people's homes [5]. Pumas have a good reason to be fearful of humans in this region, as they were bounty hunted in California for decades and even today humans are their primary source of mortality in the Santa Cruz Mountains (Wilmers unpublished data).

We conducted a playback experiment on pumas at their active kill sites. We first located puma kill sites from recent GPS tracks of collared individuals (IACUC no. WILMC1011). We downloaded recent GPS locations successfully transmitted through GSM or Iridium technologies and identified potential fresh kill sites as clusters of locations within 100 m of one another that occurred between sunset and sunrise. We field-investigated potential kill sites that were no more than 3 days old and at which the puma was present the previous night. If a fresh kill was found, we tied the carcass down so it could not be dragged out of the view of our cameras. Any behavioural effects of tying down the carcass were experienced for both control and experimental playback treatments, therefore baseline disturbance levels should not influence the relative difference in response between treatments.

To test whether pumas fear humans and quantify the cost of this fear, we broadcast predator (human) or non-predator (Pacific tree frog, *Pseudacris regilla*) playbacks at puma kill sites following well-established experimental methods [10,19,20]. Tree frog vocalizations provide an ideal control – like humans, tree frogs occur throughout the study area, but unlike humans they are neither predators, prey, nor competitors of pumas, and thus represent an equally familiar but benign stimulus. Tree frog vocalizations further provide an ideal control because they may naturally be heard both night and day, whenever pumas are active. Controls in other playback studies testing for fear responses in wildlife include running water (study organism: moose; [22]), seals (study organism: raccoon; [10]), sheep (study organism: European badger; [3]) and assorted non-threatening birds (study organism: song sparrow; [20]).

We recorded puma responses to playbacks using an Automated Behavioral Response (ABR) system (i.e. video-enabled camera trap linked to a playback unit triggered by the camera's activation) [21]. We deployed the playback speaker 400–450 cm from the centre of the carcass. Videos were 30 s long, the playback being broadcast for 10 s in the middle of the video. If the puma repeatedly triggered the camera it could hear the playback as often as twice per minute. We used seven exemplars of each playback type [23], the human exemplars all consisting of a single individual speaking conversationally. We edited all exemplars for consistency in amplitude and quality using Audacity® (v. 2.1.0, Audacity Team 2014), and broadcast the playbacks at a consistent peak sound pressure level of 80 dB at 1 m (measured using Radioshack 33-2055 Digital Sound Level Meter set to fast response and C weighting). This volume was chosen to mimic the natural volume of human conversation. Using these exemplars we composed 30 min playlists of each treatment. The playlists alternated between frogs and humans every 30 min; which treatment the puma heard first being determined by when it triggered the camera, and was thus effectively random. An individual puma might be exposed to either or both treatments over 24 h, depending upon its reaction. For pumas that heard both treatments, there was no significant difference in the proportion of each treatment first heard ($Z = 1.63$, $p = 0.103$). Pumas were exposed to each treatment only once over the course of the study.

We tested for the fear response of pumas and its ecological cost as follows: (i) We examined the puma's initial response to

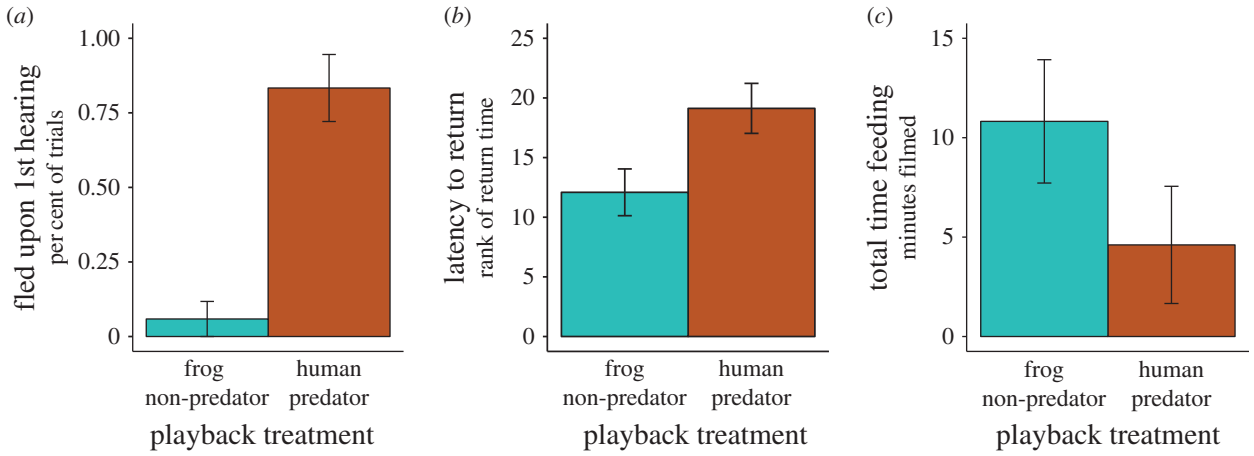


**Figure 1.** Responses of pumas to predator (human) and non-predator (frog) playbacks at puma feeding sites. (*a*) Proportion of pumas that fled following their first exposure to frog or human playbacks. (*b*) Latency in time to return (rank) after initial payback exposure. (*c*) Total time spent feeding during the first 24 h of playback treatment. Bars represent standard error. Although transformation of feeding data was required to meet normalization assumptions for our analysis, here we show mean and standard error of raw feeding time measures for purposes of visualization. (Online version in colour.)

the playbacks by quantifying whether the puma fled (ran away) upon first hearing a treatment. We tested for significant differences in fleeing using Fisher's exact test. (ii) We assessed recovery time following puma initial exposure to each playback as the time difference between their first exposure to a playback treatment and the next video in which they subsequently appeared (hereafter, 'latency to return time'). We ranked the latency to return time for each trial, assigning the highest rank to individuals who did not return. We tested for a treatment effect by applying a Mann–Whitney *U* test to the ranked return times. Some pumas were exposed to both treatments enabling us to additionally test these two responses (fleeing and latency) using repeated-measures Wilcoxon matched pairs tests, which provided qualitatively the same answers, reinforcing the robustness of the results. Because there is no qualitative difference, but these repeated-measure tests do necessitate excluding some individuals, we report the results of the between-group comparisons to best reflect the full dataset. (iii) We measured the aggregate effect of hearing a playback treatment on feeding time by calculating the total time a puma was observed feeding during each treatment over the course of 24 h. We Box-Cox transformed these data to meet normality assumptions and tested for differences using ANOVA. Again, because some pumas were exposed to both treatments, we began by including individual identity as a random effect in the feeding analysis (the only parametric test), but because this did not explain any additional variation we removed it from the model and accordingly report results from the univariate (predator versus non-predator) fixed effects model.

## 3. Results

We successfully conducted 29 experimental trials on 17 pumas. All 17 heard non-predator (frog) playbacks and 12 were exposed to both predator (human) and non-predator (frog) playbacks. Pumas fled in the majority of cases (83%) upon first hearing humans and only once upon first hearing frogs (6%; figure 1*a*; Fisher's exact $p < 0.001$). The latency to return time after pumas first heard a treatment was significantly greater in response to human playbacks (figure 1*b*; M-W $U_{12,17} = 151.5$, $p = 0.028$) because pumas returned to the carcass less often following their first hearing of a human playback (42% of trials) than following their first hearing of a non-predator (frog) playback (18%), or if they did return, they took longer to do so after first hearing humans (median = 20 min, range = 0–257) than after first hearing frogs (median = 2 min, range = 0–40). Feeding time was significantly less for the human treatment than the non-predator (frog) treatment ($F_{1,27} = 5.74$, $p = 0.024$; figure 1*c*). Over the course of 24 h, pumas fed for less than half as long when exposed to humans (4.6 ± 2.9 SE min; median = 0.03 min) as when exposed to frogs (10.4 ± 3.1 SE min; median = 4.5 min).

## 4. Discussion

Our results experimentally demonstrate that fear of the human 'super predator' induces substantial behavioural changes in pumas, ultimately leading to significant reductions in time spent feeding. We observed almost unanimous fleeing behaviour in response to the human playback treatment, directly tying a strong fear response to subsequent declines in feeding. Our previous work showed that pumas nearly halve their feeding time of deer in suburban areas compared to areas with less housing [5]. The halving of feeding time during human trials compared to non-predator trials that we observed in this study suggests that this difference in puma behaviour at kills based on nearby housing densities can be fully accounted for by fear, and that this consequently causes pumas to increase their kill rates by 36% [5]. In a previous study we found that deer occupancy was not influenced by housing density, therefore it is unlikely that relative deer availability explains observed changes in kill rate [18]. Our results support the conclusion that increased kill rates in residential areas are driven by a top-down mechanism (fear of humans), rather than a bottom-up mechanism (availability of prey). Thus, non-consumptive forms of human disturbance may alter the ecological role of large carnivores by affecting the link between these top predators and their prey.

Prey generally respond to both direct (e.g. predator vocalizations) and indirect (e.g. moonlight or cover) cues of predation risk, and the strength of their response depends upon both the nature and number of cues. A single direct cue typically induces a stronger response than a single indirect cue, but multiple indirect cues may induce an equivalent or even stronger response than a single direct one [24–26]. Our experiment demonstrates that pumas respond fearfully to a direct cue indicative of the immediate presence of the human 'super predator' (i.e. hearing

human vocalizations). In human-dominated landscapes, pumas are exposed to multiple indirect cues indicative of the presence of the human 'super predator' (e.g. anthropogenic lighting, sounds of vehicles and dogs), and our previous work shows that pumas respond to these indirect cues [5,6,18]. Our purpose in testing the responses of pumas to human vocalizations was to evaluate the perception of humans *as* predator, as explained above. In the present study, exposure to a single direct cue (hearing human vocalizations) had the same magnitude of effect on feeding time as did cumulative indirect (e.g. lighting, vehicles) and less direct (e.g. hearing humans at a distance) cues [5], as might be expected in the response of any prey to any predator. Fear-induced trophic cascades are not caused by responses to a specific cue, but by prey responding to any and every cue signalling the presence of the predator it fears [9,10,25].

Our results are consistent with theoretical predictions made from other playback experiments that have demonstrated the ability for humans to cause fear responses in wildlife [3] and for fear responses in carnivores to cascade to lower trophic levels [10]. We have combined these concepts in context of large carnivores due to their important regulatory role and susceptibility to disproportionately high mortality rates via the human 'super predator' [1]. Our results show that large carnivores are not exempt from human-induced fear, and that human impacts on their feeding behaviour might have surprising cascading effects.

In this study, we implemented a novel ABR playback experiment [21] to quantify a large carnivore's behavioural response to humans. Such direct testing of human disturbance has not previously been done on a large carnivore due to the challenge of observing these animals in the wild. Our use of recent puma kill sites accompanied by the integrated ABR technology allowed us to make inferences on humans as a driver of risk–foraging trade-offs in a large carnivore. Similar methods could be executed on other elusive species to investigate a diversity of risk responses to invasive predators, extirpated predators or competing predators.

Overlap between large carnivores and humans is increasing in regions where continued agricultural and residential development coincides with the recovery of large carnivore populations [27,28]. Although the coadaptation of humans and carnivores can lead to coexistence in human-dominated landscapes [29], carnivore behavioural adaptations might result in unintended indirect effects on other species [11]. Our work suggests that fear-induced trophic cascades instigated by the human 'super predator' are likely to contribute to altered ecological dynamics in human-dominated landscapes. As the habitats used by wildlife and humans are increasingly shared, additional work is needed on the extent to which fear in top predators cascades through ecosystems.

Data accessibility. Data have been made available in the Dryad data repository: http://dx.doi.org/10.5061/dryad.6pn0b [30].

Authors' contributions. J.A.S., M.C., C.C.W. and L.Y.Z. conceived of; J.A.S., J.P.S., M.C., C.C.W. and L.Y.Z. designed; and J.A.S., A.C. and C.C.W. conducted the study. J.A.S., M.C., A.C. and D.R. processed and analysed data. J.A.S. wrote the manuscript, with help from J.P.S., M.C., L.Y.Z. and C.C.W. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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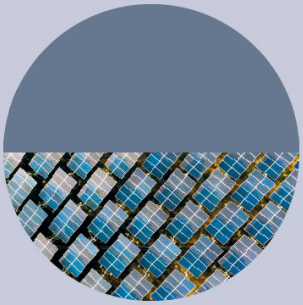

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# Urban–wildland fires: how California and other regions of the US can learn from Australia

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**Abstract**
Most urban–wildland interface (UWI) fires in California and the other regions of the US are managed in a similar fashion: fire agencies anticipate the spread of fire, mandatory evacuations are ordered, and professional fire services move in and attempt to suppress the fires. This approach has not reduced building losses in California. Conversely, losses and the associated suite of environmental impacts, including reduced air quality, have dramatically increased over the last three decades. In contrast to California, Australia has developed a more effective 'Prepare, stay and defend, or leave early' policy. Using this approach, trained residents decide whether they will stay and actively defend their well-prepared property or leave early before a fire threatens them. Australian strategies have the distinct advantage of engaging and preparing those most affected by such fires: homeowners. Investing more in fire suppression alone, the common response after large UWI fires in California, will not reduce losses. US society has attempted to accommodate many of the natural hazards inherent to the landscapes that we inhabit; by examining the Australian model, we may approach a more sustainable coexistence with fire as well. However, it should be noted that some California communities are so vulnerable that a 'Prepare and leave early' strategy may be the only option.

**Keywords:** fire policy, fire management, wildland urban interface, wildfire, land use planning

## 1. Introduction

Wildfires in the urban–wildland interface (UWI) continue to devastate communities in California (figure 1) and across the US. Despite known risks, people continue to move into wildfire-prone areas at high rates. The issue is particularly acute in California where a recent analysis indicated that over five million homes are located in the UWI (Radeloff *et al* 2005, Theobald and Romme 2007). This number is the highest in the US, and is expected to increase further as urban dwellers seek the 'natural amenities'—e.g., open space and recreational opportunities—provided by wildland areas. Similar trends elsewhere in the world are exacerbated by long-term economic conditions, such as the declining value of rural commodities, which result in land being of greater value for housing than for other uses.

Responses after large UWI fires in California have been consistent and largely focused on the procurement of additional

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**Figure 1.** Santiago Canyon Fire in Foothill Ranch, Orange County, California (October 2007). Courtesy of Alex Miroshnichenko (Miro-Foto).

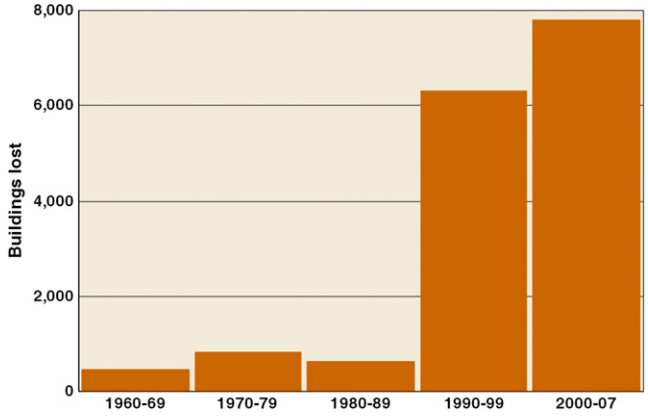


**Figure 2.** Number of buildings lost from the 25 most destructive UWI fires in California history from 1960–2007.

fire suppression resources, particularly at the state level. The common argument presented is: 'if we had more fire engines, aircraft, and fire fighters then we could have prevented this catastrophic loss of homes'. While fire suppression is a critical component of fire management in the UWI, it alone will not reduce the losses of life and property. A new approach is needed, and that is the goal of our joint examination of the problem by both American and Australian scientists. In a novel collaboration, we present ideas that could be used to fundamentally change fire management in the UWI across the US. Such a new approach must also be examined critically, since it should neither encourage further fragmentation of natural landscapes nor give a false sense of safety to those in the most vulnerable situations.

## 2. The need for a new approach

As a society we have attempted to accommodate some of the natural hazards inherent to the landscapes that we inhabit. For example, buildings in earthquake-prone areas are designed to withstand events of a given magnitude. Building on floodplains is typically restricted, and land-use planners are familiar with the concept of the 100- or 250-year flood event. In California and the rest of the US we have yet to adopt this line of thinking for fires—instead we focus much more on *fighting* fire than on coexisting with it.

Fuels, topography, and weather determine the level of fire hazard in any given area (Agee and Skinner 2005). Most of California experiences annual summer drought, and there are many different local patterns of fire weather. Some of the most extreme fire weather conditions, however, are generated by 'Santa Ana' winds in southern California (Schroeder *et al* 1964). These foehn winds—generated as air moves downward from a higher elevation—cause hot, dry, and very strong winds for days at a time. When these episodes coincide with dry fuels in autumn, fires can become very large and are unconstrained by the age and spatial patterns of shrubland fuels (Moritz *et al* 2004), pushing fires into the UWI (figure 1). Extreme fire weather can also occur in south east Australia as demonstrated by the 1983, 2003, and 2009 bushfires.

There is a strong link between fire activity and population patterns throughout California and humans are the dominant source of ignitions for UWI fires (Syphard *et al* 2007). Because substantial population increases are projected in coming decades, the problem of human ignitions will only get worse. In addition, some of the largest fires in California and Australia are often those intentionally set by arsonists, who target the worst conditions and most vulnerable locations. The majority of Californian and Australian ecosystems are fire adapted and altered fire regimes have been a negative influence on their sustainability (Pyne 1991, Sugihara *et al* 2006, Stephens *et al* 2007) further confounding management of the UWI and surrounding wildlands (Dombeck *et al* 2004, Donovan and Brown 2007).

Collaborative research between Australia and California on the performance of construction materials and landscaping during wildfires, quantification of fire hazard and risk in changing climates, effectiveness of fuels treatments, and policy development would enable both countries to advance more quickly in developing sustainable UWI areas.

## 3. Current UWI fire management in California

Most UWI fires in California and other regions in the US are managed in a similar fashion. Fire agencies first attempt to anticipate the spread of the fire, and mandatory evacuations are ordered. With the public evacuated, professional fire services move in and attempt to suppress the fires. This approach has not reduced building losses from UWI fires in California. Instead, losses have dramatically increased over the last three decades (figure 2). Mandatory evacuations may save lives if implemented well before the time a wildfire arrives to a particular location. However, evacuations at the last minute, when people may be overrun by fast-moving fires, create the most deadly periods in UWI fires (Gill 2005, Handmer and Tibbits 2005). Some people pack their cars with possessions and then procrastinate or wait until the wildfire is in close proximity before leaving, this can be very dangerous.

UWI fire policy in California and other regions of the US has developed piecemeal. Historically, large-scale urban conflagrations were the result of structure-to-structure fires, fueled by wood buildings. These types of urban fires, where hundreds of buildings are lost, are uncommon now because urban areas contain fewer wood buildings and most buildings include a multitude of features such as fire alarms, fire-resistant walls, and sprinklers.

As the recent 2007 and 2008 fires in southern California have demonstrated, we still have a long way to go in reducing similar losses in UWI fires (Mutch 2007, Paveglio *et al* 2008). As homes continue to be built in flammable wildland areas, the Californian approach to building has yet to catch up to the types of hazards faced by homeowners (CFRO 2005). For example, it is evident that most homes ignite in UWI fires (figure 1) due to embers that can travel over 1–2 km. At a minimum, therefore, vents that resist ember entry into attics and fire-resistant roofing and other building materials are key. While there is good evidence as to the efficacy of this type of 'fire safe' approach to building and maintaining homes (Cohen 2000, Blanchi and Leonard 2008), it has remained largely unregulated in the US.

## 4. What California can do reduces losses in the UWI

### *4.1. UWI building codes*

In California, enforcement of new building codes that include ignition-resistant construction standards only began in early 2008 (CBC 2007). These codes will apply only to new buildings in very high hazard UWI areas and areas where the state has financial responsibility for fire protection. Local jurisdictions will have the ability to accept or reject their zoning designation, thereby influencing where stricter building codes apply. While we believe that this new policy is a step forward, much more needs to be done.

Out of necessity, revised building codes are a compromise between science, policy, and economic interests. Even so, a more rigorous and objective approach to assessing structure vulnerabilities is needed, so that each revision to UWI standards and policies is based on the best scientific analysis possible. All UWI policies should be reviewed and updated as new information becomes available.

### *4.2. Land-use planning*

Large portions of California's 58 counties are under local land-use planning control, and several jurisdictions have adopted local ordinances to mandate defensible space and fire-resistant materials in home construction in the UWI (e.g. Ventura and Los Angeles counties). Most local jurisdictions, however, have employed a variety of standards over the years, changing requirements as priorities and economic conditions change. The resulting mixture of different aged housing stock—and thus structural vulnerabilities—makes long-term standardized solutions problematic. The continued expansion of the UWI and fragmentation of fire-prone wildlands is also directly related to increases in the number of ignitions. Importantly, the UWI poses a series of additional environmental challenges, including ecosystem fragmentation, increased exposure to invasive species, and water and air pollution (Alavalapati *et al* 2005).

Alternative policies and/or regulatory approaches aimed at reducing the inconsistencies in local land-use planning should be implemented. For example, one approach would be to move some local, land-use planning authority to the state level. This would mean in reference to fire in the UWI, any new development would have to be reviewed by a state level, land-use planning agency. This standardized review would include both materials used in construction, construction methods, and land-use planning objectives, based on a strategic plan to protect the many public assets that fire affects. This type of comprehensive planning may be especially important in the face of climate change (Moritz and Stephens 2008), an issue that links fire, development patterns, and ecosystem services in broader context.

As a model, in the state of New South Wales in Australia, the Rural Fire Service performs a similar service (albeit at a sub-division level rather than the level of individual houses). In 1997 the Rural Fire Act was passed in New South Wales and this consolidated 142 separate fire municipalities into one organization with similar standards; in 2002 this act was amended to incorporate the review of new housing construction in all wildlands. Such a strategy has advantages because one set of UWI standards is applied to the whole state, and each review includes a mandatory fire perspective. This approach has the best chance of success if planning and building provisions are combined into a holistic process.

### *4.3. Fire suppression*

The costs of fire suppression continue to rise at both federal and state levels in the US (Stephens and Ruth 2005). A large proportion of 'fire' budgets are focused solely on fire suppression with more limited funds for the reduction of hazardous fuels and public education (Steelman and Burke 2007). However, a recent study by the Natural Resources Defense Council reported an average cost of only $2510/home to make the needed improvements (e.g., vent screening and enclosing open eaves to prevent ember intrusion) to create more fire-resistant homes in a community in the Sierra Nevada foothills (Mall and Matzner 2007). Even if subsidized by state or local governments, or insurance companies, these costs are substantively lower than the losses incurred in massive UWI fires.

### *4.4. Insurance issues*

With the numbers of structures lost in California wildfires, many homeowners now risk losing, or never being able to obtain, fire insurance. Although the State of California has developed a program to offer insurance to those homeowners unable to obtain private insurance, the price is higher, and it is not available everywhere it is needed. Regardless, insurers could play a much larger role in providing incentives to homeowners to reduce structure-based wildfire hazards, and therefore losses. However, an insurance-based approach

cannot fully solve the UWI fire challenge because a home-based policy disregards non-monetary goods and services (uninsured personal property, recreation, aesthetics) (Talberth *et al* 2006).

In New South Wales and Victoria, Australia, significant components (approximately 17%) of private fire insurance premiums paid by individuals are used in fire mitigation practices. These resources are used to fund rural fire services, neighborhood community groups regarding fire, and public outreach and education (Henri 2003). Connecting fire insurance companies to UWI homeowners can increase incentives to reduce the vulnerability of homes through the marketplace (i.e. lower premiums for houses that resist ember attack, have access to water supplies, include multiple access/egress opportunities).

## 5. The Australian policy

The 'Stay or Go'—or more accurately 'Prepare, stay and defend, or leave early'—approach has recently been endorsed by all Australian fire services, as well as by most police forces (AFAC 2005); there is a similar approach in southern France although this is not based on a national policy.

The Australian position is that all residents should prepare their property against fire and decide whether to stay and actively defend their property or leave early before a fire threatens the area and road travel becomes dangerous. If they decide to stay, they are advised to prepare their property through vegetation (fuel) management, undertaking house protection measures, and ensuring they have the resources, both physical and psychological, to actively defend their property. The approach does not entail or encourage people to passively 'shelter in place' which is dangerous (Gill 2005). The common American usage of the phrase 'shelter in place' in the context of fire implies a much more passive response than what the Australian policy requires.

There is considerable evidence that well-prepared houses can provide a safe place for people during wildfires, based on the key assumption that a fire front passes quickly and that houses can survive this period and protect occupants from radiant heat, smoke and embers. This is well supported by research on how houses ignite and are destroyed largely through ember attack (Cohen 2000, Blanchi and Leonard 2008). Risk from embers can be reduced by advance preparation, such that when small fires are ignited by embers, they can be extinguished if residents are present and prepared, and actively defending their property.

No option is risk free, but evidence suggests that the most common avoidable cause of death is being caught outside of a structure as the fire front passes with its lethal radiant heat and smoke. Fleeing at the last minute often involves driving or running through flames, ember storms, and intense heat and smoke, with accompanying disorientation and poor visibility. This is the most dangerous option.

Evidence from Australia has come from oral histories, documented practice by fire agencies and those at risk, post-fire public inquiries, scientific publications, and a fatality data-base (Handmer and Tibbits 2005, Gill 2005, Handmer and Haynes 2008, Leicester and Handmer 2008). Most of this material deals with extreme fires—the worst Australian fires in the last 70 years—and their findings indicate:

- *Evidence supports current Australian practice*. The most risky thing to do, and the cause of most fatalities, is to leave at the last moment as the fire front arrives and when roads may be blocked by smoke, electrical power lines, stalled cars, and burning debris.
- Building research confirms that *embers ignite houses* and these fires can be put out by vigilant trained homeowners.
- The critical factor in *building survival is the presence of people.*
- There is *no legal impediment*, but there are some gaps such as some Australian police agencies ordering mandatory evacuations during UWI fires at the same time as fire services want prepared people to stay (Tibbits and Whittaker 2007).
- There are *many implementation issues* to do with information provision, expectations that fire agencies will be at every house, belief that houses explode in fires, confidence, commitment, and high risk decisions. This therefore requires a strong and sustained commitment to public education and outreach.

In Victoria, Australia, the 'Operation Fireguard' program attempts to educate all communities at risk to wildfire attack (CFA 2004, 2007). Training courses are held every year preceding the onset of the fire season, and there are numerous newspaper articles on both preparation and action plans. All residents are exhorted to prepare an 'action plan' prior to the start of the fire season. Within this action plan they select whether they will choose the 'stay and defend' option or the 'leave early' option. The 'Prepare, stay and defend, or leave early' strategy has frequently worked well in Australia, but experience shows that for this to happen all critical components of this strategy must be in place, particularly (a) the effective education of the community, (b) the psychological, infrastructure, landscaping, and equipment preparation of those who plan to stay and (c) an effective early warning system to communicate to those living in the UWI.

## 6. People living in the UWI: a potential resource regarding wildfire

The Australian approach to UWI fire management has the distinct advantage of engaging those most affected by such fires: homeowners. Homeowners that prepare for inevitable UWI fires can be a positive resource in fire management, instead of simply people to be evacuated, as in the California case. It is recognized that some UWI communities are dominated by vacation homes that are only occupied a few weeks each year. The Australia UWI policy would not directly apply in these areas because of the general absence of people.

In both the US and Australia, most new residents in the UWI have arrived there from cities and have little experience of natural hazards such as fire (Pyne 1991, Moritz and Stephens 2008). This is all the more reason for engagement. By engaging and training those potentially affected by UWI fires,

losses could be reduced in California and other regions of the US. However, it is not clear if factors unique to some California UWI communities might make it impossible to implement a policy similar to that in Australia. There may be some regions where the local climate, topography, and infrastructure may render a 'Prepare, stay and defend or leave early' option to be inadvisable. In these locations, a focus on preparing your property to resist ignitions and leaving early may be the only viable option. UWI areas surrounded by crown fire adapted ecosystems such as chaparral or mountain ash (*Eucalyptus regnans*) forests could be particularly hazardous.

Investing solely in more resources for fire suppression in an attempt to reduce losses from California UWI fires is not justified. There will never be enough suppression resources alone to reduce losses with an ever-expanding UWI. Part of the solution is a more sustainably designed and built UWI, inhabited by informed and prepared homeowners.

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# HUMAN INFLUENCE ON CALIFORNIA FIRE REGIMES

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*Abstract*. Periodic wildfire maintains the integrity and species composition of many ecosystems, including the mediterranean-climate shrublands of California. However, human activities alter natural fire regimes, which can lead to cascading ecological effects. Increased human ignitions at the wildland–urban interface (WUI) have recently gained attention, but fire activity and risk are typically estimated using only biophysical variables. Our goal was to determine how humans influence fire in California and to examine whether this influence was linear, by relating contemporary (2000) and historic (1960–2000) fire data to both human and biophysical variables. Data for the human variables included fine-resolution maps of the WUI produced using housing density and land cover data. Interface WUI, where development abuts wildland vegetation, was differentiated from intermix WUI, where development intermingles with wildland vegetation. Additional explanatory variables included distance to WUI, population density, road density, vegetation type, and ecoregion. All data were summarized at the county level and analyzed using bivariate and multiple regression methods. We found highly significant relationships between humans and fire on the contemporary landscape, and our models explained fire frequency ($R^2 = 0.72$) better than area burned ($R^2 = 0.50$). Population density, intermix WUI, and distance to WUI explained the most variability in fire frequency, suggesting that the spatial pattern of development may be an important variable to consider when estimating fire risk. We found nonlinear effects such that fire frequency and area burned were highest at intermediate levels of human activity, but declined beyond certain thresholds. Human activities also explained change in fire frequency and area burned (1960–2000), but our models had greater explanatory power during the years 1960–1980, when there was more dramatic change in fire frequency. Understanding wildfire as a function of the spatial arrangement of ignitions and fuels on the landscape, in addition to nonlinear relationships, will be important to fire managers and conservation planners because fire risk may be related to specific levels of housing density that can be accounted for in land use planning. With more fires occurring in close proximity to human infrastructure, there may also be devastating ecological impacts if development continues to grow farther into wildland vegetation.

*Key words: California, USA; fire; fire history; housing density; nonlinear effects; regression; wildland–urban interface.*

## Introduction

Fire is a natural process in many biomes and has played an important role shaping the ecology and evolution of species (Pyne et al. 1996, Bond and Keeley 2005). Periodic wildfire maintains the integrity and species composition of many ecosystems, particularly those in which taxa have developed strategic adaptations to fire (Pyne et al. 1996, Savage et al. 2000, Pausas et al. 2004). Despite the important ecosystem role played by fire, human activities have altered natural fire regimes relative to their historic range of variability. To develop effective conservation and fire management strategies to deal with altered fire regimes, it is necessary to understand the causes underlying altered fire behavior and their human relationships (DellaSalla et al. 2004). Nowhere is this more critical in the United States than in California, which is the most populous state in the nation, with roughly $35 \times 10^6$ people. Most of the population lives in lower elevations dominated by hazardous chaparral shrublands susceptible to frequent high-intensity crown fires.

In California, as elsewhere, the two primary mechanisms altering fire regimes are fire suppression, resulting in fire exclusion, and increased anthropogenic ignitions, resulting in abnormally high fire frequencies (Keeley and

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Fotheringham 2003), though climate change, vegetation manipulation, and other indirect factors may also play a role (Lenihan et al. 2003, Sturtevant et al. 2004). For most of the 20th century, fire suppression effectively excluded fire from many western U.S. forest ecosystems, such as ponderosa pine. In these ecosystems, fire exclusion contributed to unnatural fuel accumulation and increased tree density (Veblen et al. 2000, Allen et al. 2002, Gray et al. 2005). Recently, when wildfires have hit many of these forests, hazardous fuel loads have contributed to high-intensity crown fires that are considered outside the historical range of variability (Stephens 1998). While these patterns are widely applicable to many forested landscapes in the western United States, California chaparral shrublands have experienced such substantial human population growth and urban expansion that the increase in ignitions, coupled with the most severe fire weather in the country (Schroeder et al. 1964), have acted to offset the effects of suppression to the point that fire frequency exceeds the historic range of variability (Keeley et al. 1999). Because anthropogenic ignitions tend to be concentrated near human infrastructure, more fires now occur at the urban fringe than in the backcountry (Pyne 2001, Keeley et al. 2004). Profound impacts on land cover condition and community dynamics are possible if a disturbance regime exceeds its natural range of variability, and altered fire regimes can lead to cascading ecological effects (Landres et al. 1999, Dale et al. 2000). For example, too-frequent fire can result in habitat loss and fragmentation, shifting forest composition, reduction of small-mammal populations, and accompanying loss of predator species (Barro and Conard 1991, DellaSalla et al. 2004).

Landscape-level interactions between human activities and natural dynamics tend to be spatially concentrated at the wildland–urban interface (WUI; see Plate 1), which is the contact zone in which human development intermingles with undeveloped vegetation (Radeloff et al. 2005). The WUI has received national attention because housing developments and human lives are vulnerable to fire in these locations and because anthropogenic ignitions are believed to be most common there (Rundel and King 2001, USDA and USDI 2001). The majority of WUI fire research has focused on strategies to protect lives and structures (e.g., Cohen 2000, Winter and Fried 2000, Winter et al. 2002, Shindler and Toman 2003) or on the assessment of fire risk using biophysical or climate variables that influence fire behavior (Bradstock et al. 1998, Fried et al. 1999, Haight et al. 2004). However, it is also important to understand how the WUI itself (or other indicators of human activity) affects fire and to quantify the spatial relationships between human activities and fire (Duncan and Schmalzer 2004).

The influence of proximity to the WUI and other human infrastructure appears to vary markedly with region. In the northern Great Lakes states, areas with higher population density, higher road density, and lower distance to nonforest were positively correlated with fire (Cardille et al. 2001). Also, in southern California, a strong positive correlation between population density and fire frequency was reported (Keeley et al. 1999). However, no relationship between housing count and fire was found in northern Florida counties (Prestemon et al. 2002); population density and unemployment were positively related, and housing density and unemployment were negatively related to fire in a different analysis of Florida counties (Mercer and Prestemon 2005). A negative relationship between housing density and fire was also found in the Sierra Nevada Mountains of California (CAFRAP 2001).

In addition to potential regional differences, it is also difficult to draw general conclusions from these studies because they used different indicators of human activities, their data sets differed in spatial and temporal scale, and they were conducted in small areas where ranges of variability in both fire frequency and level of development were limited. Human–fire relationships may also vary based on factors that were not accounted for, such as pattern of development. Another explanation for the discrepancy is that relationships between human activities and fire may be nonlinear in that humans may affect fire occurrence positively or negatively, depending on the level of influence. These nonlinear effects were apparent in data from a recent study in the San Francisco Bay region, where population growth was positively related to fire frequency over time up to a point, but then fire frequency leveled off as population continued to increase (Keeley 2005).

Whether positive or negative, the significance of the relationships between human activities and fire that were detected in previous studies stresses the importance of further exploring links between anthropogenic and environmental factors and their relative influence on wildfire patterns across space and time. Therefore, our research objective was to quantify relationships between human activities and fire in California counties using temporally and spatially rich data sets and regression models. Although fire regimes encompass multiple characteristics, including seasonality, intensity, severity, and predictability, we restricted our analysis to questions about fire frequency and area burned to determine: (1) what the contemporary relationship between human activities and fire is; (2) how human activities have influenced change in fire over the last 40 years; and (3) whether fire frequency and area burned vary nonlinearly in response to human influence.

Humans are responsible for igniting the fires that burn the majority of area in California (Keeley 1982); therefore, we expected our anthropogenic explanatory variables to significantly explain fire activity on the current landscape and over time. In addition to population density (which simply quantifies the number of people in an area), we expected the spatial pattern of human development (indicated by housing density and

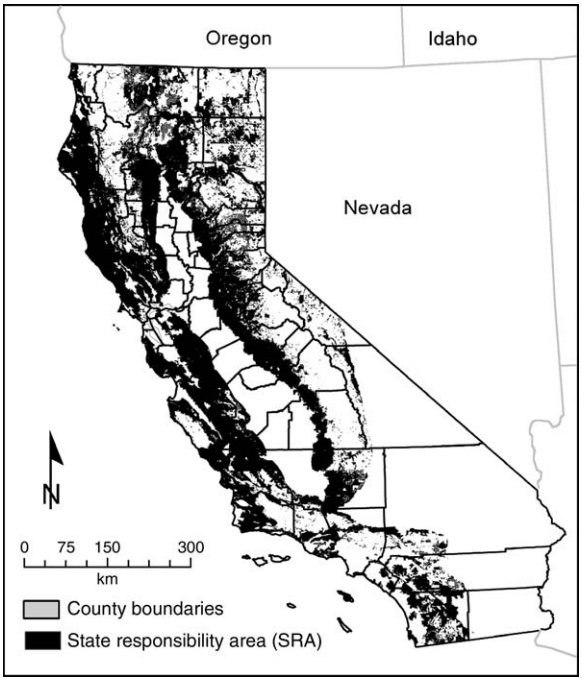


FIG. 1. Map of California Department of Forestry and Fire Protection (CDF) state responsibility areas (SRAs) within county boundaries of California, USA.

land cover combinations and distance variables) to be an important influence on fire because we assumed that anthropogenic ignitions are most likely to occur where human presence is greatest. We also expected that the relationships between human activities and fire would be both positive and negative because humans ignite fires, but development patterns affect fuel continuity and the accessibility of fire suppression resources. Finally, we included several environmental variables in the analysis because we expected the human relationships to be mediated by these other biophysical variables that shape the pattern and frequency of fire (Wells et al. 2004).

## METHODS

### *Study area*

California is the second largest state in the continental United States and is the most populous and physically diverse. Most of the state has a mediterranean climate, which, along with a heterogeneous landscape, contributes to tremendous biodiversity (Wilson 1992). Because the state contains a large proportion of the country's endangered species, it is considered a "hotspot" of threatened biodiversity (Dobson et al. 1997). There is extensive spatial variation in human population density: large areas in the north are among the most sparsely populated in the country, but metropolitan regions in the south are growing at unprecedented rates (Landis and Reilly 2004). Much of the landscape is highly fire-prone, but fire regimes vary, and fire management is divided among many institutions. Humans have altered California's fire regimes, and its fire-related financial losses are among the highest in the country (Halsey 2005).

### *Data*

*Dependent variables: fire statistics.*—We assembled our fire statistics from the California Department of Forestry and Fire Protection (CDF; Sacramento, California, USA) annual printed records, which included information on all fires for which the CDF took action between 1931 and 2004. For all state responsibility areas (SRA; Fig. 1), fire statistics are recorded by county and include numbers by size class, total area burned, vegetation type, and cause. Because the statistics did not include spatially explicit information on individual fires, we weighted the data by the area within the SRA in each county by calculating proportions to use as our dependent variables. These fire statistics were substantially more comprehensive than the readily available electronic Statewide Fire History Database, which excludes most fires <40 ha, which in many counties represents >90% of the fires. Although both anthropogenic and lightning ignitions would be important to consider for fully understanding fire patterns in other regions (e.g., Marsden 1982), humans were responsible for ~95% of both the number of fires and area burned in California in the last century. We restricted our analysis to these anthropogenic fires because our focus was on human relationships with fire. Although the fire statistics were not spatially explicit, we developed GIS grids at 100-m resolution to derive data for all of the explanatory variables. The data for these explanatory variables were only extracted and averaged from within the SRA boundaries corresponding to the fire data.

Out of the 58 counties in California, we had fire statistics for 54 of them for the year 2000. Therefore, to assess the contemporary relationship between fire and human activities (hereafter referred to as the "contemporary analysis"), we analyzed the data from these counties using the annual number of fires and area burned as our dependent variables (Table 1).

Based on a preliminary exploration of the fire history data (averaged across all counties), we observed two distinct trends during the last 50 years. First, the number of fires substantially increased until 1980 and then decreased until 2000; and second, the average area burned changed inversely to the number of fires, but the differences over time were less dramatic and not statistically significant (Fig. 2). Considering these trends, we broke the historic analysis into two equal time periods (1960–1980 and 1980–2000) to compare the relative influence of the explanatory variables on both the increase (i.e., from 1960 to 1980) and decrease (from 1980 to 2000) in fire activity. The year 1980 is used to compute differences for both time periods because the census data that formed the basis for many of our explanatory variables were only available by decade. We averaged the number of fires and the area burned for 10-

TABLE 1. Variables analyzed in the regression models.

| Variable | Source | Processing |
|---|---|---|
| 2000 data | | |
| Dependent variables | | |
| Number of fires | CDF | proportion in SRA, square-root transformed |
| Area burned | CDF | proportion in SRA, square-root transformed |
| Explanatory variables | | |
| Human | | |
| Intermix WUI | SILVIS | proportion in SRA |
| Interface WUI | SILVIS | proportion in SRA |
| Low-density housing | SILVIS | proportion in SRA |
| Distance to intermix WUI | SILVIS | mean Euclidean distance in SRA |
| Distance to interface WUI | SILVIS | mean Euclidean distance in SRA |
| Population density | SILVIS | proportion in SRA |
| Road density | TIGER | mean km/km$^2$ in SRA |
| Distance to road | TIGER | mean Euclidean distance in SRA |
| Biophysical | | |
| Ecoregion | CDF | discrete class |
| Vegetation type | CDF | area burned in vegetation type/area burned in SRA |
| Historic data, 1960–1980 and 1980–2000 | | |
| Dependent variables | | |
| Change in number of fires | CDF | difference between decadal averages, proportion in SRA, square-root transformed |
| Change in area burned | CDF | difference between decadal averages, proportion in SRA, square-root transformed |
| Explanatory variables | | |
| Human | | |
| Change in housing density | SILVIS | difference between decades |
| Change in distance to low-density housing | SILVIS | difference between mean Euclidean distance in SRA |
| Initial housing density | SILVIS | mean housing density in either 1960 or 1980 |
| Initial distance to low-density housing | SILVIS | mean Euclidean distance in SRA in either 1960 or 1980 |
| Biophysical | | |
| Ecoregion | CDF | discrete class |
| Vegetation type | CDF | mean area burned in vegetation type/area burned in SRA over time period |

*Notes:* Key to abbreviations: WUI, wildland–urban interface; SRA, state responsibility area. Sources are as follows: CDF, California Department of Forestry and Fire Protection, Sacramento, California, USA, *unpublished data*; SILVIS, Radeloff et al. (2005); TIGER, U.S. Census Bureau (2000).

year time periods that bracketed the dates of the census data (e.g., 1955–1964 [1960], 1975–1984 [1980], 1995–2004 [2000]) and then calculated the difference in averages from the 1960–1980 and 1980–2000 periods for our dependent variables (Table 1). By averaging the fire data, we smoothed some of the annual variability that may have occurred due to stochastic factors such as weather.

*Explanatory variables: housing data.*—Data for most of the anthropogenic variables were available through a nationwide mapping project that produced maps of the WUI in the conterminous United States using housing density data from the 1990 and 2000 U.S. Census (U.S. Census Bureau 2002) and land cover data from the USGS National Land Cover Dataset (Radeloff et al. 2005). The maps were produced at the finest demographic spatial scale possible, the 2000 decennial census blocks. The vegetation data were produced at 30-m resolution. These maps delineated two types of WUI in accordance with the Federal Register definition (USDA and USDI 2001). "Intermix WUI" is defined as the intermingling of development with wildland vegetation; the vegetation is continuous and occupies >50% of the area. "Interface WUI" is defined as the situation in which development abuts wildland vegetation; there is <50% vegetation in the WUI, but it is within 2.4 km of an area that has >75% vegetation. In both types of WUI communities, housing must meet or exceed a density of more than one structure per 16 ha (6.17 housing units/km$^2$). Interface WUI tends to occur in buffers surrounding higher-density housing, whereas intermix WUI is more dispersed across the landscape (Fig. 3A, B).

The WUI data were only produced for 1990 and 2000 due to the lack of historic land cover data, but housing density data were available from 1960 to 2000. Historic housing density distribution was estimated using back-casting methods to allocate historic county-level housing unit counts into partial block groups (as described in Hammer et al. 2004). We used both intermix and interface WUI as explanatory variables (proportions within the county SRAs) in the current analysis to evaluate how these different patterns of vegetation and housing density affected fire activity. We also used low-density housing (housing density $\geq$6.17 housing units/km$^2$ and <49.42 housing units/km$^2$) to determine whether it could act as a substitute for WUI as an explanatory variable in the historic analysis (Table 1).

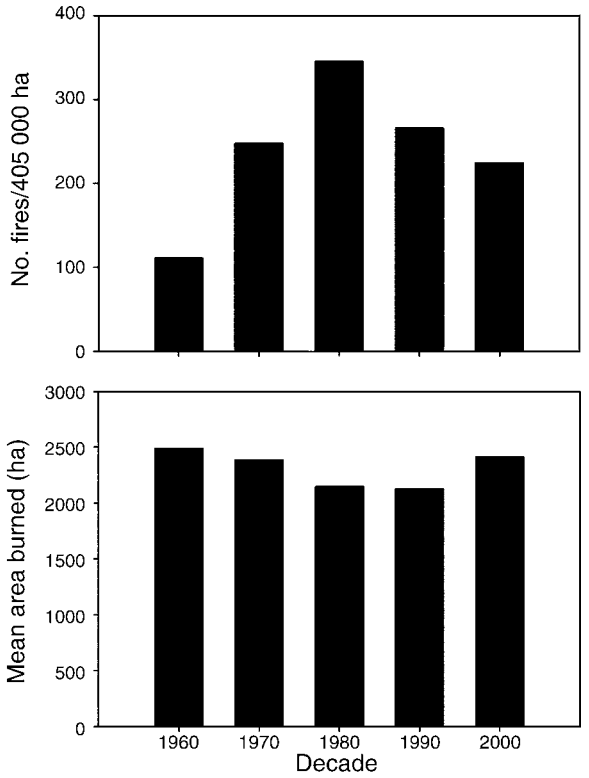


FIG. 2. Trends in number of fires and area burned for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

Looking at an overlay of fire perimeters from the electronic Statewide Fire History Database (from the last 25 years; *available online*)[7] on the WUI data, it was apparent that many fires occurred close to the WUI, but not necessarily within the WUI (Fig. 3C, D). Therefore, we calculated the mean distance to intermix and interface WUI to evaluate as explanatory variables (Table 1). These means were calculated by iteratively determining the Euclidean distances from every grid cell in the county SRA boundaries and then averaging the distances across all cells to determine means for the counties. We also included population density data from the 2000 Census.

For the historic analysis, we calculated changes in mean housing density and mean distance to low-density housing between the 1960–1980 and 1980–2000 periods to relate to change in the dependent variables. We excluded the proportion of low-density housing from our analysis because it was highly correlated with mean housing density ($r = 0.84$). Unlike the historical fire data that switched in their direction of change over time, housing density continued to increase while the mean distance to low-density housing continued to decline (Fig. 4). We included the initial values of these data (e.g., 1960 and 1980) to account for the fact that the same magnitude of change may have different effects on the dependent variables depending on the starting value of the explanatory variables (Table 1).

*Explanatory variables: road data.*—The quality of road data can vary according to data source (Hawbaker and Radeloff 2004), so we compared the U.S. Geological Survey digital line graph (DLG; U.S. Geological Survey 2002) and the US TIGER 2000 GIS (U.S. Census Bureau 2000) layers of roads to determine whether there were substantial differences that could affect the interpretation of the results. After calculating and summarizing road density by county, we found a strong positive correlation ($r = 0.97$). Therefore, we used the TIGER data because they were produced in 2000, the same year as the contemporary analysis. The more current TIGER data generally capture new development that might not be included in the DLG data. We evaluated mean road density and mean distance to roads in the current analysis (Table 1), but road data were unavailable for the historic analysis.

*Explanatory variables: environmental.*—In the absence of human influence, fire behavior is primarily a function of biophysical variables (Pyne et al. 1996, Rollins et al. 2002). These can vary widely across a county, but ecoregions capture broad differences by stratifying landscapes into unique combinations of physical and biological variables (ECOMAP 1993). Our ecoregion data were the geographic subdivisions of California defined for The Jepson Manual (Hickman 1993), designated through broadly defined vegetation types and geologic, topographic, and climatic variation (Fig. 5).

Because vegetation type influences the ignitability of fuel and the rate of fire spread (Bond and van Wilgen 1996, Pyne et al. 1996), we also evaluated the proportion of area burned within three broad vegetation types: shrubland, grassland, and woodland (Fig. 5). Differences in fire regimes between broadly defined vegetation types can be striking, particularly between shrubland and woodland in southern California (Wells et al. 2004). The CDF fire statistics included information on the proportion of area burned in these vegetation types. For the historic analysis, we averaged the proportion of fires burned within different vegetation types over the entire decade (Table 1).

### *Analytical methods*

*Diagnostics and data exploration.*—Before developing regression models, we examined scatter plots for each variable. Nonlinear trends were apparent (e.g., Fig. 6), suggesting that we needed to include quadratic terms for the explanatory variables in the regressions. Unequal variances in the residual plots prompted us to apply a square-root transformation to the dependent variables. We also plotted semivariograms of the models' residuals (using centroids from the SRA boundaries) and found no evidence of spatial autocorrelation. To check for

[7] ⟨http://frap.cdf.ca.gov/data/frapgisdata/select.asp⟩

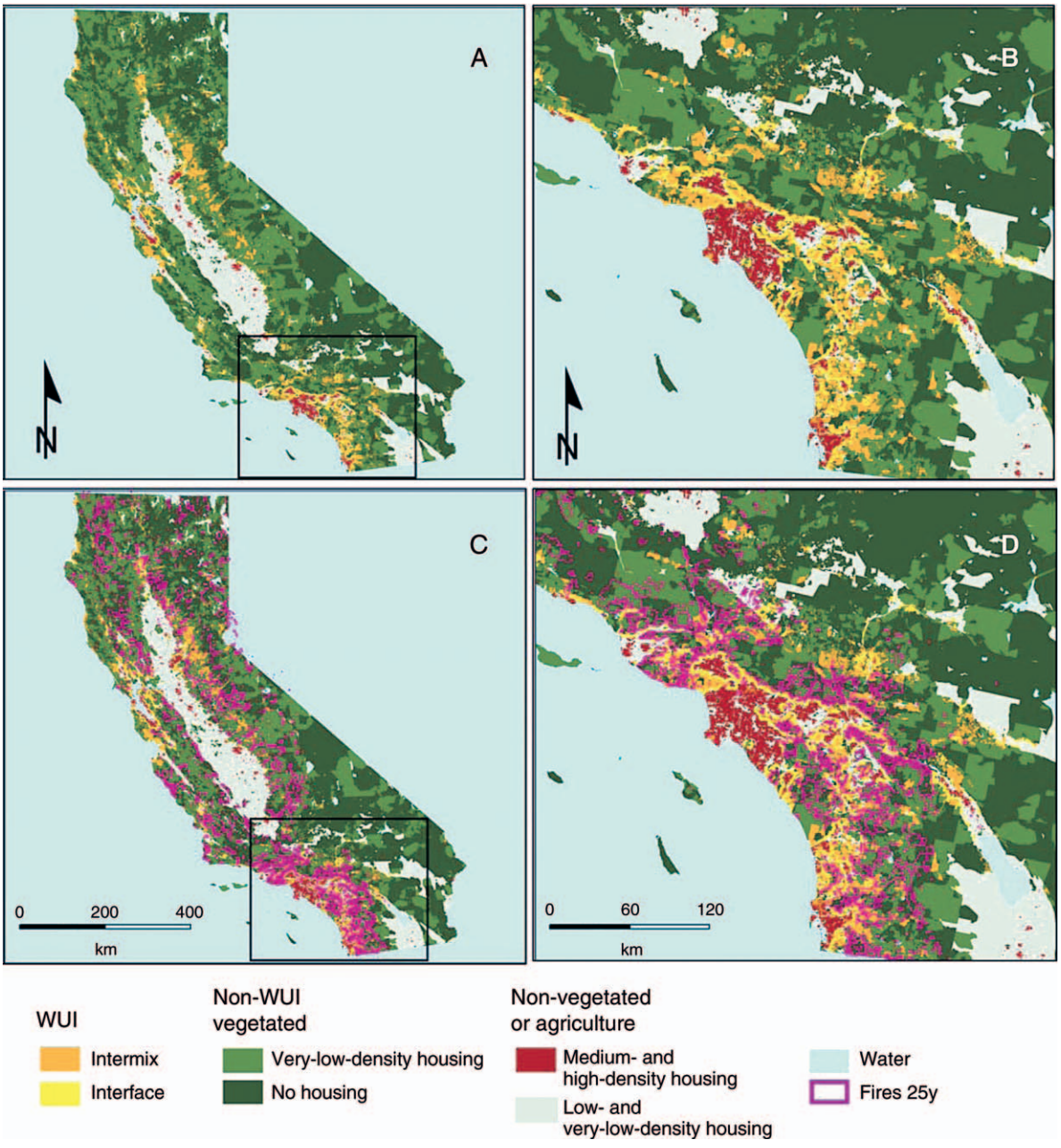


FIG. 3. The wildland–urban interface (WUI) in 2000 with and without fire perimeter overlays (from 1979 to 2004) in (A, C) California and (B, D) southern California. Housing density is defined as follows: very low, >0–6.17 housing units/km$^2$; low, 6.17–49.42 housing units/km$^2$; medium, 49.42–741.31 housing units/km$^2$; and high, >741.31 housing units/km$^2$ (USDA and USDI 2001). "Fires 25y" refers to 25 years of fire perimeters, from 1980 to 2005.

multicollinearity, we calculated the correlation coefficients between all of the explanatory variables and only included noncorrelated variables ($r \leq 0.7$) in the multiple regression models.

The areas of CDF jurisdiction for each county varied slightly over time. Therefore, we compared separate regressions from the full historic data set ($n = 37$) to a subset of the data excluding counties that experienced a greater than 20% change in area over time ($n = 23$). For both the 1960–1980 regressions and the 1980–2000 regressions, every one of the explanatory variables that was significant in the subset was also significant in the full data set, with very similar $R^2$ values; therefore, we felt confident proceeding with the full data set for the historic analysis because we had greater power with the larger sample size.

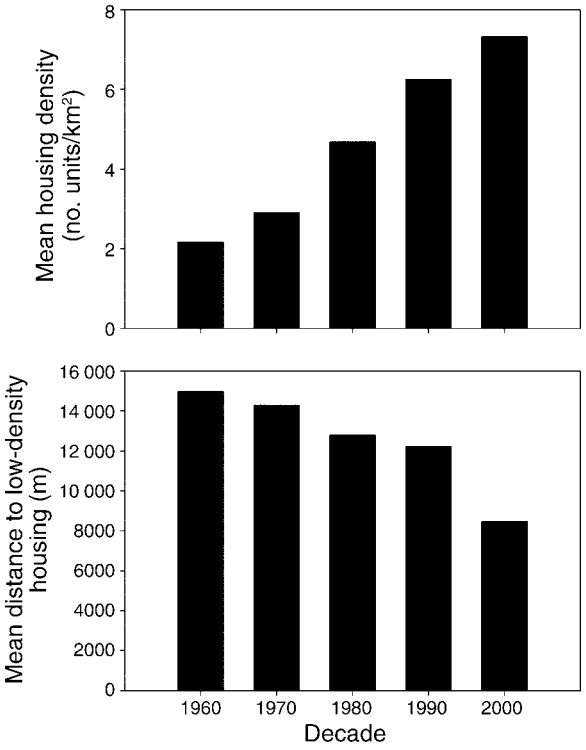


FIG. 4. Trends in housing density and distance to low-density housing (6.17–49.42 housing units/km$^2$) for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

### *Statistical analysis*

We used the same regression modeling approach for both the current and historic analyses. First, we developed bivariate regression models for all of the explanatory variables and their quadratic terms so that we could evaluate their independent influence on fire frequency and area burned. To account for the interactions between variables (and their quadratic terms), we also built multiple regression models using the R statistical package (R Development Core Team 2005). For all models, we first conducted a full stepwise selection analysis (both directions) using Akaike Information Criteria to identify the best combination of predictor variables (Burnham and Anderson 2002). Some of the models retained a quadratic term without including the lower-order variable. In these models, we added the lower-order term, rebuilt the model, and then proceeded with a backwards elimination process until all predictor variables in the model were significant with $P$ values $\leq 0.05$.

## RESULTS

### *Current analysis*

*Bivariate regressions.*—Many of the anthropogenic variables were highly significant in explaining the number of fires in 2000. The quadratic term for each of these variables was also significant, and the direction of influence was both positive and negative (Fig. 7). Compared to the other variables, population density explained the greatest amount of variability. The proportion of intermix WUI and low-density housing in the counties also explained significant variation in the number of fires; but the proportion of interface WUI was insignificant. The number of fires was significantly related to the mean distance to both types of WUI, but neither of the road variables was significant. All three vegetation types, particularly shrubland, significantly influenced the number of fires, but ecoregion was insignificant.

For the anthropogenic variables, the number of fires was highest at intermediate levels of population density (from ~35 to 45 people/km$^2$; Fig. 6), proportion of intermix WUI (~20–30% in the county), and proportion of low-density housing (~25–35% in the county). It was also highest at the shortest distances to intermix and interface WUI, but started to level off at ~9–10 km for intermix (Fig. 6) and 14–15 km for interface WUI.

Unlike the number of fires, none of the anthropogenic variables were significantly associated with the area burned in 2000. In fact, shrubland was the only variable that explained significant variation in area burned.

*Multiple regression.*—When all of the variables were modeled in the multiple regressions, the resulting model for number of fires in 2000 included population density, the proportion of intermix WUI and its quadratic term, grassland and its quadratic term, and shrubland (Table 2). The model was highly significant with an adjusted $R^2$ value of 0.72.

The multiple regression model for area burned in 2000 included distance to road, shrubland, and woodland, and all three variables had significant positive relationships (no quadratic terms were retained). This model was also highly significant with an adjusted $R^2$ of 0.50.

### *Historical analysis 1960–1980*

*Bivariate regressions.*—Change in the number of fires (net increase) from 1960 to 1980 was significantly explained by each of the human-related variables except for change in the mean distance to low-density housing (Fig. 8). The quadratic term was also significant in the separate models, except for the initial distance to low-density housing (in 1960), which had a negative influence on the change in number of fires. Change in number of fires was also significantly related to ecoregion and shrubland vegetation.

The only three variables with significant influence on the change in area burned (net decrease) were the three vegetation types.

*Multiple regression.*—The explanatory variables that were retained in the multiple regression model for change in the number of fires from 1960 to 1980 included mean housing density in 1960 and its quadratic term, grassland vegetation, and ecoregion (Table 2). The adjusted $R^2$ value was highly significant at 0.72.

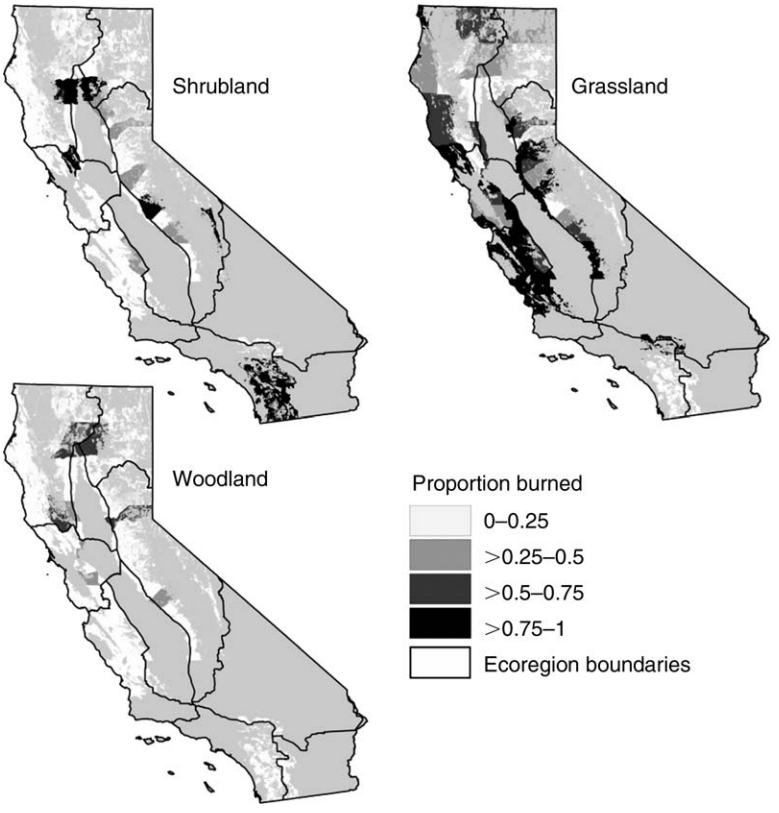


FIG. 5. Maps showing ecoregion boundaries and the proportion of area burned in shrubland, grassland, and woodland in 2000.

Mean housing density in 1960 was positively associated with change in area burned from 1960 to 1980, and the distance to low-density housing had first a positive, then a negative influence because the quadratic term was included. Other variables retained in the multiple regression model included shrubland and its quadratic term, grassland, woodland, and ecoregion.

### *Historical analysis 1980–2000*

*Bivariate regressions.*—Initial housing density (in 1980) was the only significant explanatory variable explaining change in number of fires (net decrease) from 1980 to 2000 (Fig. 9). Woodland vegetation was the only significant variable out of the separate models explaining change in area burned from 1980 to 2000 (net increase). The quadratic terms were significant for both of these models.

*Multiple regression.*—The multiple regression model explaining change in number of fires from 1980 to 2000 included change in housing density, initial housing density (in 1980), and woodland vegetation; the quadratic term was also significant for these three variables (Table 2). Although the model was significant, the $R^2$ was substantially lower than the 1960–1980 model, at 0.26.

The multiple regression model explaining change in area burned included initial housing density (in 1980) and its quadratic term, initial distance to low-density

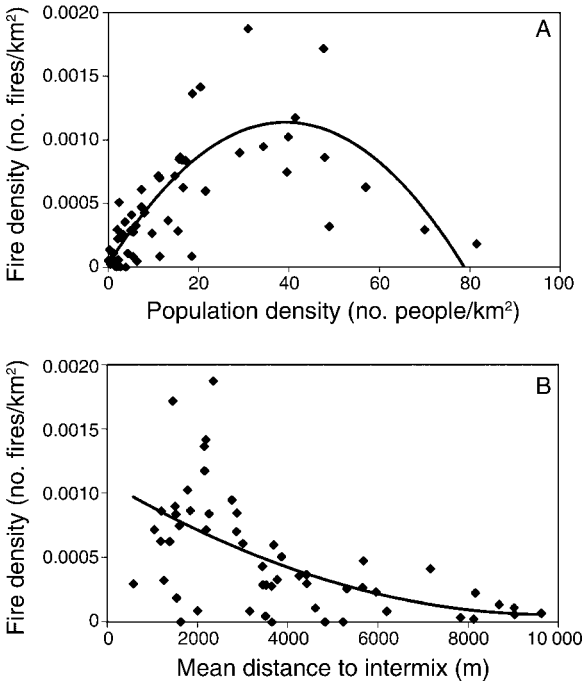


FIG. 6. The relationships between (A) the proportion of the number of fires and population density and (B) the proportion of the number of fires and mean distance to intermix wildland–urban interface (WUI).

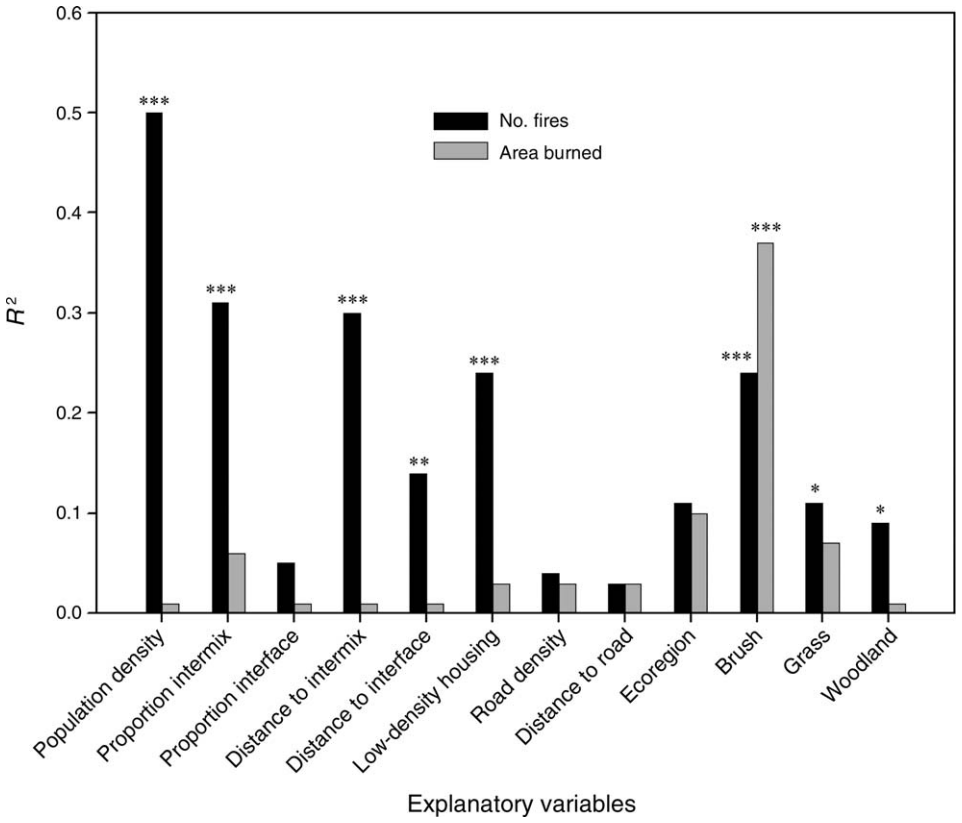


FIG. 7. $R^2$ values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned in 2000.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

housing, woodland vegetation and its quadratic, and ecoregion. This model had better explanatory power than the number of fires model, with an $R^2$ of 0.41.

## DISCUSSION

The expression of fire on a landscape is influenced by a combination of factors that vary across spatial and temporal scales and involve both physical and biological characteristics. Fire behavior has long been viewed as a largely physical phenomenon illustrated by the classic fire environment triangle that places fire as a function of weather, fuels, and topography (Countryman 1972), but clearly the human influence on modern fire regimes must also be understood to meet fire management needs (DellaSalla et al. 2004). We first asked what the current relationship is between human activities and fire in California and found that humans and their spatial distribution explained a tremendous proportion of the variability in the number of fires, but that area burned was more a function of vegetation type. Anthropogenic ignitions are the primary cause of fire in California and were the focus of our analysis, so we were not surprised by the strong human influence. Nevertheless, the high explanatory power of the models underscores the importance of using locally relevant anthropogenic factors as well as biophysical factors in fire risk assessments and mapping. The models also identify which indicators of human activity are most strongly associated with fire in California. For number of fires, the proportion of intermix WUI explained more variation than any other variable except for population density, suggesting that the spatial pattern of housing development and fuel are important risk factors for fire starts.

Human-caused ignitions frequently occur along transportation corridors (Keeley and Fotheringham 2003, Stephens 2005), so it was surprising that neither road density nor average distance to road were significant in explaining fire frequency. Although roads are important in local-scale ignition modeling, detecting their influence on fire ignitions may be difficult at an aggregated, county level since they are narrow, linear features. On the other hand, distance to roads was the only anthropogenic variable associated with area burned, having a positive influence when grassland and shrubland were also accounted for in the multiple regression model, which may reflect the difficulty of fire suppression access contributing to fire size.

Humans influence fire frequency more than area burned because anthropogenic ignitions are responsible

TABLE 2. Variables retained in the multiple regression models for the current and historic analyses.

| Analysis and explanatory variable | Coefficient and intercept | *P* |
|---|---|---|
| Current | | |
| 2000 | | |
| No. fires | | |
| Population density | 0.0006 | <0.01 |
| Proportion intermix | 0.0702 | <0.01 |
| (Proportion intermix)$^2$ | −0.2629 | <0.01 |
| Grassland | 0.0496 | <0.01 |
| (Grassland)$^2$ | −0.0441 | <0.01 |
| Shrubland | 0.0093 | 0.02 |
| Overall model (adjusted $R^2$: 0.72) | 0.0001 | <0.01 |
| Area burned | | |
| Distance to road | 0.00004 | <0.01 |
| Shrubland | 0.0833 | <0.01 |
| Woodland | 0.0559 | <0.01 |
| Overall model (adjusted $R^2$: 0.50) | −0.0052 | <0.01 |
| Historic | | |
| 1960–1980 | | |
| No. fires | | |
| Initial housing | 2.7649 | <0.01 |
| (Initial housing)$^2$ | −0.1523 | <0.01 |
| Grassland | 4.6311 | 0.05 |
| Ecoregion | ...† | <0.01 |
| Overall model (adjusted $R^2$: 0.72) | 0.6443 | <0.01 |
| Area burned | | |
| Initial housing | 0.0188 | <0.01 |
| Initial distance | 0.00002 | <0.01 |
| (Initial distance)$^2$ | $-2 \times 10^{-10}$ | <0.01 |
| Shrubland | −0.3641 | 0.12 |
| (Shrubland)$^2$ | 0.8778 | 0.01 |
| Grassland | 0.0371 | <0.01 |
| Woodland | 0.0449 | 0.01 |
| Ecoregion | ...† | 0.03 |
| Overall model (adjusted $R^2$: 0.51) | −0.373 | <0.01 |
| 1980–2000 | | |
| No. fires | | |
| Change housing | 3.0666 | 0.01 |
| (Change housing)$^2$ | −0.2661 | 0.01 |
| Initial housing | −1.8269 | 0.01 |
| (Initial housing)$^2$ | 0.0505 | 0.03 |
| Woodland | 38.1957 | 0.03 |
| (Woodland)$^2$ | −107.0112 | 0.02 |
| Overall model (adjusted $R^2$: 0.26) | −1.894 | 0.01 |
| Area burned | | |
| Initial housing | −0.0114 | 0.01 |
| (Initial housing)$^2$ | 0.0003 | 0.05 |
| Initial distance | −0.000003 | <0.01 |
| Woodland | 0.0292 | 0.18 |
| (Woodland)$^2$ | −1.2831 | 0.02 |
| Ecoregion | ...† | 0.05 |
| Overall model (adjusted $R^2$: 0.41) | 0.0409 | <0.01 |

† Coefficients are not listed for categorical variables.

for fire initiation, but fire spread and behavior is ultimately more a function of fuel availability and type (Bond and van Wilgen 1996, Pyne et al. 1996). Yet humans do have some control over fire size through suppression and, indirectly, through fuel connectivity (Sturtevant et al. 2004), although fires are extremely difficult to suppress in California shrublands under high-wind conditions that typify the most destructive fires (Keeley and Fotheringham 2003). Therefore, human effects on area burned may cancel one another out to some extent because fire suppression can minimize the increase in area burned that would result from increased ignitions, at least at the WUI. Fire suppression resources are more likely to be concentrated on structural protection in developed areas (Calkin et al. 2005), which would explain the positive relationship between area burned and distance to road. Roads can serve as firebreaks and can also provide access routes for firefighters.

The inclusion of vegetation type in the multiple regression models illustrates that, despite the strong influence of humans, fire occurrence remains a function

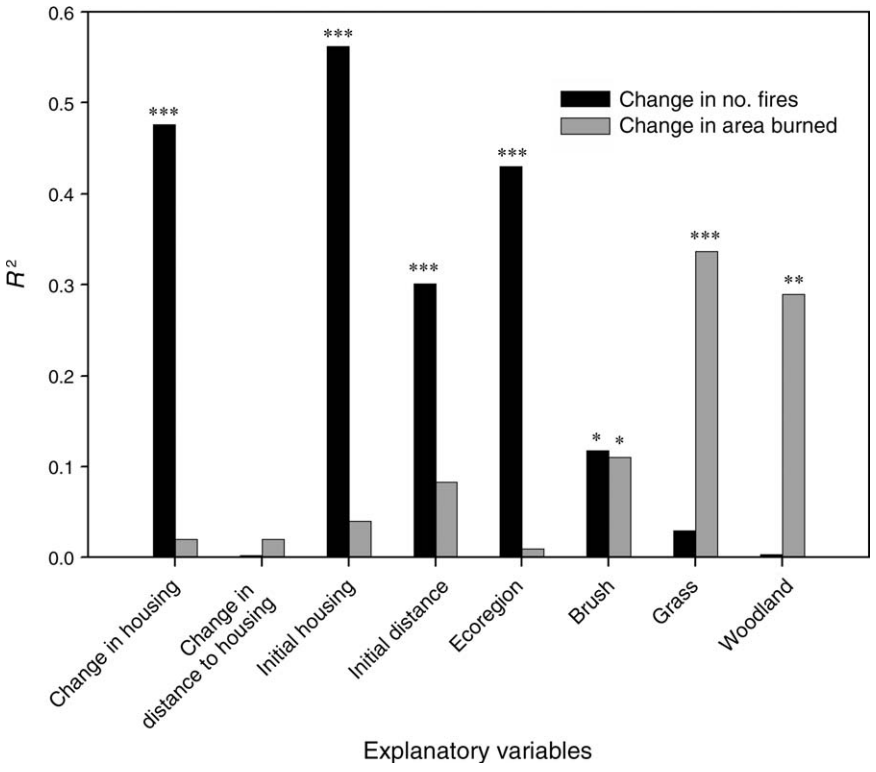


FIG. 8. $R^2$ values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1960 to 1980.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

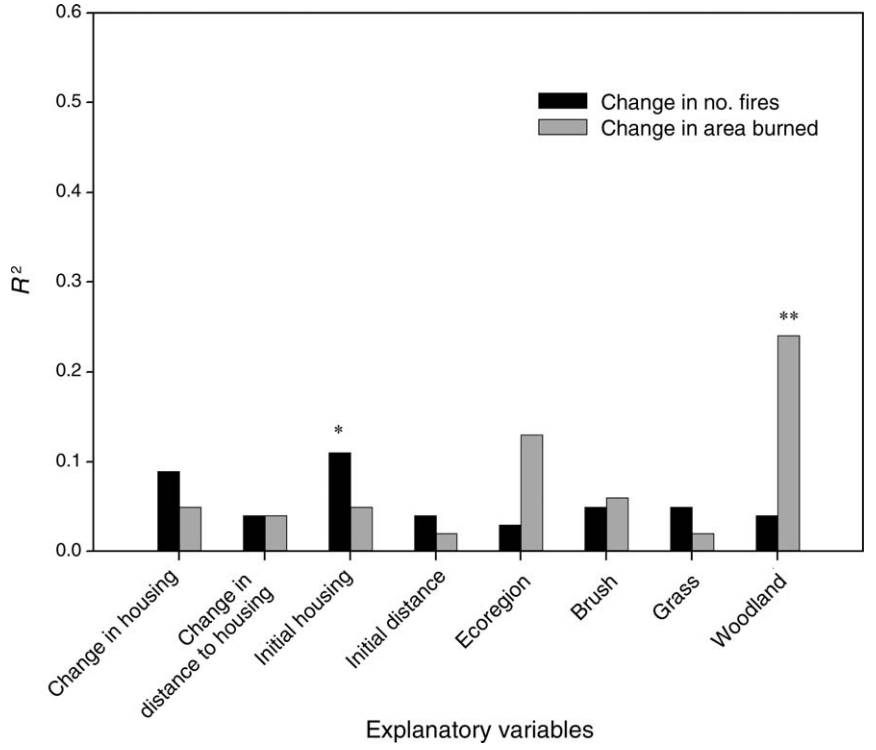


FIG. 9. $R^2$ values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1980 to 2000.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

PLATE 1. (Left) Wildland–urban interface (WUI) and (right) burned-over fuel break, both at the eastern end of Scripps Ranch (San Diego County, California, USA) after the autumn 2003 Cedar Fire (largest fire in California since the beginning of the 20th century). Photo credits: J. E. Keeley.

of multiple interacting social and environmental variables. For number of fires and area burned, shrubland had the strongest explanatory power of the vegetation types. Chaparral and coastal sage scrub are both extremely fire-prone vegetation types and high human population density tends to be distributed in these types; other studies have shown that they have experienced a higher rate of burning than other vegetation types in the southern part of the state in the last century (Keeley et al. 1999, Keeley 2000, Wells et al. 2004). Increased ignitions in highly flammable vegetation types can lead to very hazardous conditions (Halsey 2005).

The second question we asked was "How do human activities relate to change in fire?" In the last 40 years, the most substantial change was the increase in number of fires from 1960 to 1980. The decrease in number of fires was less dramatic between 1980 and 2000; and the change in area burned was relatively small in both time periods. Housing development patterns were most influential when change was greatest, from 1960 to 1980, and for trends in fire frequency (vs. area burned).

Although anthropogenic influence was partially responsible for the change in area burned, the apparent inverse relationship between change in fire frequency and change in area burned may be spurious. In other words, the explanation for a decrease in number of fires may be independent of the concurrent increase in area burned. Trends in area burned are naturally cyclic due to broad-scale factors such as climate. Recent research has shown that change in climate was a major factor driving fire activity in the western United States in the last several decades (Westerling et al. 2006); however, that research was restricted to large montane fire events on federally owned land above 1370 m. Therefore, while climate change may have played some role in our observed change in area burned, we cannot extend those results to our analysis because we included fires of all sizes under multiple land ownership classes, and historical fire patterns in the lower elevations do not correspond to patterns in montane forests (Halsey 2005).

Fire both constrains and is constrained by the fuel patterns it creates, resulting in cycles of fire activity and temporal autocorrelation in area burned, in part because young fuels are often less likely to burn (Malamud et al. 2005). Temporal autocorrelation effects vary with ecosystem, fuel type, and the area of analysis; but in all vegetation types, temporal dependence diminishes over time due to post-fire recovery. Therefore, we assumed that the effects would be low in our study because we were looking at change over 20-year time periods. Furthermore, the chaparral vegetation that dominates much of California recovers very quickly following fire, meaning that the effect of temporal autocorrelation in this vegetation type would last for only brief periods of time. Also, under extreme weather conditions, young age classes are capable of carrying fires in the southern portions of California (Moritz 1997, Moritz et al. 2004).

In general, the anthropogenic influence on fire frequency and extent was complicated through the combination of positive and negative effects, which helps to answer our third question: "Do fire frequency and area burned vary nonlinearly in response to human influence?" Nonlinear effects were evident in the scatter plots and confirmed by the significance of quadratic terms in most of the models. The regression models indicate that humans were responsible for first increasing and then decreasing fire frequency and area burned. These dual influences may explain why prior studies presented conflicting results, because a positive or negative response was dependent on the level of human presence. Aside from the fact that we intentionally tested hypotheses regarding nonlinear relationships, our data also contained a wide range of human presence due to the large extent and diversity of the state of California.

The scatter plots illustrate how these human–fire relationships occurred. For both the number of fires and area burned, and in the current and historic analyses, the

maximum fire values occurred at intermediate levels of human presence (as in Fig. 6A); and when human activity was either lower or higher, fire activity was lower. Initial increase in fire occurrence with increasing population is reasonable since human presence results in more ignitions. However, it appears that when human population density and development reach a certain threshold density, ignitions decline, and this is likely the result of diminished and highly fragmented open space with fuels insufficient to sustain fire. In addition, above a certain population threshold, fire suppression resources are likely to be more concentrated in the WUI. Inverse relationships were evident in the scatter plots of distance (Fig. 6B). In these, fire frequency and area burned were greatest at short distances to WUI; and at longer distances, the trend lines leveled off. These distance relationships indicate that more fires would be expected in close proximity to settled areas where ignitions are likely to occur.

The inclusion of quadratic terms in the multiple regression models supports the concept that fire frequency and area burned were dependent on the level of human activity. Initial housing density was important in all four historic multiple regression models, and initial distance to low-density housing was important in both of the historic area-burned models. The change in number of fires for both periods was also related to change in housing density, in bivariate regression models for the earlier period and in the multiple regression model for the later period (1980–2000). These results further emphasize that fire activity was a function of a certain level of human presence. In addition to the strong influence of human presence, ecoregion and vegetation types were also highly significant in the multiple regression models, suggesting that the particular level of human activity that was most influential in explaining fire activity was dependent upon biophysical context.

The primary value of the multiple regression models was to identify the most influential variables and their direction of influence when accounting for other factors. While they explained how fire activity varied according to context-dependent interactions, their purpose was not to provide a formula for determining fire risk at a landscape scale. Environmental and social conditions differ from region to region, and processes such as fire and succession are controlled by a hierarchy of factors, with different variables important at different scales (Turner et al. 1997). Nevertheless, these models provide strong evidence about the strength and nature of human–fire relationships. That these relationships are significant across a state as diverse as California suggests that human influence is increasingly overriding the biophysical template; yet, managers must account for the interactions with ecoregion and vegetation type when making management decisions. Determining the conditions (e.g., thresholds) for nonlinear anthropogenic relationships will be important to understand how fire risk is distributed across the landscape.

At the coarse scale of our analysis, we can estimate these thresholds based on the nonlinear relationships in our scatter plots (as in Fig. 6) and suggest that fire frequency is likely to be highest when population density is between 35 and 45 people/km$^2$, proportion of intermix WUI is ~20–30%, proportion of low-density housing is ~25–35%, the mean distance to intermix WUI is <9 km, and the mean distance to interface WUI is <14 km. Our next step is to more precisely define these relationships at scales finer than the county level (where management decisions often occur) and to understand the conditions under which human activities positively or negatively influence fire.

These results imply that fire managers must consider human influence, together with biophysical characteristics such as those represented in the LANDFIRE database, when making decisions regarding the allocation of suppression and hazard mitigation resources. If human presence is not explicitly included in decision making, inefficiencies may result, because fire occurrence is related to human presence on the landscape. In particular, we identify an intermediate level of housing density and distance from the WUI at which the effects of human presence seem to be especially damaging, i.e., a point at which enough people are present to ignite fires, but development has not yet removed or fragmented the wildland vegetation enough to disrupt fire spread. This intermediate level of development is one that large areas of the lower 48 states, particularly in the West and Southwest, will achieve in the coming decade. Hence, the WUI's location, extent, and dynamics will continue to be essential information for wildland fire management.

## Conclusion

In addition to the risk to human lives and structures, changing fire regimes may have substantial ecological impacts, and the results in this analysis support the hypothesis that humans are altering both the spatial and temporal pattern of the fire regime. Although the overall area burned has not changed substantially, the distribution of fires across the landscape is shifting so that the majority of fires are burning closer to developed areas, and more remote forests are no longer burning at their historic range of variability (Pyne 2001). In either case, the ecological impacts may be devastating. Due to lack of dendrochronological information, historic reference conditions are difficult to determine in stand-replacing chaparral shrublands. Although chaparral is adapted to periodic wildfire, there is substantial evidence that fires are burning at unprecedented frequencies, and this repeated burning (at intervals closer than 15–20 years apart) exceeds many species' resilience and has already resulted in numerous extirpations (Zedler et al. 1983, Haidinger and Keeley 1993, Halsey 2005).

If present trends continue in California, the population may increase to $90 \times 10^6$ residents in the next 100 years. Recent trends in housing development patterns also indicate that growth in area and number of houses in intermix WUI has far outpaced the growth in interface WUI (Radeloff et al. 2005; Hammer et al., *in press*). Our results showing that fire frequency and area burned tend to be highest at intermediate levels of development (more typical of intermix than interface) suggest that fire risk is a function of the spatial arrangement of housing development and fuels. Therefore, in addition to more people in the region that could ignite fires, future conditions that include continued growth of intermix WUI may also contribute to greater fire risk. Land use planning that encourages compact development has been advocated to lessen the general impacts of growth on natural resources (Landis and Reilly 2004), and we suggest that reducing sprawling development patterns will also be important to the control of wildfires in California.

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Conservation Biology

*Contributed Paper*

# Conservation Threats Due to Human-Caused Increases in Fire Frequency in Mediterranean-Climate Ecosystems

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**Abstract:** *Periodic wildfire is an important natural process in Mediterranean-climate ecosystems, but increasing fire recurrence threatens the fragile ecology of these regions. Because most fires are human-caused, we investigated how human population patterns affect fire frequency. Prior research in California suggests the relationship between population density and fire frequency is not linear. There are few human ignitions in areas with low population density, so fire frequency is low. As population density increases, human ignitions and fire frequency also increase, but beyond a density threshold, the relationship becomes negative as fuels become sparser and fire suppression resources are concentrated. We tested whether this hypothesis also applies to the other Mediterranean-climate ecosystems of the world. We used global satellite databases of population, fire activity, and land cover to evaluate the spatial relationship between humans and fire in the world's five Mediterranean-climate ecosystems. Both the mean and median population densities were consistently and substantially higher in areas with than without fire, but fire again peaked at intermediate population densities, which suggests that the spatial relationship is complex and nonlinear. Some land-cover types burned more frequently than expected, but no systematic differences were observed across the five regions. The consistent association between higher population densities and fire suggests that regardless of differences between land-cover types, natural fire regimes, or overall population, the presence of people in Mediterranean-climate regions strongly affects the frequency of fires; thus, population growth in areas now sparsely settled presents a conservation concern. Considering the sensitivity of plant species to repeated burning and the global conservation significance of Mediterranean-climate ecosystems, conservation planning needs to consider the human influence on fire frequency. Fine-scale spatial analysis of relationships between people and fire may help identify areas where increases in fire frequency will threaten ecologically valuable areas.*

**Keywords:** fire, land cover, Mediterranean, MODIS, population density, remote sensing

Amenazas a la Conservación Debido a Incrementos en la Frecuencia de Incendios Causados por Humanos en Ecosistemas de Clima Mediterráneo

**Resumen:** *El fuego periódico es un proceso natural importante en los ecosistemas de clima mediterráneo, pero el incremento de la recurrencia de fuego amenaza la frágil ecología de esas regiones. Debido a que la mayoría de los incendios son causados por humanos, investigamos el efecto de los patrones de población humana sobre la frecuencia del fuego. Investigaciones previas en California sugieren que la relación entre la densidad poblacional y la frecuencia de incendios no es lineal. Hay pocas igniciones humanas en áreas con baja densidad poblacional, así que la frecuencia de incendios es baja. A medida que aumenta la densidad poblacional, los incendios causados por humanos y la frecuencia de incendios también incrementa; pero al*

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*llegar a un umbral de densidad, la relación se vuelve negativa ya que los combustibles son escasos y se concentran recursos para la supresión de fuego. Probamos sí esta hipótesis también aplica a los otros ecosistemas de clima mediterráneo en el mundo. Utilizamos bases de datos de satélite de población, actividad de fuego y cobertura de suelo para evaluar la relación espacial entre humanos y fuego en los cinco ecosistemas de clima mediterráneo en el mundo. Tanto las densidades medias y medianas fueron consistente y sustancialmente más altas en áreas con fuego como sin fuego, pero los incendios alcanzaron su máximo en densidades poblacionales intermedias, lo que sugiere que la relación espacial es compleja y no lineal. Algunos tipos de cobertura de suelo tuvieron incendios más frecuentemente de lo esperado, pero no se observaron diferencias significativas en las cinco regiones. La asociación consistente entre mayores densidades poblacionales y fuego sugiere que, independientemente de las diferencias entre tipos de cobertura de suelo, los regímenes de fuego naturales o la población total, la presencia de gente en regiones de clima mediterráneo afecta fuertemente a la frecuencia de incendios; por lo tanto, el crecimiento poblacional en áreas escasamente pobladas es preocupante para la conservación. Considerando la sensibilidad de las especies de plantas a incendios recurrentes y la significancia para la conservación de los ecosistemas de clima mediterráneo, la planificación de la conservación requiere que se considera la influencia humana sobre la frecuencia de incendios. El análisis espacial a fina escala de las relaciones entre gente y fuego puede ayudar a identificar áreas en las que el incremento en la frecuencia de fuego amenazará a áreas valiosas ecológicamente.*

**Palabras Clave:** cobertura de suelo, densidad poblacional, fuego, Mediterráneo, MODIS, percepción remota

## Introduction

The biodiversity of Mediterranean-climate ecosystems is among the highest of any biome in the world. The five regions in the world with Mediterranean climates (the Mediterranean Basin, central Chile, the Cape Region of South Africa, southwestern Australia, and parts of California and northern Baja California in North America) collectively occupy <5% of the Earth's unglaciated land surface, yet they contain 20% of the world's flora (Cowling et al. 1996), and many species are endemic (Mittermeier et al. 1998). Because of rapid global change and increasing anthropogenic pressure, all Mediterranean regions are of high global conservation concern (Médail & Quézel 1999; Olson & Dinerstein 2002; Vogiatzakis et al. 2006).

Although Mediterranean-climate ecosystems are geographically disjunct, they are classic examples of convergence in ecosystem structure and dynamics (Cody & Mooney 1978). The Mediterranean climate is characterized by cool, wet winters and warm to hot, dry summers, and the summer drought produces water stress that affects the seasonal distribution of wildfires. Vegetation in Mediterranean-climate regions is dominated by evergreen, woody, sclerophyllous shrubs that are very flammable and support crown fires (Christensen 1985). Nevertheless, specialized postfire persistence traits (e.g., seed banking in the soil and canopy and resprouting) make plant species resilient to periodic wildfire (Naveh 1975). The presence of fire-stimulated reproduction indicates an adaptive response to fire, and seed banking evolved independently in all Mediterranean-climate ecosystems except Chile (Bond & van Wilgen 1996). Nevertheless, all the woody shrubs in Chile resprout in response to fire, which is now frequent due to anthropogenic ignitions (Montenegro et al. 2004).

Fire in Mediterranean-climate ecosystems predates humans (except in Chile), and natural fire frequencies have varied between and among regions over time and in response to climate fluctuations (Rundel 1998). The history of human impact on fire regimes also differs among regions. For example, humans ignited fires in the Mediterranean Basin for thousands of years to support agropastoral activities (Lozano et al. 2008), Native Americans ignited fires in California since the early Holocene (Keeley 2002), and small populations of hunter-gatherers ignited fires in other regions until a few centuries ago (Rundel 1998). Evidence regarding early human influence on fire is circumstantial and controversial, but human activity is now thought to be a major determinant of the timing and location of fire. In fact, humans ignite most fires in Mediterranean regions (Bond & van Wilgen 1996). Current human influence on fire regimes and the potential ecological impact of their influence on fire is similar among Mediterranean-climate regions and differs strongly from fire problems in other forested systems.

In dry coniferous forests, like those in the western United States, the primary concern is a lack of fire primarily due to 20th-century fire suppression. Lower fire frequency in forests that naturally experienced high-frequency, low-intensity surface fires resulted in high accumulation of surface and canopy fuels (Parsons & Landres 1998). Fuel accumulation increases the likelihood fires will become uncharacteristically large and intense, which can kill even large, surface-fire-resistant trees.

Conservation threats and changes in fire regimes in Mediterranean-climate regions, however, are different. The shrublands are adapted to fire-return intervals that

are generally longer than those historically experienced in conifer forests (Sugihara et al. 2006). Despite their capacity for rapid postfire regeneration, many shrubland plant species are sensitive to repeated burning. Serotinous species are particularly vulnerable (e.g., Wark et al. 1987; Pausas 1999; Syphard et al. 2006), but repeated burning may also extirpate resprouting species by reducing their capacity to regenerate and constraining their reproductive ability (e.g., Haidinger & Keeley 1993; Montenegro et al. 2004; Espelta et al. 2008). A related issue is that exotic species may facilitate fire and may expand under frequent fire (Mack & D'Antonio 1998). In California biodiversity is critically threatened by shrubland conversion to exotic annual grasses caused by atypically frequent fire (Keeley et al. 2005). Therefore, where the primary concern in dry coniferous forests is fire exclusion, the problem in Mediterranean-climate regions is repeated fires in the same location (Montenegro et al. 2004; Badia-Perpinyà & Pallares-Barbera 2006; Forsyth & van Wilgen 2008), although the intensity of fires may vary from region to region because of differences in prescribed management practices. Thus, understanding the causes and spatial distribution of altered fire regimes in Mediterranean-climate ecosystems has become a major research priority with strong conservation implications (Lavorel et al. 1998) and is particularly important given population growth in Mediterranean-climate ecosystems.

Studies in California show that area burned and number of fires are highest when population and housing densities are intermediate (Keeley 2005; Syphard et al. 2007). Fires initially increase with population and housing density and then decline where a threshold density is reached. There are several interrelated reasons for this. Ninety-five percent of California's fires are human caused; therefore, anthropogenic ignitions are lower in areas with low population density. As population and housing densities increase, fuels are still abundant and contiguous enough to carry fire, and the number and frequency of fires increase (Syphard et al. 2007). As population density increases further and an area is developed, wildland fuel is reduced and fragmented and fire-suppression resources are concentrated, resulting in lower fire frequencies at high population densities. Finally, even if fire frequency remains stable, fires may cluster in certain areas (e.g., human settlements) or land-cover types (Nunes et al. 2005; Forsyth & van Wilgen 2008), resulting in high fire frequency in localized areas.

Although the relationship between human population densities and fires has been studied in California, less is known about fire trends and patterns in other Mediterranean ecosystems. In recent years, fire frequency has escalated because of population growth and human ignitions in Chile (e.g., Montenegro et al. 2004) and South Africa (Forsyth & van Wilgen 2008), and fires increased exponentially in many areas in the Mediterranean Basin, in part due to the abandonment of traditional land-use practices (Pausas & Vallejo 1999). Interactions between fire and exotic species have been exacerbated by recurrent human-caused fires in Chile (Montenegro et al. 2004), South Africa (Bond & van Wilgen 1996), the Mediterranean Basin (Kark & Sol 2005; Vogiatzakis et al. 2006), and Australia (Offor 1990). In Spain fire ignitions cluster near urban areas (Badia-Perpinyà & Pallares-Barbera 2006), and population density has been correlated with the number of fires and area burned (Vázquez de la Cueva et al. 2006). Results of previous studies thus suggest that the relationship between human populations and fire frequency may be similar in all Mediterranean-climate ecosystems, but this idea has not been examined systematically across the different areas. Whether fire frequencies consistently peak at intermediate densities of human population is unclear. Nor is it clear whether certain land-cover types are more likely to burn.

Our objective was to quantify the relationship between humans and fire in Mediterranean-climate ecosystems across the globe. We asked, Are population densities higher in places where fires occur than in places without fires? Are fires consistently most frequent at intermediate population densities? Are certain land-cover types in each region more prone to fires?

## Methods

### Study Area

We used Bailey's ecoregion boundaries to demarcate Mediterranean-climate ecoregions (Bailey 1989). (Table 1). This is a hierarchical system with four levels (domains, divisions, provinces, and sections). For all five

**Table 1. Number of Bailey's ecoregions, total area, and biogeographic characteristics* of Mediterranean-climate regions.**

| | *Number of ecoregions* | *Total area ($km^2$)* | *Number of native vascular plants* | *Endemic species (%)* | *Threatened species (%)* |
|---|---|---|---|---|---|
| Mediterranean Basin | 25 | 2,392,048 | 23,300 | 50 | 18 |
| North America | 5 | 407,654 | 4,300 | 35 | 17 |
| Chile | 2 | 74,863 | 2,100 | 23 | unknown |
| South Africa | 1 | 69,401 | 8,550 | 68 | 15 |
| Southwest Australia | 1 | 118,882 | 8,000 | 75 | 18 |

*Biogeographic characteristics based on Calow (1998) and Vogiatzakis et al. (2006).*

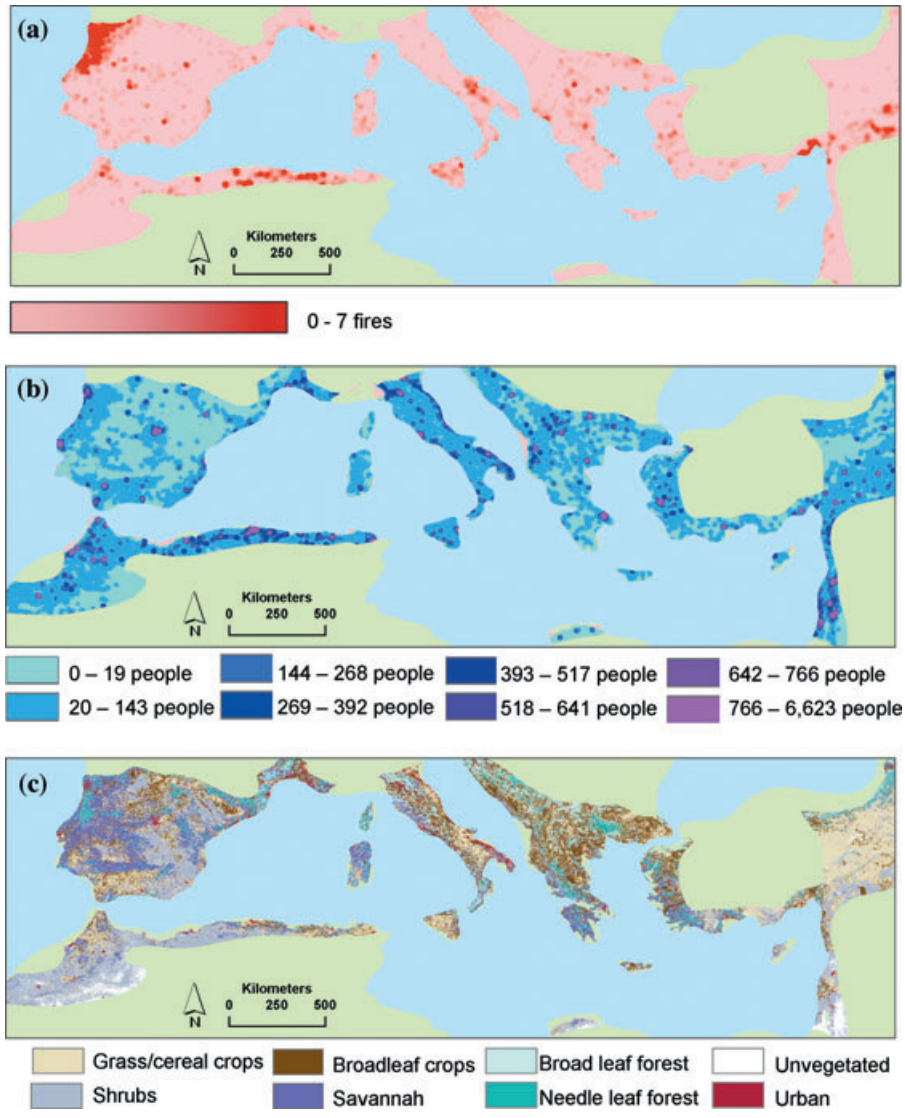


*Figure 1. For the Mediterranean Basin, (a) MODIS active-fire detections in 2005, (b) LandScan population density in 2005, and (c) MODIS land-cover data. Fire and population density values are averaged across 225-km$^2$ pixels.*

continents, we selected all ecoregions classified as either the Mediterranean Division or the Mediterranean Regime Mountains. To ensure comparability of area calculations, all spatial data were projected into an Albers equal area projection.

### Processing of Population Data

We used population data from the LandScan Global Population Product because it has the finest resolution (<1 km) of any global population data set (Dobson et al. 2000). The LandScan database represents ambient population, accounting for diurnal movement and travel patterns. Every grid cell is allocated a population count based on a distribution model that incorporates the best available data on human population for every country, proximity of people to roads, land cover, nighttime lights, and urban density.

Because the accuracy and precision of LandScan are continually being improved, we restricted our analysis to 2005, the year with the most current data (Fig. 1). For comparison purposes, we divided the population counts by area and analyzed population density.

### Processing of MODIS Fire Data

We used fire data from the Moderate Resolution Imaging Spectroradiometer (MODIS) to assess fire activity in Mediterranean-climate ecoregions because of its unmatched spatial and temporal detail (Justice 2002). With two polar-orbiting satellites, the MODIS active-fire product provides daily global information on fires. These data show actively burning fires based on radiant energy and comparisons of target pixels with surrounding pixels (Giglio et al. 2003).

Instead of mapping individual fires and area burned, MODIS indicates pixels in which fire activity was detected. Thus, there could be more than one fire active within a 1-km$^2$ MODIS pixel (Csiszar et al. 2006). In addition, fires occupying only a portion of a pixel can

be detected (Dozier 1981). Although many small fires are missed, MODIS consistently detects larger fires that are ecologically relevant (Hawbaker et al. 2008), and the number of contiguous MODIS fire pixels tends to correlate with fire size (Giglio et al. 2006).

We analyzed MODIS fire data from the Land Processes Distributed Active Archive Center (LPDAAC, http://edcdaac.usgs.gov/modis/dataproducts.asp) for both sensors every day in 2005 to match the date of the population data. Using the boundaries of the Mediterranean ecoregions, we put all images into a mosaic (i.e., joined them together to form daily continuous tiles) for both sensors and summarized the daily data to create annual maps of fire for each region (Fig. 1). We included fire detections from all classified confidence levels because detection accuracy varies little whether fires are classified as low or high confidence (Hawbaker et al. 2008).

### Processing of MODIS Land-Cover Data

In addition to the active-fire product, we used the 2003 MODIS 1 km Land Cover Dataset (Friedl et al. 2002) to analyze fire activity by land-cover class (Fig. 1). We used the LAI/fPAR Biome land-cover classification scheme because it was designed to capture differences in vegetation structural types (grasslands and cereal crops, shrubs, broadleaf crops, savannah, broadleaf forest, needle leaf forest, unvegetated, and urban; Myneni et al. 1997).

### Analysis

In California fires are most likely to occur when the distance to housing is $<15$ km (Syphard et al. 2007). Because scale dependencies of ecological patterns and processes vary by region (Shugart 1998) and because people are mobile and affect their surroundings, we conducted our analysis of humans and fire at three levels of resolution (1, 15, and 45 km). Land-cover analyses were conducted only at the 1-km resolution, however, because we did not consider relationships between land cover and population measures.

We conducted a moving-window GIS analysis to summarize data across the entire land area. Within each window and at each resolution, we summarized the population density and the number of fires. Satellite fire detections can be obscured by clouds, and the MODIS active-fire product explicitly masks cloud cover in every daily image (Giglio et al. 2003). Therefore, we excluded cloud pixels, calculated the number of "observable days" within each window, and used this number to calculate average fire frequency. Uncertainty due to land-cover misclassification, undetected fires, and errors in population distribution was assumed to be consistent among the Mediterranean-climate ecoregions.

To determine whether population densities were higher in areas with fires, we selected all pixels and windows where there was one or more fires and calculated the mean and median population densities. We compared those with mean and median population densities in pixels and windows where no fires occurred. If there is a relationship between humans and fire, the proportion of fire should be higher where population is higher and lower where population is lower. We did not conduct a statistical test to determine whether the distributions differed because our data represent a complete enumeration, not a sample, and any difference would be statistically significant. Instead, we distributed the population data into 25 equally spaced categories and plotted the proportion of fires that occurred within each category for the three window sizes. The resulting bar charts showed whether more fires occurred at low, intermediate, or high population densities.

To determine whether fires burned more often (selectively) in different land-cover types, we calculated the total proportion of land-cover types in each region, then selected only the pixels with fires and recalculated the proportion. We calculated the ratio of the proportion of fires in the land-cover types and the proportion of the land-cover types in the landscape. A ratio of 1.0 means fire occurred in a land-cover type as often as would be expected by chance, $>1.0$ means fire occurred in the land-cover type more often, and $<1.0$ means fire occurred less often than expected by chance.

## Results

We observed substantial differences in population density among the regions. Both the mean and median population densities in southwestern Australia were lowest of all the regions, and those in the Mediterranean Basin were highest. Although median population densities were substantially lower than mean population densities for all regions, the difference in North America was so substantial that mean population density was highest among the regions, but median population density was equal to that in southwestern Australia.

Pixels or windows with fires typically had higher population densities than pixels or windows without fires (Fig. 2). The only exception was in the 1-km pixels in North America, where mean population density was higher in the pixels without fires. Median population densities were nearly equal with and without fire in 1-km pixels in North America, South Africa, and southwestern Australia.

The relationship between population density and fire was more pronounced at 15 km than at 1 km, and at 45 km the mean population densities in areas with fires were much higher than where there were no fires (Fig. 2a). The median population density with fire was almost 3 times larger than the population density without fire at 45-km resolution.

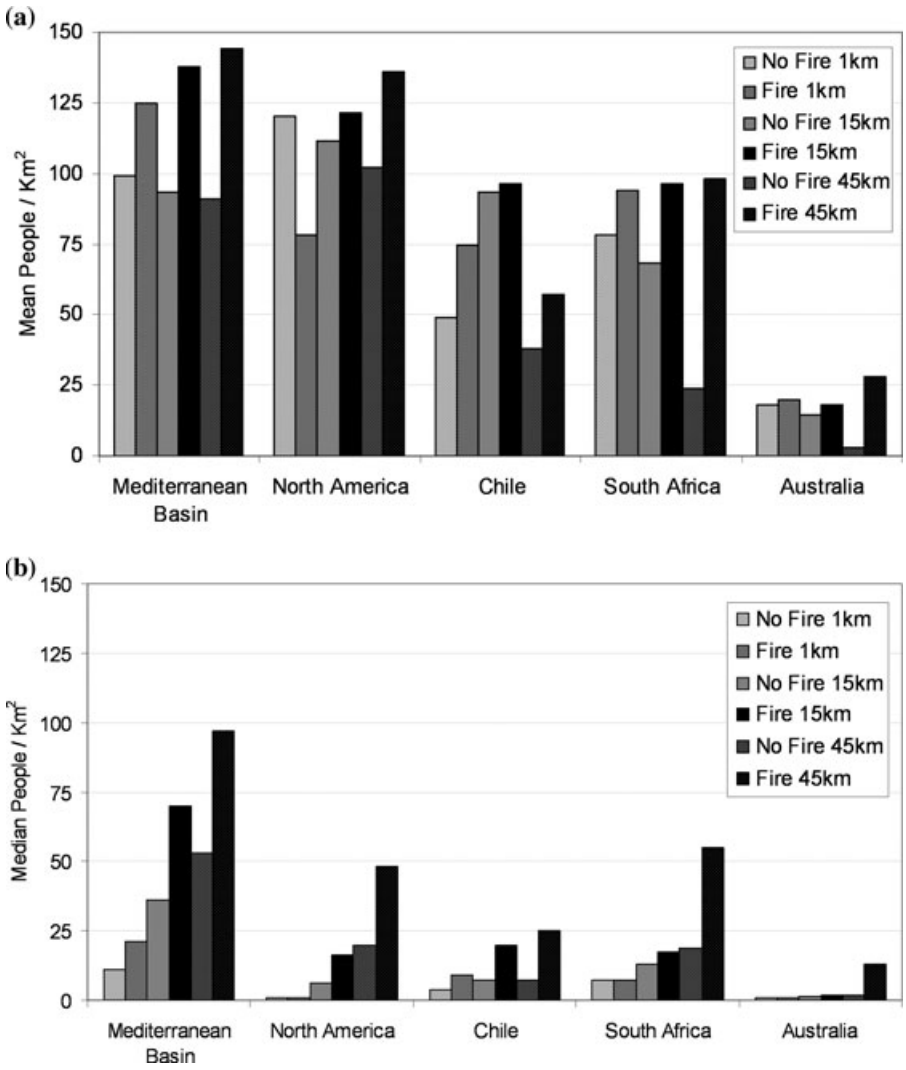


*Figure 2. (a) Mean and (b) median population densities in areas with and without fires for 1-, 15-, and 45-km resolution windows. The y-axis scales differ.*

Although population densities were, on average, higher where there were fires, the largest proportion of fires peaked at intermediate population densities (Fig. 3). Patterns of variation and peak population densities varied from region to region though, particularly at the 1- and 15-km window sizes. In addition, the peak in proportion of fires occurred in areas of lower population densities in North America at the 1-km resolution. In Chile and southwestern Australia, peak in proportion of fires occurred at the higher end of the population density distribution in the 1- and 45-km window sizes. The most consistent trend was apparent at the 45-km window size, where the highest proportion of fires occurred between 100 and 250 people per 45 $km^2$.

Land cover in the five regions included grasslands and cereal crops, shrubs, and savanna, with lower proportions of broad-leaf crops, broad-leaf forest, needle-leaf forest, unvegetated, and urban cover (Fig. 4). Distribution of these land-cover types, however, varied widely from region to region. Grasslands and cereal crops accounted for 40% of land cover in South Africa and southwestern Australia, but in Chile and North America they were just 20% of land cover. Substantially more needle-leaf forest was present in North America (21%) than in the other regions (<10%), and much of Chile was unvegetated (23%).

Some land-cover classes burned proportionately more than expected by chance given their areal distribution in the regions, but patterns were not consistent (Table 2; Fig. 4). In North America and Chile grasslands and cereal crops burned substantially more than expected but only as much as expected in the other three regions. Broad-leaf forest burned more than expected in southwestern Australia but not in the other regions. In North America shrubs burned more than expected and needle-leaf forest burned less than expected, but in the Mediterranean Basin, shrubs burned less than expected and needle-leaf forest burned more. In all regions, except for North America, more fires occurred in savannah than expected. Overall, very little fire occurred in unvegetated or urban areas.

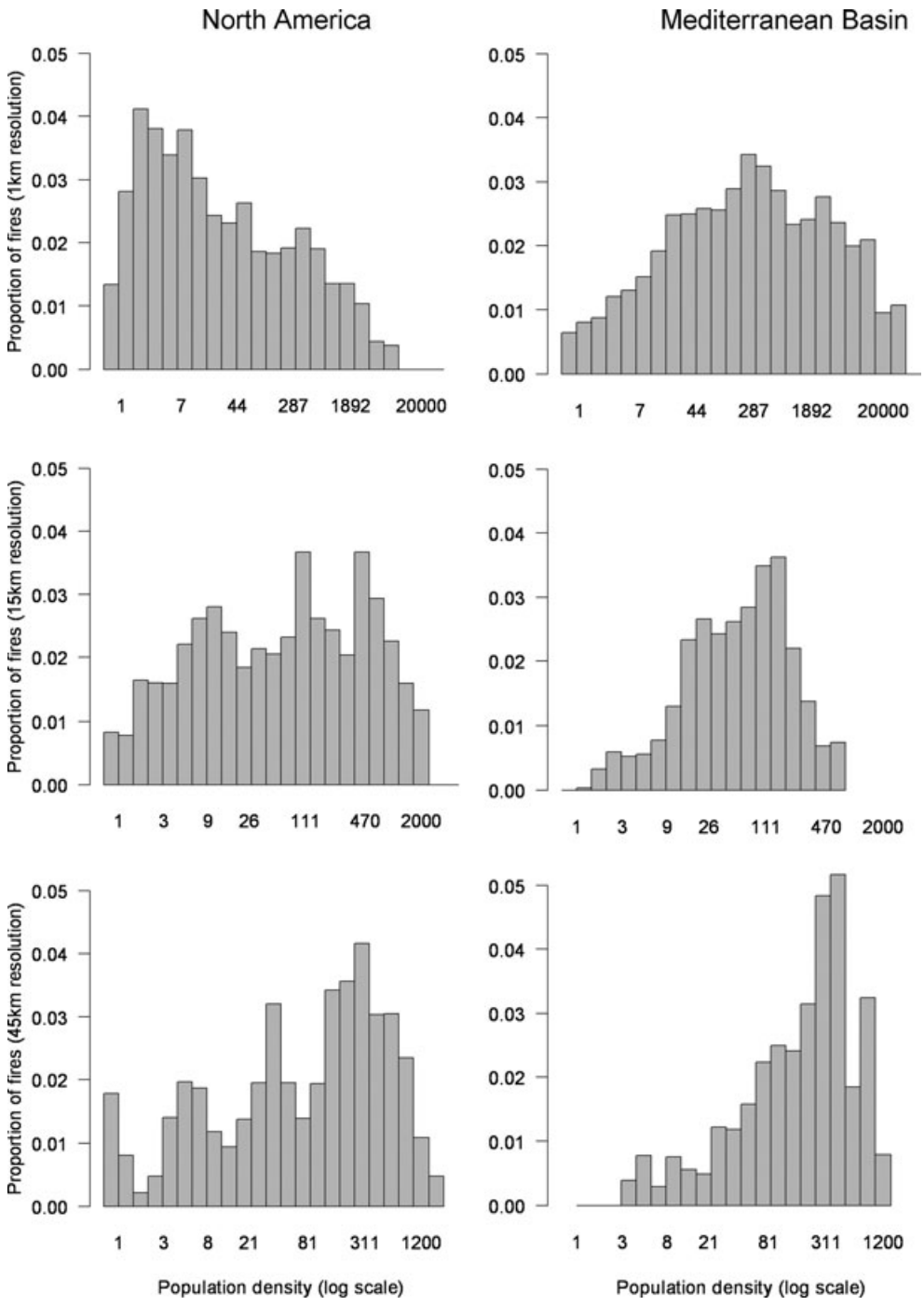


*Figure 3. Proportion of fires within population density classes for 1-, 15-, and 45-km resolution windows.*

## Discussion

We found strong evidence that people are associated with the frequency and spatial distribution of fire similarly in all five Mediterranean-climate regions. Both mean and median population densities were consistently and substantially higher in areas with fire than in areas that did not burn; fires in Mediterranean-climate regions tended to occur close to people. Despite their convergence in ecosystem structure and function, Mediterranean-climate regions do vary in fire history, land-use history, or socioeconomic and political conditions (Pignatti et al. 2002; Carmel & Flather 2004; Vogiatzakis et al. 2006). Because of these differences, variations among the regions in population densities and land cover are not surprising. But these differences make the consistency of spatial relationships between people and fire across the five regions even more striking. The spatial pattern of fires

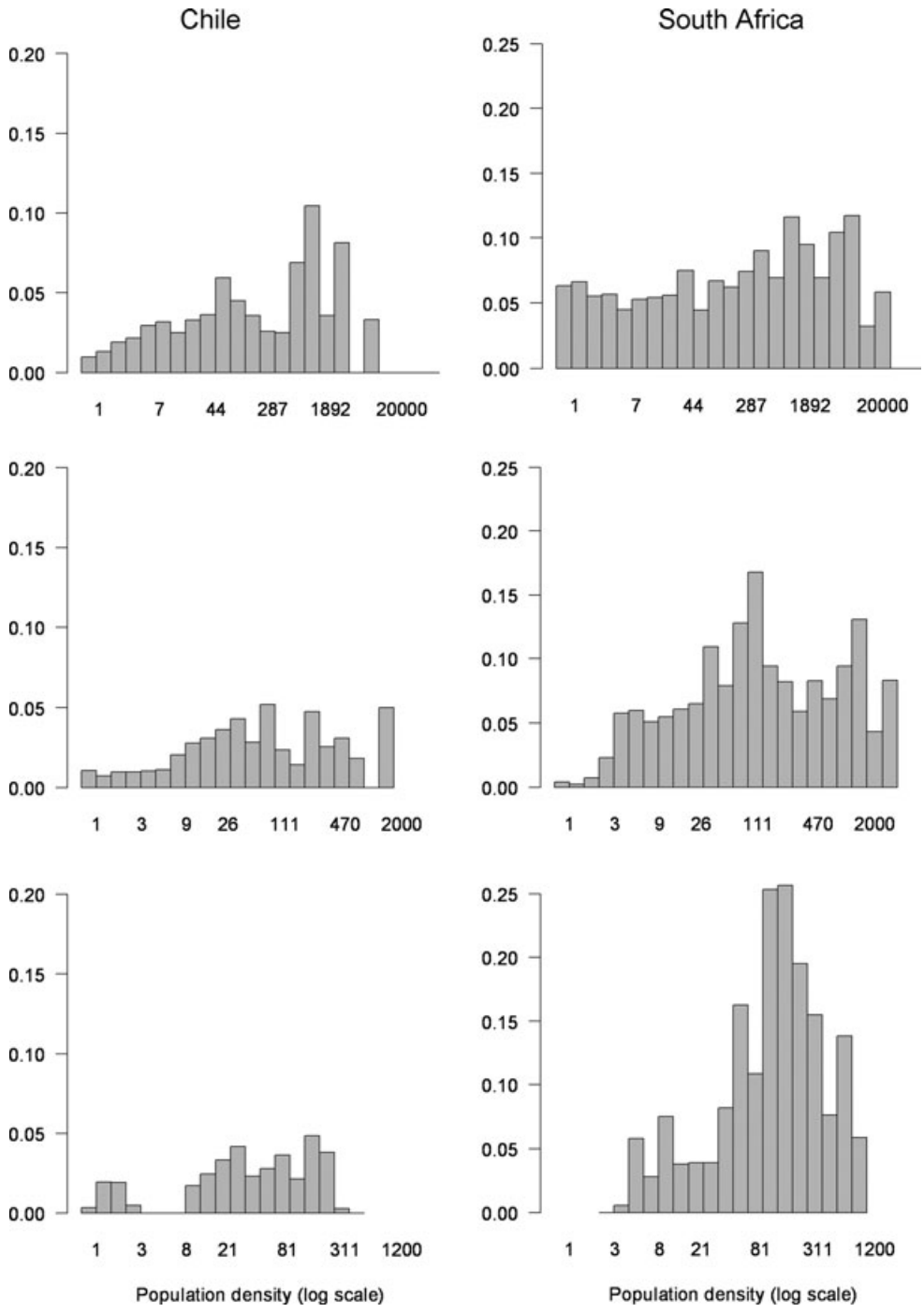


*Figure 3. (continued)*

in any region depends on complex interactions between ignition sources, landscape characteristics, and fuel continuity (Whelen 1995). So the consistent relationship between fire and population density suggests that the presence of people in Mediterranean-climate regions overrides these other factors.

Understanding the distribution of fire in Mediterranean-climate ecosystems is critical due to the vulnerability of its unique vegetation to repeated burning. Unlike other ecoregions in which decreased fire frequency threatens some species (Allen et al. 2002), in Mediterranean-climate ecoregions, the conservation concern is increased fire frequency (e.g., Keeley et al. 1999; Montenegro et al. 2004; Badia-Perpinyà & Pallares-Barbera 2006). The persistence of native plants is threatened and may have cascading ecological effects (Barro & Conard 1991; DellaSalla et al. 2004). Because Mediterranean regions are highly heterogeneous, the

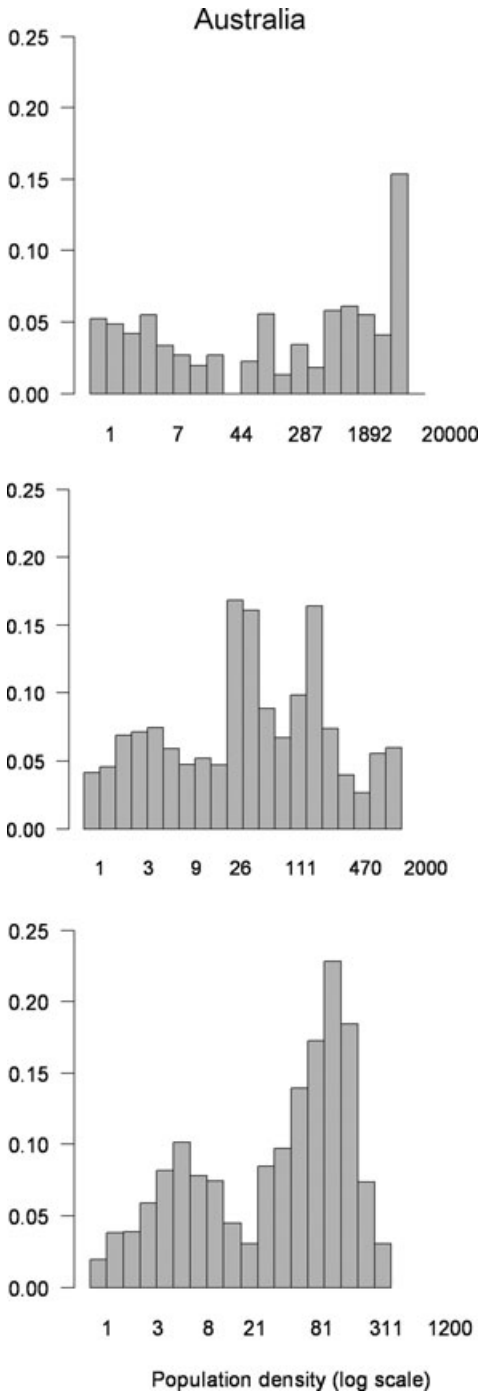


*Figure 3. (continued)*

sensitivity of different plant species to specific fire frequencies will vary (Public Library of Science ONE DOI:10.1371/journal.pone.0000938. 2007). Nevertheless, identifying where the landscape is likely to burn frequently is an important step in identifying areas vulnerable to the extirpation of native species.

The association of people with the spatial distribution of fire occurrence is likely due to the fact that humans now cause the majority of ignitions in all five Mediterranean-climate regions (Bond & van Wilgen 1996), and human ignitions are likely to occur close to roads and human infrastructure (e.g., Yang et al. 2007; Syphard et al. 2008). Nevertheless, our results also showed that fire occurrence consistently peaked where population densities were intermediate, which suggests that fire patterns in Mediterranean-climate regions are related to the spatial arrangement between people, urban development, and fuel. When population density is lowest, human ignitions are also low but increase with population density. Nevertheless, there appears to be a threshold above which fire occurrence declines, possibly due to less open space and fuel fragmentation caused by urban development or other land-use change. Fire-suppression resources also tend to be concentrated near urban areas (Calkin et al. 2005), and intermediate-density housing when located within wildland vegetation is classified as the wildland–urban interface (WUI) in the United States and given special fire-management considerations (Radeloff et al. 2005).

**Table 2. Ratio of the proportion of fires by land-cover type and proportion of land-cover type in the landscape.***

| *Land-cover type* | *Mediterranean Basin* | *North America* | *Chile* | *South Africa* | *SW Australia* |
|---|---|---|---|---|---|
| Grass/cereal | 0.79 | 1.76 | 1.72 | 1.09 | 0.85 |
| Broad crops | 1.07 | 1.70 | 1.65 | 0.55 | 0.49 |
| Shrubs | 0.42 | 1.35 | 1.00 | 0.79 | 0.43 |
| Savannah | 2.01 | 0.72 | 1.51 | 1.46 | 1.35 |
| Broad leaf | 0.80 | 0.45 | 1.02 | 1.62 | 1.90 |
| Needle leaf | 2.01 | 0.54 | 1.03 | 0.94 | 2.64 |
| Unvegetated | 0.06 | 0.17 | 0.03 | 0.13 | 0.06 |
| Urban | 1.92 | 0.89 | 1.88 | 1.41 | 0.96 |

**A ratio of 1.0 means fire occurred in a land-cover type as often as would be expected by chance, >1.0 means that fire occurred more often than expected, and <1.0 less often than expected by chance.*

The relationship between people and fire in our study was most pronounced at the 15- and 45-km scales of analysis. Many ecological processes and spatial relationships have characteristic scales or space and time intervals over which the process can be detected (Shugart 1998). One explanation for the scale effect in our results is that analysis with the 15- and 45-km window sizes could include pixels where fires did, and did not, burn. The observed relationship and scale dependence of the results may therefore have been related to the relative proportion of burned cells within a window. At the 1-km resolution, the pixel either burned or it did not, and the analysis did not account for neighborhood effects.

Although our primary focus was to assess the relationship between population density and fire, other researchers have shown that land use and land cover may be important covariates of fire patterns due to their effects on fuel types, flammability, and human use of fire (e.g., Viedma et al. 2006; Baeza et al. 2007). In our analysis some land-cover types burned more frequently than expected, but no systematic differences were observed.

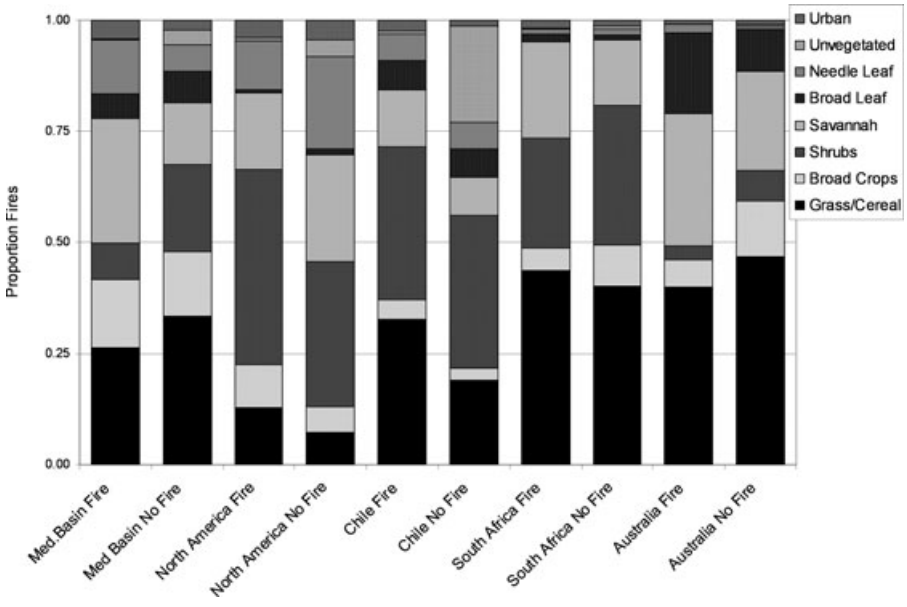


*Figure 4. Aerial proportion of land-cover classes in the ecoregions and within pixels with an active fire in 2005.*

Therefore, the patterns we observed in land-cover types were likely related to unique combinations of human land use and management practices within each region. For example, in North America, needle-leaf forest burned less than expected, whereas shrublands burned more. Fire suppression has successfully excluded fire from California's high-elevation-mixed conifer forests. On the other hand, the disproportionately high level of fire in shrubs is likely due to housing development and increased human ignitions in low-elevation areas where these shrubs (i.e., chaparral) are common (Keeley et al. 1999). More fires than expected in needle-leaf forests in the Mediterranean Basin may be due to land abandonment, which has resulted in substantial increases of fire in pine forests (Pausas & Vallejo 1999).

In North America and Chile fire burned more in grasslands and cereal crops than expected. Grasslands can sustain and even promote higher fire frequencies than other land-cover types (Mack & D'Antonio 1998), a major conservation concern in southern California, where exotic annual grasses have replaced native shrublands under unnaturally high fire frequencies (Haidinger & Keeley 1993). Problems with exotic annual grasses have also been reported in Chile and Australia (Pignatti et al. 2002) and may become more pronounced if fire frequency continues to increase.

## Conclusions

Mediterranean-climate ecosystems are among the most biologically diverse regions in the world with rates of endemism ranging from 23% (Chile) to 75% (southwestern Australia), and at least 15% of the taxa in Mediterranean-climate ecosystems are threatened (Calow 1998). Our results suggest that conservation planners in Mediterranean-climate regions should seriously consider human alteration of fire patterns. Although we used fire data for only 1 year, the consistency in our results demonstrates that, regardless of the overall fire frequency in a region and its annual weather-driven variations, it may be possible to predict where fires are concentrated. Our results therefore provide a foundation for further research and planning to identify where frequent fire threatens vulnerable Mediterranean-climate plant species.

Future research should identify regionally specific ranges of population densities where fire occurrence is highest, be conducted at the scales most relevant to planning and management, and incorporate other drivers of fire pattern, such as biophysical variables. Finally, compact development should be studied for its potential to mitigate the effects of human presence by limiting expansion into undeveloped vegetation. Education efforts to reduce human-caused ignitions were once the foundation of outreach programs, such as Smokey Bear; perhaps the time has come to bring the bear back from semiretirement.

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# Comparing the role of fuel breaks across southern California national forests

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ABSTRACT

Fuel treatment of wildland vegetation is the primary approach advocated for mitigating fire risk at the wildland–urban interface (WUI), but little systematic research has been conducted to understand what role fuel treatments play in controlling large fires, which factors influence this role, or how the role of fuel treatments may vary over space and time. We assembled a spatial database of fuel breaks and fires from the last 30 years in four southern California national forests to better understand which factors are consistently important for fuel breaks in the control of large fires. We also explored which landscape features influence where fires and fuel breaks are most likely to intersect. The relative importance of significant factors explaining fuel break outcome and number of fire and fuel break intersections varied among the forests, which reflects high levels of regional landscape diversity. Nevertheless, several factors were consistently important across all the forests. In general, fuel breaks played an important role in controlling large fires only when they facilitated fire management, primarily by providing access for firefighting activities. Fire weather and fuel break maintenance were also consistently important. Models and maps predicting where fuel breaks and fires are most likely to intersect performed well in the regions where the models were developed, but these models did not extend well to other regions, reflecting how the environmental controls of fire regimes vary even within a single ecoregion. Nevertheless, similar mapping methods could be adopted in different landscapes to help with strategic location of fuel breaks. Strategic location of fuel breaks should also account for access points near communities, where fire protection is most important.

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## 1. Introduction

Wildfire is a key natural process in many ecosystems, but fire frequency, extent, and/or severity have surged across the globe in recent decades (Bowman et al., 2009; Flannigan et al., 2009; Westerling et al., 2006). The social and economic consequences of these fires are immense, with dramatic increases in property destruction and firefighting expenditures (Butry et al., 2001; NIFC, 2009). Altered fire regimes also threaten ecosystem integrity and biodiversity (Pausas and Keeley, 2009; Pyne, 2004). In many parts of the world the fire problem has been exacerbated by the continued expansion of the wildland–urban interface, where homes and lives are most vulnerable to wildfires, and where human ignitions increase the likelihood of fire occurring (Radeloff et al., 2005; Syphard et al., 2007). Mitigating the risk of wildfire at the wildland–urban interface, therefore, is now described as a major objective in the National Fire Plan (2001), the Healthy Forests Restoration Act (2003), and other federal fire management documents. The primary approach advocated for mitigating fire risk is to reduce hazardous fuel loads through fuel treatments of vegetation in wildland areas. In the last decade, expenditures on fuel treatments and area treated has increased markedly (Mell et al., 2010), with U.S. federal land management agencies receiving billions of dollars and treating millions of hectares of land (Schoennagel et al., 2009).

Despite this recent surge in treatment area and expenditure, fuel treatments have been a cornerstone of fire management in the U.S.A. for the better part of the 20th century. Yet, little systematic research has been conducted to understand what role fuel treatments have played in controlling fire, which factors influence this role, or how the role of fuel treatments may vary over space and time. A number of simulation studies have improved our understanding of potential fuel treatment effectiveness in modifying forest fire behavior (e.g., Finney et al., 2007; Miller and Urban, 2000; Schmidt et al., 2008). However, most empirical studies have focused on relatively localized effects when fires have intersected fuel treatments on forests (e.g., Finney et al., 2005; Martinson and Omi, 2003; Raymond and Peterson, 2005; Schoennagel et al., 2004). Due to this relatively small temporal and spatial scale (but see

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Syphard et al., in press-b), these studies have not contributed to an understanding of factors that influence sustainable fuel treatment performance over broad landscapes. This is important because many parts of the western U.S. that intersect with urban environments comprise heterogeneous landscapes that include forest and non-forested ecosystems and because strategic planning requires an understanding of how repeated fire events over time are affected by fuel treatments.

Due in part to the paucity of appropriate research, there is no comprehensive fire policy in the United States that provides forest mangers with science-based guidance on where, how, and when fuel treatments should be conducted (Agee et al., 2000; Franklin and Agee, 2003). Instead, within-agency policies are established and implemented according to the agencies' missions and objectives, and many policies are not publicly reviewed or debated (Franklin and Agee, 2003). Developing scientifically based general principles and guidelines for using fuel treatments to control fires could benefit managers if these guidelines were to facilitate decision-making with regards to strategic placement and tactical response. Given limits in time and money, managers need to prioritize where to place new fuel treatments and to determine the level of maintenance needed for current fuel treatments (Dellasala et al., 2004). Thus, a scientifically based methodology and set of principles could make the decision-making process not only easier but more defensible as well. Furthermore, a better understanding of the factors that influence the role of fuel treatments could lead to the identification of additional management considerations and the development of improved management practices.

The primary problem with development of general guidelines for fuel treatments is that fire-prone regions are highly variable with regards to their natural fire regimes and the factors that control them. Fire regimes vary as a function of forest type, fuels, terrain, climate, and ignition sources (Pyne et al., 1996; Keeley et al., 2009), and fuel treatment effectiveness may also vary according to these factors (Schoennagel et al., 2004). In addition, human development and other infrastructure strongly influence fire regimes and vulnerability to fire. Humans start and stop fires both directly (e.g., via suppression or accidental ignitions) and indirectly (e.g., via land use planning, land cover change, exotic species introduction, climate change), and their influence varies by scale and by locale (Cardille et al., 2001; Prestemon et al., 2002; Syphard et al., 2009). These variations in fire regime and human influence complicate the notion of general principles because management programs need to account for these differences (Noss et al., 2006).

Another reason that a "one size fits all" approach to fire management is problematic is that fuel treatment objectives are likely to vary from region to region, particularly for wildland areas versus the wildland–urban interface (Keeley et al., 2009). In wildland areas, particularly in western U.S. forests, fuel treatments are intended to change fire behavior and to reduce the severity of fire effects, whereas fuel treatments in the wildland–urban interface are intended to prevent fire from spreading into communities (Radeloff et al., 2005; Reinhardt et al., 2008). Therefore, the effectiveness of fuel treatments, and the factors that contribute to their effectiveness, may change as a function of fuel treatment objectives.

One way to determine how well certain guidelines may transfer from region to region is to identify which factors affecting fuel treatment outcome are most likely to vary. Identifying these could help to determine what aspects of plans need to be developed separately for each management area. Common decision-making tools could be developed that account for regional differences in those variables. If there are factors that are universally influential across different regions or landscapes, these could help in the development of general management considerations.

In California, where a substantial portion of the landscape comprises non-forested ecosystems such as chaparral and sage scrub, fuel breaks have been a major part of fire management activities since the 1930s (Davis, 1965). Unlike forests where mechanical fuel treatments remove only surface fuels (preserving larger, older trees), fuel break construction in chaparral typically involves complete removal of vegetation, chemical herbicides, and permanent conversion of native shrublands to weedy herbaceous associations (Wakimoto, 1977).

In southern California, differences in natural fire regimes and the way fire regimes have been altered by past land use complicate fire management in the region. In the shrubland-dominated foothills and coastal valleys, fire frequency has substantially increased along with population growth and urban expansion (Keeley et al., 1999; Syphard et al., 2007). This increased fire frequency not only threatens homes and lives, but many shrublands cannot tolerate repeated fires and under such conditions are often replaced with non-native grasslands (Keeley and Fotheringham, 2003; Syphard et al., 2006). In shrubland-dominated regions, fuel manipulation projects involve a trade-off. On one hand, fuel breaks are needed to protect homes and lives, which are at an elevated risk in these crown fire shrublands; on the other hand, construction of fuel breaks typically involves complete removal of vegetation and may result in a range of ecological impacts. Thus, fire management in the region is greatly complicated by the need to balance both fire and resource management.

In the less extensive montane coniferous forests in the region, fire frequency has been unnaturally low during the last century, and fire hazard has consequently increased due to accumulated fuels associated with fire suppression and logging (Keeley, 2006), problems similar to other forests in the western U.S. (Miller et al., 2009). Because thinning and fuel manipulation is intended to improve forest vigor and reduce risk of catastrophic loss to wildfire (often by restoring forests to more historic conditions), fuel treatments and resource benefits are likely to be compatible in these forested regions (Schwilk et al., 2009). However, this model of fuel accumulation and ecological compatibility with fuel treatments has often been inappropriately applied to chaparral (Keeley and Fotheringham, 2004, 2006).

To better understand the factors that influence the role of fuel treatments in controlling large fires in southern California, and how the role of fuel treatments varies across different landscapes, we assembled a spatial database of fuel breaks and fires from the last 30 years in four national forests. For this analysis, we only considered fuel manipulation projects that were clearly intended to serve as fuel breaks, which are defined as wide blocks, or strips, on which vegetation was manipulated to create lower fuel volume and reduced flammability (Green, 1977). Thus, prescribed fires and burn piles were excluded, as were any dozer lines created to aid suppression activities during the time that a fire was burning. We analyzed relationships among fires and fuel breaks to answer:

(1) What are the most important environmental and management variables affecting the role of fuel breaks in controlling large fires, and do these factors vary among national forests?
(2) What are the primary factors affecting the spatial pattern of fires and fuel break intersections, and do they vary among national forests?

Because we restricted our analysis to U.S. Forest Service national forests, we assumed these landscapes would be broadly similar in the tactical approaches used in the construction and maintenance of fuel breaks. Thus, this study could help determine how well management approaches for one national forest may transfer to other national forests. Also, on these largely non-forested landscapes we assumed that the primary management objective for fuel breaks in the region is to control the spread of fire and protect communities.

**Table 1**
Characteristics of fires and fuel breaks in the four southern California national forests. Fire rotation was calculated from 1980 to 2007.

| | Angeles | Cleveland | Los Padres | San Bernardino |
|---|---|---|---|---|
| Area (ha) | 26,375 | 21,117 | 61,464 | 30,408 |
| Number of fires since 1980 | 175 | 118 | 96 | 253 |
| Fire rotation period (years) | 32 | 14 | 35 | 30 |
| Fuel break length (km) | 1834 | 482 | 550 | 1199 |

## 2. Methods

### 2.1. The national forests of southern California

The area of study included the Los Padres, Angeles, San Bernardino, and Cleveland National Forests (Table 1), an area spanning the extent of the state's South Coast Ecoregion (Keeley, 2006), which encompasses approximately 3.4 million ha (8% of the state) and is home to more than 19 million people (US Census 2000) (Fig. 1). Although the region is the most threatened hotspot of biodiversity in the continental US (Hunter, 1999), the national forest lands together occupy more than 1.5 million ha and offer some measure of protection for the region's biodiversity.

The South Coast Ecoregion is characterized by a Mediterranean-type climate, with cool, wet winters and warm, dry summers. Chaparral shrublands are the most extensive vegetation type, but there is extraordinary ecosystem diversity in the region, owing largely to a relatively sharp elevational gradient from sea level to more than 3500 m. Therefore, chaparral forms a mosaic with other vegetation types, including coastal sage scrub shrublands, grasslands, oak woodlands, and montane coniferous forests, and natural fire regimes are correspondingly variable (Keeley, 2006; Wells et al., 2004).

Fire management on the national forests is the responsibility of the U.S. Forest Service. The two primary strategies for management are to (1) suppress all actively burning fires, and (2) reduce the extent of future fires through mechanical construction of fuel breaks and limited use of prescription burning. We focus exclusively on fuel breaks in this study.

### 2.2. Data for dependent variables: fuel break outcome and fire/fuel break intersections

We acquired information on historic fuel breaks and their location from U.S. forest service staff on each of the four forests. We developed a digital spatial database of fuel breaks for the four forests by combining existing GIS layers with files that we created ourselves by digitizing fuel breaks that had been drawn on paper maps. Due to the substantial number of fuel breaks that were hand drawn, we conducted follow-up interviews to validate the newly digitized data.

On all the forests, we overlaid the fuel break GIS layer with fire perimeter polygons compiled by the California Department of Forestry-Fire and Resource Assessment Program (CALFIRE). The fire perimeter data represent the largest fires, with a minimum mapping unit of 4.04 ha (10 acres).

To evaluate factors affecting fuel break outcome, we first used a GIS overlay to identify all events in which a fire intersected a fuel break (within a 100 m buffer distance to account for potential data uncertainty). These events were considered potential case studies to retain for subsequent analysis. To be included for consideration, the date of the fire had to be later than the date of fuel break construction. For the case studies, we conducted a preliminary assessment as to whether fires stopped or crossed over fuel breaks, and then confirmed the outcome during personal interviews with firefighters who had first-hand knowledge of the event.

**Table 2**
Variables considered and retained in the multiple regression models explaining number of fire and fuel break intersections in three national forests. All variables retained in the models are designated through a significance symbol.

| | Angeles | Los Padres | San Bernardino |
|---|---|---|---|
| Elevation | * | | * |
| Slope | | | |
| Solar radiation | | * | |
| USFS fuel model | * | | * |
| Distance road | | ** | |
| Distance development | | | |
| Distance trails | | ** | |
| Historic fire frequency | *** | ** | *** |
| Ignition density | * | * | |
| Deviance explained | 37.27 | 27.55 | 54.7 |

* $p = 0.05$.
** $p = 0.01$.
*** $p = 0.001$.

Although data for some of the explanatory variables were acquired during personal interviews, we also used a GIS to extract information for other explanatory variables to relate to the fuel break outcome. See below for description of explanatory variables. For this analysis, we extracted data only from the portion of the fuel break that intersected the fire and averaged values across that area. In some cases, fires stopped at a portion of the fuel break, but ultimately crossed over the fuel break. For those cases, we classified the fuel break as not having stopped fire (for statistical analysis purposes only), and we only extracted explanatory variables for the section of the fuel break where the fire crossed over.

To analyze factors influencing the number of times fires intersected fuel breaks, we spatially stratified and classified all fuel breaks according to the number times they intersected fires during the study period. We only considered fires that had occurred since 1980, and to ensure that all fuel breaks had an equal chance of experiencing a fire, we only looked at fuel breaks that had been constructed before 1980. From this spatially stratified layer, we randomly selected point samples (greater than 1 km apart, to avoid spatial autocorrelation) to extract environmental data used as explanatory variables. The dependent variable was number of intersections at each sample location.

### 2.3. Explanatory variables for role of fuel breaks

The factors we considered as potentially influencing the role of fuel breaks on the forests included human and biophysical variables that have previously explained landscape-scale fire patterns in the region (Syphard et al., 2008), and that we used in a previous study of fuel breaks on a single national forest (Table 2, Syphard et al., in press-a). In addition to static landscape features, we also considered variables related to the actual event when a fire intersected a fuel break, including characteristics of fires, fuel breaks, vegetation age, and firefighting activities.

For the human variables, we considered distance to roads, trails, and development (Table 2) because fire ignitions in the region tend to occur near human activities (Syphard et al., 2008). We also hypothesized that these human variables may influence firefighting access and resources. For these three variables, we developed continuous grid surfaces reflecting the Euclidean distance to the nearest feature (road, trail, or development) and extrapolated values from those grids for the areas where fuel breaks intersected fires.

Biophysical variables (including climate, terrain, and fuels) influence fire spread rate, fuel moisture, flammability, and fire intensity (Pyne et al., 1996; Whelan, 1995). Therefore, we evaluated the potential influence of elevation, slope, solar radiation, vegetation age, and fuel model on fuel break outcome (Table 2). After

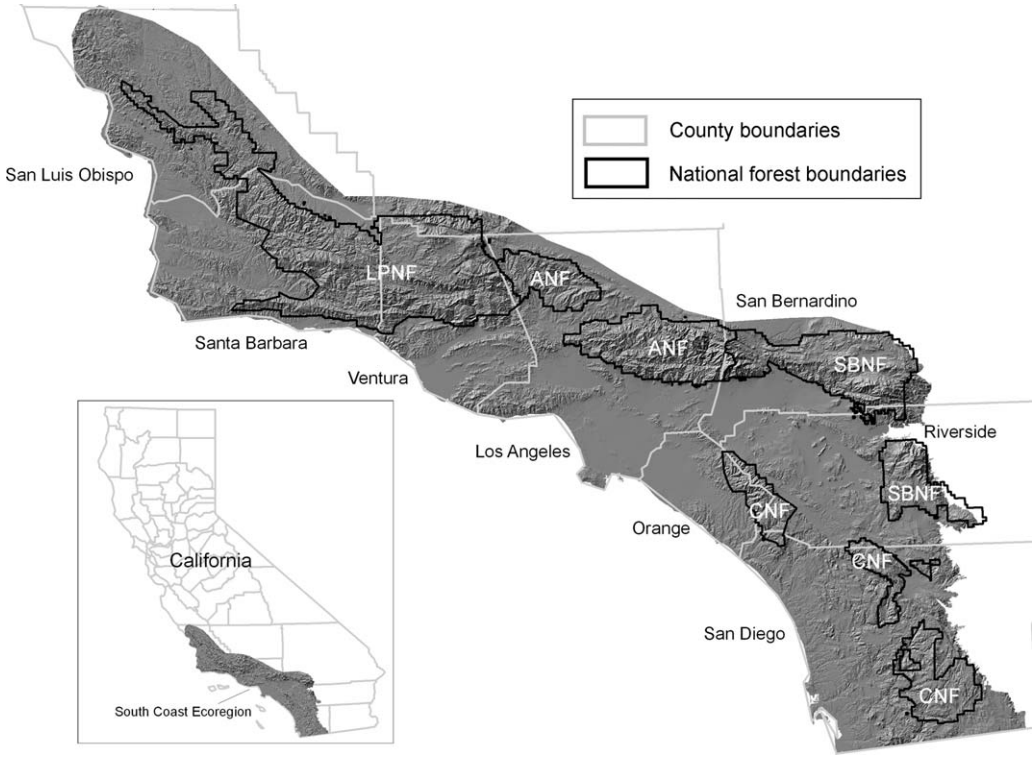


**Fig. 1.** Study area showing the four national forests of southern California. ANF is Angeles National Forest, CNF is Cleveland National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

preliminary regression analysis, we found that climate variables were significantly correlated with terrain variables, so we did not include them. Because most fires are stand-replacing in southern California shrublands, we determined vegetation age by calculating the time since last fire in the area immediately adjacent to the fuel break before the fire intersected it.

Severe weather conditions are likely to strongly influence fire spread rates and intensity (Moritz et al., 2004; Keeley and Zedler, 2009), and lead to conditions that are dangerous for firefighters (Halsey, 2005). However, previous analysis indicated that, because weather is highly variable over space and time, it is difficult to attribute exact weather conditions to the moment of intersection (Syphard et al., in press-a). Instead, we considered fire size and season as potential explanatory variables because they indirectly reflect the severity of weather conditions (Finney, 2003; Westerling et al., 2004), particularly because of the importance of autumn Santa Ana winds in this region (Moritz et al., 2010). We calculated fire size from the fire perimeter data through GIS calculations, and we derived fire season from the attributes of the fire perimeter data. We reclassified the months of the fires into winter and spring (January through May), summer (June through August), and autumn (September through November) to reduce the degrees of freedom in the data.

We obtained information on fuel break condition and firefighting activities through personal interviews with firefighters and managers who were most familiar with the fire events. Fuel break length was calculated from the GIS files, but data on fuel break width were largely unavailable for all four forests. Because written fuel break maintenance records were often unavailable, we determined how well the fuel break had been maintained by asking fire personnel to indicate the condition of the fuel break at the time the fire intersected it on a scale from one to three. The ranking reflected poor to excellent conditions, with poor reflecting fuel breaks where the vegetation had almost entirely regrown, and excellent reflecting fuel breaks that were either entirely grass, or no vegetation had regrown. To evaluate the importance of management activities, we also asked personnel to indicate whether they were able to gain access to the fuel break for firefighting (yes or no) and whether they had sufficient resources available (including manpower and equipment) to fight the fire, again on a scale of one to three, from poor (no resources) to excellent (full resources).

### 2.4. Explanatory variables for mapping number of intersections

To explain and map areas where fires and fuel breaks are most likely to intersect, we evaluated the same human and biophysical variables as for the fuel break outcome (Table 2). However, we did not consider fire and management variables related to single events because we were interested in trends across the entire study period (1980–2007). In addition, we hypothesized that significantly more fire and fuel break intersections would occur in areas that were historically fire-prone. Therefore, we additionally explored historic fire frequency (derived through overlay of fire perimeters from 1878 to 2007) as well as spatially interpolated ignition density as explanatory variables.

### 2.5. Fuel treatment outcome: structural equation modeling

Structural equation modeling provides advantages over traditional multiple regression analysis because it uses existing information to examine potential causal pathways among intercorrelated variables and identify indirect relationships (Bollen, 1989; Grace and Pugesek, 1998). The model is statistically evaluated to determine the degree of consistency with empirical data and compare the outcomes of alternative models. Although structural equation modeling is a confirmatory approach that tests a priori hypotheses of about interrelationships among variables, it is often essential to use exploratory regression and correlation analysis to suggest which pathways to explore (Grace, 2006).

For the different national forests, we initially conducted correlation analyses and built simple and multiple logistic regression models to explore the relationships among the explanatory variables and fuel break outcome. We used logistic regression because the response variable for fuel treatment outcome was binary, indicating whether the fuel treatment stopped the fire or not. Based on the hypothesized interrelationships developed through correlation and regression analysis, we developed and tested structural equation models using Mplus version 5.1 software. Because we modeled categorical outcomes, we used the weighted least-squares with mean and variance adjustment (WLSMV) estimator. To ensure that we retained only the important pathways in the final models, we sequentially removed one path at a time to ensure that, if a path were removed, the chi-square did not increase more than 3.84 points (the single degree-of-freedom test) (James B. Grace, personal communication). We also examined the fit of alternative models through *p*-values, root mean square error of approximation, and weighted root mean square residual (Hooper et al., 2008).

### 2.6. Number of intersections: multiple regression and predictive mapping

To evaluate the relative influence of the explanatory variables on the number of times fires intersected fuel breaks on the forests, we developed simple and multiple Poisson regression models that were appropriate for count response variables (Agresti, 1996). Because the objective of this part of our study was to create predictive maps (rather than explore causal pathways), we only used multiple regression analysis, as opposed to structural equation modeling. We first conducted simple regression models with each variable (and quadratic terms for continuous variables) to establish rankings for entering the variables into a multiple regression.

For the multiple regression models, we entered variables according to the amount of deviance they explained [$D^2$, equivalent to the $R^2$ in ordinary least square models (Guisan and Zimmermann, 2000)] and only considered those variables that were significant at $p \leq 0.15$. We evaluated correlation coefficients in the models for all of the forests and avoided including two variables with a bivariate correlation $\geq 0.3$. For each forest, we evaluated alternative plausible multiple regression models with different combinations of predictor variables and selected the best model as the one that explained the highest percentage deviance with the lowest Akaike information criterion (AIC) (Quinn and Keough, 2002). We also checked to ensure that overdispersion was not present in the models.

After selecting the best multiple regression models, we converted them into continuous map surfaces that reflected the predicted number of fires that would intersect fuel breaks across the entire forest. We created these maps by applying the Poisson regression formula and predicted coefficients onto the GIS layers of the significant explanatory variables (as in Syphard et al., 2008). We evaluated the correspondence of the predicted number of intersections to the actual intersections that occurred through Pearson correlation coefficients. We also quantified the magnitude of discrepancy among predicted and observed values by calculating the root mean square error (RMSE).

To test how well the models that explained the number of intersections on one national forest matched the models in the other forests, we applied the models developed on each forest to the entire South Coast Ecoregion and compared the maps. To quantify the spatial correspondence among the maps, we used a Pearson's correlation coefficient to calculate pairwise correlations (Termansen et al., 2006; Syphard and Franklin, 2009). High correlations among maps would indicate that the factors controlling the spatial pattern of fire and fuel break intersections were similar among the forests, and low correlations would suggest that those factors vary.

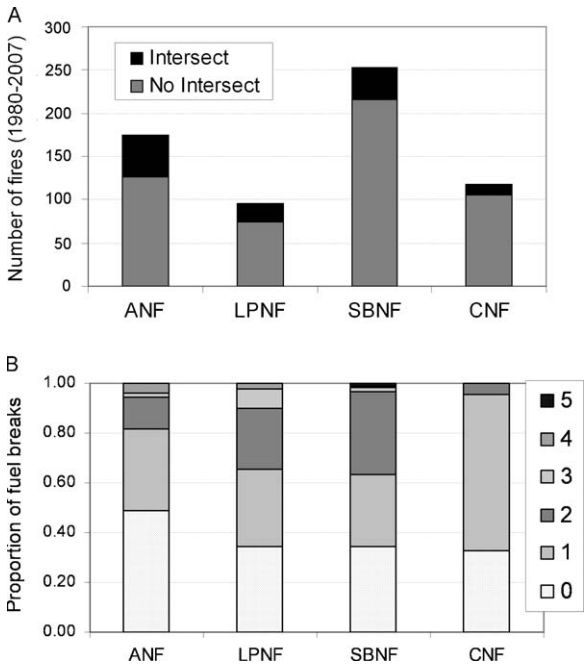


**Fig. 2.** Number of fires that occurred in four national forests divided into those that intersected a fuel break and those that did not intersect a fuel break (A); and proportion of fuel break area intersected by 0–5 fires from 1980 to 2007 (B). ANF is Angeles National Forest, CNF is Cleveland National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

## 3. Results

### 3.1. Summary of fuel break and fire intersections and outcomes

During the 28 years of the analysis, 641 fires occurred within the boundaries of the four national forests. On average, 23% of those fires intersected a fuels treatment, but the proportion of intersections varied among the forests (Fig. 2A). In fact, the number of intersections among fires and fuel breaks on the Cleveland National Forest was only 13 (11% of the intersections), and this small number precluded us from including that forest in our statistical analyses.

For the fuel breaks that we considered in our spatial analysis of intersections (i.e., those constructed on or before 1980), approximately 25–50% of the fuel break area never intersected a fire. On the other hand, approximately 10–45% of the fuel break area intersected multiple (two or more) fires. The proportion of fuel break area that intersected fires varied among the four forests (Fig. 2B).

When fires intersected fuel breaks, the percentage that stopped at the fuel breaks ranged from 22 to 47%, and the percentage that crossed over the fuel breaks ranged from 29 to 65%, depending on the forest (Fig. 3). We distinguished another group of fuel break intersections where fires crossed over fuel breaks, but the fuel breaks did change fire behavior enough to facilitate firefighter access and eventually help with the suppression of the fire. When this group is considered along with the other cases in which the fuel break held a portion of the fire, the percentage ranged from 10 to 23% (Fig. 3).

### 3.2. Fuel treatment outcome: structural equation modeling

Among the three national forests that we analyzed, there were seven variables that significantly affected fuel break/fire outcomes. However, the structural equation models revealed differences in the number and combination of important variables as well as

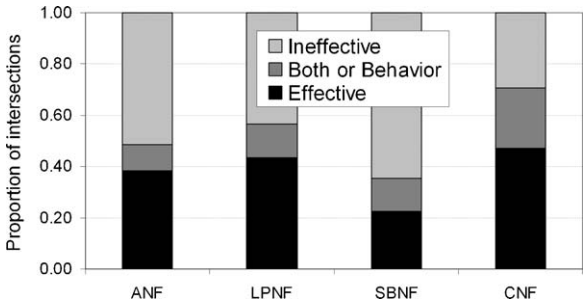


**Fig. 3.** Proportion of fire and fuel break intersections in four forests divided into those that effectively stopped a fire (Effective); those in which only a portion stopped a fire or that changed fire behavior (Both or Behavior); and those in which the fires crossed over the fuel break (Ineffective). ANF is Angeles National Forest, CNF is Cleveland National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

differences in the interrelationships among them. We tested alternative models with different explanatory variables and different direct and indirect effects. The final model varied among the forests (Fig. 4). Despite these differences, most of the variables were common to at least two of the three forests; and three variables were common to all forests: firefighter access, fire size, and fuel break condition.

Firefighter access was the only variable to directly improve the outcome in all three forests, and it was the most influential variable for the Los Padres and Angeles National Forests. The proportion of events in which firefighters had access to fuel breaks was slightly lower in the Angeles than in the other two forests (Fig. 5C). On the Los Padres and San Bernardino forests, fire size was directly and negatively related to fuel break outcome; in the Angeles, fire size negatively affected firefighter access and thus indirectly influenced fuel break outcome. On average, the fires were smaller in the Angeles, but fire sizes were highly variable on all of the forests (Fig. 6). On the Los Padres and Angeles forests, fuel break condition facilitated firefighter access to fuel break and thus indirectly improved fuel break outcome; the relationship was direct in the San Bernardino, which reported the largest proportion of fuel breaks with low scores for fuel break condition (Fig. 5B).

The Los Padres was the only forest for which season was not important in explaining fuel break outcome, as later-season fires (i.e., September through November) had a direct negative influence on outcome for the Angeles; and for the San Bernardino, later-season fires contributed to increased fire size, so the effect was indirectly negative. Most of the fires on the Los Padres occurred in the summer months, whereas fires in the autumn were most common for the other two forests (Fig. 5E). The Los Padres was the only forest in which firefighting resources were not influential in explaining outcome. On both the Angeles and San Bernardino, resources indirectly improved fuel treatment outcome; but on the Angeles, the primary relationship was by improving access and on the San Bernardino, the primary relationship was through reduction in fire size. The overall distribution of firefighting resources, according to the interviews, was variable among the forests (Fig. 5A). Finally, the Los Padres was the only forest in which fuel break length had a significant direct and positive impact on fuel treatment outcome, and this forest had longer fuel breaks, on average, than the other two forests (Fig. 6).

The Angeles was the only forest in which vegetation age was not important. On the Los Padres, younger vegetation surrounding the fuel breaks improved firefighter access to the treatment, so the relationship was indirectly negative. On the San Bernardino, the relationship was direct and positive. Although the average vegetation age was lowest on the San

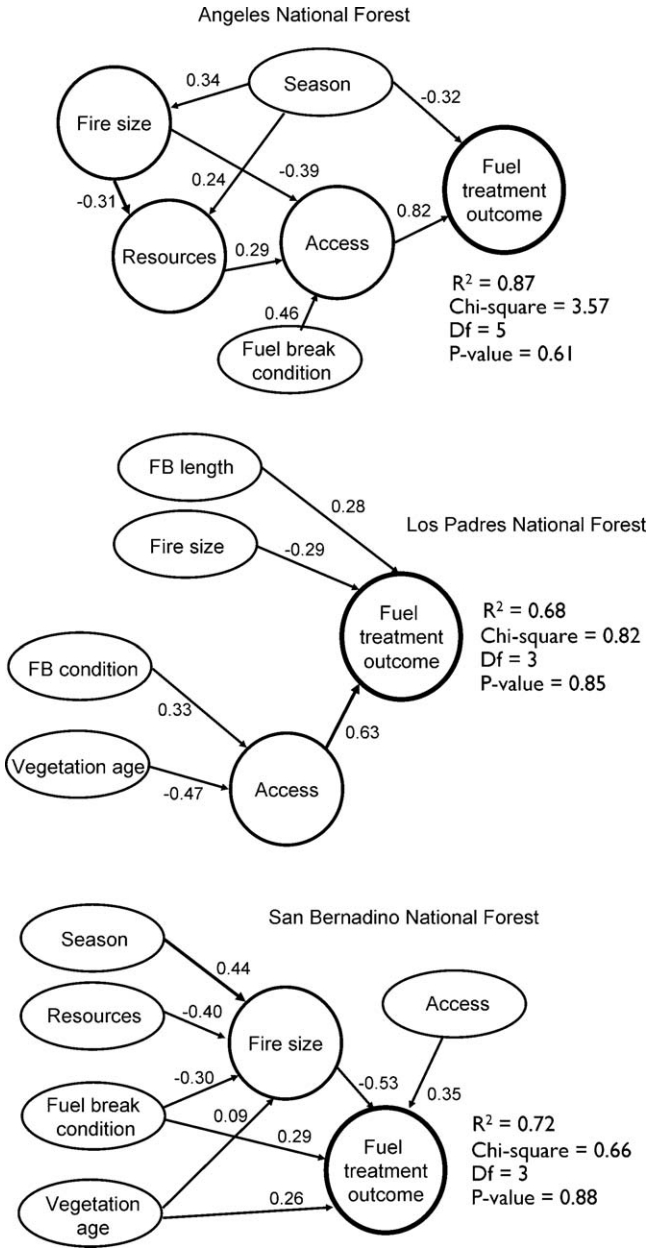


**Fig. 4.** Structural equation model of factors that directly and indirectly explain why fires stopped at fuel breaks in the Angeles, Los Padres, and San Bernardino National Forests. Solid arrows represent direction of effect, and coefficients shown along arrows are standardized values. Circles represent endogenous (or dependent) variables in the models. Due to insufficient number of fuel break/fire intersections the Cleveland National Forest was not included.

Bernardino, there was a lot of variability in age for all the forests (Fig. 6).

### 3.3. Number of intersections: multiple regression and predictive mapping

Of the variables we considered for explaining the number of fire and fuel break intersections in the forests, historic fire frequency was the only one that was retained in all three of the multiple regression models (Table 2). For all three forests, the number of intersections was strongly and positively related to the number of fires that had occurred since 1878 (date of the earliest fire in the database). Ignition density was also positively related to the number of intersections on the Angeles and Los Padres National

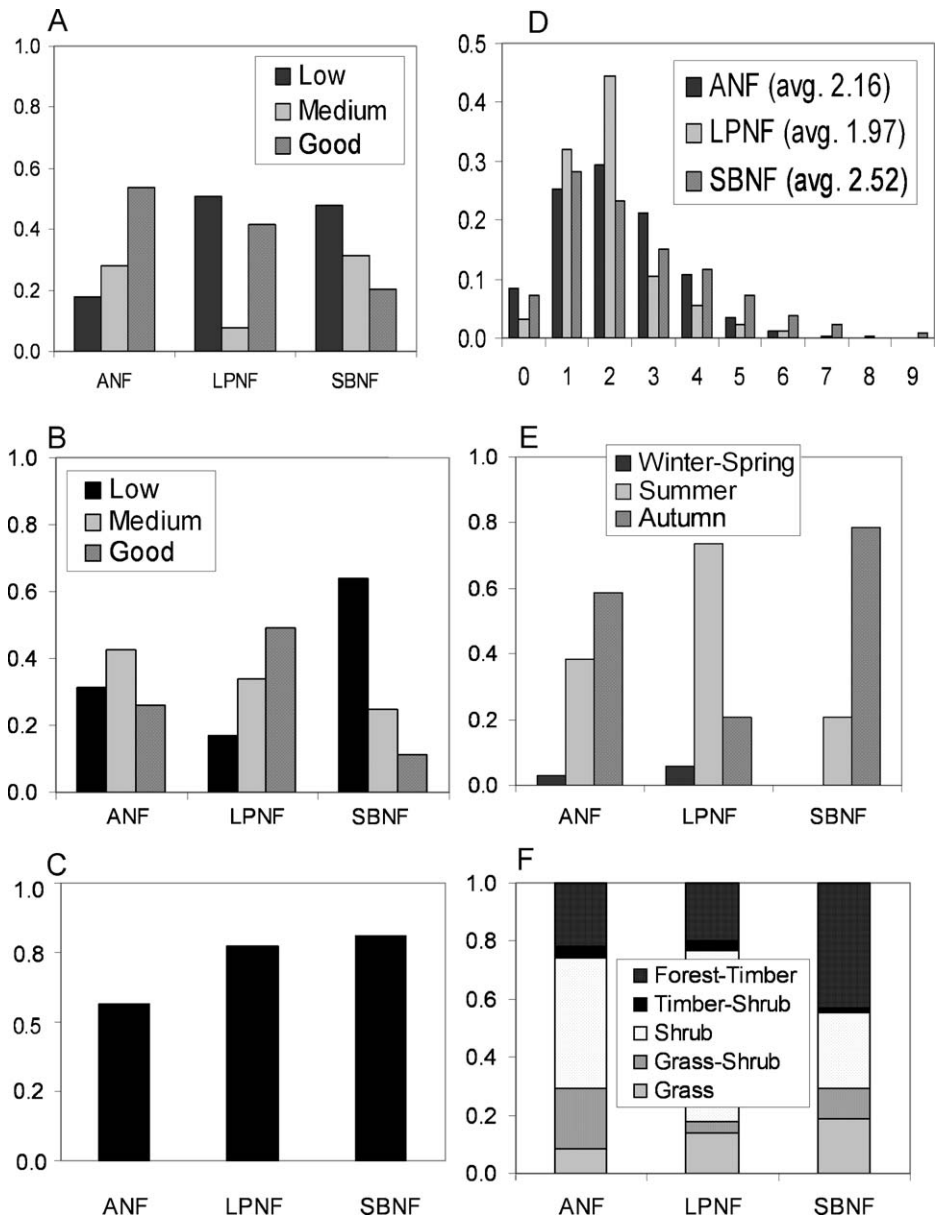


**Fig. 5.** Distribution of categorical variables for three national forests that were significant in any of the statistical models. The *y*-axis for all charts represents the proportion of observations within each forest. The charts represent (A) firefighting resources; (B) fuel break condition; C) Access to fuel break; (D) historic fire frequency (with the average for each forest indicated in the legend); (E) season when intersection occurred; (F) fuel type. ANF is Angeles National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

Forests, but was not retained in the model for the San Bernardino National Forest. The Los Padres had the lowest average number of fires and lowest ignition density, whereas the San Bernardino had the highest fire frequency and ignition density (Figs. 5D and 6).

For both the Angeles and San Bernardino National Forests, the number of intersections was negatively related to elevation, which was slightly higher on average on the San Bernardino than the other forests (Fig. 6). The fuel model parameter was also significant in explaining model variation for only the Angeles and San Bernardino. A larger number of intersections occurred in forest and timber fuel models on the San Bernardino National Forest ("TU" or "TL", Scott and Burgan (2005)), whereas the shrub models ("SH", Scott and Burgan (2005)) were more influential in the Angeles (Fig. 5F). Three variables were retained in the multiple-regression model for the Los Padres that were not important in the other forests. On the Los Padres, fires were more likely to intersect fuel breaks when fuel breaks were in close proximity to trails, distance to roads was intermediate, and winter solar radiation was low. Both the average distance to trails and solar radiation were lower on the Los Padres than in the other two forests, but the average distance to roads was similar, with high variation in the three forests (Fig. 6).

The three map surfaces developed by applying the multiple-regression model formulas and coefficients to the GIS maps of the significant variables reflect a continuous probability distribution of where fires and fuel breaks are most likely to intersect (Fig. 6). The Pearson's correlation coefficients between the observed number of intersections and the number of intersections predicted by the model ranged between 0.59 and 0.74 (Table 3), and the root mean squared error ranged from 0.28 to 1.31 intersections. The correlations among the three maps generated by the differ-

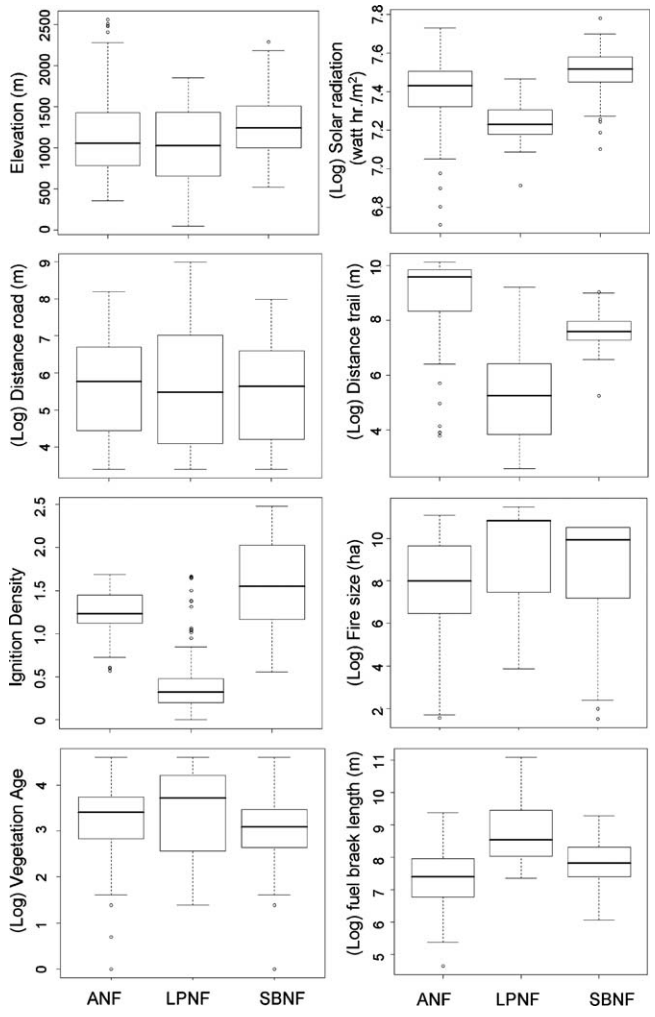


**Fig. 6.** Distribution of continuous variables for three national forests that were significant in any of the statistical models.

ent multiple-regression models were lower, particularly for the Los Padres model (correlation of 0.21 with the Angeles and 0.16 with the San Bernardino). The Angeles and San Bernardino maps, however, had a much stronger correlation (0.54) (Fig. 7).

## 4. Discussion

The four southern California national forests studied here all share several features in common; they are in rugged terrain, are dominated by non-forested ecosystems, and contain a substantial amount of wildland–urban interface. These national forests, however, differ in the proportions of vegetation types, biophysical characteristics, and the relative proportions of wildland–urban interface and intermix landscapes. These differences are part of the reason the significant factors explaining fuel break/fire outcomes and number of intersections were different among forests. Nevertheless, several factors were consistently important across all forests in explaining the number of intersections between fuel breaks and big fires and the role of fuel breaks in altering fire spread. These similarities support several general conclusions about the role of fuel breaks in controlling large fires in southern California.

**Table 3**
Pearson correlation coefficients among prediction maps for three national forests and among predicted and observed number of intersections within each forest. Root mean squared error (RMSE) is calculated between the observed and predicted number of intersections within each forest.

| | Angeles | Los Padres | San Bernardino |
|---|---|---|---|
| Angeles map | 1.00 | 0.21 | 0.54 |
| Los Padres map | 0.21 | 1.00 | 0.16 |
| San Bernardino map | 0.54 | 0.16 | 1.00 |
| Observed *N* intersections | 0.61 | 0.59 | 0.74 |
| RMSE | 1.31 | 0.76 | 0.28 |

One conclusion is that the primary role of fuel breaks in the region is to facilitate fire management activities. Two of the three fire management variables we considered (access and fuel break condition) were important in all three structural equation models (Fig. 4), and firefighter resources was important for two of the forests (Angeles and San Bernardino). Furthermore, while other important variables in the models (related to vegetation structure, fire size, and season) were not directly related to management, these variables often indirectly influence management, for example, by affecting access to treatment areas. Demonstrating the strength of these indirect effects is one of the benefits to structural equation modeling (Grace, 2006).

Firefighter access to fuel breaks was the most influential factor in fuel treatment outcome for the Los Padres and Angeles, and was also highly significant for the San Bernardino. The high level of significance for this variable supports the notion that, without firefighters present to control fires, fires will generally not stop at fuel breaks. Although three fires stopped on their own at the top of ridges on the San Bernardino, these fires constituted less than 1% of the cases. Only one fire stopped passively on the Los Padres, and none of the fires in our analysis stopped without firefighters on the Angeles. Despite this conclusion, it is important to point out that the fire perimeter database only includes fires greater than 10 ha; therefore, it is possible that some smaller fires do stop passively (i.e., without fire fighting actions) at fuel breaks. Many fire management personnel understand that fuel breaks are unlikely to passively stop most fires, particularly during extreme weather conditions, but the public, news media, and policy-makers may unrealistically expect otherwise. Our results show that such beliefs could lead to a false sense of security about the protective value of fuel breaks.

Most of the largest fire events in southern California occur during severe weather conditions in autumn, prior to winter rains, when dry, offshore Santa Ana winds can exceed 30 $ms^{-1}$ (Miller and Shlegel, 2006; Moritz et al., 2010). Fighting fires during these weather conditions can be extremely dangerous, and during these wind events, multiple fires often break out simultaneously. These severe weather conditions likely explain why fire size was another variable that was highly significant in explaining fuel treatment outcome in all three forests. Discussions during the interviews confirmed that fires were more difficult to control, and likely to become large, under severe weather conditions. There are a number of reasons for this: the speed of such fires, which can cover 10,000 ha within a day or two, and thus the lack of time for accessing fuel breaks, the danger of aggressively attacking fires under such conditions, and firefighting resources spread too thin because of multiple fire fronts. Consistent with the effect of fire size, fire season was significant on the Angeles and San Bernardino because Santa Ana winds typically occur during the fall (and this was the season when fuel treatment/fire outcomes were poorest). The reason that season was not important for the Los Padres, but fire size was, is that Santa Ana winds are much less predictable there (Moritz et al., 2004, 2010). The Los Padres regularly experiences strong, hot wind downcanyon wind events known as "sundowners," typically in summer (Ryan, 1996), but these are not annual events as are Santa Ana winds. It is possible for severe-weather fire events to occur in any season, not just the fall, across the entire southern California region. This explains why fire size was important on all three forests.

In addition to fire management and fire weather (i.e., size and season), there was evidence that vegetation structure played an

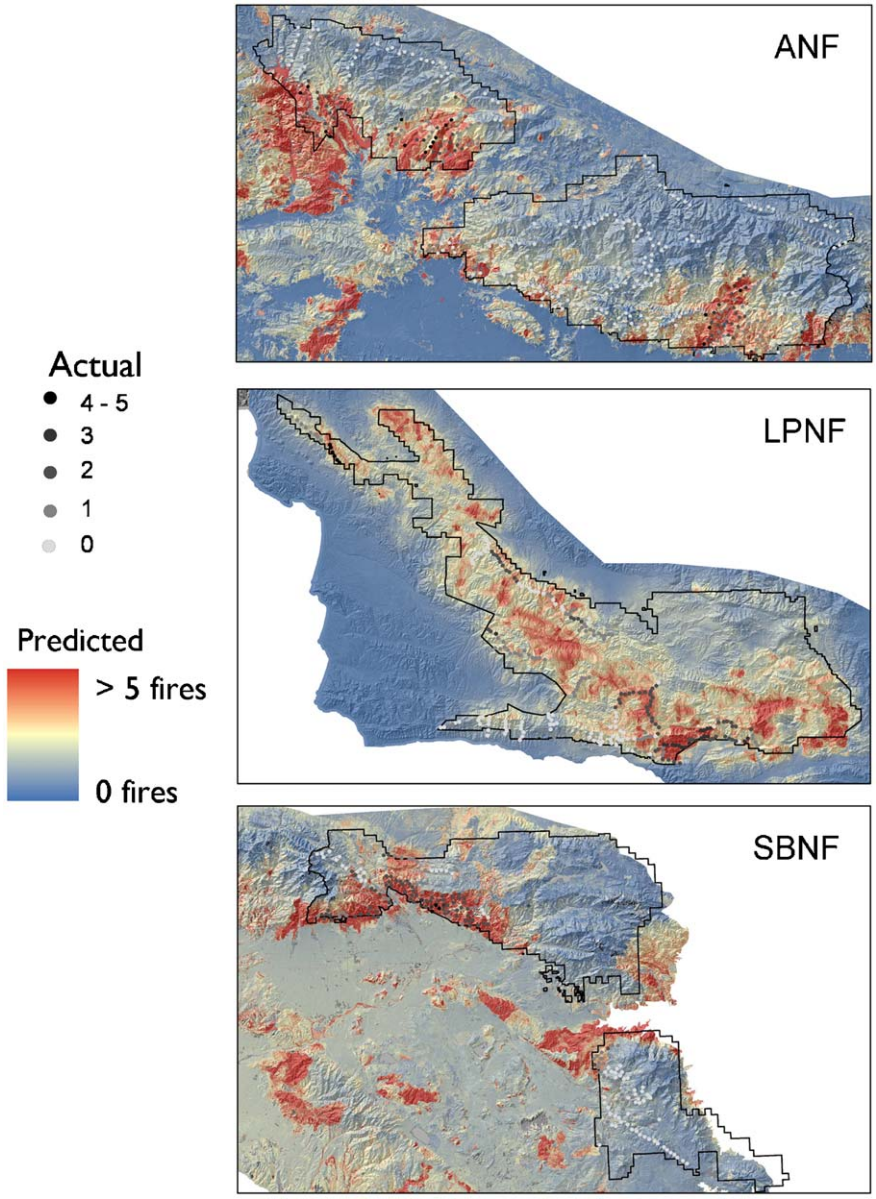


**Fig. 7.** Maps showing predicted distribution of areas most likely to intersect fuel breaks in the Angeles, Los Padres, and San Bernardino National Forests. The sample points along the fuel breaks also show the actual number of times fires intersected fuel breaks at those locations from 1980 to 2007.

important role in improving fuel break outcome in all three forests, and this was generally because well-maintained fuel breaks were much easier for firefighters to access in time to prepare the fuel break for suppression activities. Because young vegetation typically has a lower fuel load than old vegetation, one of the premises of conducting fuel manipulation is that young vegetation can directly slow or stop the spread of fire. However, in southern California shrublands, stand age and fuel loads play a limited role in stopping the spread of fire, particularly during extreme weather conditions, when fires often spread through or over very young age classes (Keeley and Zedler, 2009; Moritz, 1997; Moritz et al., 2004). Accordingly, while vegetation age was significant in the Los Padres, younger vegetation did not directly prevent fires from spreading, but helped facilitate firefighter access to fuel breaks. There are some parts of the Los Padres where, because of the lack of consistent Santa Ana influence, fuel age may play a role in controlling fire spread (Moritz, 1997). This particularly applies to the coastal area near the city of Santa Barbara. Regardless, the most significant relationship was between vegetation age and firefighter access.

Fuel break condition (i.e., how well it was maintained) played a similar role as vegetation age, and it was influential in all three forests. While the relationship was direct on the San Bernardino, better-maintained fuel breaks improved access to fuel breaks in the Los Padres and the Angeles, and thus, the relationship was indirect. Southern California chaparral forms a dense, continuous cover that is extremely difficult to maneuver in (Halsey, 2005), which likely explains why well-maintained fuel breaks improved the outcome.

As in the models for fuel break outcome, the models explaining the number of fire and fuel break intersections reflected regional landscape diversity and differences among the forests, while nevertheless suggesting several general conclusions. By far the most significant variable, and the only variable consistently significant for all forests, was historic fire frequency. This result is not surprising because areas that have burned most frequently in the past are likely to be most fire-prone in general. Ignition density patterns were also significant for two of the forests. Nevertheless, fire history was not the only factor explaining why fuel breaks intersect fires more in some places than in others. Fire and fuel break

intersections were a function of a combination of biophysical and human variables for all the forests, but the biophysical variables were generally more important than the human ones. This is consistent with other regional studies that have shown biophysical factors to be strongly related to patterns of fire occurrence and area burned, whereas human variables are most significant for explaining ignition patterns and fire frequency (Parisien and Moritz, 2009; Syphard et al., 2007, 2008).

The maps of predicted distribution of areas where fuel breaks are most likely to intersect with large fires did not correlate well among the forests, yet there was good correlation among observed and predicted number of intersections within the forests. In other words, the combination of factors that best predicted the number of intersections in one forest did not match well with the combination of factors that best predicted the intersections in the other forests. These differences reflect how the environmental controls of fire regimes vary from region to region, even within a single ecoregion. Therefore, a "one size fits all" management approach would be inappropriate if the objective were to map likely areas for fires and fuel treatments to intersect. While developing a model for one region and applying it to a different region may be inappropriate, the modeling methodology adopted here could easily be applied anywhere. These types of maps could be part of a manager's toolset in helping to identify areas where new fuel breaks could be constructed or where current fuel breaks should be maintained.

We cannot directly attribute differences in the influential variables of our models to differences among the forests because we only statistically analyzed three national forests. Nevertheless, the differences among the national forests do provide a perspective on the variability of the region, despite the fact that it all falls within the same ecoregion. This is striking considering that southern California has a distinctive fire regime, owing to the defining characteristics of the region's Mediterranean-type climate. Because of the cool, wet winters and hot, dry summers, and the specific properties of chaparral, this vegetation is particularly flammable for a substantial portion of the year and burns in large, stand-replacing, high-intensity fires (Pyne et al., 1996). The region's fire regime and fire management issues are typically most starkly contrasted against those in forested regions (Keeley et al., 2009). While it has been recognized that many fire management practices in forested regions are inappropriate for southern California shrublands (Halsey, 2005; Keeley and Fotheringham, 2006), this study shows how certain aspects of fire management may need to be individually tailored at even finer scales, dependent on terrain, proximity to urban environments, regional weather patterns, and fuel type composition.

In southern California, fuel treatments can lead to ecological degradation because they often involve complete removal of vegetation, facilitate the spread of exotic species, and may thus indirectly contribute to increased fire frequency in a region where recurrent fire already threatens the native shrublands (Merriam et al., 2006, 2007). These resource costs should be considered relative to the benefits of protecting communities, and these trade-offs should be considered when constructing new fuel breaks in the region. This is in contrast to forested regions, where the objective of protecting communities is often coupled with the objective of reshaping the age structure and composition of forests to resemble historic conditions (Reinhardt et al., 2008). In these forests, fuel breaks and resource benefits generally are mutually beneficial. Regardless of the region, mitigating fire risk to communities is a priority for federal land managers, yet most fuel treatments are not placed within the wildland–urban interface where they may have the greatest potential for protecting homes. Across the western United States, only 3% of the area treated from 2004 to 2008 was located in this interface (Schoennagel et al., 2009).

Many new fuel breaks are currently being constructed in southern California. In fact, the most likely reason there were not enough fire and fuel break intersections to complete a statistical analysis in the Cleveland National Forest is because a large proportion of the fuel treatments have been recently constructed. Despite the large amount of new fuel break construction, the results of this study show that many fires never actually intersect fuel breaks, and large areas of fuel breaks never intersect fire. Also, the forests that had the highest density and area of fuel breaks did not have the highest overall effectiveness of fuel breaks, suggesting that treating more area alone does not necessarily increase the safety of a region. It may be more effective to have fewer fuel breaks in strategically placed locations than to have greater area of fuel breaks overall, at least in terms of protecting communities. The results from all three forests show that fuel breaks played an important role in controlling large fires primarily where they provided access for firefighting activities. Strategically locating fewer fuel breaks could also reduce the potential for resource costs.

Discussion in the interviews revealed that many strategic decisions do go into placing fuel breaks. While these decisions are often based on years of fire management experience, quantitative and spatially explicit analyses could potentially be helpful in refining these strategic decisions. For example, maps like the ones generated here, showing where fuel treatments are mostly likely to intersect fires, could be combined with further spatial analyses of where access is best and where communities need the most protection. In particular, this study strongly supports the notion of constructing fuel breaks along the wildland–urban interface where firefighters will have better access to the fuel breaks, and where the fuel breaks will provide an immediate line of defense adjacent to homes that are at risk. The case studies from all four national forests demonstrate that fuel breaks will not stop fires without firefighter presence. Therefore, constructing fuel breaks in remote, backcountry locations will do little to save homes during a wildfire because most firefighters will be needed to protect the wildland–urban interface, and fires will not be stopped by those fuel breaks that are located farther away. Finally, because access to fuel breaks was consistently improved when vegetation structure was favorable, this study suggests that maintaining fuel breaks in strategic locations may be just as important as constructing new fuel breaks.

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# Housing Arrangement and Location Determine the Likelihood of Housing Loss Due to Wildfire

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## Abstract

Surging wildfires across the globe are contributing to escalating residential losses and have major social, economic, and ecological consequences. The highest losses in the U.S. occur in southern California, where nearly 1000 homes per year have been destroyed by wildfires since 2000. Wildfire risk reduction efforts focus primarily on fuel reduction and, to a lesser degree, on house characteristics and homeowner responsibility. However, the extent to which land use planning could alleviate wildfire risk has been largely missing from the debate despite large numbers of homes being placed in the most hazardous parts of the landscape. Our goal was to examine how housing location and arrangement affects the likelihood that a home will be lost when a wildfire occurs. We developed an extensive geographic dataset of structure locations, including more than 5500 structures that were destroyed or damaged by wildfire since 2001, and identified the main contributors to property loss in two extensive, fire-prone regions in southern California. The arrangement and location of structures strongly affected their susceptibility to wildfire, with property loss most likely at low to intermediate structure densities and in areas with a history of frequent fire. Rates of structure loss were higher when structures were surrounded by wildland vegetation, but were generally higher in herbaceous fuel types than in higher fuel-volume woody types. Empirically based maps developed using housing pattern and location performed better in distinguishing hazardous from non-hazardous areas than maps based on fuel distribution. The strong importance of housing arrangement and location indicate that land use planning may be a critical tool for reducing fire risk, but it will require reliable delineations of the most hazardous locations.

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## Introduction

As the frequency, extent, and severity of wildfires are surging across the world [1,2], so too are the ecological, social, and economic consequences. Residential losses associated with wildland fire have escalated globally [3–5], and recent fire events have resulted in billions of dollars of damage per event [6]. The problem is particularly critical in Mediterranean-climate regions of the world, where major metropolitan centers are juxtaposed with highly flammable ecosystems [7]. Since the 1950s, southern California has experienced the highest losses in property and life in the U.S., averaging 500 homes per year [8]. Here we show that the arrangement and location of structures strongly affects their susceptibility to being destroyed in a wildfire, and that empirically based maps developed using housing density and location can better identify hazardous locations than fuel-based maps.

The escalation of wildland fire losses is typically attributed to housing development within or adjacent to wildland vegetation (i.e., the "wildland-urban interface") [6,9], changing climate conditions [1], or an accumulation of hazardous wildland fuels [10]. The primary preventive strategy used for reducing fire impacts has been the manipulation of wildland vegetation to reduce hazardous fuels. The U.S. federal government has strongly promoted and funded fuel reduction treatments to mitigate fire hazard, and federal land management agencies spent billions of dollars (e.g., $2.7 billion from 2001–2006) to treat millions of hectares within the last decade [10]. Yet, while costs for suppression and treatment have nearly tripled since 1996 [11], the fire problem has only gotten worse.

With the growing realization that wildland fuel manipulations can alter fire outcomes only to a limited extent, the need for alternatives has risen. For example, a structure's survival during a wildfire depends largely on its building materials and the characteristics of fuels in its immediate surroundings [3], suggesting that fire hazard can be reduced by homeowner actions to protect the structure [12].

However, what remains unclear is to what extent property loss depends on the role of land planning and the placement and arrangement of homes relative to the spatial patterns of wildland fire hazards. Past land-use decision-making has allowed homes to be constructed in highly flammable areas, and this may be one of the roots of the fire problem [13]. Although it is not feasible to change current housing patterns, homes in the most hazardous locations could be identified and prioritized for fire protection efforts, and land use planning and regulation may potentially be a powerful tool for reducing future property loss [14], especially in

areas such as southern California where substantial future housing growth is expected [15], and across the western US, where further development is expected in a substantial proportion of the wildland-urban interface [16].

If land use regulation and planning are to effectively reduce wildland fire loss, they have to be based on solid understanding of what landscape factors most significantly contribute to wildfire danger and where to locate and arrange homes to reduce fire hazard. Currently, most fire hazard maps are based on expert knowledge of how fuel and fire history determine threats to a given community e.g., [17–19]. Similar fire hazard maps have been created for the state of California that identify communities at risk and areas of substantial fire threat to people. These maps are readily available [20] and widely used. Fire hazard maps, however, are only effective if they accurately delineate areas where property loss is most likely to occur. Whether this is the case or not is unknown since most have never been evaluated against empirical data.

We constructed a complete database of structure locations in two extensive, fire-prone regions of southern California and identified which structures were destroyed or damaged by wildfires since 2001 (Fig. 1). These two regions were the Santa Monica Mountains, one of the largest wildland open space areas adjacent to the Los Angeles metropolitan area and San Diego County, site of major wildfire losses in both 2003 and 2007 [20]. Based on these data, we used logistic regression and maximum entropy analysis to answer three questions: 1) What is the relative importance of housing arrangement (i.e., the spatial pattern of residential structures), location, and environment in explaining property loss from fire? 2) How well do currently available statewide fuel-based maps of fire hazard correspond to actual wildfire impacts? 3) Can fire hazard maps based on empirical data and an expanded set of explanatory variables successfully predict local-scale housing losses?

## Results

In the Santa Monica Mountains, 3% of 36,399 structures were located within the boundaries of 10 large fires that occurred from 2001 to 2009. In these fires, 173 homes, guest houses, or outbuildings were destroyed and an additional 140 were damaged. For the second study region in San Diego County, 4% of 687,869 structures were located within one of 40 fire perimeters. In these fires, 4315 structures were completely destroyed and an additional 935 were damaged.

In both study regions, the spatial arrangement of structures (Table 1) significantly influenced the likelihood of property loss (i.e., destruction or damage) (Figs. 2 and 3). Property loss was more likely in smaller, more isolated housing clusters with low- to intermediate housing density and fewer roads, although road density was insignificant after accounting for spatial autocorrelation in the Santa Monica Mountains (Table 2). Structures located near the edges of developments, or in housing clusters on steep slopes, were also more susceptible. Many relationships were nonlinear, with the highest property loss occurring when structures were at intermediate distances to other structures or housing clusters.

In addition to spatial arrangement, a structure's location on the landscape was also a highly significant predictor of property loss (Fig. 2). In both study regions, property loss was significantly related to a structure's distance from the coastline, but the relative effect varied. In the Santa Monica Mountains, property loss occurred disproportionately closer to the coast, whereas structures farther from the coast were most susceptible in San Diego County (Tables 2 and 3).

The other significant location-dependent variable affecting property loss was historical fire frequency (Fig. 2). In the Santa Monica Mountains, this was the single most important predictive variable. Here, property loss was most likely in areas of historical high fire frequency, which corresponded with wind corridors. Fire frequency was also a significant variable in San Diego County, but here the relationship was nonlinear.

Property loss was more likely to occur when structures were surrounded by wildland vegetation rather than by urban or impervious areas (Fig. 4). However, property loss was also more (Santa Monica Mountains) or as likely (San Diego County) to

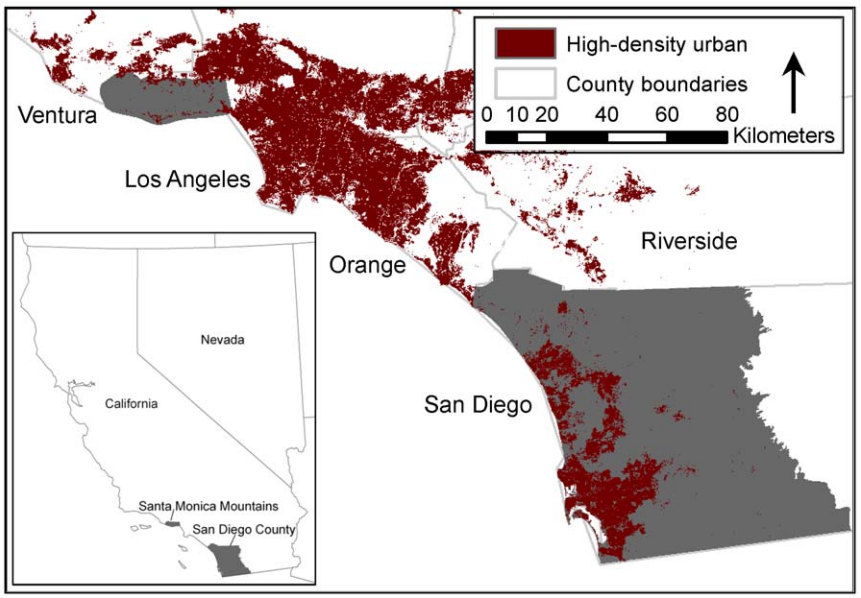


**Figure 1. The Santa Monica Mountains and San Diego County, California, USA.** Study areas in gray. The Santa Monica Mountains are located in Ventura and Los Angeles counties, and both study areas are located within the South Coast Ecoregion of California, USA. Study areas in gray.
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**Table 1.** Variables analyzed for explaining structure loss in the Santa Monica Mountains and San Diego County.

| *Variable* | *Source* | *Description* |
|---|---|---|
| Fire frequency 2001 | CDF* Fire perimeter overlays | Number of fires (2001–2010) |
| Distance to coast | Derived from coastline of county | Continuous distance in meters |
| Fire threat | CDF* | Ranking from 1 to 5 |
| Fire threat to people | CDF* | Ranking from 1 to 5 |
| Communities at risk | CDF* | Binary, at risk or not at risk |
| Housing density | Derived from digitized structures | Structures per hectare |
| Distance nearest housing cluster | Derived from 100 m buffer of structures | Continuous distance in meters |
| Housing dispersion | Derived from 100 m buffer of structures | Standard deviation/mean distance between structures in housing cluster |
| Distance to nearest structure | Derived from digitized structures | Continuous distance in meters |
| Distance to edge of housing cluster | Derived from digitized structures | Continuous distance in meters |
| Area of housing cluster | Derived from 100 m buffer of structures | Squared meters |
| Elevation | US Geological Survey digital elevation model (DEM | 30 meters |
| Slope | Derived from the DEM | Percent slope |
| Southwestness | Derived from the DEM | SW = con(aspect(<dem>) = = −12, 201,(cos(((aspect(<dem>)−255) div deg)+1) * 100))) |
| Road length | US Census Bureau TIGER/Line files | Meters |

*California Department of Forestry Fire and Resource Assessment Program.
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occur within herbaceous fuel types than within the higher fuel-volume woody types that are typically considered as the most hazardous fuels.

Variables with correlation coefficients greater or equal to 0.7 in the Santa Monica Mountains included road length and area of housing cluster (0.95) and elevation and distance to coast (0.72). In San Diego County, pairs of correlated variables also included road length and area of housing cluster (0.99), distance to nearest structure and distance to nearest housing cluster (0.71). Distance to coast was correlated with housing density (−.71) and elevation (0.89). To develop multiple-regression models, we removed elevation and road length from consideration in the Santa Monica Mountains, because they explained less variation than the variable with which they were correlated. For the San Diego County analyses, we removed distance to coast, road length, and distance to nearest housing cluster.

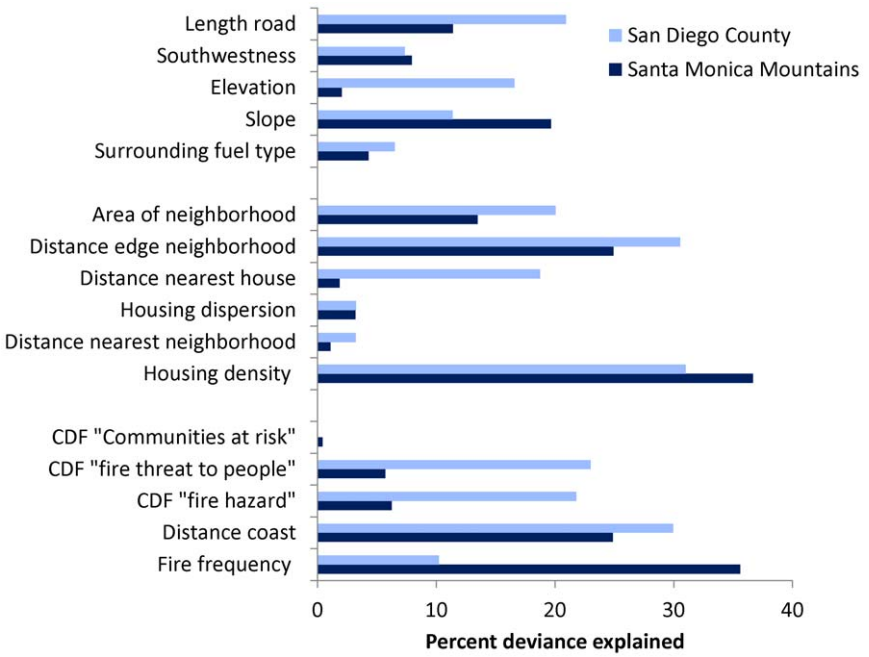


**Figure 2. Percent deviance explained for generalized additive models (GAMs).** GAMs explain the influence of firefighter access, biophysical variables, structure arrangement, and structure location on burned structures from fires during 2001–2010 in the Santa Monica Mountains, CA and San Diego County, CA. CDF – California Department of Forestry and Fire Protection.
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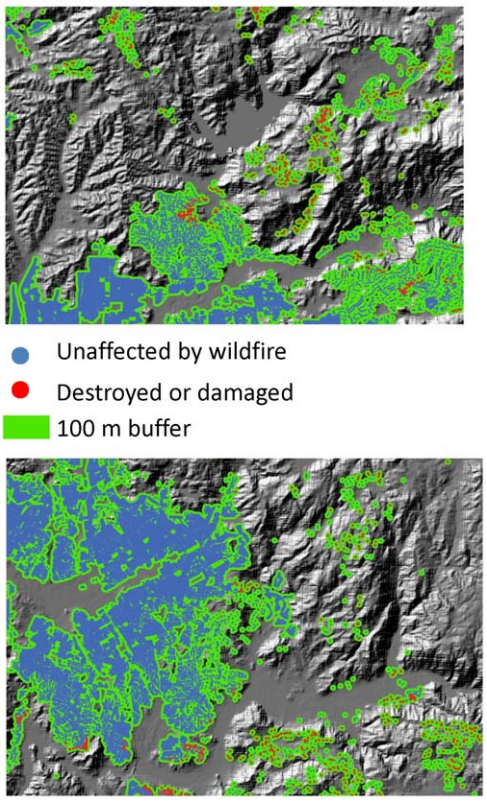


**Figure 3. Maps from portions of San Diego County illustrating how housing arrangement influences the likelihood that a house will be lost from wildfire.** Structures most likely to be burned by fires (in red) were: in areas with low to intermediate structure density; in small, dispersed housing clusters, close to the edge of the housing cluster, at intermediate distance to the nearest structure or housing cluster than structures that were unaffected (in blue).
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The multiple-regression GAM model for the Santa Monica Mountains included fire frequency, housing density, distance to edge of housing cluster, distance to coast, slope, area of housing cluster, southwestness, fuel type, housing dispersion, distance to nearest structure and housing cluster. Only nonparametric terms were selected, except fuel type, which was categorical. The deviance explained for the model was 65.7%, and the area under the curve (AUC) of receiver operating characteristic (ROC) plots, indicating the ability of the model to discriminate between burned and unburned structures on test data (20%), was 0.82.

The multiple-regression GAM model for San Diego County included housing density, distance to edge of housing cluster, area of housing cluster, elevation, fire frequency, fuel type, and housing dispersion. All terms included in the model were nonparametric except for distance to edge of neighborhood, which was linear, and fuel type. The deviance explained for the model was 45.5%, and the AUC was 0.87.

Our fire-hazard maps developed with the Maxent model using empirical data and multiple explanatory variables (Figs. 5 and 6) performed well. The AUC of receiver operating characteristic (ROC) plots on test data (15% withheld) was 0.987 for the Santa Monica Mountains and 0.923 for San Diego County.

In contrast, statewide fire-hazard maps developed using fuel rank and fire rotation were unable to predict which structures were burned by fire (Fig. 7). This poor performance of the statewide maps was also evident through visual comparison with maps of actual property loss (Figs. 5 and 6). Similarly, property loss was not substantially higher in the highest hazard or communities-at-risk areas of the statewide maps. In most cases, property loss was evenly divided among hazard levels (Fig. 8A and 8B), and even where a substantial proportion of burned structures were located in areas mapped as high fire hazard, most of the unaffected structures were also distributed in these high-hazard areas, suggesting high commission error (Fig. 8C and 8D). The most worrisome finding was that the majority of property loss occurred in areas not designated as at-risk (Fig. 8E and 8F).

The results of all sensitivity analyses indicated that the results were robust: the importance and ranking of variables remained essentially the same for all data sets at different buffer distances and certainty classifications (Table 3). Differences in results were slightly larger using different buffer distances than using all burned structures across a range of certainty levels versus all destroyed structures classified at the highest level of certainty. The main difference between the 200 and 100-m buffer analysis was that housing density was somewhat less important while distance to nearest housing cluster and southwestness were somewhat more important using the 200-m buffer in the Santa Monica Mountains. In San Diego County, housing dispersion and distance to the edge of housing cluster were somewhat more important using the 200-m buffer. We also found no substantial difference in results for the Maxent models.

After adding a spatial term, spatial autocorrelation was no longer present in the residuals of any of the models (Table 2). Also, although there were small differences in the coefficients between spatial and non-spatial models, the direction of influence consistently remained the same. The only variables that were no longer significant after accounting for spatial autocorrelation included the CDF communities at risk map, the distance to the nearest housing cluster, southwestness, and road length for the Santa Monica Mountains, and southwestness for San Diego County.

## Discussion

Wildfire is a key process that interacts with all major components of the earth system, but fire frequency, extent, and/or severity are on the rise [1,2,21,22]. Residential losses to wildfire have also escalated despite enormous investments in wildland fuel manipulation, improvements in fire-safe codes and building regulations, and advanced fire suppression tactics. Therefore, our finding that housing arrangement and location were the most important contributors to property loss supports the notion that patterns of land use may be partly responsible for property loss in the wildland-urban interface [13].

One reason that property loss is related to the arrangement of housing across the landscape may be that the amount and arrangement of human infrastructure also strongly and non-linearly influence wildfire ignitions and frequency [7,23,24]. Therefore, the places where homes are most likely to burn may also be the places where fires are most likely occur, which is partly a function of the distribution of people. Thus, there may be spatial interactions and feedbacks between fire and housing patterns.

In southern California, as in many regions, humans cause most fires [7,23–25]. Thus, population growth and housing development increase fire frequency. Yet, although urban expansion increases fire frequency in general, the highest hazard tends to be in low-density housing areas, where structures are interspersed with wildland vegetation [9]. Scattered, isolated structures are more difficult for firefighters to defend, and poor firefighter access may explain why housing clusters with fewer roads were more vulnerable in San

**Table 2.** Model coefficients for generalized linear models (GLMs) estimated with and without autocovariate terms in the Santa Monica Mountains and San Diego County.

| | *Linear* | *Autocovariate linear* | *Quadratic* | *Autocovariate quadratic* | *P-value* |
|---|---|---|---|---|---|
| *Santa Monica Mountains* | | | | | |
| Fire frequency 2001 | 0.860 | 0.440 | | | <0.001 |
| Distance coast | 0.004 | 0.002 | −7.0E-07 | −4.0E-07 | <0.001 |
| CDF Fire threat | 5.900 | 2.880 | −8.5E-01 | −3.9E-01 | <0.001 |
| CDF Fire threat people | 3.070 | 1.540 | | | <0.01 |
| CDF Communities risk | −0.540 | −0.280 | | | NS |
| Housing density | 1.010 | 1.130 | −3.9E-01 | −4.0E-01 | <0.001 |
| Distance housing cluster | 0.006 | 0.004 | −1.0E-05 | −7.0E-06 | NS |
| Housing dispersion | 2.280 | 2.670 | | | <0.001 |
| Distance structure | 0.020 | 0.020 | −3.0E-05 | −2.0E-05 | <0.001 |
| Distance edge | −0.021 | −0.017 | | | <0.001 |
| Area housing cluster | −2.0E-07 | −8.0E-08 | | | <0.001 |
| Slope | 0.033 | 0.016 | | | <0.001 |
| Elevation | −0.001 | −0.001 | | | 0.01 |
| Southwestness | −0.002 | 0.002 | | | NS |
| Road length | −2.0E-05 | −2.0E-05 | | | NS |
| *San Diego County* | | | | | |
| Fire frequency 2001 | 1.53 | 1.05 | −0.33 | −0.22 | <0.001 |
| Distance to coast | 3.0E-04 | 3.0E-09 | 2.0E-04 | 2.0E-09 | <0.001 |
| CDF Fire threat | −0.54 | −0.68 | 0.189 | 0.17 | <0.001 |
| CDF Fire threat people | 2.27 | 1.69 | | | <0.001 |
| CDF Communities risk | −0.93 | −0.51 | | | <0.001 |
| Housing density | −0.99 | −0.47 | | | <0.001 |
| Distance housing cluster | 0.005 | 0.004 | −4.0E-06 | −1.0E-06 | <0.001 |
| Housing dispersion | −3.08 | −1.68 | 0.865 | 0.542 | <0.001 |
| Distance structure | 0.007 | 0.004 | −5.0E-06 | −2.0E-06 | <0.001 |
| Distance edge | −0.02 | −0.01 | | | <0.001 |
| Area of housing cluster | −2.0E-08 | −7.0E-09 | | | <0.001 |
| Slope | 0.17 | 0.12 | | | <0.001 |
| Elevation | 0.001 | 0.003 | | | <0.001 |
| Southwestness | −0.005 | −0.003 | | | NS |
| Road length | −1.0E-06 | −7.0E-07 | | | <0.001 |

Quadratic terms were evaluated for all models, and coefficients are only provided for those models in which the quadratic term was significant in the non-spatial model.
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Diego County. However, there can also be situations in which high housing density contributes to structure-to-structure fire spread e.g., [26], depending on their flammability [27].

The importance of a structure's location on the landscape relative to the coast and historical patterns of fire frequency shows that certain places are more fire-prone than others, which in turn reflects how biophysical and human variables together create conditions that are particularly conducive to wildfire occurrence [2]. In our study areas, these relationships are also likely a function of a structure's location relative to predominant wind patterns and direction [28]. In the Santa Monica Mountains, certain fire corridors tend to burn repeatedly, and winds funnel down these corridors toward vulnerable structures located directly in their path. Here, the high-density coastal strip is narrow, and homes are closer to continuous vegetation than in San Diego County, where high-density development extends inland for much greater distances. This may be why houses were more likely to burn at a closer distance to the coast in the Santa Monica Mountains than in San Diego County. The low-density, high-risk areas in San Diego County are located farther inland where, if an ignition occurs there under extreme wind conditions, the fire is in its initial stages. Santa Ana winds blow from west toward the coast, and they are particularly dangerous in the beginning because they are usually most explosive and fast-moving right after they start, and it takes time to mobilize firefighting resources. Thus, the significance of distance to coast may be a proxy for other variables, such as the juxtaposition of housing density, contiguous fuels, and location relative to predominant wind patterns.

The importance of historical fire frequency suggests that, at least in non-forested ecosystems, fuel age may not be an important predictor of home loss [25], despite the fact that fuel age and time-since-fire maps are often used to delineate fire hazard. In fact, substantial property loss occurred when the primary surrounding fuel type was low fuel-volume grasslands. Although this result may seem counter-

**Table 3.** Percent deviance explained in generalized additive models (GAMs) for structures that were destroyed or damaged (Burned) and destroyed with the highest certainty (Destroyed); and for burned structures analyzed using a 200 m buffer distance (200 m).

| | *Burned* | *Destroyed* | *200 m* | *Relationship* |
|---|---|---|---|---|
| *Santa Monica Mountains* | | | | |
| Fire frequency 2001 | 35.59 | 31.63 | NA | Positive |
| Distance coast | 24.86 | 22.85 | NA | Intermediate |
| CDF fire threat | 6.23 | 4.37 | NA | Intermediate |
| CDF fire threat people | 5.69 | 5.01 | NA | Positive |
| CDF Communities at risk | 0.42 | 0.81 | NA | Negative |
| Housing density | 36.68 | 33.19 | 14.04 | Intermediate |
| Distance housing cluster | 1.08 | 1.46 | 14.23 | Intermediate |
| Housing dispersion | 3.18 | 2.23 | 4.24 | Positive |
| Distance structure | 1.85 | 2.17 | NA | Intermediate |
| Distance edge | 24.92 | 33 | 16 | Negative |
| Area of housing cluster | 13.47 | 12.88 | 18.06 | Negative |
| Surrounding fuel type | 4.3 | 3.18 | NA | NA |
| Slope | 19.66 | 17.79 | 18.31 | Positive |
| Elevation | 2.04 | 0.78 | 1.62 | Negative |
| Southwestness | 7.93 | 8.91 | 16.1 | NA |
| Road length | 11.4 | 11.2 | 13.98 | Negative |
| San Diego County | | | | |
| Fire frequency 2001 | 10.2 | 10.6 | NA | Intermediate |
| Distance coast | 30.0 | 28.19 | NA | Intermediate |
| CDF fire threat | 21.8 | 20.4 | NA | Intermediate |
| CDF fire threat to people | 23.9 | 24.1 | NA | Positive |
| CDF Communities at risk | 0.0 | 0.02 | NA | Negative |
| Housing density | 31.0 | 28.16 | 21.59 | Negative |
| Distance housing cluster | 3.2 | 2.92 | 0.97 | Intermediate |
| Housing dispersion | 3.3 | 2.85 | 8.62 | Parabolic |
| Distance structure | 18.7 | 15.73 | NA | Intermediate |
| Distance edge | 30.5 | 28.74 | 54.76 | Negative |
| Area of housing cluster | 20.1 | 16.41 | 10.63 | Negative |
| Surrounding fuel type | 6.5 | 4.90 | NA | NA |
| Slope | 11.4 | 13.94 | 10.61 | Positive |
| Elevation | 16.6 | 25.5 | 19.75 | Positive |
| Southwestness | 7.3 | 6.98 | 4.17 | NA |
| Road length | 20.9 | 19.6 | 15.4 | Negative |

The buffer distance used in all other analysis was 100 m. Relationship describes the shape of the response curve for all models. Ïntermediate signifies a nonlinear relationship in which values were highest at intermediate levels of the variable. Values listed as NA in 200 m were for variables that were only analyzed at the level of the individual house.

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intuitive, herbaceous fuels tend to have low fuel moisture, facilitate high wind speeds and fire spread, and have low heat requirements for ignition, thus promoting longer fire seasons and high fire frequency [29,30]. Grasslands also tend to ignite quickly, then carry fires into shrublands or woodlands [31]. These results suggest a need to reexamine the assumptions used in existing hazard maps and the management practice of converting shrublands to grasslands.

Fire hazard in the CDF statewide maps, as with most hazard maps [17–19,32], depends largely on the assumption that fuel properties are the primary contributors to fire danger. However, our empirical data indicate that, at least at the local scale considered here, fuel was not as significant as measurable factors related to the arrangement and location of structures. This is likely because the influence of fuel is complex and interacts with other risk factors [33]. Therefore, our empirical maps developed using a more comprehensive set of predictor variables, including fuel type, housing arrangement and location, and other environmental variables, performed better in distinguishing hazardous from non-hazardous areas.

Another reason for the discrepancy in map performance may be related to differences in mapping approach: while our approach used empirical data on actual structure loss, the statewide maps were developed based on a priori assumptions of where hazard is expected to be highest. At larger scales, such as the state level, the CDF fuel-based maps would likely perform better at picking out where homes are most vulnerable to fires. We also did not evaluate the CDF maps developed for local responsibility areas, which may better capture finer-scale patterns of hazard in local jurisdictions.

The fact that unburned structures in our analysis were more likely to be located in ''communities at risk,'' whereas burned structures were more likely to be located outside of high-risk areas is potentially due to two reasons. At the most basic level, this may simply be caused by an incorrect identification of communities at risk. However, we caution that the discrepancy may also be due to scale effects and the definition of ''community at risk.'' At a broad scale, ''communities at risk'' are likely located within areas that generally have the potential for hazardous fires, and places with more houses in such a danger zone are more likely to be identified as a ''community at risk.'' However, at the structure level, low-housing density significantly increases the chance a house will burn – while it decreases the likelihood that at home will be included in a ''community at risk.'' In summary, our results support the notion that property loss is a function of many physical and biological factors, in addition to characteristics of home construction and maintenance that we did not consider, such as roofing, construction materials, and home landscaping.

The effects of housing arrangement and location on the likelihood that a house will be destroyed or damaged by wildfire suggest that land use planning may be a critical tool for reducing fire hazard. Restricting development from hazardous locations has been effective for other hazards, such as flooding and the prevention of building on floodplains [34]. In the case of fire, new structures should be located and arranged in ways that not only minimize their exposure to hazard, but may also limit the increase in fire occurrence that often accompanies urban development. For example, our results suggest that in both study areas, new development would have a lower likelihood of burning if it were located away from fire-prone areas, such as wind corridors or steep slopes, and if new structures were arranged in intermediate-to high-density neighborhoods designed to minimize the amount of interface between homes and wildland vegetation. New development within large, existing urban areas, which typically also have better firefighter access, would also lower the likelihood of burning, compared to new development in more isolated, remote settings. Land use planning that considers minimizing future structure loss and prioritizing other fire prevention actions would be more informed with maps that reliably differentiate the most hazardous locations than with maps currently used for this purpose. Although the direction of influence was the same for most variables in the two study regions, the relative importance varied, and the distance from coast and elevation had opposite effects. This supports the notion that hazard is place-specific [35], and fire hazard mapping should therefore be individualized for specific landscapes.

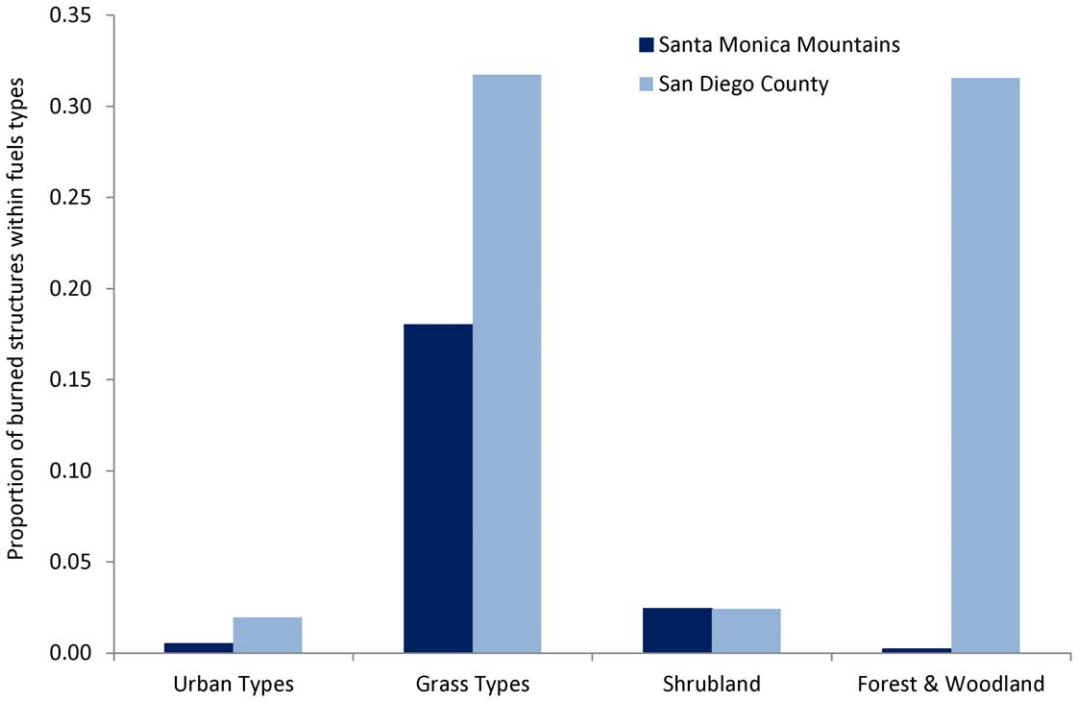


**Figure 4. Proportion of burned structures within broad fuels types in the Santa Monica Mountains and San Diego County.**
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## Materials and Methods

### Data and digitizing structures

We explained property loss by comparing structures that were burned (i.e., destroyed or damaged) by wildfires to those structures that were unaffected. The likelihood of a house burning in a fire has two major components: the first is the likelihood that there will be a fire, and the second is the likelihood that a structure will burn if there is a fire. That 'total' likelihood required us to include both structures inside and outside of fire perimeters in the model. We

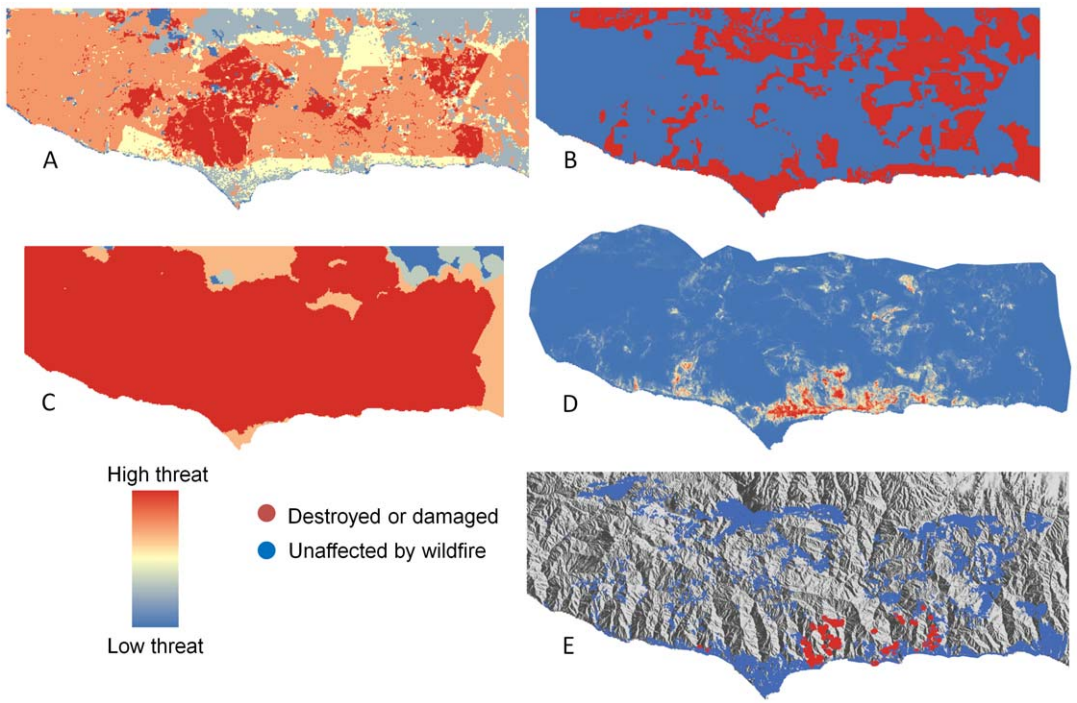


**Figure 5. Fire hazard maps versus actual burned structures in the Santa Monica Mountains.** (A) CDF "Fire threat" (B) CDF "Communities at risk" (C) CDF "Fire threat to people (D) Empirically based map showing probability of structure being burned by fire (E) Structures that were destroyed or damaged (red) and unaffected (blue) by wildfire from 2001–2010. CDF – California Department of Forestry and Fire Protection.
doi:10.1371/journal.pone.0033954.g005

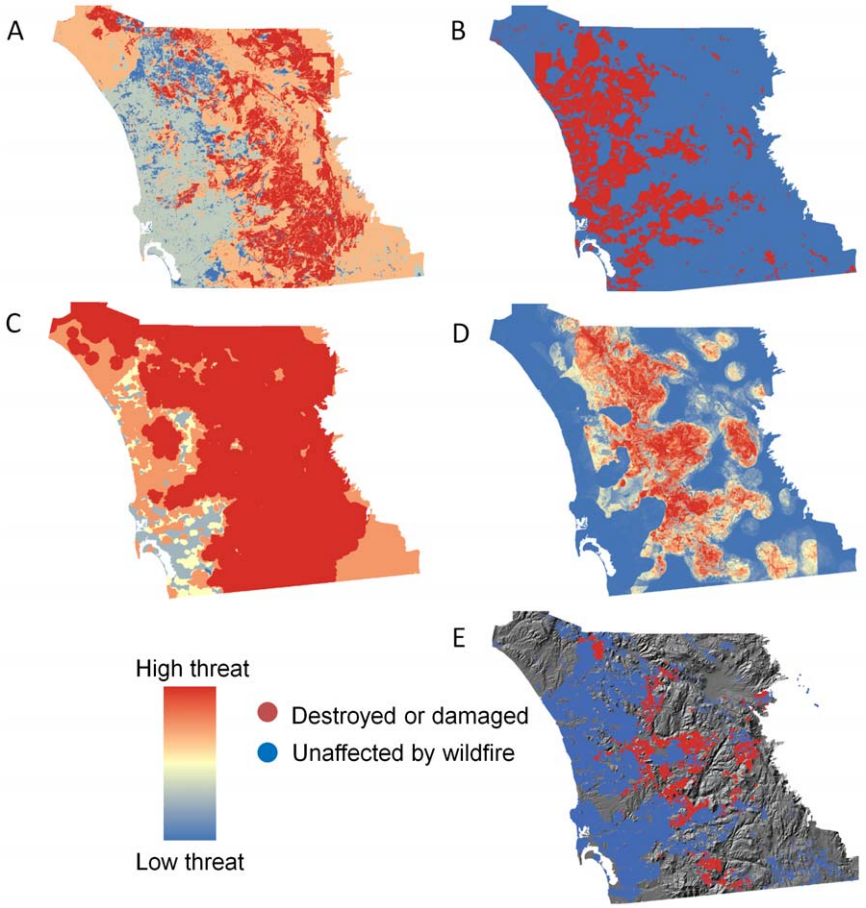


**Figure 6. Fire hazard maps versus actual burned structures in San Diego County.** (A) CDF "Fire threat" (B) CDF "Communities at risk" (C) CDF "Fire threat to people (D) Empirically based map showing probability of structure being burned by fire (E) Structures that were destroyed or damaged (red) and unaffected (blue) by wildfire from 2001–2010. CDF – California Department of Forestry and Fire Protection.
doi:10.1371/journal.pone.0033954.g006

also wanted to account for the full range of variation for the explanatory variables because planning decisions occur at a landscape scale, not just for a subset of structures within fire perimeters. Therefore, we digitized and analyzed all residential structures within the Santa Monica Mountains National Recreation Area in Ventura and Los Angeles counties, California as well as the portion of San Diego County that falls within the South Coast Ecoregion. Using onscreen digitizing, we carefully scanned the most recent aerial imagery available in Google Earth for each study area and placed a point over every visible structure. We digitized all structures, including homes, outbuildings, and guest houses, because we assumed that the factors explaining which homes burned were similar to those explaining the burning of other structures. Because most of the vegetation in our study areas is non-forested, there were very few occasions in which vegetation canopy obscured structures in the imagery. Structures were in all cases at least partly visible, even if they were covered by vegetation, and we looked at earlier images available in Google Earth to confirm where structures were located. The canopy cover was generally lower farther back in time.

Due to the large number of structures in San Diego County, many of which are located in high-density urban core areas, we used a parcel map to facilitate the digitizing process. For small parcels (area $<900$ m$^2$, equivalent to one $30\times30$ m pixel of the environmental data, see below), we placed the point representing the structure in the centroid of the polygon instead of digitizing the exact location of the structure within the parcel boundary. We assumed the location of the structure within the boundary of small parcels would not significantly alter the overall calculations of spatial pattern among structures. However, for large parcels, the location of the structure within the parcel boundary may be important because the parcel may include more than one pixel, and thus, the environmental data are associated with the structure may depend on structure location. Distance calculations to other structures could also be more substantially influenced by the location of structures in large parcels, which is why we analyzed the Google Earth imagery to place those structures accurately. We did not digitize houses under construction at the date the remote sensing imagery was recorded.

To identify burned structures, we developed an initial address list and spatial database of structures destroyed or damaged by fires from a variety of records, including official incident reports, county assessors' offices, public works departments, city records, and newspaper reports. Because these records were incomplete, we also used Google Earth imagery for a systematic visual analysis to correct geocoded locations and to identify additional structures that had not been documented. For this analysis, we identified burned structures by comparing pre-fire to post-fire images that are available in Google Earth. To develop a data set of houses to inspect for property loss, we selected all structures that fell within and up to 80 m outside any perimeter of a fire that occurred since 2001 in both study areas. We used 80 m because it is twice the distance beyond which flame fronts are not expected to ignite

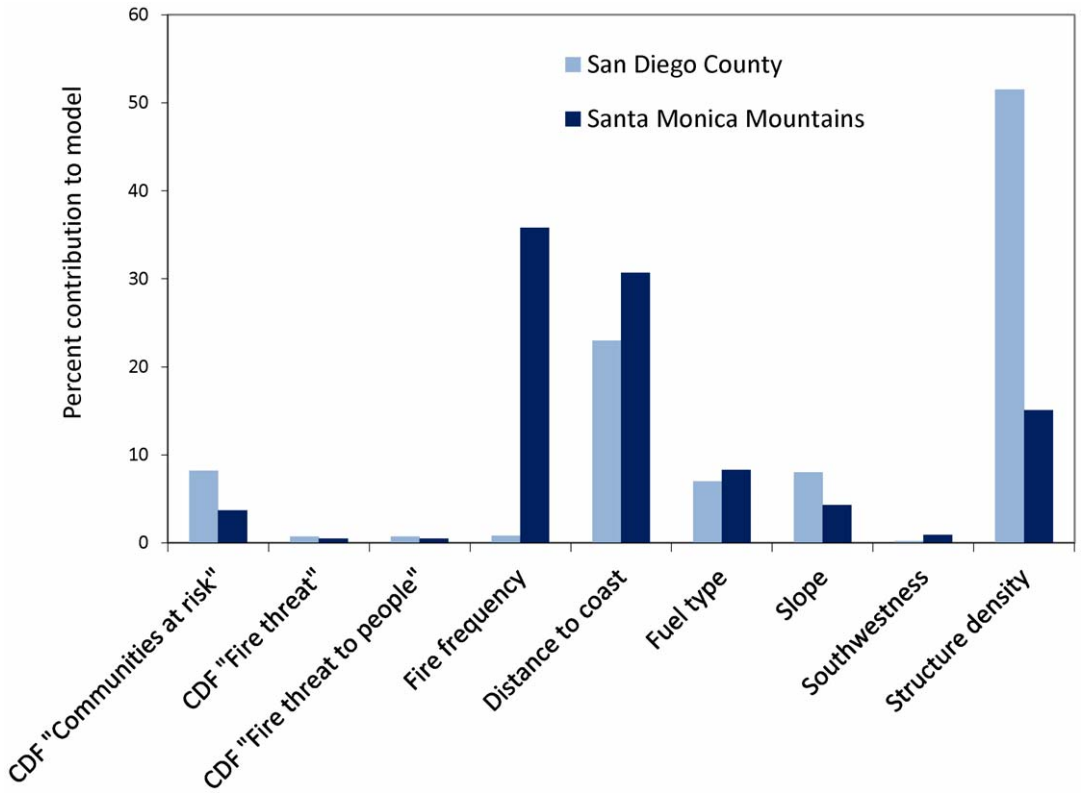


**Figure 7. The percent contribution of explanatory variables in Maxent empirical fire hazard model.** CDF – California Department of Forestry and Fire Protection.
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wood [36].The determination of destroyed or damaged structures was based on data collected from official records combined with visual inspection of imagery. Destroyed structures were those in which the house had completely burned to the ground, whereas damaged structures where those that had partially burned. Because damaged structures were more difficult to identify in the imagery, we ruled that if a fire had clearly burned into the property (i.e., if vegetation had visibly been burned), the structure was classified as damaged.

For both the destroyed and damaged structures, we assigned an estimate of certainty for the classification and conducted sensitivity analyses to test if results were similar for destroyed structures that were classified with the highest level of certainty versus a complete dataset with all destroyed and damaged homes at all certainty levels. In our classification, we indicated "1" for uncertain if the house was damaged or destroyed; "2" for fairly certain; "3" for absolutely certain. Since the results were similar (Table 3), we used the full dataset in our analyses to obtain the largest sample size. Although rare, if two buildings burned on a parcel, we only included one in our analysis. For those structures that burned in more than one fire, which only occurred in San Diego, we only used the data for the first fire to avoid double counting of structures in the spatial analysis.

## Explanatory variables

To fully explore the influence of housing arrangement and pattern, we analyzed both the spatial relationships among individual structure locations and the arrangement of structures within housing clusters. Housing clusters were defined as groups of houses with a maximum distance of 100 m from each house to any other house [24]. We calculated these housing clusters by creating a 100 m buffer around each structure and dissolving overlapping boundaries. Thus, areas with many homes within 100 m of each other constituted one large housing cluster, while smaller housing clusters contained fewer or more isolated homes. This allowed spatial analysis based on the spatial and biophysical properties of the structure locations as well as spatial and biophysical properties of the housing clusters within which structures were located. Thus, some variables were calculated for the housing cluster in which the structure was located and the values for that housing cluster were assigned back to the structure. Other variables were calculated only for the location in which the structure was located.

Because our objective was to better understand the landscape factors that significantly contribute to the likelihood that a house will burn in a wildfire, particularly focusing on those factors that are relevant to land use planning, we only assessed variables affecting exposure of structures to wildfires (i.e., fires spreading into the property and reaching the structure, or embers landing on a structure). We did not consider factors such as urban landscaping or housing construction materials within the home ignition zone that determine whether the house survived the exposure. To evaluate the influence of housing arrangement and location on susceptibility to wildfire, we considered a suite of variables representing different spatial configurations and locations of structures as well as additional environmental variables that may affect property loss due to their potential control over fire spread behavior, fuel moisture, or flammability [23,37] (Table 1).

**Housing arrangement variables.** We evaluated the area of the housing cluster to test the hypothesis that small, isolated groups of structures are more susceptible to wildfire than large groups of structures. Housing density was calculated as the number of structures divided by the area of the housing cluster. For every

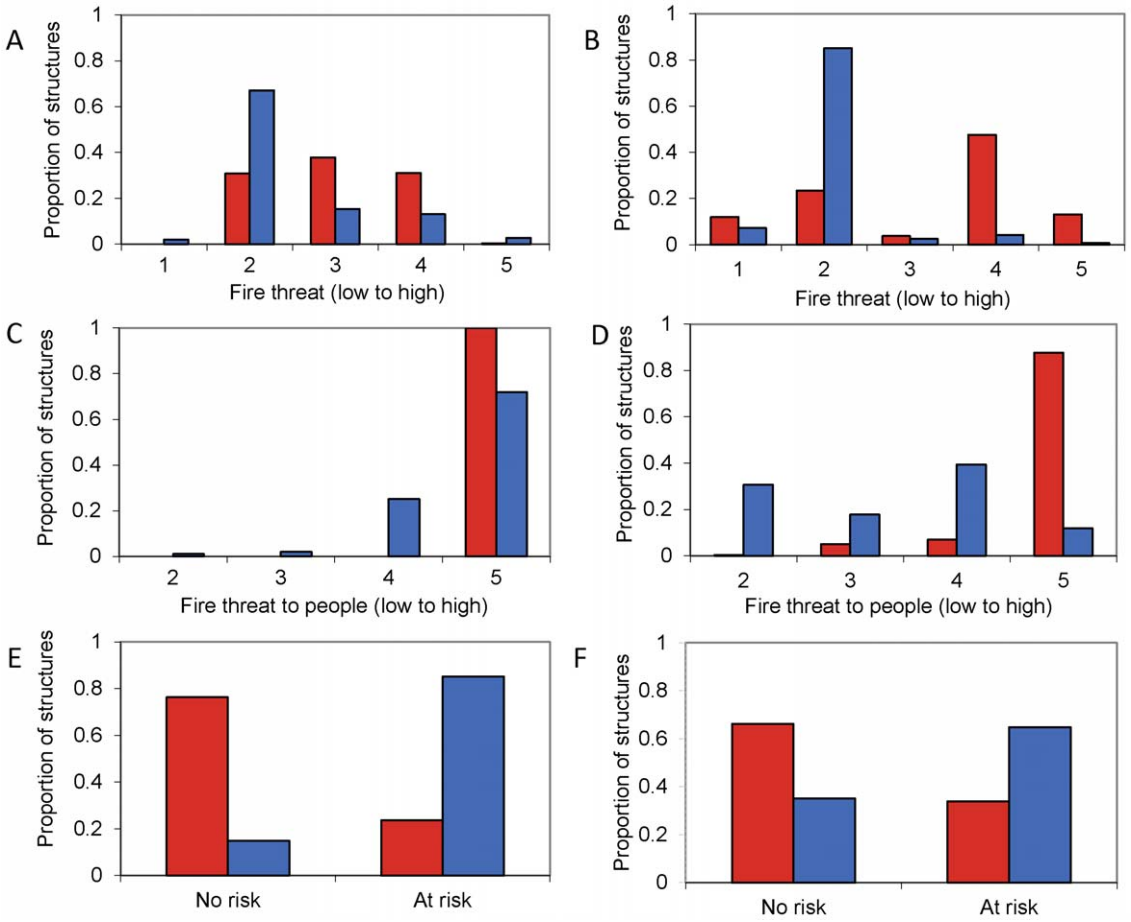


**Figure 8. Distribution of actual burned structures in classes of statewide fire hazard maps.** Proportion of structures burned (in red) or unaffected (in blue) distributed within map classes of: (A) CDF "Fire threat" in Santa Monica Mountains. (B) CDF "Fire threa" in San Diego County. (C) CDF "Fire threat to people" in Santa Monica Mountains (D) CDF "Fire threat to people" in San Diego County (E) CDF "Communities at risk" in Santa Monica Mountains (F) CDF "Communities at risk" in San Diego County. CDF – California Department of Forestry and Fire Protection.
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structure, we calculated the distance to the edge of the housing cluster to evaluate whether structures in the interior of housing clusters were less susceptible to wildfire than structures at the edge. To assess local spatial patterns, we calculated the distance from each structure to its nearest neighbor, and for overall landscape configuration of structures, we calculated the distance from each housing cluster to the next nearest housing cluster. Finally, we calculated the coefficient of variation, or, the standard deviation of distance among structures in a housing cluster divided by the mean to assess housing dispersion, or, regularity of housing pattern.

**Housing location variables.** To test whether structures located in fire-prone parts of the landscape were more likely to be burned, we overlaid fire perimeter polygons compiled by the California Department of Forestry (CDF)-Fire and Resource Assessment Program and created a continuous raster map representing the number of times an area had burned from the beginning of record-keeping, 1878, until 2001. We did not include any fires that occurred after 2001 to ensure that our count of fire frequency was independent of those fires that burned the structures in our analysis. We calculated the distance from the coast for every structure as another way to test whether a structure's location influences its likelihood to be burned. In southern California, a number of variables that influence fire patterns, including climate, terrain, and vegetation distribution, are correlated with the distance to the coast. Distance to the coast is also correlated with housing patterns, and may influence how a house is arranged relative to the major wind corridors in the region [38]. Although the inclusion of weather data at the time of fires would be more directly related to fire behavior and danger, the high variability of weather over space and time limits the ability to relate specific weather data to the place and time that fires burn structures. First, we did not know the exact time that fires burned structures, and thus could not retrieve the temporally matching weather data. Second, weather stations are generally located too far away from where fires burned homes to reflect local variability in weather conditions.

**Biophysical variables.** Terrain-derived variables included the average elevation and percent slope of the housing cluster as well as a cosine-transformation of aspect to create an index of 'southwestness,' which could account for the influence of solar radiation and aspect on fuel properties and fire behavior. For each structure, we also determined fuel type in the surrounding by identifying the most common fuel model within a 1 km buffer of the structure. This buffer allowed us to identify the vegetation types fires spread through before reaching the property. Our objective for this analysis was to determine which broad-based fuel classes were most closely associated with structure loss. If more than one fuel type occurred in the buffer, we used the fuel type present in the majority of the area. We obtained spatial fuel model

data, developed for fire behavior modeling, from statewide maps developed by the U.S. Forest Service (N. Amboy) at 30 m resolution. The fuel models provided in the USFS maps were created through remote sensing and classified according to Scott and Burgan [39]. From this map, we grouped together the fuel models from broad fuel types (representing grassland, shrubland, and timber). We also grouped agriculture, barren land, and urban land into one type representing mostly urban landscaping and impervious surface (i.e., with little wildland vegetation).

**Firefighter access.** As a way of indirectly assessing firefighter access to the structure, we calculated the length of road within each housing cluster using the 2000 US Topologically Integrated Geographic Encoding and Referencing system TIGER/line files from the US Census.

## Statewide fire hazard maps

Statewide fire hazard maps were available online from the California Department of Forestry and Fire Protection (CDF) [20].We downloaded the Wildland Urban Interface (WUI) "fire threat" data product that includes a series of maps that rank the wildland fire threat to human development. The term "fire threat" in these maps is used analogously to the way we use the term fire "hazard" or, a phenomenon or place where harm is likely to occur.

The "fire threat" map is based on the hazard ranking of different fuels types combined with the fire rotation period, or, the average area burned during the period of record for different vegetation types. Fuels types with higher fuel loads and vegetation types that burned most frequently were considered most hazardous. The "fire threat to people" map is based on a cost-distance calculation that estimates distances from areas of high fire hazard. As an example, the highest "fire threat to people" is calculated as a maximum of 2400 m from "extreme threat" in the fire threat map. Finally, the "communities at risk" map depicts U.S. Census communities with more than 1 house per 8.09 ha (20 acres) that are located in areas with "high fire threat to people."

The CDF provides additional fire hazard severity maps developed separately for state and local responsibility areas. The finer-scale maps for local responsibility areas, which include incorporated cities, cultivated agricultural lands, and portions of the desert, are limited in extent and only overlap a small portion of our study areas. Due to the limited extent of the local responsibility area maps, and the fact that the state responsibility maps were still being refined, we did include these in our analysis. Their proposed modeling approach will be based upon the existing fire threat and communities at risk maps and will be refined to include additional methods that characterize brand production from vegetative fuels.

To evaluate how well the CDF statewide fire hazard maps corresponded to actual burned structures, we included the three maps as predictor variables in our statistical analyses and quantified the distribution of burned and unaffected structures within the different classes of each map.

## Analysis

To identify the variables that best explain property loss and to estimate the relative contribution of each variable, we developed generalized additive models (GAMs) using a binary response (i.e., house burned or unaffected by fire) and logit link. We used three target degrees of freedom for smoothing splines for our continuous explanatory variables. Because we wanted to compare the independent relative variance explained for all explanatory variables, we estimated separate regression models for each variable. However, we also calculated the correlation coefficients among all variables and developed multiple-regression models with non-correlated variables for each study area. We used a stepwise selection procedure, entering variables according to amount of deviance explained and exploring both forward and backwards directions. We used AIC as the selection criterion for variable selection. To develop the models, we split the data for training and testing (withholding 20% of the data for testing) so we could calculate the area under the curve (AUC) of receiver operating characteristic (ROC) plots on an independent dataset to quantify model performance.

We used GAMs because prior studies reported nonlinear relationships between fire patterns and many of our predictor variables [7,23,24]. Unlike parametric statistical methods, such as generalized linear models (GLMs), in which nonlinear relationships are specified *a priori* (e.g., through polynomial terms) in the model, GAMs allow the structure of the data to determine the shape of the response curves. Thus, GAMs provide a more flexible and automated approach for identifying and describing nonlinear relationships [40,41]. We used the GAMs to estimate the shape of response curves and to calculate deviance explained ($D^2$, analogous to R-squared in linear regression) for all explanatory variables.

Although non-parametric methods, such as GAMs, tend to be less sensitive to the effects of spatial autocorrelation than other model approaches [42], we wanted to ensure that spatial autocorrelation did not significantly influence the results of our analysis. The main concerns about spatial autocorrelation in regression models are inflated significance values and biased coefficients [42,43]. GAMs do not estimate regression coefficients, which are replaced with smoothing functions. This is why we also fit GLMs to our data because they are parametric models similar to GAMs, but they estimate coefficients. Therefore, the GLMs allowed us tocheck the influence of autocorrelation on both coefficients and the significance of variables. The GLMs also allowed us to test whether our results were robust by comparing two modeling methods. We first developed non-spatial GLMs, and fit linear and quadratic terms for all variables (except for fuel type, which was categorical). After detecting residual autocorrelation in these nonspatial models using Moran's I [43], we calculated an autocovariate term to account for the influence of neighboring values on predictions, and included as the term as an additional explanatory variable in models. To calculate the autocovariate term, we specified a neighborhood radius of 1, which finds the minimum distance for which all observations (i.e., structure locations) are linked to at least one neighbor. The influence of structures located within any neighborhood radius was weighted by inverse distance. . After fitting these autocovariate models, we used Moran's I to recheck for spatial autocorrelation of model residuals, compared the coefficients to the nonspatial models, and checked variable significance after incorporating the autocovariate term..All model fitting and evaluation were accomplished using the gam, spdep, vegan, and ROCR packages for R [44].

## Empirical fire mapping

To develop empirical fire hazard models and maps, we selected Maxent [45], a machine-learning method that is best recognized for creating species distribution models and maps. We selected Maxent because it outperforms other presence-only and presence-background species distribution modeling methods [41] and has been applied successfully to map the distribution of fire [46]. Maxent assumes that the best approximation of an unknown distribution (e.g., fire hazard) is the one with maximum entropy. The model iteratively evaluates contrasts between values of explanatory variables at locations of the response variable (i.e.,

burned structures) and for averages of the explanatory variables across the entire study area. The output is an exponential function that assigns a hazard probability (i.e., probability of structure being burned) to each site or cell of a map. In the output map, areas of predicted high risk that do not have structures on them represent environmental conditions similar to those in which structures have actually burned.

Because mapped predictor variables were required for the modeling, so that conditions similar to those where structures were burned could be delineated continuously across the landscape, we created maps representing a subset of the variables that we explored with the regression analysis. These variables represented a combination of structure arrangement, location, and biophysical variables, including: interpolated structure density, distance to coast, fuel type, slope, historical fire frequency, and southwestness. We developed models that included CDF fire hazard maps as predictors to test their importance relative to the other predictor variables. However, for generating maps and quantifying model performance, we only used models that did not include CDF predictor variables.

### Sensitivity tests

The results of our analysis may have been affected by the size of the buffer that we used around structures to create housing clusters, the degree of impact of fire on the structure (i.e., destroyed or damaged), and certainty of the classification (i.e., 1–3). Therefore, to evaluate how sensitive our results were to these variables, we created housing clusters around structures using a 200 m buffer and compared the regression results for which housing cluster was relevant in the to those obtained when using a 100 m buffer. We also performed separate regressions using only those structures that had been destroyed with complete certainty (a "3") and compared those to the regressions of all burned structures at all certainty levels. For the Maxent analysis, we also compared models using only structures that were destroyed with the highest level of certainty to models using all burned structures at all certainty levels.

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## Author Contributions

Conceived and designed the experiments: ADS JEK ABM TJB VCR. Performed the experiments: ADS ABM TJB. Analyzed the data: ADS JEK ABM. Wrote the paper: ADS JEK ABM TJB VCR.

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# Land Use Planning and Wildfire: Development Policies Influence Future Probability of Housing Loss

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## Abstract

Increasing numbers of homes are being destroyed by wildfire in the wildland-urban interface. With projections of climate change and housing growth potentially exacerbating the threat of wildfire to homes and property, effective fire-risk reduction alternatives are needed as part of a comprehensive fire management plan. Land use planning represents a shift in traditional thinking from trying to eliminate wildfires, or even increasing resilience to them, toward avoiding exposure to them through the informed placement of new residential structures. For land use planning to be effective, it needs to be based on solid understanding of where and how to locate and arrange new homes. We simulated three scenarios of future residential development and projected landscape-level wildfire risk to residential structures in a rapidly urbanizing, fire-prone region in southern California. We based all future development on an econometric subdivision model, but we varied the emphasis of subdivision decision-making based on three broad and common growth types: infill, expansion, and leapfrog. Simulation results showed that decision-making based on these growth types, when applied locally for subdivision of individual parcels, produced substantial landscape-level differences in pattern, location, and extent of development. These differences in development, in turn, affected the area and proportion of structures at risk from burning in wildfires. Scenarios with lower housing density and larger numbers of small, isolated clusters of development, i.e., resulting from leapfrog development, were generally predicted to have the highest predicted fire risk to the largest proportion of structures in the study area, and infill development was predicted to have the lowest risk. These results suggest that land use planning should be considered an important component to fire risk management and that consistently applied policies based on residential pattern may provide substantial benefits for future risk reduction.

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## Introduction

The recognition that homes are vulnerable to wildfire in the wildland-urban interface (WUI) has been established for decades [e.g., 1,2]; but with a recent surge in structures burning, this issue is now receiving widespread attention in policy, the media, and the scientific literature. Single fire events, like those in Greece, Australia, southern California, and Colorado have resulted in scores of lost lives, thousands of structures burned, and billions of dollars in expenditures [3–6]. With the potential for increasingly severe fire conditions under climate change [7] and projections of continued housing development [8], it is becoming clear that more effective fire-risk reduction solutions are needed. "Fire risk" here refers to the probability of a structure burning in a wildfire within a given time period.

Traditional fire-risk reduction focuses heavily on fire suppression and manipulation of wildland vegetation to reduce hazardous fuels [9]. Enormous resources are invested in vegetation management [10], but as increasing numbers of homes burn down despite this massive investment, the "business-as-usual" approach to fire management is undergoing reevaluation. One issue is that fuel treatments may not be located in the most strategic positions, i.e., in the wildland-urban interface [11]. Yet, even if treatments surrounded all communities, scattered development patterns are difficult for firefighters to reach [12–14], and fuel treatments do little to protect homes without firefighter access [15–16]. Fuel treatments may also be ineffective against embers or flaming materials that blow ahead of the fire front [17].

One alternative to traditional fire management that is receiving widespread attention is to prepare communities through the use of fire-safe building materials or creating defensible space around structures [17–18]. These actions represent an important shift in emphasis from trying to prevent wildfires in fire-prone areas to better anticipating fires that are ultimately inevitable. Nevertheless, the cost of building and retrofitting homes to be fire-safe can be prohibitive, and these actions do not guarantee immunity from fire [19].

Land use planning is an alternative that represents a further shift in thinking, beyond the preparation of communities to withstand an inevitable fire, to preventing new residential structures from being exposed to fire in the first place. The reason homes are vulnerable to fires at the wildland-urban interface is a function of its very definition: "where homes meet or intermingle with wildland vegetation" [20]. In other words, the location and

pattern of homes influence their fire risk, and past land-use decision-making has allowed homes to be constructed in highly flammable areas [21]. Land use planning for fire safety is beginning to receive some attention in the literature [22–23], and there is growing recognition of the potential benefits of directing development outside of the most hazardous locations [8,19,24].

Despite recent attention in the literature, land use planning for wildfire has yet to gain traction in practice, particularly in the United States. However, fire history has been used to help define land zoning for fire planning in Italy [22], and bushfire hazard maps are integrated into planning policy in Victoria, Australia [25]. Although some inertia inevitably arises from complications with existing policy and plans, a primary impediment to the design and implementation of fire-smart land use planning is lack of guidance about specific locations, patterns of development, or appropriate methodology to direct the placement of new development. Without a solid knowledge base to draw from, planners will be misinformed about which planning decisions may result in the greatest overall reduction of residential landscape risk. Even worse, poor science could result in placement of homes in areas that actually have high fire hazard.

Research on how planning decisions contributed to structures burning in the past provides some guidance about what actions may work in the future. Analysis of hundreds of homes that burned in southern California the last decade showed that housing arrangement and location strongly influence fire risk, particularly through housing density and spacing, location along the perimeter of development, slope, and fire history [26]. Although high-density structure-to-structure loss can occur [27–28], structures in areas with low- to intermediate- housing density were most likely to burn, potentially due to intermingling with wildland vegetation or difficulty of firefighter access. Fire frequency also tends to be highest at low to intermediate housing density, at least in regions where humans are the primary cause of ignitions [29–30].

These results suggest, for example, that placing new residential development within the boundaries of existing high-density developments or in areas of low relief may reduce fire risk. However, it is difficult to know whether broad-scale planning policies would actually result in the intended housing arrangement and pattern at the landscape scale, and whether those patterns would result in lower fire risk. Our objective here was to simulate three scenarios of future residential development, and to project wildfire risk, in a rapidly urbanizing and fire-prone region where we have studied past structure loss [25]. We based all future development on an econometric subdivision model, but we varied the emphasis of subdivision decision-making based on three broad and common growth types.

Although cities vary in extent, fragmentation, and residential density [31–32], urban form typically adheres to a set of common patterns [33–34], and we based our development scenarios on the three primary means by which residential development typically occurs: infill, expansion, or leapfrog [34]. Infill is characterized by development of vacant land surrounded by existing development, typically in built-up areas where public facilities already exist. [35–36], and should result in higher structure density rather than increased urban extent. Expansion growth occurs along the edge of existing development, extends the size of the urban patch to which it is adjacent, and may have variable influence on structure density. Leapfrog growth occurs when development occurs beyond existing urban areas such that the new structure is surrounded by undeveloped land. This type of growth would expand the urban extent and initially result in lower structure density; but these areas may eventually become centers of growth from which infill or expansion can occur. We asked:

1) Do residential development policies reflecting broad growth types affect the resulting pattern and footprint of development across the landscape?
2) Do differences in extent, location, and pattern of residential development translate into differences in wildfire risk, based on the current configuration of structures?
3) Which development process, infill, expansion, or leapfrog, results in the lowest projected fire risk across the landscape?

## Methods

### Study Area

The study area included all land within the South Coast Ecoregion of San Diego County, California, US, encompassing an area of 8312 $km^2$. The region is topographically diverse with high levels of biodiversity, and urban development has been the primary cause of natural habitat loss and species extinction [37]. Owing to the Mediterranean climate, with mild, wet winters and long summer droughts, the native shrublands dominating the landscape are extremely fire-prone. San Diego County was the site of major wildfire losses in 2003 and 2007 [38], although large wildfire events have occurred in the county since record-keeping began, and are expected to continue, as fire frequency has steadily increased in recent decades [29,39]. The county is home to more than three million residents, and approximately one million more people are expected by 2030 [40]. Although most residential development has been concentrated along the coast, expansion of housing is expected in the eastern, unincorporated part of the county.

### Econometric Subdivision Model

A host of alternative modeling approaches exist to simulate future land use scenarios [41], including a cellular automaton model that we previously applied to the study area [42]. We chose to use an econometric modelling approach for this study because we wanted to capture fine-scale, structure-level patterns and processes that are correlated with housing loss to wildfire [26]; and econometric models may perform better at the scale of individual parcels [43].

Although we based the three development scenarios on generalized planning policies, we also wanted to ensure that the residential projections were realistic and adhered to current planning regulations. The objective of the econometric modeling was to estimate the likelihood that residential parcels will subdivide in the future. Therefore, we used a probit model to estimate the transition probability of each parcel based on a range of potential explanatory variables typically associated with parcel subdivision and housing development [44–45].

To develop the model of subdivision probability, we acquired GIS data of the county's parcel boundaries in years 2005 and 2009 from the San Diego Association of Governments (SANDAG). The dependent variable was equal to 1 if a parcel subdivided between 2005 and 2009, and zero otherwise. Using these data layers we first determined which parcels were legally able to subdivide given current land use regulations. Minimum lot size restrictions are typically considered the most import restriction for determining future land use. We deemed a parcel eligible for subdivision if the current lot size was greater than twice the minimum legal size given the land class. To determine which parcels subdivided between 2005 and 2009, we queried parcel IDs where the total

area was reduced by at least the minimum lot size between the two time periods. Finally, we were able to generate a suite of variables that determine the likelihood of a parcel developing in the future (Table S1).

We overlaid the parcel boundaries over a range of GIS layers representing our explanatory variables. These data are available to download at (http://www.sandag.org/index.asp?subclassid = 100&fuseaction = home.subclasshome). Our explanatory variables included: parcel size, parcel size squared, six dummy variables which capture non-linear effects of parcel size, distance to the coast, distance to the coast squared; distance to city center and its square, current zoning, slope, land use, roads, if the parcel is in a protected area, if the parcel is in a development area, if the parcel is in the redevelopment area (Table 1).

## Spatial Model of Future Development under Planning Alternatives

The outcome of the land use change econometric model is the subdivision probability for each parcel for a five-year time step. Based on these probabilities, we developed a GIS spatial simulation model of future land use under three distinct planning scenarios: infill (development in open or low density parcels within already developed areas), expansion (development on the fringe of developed areas), and leapfrog (development in open areas). The model runs in four 5-year time steps from 2010 to 2030, and generates the spatial locations of new housing units in the county.

Although development decisions could feasibly depend on fire risk, we did not model that here. There is no evidence that fire has influenced past regional planning decisions, so it was not used as an explanatory variable in the econometric model. Although we could have evaluated the potential for future development decisions to be based in part on fire risk, this would have required simulation of feedbacks between fires and probability of development. Because our objective in this study was to isolate the effects of the three distinct growth types, we modeled fire risk only as a function of development pattern and not vice versa.

We constructed a complete spatial database of existing residential structures in the study area [26]. These structures and their corresponding parcel boundaries served as the initial conditions for all three scenarios of the spatial simulation model. The current and projected future GIS layers of structures were also subsequently used in the fire risk model (see below). The

**Table 1.** Variables and results from the probit regression model of parcel subdivision in San Diego County.

| Subdivided (1 = yes,0 = no) | Coefficient | Std. Err. | z | P>\|z\| | [95% Conf. Interval] | |
|---|---|---|---|---|---|---|
| **Acres of lot** | 0.0026342 | 0.00075 | 3.51 | 0 | 0.001164 | 0.004105 |
| **Acres of lot $^2$** | −3.02E-06 | 1.29E-06 | −2.34 | 0.019 | −5.55E-06 | −4.93E-07 |
| **Distance to ocean** | −7.42E-06 | 1.33E-06 | −5.59 | 0 | −0.00001 | −4.82E-06 |
| **Distance to ocean $^2$** | 2.33E-11 | 8.28E-12 | 2.82 | 0.005 | 7.11E-12 | 3.96E-11 |
| **Distance to major road** | 2.17E-07 | 2.74E-06 | 0.08 | 0.937 | −5.16E-06 | 5.59E-06 |
| **Distance to major road $^2$** | −1.94E-11 | 1.70E-11 | −1.14 | 0.252 | −5.27E-11 | 1.38E-11 |
| **Distance to nearest city center** | −0.0000115 | 1.70E-06 | −6.76 | 0 | −1.5E-05 | −8.16E-06 |
| **Distance to nearest city center $^2$** | 2.89E-11 | 9.70E-12 | 2.98 | 0.003 | 9.91E-12 | 4.79E-11 |
| **Slope between 0–5%** | 0.6211289 | 0.211761 | 2.93 | 0.003 | 0.206085 | 1.036173 |
| **Slope between 5–10%** | 0.3911427 | 0.210684 | 1.86 | 0.063 | −0.02179 | 0.804076 |
| **Slope between 10–25%** | 0.0716669 | 0.212725 | 0.34 | 0.736 | −0.34527 | 0.4886 |
| **Rural Residential** | −0.3563149 | 0.071512 | −4.98 | 0 | −0.49648 | −0.21615 |
| **Single Family** | 0.1361149 | 0.068678 | 1.98 | 0.047 | 0.001509 | 0.270721 |
| **Multi-Family** | −0.2505093 | 0.151486 | −1.65 | 0.098 | −0.54742 | 0.046397 |
| **Road** | 0.015329 | 0.086094 | 0.18 | 0.859 | −0.15341 | 0.184069 |
| **Open Space** | −0.7440933 | 0.099145 | −7.51 | 0 | −0.93841 | −0.54977 |
| **Orchard/Vineyard** | −0.5813305 | 0.097867 | −5.94 | 0 | −0.77315 | −0.38951 |
| **Agriculture** | −0.9785208 | 0.132734 | −7.37 | 0 | −1.23867 | −0.71837 |
| **Vacant Land** | −0.5222501 | 0.074586 | −7 | 0 | −0.66844 | −0.37606 |
| **Zoned protected** | 0.253769 | 0.076881 | 3.3 | 0.001 | 0.103086 | 0.404452 |
| **Area marked for redevelopment** | −0.2680261 | 0.14069 | −1.91 | 0.057 | −0.54377 | 0.007722 |
| **Area marked for development** | 0.5780101 | 0.064103 | 9.02 | 0 | 0.452371 | 0.703649 |
| **Parcel between 10–20 acres** | −0.3379532 | 0.065899 | −5.13 | 0 | −0.46711 | −0.20879 |
| **Parcel between 5–10 acres** | −0.6119036 | 0.067012 | −9.13 | 0 | −0.74325 | −0.48056 |
| **Parcel between 2–5 acres** | −1.16297 | 0.07062 | −16.47 | 0 | −1.30138 | −1.02456 |
| **Parcel between 1–2 acres** | −1.563956 | 0.090286 | −17.32 | 0 | −1.74091 | −1.387 |
| **Parcel between.5–1 acres** | −1.999939 | 0.099893 | −20.02 | 0 | −2.19573 | −1.80415 |
| **Parcel between.25–.5 acres** | −2.178273 | 0.117101 | −18.6 | 0 | −2.40779 | −1.94876 |
| **Constant** | −1.397931 | 0.227467 | −6.15 | 0 | −1.84376 | −0.9521 |

Sample size 113 001, LR Chi$^2$ 1535.23, pro>chi 0, pseudo $R^2$ 0.22. Further description of the variables is provided in Table S1.
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dataset of existing housing includes locations of 687,869 structures, of which 4% were located within the perimeter of one of 40 fires that burned since 2001. During these fires, 4315 structures were completely destroyed, and another 935 were damaged.

For future development scenarios, we wanted to allocate an equal number of new structures to the landscape. This was to ensure that any predicted difference in fire risk was a function of the arrangement and location of structures, not the total number of structures. Nevertheless, differences in the total number of structures were simulated with each of the 5-year time steps. We determined the number of housing units to add during the simulations based on projections made by San Diego County [46]. Using factors such as development proposals, general plan densities, and information from jurisdictions, the county estimated that between 331,378 units and 486,336 units could be supported within the developable residential land by 2030. Because the eastern, desert portion of the county was not included in our study area, we used a conservative approach and simulated the addition of 331,378 new dwelling units. We divided this number by four to define the number of new dwelling units to add at each time step, assuming a linear growth rate.

One output of the econometric model was the prediction of the maximum number of new dwelling units that could be added to each parcel. However, dwelling units may consist of apartments as well as single family homes. The mix of single and multifamily units in the region has remained relatively constant over time, and the overall trend has been a mix of roughly 1/3 multifamily and 2/3 single family units. Because the fire risk model is based on points representing structure locations across the landscape, regardless of the number of dwelling units per structure, we needed to generate a conversion factor from dwelling units to structures. We therefore defined a minimum lot size of 0.25 acre on which no more than a single structure could be built, regardless of the number of dwelling units in it (i.e., a single family home or apartment complex). Then, once a parcel was selected for development by the model (see details below), we divided its total area by the maximum number of dwelling units to be added, according to the econometric model. If the result was larger than 0.25, we subdivided parcels according to the result. If not, we quantified how many 0.25 acre parcels fit into the original parcel, and generated the new parcel boundaries accordingly.

Using the initial map of parcels (year 2010), we classified each parcel that was defined as eligible for development (in the previous stage) as suitable for one of the three planning scenarios described above, according to the number of developed parcels in its immediate neighborhood (i.e., those parcels that share a boundary with the focal parcel). We defined 'developed parcels' as ones that had more than one house per 20 acres (8.09 ha). Therefore, according to these density thresholds, we allowed some parcels with nonzero housing density to be considered as 'undeveloped' because these large, rural parcels might contain a single or a handful of houses but they exist within a large open area. In other words, the overall land cover of these parcels was effectively undeveloped, and we therefore assumed that development in adjacent parcels would be akin to development in open areas.

We defined infill parcels as those that were completely surrounded by developed parcels. Expansion parcels had at least one neighboring parcel that was undeveloped; and leapfrog parcels were those with no developed parcels in their immediate surroundings. We reclassified the type of each available parcel in the same manner after each time step, to account for changing dynamics in the development map of the county.

We conducted three simulations, one for each development scenario (infill, expansion, and leapfrog). In each simulation, all parcels were eligible to subdivide, regardless of their class. Therefore, to build a simulation for a specific scenario, we increased the development probability of parcels of the selected scenario by 20%, to favor their development compared to the other types of parcels, without prohibiting development in the other parcel types. This approach was necessary because the projected number of dwelling units was much larger than it would be possible to fit in infill and leapfrog class parcels solely. For example, as the spatial coverage of developed parcel expands, there is less contiguous area that is undevelopable and suitable for leapfrog development. Therefore, the scenarios are not exclusive, but rather a mixture of the three development types. Yet, in each scenario, there is one main type of development, and smaller amounts of development events of the other two types.

Due to the immense computational demand of the simulations, we adopted a deterministic, rather than a stochastic approach to decide on which parcels were subdivided. After enhancing the transition probability according to the corresponding scenario, we ranked and then sorted all parcels according to their probability of subdivision. We then sequentially selected parcels, while simultaneously tallying the number of dwelling units in them, until the development target in that time step (one fourth of the total number of dwelling units to be added: 82,795) was reached. Once the development target was reached, we moved to the next time step. After each time step, the remaining parcels that were still eligible for development were re-classified to development types according to the new spatial configuration of the landscape.

Once a parcel was selected for subdivision, and the number of new parcels to develop in it was calculated (as detailed above), an equal-area spatial splitting model was employed to split the parent parcel to the predefined number of equal-area child parcels. We developed a simple splitting model which is based on iterative splitting of larger parcels into two smaller parcels using a straight line splitting boundary. Once the parcel was fully split into the needed number of sub-parcels, we allocated a new structure inside each new parcel by generating a point at its centroid (center of gravity). The point datasets of all structure locations per time step per scenario were passed over to the fire risk model, which is described below.

## Fire Risk Modeling and Analysis

To project the distribution of fire risk under alternative scenarios, we used MaxEnt [47–48], a map-based modeling software used primarily for species distribution modeling [48], but we have used it successfully for ignition modeling [50] and for projecting current fire risk in the study area [26]. For this study, we slightly modified the model from Syphard et al. [26]. The dependent variable was the location of structures destroyed by fire between 2001 and 2010. Although inclusion of damaged structures in the data set does not significantly affect results [26], we only included completely destroyed structures to avoid the introduction of any uncertainty.

The MaxEnt software uses a machine-learning algorithm that iteratively evaluates contrasts among values of predictor values at locations where structures burned versus values distributed across the entire study area. The model assumes that the best approximation of an unknown distribution (i.e., structure destruction) is the one with maximum entropy. The output is an exponential function that assigns a probability to every cell of a map. Thus, the resulting continuous maps of fire risk represented the probability of a structure being destroyed by fire. In these output maps, areas of predicted high fire risk that did not have structures on them represented environmental conditions similar to those in which structures have actually burned.

We based the explanatory variables on those that were significantly related to burned structures in Syphard et al. [26], including maps depicting housing arrangement and pattern, housing location, and biophysical factors. Housing pattern variables reflected individual structure locations as well as the arrangement of structures within housing clusters. We calculated housing clusters, defined as groups of structures located within a maximum of 100 m from each other, by creating 100 m buffers around all structures and dissolving the overlapping boundaries [51].

Because burned structures were significantly related to small housing clusters [26], we calculated the area of every cluster as an attribute, and then created raster grids based on that attribute. Low-to intermediate housing density and distance to the edge of the cluster were also significant explanatory variables relative to housing pattern and location [26], so we also created raster grids for those. GIS buffer measures at 1-km have been found to explain approximately 90% of the variation in rural residential density [52], so we developed density grids using simple density interpolation based on a 1-km search radius, with area determined through square map units. To create grids representing distance to the edge of clusters, we first collapsed the cluster polygons into vector polyline files, and then created grids of interpolated Euclidean Distance to the edge within each cluster.

Because the MaxEnt model randomly selects background samples in the map to compare with locations of destroyed structures, we used a mask to restrict sampling to the developed environment within cluster boundaries; the distance to the edge of the cluster would represent a different relationship inside a cluster boundary versus outside in the wildland. We also modified the grids to ensure that any random sample located within the 100m buffer zone would receive a value of 100m; thus, all points within the buffer were considered ''the edge of the development''.

After creating the grids representing housing pattern and arrangement of the current configuration of structures, we applied the same algorithms to the maps of simulated future structure locations. We thus generated grids representing future housing pattern and arrangement under alternative development scenarios. The other explanatory variables, including fire history, slope, fuel type, southwest aspect, and distance to coast [26] remained constant through time for current and future scenarios. Although historic fire frequency and fuel type typically change through time, we did not simulate their dynamics here because we wanted to isolate the effect of planning decisions on housing pattern and arrangement while holding everything else constant.

We conditioned the MaxEnt model on present distributions of housing using ten thousand random background points and destroyed structures located no closer than 500-m to minimize any effect of spatial autocorrelation. We used 80% (260 records) of these data for model training, and 20% [66 records) for testing. We repeated the process using cross-validation with five replicates and used the average of these five models for analyses. For smoother functions of the explanatory variables, we used hinge features, linear, and quadratic with an increase in regularization of beta set at 2.5, based on Elith et al. [48]. The smoother response curves minimize over fitting of the model. We conducted jackknife tests of explanatory variable importance.

We first developed the model using mapped explanatory variables derived from the current configuration of structures. To project fire risk under the different time steps of the alternative development scenarios, projected the model conditioned upon current conditions onto maps representing future conditions by substituting the grids representing future housing pattern and arrangement. This is similar to how potential future distributions of species are projected under climate change scenarios [49].

To quantify differences among current and future alternative scenarios, we calculated metrics representing housing density, pattern, and footprint to determine the extent to which the planning policies produced differences in housing pattern and location. We compared the modeled structure fire risk of the scenarios by overlaying all maps of structure locations with their respective mapped output grids from the MaxEnt models and calculating probability of burning for every structure point. We also calculated total area of risk by selecting three threshold criteria [53]. These criteria, at 0.05, 0.25, and 0.5 represented three different degrees of risk, and we calculated the proportion of structures that were located in risk areas for every time step in all scenarios.

## Results

The probit econometric model, run on 113 001 observations, showed that larger parcels were most likely to subdivide, although the relationship between parcel size and subdivision probability was non-linear (Table 1). Parcels closer to existing roads, the ocean, those with lower slopes, and those designated as fit for development were all most likely to develop. Parcels designated in redevelopment areas were less likely to develop. Overall, the model had a pseudo r –squared of 0.22.

The land use simulation model, based on a combination of the econometric subdivision model and three different growth policies, resulted in substantial differences in the extent and pattern of housing of the three scenarios. The total area of housing development, or the housing footprint, was largest for simulations where leapfrog growth dominated, followed by expansion-type development, and then infill (Figure 1a). The differences in the housing footprint became larger among the scenarios over time, but the largest difference was between infill and the other two development types. As the housing footprint expanded in the three scenarios, the corresponding housing density declined, so that leapfrog growth resulted in the lowest housing density per 1-km, followed by expansion and then infill (Figure 2b). Despite the near inverse of this relationship, there was generally a larger separation among scenarios with regard to housing density. With larger housing footprints and lower housing density, the number of separate housing clusters increased while their size decreased (Figure 2c).

In the first two time steps of the model (2015 and 2020), the simulated development pattern closely followed the desired pattern in the scenario, although some of the growth in the infill scenario ended up becoming expansion or leapfrog (Table 2). In the last two time steps (2025 and 2030), there were not enough infill parcels left, and thus, the majority of growth in these simulations became expansion, followed by infill, and then leapfrog. In the last time step, there were not enough isolated parcels in the leapfrog scenario and thus, the majority of development became expansion. Thus in general, as more development occurred in the simulations by the year 2030, the majority took the form of expansion.

The area under the curve (AUC) of receiver operating characteristic (ROC) plots, indicating the ability of the MaxEnt model to discriminate between burned and unburned structures, averaged across five cross-validated replicate runs was 0.91. The AUC represents the probability that, for a randomly selected set of observations, the model prediction was higher for a burned structure than for an unburned structure [49].The two most important variables in the model according to the internal jackknife tests in MaxEnt [47] were related to housing pattern:

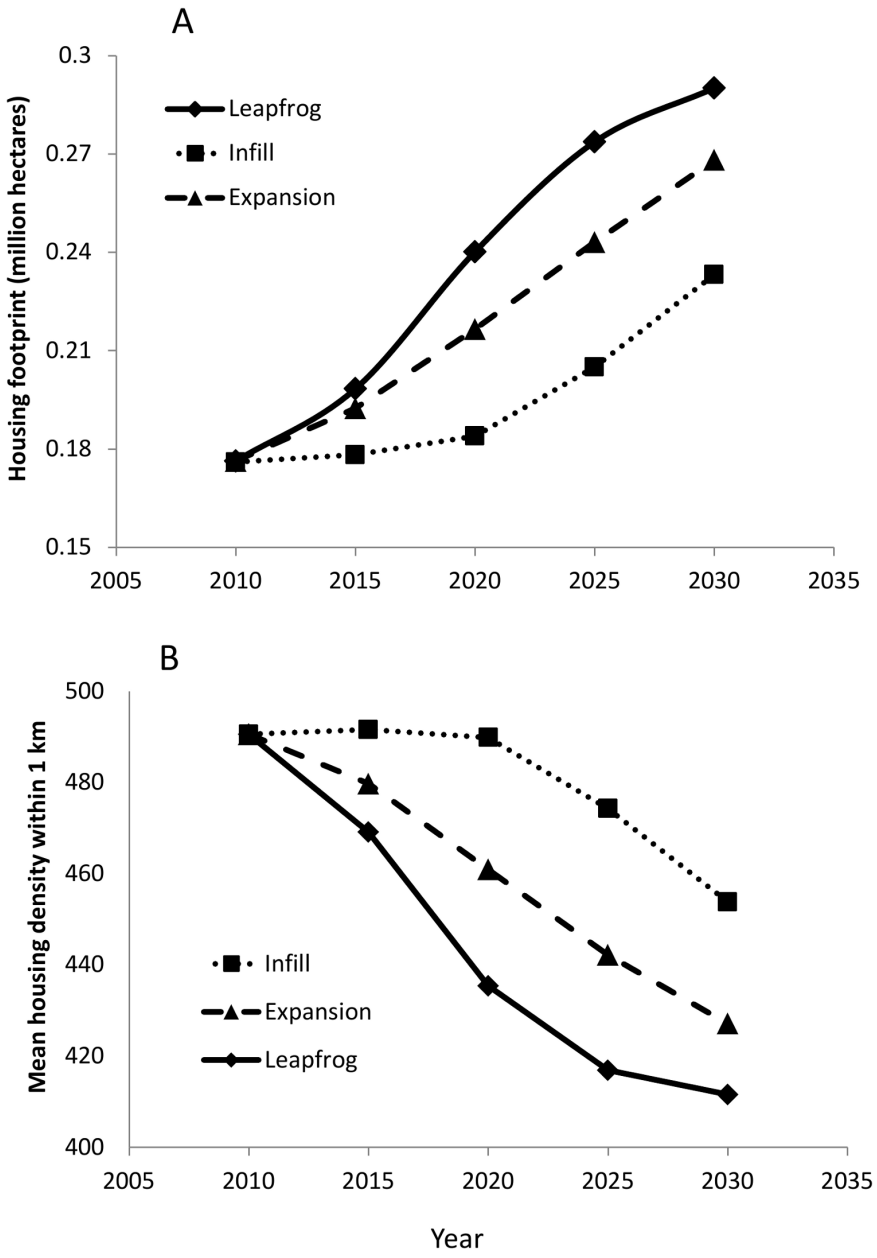


**Figure 1. Trends of development extent and pattern for three planning policy simulations from 2010–2030, including A) total housing footprint representing the area of land within all housing clusters, and B) mean housing density averaged across all housing clusters.**
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low to intermediate housing density and small cluster size and housing density (Figure 3). The distance to the edge of housing cluster was a less important contribution.

Maps showing the probability of a structure being destroyed in a wildfire, displayed as a gradient from low to high risk, show broad agreement relative to the general areas of the landscape that are riskiest, with correlation coefficients ranging from 0.85–0.91 (Figure 4). Nevertheless, subtle differences are apparent in the three development-scenario maps by year 2030, with the highest-risk areas in the expansion scenario located farther east than infill, and the highest-risk areas in leapfrog occupying a wider extent than either of the other two scenarios.

Differences among current housing and the three development scenarios are clearly illustrated through the mean landscape risk, or total probability of all structures burning (Figure 5). All three development scenarios were predicted to experience an increase in mean landscape risk over the duration of the simulations, except for infill at year 2015. The highest landscape risk to structures was predicted for the leapfrog scenario, followed by expansion, and then infill. The increase in risk over time is more gradual for the infill scenario than the other two scenarios.

The ranking of scenarios varied according to the proportion of structures located within different levels of risk defined through binary thresholding (Figure 6). When the continuous risk maps were thresholded at the lowest number of 0.05, a large proportion

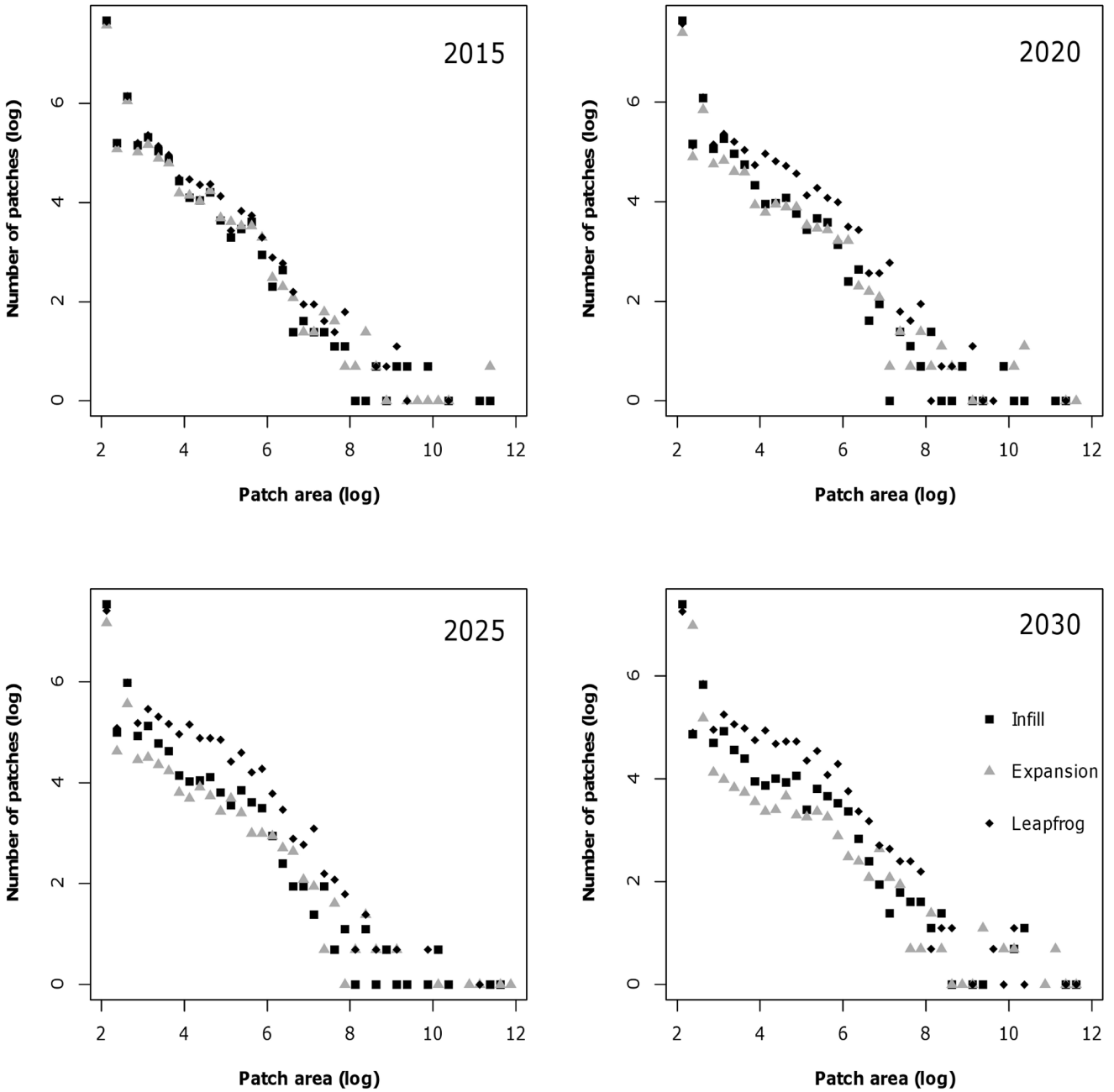


**Figure 2. Trends in number of patches and patch area for three planning policy simulations from 2010–2030.** Numbers were log-transformed for better visual representation of the scenarios.
doi:10.1371/journal.pone.0071708.g002

of structures in all scenarios fell within areas defined as risky according to this criterion. At this threshold, the proportion of structures in high-risk areas increased linearly for the expansion and leapfrog development scenarios while the proportion of infill homes increased more gradually. When risk was defined more conservatively at 0.25, temporal trends for the leapfrog and infill scenarios were similar to the 0.05 threshold. However, the proportion of structures at risk in the expansion scenario initially increased to 2020, but this proportion leveled off and declined by 2030. When the threshold was highest at 0.50, a very low proportion of structures in any scenario were located in areas at risk. But in these high-risk areas, the expansion scenario switched places with infill to have the lowest proportion of structures at risk in all time steps. Leapfrog had the largest proportion of homes at risk. This proportion of homes located in areas at risk with a threshold at 0.5 declined over time for all three scenarios.

## Discussion

Our simulations of residential development showed that planning policies based on different growth types, applied locally for subdivision of individual parcels, will likely produce substantial and cumulative landscape-level differences in pattern, location, and extent of development. These differences in development pattern, in turn, will likely affect the area and proportion of

**Table 2.** Pattern of simulated development under infill, expansion, and leapfrog growth policies.

| | | Actual development | | |
|---|---|---|---|---|
| **Development scenario** | **year** | *Infill* | *Expansion* | *Leapfrog* |
| *Infill* | 2015 | 9450 | 18 | 6 |
| | 2020 | 11787 | 153 | 29 |
| | 2025 | 236 | 624 | 144 |
| | 2030 | 325 | 890 | 179 |
| *Expansion* | 2015 | 0 | 772 | 0 |
| | 2020 | 0 | 1243 | 2 |
| | 2025 | 0 | 1871 | 1 |
| | 2030 | 0 | 2662 | 0 |
| *Leapfrog* | 2015 | 0 | 10 | 408 |
| | 2020 | 0 | 5 | 1132 |
| | 2025 | 1 | 83 | 3563 |
| | 2030 | 34 | 917 | 0 |

The numbers in the table denote the numbers of patches of a given development type.
doi:10.1371/journal.pone.0071708.t002

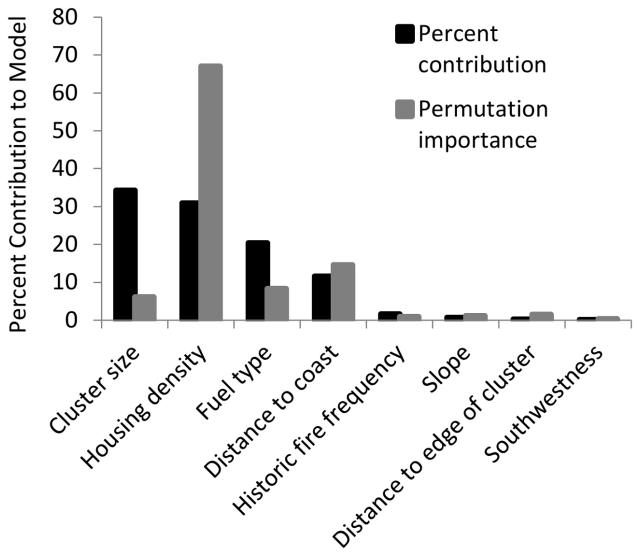


**Figure 3. The importance of explanatory variables averaged across five cross-validated replications in the MaxEnt fire risk model.** Percent contribution is determined as a function of the information gain from each environmental variable throughout the MaxEnt model iterations. Permutation importance reflects the drop in model accuracy that results from random permutations of each environmental variable, normalized to percentages.
doi:10.1371/journal.pone.0071708.g003

structures at risk from burning in wildfires. In particular, the scenarios with lower housing density and larger numbers of small, isolated clusters of development, i.e., leapfrog followed by expansion and infill, were generally predicted to have the highest predicted fire risk to the largest proportion of structures in the study area. Nevertheless, rankings of scenarios were affected by the definition of risk.

Theoretically, it makes sense that leapfrog development produced fragmented development with larger numbers of small patches, lower housing density, and a larger housing footprint; and that infill resulted in the opposite, with expansion in the middle. By definition, leapfrog development requires open space around all sides of the newly developed parcel, whereas infill requires development on all sides, and expansion requires development on one side and open space on another. Implementing these planning policies on real landscapes, however, can be complex if there are more houses to build than there are parcels that meet the definitions of the three planning rules, and thus not all development conforms strictly to the policy [54]. In our simulations, parcels meeting the definition of each growth type had a higher probability of subdividing; yet, as we were simulating a real landscape, many newly developed parcels did not meet the scenario criteria. That the three scenarios nevertheless produced substantial differences in landscape-level development patterns shows that decision-making at the individual level can lead to meaningful broad-scale effects.

The objective of the econometric model was to provide a baseline probability to predict which parcels were most likely to subdivide; thus, the econometric model itself provides no explanation of how a given policy affects likelihood of subdivision, although it does indicate the correlation between the policy and the outcome. In our setting, which areas are protected, marked for redevelopment, or marked for development may be endogenous to the land owner decision to subdivide. In the case of these variables especially, our results should not be interpreted as causal predictors. Likewise, we use data only from 2005–2009 to predict changes to 2030. If major changes in the land market take place over this time horizon our model will not be able to take this into account.

Although some differences in predicted fire risk among the three scenarios likely stemmed from location of new structures relative to variables such as distance to coast, fuel type, or slope, the most important variables in the fire risk model were housing density and cluster size, with most structure loss historically occurring in areas with low housing density and in small, isolated housing clusters. Thus, leapfrog development was generally the riskiest scenario and infill the least risky. The most surprising result was the variation in predicted risk for the expansion scenario over time and at different thresholds. While leapfrog and infill showed similar trajectories across thresholds, expansion went from being the highest-risk scenario at the low threshold to being the lowest-risk scenario at the highest threshold. Because the threshold is merely a way to group structures into a binary classification, this means that, while the average risk calculated across all homes shows expansion to rank in the middle of infill and leapfrog throughout the simulation (Figure 5), the other two scenarios have a relatively larger proportion of homes that are modeled to be at a very high risk (i.e., 0.25 or 0.5), particularly by the end of the simulations. Because the total number of structures with a risk greater than 0.25 or 0.5 is relatively low in all scenarios, this difference in distribution of homes at the highest risk is not reflected in the mean. Another reason for the shift in rank of expansion over time is that, as more development occupied the landscape, there were fewer parcels remaining to accomplish infill or leapfrog type growth in the other scenarios. Thus, by the end of the simulations in year 2030, the majority of growth in all scenarios was expansion, and there was some convergence between scenarios. Finally, the change in risk of expansion growth over time may reflect that, despite the relatively low importance of distance to edge of cluster as an explanatory variable, expansion growth is characterized as having an initially fragmented landscape pattern that eventually merges into large patches with low edge.

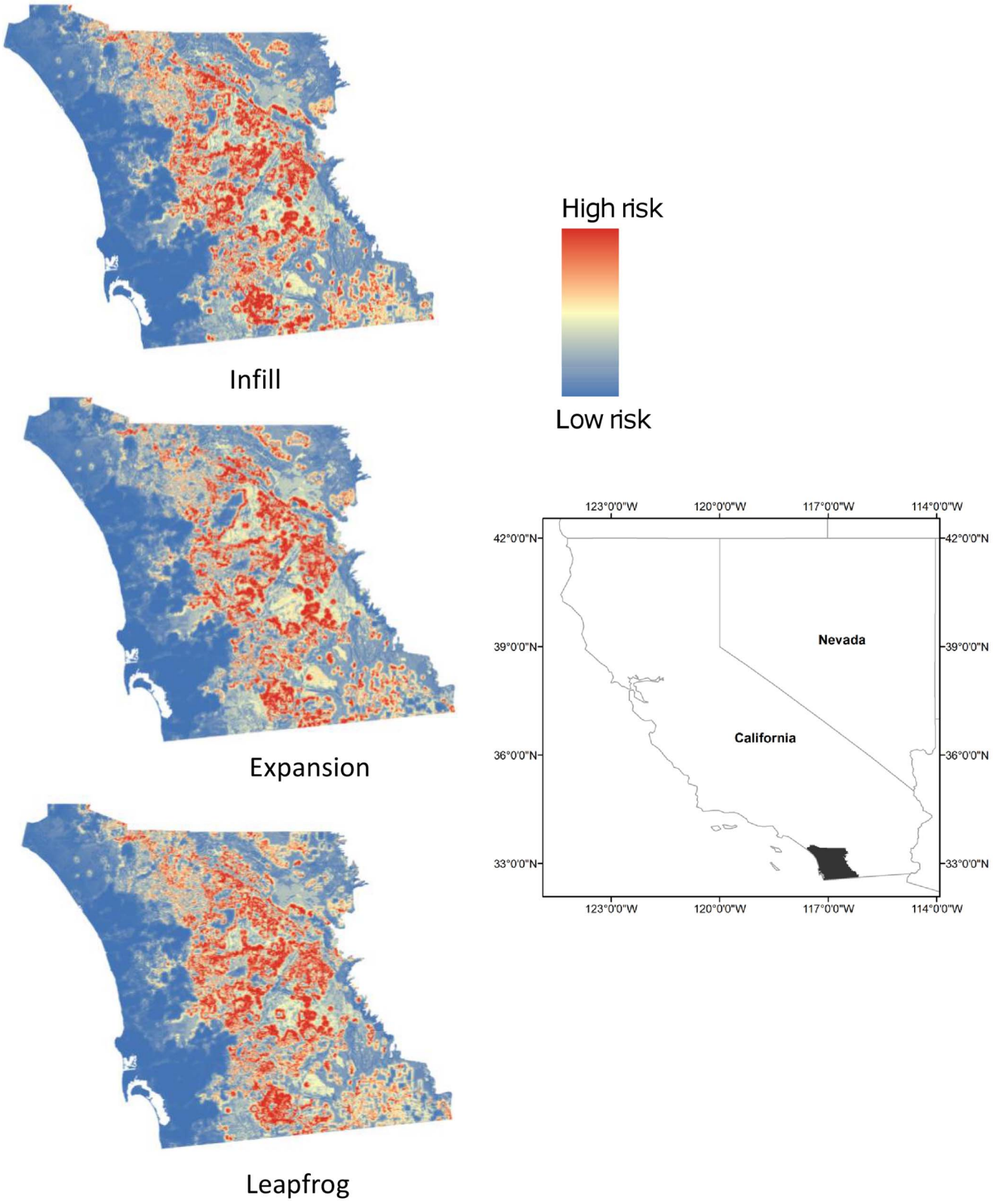


**Figure 4. Maps of the study area showing projected wildfire risk at year 2030 for simulations of residential development under policies emphasizing infill, expansion, or leapfrog growth.**
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Although leapfrog development clearly ranked highest in terms of fire risk, the interpretation of which planning policy is best may depend on fire management objectives and resources, as well as other considerations such as biodiversity or ecological impacts.

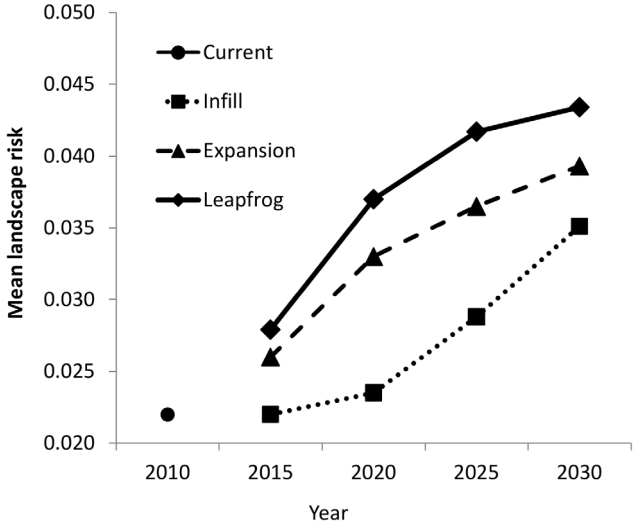


**Figure 5. Projected landscape fire risk, reflecting the probability of burning in a wildfire averaged across all residential structures on the current landscape and in three development scenarios of infill, expansion, and leapfrog for year 2030.**
doi:10.1371/journal.pone.0071708.g005

The spatial pattern of development affects multiple ecological functions and services [55], with potentially varying conservation implications; both leapfrog and expansion development consumed more land than infill, which would likely lead to more ecological degradation [56]; nevertheless, higher-density clustered development may be dominated by more invasive species [57]. Trade-offs between fire protection and conservation are common, but techniques are available for identifying mutually beneficial solutions [58].

Different perceptions of the fire risk results could also potentially translate into different planning priorities for management. For example, if the priority is to plan for the lowest overall risk to structures, then the mean landscape risk clearly delineates the rankings of options, with infill being the winner. However, if the objective is to reduce the number of structures at the highest risk threshold, i.e., $>=0.5$, then expansion is the best option, at least by 2030. An important consideration for fire management is the total area that needs to be protected, as well as the length of wildland-urban interface [8,13]. Therefore, despite the lower number of structures at the highest risk thresholds, expansion creates more edge than infill and may translate into greater challenges for firefighter protection.

Although we did not create separate scenarios for high or low growth, the results at different time steps can be substituted to envision the potential outcome of developing more or fewer houses. In the short term, the total fire risk is projected to increase proportionately as more land is developed. However, given the inverse relationship between housing density and fire risk, it is possible that this trend could reverse if housing growth eventually resulted in expansive high-density development.

Land use planning is one of a range of options available for reducing fire risk, and the best outcome will likely be achieved through a combination of strategies that include homeowner actions, improvements in fire-safe building codes, and advanced fire suppression tactics. Although we isolated the effect of land use planning policy in the three development scenarios, the fire risk model nevertheless showed that the pattern and location of structures in this study area were the most important out of a suite of factors influencing structure loss. We used a correlative approach that did not incorporate mechanisms or feedbacks, but our models clearly illustrated differences in the cumulative effects of individual planning decisions. The relationship between spatial pattern of development and fire risk is likely related to the intermixing of development and wildland vegetation [29,59]; thus, these results likely apply to a wide range of fire-prone ecosystems with large proportions of human-caused ignitions. Nevertheless, because fire risk is highly variable over space and time, and due to a range of human and biophysical variables [60], we recommend planners develop their own models for the best understanding of where the most fire-prone areas are in their region [19].

With projections of substantial global change in climate and human development, we recommend that land use planning should be considered as an important component to fire risk management, potentially to become as successful as the prevention of building on flood plains [61]. History has shown us that preventing fires is impossible in areas where large wildfires are a natural ecological process [4,9]. As Roger Kennedy put it, "the

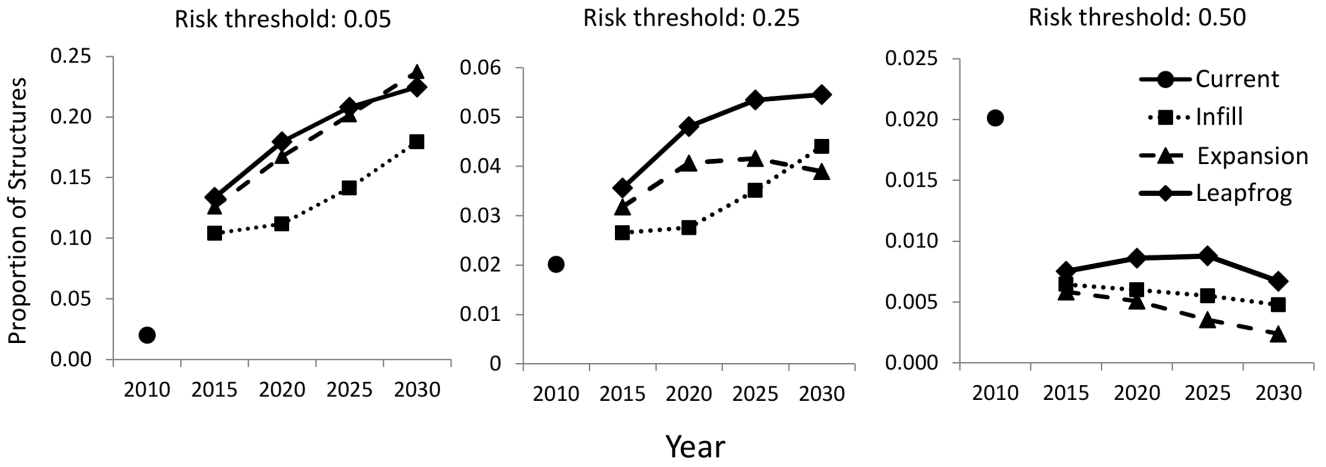


**Figure 6. Proportion of residential structures that are located in areas of high fire risk defined using thresholds from the fire risk model of 0.05, 0.25, and 0.5 for current structures and for structures simulated under infill, expansion, and leapfrog growth policies.**
doi:10.1371/journal.pone.0071708.g006

problem isn't fires; the problem is people in the wrong places [62]."

## Supporting Information

**Table S1 Definitions and summary statistics for variables used in the probit model.**
(DOCX)

## Acknowledgments

We thank V.C. Radeloff for insightful discussions, and we are grateful for the helpful suggestions from Susan Jones, Rob Klinger, Ben Bond-Lamberty, and the anonymous reviewers. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## Author Contributions

Conceived and designed the experiments: ADS JEK ABM VB. Performed the experiments: ADS ABM VB. Analyzed the data: ADS ABM VB. Wrote the paper: ADS JEK ABM VB.

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# The role of defensible space for residential structure protection during wildfires

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**Abstract.** With the potential for worsening fire conditions, discussion is escalating over how to best reduce effects on urban communities. A widely supported strategy is the creation of defensible space immediately surrounding homes and other structures. Although state and local governments publish specific guidelines and requirements, there is little empirical evidence to suggest how much vegetation modification is needed to provide significant benefits. We analysed the role of defensible space by mapping and measuring a suite of variables on modern pre-fire aerial photography for 1000 destroyed and 1000 surviving structures for all fires where homes burned from 2001 to 2010 in San Diego County, CA, USA. Structures were more likely to survive a fire with defensible space immediately adjacent to them. The most effective treatment distance varied between 5 and 20 m (16–58 ft) from the structure, but distances larger than 30 m (100 ft) did not provide additional protection, even for structures located on steep slopes. The most effective actions were reducing woody cover up to 40% immediately adjacent to structures and ensuring that vegetation does not overhang or touch the structure. Multiple-regression models showed landscape-scale factors, including low housing density and distances to major roads, were more important in explaining structure destruction. The best long-term solution will involve a suite of prevention measures that include defensible space as well as building design approach, community education and proactive land use planning that limits exposure to fire.

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## Introduction

Across the globe and over recent decades, homes have been destroyed in wildfires at an unprecedented rate. In the last decade, large wildfires across Australia, southern Europe, Russia, the US and Canada have resulted in tens of thousands of properties destroyed, in addition to lost lives and enormous social, economic and ecological effects (Filmon 2004; Boschetti *et al.* 2008; Keeley *et al.* 2009; Blanchi *et al.* 2010; Vasquez 2011). The potential for climate change to worsen fire conditions (Hessl 2011), and the projection of continued housing growth in fire-prone wildlands (Gude *et al.* 2008) suggest that many more communities will face the threat of catastrophic wildfire in the future.

Concern over increasing fire threat has escalated discussion over how to best prepare for wildfires and reduce their effects. Although ideas such as greater focus on fire hazard in land use planning, using fire-resistant building materials and reducing human-caused ignitions (e.g. Cary *et al.* 2009; Quarles *et al.* 2010; Syphard *et al.* 2012) are gaining traction, the traditional strategy of fuels management continues to receive the most attention. Fuels management in the form of prescribed fires or mechanical treatments has historically occurred in remote, wildland locations (Schoennagel *et al.* 2009), but recent studies suggest that treatments located closer to homes and communities may provide greater protection (Witter and Taylor 2005; Stockmann *et al.* 2010; Gibbons *et al.* 2012). In fact, one of the most commonly recommended strategies in terms of fuels and fire protection is to create defensible space immediately around structures (Cohen 2000; Winter *et al.* 2009). Defensible space is an area around a structure where vegetation has been modified, or 'cleared,' to increase the chance of the structure surviving a wildfire. The idea is to mitigate home loss by minimising direct contact with fire, reducing radiative heating, lowering the probability of ignitions from embers and providing a safer place for fire fighters to defend a structure against fire (Gill and Stephens 2009; Cheney *et al.* 2001). Many jurisdictions provide specific guidelines and practices for creating defensible space, including minimum distances that are required among trees and shrubs as well as minimum total distances from the structure. These distances may be enforced through local ordinances or state-wide laws. In California, for example, a state law in 2005 increased the required total distance from 9 m (30 ft) to 30 m (100 ft).

Despite these specific guidelines on how to create defensible space, there is little scientific evidence to support the amount and location of vegetation modification that is actually effective

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at providing significant benefits. Most spacing guidelines and laws are based on 'expert opinion' or recommendations from older publications that lack scientific reference or rationale (e.g. Maire 1979; Smith and Adams 1991; Gilmer 1994). However, one study has provided scientific support for, and forms the basis of, most guidelines, policy and laws requiring a minimum of 30 m (100 ft) of defensible space (Cohen 1999, 2000). The modelling and experimental research in that study showed that flames from forest fires located 10–40 m (33–131 ft) away would not scorch or ignite a wooden home; and case studies showed 90% of homes with non-flammable roofs and vegetation clearance of 10–20 m (33–66 ft) could survive wildfires (Cohen 2000). However, the models and experimental research in that study focussed on crown fires in spruce or jack pine forests, and the primary material of home construction was wood. Therefore, it is unknown how well this guideline applies to regions dominated by other forest types, grasslands, or nonforested woody shrublands and in regions where wooden houses are not the norm.

Some older case studies showed that most homes with non-flammable roofs and 10–18 m (33–ft) of defensible space survived the 1961 Bel Air fire in California (Howard *et al.* 1973); most homes with non-flammable roofs and more than 10 m (33 ft) of defensible space also survived the 1990 Painted Cave fire (Foote and Gilless 1996). Also, several fire-behaviour modelling studies have been conducted in chaparral shrublands. One study showed that reducing vegetative cover to 50% at 9–30 m (30–ft) from structures effectively reduced fireline intensity and flame lengths, and that removal of 80% cover would result in unintended consequences such as exotic grass invasion, loss of habitat and increase in highly flammable flashy fuels (A. Fege and D. Pumphrey, unpubl. data). Another showed that separation distances adequate to protect firefighters varied according to fuel model and that wind speeds greater than 23 km $h^{-1}$ negated the effect of slope, and wind speed above 48 km $h^{-1}$ negated any protective effect of defensible space (F. Bilz, E. McCormick and R. Unkovich, unpubl. data, 2009). Results obtained through modelling equations of thermal radiation also found safety distances to vary as a function of fuel type, type of fire, home construction material and protective garments worn by firefighters (Zárate *et al.* 2008).

Although there is no empirical evidence to support the need for more than 30 m (100 ft) of defensible space, there has been a concerted effort in some areas to increase this distance, particularly on steep slopes. In California, a senate bill was introduced in 2008 (SB 1618) to encourage property owners to clear 91 m (300 ft) through the reduction of environmental regulations and permitting needed at that distance. Although this bill was defeated in committee, many local ordinances do require homeowners to clear 91 m (300 ft) or more, and there are reports that some people are unable to get fire insurance without 91 m (300 ft) of defensible space (F. Sproul, pers. comm.). In contrast, homeowner acceptance of and compliance with defensible space policies can be challenging (Winter *et al.* 2009; Absher and Vaske 2011), and in many cases homeowners do not create any defensible space.

It is critically important to develop empirical research that quantifies the amount, location and distance of defensible space that provides significant fire protection benefits so that guidelines and policies are developed with scientific support. Data that are directly applicable to southern California are especially important, as this region experiences the highest annual rate of wildfire-destroyed homes in the US. Not having sufficient defensible space is obviously undesirable because of the hazard to homeowners. However, there are clear trade-offs involved when vegetation reduction is excessive, as it results in the loss of native habitats, potential for increased erosion and invasive species establishment, and it potentially even increases fire risk because of the high flammability of weedy grasslands (Spittler 1995; Keeley *et al.* 2005; Syphard *et al.* 2006).

It is also important to understand the role of defensible space in residential structure protection relative to other factors that explain why some homes are destroyed in fires and some are not. Recent research shows that landscape-scale factors, such as housing arrangement and location, as well as biophysical variables characterising properties and neighbourhoods such as slope and fuel type, were important in explaining which homes burned in two southern California study areas (Syphard *et al.* 2012; 2013). Understanding the relative importance of different variables at different scales may help to identify which combinations of factors are most critical to consider for fire safety.

Our objective was to provide an empirical analysis of the role of defensible space in protecting structures during wildfires in southern California shrublands. Using recent pre-fire aerial photography, we mapped and measured a suite of variables describing defensible space for burned and unburned structures within the perimeters of major fires from 2001 to 2010 in San Diego County to ask the following questions:

1. How much defensible space is needed to provide significant protection to homes during wildfires, and is it beneficial to have more than the legally required 30 m (100 ft)?
2. Does the amount of defensible space needed for protection depend on slope inclination?
3. What is the role of defensible space relative to other factors that influence structure loss, such as terrain, fuel type and housing density?

## Methods

### *Study area*

The properties and structures analysed were located in San Diego County, California, USA (Fig. 1) – a topographically diverse region with a Mediterranean climate characterised by cool, wet winters and long summer droughts. Fire typically is a direct threat to structures adjacent to wildland areas. Native shrublands in southern California are extremely flammable during the late summer and fall (autumn) and when ignited, burn in high-intensity, stand-replacing crown fires. Although 500 homes on average have been lost annually since the mid-1900s (Calfire 2000), that rate has doubled since 2000. Most of these homes have burned during extreme fire weather conditions that accompany the autumn Santa Ana winds. The wildland–urban interface here includes more than 5 million homes, covering more than 28 000 $km^2$ (Hammer *et al.* 2007).

### *Property data*

The data for properties to analyse came from a complete spatial database of existing residential structures and their

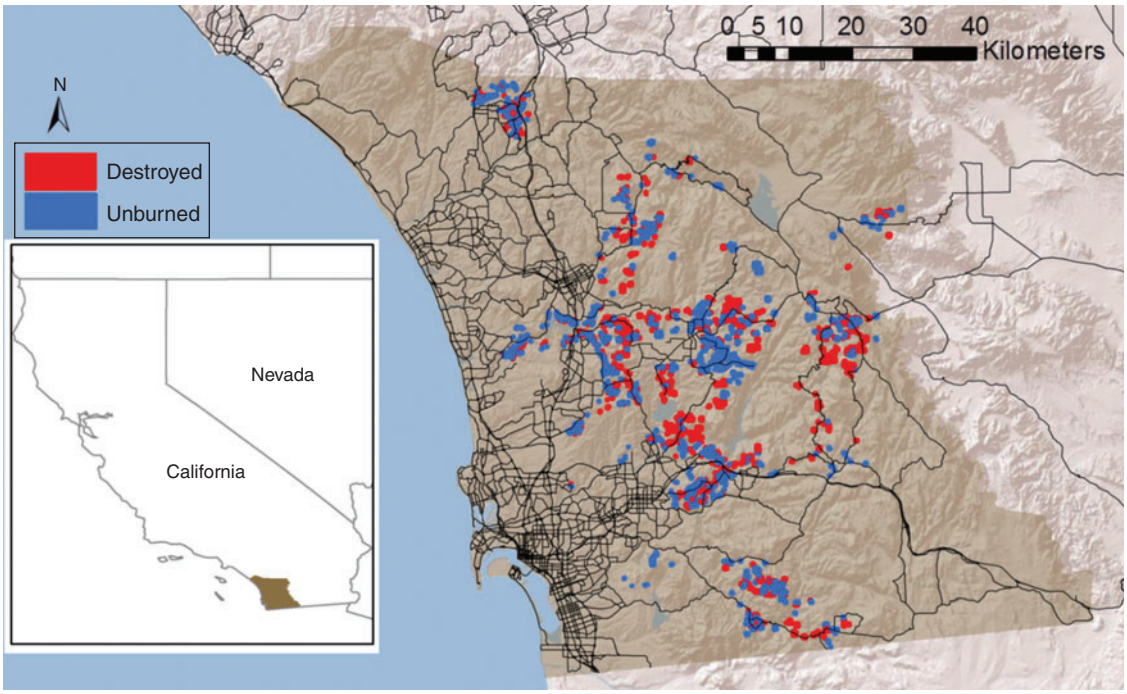


**Fig. 1.** Location of destroyed and unburned structures within the South Coast ecoregion of San Diego County, California, USA.

corresponding property boundaries developed for San Diego County (Syphard *et al.* 2012). This dataset included 687 869 structures, of which 4315 were completely destroyed by one of 40 major fires that occurred from 2001 to 2010. Our goal was to compare homes that were exposed to wildfire and survived with those that were exposed and destroyed. To determine exposure to fire, we only considered structures located both within a GIS layer of fire perimeters and within areas mapped as having burned at a minimum of low severity through thematic Monitoring Trends in Burn Severity produced by the USA Geological Survey and USDA Forest Service. From these data, we used a random sample algorithm in GIS software to select 1000 destroyed and 1000 unburned homes that were not adjacent to each other, to minimise any potential for spatial autocorrelation. Our final property dataset included structures that burned across eight different fires. More than 97% of these structures burned in Santa Ana wind-driven fire events (Fig. 1).

### *Calculating defensible space and additional explanatory variables*

To estimate defensible space, we developed and explored a suite of variables relative to the distance and amount of defensible space surrounding structures, as well as the proximity of woody vegetation to the structure (Table 1). We measured these variables based on interpretation of Google Earth aerial imagery. We based our measurements on the most recent imagery before the date of the fire. In almost all cases, imagery was available for less than 1 year before the fire.

Our definition of defensible space followed the guidelines published by the California Department of Forestry and Fire Protection (Calfire 2006). 'Clearance' included all areas that were not covered by woody vegetation, including paved areas or grass. Although Google Earth prevents the identification of understorey vegetation, woody trees and shrubs were easily distinguished from grass, and our objective was to measure horizontal distances as required by Calfire rather than assess the relative flammability of different vegetation types. Trees or shrubs were allowed to be within the defensible space zone as long as they were separated by the minimum horizontal required distance, which was 3 m (10 ft) from the edge of one tree canopy to the edge of the next (Fig. 2). Although greater distances between trees or shrubs are recommended on steeper slopes, we followed the same guidelines for all properties. For all structures, we started the distance measurements by drawing lines from the centre of the four orthogonal sides of the structure that ended when they intersected anything that no longer met the requirements in the guidelines. A fair number of structures are not four sided; thus, the start of the centre point was placed at a location that approximated the farthest extent of the structure along each of four orthogonal sides.

We developed two sets of measurements of the distance of defensible space based on what is feasible for homeowners within their properties *v.* the total effective distance of defensible space. We made these two measurements because homeowners are only required to create defensible space within their own property, and this would reflect the effect of individual homeowner compliance. Therefore, even if cleared vegetation extended beyond the property line, the first set of distance measurements ended at the property boundary. The second set of measurements ignored the property boundaries and accounted for the total potential effect of treatment. For all measurements, we recorded the cover types (e.g. structure $>3$ m (10 ft) long, property boundary, or vegetation type) at which the distance measurements stopped (Table 1). Because property

**Table 1. Defensible space variables measured for every structure**

Urban veg, landscaping vegetation that was not in compliance with regulations within urban matrix; wildland veg, wildland vegetation that was not in compliance with regulations; orchard, shrub to tree-sized vegetation in rows; urban to wildland, landscaping vegetation that leads into wildland vegetation; structure, any building longer than 3 m (10 ft)

| Variable | Definition |
|---|---|
| Distance defensible space within property | Measure of clearance from side of structure to property boundary calculated for four orthogonal directions from structure and averaged |
| Total distance defensible space | Measure of clearance from side of structure to end of clearance calculated for four orthogonal directions from structure and averaged |
| Cover type at end of defensible space | Type of cover encountered at end of measurement (urban veg, wildland veg, orchard, urban to wildland, structure) |
| Percentage clearance | Percentage of clearance calculated across the entire property |
| Neighbours' vegetation | Binary indicator of whether neighbours' uncleared vegetation was located within 30 m (100 ft) of the main structure |
| Vegetation touching structure | Number of sides on which woody vegetation touches main structure (1–4) Structure with more than 4 sides were viewed as a box and given a number between 1 and 4 |
| Vegetation overhanging roof | Was vegetation overhanging the roof? (yes or no) |

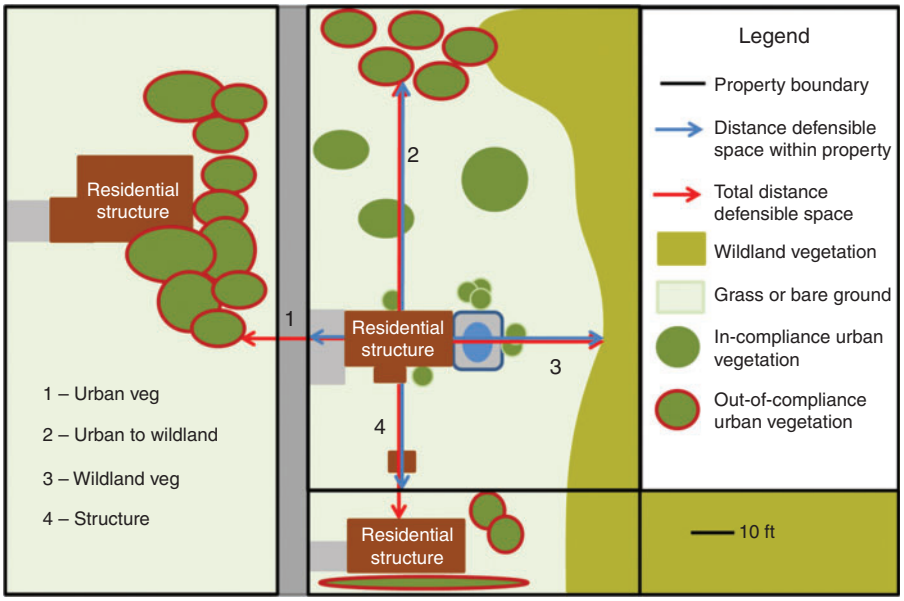


**Fig. 2.** Illustration of defensible space measurements. See Table 1 for full definition of terms.

owners usually can only clear vegetation on their own land, it is possible that the effectiveness of defensible space partly depends upon the actions of neighbouring homeowners. Therefore, we also recorded whether or not any neighbours' un-cleared vegetation was located within 30 m (100 ft) of the structure.

To assess the total amount of woody vegetation that can safely remain on a property and still receive significant benefits of defensible space, we calculated the total percentage of cleared land, woody vegetation and structure area across every property. This was accomplished by overlaying a grid on each property and determining the proportion of squares falling into each class. Preliminary results showed these three measurements to be highly correlated, so we only retained percentage clearance for further analysis. To evaluate the relative effect of woody vegetation directly adjacent to structures, we also calculated the number of sides of the structure with vegetation touching and recorded whether any trees were overhanging structures' roofs.

In addition to defensible space measurements, we evaluated other factors known to influence the likelihood of housing loss to fire in the region (Syphard *et al.* 2012, 2013). Using the same data as in Syphard *et al.* (2012, 2013), we extracted spatial information from continuous grids of explanatory variables for the locations of all structures in our analysis. Variables included interpolated housing density based on a 1-km search radius; percentage slope derived from a 30-m digital elevation model (DEM); Euclidean distance to nearest major and minor road and fuel type, which was based on a simple classification of US Forest Service data (Syphard *et al.* 2012), including urban, grass, shrubland and forest & woodland.

### *Analysis*

We performed several analyses to determine whether relative differences in home protection are provided by different distances and amounts of defensible space, particularly beyond the legally required 30 m (100 ft), and to identify the effective treatment distance for homes on low and steep slopes.

### *Categorical analysis*

For the first analysis, we divided our data into several groups to identify potential differences among specific categories of defensible space distance around structures located on shallow and steep slopes. We first sorted the full dataset of 2000 structures by slope and then split the data in the middle to create groups of homes with shallow slope and steep slope. We divided the data in half to keep the number of structures even within both groups and to avoid specifying an arbitrary number to define what constitutes shallow or steep slope. The two equal-sized subsets of data ranged from 0 to 9%, with a mean of 8% for shallow slope, and from 9 to 40%, with a mean of 27% for steep slope. Within these data subsets, we next created groups reflecting different mean distances of defensible space around structures. We also performed separate analyses based on whether defensible space measurements were calculated within the property boundary or whether measurements accounted for the total distance of defensible space.

Within all groups, we calculated the proportion of homes that were destroyed by wildfire. We performed Pearson's Chi-square tests of independence to determine whether or not the proportion of destroyed structures within groups was significantly different (Agresti 2007). We based one test on four equal-interval groups within the legally required distance of 30 m (100 ft): 0–7 m (0–25 ft), 8–15 m (26–50 ft), 16–23 m (51–75 ft) and 24–30 m (76–100 ft). A second test was based on three groups (24–30 m (75–100 ft), 31–90 m (101–300 ft) and >90 m (>300 ft) or >60 m (>200 ft)) to evaluate whether groups with mean defensible space distances >30 m (>100 ft) were significantly different from groups with <30 m (<100 ft). When defensible space distances were only measured to the property boundary, few structures had mean defensible space >90 m (>300 ft). Therefore, we used a cut-off of 60 m (200 ft) to increase the sample size in the Chi-square analysis. In addition to the Chi-square analysis, we calculated the relative risk among every successive pair of categories (Sheskin 2004). The relative risk was calculated as the ratio of proportions of burned homes within two groups of homes that had different defensible space distances.

### *Effective treatment analysis*

In addition to comparing the relative effect of defensible space among different groups of mean distances, as described above, we also considered that the protective effect of defensible space for structures exposed to wildfire is conceptually similar to the effect of medication in producing a therapeutic response in people who are sick. In addition to pharmacological applications, treatment–response relationships have been used for radiation, herbicide, drought tolerance and ecotoxicological studies (e.g. Streibig *et al.* 1993; Cedergreen *et al.* 2005; Knezevic *et al.* 2007; Kursar *et al.* 2009). The effect produced by a drug or treatment typically varies according to the concentration or amount, often up to a point at which further increase provides no additional response. The effective treatment (ET50), therefore, is a specific concentration or exposure that produces a therapeutic response or desired effect. Here we considered the treatment to be the distance or amount of defensible space.

Using the software package DRC in R (Knezevic *et al.* 2007; Ritz and Streibig 2013), we evaluated the treatment–response relationship of defensible space in survival of structures during wildfire. To calculate the effective treatment, we fit a log-logistic model with logistic regression because we had a binary dependent variable (burned or unburned). We specified a 2-parameter model where the lower limit was fixed at 0 and the upper limit was fixed at 1. We again performed separate analyses for data subsets reflecting shallow and steep slope, as well as from measurements of defensible space taken within, or regardless of, property boundaries. We also performed analyses to find the effective treatment of percentage clearance of trees and shrubs within the property.

### *Multiple regression analysis*

To evaluate the role of defensible space relative to other variables, we developed multiple generalised linear regression models (GLMs) (Venables and Ripley 1994). We again had a binary dependent variable (burned versus unburned), so we specified a logit link and binomial response. Although the proportion of 0s and 1s in the response may be important to consider for true prediction (King and Zeng 2001; Syphard *et al.* 2008), our objective here was solely to evaluate variable importance. We developed multiple regression models for all possible combinations of the predictor variables and used the corrected Akaike's Information Criterion (AICc) to rank models and select the best ones for each region using package MuMIn in R (R Development Core Team 2012; Burnham and Anderson 2002). We recorded all top-ranked models that had an AICc value within 2 of that of the model with lowest AICc to identify all models with empirical support. To assess variable importance, we calculated the sum of Akaike weights for all models that contained each variable. On a scale of 0–1, this metric represents the weight of evidence that models containing the variable in question are the best model (Burnham and Anderson 2002). The distance of defensible space measured within property boundaries was highly correlated with the distance of defensible space measured beyond property boundaries ($r = 0.82$), so we developed two separate analyses – one using variables measured only within the property boundary and the other using variables that accounted for defensible space outside of the property boundary as well as the potential effect of neighbours having uncleared vegetation within 30 m (100 ft) of the structure. A test to avoid multicollinearity showed all other variables within each multiple regression analysis to be uncorrelated ($r < 0.5$).

### *Surrounding matrix*

To assess whether the proportion of destroyed structures varied according to their surrounding matrix, we summarised the most common cover type at the end of defensible space measurements (descriptions in Table 1) for all structures. These summaries

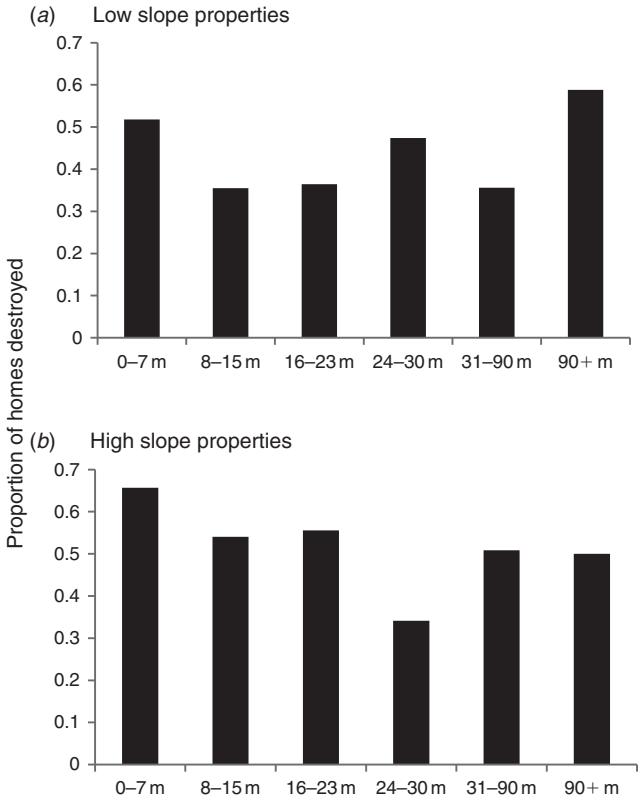


**Fig. 3.** Proportion of destroyed homes grouped by distances of defensible space based upon total distance of clearance within property boundary, for structures on (*a*) shallow slopes (mean 8%) and (*b*) steep slopes (mean 27%).

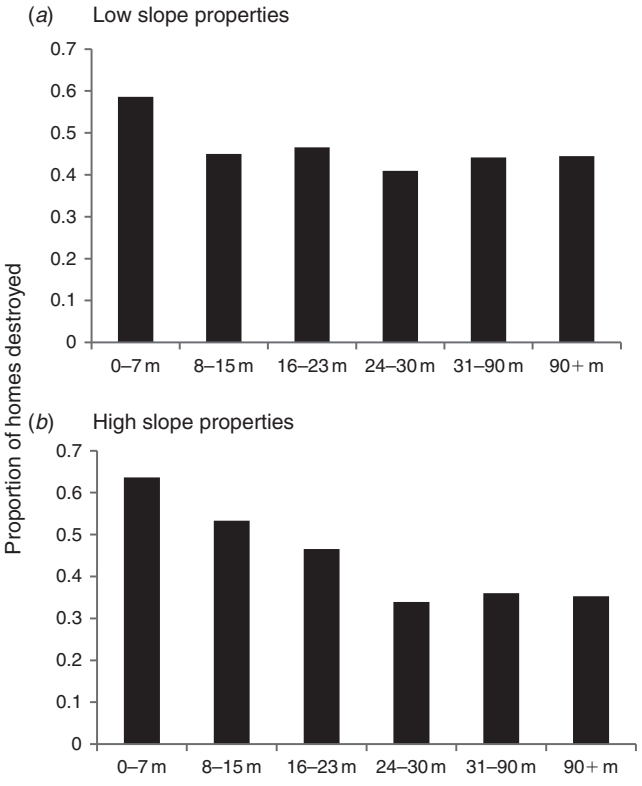


**Fig. 4.** Proportion of destroyed homes grouped by distances of defensible space based upon total distance of clearance regardless of property boundary, for structures on (*a*) shallow slopes (mean 8%) and (*b*) steep slopes (mean 27%).

were based on the majority surrounding cover type from the four orthogonal sides of the structure. We also noted cases in which there was a tie (e.g. two sides were urban vegetation and two sides were structures).

## Results

### *Categorical analysis*

When the distance of defensible space was measured both 'only within property boundaries' (Fig. 3) and 'regardless of property boundaries' (Fig. 4), the Chi-square test showed a significant difference ($P < 0.001$) in the proportion of destroyed structures among the four equal-interval groups of distance ranging from 0 to 30 m (0–100 ft). This relationship was consistent on both shallow-slope and steep-slope properties, although the relative risk analysis showed considerable variation among classes (Table 2) There was a steadily decreasing proportion of destroyed structures at greater distances of defensible space up to 30 m (100 ft) on the steep-slope structures with defensible space measured regardless of property boundaries (Fig. 4*b*). Otherwise, the biggest difference in proportion of destroyed structures occurred between 0 and 7 m (0–25 ft) and 8–15 m (26–50 ft) (Figs 3*a–b*, 4*a*).

When the distance of defensible space was measured in intervals from 24 m (75 ft) and beyond, the Chi-square test showed no significant difference among groups ($P = 0.96$ for shallow-slope properties and $P = 0.74$ for steep-slope properties) (Figs 3, 4), although again, the relative risk analysis showed considerable variation (Table 2).There was a slight increase in the proportion of homes destroyed at longer distance intervals when the defensible space was measured only to the property boundaries (Fig. 3*a–b*). This slight increase is less apparent when distances were measured regardless of boundaries (Fig. 4*a–b*).

The relative risk calculations showed that the ratio of proportions was generally more variable among successive pairs when the distances were measured within property boundaries (Table 2). For these calculations, the risk of a structure being destroyed was significantly lower when the defensible space distance was 8–15 m (25–50 ft) compared to 0–7 m (0–25 ft) on both shallow- and steep-slope properties. On the steep-slope properties, there was an additional reduction of risk when comparing 24–30 m (75–100 ft) to 16–23 m (50–75 ft). However, the risk of a home being destroyed was slightly significantly higher when there was 31–90 m (101–225 ft) compared to 16–23 m (50–75 ft). For distances that were measured regardless of property boundary (total clearance), the only significant differences in risk of burning were a reduction in risk for 8–15 m (25–50 ft) compared to 0–7 m (0–25 ft).

**Table 2. Number of burned and unburned structures within defensible space distance categories (m), their relative risk and significance**
A relative risk of 1 indicates no difference; <1 means the chance of a structure burning is less than the other group; >1 means the chance is higher than the other group. The relative risk is calculated for pairs that include the existing row and the row above. Confidence intervals are in parentheses

| | Distance within property | | | | Total distance | | | |
|---|---|---|---|---|---|---|---|---|
| | Burned | Unburned | Relative risk | *P* | Burned | Unburned | Relative risk | *P* |
| Shallow slope | | | | | | | | |
| 0–7 | 200 | 186 | | | 162 | 114 | | |
| 8–15 | 109 | 198 | 0.69 (0.12) | <0.001 | 108 | 132 | 0.77 | 0.002 |
| 16–23 | 51 | 89 | 1.03 (0.30) | 0.850 | 78 | 90 | 1.03 | 0.770 |
| 24–30 | 36 | 40 | 1.30 (0.39) | 0.110 | 50 | 70 | 0.90 | 0.430 |
| 31–90 | 28 | 47 | 0.79 (0.24) | 0.220 | 79 | 99 | 1.06 | 0.640 |
| 60 or 90+ | 10 | 6 | 1.67 (0.63) | 0.040 | 8 | 9 | 1.01 | 0.830 |
| Steep slope | | | | | | | | |
| 0–7 | 245 | 128 | | | 224 | 128 | | |
| 8–15 | 174 | 148 | 0.82 (0.10) | 0.001 | 158 | 139 | 0.84 | 0.008 |
| 16–23 | 85 | 68 | 1.03 (0.16) | 0.750 | 73 | 83 | 0.87 | 0.210 |
| 24–30 | 29 | 56 | 0.61 (0.17) | 0.004 | 26 | 50 | 0.73 | 0.080 |
| 31– | 29 | 28 | 1.49 (0.48) | 0.050 | 39 | 68 | 1.06 | 0.760 |
| 60 or 90+ | 5 | 5 | 0.98 (0.47) | 0.950 | 4 | 8 | 0.91 | 0.830 |

**Table 3. Effective treatment results reflecting the distance (in metres, with feet in parentheses) and percentage clearance within properties that provided significant improvement in structure survival during wildfires**
The property mean is the average distance of defensible space or percentage clearance that was calculated on the properties before the wildfires and provides a means to compare the effective treatment result to the actual amount on the properties

| | All parcels effective treatment ($n = 2000$) | Parcel mean | Shallow slope (mean 8%) effective treatment ($n = 1000$) | Parcel mean | Steep slope (mean 27%) effective treatment ($n = 1000$) | Parcel mean |
|---|---|---|---|---|---|---|
| Defensible space within parcel | 10 (33) | 13 (44) | 4 (13) | 14 (45) | 25 (82) | 11 (35) |
| Total distance defensible space | 10 (32) | 19 (63) | 5 (16) | 20 (67) | 20 (65) | 18 (58) |
| Mean percentage clearance on property | 36 | 48 | 31 | 51 | 37 | 35 |

### *Effective treatment analysis*

Analysis of the treatment–response relationships among defensible space and structures that survived wildfire showed that, when all structures are considered together, the mean actual defensible space that existed around structures before the fires was longer than the calculated effective treatment (Table 3). Regardless of whether the defensible space was measured within or beyond property boundaries, the estimated effective treatment of defensible space was nearly the same at 10 m (32–33 ft).

The effective treatment distance was much shorter for structures on shallow slopes (4–5 m (13–16 ft)) than for structures on steep slopes (20–25 m (65–82 ft)), but in all cases was <30 m (<100 ft). Although longer distances of defensible space were calculated as effective on steeper slopes, these structures actually had shorter mean distances of defensible space around their properties than structures on low slopes (Table 3).

The calculated effective treatment of the mean percentage clearance on properties was 36% for all properties, 31% for structures on shallow slopes and 37% for structures on steep slopes (Table 3). In total, the properties all had higher actual percentage clearance on their property than was calculated to be effective. However, this mainly reflects the shallow-slope properties, as those structures on steep slopes had less clearance than the effective treatment.

### *Multiple regression analysis*

When defensible space was measured only to the property boundaries, it was not included in the best model, according to the all-subsets multiple regression analysis (Table 4). However, it was included in the best model when factoring in the distance of defensible space measured beyond property boundaries (Table 5). In both multiple regression analyses, low housing density and shorter distances to major roads were ranked as the most important variables according to their Akaike weights. Slope and surrounding fuel type were also in both of the best models as well as other measures of defensible space, including the percentage clearance on property and whether vegetation was overhanging the structure's roof. The number of sides in which vegetation was touching the structure was included in the best model when defensible space was only measured to the property boundary. The total explained deviance for the multiple regression models was low (12–13%) for both analyses.

**Table 4. Results of multiple regression models of destroyed homes using all possible variable combinations and corrected Akaike's Information Criterion (AICc)**

Includes variables measured within property boundary only. Top-ranked models include all those ($n = 12$) with AICc within 2 of the model with the lowest AICc. Relative variable importance is the sum of 'Akaike weights' over all models including the explanatory variable

| Variable in order of importance | Relative variable importance | Model-averaged coefficient | Number inclusions in top-ranked models |
|---|---|---|---|
| Housing density | 1 | −0.003 | 12 |
| Distance to major road | 1 | −0.0005 | 12 |
| Percentage clearance | 1 | −0.02 | 12 |
| Slope | 1 | 0.03 | 12 |
| Vegetation overhang roof | 1 | 0.5 | 12 |
| Fuel type | 0.67 | Factor | 9 |
| Vegetation touch structure | 0.49 | 0.07 | 6 |
| Distance defensible space within property | 0.45 | −0.0002 | 5 |
| South-westness | 0.36 | −0.0007 | 3 |
| Distance to minor road | 0.28 | −0.0002 | 1 |
| $D^2$ of top-ranked model | | | 0.123 |

**Table 5. Results of multiple regression models of destroyed homes using all possible variable combinations and corrected Akaike's Information Criterion (AICc)**

Includes variables measured beyond property boundary. Top-ranked models include all those ($n = 6$) with AICc within 2 of the model with the lowest AICc. Relative variable importance is the sum of 'Akaike weights' over all models including the explanatory variable

| Variable in order of importance | Relative variable importance | Model-averaged coefficient | Number inclusions in top-ranked models |
|---|---|---|---|
| Housing density | 1 | −0.003 | 6 |
| Distance to major road | 1 | −0.0005 | 6 |
| Total distance defensible space | 1 | −0.004 | 6 |
| Percentage clearance | 1 | −0.01 | 6 |
| Vegetation overhang roof | 0.99 | 0.4 | 6 |
| Slope | 0.99 | 0.03 | 6 |
| Fuel type | 0.86 | Factor | 4 |
| South-westness | 0.42 | −0.0009 | 2 |
| Distance to minor road | 0.36 | −0.0009 | 2 |
| Neighbours' vegetation | 0.27 | 0.08 | 1 |
| Vegetation touch structure | 0.27 | 0.18 | 1 |
| $D^2$ of top-ranked model | | | 0.125 |

### *Surrounding matrix*

The cover type that most frequently surrounded the structures at the end of the defensible space measurements was urban vegetation, followed by urban vegetation leading into wildland vegetation, and wildland vegetation (Fig. 5). Many structures were equally surrounded by different cover types. There were no significant differences in the proportion of structures destroyed depending on the surrounding cover type. However, a disproportionately large proportion of structures burned (28 *v.* 9% unburned) when they were surrounded by urban vegetation that extended straight into wildland vegetation.

## Discussion

For homes that burned in southern Californian urban areas adjacent to non-forested ecosystems, most burned in high-intensity Santa Ana wind-driven wildfires and defensible space increased the likelihood of structure survival during wildfire. The most effective treatment distance varied between 5 and 20 m (16–58 ft), depending on slope and how the defensible space was measured, but distances longer than 30 m (100 ft) provided no significant additional benefit. Structures on steeper slopes benefited from more defensible space than structures on shallow slopes, but the effective treatment was still less than 30 m (100 ft). The steepest overall decline in destroyed structures occurred when mean defensible space increased from 0–7 m (0–25 ft) to 8–15 m (26–50 ft). That, along with the multiple regression results showing the significance of vegetation touching or overhanging the structure, suggests it is most critical to modify vegetation immediately adjacent to the house, and to move outward from there. Similarly, vegetation overhanging the structure was also strongly correlated with structure loss in Australia (Leonard *et al.* 2009).

In terms of fuel modification, the multiple regression models also showed that the percentage of clearance was just as, or more important than, the linear distance of defensible space.

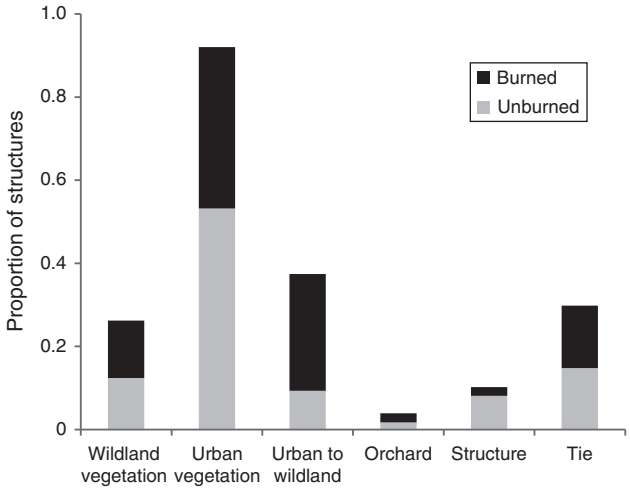


**Fig. 5.** Proportion of destroyed and unburned structures based on the primary surrounding cover type at the end of defensible space measurements. There were no significant differences in the proportion of burned and unburned structures within cover types ($P = 0.14$). Cover types are defined in Table 1.

However, as with defensible space, percentage clearance did not need to be draconian to be effective. Even on steep slopes, the effective percentage clearance needed on the property was <40%, with no significant advantage beyond that. Although these steep-slope structures benefited more from clearance, they tended to have less clearance than the effective amount, which may be why slope was such an important variable in the multiple regression models. Shallow-slope structures, in contrast, had more clearance on average than was calculated to be effective, suggesting these property owners do not need to modify their behaviours as much relative to people living on steep slopes.

Although the term 'clearance' is often used interchangeably with defensible space, this term is incorrect when misinterpreted to mean clearing all vegetation, and our results underline this difference. The idea behind defensible space is to reduce the continuity of fuels through maintenance of certain distances among trees and shrubs. Although we could not identify the vertical profile of fuels through Google Earth imagery, the fact that at least 60% of the horizontal woody vegetative cover can remain on the property with significant protective effects demonstrates the importance of distinguishing defensible space from complete vegetation removal. Thus, we suggest the term 'clearance' be replaced with 'fuel treatment' as a better way of communicating fire hazard reduction needs to home owners.

The percentage cover of woody shrubs and trees was not evenly distributed across properties, and we did not collect data describing how the cover was distributed. Considering the importance of defensible space and vegetation modification immediately adjacent to the structure, it should follow that actions to reduce cover should also be focussed in close proximity to the structure. The hazard of vegetation near the structure has apparently been recognised for some time (Foote *et al.* 1991; Ramsey and McArthur 1994), but it is not stressed enough, and rarely falls within the scope of defensible space guidelines or ordinances.

In addition to the importance of vegetation overhanging or touching the structure, it is important to understand that ornamental vegetation may be just as, if not more, dangerous than native vegetation in southern California. Although the results showed no significant differences in the cover types in the surrounding matrix, there was a disproportionately large number of structures destroyed (28% burned *v.* 9% unburned) when ornamental vegetation on the property led directly into the wildland. Ornamental vegetation may produce highly flammable litter (Ganteaume *et al.* 2013) or may be particularly dangerous after a drought when it is dry, or has not been maintained, and species of conifer, juniper, cypress, eucalypt, *Acacia* and palm have been present in the properties of many structures that have been destroyed (Franklin 1996). Nevertheless, ornamental vegetation is allowed to be included as defensible space in many codes and ordinances (Haines *et al.* 2008).

One reason that longer defensible space distances did not significantly increase structure protection may be that most homes are not destroyed by the direct ignition of the fire front but rather due to ember-ignited spot fires, sometimes from fire brands carried as far as several km away. Although embers decay with distance, the difference between 30 and 90 m (100 and 300 ft) may be small relative to the distance embers travel under the severe wind conditions that were present at the time of the fires. The ignitability of whatever the embers land on, particularly adjacent to the house, is therefore most critical for propagating the fire within the property or igniting the home (Cohen 1999; Maranghides and Mell 2009).

Aside from roofing or home construction materials and vegetation immediately adjacent to structures (Quarles *et al.* 2010; Keeley *et al.* 2013), the flammability of the vegetation in the property may also play a role. Large, cleared swaths of land are likely occupied at least in part by exotic annual grasses that are highly ignitable for much of the year. Conversion of woody shrubs with higher moisture content into low-fuel-volume grasslands could potentially increase fire risk in some situations by increasing the ignitability of the fuel; and if the vegetation between a structure and a fire is not readily combustible, it could protect the structure by absorbing heat flux and filtering fire brands (Wilson and Ferguson 1986).

The slight increase in proportion of structures destroyed with longer distances of defensible space within parcel boundaries was surprising. However, that increase was not significant in the Chi-square analysis, although there were some significant differences in the pairwise relative risk analysis. Nevertheless, the largest significant effect of defensible space was between the categories of 0–7 m (0–25 ft) to 8–15 m (26–50 ft), and it may be that differences in categories beyond these distances are not highly meaningful or reflect an artefact of the definition of distance categories. These relationships at longer distances are likely also weak compared to the effect of other variables operating at a landscape scale. Although the categorical analysis allowed us to answer questions relative to legal requirements and specific distances, the effective treatment analysis was important for identifying thresholds in the continuous variable.

The multiple regression models showed that landscape factors such as low housing density and longer distances to major roads were more important than distance of defensible space for explaining structure destruction, and the importance of

these variables is consistent with previous studies (Syphard *et al.* 2012, 2013), despite the smaller spatial extent studied here. Whereas this study used an unburned control group exposed to the same fires as the destroyed structures, previous studies accounted for structures across entire landscapes. The likelihood of a fire destroying a home is actually a result of two major components: the first is the likelihood that there will be a fire, and the second is the likelihood that a structure will burn in that fire. In this study, we only focussed on structure loss given the presence of a fire, and the total explained variation for the multiple regression models was quite low at ~12%. However, when the entire landscape was accounted for in the total likelihood of structure destruction, the explained variation of housing density alone was >30% (Syphard *et al.* 2012). One reason for the relationship between low housing density and structure destruction is that structures are embedded within a matrix of wildland fuel that leads to greater overall exposure, which is consistent with Australian research that showed a linear decrease of structure loss with increased distance to forest (Chen and McAneney 2004). That research, however, only focussed on distance to wildland boundaries and did not quantify variability in defensible space or ornamental vegetation immediately surrounding structures. Thus, fire safety is important to consider at multiple scales and for multiple variables, which will ultimately require the cooperation of multiple stakeholders.

## Conclusions

Structure loss to wildfire is clearly a complicated function of many biophysical, human and spatial factors (Keeley *et al.* 2009; Syphard *et al.* 2012). For such a large sample size, we were unable to account for home construction materials, but this is also well understood to be a major factor, with older homes and wooden roofs being most vulnerable (Franklin 1996; Cohen 1999, 2000). In terms of actionable measures to reduce fire risk, this study shows a clear role for defensible space up to 30 m (100 ft). Although the effective distances were on average much shorter than 30 m (100 ft), we recognise that additional distance may be necessary to provide sufficient protection to firefighters, which we did not address in this study (Cheney *et al.* 2001). In contrast, the data in this study do not support defensible space beyond 30 m (100 ft), even for structures on steep slopes. In addition to the fact that longer distances did not contribute significant additional benefit, excessive vegetation clearance presents a clear detriment to natural habitat and ecological resources. Results here suggest the best actions a homeowner can take are to reduce percentage cover up to 40% immediately adjacent to the structure and to ensure that vegetation does not overhang or touch the structure.

In addition to defensible space, this study also underlines the potential importance of land use planning to develop communities that are fire safe in the long term, in particular through their reduction to exposure to wildfire in the first place. Localised subdivision decisions emphasising infill-type development patterns may significantly reduce fire risk in the future, in addition to minimising habitat loss and fragmentation (Syphard *et al.* 2013). This study was conducted in southern California, which has some of the worst fire weather in the world and many properties surrounded by large, flammable exotic trees. Therefore, recommendations here should apply to other non-forested ecosystems as well as many forested regions.

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# Chapter 12
# Chaparral Landscape Conversion in Southern California

**Alexandra D. Syphard, Teresa J. Brennan, and Jon E. Keeley**

*Southern California, where the American Dream came too true*

*–Lawrence Ferlinghetti*

**Abstract** The low-elevation chaparral shrublands of southern California have long been occupied and modified by humans, but the magnitude and extent of human impact has dramatically increased since the early 1900s. As population growth started to boom in the 1940s, the primary form of habitat conversion transitioned from agriculture to urban and residential development. Now, urban growth is the primary contributor, directly and indirectly, to loss and fragmentation of chaparral landscapes. Different patterns and arrangements of housing development confer different ecological impacts. We found wide variation in the changing extent and pattern of development across the seven counties in the region. Substantial growth in lower-density exurban development has been associated with high frequency of human-caused ignitions as well as the expansion of highly flammable non-native annual grasses. Combined, increases in fire ignitions and the extent of grassland can lead to a positive feedback cycle in which grass promotes fire and shortens the fire-return interval, ultimately extirpating shrub species that are not adapted to short fire intervals. An overlay of a 1930s vegetation map with maps of contemporary vegetation showed a consistent trend of chaparral decline and conversion to sage scrub or

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grassland. In addition, those areas type-converted to grassland had the highest fire frequency over the latter part of the twentieth century. Thus, a continuing trend of population growth and urban expansion may continue to threaten the extent and intactness of remaining shrubland dominated landscapes. Interactions among housing development, fire ignitions, non-native grasses, roads, and vehicle emissions make fire prevention a complex endeavor. However, land use planning that targets the root cause of conversion, exurban sprawl, could address all of these threats simultaneously.

**Keywords** Chaparral · Fire · Housing development · Land use change · Non-native species · Vegetation change

## 12.1 Introduction

For thousands of years, humans have occupied the vast shrublands blanketing the foothills and mountains of southern California. Native Americans altered their environment to protect and sustain themselves, particularly via controlled burning to open up shrubland landscapes (see Chap. 4). Subsequently, the arrival of Euro-American settlers in the late eighteenth century brought about a sequence of progressively intense phases of rapid population growth and landscape conversion. The California Gold Rush and statehood brought one of the first population booms in 1850, and shortly thereafter, the region was linked to the railroad, enabling faster and safer immigration to the region from the rest of the country. Transportation via automobile soon became possible in the early 1900s, which facilitated even more immigration; plus, it enabled the beginning of suburban development outside of the region's main urban centers, such as Los Angeles and San Diego.

Throughout the progression of the twentieth century, southern California has continued to offer a wide range of economic opportunities. When coupled with the mild Mediterranean-type climate, these have made the region one of the most desirable places to live in the US. In particular, people flocked to the region with the discovery of oil at the turn of the century, which was then followed by growth in numerous other industries, including military defense production, agriculture, and the film industry. In the middle of the century, human population growth exploded; the accompanying massive change in land use dramatically altered the extent and composition of the native vegetation communities in the region. Although large expanses of native shrublands still exist in many areas, southern California has come to be viewed by the world as the land of freeways, strip malls, and endless housing developments.

In this chapter, we explore the trends and drivers of vegetation change in southern California since the early 1900s. In particular, we focus on the interactions between direct habitat conversion through urban growth and indirect changes

brought on by non-native annual grasses, increased frequency of fires, and the resultant loss of native shrublands.

## 12.2 Habitat Conversion

### *12.2.1 Overview of Land Use Change*

By the middle Holocene, Indian populations dominated much of coastal California, and they had a significant impact on landscape patterns through repeated burning and displacement of chaparral with more productive herbaceous communities (see Chap. 4). In the late eighteenth century, Spanish settlements initiated a new wave of changes with the introduction of a wide selection of non-native annual grasses and forbs (Mack 1989). The economy of these early settlements was based on cattle production, and the Mexican vaqueros would often burn off shrublands to increase grazing lands (Kinney 1887). Ever since then, rangeland management has had a significant component of repeated burning of shrublands to increase forage for livestock (Keeley and Syphard 2018).

One of the most significant changes in plant community composition with Euro-American settlement was the replacement of native vegetation with non-native grassland. As a result, non-native annuals were likely a large component of California grasslands by the 1850s (Burcham 1956). Livestock grazing undoubtedly has contributed substantially to this shift (D'Antonio et al. 1992), often in combination with severe droughts (Burcham 1956). Nevertheless, even in the absence of grazing, non-native annuals introduced by Euro-American settlers likely outcompeted native bunch grasses (Bartolome and Gemmill 1981). Intentional conversion of shrublands to create grassland for grazing was common across California (Burcham 1956; Keeley and Fotheringham 2003). Similar patterns of type-conversion have occurred over the 10,000-year history of human occupation in the Mediterranean Basin, where transitions from woody to herbaceous species have also been caused by human disturbance via livestock grazing and accelerated burning due to anthropogenic ignitions. However, in California, this loss of woody cover degrades natural systems and diminishes their conservation value by displacing native flora with non-native species. In the Mediterranean Basin, type-conversion replaces woody natives with herbaceous natives, and thus, native biodiversity increases.

In the early twentieth century, conversion of natural habitat into agricultural lands was the most dominant form of land use change, and by the 1930s, approximately 20% of the land within the South Coast Ecoregion had become croplands, with citrus and other fruit trees becoming especially extensive. At this time, southern California was considered one of the top agricultural regions in the US. However, with population growth and evolving economic opportunities, farming was largely wiped out in the middle of the century in favor of commercial and residential

development, a trend that was common nationwide (Alig and Plantinga 2004). In the South Coast Ecoregion of California, less than five percent of the croplands mapped in the 1930s were still present by the early 2000s (derived from data described in next section).

Urban and residential development is now the top contributor to both direct and indirect habitat conversion in southern California. Not only have the major metropolitan areas become denser, but the freeway system developed in the 1940s initiated what has been an ongoing trend of "sprawl" outward from coastal cities into the inland foothills and mountains. This growth was so rapid and extensive that the San Fernando Valley outside of Los Angeles took on the name of "America's Suburb" (Roderick 2002). Across the world, southern California is still perceived as synonymous with urban sprawl.

### *12.2.2 Spatial and Temporal Patterns of Housing Growth*

The spatial pattern of housing development has important implications for landscape conversion because low-density, sprawling-type development typically consumes more land and wildlife habitat than high-density development (Odell et al. 2003). As a consequence, low-density development may have a more negative impact on biodiversity and ecosystem services (Hansen et al. 2005). On the other hand, higher-density, clustered development may be more ecologically degraded with a larger dominance of non-native species (Lenth et al. 2006). Despite these trade-offs, compact urban development has been shown to minimize ecological disruption relative to sprawling development (Sushinsky et al. 2013).

The term wildland-urban interface (WUI) has emerged in the last couple of decades to describe the characteristics and social-ecological effects of those areas where housing development is adjacent to or interspersed with wildland vegetation (Radeloff et al. 2005). Two types of WUI are typically defined, largely as a function of housing density and the extent to which houses are surrounded by wildland vegetation. The "interface WUI" describes those areas where human settlements are denser and form an edge with wildland vegetation, whereas "intermix WUI" reflects areas where sparser, lower-density housing is interspersed with wildland vegetation. Although the exact definition of intermix or interface WUI may vary slightly with regards to how it is mapped (Stewart et al. 2007), these terms have provided a useful framework for understanding how and where human settlements interact with the natural environment, and how different forms of development may differentially affect habitat change and ecological impacts (Bar-Massada et al. 2014).

The spatial pattern of urban development in any given area can vary dramatically over time, but it typically emerges as a result of different characteristic growth types (Herold et al. 2003; Dahal et al. 2017). At one end, compact and high-density development patterns usually result from infill-type growth, where new structures are built within or expand outward from existing urban areas. At the other end,

low-density, fragmented, exurban development patterns result from leapfrog-type growth in which new development occurs outside of urban areas and is typically surrounded by wildland vegetation. This lower-density exurban development, characteristic of the intermix WUI, is often the result of homeowner preferences and behaviors, including a desire to live closer to natural amenities (Netusil 2005) or lower land prices at greater distances from the urban core (Wu and Plantinga 2003).

Given the importance of both spatial extent and pattern of housing growth in terms of natural habitat conversion, we quantified historical housing trends in the South Coast Ecoregion from 1940 to 2010. To do this, we evaluated historical housing density maps (Hammer et al. 2004, available at http://silvis.forest.wisc.edu/maps/housing) within the footprint of a modified South Coast Ecoregion boundary (i.e., as in Syphard et al. 2011) that includes the full extent of the Los Padres National Forest. The maps were developed as part of a national data product in which housing density was mapped within partial census block groups and reported as housing units per square kilometer.

We quantified the extent of both low- and medium- to high-density housing from 1940 to 2010 within the seven counties that are located within the ecoregion. Instead of clipping the counties to the ecoregion boundary, we assessed housing growth for the complete extent of each county. To threshold the continuous housing data into classes of low- and medium-high-density, we selected all areas with a housing density between 6.17 and 49 houses per $km^2$ and classified them as "low density." The number 6.17 corresponds to the minimum housing density cutoff for defining low-density WUI (Radeloff et al. 2005). The threshold of $\geq$50 houses per square kilometer corresponds to those areas defined as medium- or high-density WUI. For each county in each decade, we summarized the total extent of each housing density type and calculated its proportion of the county area.

In all seven counties, housing development, and hence direct habitat conversion, increased substantially from 1940 to 2010 across the region, but the extent of development and pattern of housing growth varied over time and by county (as can be seen in the widely varying range of the Y axis in Fig. 12.1). Medium- to high-density development has dominated the counties closest to Los Angeles, but low-density housing growth has predominated in San Luis Obispo, Riverside, and San Diego counties (Figs. 12.1 and 12.2). Except for Los Angeles, which exhibited slow, steady growth in both housing-density types over time, a pulse in growth was apparent during and shortly after the 1990s for the other counties, which is consistent with nation-wide trends (Glaeser and Shapiro 2003). Orange County stands out in that, as medium-high density increased over time, low-density development has shown a slight decline across most of the record. This also has been evident in recent decades for Santa Barbara and San Luis Obispo Counties, suggesting that, in addition to urban expansion, existing urban areas in these counties may also be infilling and becoming denser. The two southern-most counties (San Diego and Riverside), on the other hand, show no sign of slowing in the expansion of low-density development.

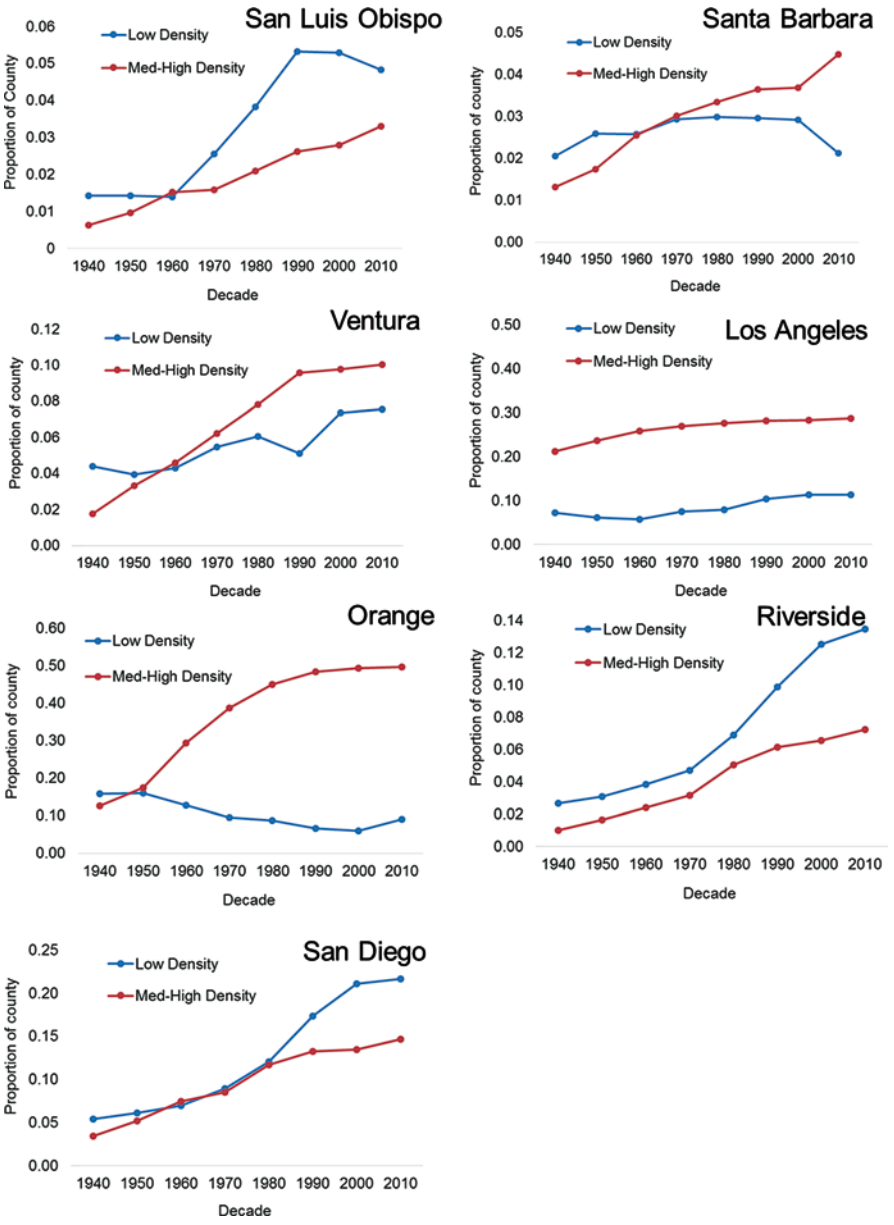


**Fig. 12.1** Growth in area (proportion of county) of low and medium-high housing density from 1940 to 2010 within the full boundaries of the seven counties overlapping the South Coast Ecoregion of southern California

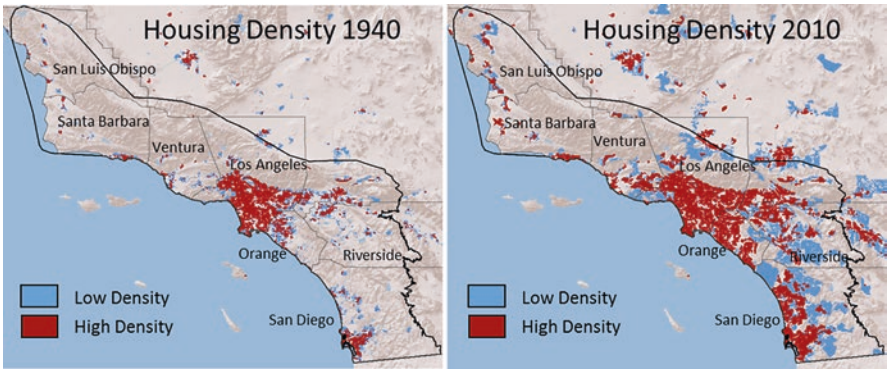


**Fig. 12.2** Maps of low and medium-high housing density in 1940 and 2010 in the South Coast Ecoregion of southern California

### *12.2.3 Indirect Habitat Loss and Conversion*

In addition to causing direct conversion of native habitat, housing development in southern California indirectly contributes to chaparral conversion, primarily by facilitating an interaction between increased fire frequency and the expansion of weedy non-native annual grasslands.

Although periodic wildfire is an essential component of chaparral ecosystems, fire frequency has been increasing in southern California to the extent that most of the landscape is burning at fire-return intervals (i.e., the time between fires at a defined area) that are uncharacteristically short relative to pre-EuroAmerican settlement conditions (Safford and Van de Water 2014). In some areas, fires are now so frequent that they outpace the historical baseline by a wide margin; for example, return intervals that once averaged 30 to more than 150 years are now shorter than 10 years in some areas (Keeley and Syphard 2018).

Given that humans cause more than 95% of the fires in the region (Syphard et al. 2007), the trend of increasing fire frequency is primarily explained by population growth and expansion of development into wildland vegetation. Although human-caused fires generally increase with human population, this relationship is mediated by population or housing density. That is, across California and other Mediterranean-type climate regions, studies show that the ignition frequencies tend to peak at low-intermediate population density, such as the WUI intermix areas (Syphard et al. 2007, 2009; Archibald et al. 2010; Syphard and Keeley 2015). The likely explanation for this is that these intermix WUI areas have both enough people to start frequent fires, which wild areas lack, and sufficient wildland areas to facilitate fire spread, which urban areas lack. These are also the areas most difficult to access for fire suppression (Gude et al. 2008).

In addition to increased fire frequency, exurban development provides conduits for non-native species to expand into wildland vegetation, via land disturbance, road networks, and residential landscaping (Gavier-Pizarro et al. 2010). Even fuelbreaks

designed to control wildfires facilitate establishment and spread of non-native species (Merriam et al. 2006). In recent studies, which assessed the ecological effects of mechanical fuel treatments on chaparral (such as removing vegetation with bulldozers), it was found that treated sites had a significantly lower cover and density of shrubs and a significantly higher cover and density of herbaceous plants (Brennan and Keeley 2015). The increase in herbaceous plants was dominated by non-native species and in particular by non-native annual grasses. Sites that were treated a second time had more than twice the cover and density of non-native species than single treatments and were clearly showing more signs of degradation and type-conversion, that is, a shift in physiognomic structure from woody shrubland to herbaceous cover. These treatments are frequently used near housing developments within the WUI; and over time, with periodic retreatment, will most likely be completely type-converted to non-native annual grasslands.

The weedy annual grasses that have invaded vast portions of southern California are highly flammable and tolerant of rapidly repeating fires. In the absence of disturbance, chaparral shrublands are relatively resistant to invasion by non-native species, in part due to their dense cover and closed canopy. However, increased human ignitions in these fire-prone grasslands has lengthened the fire season, thereby increasing canopy opening and providing new establishment opportunities for these well-dispersed grasses. This positive feedback process between fires and grass expansion is typically referred to as a grass-fire cycle, and it is recognized as a potential problem in ecosystems across the world (e.g., D'Antonio and Vitousek 1992; Rossiter et al. 2003; Brooks et al. 2004; Bowman et al. 2014), including southern California shrublands (Keeley et al. 2012).

The larger ecological issue is that, despite native shrublands' resilience to periodic wildfire, too-short intervals between fires can lead to their extirpation. This is because many species require a minimum amount of time between fires to recover and regenerate. Non-resprouting species—i.e., obligate seeders—may require up to 25 years to fully establish a seedbank that can effectively recruit new plants after fire (Keeley 1986). Although re-sprouting chaparral species are resilient to shorter intervals between fires than non-re-sprouters, even re-sprouters were reduced when multiple fires occurred within in a six-year interval (Haidinger and Keeley 1993). Thus, as native shrubland species are extirpated, providing opportunities for further grass expansion, the potential exists for large scale vegetation type-conversion.

A number of studies in southern California have provided evidence of vegetation type-conversion from shrubland to grassland. Particularly widespread has been the conversion of coastal sage scrub to non-native grasses (Minnich and Dezzani 1998; Cox et al. 2014). Talluto and Suding (2008) found nearly 50% replacement of sage scrub by annual grasses within a 76-year study period in parts of Orange and Riverside Counties, with a substantial amount being due to fire frequency. Because sage scrub is generally more tolerant of higher fire frequencies than chaparral, chaparral may be even more vulnerable to vegetation type-conversion, depending on species composition and site factors. In some cases, it may even transition to sage scrub vegetation before finally transitioning to herbaceous cover (Syphard et al. 2006).

Chaparral conversion to grasslands after repeated fires has been documented in many localized studies (e.g., Zedler et al. 1983; Haidinger and Keeley 1993; Lippitt et al. 2012; Keeley and Brennan 2012). Given the consistency in these findings across the southern California region, and the fact that large areas across the region have experienced short fire-return intervals, there is reason to suspect that widespread conversion due to repeated fires has already occurred (Keeley 2010). Nevertheless, the empirical evidence for larger landscape scale changes in chaparral has been sparse, with one recent study even questioning the potential for widespread vegetation type change in chaparral to occur (Meng et al. 2014).

## 12.3 Landscape Scale Vegetation Type-Conversion

As a general means of quantifying historical vegetation change in concert with mean historical fire frequency in southern California, we overlaid contemporary maps of existing vegetation with an historical map delineating broad scale vegetation types and then integrated data on fire frequency. We estimated change using maps from multiple data sources because of the potential for vegetation to be mapped differently. Although variation is much more likely given finer scale vegetation classification schemes, there may even be differences in the way broad vegetation types are mapped due to differences in mapping methods, scales, and definitions.

The historical vegetation type maps (VTM) were developed between the years 1929 and 1934 (Wieslander 1935) as part of an extensive statewide mapping project. In addition to detailed species level plot information, vegetation types and dominant species were mapped on 15-minute topographic quadrangles in the field with a minimum mapping unit of 16 ha (39.5 acres) (Kelly et al. 2005; Kelly 2016). The first contemporary map we evaluated represents existing vegetation and was produced by the US Forest Service using a combination of satellite imagery, field verification, and expert guidance (CalVeg, http://www.fs.fed.us/r5/rsl/projects/classification/system.shtml). The majority of the area in this map was most recently updated in 2002. However, the national forest lands were updated more recently, in 2003, 2009, or 2010. The entire region was mapped at a scale of 1:24,000.

Both the VTM and CalVeg maps provide classification according to the California Wildlife Habitat Relationships System (Mayer and Laudenslayer 1988). Therefore, for both of these maps, we grouped vegetation classes into life-forms, including tree, shrub, coastal sage scrub, and herbaceous. For the other categories, which are mostly unvegetated (e.g., urban/developed land) or wetland, we lumped them into a class named "other."

We also evaluated the 2013 Landfire existing vegetation maps, which were developed based on a combination of decision tree models, field data, Landsat 7 imagery, elevation, and biophysical gradient data (http://landfire.cr.usgs.gov/viewer/ [2013, May 8]). The map comes as a grid at 30 m (0.2 acres) resolution. We developed map classes to match the vegetation types in the other two maps using the map

**Table 12.1** Proportion of vegetation types within the historical (VTM) and contemporary (San Diego County, CalVeg, and Landfire) maps

| Vegetation Type | VTM | San Diego | CalVeg | Landfire |
|---|---|---|---|---|
| Grass | 0.06 | 0.09 | 0.12 | 0.27 |
| Sage scrub | 0.29 | 0.24 | 0.10 | 0.06 |
| Shrubland | 0.45 | 0.35 | 0.43 | 0.19 |
| Tree | 0.08 | 0.09 | 0.12 | 0.18 |
| Other | 0.13 | 0.23 | 0.23 | 0.29 |
| Total | 1.0 | 1.0 | 1.0 | 1.0 |

attribute based on the National Vegetation Classification System Physiognomic Order. Any area that was classified as "sparsely vegetated," "barren," "water," "developed," or "agriculture" in the Landfire vegetation type classification, we converted to the "other" class.

At a finer resolution for a subset of the South Coast Ecoregion, we compared the VTM map to a detailed 2012 vegetation community map that spans part of San Diego County (https://databasin.org/datasets/bcd5db8e6aa540e6b06a371bde0afde3). This map was developed with a 1 ha (2.5 acre) minimum mapping unit for terrestrial vegetation and has an accuracy of at least 80% as determined through extensive field verification reports. The map was classified according to Sproul et al. (2011), and again, we grouped these into the same life-form vegetation classes and an "other" class.

After re-classifying the vegetation maps into physiognomic types, we quantified the proportion of each vegetation or cover type within each map. We then overlaid the contemporary maps with the VTM map and summarized the mean historical fire frequency that occurred within each change class up to 2013. To estimate the transitions between life-form classes, we assessed changes from shrub to grass, sage scrub to grass, shrub to sage scrub, tree to earlier successional class (shrub, sage scrub, or grass), successional (e.g., grass to sage scrub, sage scrub to shrub, shrub to tree), no change in vegetation, or other (i.e., unvegetated in either map. We used the California Department of Forestry–Fire and Resource Assessment Program (CDF-FRAP 2013) map of overlapping historical fire perimeters (wildfire only) to create a continuous 30 m grid with each cell representing the number of times it had burned since 1878 (http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download). In this database, any grid cell location may have burned 0–13 times during the time period, although this may under-estimate fire frequency due to the minimum mapping unit of this dataset (Syphard and Keeley 2017).

The contemporary vegetation maps showed consistent trends of increasing grass, tree, and other cover types and decreasing sage scrub and shrubs over time (Tables 12.1 and 12.2, Fig. 12.3). There were substantial areas of agreement in the delineation of all vegetation types that did not change between the VTM map and contemporary maps (Figs. 12.4 and 12.5), particularly in CalVeg and the higher-resolution San Diego County map. The Landfire map, however, delineated a much larger pro-

**Table 12.2** Proportion of chaparral in the historical (VTM) map that transitioned to other vegetation types in contemporary (San Diego County, CalVeg, and Landfire) maps

| Chaparral Change Class | San Diego | CalVeg | Landfire |
|---|---|---|---|
| Chaparral to chaparral | 0.33 | 0.22 | 0.24 |
| Chaparral to sage scrub | 0.07 | 0.22 | 0.26 |
| Chaparral to grass | 0.12 | 0.10 | 0.26 |
| Chaparral to tree | 0.40 | 0.27 | 0.17 |
| Chaparral to other | 0.09 | 0.20 | 0.07 |
| Total | 1.0 | 1.0 | 1.0 |

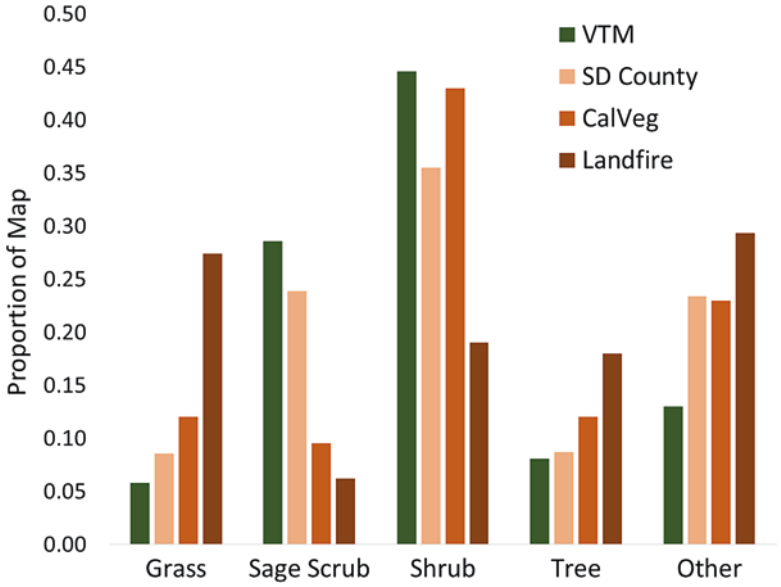


**Fig. 12.3** Proportion of vegetation type within four vegetation maps of the South Coast Ecoregion (VTM 1930s; CalVeg 2002; Landfire 2013) and San Diego County (2012)

portion of the landscape as grassland than the other two contemporary maps (Fig. 12.4c). This is reflected in the vast areas of the landscape that were mapped as having changed from sage scrub or shrub to grass (Fig. 12.6a).

In terms of fire frequency, the analysis showed highest mean fire frequencies in classes where either sage scrub or shrub converted to grass, or where shrub converted to sage scrub (Fig. 12.7). The mean number of fires summed across grid cells in each change class ranged from 1.55 to 2.41, but the actual number of times areas burned during the 135-year span of the fire history data ranged from 0 to13.

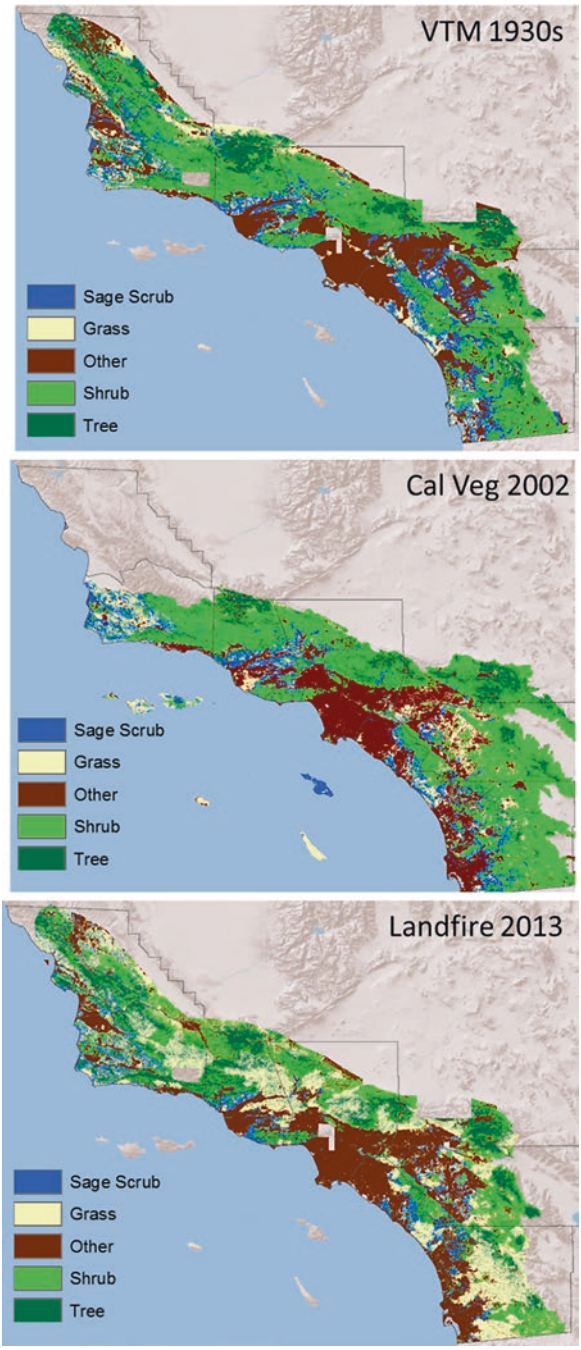


**Fig. 12.4** Vegetation types as mapped in the 1930s (VTM), 2002 (CalVeg maps), and 2013 (Landfire)

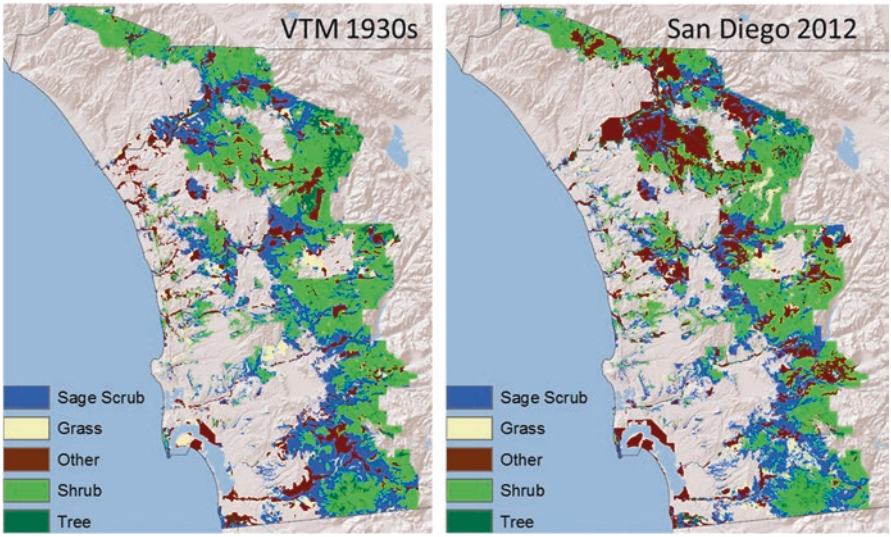


**Fig. 12.5** Comparison of vegetation type classes as mapped in the 1930s (VTM) and in 2012 (San Diego County map)

### *12.3.1 Challenges in Quantifying Vegetation Change*

The wide variation apparent among the three contemporary maps illustrates the challenge in overlapping different vegetation maps to accurately delineate and quantify vegetation change, particularly if the objective is to map change at a fine scale. There are multiple sources of uncertainty inherent in any ecological analysis (Regan et al. 2002), and spatial data are particularly susceptible to errors in map boundaries and classification (Goodchild and Gopal 1989). Nevertheless, when vegetation map classes are collapsed into broad categories reflecting vegetation formations, map accuracy can be relatively high (Goodchild et al. 1991).

Clearly, the extent and location of vegetation type-conversion cannot be precisely determined from our analysis, and the vast areas of type change from shrub or scrub to grass mapped using the Landfire data should be interpreted with some caution given that many of these areas were not mapped as grass in the other two contemporary maps. Nevertheless, despite the variation among contemporary maps, the results of all three overlays were remarkably consistent in the kind of change measured. Thus, even using the most conservative estimates, there has been a clear trend of chaparral decline and conversion to either sage scrub or grassland over the last 70–80 years. Furthermore, fire frequency tends to be highest where these changes have been mapped (Fig. 12.7).

In the southern California landscape, the most likely explanation for the differences in maps is the treatment of mixed classes. Depending on the scale of the analysis relative to the heterogeneity of the vegetation, mixed grass and shrub stands must often be lumped into one class or the other. Thus, many of the areas mapped

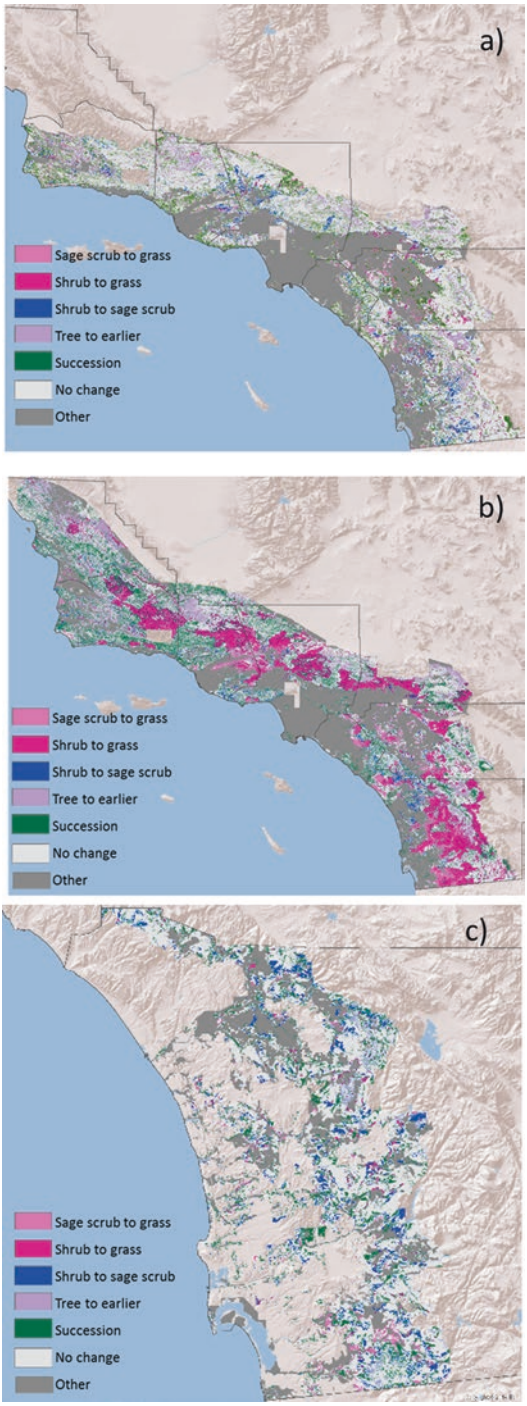


**Fig. 12.6** Maps of vegetation type change from (**a**) the 1930s to 2002 (CalVeg), (**b**) the 1930s to 2013 (Landfire), and (**c**) the 1930s to 2012 (San Diego County map)

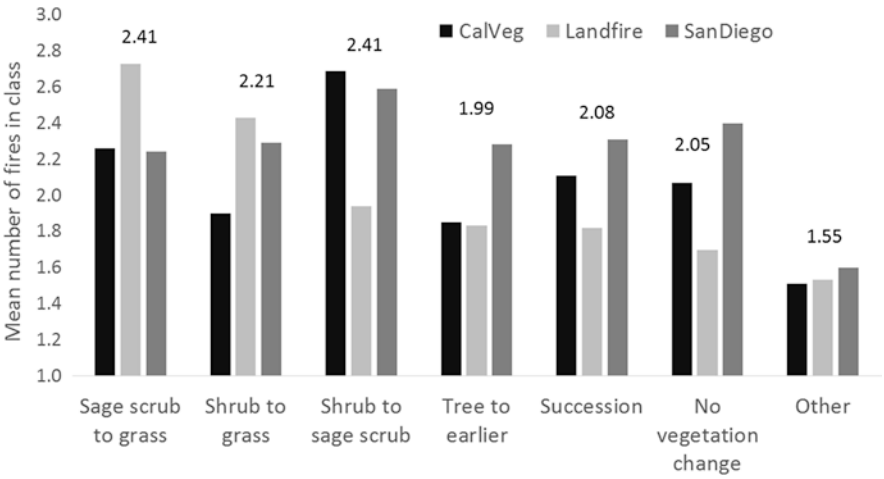


**Fig. 12.7** Mean number of fires from 1878–2013 within each vegetation type change class between the 1930s and 2002, using data from CalVeg (2002), Landfire (2013), and San Diego County maps (2012). Numbers above the bars indicate the mean fire frequency averaged across the three maps. "Tree to other" reflects any changes in which trees changed to shrub, sage scrub, or grass. "Succession" reflects any changes in which grass changed to shrub or sage scrub, or sage scrub changed to shrub

as grass in the Landfire map, and mapped as some type of shrubland in the CalVeg or San Diego County map, were probably some mixture of shrub and grass.

Whether these classes were purely grass or represented some mixture with shrubs is one of the central challenges in quantifying landscape scale vegetation change. It also provides one reason for questioning Meng et al.'s (2014) conclusion that widespread vegetation type-conversion is not an immediate threat in southern California, as vegetation type-conversion does not occur as a complete shift at one moment in time. Instead, it occurs as a gradual and cumulative process, which often begins with the elimination of non-resprouting species within mixed stands, habitat simplification, and biodiversity loss (Keeley et al. 2005). In addition, because sage scrub can withstand higher fire frequencies than chaparral, vegetation change may begin with a gradual shift from stands of pure chaparral to mixed stands of chaparral, sage scrub, and grass. This type of transition is suggested in the results here that show substantial change from shrub to sage scrub under higher mean fire frequencies. Given that different species have varying sensitivities to repeat fires, and that overlapping fires exhibit fragmented spatial patterns, multiple repeat fire events are probably necessary for significant vegetation change to be discernable. Thus, one of the methodological challenges in landscape scale analyses like those in Meng et al. (2014) is that type-conversion is only inferred, and the gradual process of vegetation change cannot be documented at a specific location over time the way it can in field studies (Halsey and Syphard 2015). Another challenge is that substantial chaparral conversion had already occurred before vegetation maps became available for modern analysis. There is evidence of chaparral conversion prior to the twentieth cen-

tury (Cooper 1922), and evidence has also been documented in field studies. In summary, vegetation change is complex, gradual, and related to site factors in addition to long-term fire history and plant community composition. These factors need to be resolved and better understood when considering the potential for future chaparral conversion.

## 12.4 Ecological and Social Consequences of Chaparral Loss

In addition to the loss of plant biodiversity that occurs with habitat conversion, many rare and sensitive animal species depend on vegetation structure for their habitat (see Chaps. 2 and 3). The native coastal sage and chaparral shrublands, as well as riparian areas and oak woodlands, provide important habitat for a wide range of bird, insect, mammal, and herpetofauna species, and the negative effects of habitat loss and fragmentation have been documented for decades in numerous studies (e.g., Bolger 1991; Soulé et al. 1992; Bolger et al. 2000; Riley et al. 2003; Ruell et al. 2012). Recent studies are also beginning to show how interactions among direct and indirect effects (e.g., fire, climate change, non-native species) of urban development contribute to biodiversity loss (e.g., Franklin et al. 2014; Conlisk et al. 2015; Jennings et al. 2016).

Changes in vegetation structure that occur with the conversion of shrublands to grasslands also impact the physical and hydrological properties of the soil (Martinez-Fernandez et al. 1995; Williamson et al. 2004). The increased density of plants combined with changes in the canopy shape and root distribution of individuals significantly alter how rainfall and organic matter are channeled into and through the soil (Lee and Lauenroth 1994; Martinez-Meza and Whitford 1996). The resultant changes affect the infiltration capacity and water retention of the soil as well as the concentration and dispersal of nutrients and carbon (Gutierrez et al. 1995; Martinez-Fernandez et al. 1995). Shrublands that have been converted to grasslands have more extreme soil temperatures and they tend to develop a thicker, more variable surface (A) horizon with a significantly higher soil bulk density (Williamson et al. 2004). These changes in root distribution decrease the stability of slopes while increasing the potential for hazardous debris flows (Gabet and Dune 2002). External factors such as fire and flooding can further exacerbate the system by increasing runoff and soil erosion, which in turn have the potential to affect water quality and reservoir infilling (Hubbert et al. 2012). Finally, shrublands have substantially better capacity for ecosystem carbon sequestration than grasses (Petrie et al. 2015), which has critical implications in this era of rapid climate change.

Development patterns and chaparral conversion are not only important in terms of ecological effects, but from a social perspective, the intermix WUI areas are also the locations where houses are most likely to be destroyed by wildfire in southern California (Syphard et al. 2012). Large fires at the WUI have been occurring for decades in the region, with an average of 500 houses lost per year in the last 50 years. Furthermore, the rate of destroyed houses and lost lives in the last 10–15 years has been unprecedented (Keeley et al. 2013).

## 12.5 Discussion and Future Changes

As we march into the twenty-first century, the acceleration of global change is bound to occur, especially given the projections of continued population growth. For example, the San Diego Association of Governments expects a 140% increase in population by 2050 across the county (www.sandag.org/2050forecast). Thus, continuation of direct habitat conversion, particularly in the form of urban development, will continue to reduce and fragment chaparral habitat, as well as increase the length and extent of the WUI (Landis and Reilly 2003; Hammer et al. 2009). Furthermore, these land use changes will likely continue to interact with indirect drivers of conversion, including fire and invasion by non-native grasses.

Climate change will also likely result in chaparral species' range shifts, and possibly type-conversion, through habitat shifts and modifying phenology (Chen et al. 2011; Beltrán et al. 2014, see Chap. 14). However, it is the interaction of climate with the drivers discussed here that may be of most concern (Syphard et al. 2013b; Franklin et al. 2014). For example, future projections suggest that land use change will likely either override or compound the impacts of climate change on shrubland habitat conversion across the state of California (Mann et al. 2014; Riordan and Rundel 2014), and in southern California, loss of chaparral species' suitable habitat may be exacerbated by urban growth, with fire being the most serious threat for obligate seeding chaparral species (Syphard et al. 2013b; Bonebrake et al. 2014). Fire regimes, however, are more likely to be altered due to land use change rather than climate change in chaparral shrublands, as fire activity has not been significantly correlated with historical patterns of temperature and precipitation in these areas (Keeley and Syphard 2015, 2016, 2018). This may be due to the fact that climatic conditions are already suitable for extreme fire activity every year on these landscapes. On the other hand, changing patterns and timing of ignitions may have profound impacts on fire activity and its social and ecological consequences (Syphard and Keeley 2015).

Although the South Coast Ecoregion is relatively homogenous in terms of broad scale climatic and vegetation patterns, questions of scale and geographical context will be important when considering future management needs and priorities. For example, species with similar functional traits and sensitivities to certain threats may be differentially exposed to those threats depending on their distributions (Syphard et al. 2013b). That is, areas with the fastest climate change may not always be the same as the areas of fastest land use change or disturbance regime shifts.

Within the South Coast Ecoregion, different counties have unique histories of development and urban growth, which explains why our data show such variation in the extent and spatial pattern of housing density. Accordingly, habitat loss and fragmentation have and will continue to vary across the region. One of the most serious concerns related to chaparral conversion may be the ongoing expansion of low-density development in counties like San Diego, which still contain substantial areas of intact chaparral. Not only does continued development threaten to reduce shrubland extent and continuity, but intermix WUI is the area most prone to non-native annual grass expansion, increased fire frequency, and corresponding fire risk.

One major concern associated with the increase in fires in the southern California region is that vast areas are now covered with very young chaparral due to the enormous extent of recent wildfires. Also, there have already been extensive areas within southern California that have recently burned at anomalously short intervals (Keeley et al. 2009). These trends greatly increase the risk for future conversion to annual non-native grass. An additional potential factor is increased atmospheric pollution. Non-native grasses respond favorably to elevated atmospheric nitrogen deposition, which will likely accelerate with ongoing development (Cox et al. 2014).

Given the profound recent loss of human lives and property in southern California associated with wildfire, there has been a growing sense of urgency to identify new ways to reduce fire risk and ensure community safety. Aside from active fire suppression to control burning wildfires, the most prevalent form of management has been to burn, modify, or clear wildland vegetation to control fire behavior. While fuelbreaks can be safe and effective tools for firefighter access to chaparral communities, research shows that vegetation management in terms of prescribed fire and fuelbreaks provide little benefit for controlling the most damaging weather-driven fires (Syphard et al. 2011; Price et al. 2012; Penman et al. 2014). Given that vegetation management is a driver of chaparral conversion, trade-offs could be carefully considered in the design and placement of fuelbreaks, which ideally could be strategically placed for firefighter defense of communities.

In addition to strategically placed fuelbreaks, homeowner property preparation in terms of building construction and design and defensible space may significantly reduce the risk of a house being destroyed in a wildfire (Cohen 2004; Quarles et al. 2010; Syphard et al. 2014, 2016a). However, while defensible space does provide significant protection, the effect results primarily from modifying vegetation immediately adjacent to the structure. Research has shown there is no added benefit of treating areas farther than 100 ft. (30 m) from the property, even on steep slopes. In addition, only 40% reduction in woody cover was needed for significant protection (Syphard et al. 2014). This is important with regards to habitat, as there has been a recent push from county governments and insurance companies for homeowners to clear up to 300 ft. (60 m) of defensible space around their houses, which cumulatively could result in substantial areas of habitat loss (Keeley et al. 2013).

Considering house losses from wildfire at both local and landscape scales, the most significant factor that explains whether or not a house is destroyed has been its location and arrangement relative to other houses on the landscape (Syphard et al. 2012; Alexandre et al. 2015). Therefore, land use planning may be the most effective long-term solution for not only preventing house loss to wildfires, but also for maximizing biodiversity. Simulation studies showed that land use planning decisions, either through growth policies or through private land acquisition, could result in mutual benefits for both fire risk reduction and biodiversity conservation (Syphard et al. 2013a, 2016b; Butsic et al. 2017). In particular, both house loss and ecological impacts are likely to be most effectively minimized if future development is designed to be compact and clustered, with development restricted in either high-fire-hazard or species-rich areas, which tend to occur in the same areas (Syphard et al. 2016b). Ignition prevention efforts may also be highly effective as

part of a comprehensive fire management program (Prestemon et al. 2010; Syphard and Keeley 2015).

## 12.6 Conclusion

The sprawling development pattern in southern California has been the primary driver of contemporary chaparral conversion, both through the direct removal and fragmentation of habitat, but also through its indirect role in driving annual grass expansion associated with increased fire frequency. It is also indirectly responsible for other factors such as fuelbreaks to protect communities scattered throughout the wildland, climate change, and perhaps even the increase of nitrogen deposition. For example, the increasing road density and traffic volumes associated with increased population and urban development have and will continue to have numerous effects that threaten chaparral ecosystems. Roads are often the source of fire ignitions (Syphard and Keeley 2015), promote the spread of non-native species (Bar-Massada et al. 2014), contribute to elevated ozone and nitrogen deposition that favors grasses over shrubs (Fenn et al. 2010), and fragment habitat needed for sensitive fauna (Poessel et al. 2014).

Thus, as we move into the future, it may be well worth the effort to seriously consider how developments are designed and arranged across the landscape. Land use planning could systematically address the root causes of fire risk as well as habitat loss (Moritz et al. 2014). It could lower ignitions through reduced human presence in flammable areas, lower non-native species expansion by reducing corridors to invasion, and lower the risk of property loss by arranging houses so that they are less fire-prone (Syphard et al. 2012, 2013a). Land use planning can thus address multiple impacts of global change across California shrublands, and may ultimately be the most powerful tool for a sustainable future.

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# The relative influence of climate and housing development on current and projected future fire patterns and structure loss across three California landscapes

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ABSTRACT

Climate and land use patterns are expected to change dramatically in the coming century, raising concern about their effects on wildfire patterns and subsequent impacts to human communities. The relative influence of climate versus land use on fires and their impacts, however, remains unclear, particularly given the substantial geographical variability in fire-prone places like California. We developed a modeling framework to compare the importance of climatic and human variables for explaining fire patterns and structure loss for three diverse California landscapes, then projected future large fire and structure loss probability under two different climate (hot-dry or warm-wet) and two different land use (rural or urban residential growth) scenarios. The relative importance of climate and housing pattern varied across regions and according to fire size or whether the model was for large fires or structure loss. The differing strengths of these relationships, in addition to differences in the nature and magnitude of projected climate or land use change, dictated the extent to which large fires or structure loss were projected to change in the future. Despite this variability, housing and human infrastructure were consistently more responsible for explaining fire ignitions and structure loss probability, whereas climate, topography, and fuel variables were more important for explaining large fire patterns. For all study areas, most structure loss occurred in areas with low housing density (from 0.08 to 2.01 units/ha), and expansion of rural residential land use increased structure loss probability in the future. Regardless of future climate scenario, large fire probability was only projected to increase in the northern and interior parts of the state, whereas climate change had no projected impact on fire probability in southern California. Given the variation in fire-climate relationships and land use effects, policy and management decision-making should be customized for specific geographical regions.

## 1. Introduction

As one of the most fire-prone places in the world, California is globally recognized for its long history of wildfire-related losses of homes and human lives. Wildfire is also important for shaping ecological structure and function (van Wagtendonk, 2018), but many of California's diverse fire regimes, as those across the world, are changing in response to past fire management (e.g., Steel et al., 2015), invasive species (e.g., Syphard et al., 2017a), land use change (e.g., Mann et al., 2016), and climate change (e.g., Westerling and Bryant, 2008). Climate and land use patterns, in particular, are expected to change dramatically in the coming century, raising concern about their effects on fire regimes and subsequent impacts to human communities across the world. California is expected to embody a wide range of these changes and their impacts, and the risk to human communities is complex because it requires predicting how and where climate or land use change will alter fire patterns, i.e., the long-term spatial and temporal characteristics of fire events on a landscape. Manifestation of change will depend upon both the nature and

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strength of the drivers and their relative impacts in different regions.

There is evidence from historical patterns and modeling studies that climate change will lead to large changes in fire extent and severity (e.g., Westerling et al., 2006; Jolly et al., 2015; Abatzoglou and Williams, 2016; Restaino and Safford, 2018). However, the relationships between climate and fire are nuanced and complex (Krawchuk et al., 2009; Bradstock, 2010; Doerr and Santín, 2016) and vary in nature and strength geographically (Littell et al., 2009; Hessl, 2011; Keeley and Syphard, 2017). One of the clearest factors that determines whether a fire becomes large is wind speed (Abatzoglou et al., 2018). Large, wind-driven fire events have been responsible for the vast majority of structures lost in California wildfires (Keeley et al., 2009), including the recent fires in 2017 and 2018. Beyond weather, climate controls fire size directly via temperature, and also via its short and long-term effects on fuel volume and moisture content, which are important controls on fire behavior (Keeley and Syphard, 2016). Thus, given that hot, dry conditions are generally associated with fire, and that temperatures and moisture deficit are projected to increase globally, there is widespread concern that climate change will lead to greater fire activity. However, feedbacks between climate, vegetation, and fire are likely to mediate these effects (Bowman et al., 2014; Parks et al., 2016; Syphard et al., 2018).

Adding to the complexity, changes in human land use and population are also expected to alter spatial and temporal characteristics of future wildfires, and these effects may also interact with climate-driven effects. Humans affect fire patterns in a variety of ways, including deliberate or accidental ignitions, prescribed burning and mechanical vegetation treatments, and suppression activities; humans also change fire behavior and extent through landscape fragmentation, cultivation practices, landscaping, and flammability of buildings. Given the diversity of these effects, recent studies highlight that one of the main problems for prediction of fire patterns and related human impact is that human presence may dampen or override the influence of climate in driving fire activity (Higuera et al., 2015; Ruffault and Mouillot, 2015; Mann et al., 2016; Syphard et al., 2017b). Another complexity is that the anthropogenic and biophysical factors that influence patterns of small fires have been shown to differ from the factors that drive large fires, particularly in areas where most fires are caused by humans (Syphard et al., 2008, 2017, Barros and Pereira, 2014). This is likely due to inherent geographical and biophysical differences between those fires that are easily suppressed and those that escape control (Moritz, 1997; Hantson et al., 2015).

In California, the vast majority of fires are human-caused (Syphard et al., 2007; Balch et al., 2017), but the spatial and temporal pattern of ignition causes and patterns varies widely across the state (Keeley and Syphard, 2018). Contrary to what might be expected, fire activity is not highest where population is highest. Instead fire frequency, and to a lesser extent, area burned, tend to peak at low- to intermediate population and housing density (Syphard et al., 2007; Westerling and Bryant, 2008; Mann et al., 2016); this relationship has also been observed in other areas across the globe (Syphard et al., 2009; Aldersley et al., 2011; Bistinas et al., 2013). This hump-shaped relationship reflects, in part the increased ignitions in rural and residential areas (compared to wildlands), balanced against lower potential for fire spread and/or greater suppression in urban areas (Butsic et al., 2015).

Beyond housing density's effect on fire patterns, studies have shown that structure loss in southern California is significantly correlated with low-to-intermediate housing density (Syphard et al., 2012, 2013, 2016). Other work in southern California and Colorado (Alexandre et al., 2016a), and a national analysis across the U.S. (Alexandre et al., 2016b), identified the spatial arrangement of housing development, in addition to topographic conditions, as consistently more important than vegetation-related variables in explaining structure loss to wildfire. Although small, isolated clusters of development were consistently associated with structure loss, in some cases, high housing density in those clusters contributed to higher structure loss. In addition, high-density development has been implicated in structure loss in some fires due to fire spread among structures (Cohen and Stratton, 2008; Price and Bradstock, 2013), as seen recently in the Coffey Park neighborhood in Sonoma County, CA in 2017 (Nauslar et al., 2018). House-to-house spread is also suspected for contributing to massive structure loss in the Camp Fire in Butte County in 2018. The role of building codes and ignition resistance has yet to be examined in such loss patterns, however.

Despite clear evidence of a nonlinear relationship between housing density and patterns of fire, and subsequently on patterns of structure loss, much is unknown regarding the scale and potential thresholds that define the relationship between housing density and fire. For example, Bistinas et al. (2013) reported regionally varying thresholds determining the shape of the nonlinear relationship between population density and area burned across the globe. Much more work is needed to identify the relative roles of climate and human presence in determining fire and structure loss patterns, and to determine the extent to which these relationships vary regionally. This is particularly critical considering there have already been rapid changes in both climate patterns (Swain et al. (2018)) and land use patterns in flammable landscapes (Radeloff et al. (2018)).

To better understand the relative importance of climatic and land use factors on long-term spatial and temporal patterns of fire and structure loss and how these patterns vary from region to region, we developed an integrated modeling framework to quantify variable importance and to map the distribution of current and future projected probability of fires and structure loss in three California study areas. These regions vary biophysically but have all experienced substantial residential losses from wildfire. We first developed statistical models and maps based on the association of climate, biophysical, and anthropogenic variables with small and large fire patterns, and then we modeled structure loss as a function of those variables and the projected probabilities of large fires. After quantifying and mapping current relationships, we projected future large fire and structure loss probability under different climate and housing growth scenarios. We address the following questions:

1) How do fire patterns vary by housing density and climate?
2) How do structure loss patterns vary by housing density and climate?
3) Do these relationships vary from region to region?
4) Which is likely to be the most influential driver of future change, climate or housing development, across our study regions?

## 2. Methods

### 2.1. Study areas

The northern coastal study area (NC) includes more than 1.4 million ha of land spanning all of Lake, Sonoma, and Napa Counties, in addition to small parts of Mendocino, Glenn, Colusa, Yolo, and Solano Counties (Fig. 1). The vegetation is characterized by a mosaic of oak woodlands, grassland, chaparral, and Douglas fir/hardwood ("mixed evergreen") forests, with montane conifer forests at higher elevations. Extensive exurban development has occurred in recent decades, and numerous homes have been destroyed by fire here; in particular, the 2017 'wine country' wildfires in this region resulted in 44 lost lives and nearly 9000 destroyed buildings.

The Butte and Plumas Counties study area (BP) included the full counties, plus a 20 km buffer to incorporate a larger urban-wildland gradient (2.2 million ha). Across this gradient spanning from the Central Valley to the northern cismontane Sierra Nevada, the vegetation transitions from grassland and chaparral to mixed evergreen and then pine- and fir-dominated forests, with a very small component of subalpine forest on the highest peaks (Fig. 1). Although the higher-elevation forests are mostly protected by the U.S. Forest Service and National Park Service, substantial residential development has been

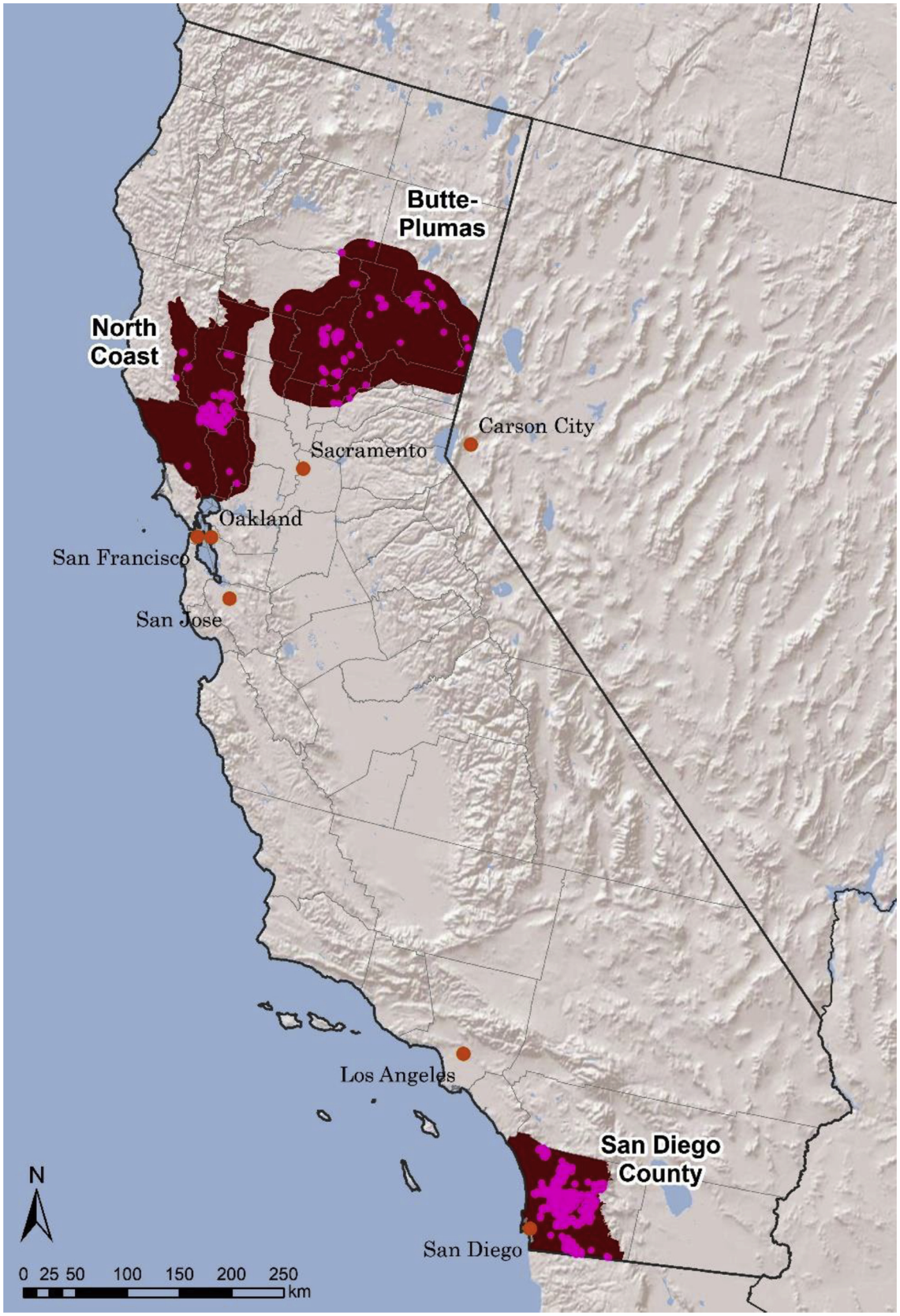


**Fig. 1.** Boundaries of three California study areas, with destroyed structure locations (2000–2015) in pink (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

occurring in the foothills. Wildfires destroyed more than 1000 structures here between 2000 and 2015 (the period we used for modeling); in 2018, the Camp Fire alone resulted in 86 fatalities and more than 18,000 destroyed structures. While all three study areas are characterized by Mediterranean climates, with warm to hot, dry summers and wet winters, BP is the only study area to receive substantial precipitation in the form of snowfall.

The third study area, coastal San Diego County (SD), is a rapidly developing, highly fire-prone region with an extensive wildland-urban interface. The majority of the study area is dominated by coastal sage and chaparral shrublands intermixed with grasslands and mixed oak woodlands, and some montane conifer forests at the highest elevations. Native shrubs are threatened by too-frequent fire, typically human-caused, which could lead to extensive replacement with more fire-prone herbaceous vegetation (Syphard et al., 2018b). Thousands of structures have been destroyed during large, Santa Ana wind-driven fire events (Keeley et al., 2009).

### 2.2. Data

For all dependent and independent variables (Table 1), we first assembled consistent statewide spatial data coverage, which we then clipped to the boundaries of the three study areas. We also rasterized all vector data, or resampled all grid data, to match the resolution of the climate variables (270 x 270 m).

#### 2.2.1. Fire data

To determine whether different factors influence fire ignitions and large fire patterns across the study areas, we created statistical models based on two sources of data (Table 1). The first dataset included the location of origin for all fires of any size from the most recent decade of data available, 2003–2013 and was available via spatial coordinates indicating the point location of fire ignition. The data, from the National Interagency Fire Program Analysis, Fire-Occurrence Database (FPA FOD), include fire size and date as attributes and are publicly available for the whole country (Short 2014). Spatial clustering of points has the potential to lead to autocorrelation, which can inflate the accuracy of statistical distribution models (Veloz, 2009). Although we were less interested in model accuracy than we were in variable importance and maintaining comparability of model results, we nevertheless spatially filtered the presence data to ensure no duplicate points within a 500-m radius, as spatial filtering can reduce the effect of sample bias (Veloz, 2009). While this distance was not systematically determined, this was the radius used in Syphard et al. (2018) that best attained the appropriate number of samples per fire, using the method described in Davis et al. (2017).

We developed a second dataset for large fire locations using a separate comprehensive statewide fire perimeter database, provided by the State of California Fire and Resource Assessment Program (FRAP, http://frap.fire.ca.gov/data/frapgisdata-subset). We only considered large fires from these data ($>=40$ ha), and, based on the method developed by Davis et al. (2017), we generated a random sample of points within all fire perimeters from a baseline period of 1985–2015, the most recent 30 years available. That is, to calculate the number of random points to generate for each fire in the database, we took the square root of the ratio of the given fire's area to the area of the smallest fire in the study area as recorded in this dataset. Because a filter distance of 500 m resulted in too-small sample sizes for many of the fires, we reduced the filter distance to 400 m.

We considered the two fire datasets to capture two different processes, where each process potentially has its own set of drivers. The 'fire ignitions' dataset reflects the spatial patterns of ignitions (which is an outcome of fire initiation processes), whereas the 'large fires' dataset reflects a discrete sample of burnt locations (which is an outcome of fire spread processes).

#### 2.2.2. Structure loss data

The dependent variable for the structure loss models was the location of any structure that had been destroyed in a fire from 2000 to 2015 (Table 1). The baseline data were developed by Alexandre et al. (2016), and included all destroyed structure locations across fires in the U.S. from 2000 – 2010. These data were created by examining, for all wildfires recorded in the Monitoring Trends and Burn Severity dataset (MTBS, https://mtbs.gov), Google Earth historical imagery from the closest dates before and after the fires. Within each fire perimeter, Alexandre et al. digitized all buildings before the wildfire; then, any building that had been completely removed in the post-fire image was considered destroyed. To update and extend these data, we followed the same methods using pre- and post-fire Google Earth imagery and digitized buildings in all three study areas that were present through 2015. Additionally, we selected all fires from the most recent Cal Fire historical perimeter database (2015 at the time of completion) and added new structures that may have been missed by Alexandre et al. (e.g., due to small fire size) or had occurred after 2010.

#### 2.2.3. Topographic data

Terrain-related variables are typically included in fire behavior and distribution models due to their direct influence on fire behavior and indirect influence on fuel characteristics and flammability (Bond and van Wilgen 1996, Pyne 1996); and they have also been significantly associated with structure loss to wildfire due to exposure (Syphard et al., 2012, Alexandre et al. 2016). Therefore, we considered a range of topographic variables in both the fire and structure loss models, including slope, topographic variability, and topographic position (Table 1).

#### 2.2.4. Climate data

We considered a range of historical and projected future climate variables, which were developed by Flint and Flint (2012) and updated through 2017 using the California Basin Characterization Model (https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html (Table 1). The data were available annually at 270 m resolution. We processed the annual data to create 30-year baseline statistical summaries from 1981 to 2010 as well as decadal future projections from 2020 to 2050. To ensure consistency with state recommendations (Kravitz, 2017), we compared two scenarios of future climate conditions from complementary CMIP-5 General Circulation Model projections regarded as relevant for California. The scenarios were CNRM-CM5 and MIROC5, which represent "warm/wet" and "hot/dry" conditions, respectively. Despite this characterization both scenarios have substantial spatial and temporal variation in projected conditions, but should still provide meaningful bookends for representative climate spaces. For both scenarios, we used the RCP 8.5 "business as usual" emissions scenario (RCP scenarios are generally similar through 2050 and only diverge in the second half of the century).

For the fire models, we considered a combination of temperature and moisture-related climate variables that have had significant associations with fire patterns in other studies due to their effects on energy and moisture gradients that influence wildland fuel condition and abundance (e.g., Whitman et al., 2015; Parisien et al., 2016; Davis et al., 2017). We also included actual evapotranspiration (AET) and climatic water deficit (CWD) in all models, as these variables have been used to account for changes in fuel abundance (AET) and moisture (CWD) (Krawchuk et al., 2014, Parks et al., 2016, Mann et al., 2016). We did not include temperature and precipitation in the structure loss models because we assumed their influence on structure loss would be indirect, via their effects on large fire probability. On the other hand, given that AET and CWD served as proxies for vegetation, and that vegetation adjacent to structures could be influential beyond the effect on large fire probability, we did include these variables.

**Table 1**
Dependent and explanatory variables used to model fire and structure loss distribution in three California study areas.

| Category | Fire models | Structure loss model | Data layer | Description and source | Time Variant |
|---|---|---|---|---|---|
| Dependent variable | x | | Fire ignitions | Fire occurrence locations delineating point of ignition from 2003 - 2013 (Short 2014) | NA |
| | x | | Large fires | Cal Fire fire perimeter database 1985 – 2015 (Department of Forestry and Fire Protection | NA |
| | | x | Structure loss | Digitizing, Alexandre et al. (2016) | NA |
| Terrain | | | | | |
| | x | x | Slope | LANDFIRE, 30-m native resolution, aggregated by mean to 270m | No |
| | x | x | Topographic roughness | Range of slope values within 810-m radius from center cell (Derived from 30-m digital elevation model) | No |
| | x | x | Topographic position index | Index of slope position and landform, Jenness 2006 (Derived from 30-m digital elevation model) | No |
| | x | x | Topographic heterogeneity | Range of elevation values within 810-m radius from center cell (Derived from 30-m digital elevation model) | No |
| Climate | | | | | |
| | x | | Temperature seasonality | Coefficient of variation across calendar year of temperatures (Derived from Flint and Flint, 2014) | Yes |
| | x | | Annual precipitation | Sum over calendar year (mm) (Flint and Flint, 2014) | Yes |
| | x | | Summer precipitation | Sum over June, July, August (mm) (Flint and Flint, 2014) | Yes |
| | x | | Annual minimum temperature | Mean low temperature of coldest month (degrees C) (Flint and Flint, 2014) | Yes |
| | x | x | Actual evapotranspiration | Total annual water evaporated from surface and transpired by plants (Flint and Flint, 2014) | Yes |
| | x | x | Climatic water deficit | Annual evaporative demand exceeding water availability (Flint and Flint, 2014) | Yes |
| Land use | | | | | |
| | x | x | Housing density | Based on 2000 U.S. Census data using the baseline projection at 2009 (Mann et al., 2014) | Yes |
| | | x | Housing cluster area | Boundaries around areas with housing density > = 0.02 units per ha (Derived) | Yes |
| | | x | Distance to cluster edge | Mean Euclidean distance to boundary of housing clusters (Derived) | Yes |
| | x | x | Distance to populated places | Census populated places of at least 10,000 inhabitants in 2010 (Derived) | No |
| | x | x | Distance to roads | TIGER line files 2015, U.S. Department of Commerce, U.S. Census Bureau | No |
| | x | x | Distance to public land | Cal Fire land ownership database 2015 (Department of Forestry and Fire Protection) | No |
| Fire | | | | | |
| | | x | Predicted large fire suitability | Output from large fire model (this paper) | Yes |

*2.2.5. Land use projections and anthropogenic data*

Our primary source of land use data were maps of current and future projected housing density that were published in Mann et al. (2014). The historical data were collected from the U.S. Census long form with models trained using historical trends from 1940 to 2000 (the latest date that the long form was available). The predictions of housing density were provided in decadal time steps, and we used the 2009 forecast as our baseline here. Created using longitudinal census data, the model calculated the total number of new houses based on demographic forecasts at the national level, and then allocated them to split-block units based on a spatio-temporal estimate of housing density. We considered two scenarios, one with concentrated urban development ("urban scenario") and the other that favored rural expansion ("rural scenario"). In the "urban development" scenario, an additional 25% of all new housing was added into urban areas (density greater than 1 house per acre), while the "rural growth" scenario pushed the 25% into areas with less than 1 house per acre.

Housing density data were initially provided as vector data, with housing density listed as an attribute for each polygon. We converted these data into 270 m raster layers using housing density as the value to grid. In previous studies of structure loss to wildfire, two additional variables, the size of the housing cluster and the distance from each structure to the edge of development, were found to be highly significant (Syphard et al., 2012; Alexandre et al., 2016a, 2016b). Given that those data had been created using point locations of all structures, we developed an approach to devise similar housing clusters by thresholding and creating borders around polygons with at least 0.01 housing units per ha, which was the value that resulted in the best fit to the data created for San Diego County (Syphard et al., 2012). The housing density variables were available for the same time periods as the climate data, with 2009 representing current conditions, and decadal projections until 2050 for the two growth scenarios. Thus, for models using baseline climate data for 1981–2010, we used housing data from 2009; and for models using climate projections from 2019 to 2029, we used the housing projection for 2029, etc.

In addition to the housing projections, we included three other variables that have been significantly associated with fire occurrence patterns in other studies (e.g., Mann et al., 2016; Syphard et al., 2018). These included proximity to primary and secondary roads, which are often associated with human-caused ignitions (Syphard and Keeley, 2015); proximity to public land, which typically consists of large uninterrupted swaths of wildland vegetation; and distance to census populated places where the city includes at least 10,000 residences (Mann et al., 2016). These maps remained static for future projections.

## 2.3. Statistical modeling

We used Maxent 3.3.3k to estimate variable importance and project mapped probabilities of current and future fires and structures loss (Phillips and Dudik, 2008; Elith et al., 2011). A statistical machine learning method, MaxEnt estimates the best approximation of a distribution via iterative comparisons between values of the environmental predictor variables at the location of presence locations (i.e., all fires, large fires, destroyed structures) versus the values of the same variables at 10,000 randomly located background points. The best distribution is identified as the one with maximum entropy, and the model outputs a continuous grid with each cell assigned a relative suitability of occurrence from an exponential function. Recognized as one of the top-performing species distribution models (Elith et al., 2006), MaxEnt has also been successfully used in a range of wildfire analyses and mapping applications (e.g., Bar-Massada et al., 2012; Batllori et al., 2013; Parisien et al., 2016; Davis et al., 2017; Tracy et al., 2018).

We developed separate models for all fires and large fires to investigate potential differences in variable importance. We also tested the output of both models as potential predictors for the structure loss model, but we found significant correlation between the output of the small fire model and distance to roads. Given that most homes are destroyed in large fires, we decided to only use the output of the large fire probability model as a predictor variable for the structure loss model.

We initially developed all models with the full range of climatic, topographic, and anthropogenic explanatory variables to compare variable importance. For projecting future conditions, we employed a variable selection and model tuning process separately for each of the three study regions to ensure the best model fit. We first used ENMTools (Warren et al., 2010) to calculate Pearson correlation coefficients for all explanatory variables using current conditions (baseline) in each study area. For any pair of variables with a correlation coefficient of $r >= 0.8$, we retained the one that had a higher mean cross-validated receiver operating characteristic curve (AUC, Fielding and Bell, 1997), based on univariate models.

We used most of the default parameters for the MaxEnt modeling, except that we used only linear, quadratic, and product features for all models, and selected regularization multipliers, that avoid overfitting by penalizing complex solutions, by running models in 0.5 increments from 0.5 to 5. The final model was chosen by selecting the multiplier that resulted in the lowest Bayesian Information Criterion (BIC). For the baseline models of all and large fires, and structure loss, we ran five cross-validated model replicates to obtain mean permutation importance values and mean out-of-sample AUCs. We averaged the predicted values from the five replicate output maps to produce the baseline maps, which are interpreted as grids of mean predicted probability of large fires or structure loss given the environment in each study area.

After conditioning the models on the baseline time period, we then projected the averaged baseline models of large fires and structure loss onto maps representing future conditions at each time step for all combinations of future climate (two scenarios) and land use (two scenarios) projections. For each future time step, we first projected large fires, and then used those projections as input to the structure loss models.

## 2.4. Analysis

We averaged large fire probability and structure loss probability for all maps generated as model output by first summarizing the predicted probabilities across all grid cells in every map, then dividing this sum by the total number of cells in the maps of the three study areas. We calculated these numbers for all model replicates in all time periods and for all climate/land use scenario combinations. The probability averages for current conditions served as a baseline to compare with the probability averages of future scenarios, which allowed an overall estimate of whether fire or structure loss probability went up or down across the region.

To identify the housing density where most structure loss occurs in each study area, we extracted the housing density of destroyed structures from the baseline housing density maps generated by Mann et al. (2014). We then compared the mean housing density of destroyed structures in each study area with the underlying housing density in each region (i.e., all burned and unburned structures), which we determined by multiplying the area of each polygon in the study area by its housing density as indicated in the attribute table. This calculation assumed housing density was evenly distributed across polygons. For polygons that overlapped the study area boundary, we calculated the number of units in the entire polygon, then prorated by the percentage

of the polygon within the study area. For both destroyed and the total structures in each study area, we plotted and compared their mean and distribution across housing density classes.

To compare the mean housing density data in our study areas to the recent destructive fire events of 2017 and 2018, we additionally acquired point locations for the destroyed structures in the 2017 Tubbs, Nunn, Atlas, and Pocket Fires in Sonoma and Napa Counties (number destroyed = 8022; http://sonomamap.maps.arcgis.com/apps/webappviewer/index.html?id=5af1dd01cb9b446db928abe51a259763), the 2018 Camp Fire in Butte County (number destroyed = 18,804; https://calfire.app.box.com/s/z03vd6hoikxa94ey25m0kuq2fsq2ln5e/folder/64813192070), the 2018 Carr Fire in Shasta County (number destroyed = 1614; https://www.arcgis.com/home/item.html?id=17d44552e0ea4c6ab2c43e80246e05b9), and the 2018 Woolsey Fire in Los Angeles and Ventura Counties (number destroyed = 1673; provided from Cal Fire to the National Park Service, Robert Taylor personal communication). All of these data were provided as part of the Cal Fire Damage Assessment and Fatality Totals (**DINS**) program. We used the same methods as above to calculate the mean housing density for destroyed and total number of structures. We calculated the total number of structures within the county boundaries where the fires were located.

To map geographical variation in structure loss probability by land use scenario, we subtracted the mapped probability of structure loss projected in the rural growth scenario models for year 2049 from the corresponding mapped probability of structure loss in the urban growth scenarios.

## 3. Results

### 3.1. Baseline statistics

From 2000–2015, there were 2081 structures destroyed in the NC study area. These destroyed structures were distributed across 17 out of a total of 202 fires during the same time period (based on the Cal Fire perimeter data). The mean size of fires where structures were destroyed (includes entire perimeters of those intersecting study area) was 5525 ha versus an overall mean fire size of 896 ha. In the BP study area, there were 451 destroyed structures that burned through 2015 in 39 out of 241 fires. The mean fire size with destroyed structures was 4018 ha versus a mean of 905 ha overall. In SD, 4338 structures were destroyed, across 20 fires out of a total 206 fires. The mean fire size when structures were destroyed was 150,647 ha versus a total mean of 1877 ha.

The mean density of destroyed structures was much lower than that of all structures in all study areas, by orders of magnitude (Fig. 2). This pattern was the same for density of destroyed structures versus all structures within counties in the recent fire events of 2017 and 2018 (Fig. 2), although the difference between destroyed and all structures was only about half for the Camp Fire and about a third for the 2017 North Coast fires. The distribution of housing density for both destroyed and all structures varied by study region, but destroyed structures were consistently located in low-density classes (Fig. 3).

Projected future trends in temperature and precipitation varied across regions for the two different climate scenarios, as did the overall housing density change. In the NC and BP study areas, the mean annual precipitation resulted in conditions with consistently more moisture in the CNRM scenario and consistently drier conditions in the MIROC scenario by 2049, with slight geographical variability (Fig S1a&b). Both GCMs projected decreased annual precipitation in the SD study area, but the drying was stronger for the MIROC scenario (Fig. S1c). The changes in summer precipitation showed much more geographical variability within study regions, but the differences in GCMs were flipped such that CNRM was projected to be drier in the summer than MIROC (Fig. S2a-c). Annual temperature was projected to increase much more substantially in the MIROC than the CNRM scenario for all three study areas by 2049, with substantially more geographical variation in the CNRM scenario (Fig. S3a-c). Decadal fluctuations, reflecting idiosyncrasies of the model run, were strongest in MIROC in the North Coast.

Changes in projected housing density patterns from 2009 to 2049 show substantial geographical variability across all three study regions (Fig. 4). For all regions, the rural scenario showed a larger areal increase of housing densities within the range where houses have been destroyed historically (Fig. 4); but the difference in rural versus urban scenarios was most substantial in NC, followed by SD, then BP. In the rural scenario, most of this increase in low-density housing occurred via growth (i.e., increased housing density) across more rural parts of the landscape, whereas in the urban scenario, a larger portion of exurban areas declined in housing density as there was a shift to more

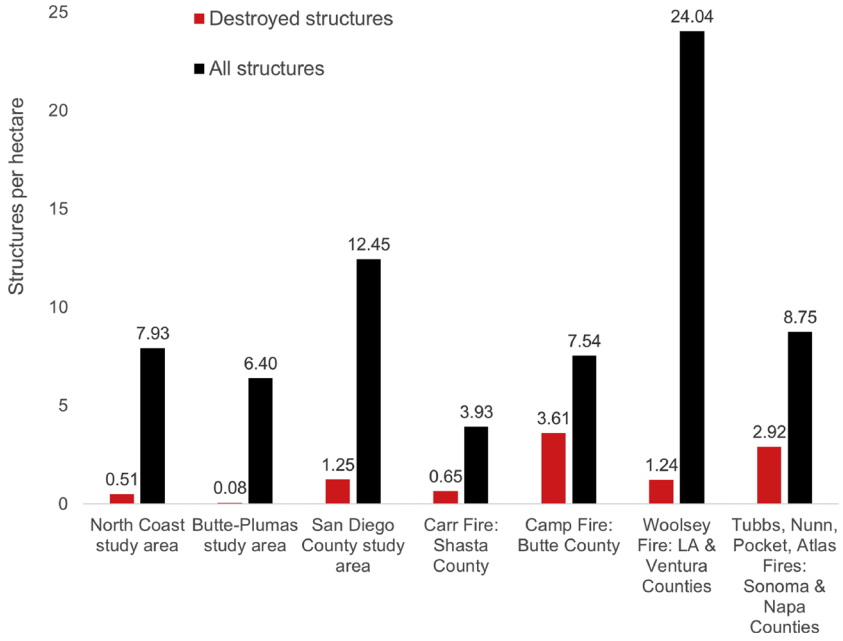


**Fig. 2.** Mean housing density for destroyed and all structures in three California study areas (using data through 2015) and for the four largest destructive fire events in 2017 and 2018.

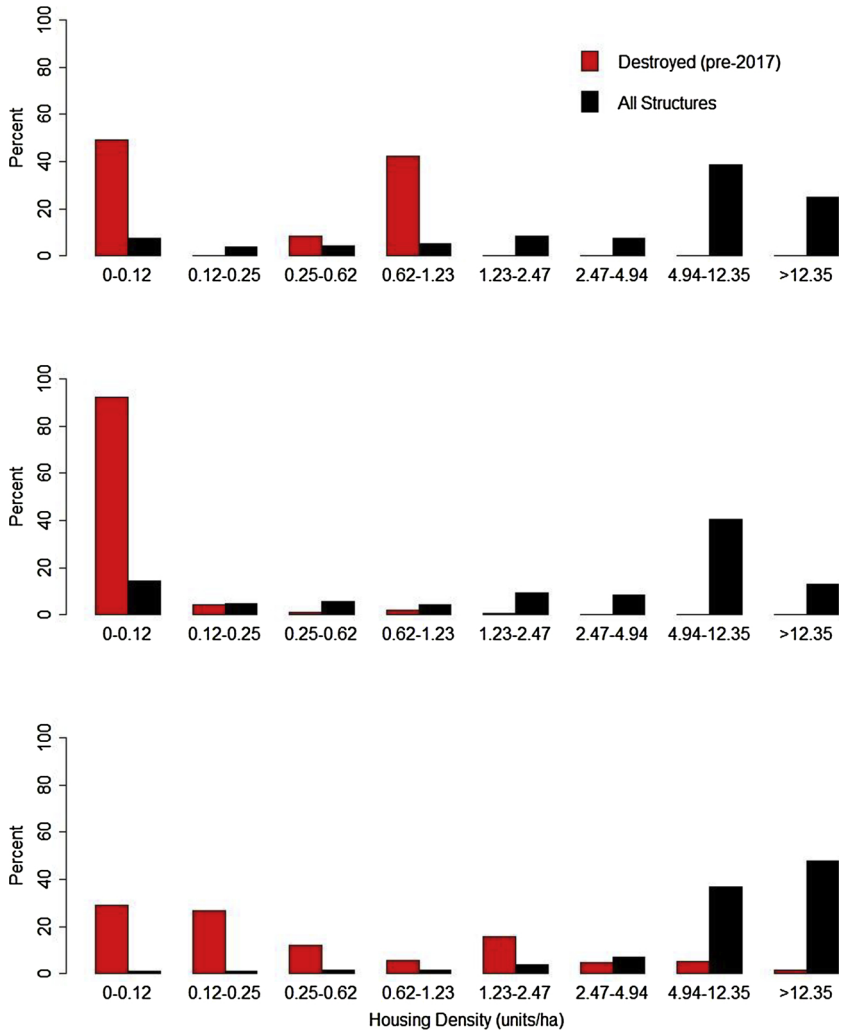


**Fig. 3.** Distribution of housing density classes (structures/ha) for destroyed and all structures in the a) North Coast, b) Butte-Plumas, and c) San Diego County study areas.

concentrated high-density housing near urban areas (Fig.4). One exception is the northern coastal portion of the SD study area, where there was some housing density decline in the rural scenario.

### 3.2. Variable importance

There were large differences in model variable importance for fire ignitions vs. large fires for all three study areas, and these were much larger than differences among regions (Table S1 – S2,Fig. 5). In particular, anthropogenic variables, particularly proximity to roads, dominated the patterns of fire ignitions, whereas topography and climate variables dominated the patterns of large fires, except in SD, where both housing density and distance to roads had about the same importance as topography and climate for large fires. In SD, housing density was almost equally as important as climate for explaining large fires. The directions of relationships differed such that fire ignitions tended to occur in close proximity to roads or populated places, but large fires occurred closer to public lands and farther from roads and populated places.

Whereas climate variables had a strong influence on fire ignitions and especially large fires, the vegetation productivity and moisture variables (AET and CWD) were not important for explaining structure loss patterns in NC or BP (Table S3 – S4, Fig. 5), and were less important than fire suitability for SD. Instead, housing variables and large fire suitability were the two most important factors explaining structure loss across all regions, with higher structure loss Univariate response curves showing the probability at low housing density (Fig. 6). SD was again different than NC or BP in that housing variables were more important than fire suitability.

### 3.3. Future projections

Overall, NC had a slightly lower baseline probability of large fires across the study area (Fig. 7a) than BP or SD, which had similar baselines (Fig. 7 b & c). Projections of future large fire probability were higher than the baseline for most time periods and climate scenarios for both the NC and BP study areas, except for MIROC in 2029 and 2049 in NC and CNRM 2019 in BP, and the results from these decades reflected oscillations that stemmed from decadal variability in the climate model projections. Large fire probability did not significantly change under either climate scenario in SD (Fig. 7c), but there was also slight decadal variability in the model run for CNRM. In all cases, differences in projected large fire suitability between the two land use scenarios were virtually absent due to the small relative importance of these variables to the model.

Compared to NC and BP (Fig. 8a & b respectively), SD had a relatively high baseline structure loss probability across the landscape (Fig. 8 c). Differences in structure loss probability for the two climate scenarios in NC and BP generally mimicked the large fire probability results in ranking and magnitude, and the decadal variability in fire

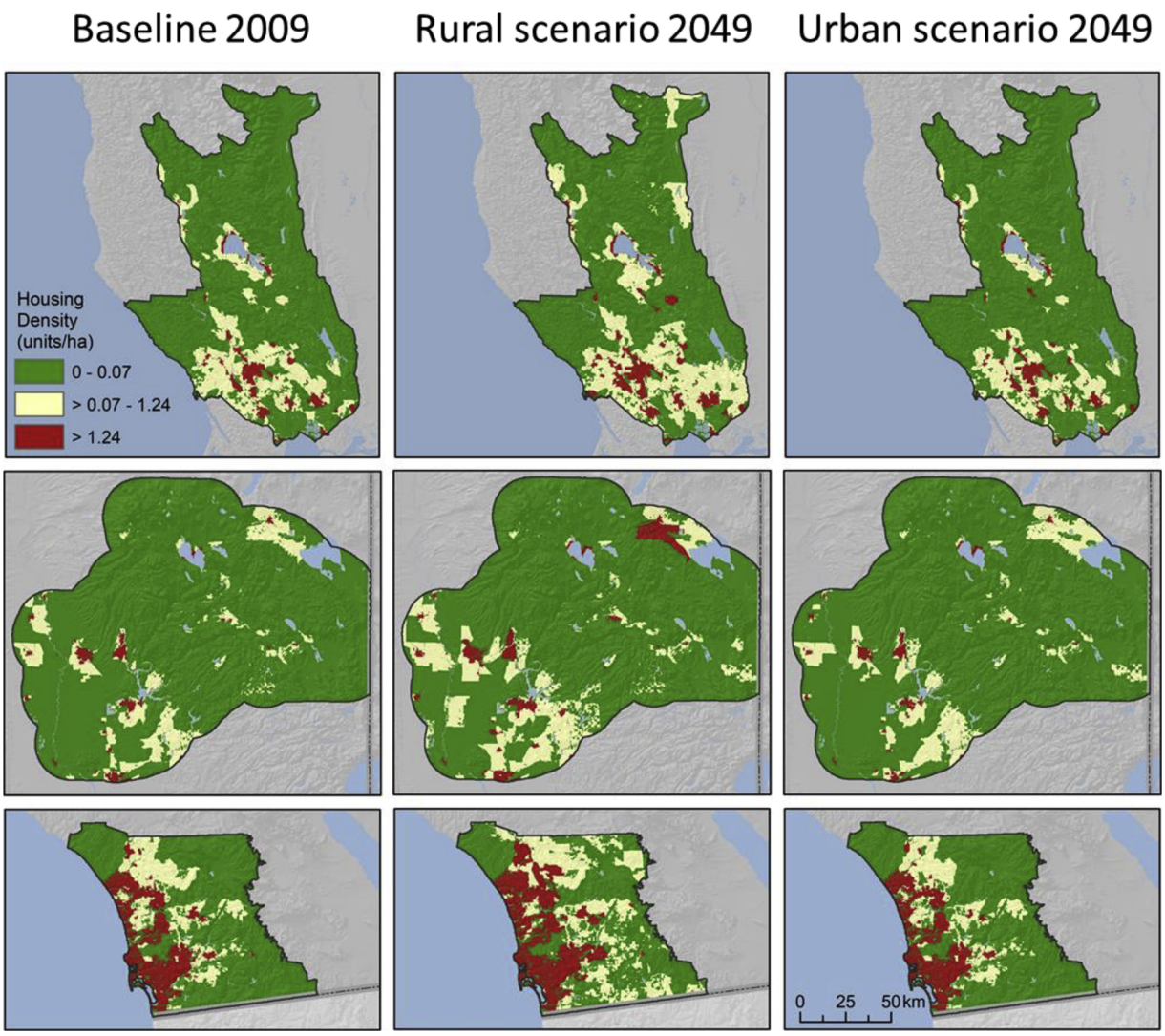


**Fig. 4.** Classified housing density in 2009, 2049 for the rural, and 2049 for the urban scenarios in the a) North Coast, b) Butte-Plumas, and c) San Diego County study areas. The middle (yellow) class represents the housing density range across the three study areas where structures have been destroyed in the past (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

probability for SD that came from climate model projections was reflected in the CNRM result. Compared to large fire probability, there was a much stronger effect of land use scenario on structure loss projections, and more variation in which scenarios exceeded baseline for NC (Fig. 8a) and SD (Fig. 8b). BP showed little variation in either climate or land use scenario probabilities. In NC, the rural land use scenario had a much larger probability of structure loss overall, and for CNRM, this difference generally determined whether probability would increase or decrease relative to the baseline. The rural scenario also resulted in higher overall structure loss probabilities in SD, but this was mostly apparent in 2049.

While structure loss was higher overall across regions and climate scenarios in the rural land use scenario (Fig. 8), there was considerable spatial heterogeneity in the effect of the land use scenario (Fig. 9). Comparing the rural land use scenario to the urban scenario in NC and SD, there were small changes to structure loss probabilities across most of the currently semi-urban and urban areas and large increases in structure loss probabilities in the currently rural areas (compare Fig. 9 to Fig. 4). In contrast, BP had locations of large increases and decreases in structure loss probabilities under the rural land use scenario compared to the urban land use scenario. However, all three regions had higher predicted structure loss in areas where there was an increase in low-density housing.

## 4. Discussion

Our projections suggest that both climate and land use will drive future changes in patterns of wildfire and subsequent likelihood of structure loss; but the relative importance and strength of different drivers will vary across and within different regions. Future changes will depend upon the nature and degree of change in both climate and land use relative to current conditions. For example, locations with increased low density rural housing are likely to see increased structure loss even in decades with lower large fire probabilities (compare decades 2029 and 2049 in Figs. 7a and 8a). Changes will also vary according to the strength and nature of regional relationships among climate, land use, fire patterns, and structure loss, with potential feedbacks among these drivers. Despite these complexities, which underscore the importance of customizing policy and management by geographical location (Keeley et al., 2009; Moritz et al., 2014), there were also key commonalities across regions. In particular, structure loss mostly occurred at fairly low housing densities. While more work needs to be done to create models that incorporate short-term weather conditions, such as wind, and feedbacks among drivers, we believe that the central importance of housing density to structure loss may be generally applicable to fire-prone landscapes.

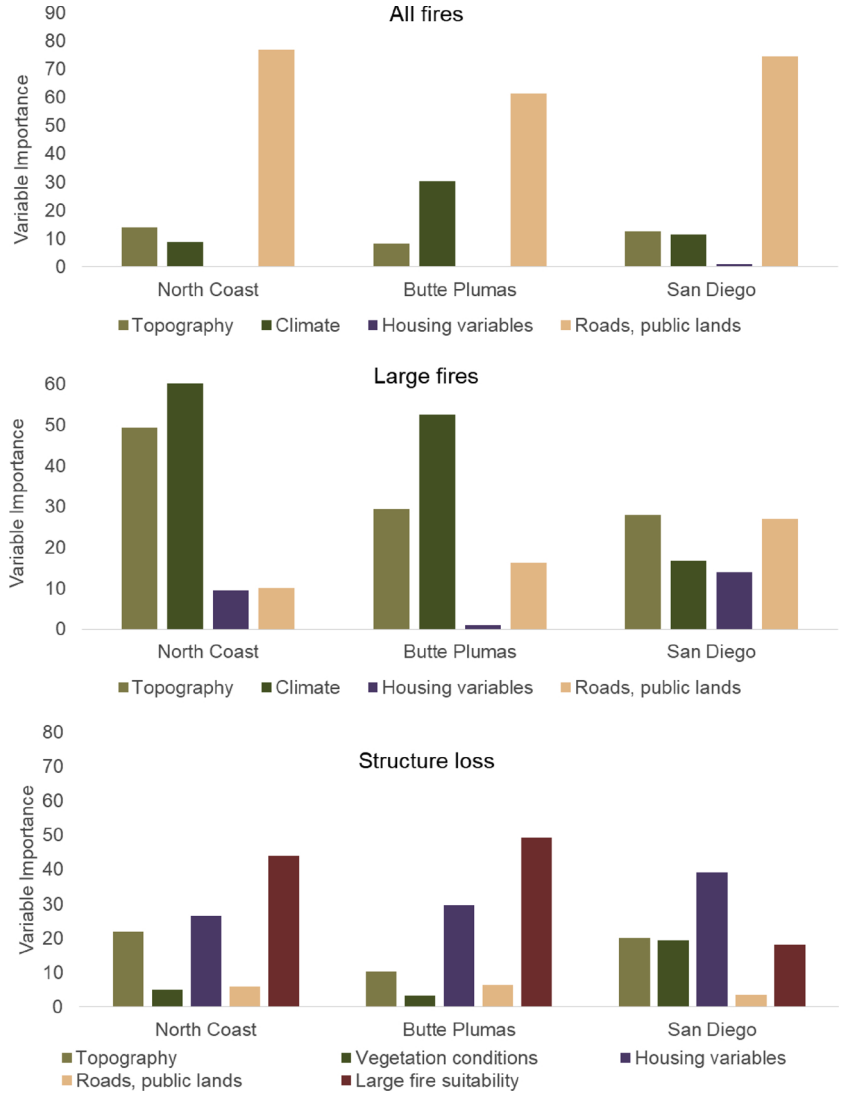


**Fig. 5.** MaxEnt variable permutation importance for fire and structure loss models in three California study areas, with variables grouped into categories. The fuel category for structure loss consisted of actual evapotranspiration and climatic water deficit.

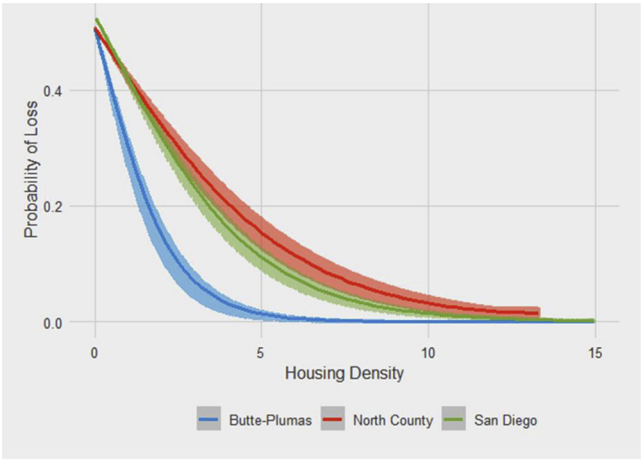


**Fig. 6.** Probability of structure loss relative to housing density (units/ha) for three California study areas, averaged across 5 model replicates.

### *4.1. High anthropogenic variable importance for fire ignitions, but not large fires*

One commonality across regions was that anthropogenic variables were most important in explaining patterns of fire ignitions, whereas large fires were more related to topography, climate, and fuel (via AET and CWD). This finding is not surprising given that most fires in California are started by humans (Syphard et al., 2007; Balch et al., 2017), near human infrastructure (Syphard and Keeley, 2016). The finding is also consistent with other studies that have shown differences between the drivers of small and large fires (e.g., Syphard et al., 2008, 2016, Barros and Perreira, 2014; Abatzoglou et al., 2018) and that large fires are more likely to occur in remote areas where fuel continuity is greater, with severe winds better able to propagate fires via long-distance ember production, and access to suppression is lower (Gray et al., 2014). The consistency with other studies, and across divergent regions in this study, has important considerations for management. For example, ignition prevention efforts may be most effective if geographically concentrated near roads and development. Thus, land use change may generally be the biggest concern for preventing fires from starting; but climate change, in addition to weather and fuel patterns, may be more critical in the consideration of large fire behavior. One exception is that, unlike other human-caused fire sources, powerline-

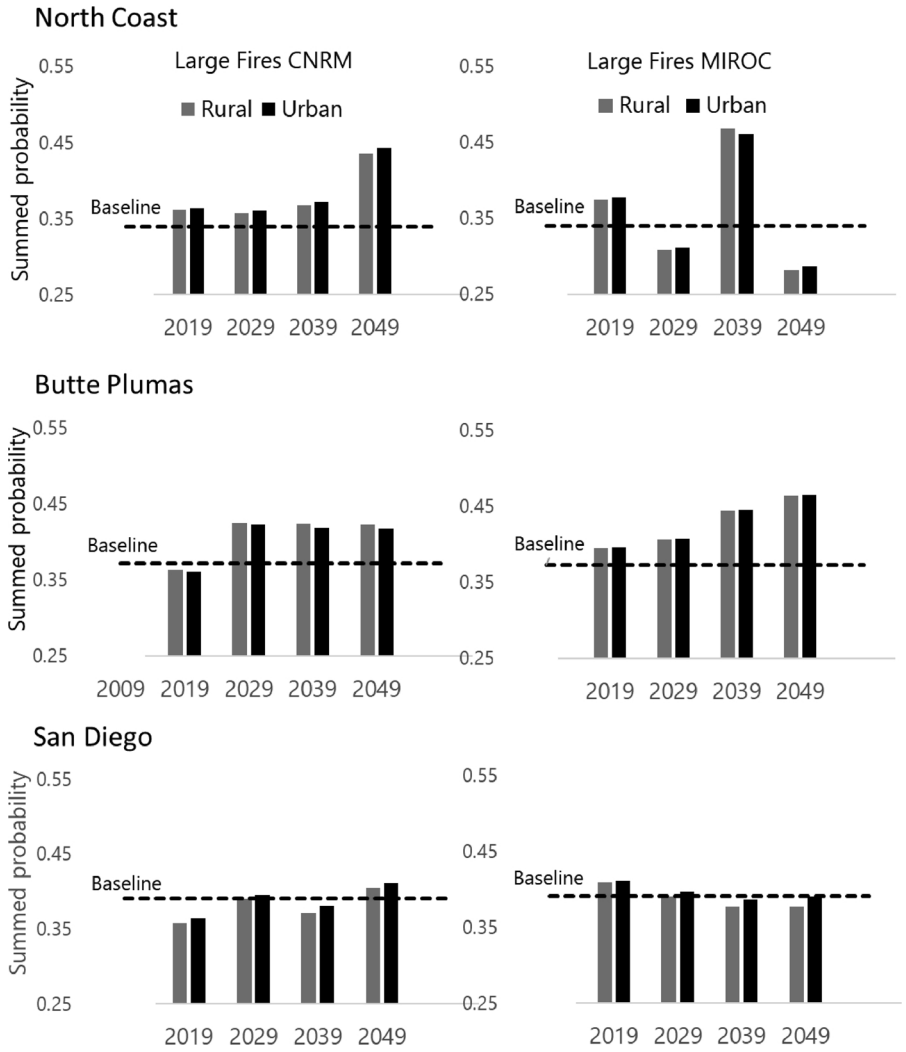


**Fig. 7.** Total projected probability of large fires under two climate and two land use scenarios for a) North Coast, b) Butte Plumas, and c) San Diego.

ignited fires tend to occur in more remote areas during severe weather, and these fires often result in large areas burned with substantial human losses (Keeley and Syphard, 2018). Understanding the relative importance of anthropogenic variables is critical given expected changes in human land use with resulting downstream impacts on deliberate or accidental ignitions, prescribed burning, mechanical vegetation treatments, and fire suppression.

The timing of ignitions, particularly corresponding with extreme fire weather, may be the most important variable to consider in determining whether fires become large and potentially destructive to human assets (Syphard et al., 2016; Abatzoglou et al., 2018). Historical analysis has also shown there to be an overall low correlation between fire frequency and area burned in California (Keeley and Syphard, 2018). Thus, small, frequent fires caused by human ignitions do not necessarily lead to highly destructive fires. Instead, the fires most likely to cause structure loss tend to be ignited in low-intermediate population or housing density (Syphard et al., 2007, 2009), adjacent to areas of high fuel loading.

Studies of historical fire-climate relationships in California (Keeley and Syphard, 2015, 2016) and across the U.S. (Littell et al., 2009; Parisien and Moritz, 2009; Syphard et al., 2017a; Littell et al., 2018) show differences in the strength and nature of climatic control over fire activity. In particular, those areas where fire is most strongly explained by climate in California are in northern, higher-elevation parts of the state, whereas in southern CA, fire-climate relationships have historically been weak (Keeley and Syphard, 2016). Other studies have shown fire-climate relationships to be weaker in areas with higher human presence (Higuera et al., 2015; Ruffault and Mouillot, 2015; Mann et al., 2016; Syphard et al., 2017b), and this is supported in our results, with the SD study area having both the highest overall housing density and the weakest link between climate and large fire suitability. SD was also the study area with the strongest relationship between anthropogenic variables and patterns of large fire suitability.

### 4.2. *Predicted future wildfire varied less across scenarios than structure loss*

Given the weak ties between climate and large fire suitability in SD, there were no major changes projected for large fires here, which is an important result given widespread concern that climate change will be responsible for increasing future fire activity across the western U.S. (Westerling et al., 2006; Barbero et al., 2015; Abatzoglou and Williams, 2016). Nevertheless, there could be other types of indirect climate change effects on fires in southern CA, such as long-term drought (Keeley and Zedler, 2009), vegetation type conversion facilitated by drier conditions (Jacobsen et al. (2007); Park et al., 2018; Syphard et al., 2018b), or changes in wind patterns (Guzman-Morales et al. (2016)). For the other two study areas, climate change was projected to increase large fire probability by the middle of the century, which corresponded to at least part of the increase in structure loss probability in these regions. In all regions, it is important to acknowledge that,

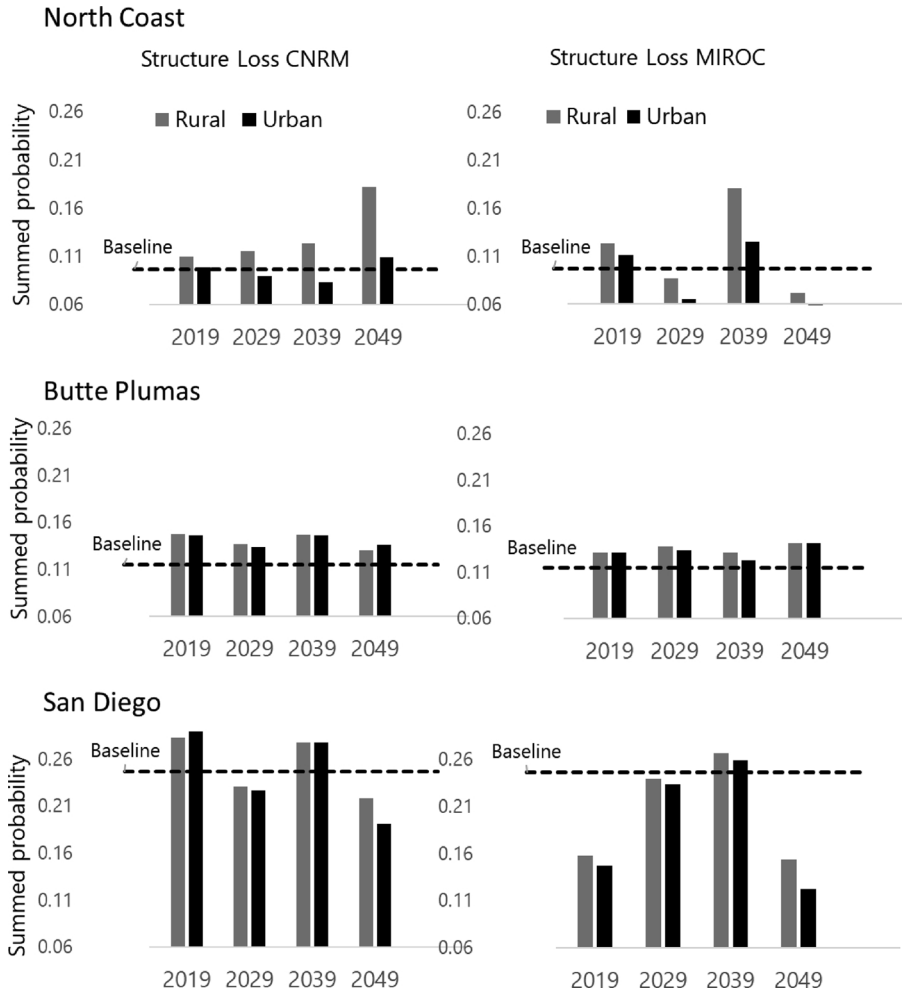


**Fig. 8.** Total projected probability of structure loss under two climate and two land use scenarios for a) North Coast, b) Butte Plumas, and c) San Diego.

despite inclusion of AET and CWD as proxies for fuel amount and condition, fire-vegetation feedbacks or vegetation type changes were not accounted for, and these could play an important, yet undetermined role in future fire activity (Syphard et al., 2018).

Particularly in the NC study area, land use change scenario played a major role in differences in structure loss probability, due to the significant relationships found in the baseline models as well as the nature of projected change in the rural versus urban scenarios. That is, there was substantially more expansion of low-density housing in the rural scenario versus the urban scenario in the NC study area, corresponding with the densities where most structures have been destroyed (i.e., the middle class in Fig. 4). This was true in BP and SD as well, but to a lesser extent. Also, for the urban scenario projections in all regions, and the rural projections for SD, there were both increases and decreases in housing density across the landscape; this patchwork of change may have dampened the apparent effect of land use on future projections of either fire or overall structure loss probability. Another important consideration is that structure loss probability may shift over time in response to changing density patterns. In other words, as some lower-density developments fill in with new homes, they may become less susceptible in the future; this is the likely reason that structure loss probability was projected to decline in some scenarios and time periods.

In modeling the decadal projections, we attempted to understand how different growth trajectories influenced model outcomes. For example, a region may initially experience low-density housing development in 2020–2030 that transitions to high density development by 2050. We hypothesized that either large fire or structure loss probability might thus vary through time as a function of the underlying housing density. However, given that land use was not one of the most important predictors of large fires, we did not observe a strong effect of oscillating housing density on fire projections. Instead, the up and down behavior in large fires, particularly in NC under MIROC, was due to idiosyncratic oscillations in climate projections that resulted from the climate model. For projections of structure loss, there was continued growth of low-density housing in the rural scenario for NC, which resulted in consistently higher structure loss probabilities over time. On the other hand, some areas of low-density development converted into high density development in San Diego County, which led to a net decline of structure loss probability by 2049. Overall, however, the biggest differences in effect of housing density was via the higher concentration of high-density development in the urban versus rural scenarios.

It is important to clarify that the land use scenarios were not meant to reflect precise changes but were designed to emphasize possible differences based on housing density and general trends towards urban or rural development. The land use change model tended to emphasize temporal and spatial spillovers; that is, any projection of housing density change in largely uninhabited areas first required either a history of growth or a spillover of growth from neighboring polygons, and this may have limited spatial expansion of housing in those areas. In other words, the model results, particularly for the rural growth scenario may understate the risks associated with low-density development. Further, we also assumed that road proximity, the distance to urban areas (areas with $\geq$10,000 residences), and the proximity to public land would remain unchanged over time, suggesting the results here are conservative.

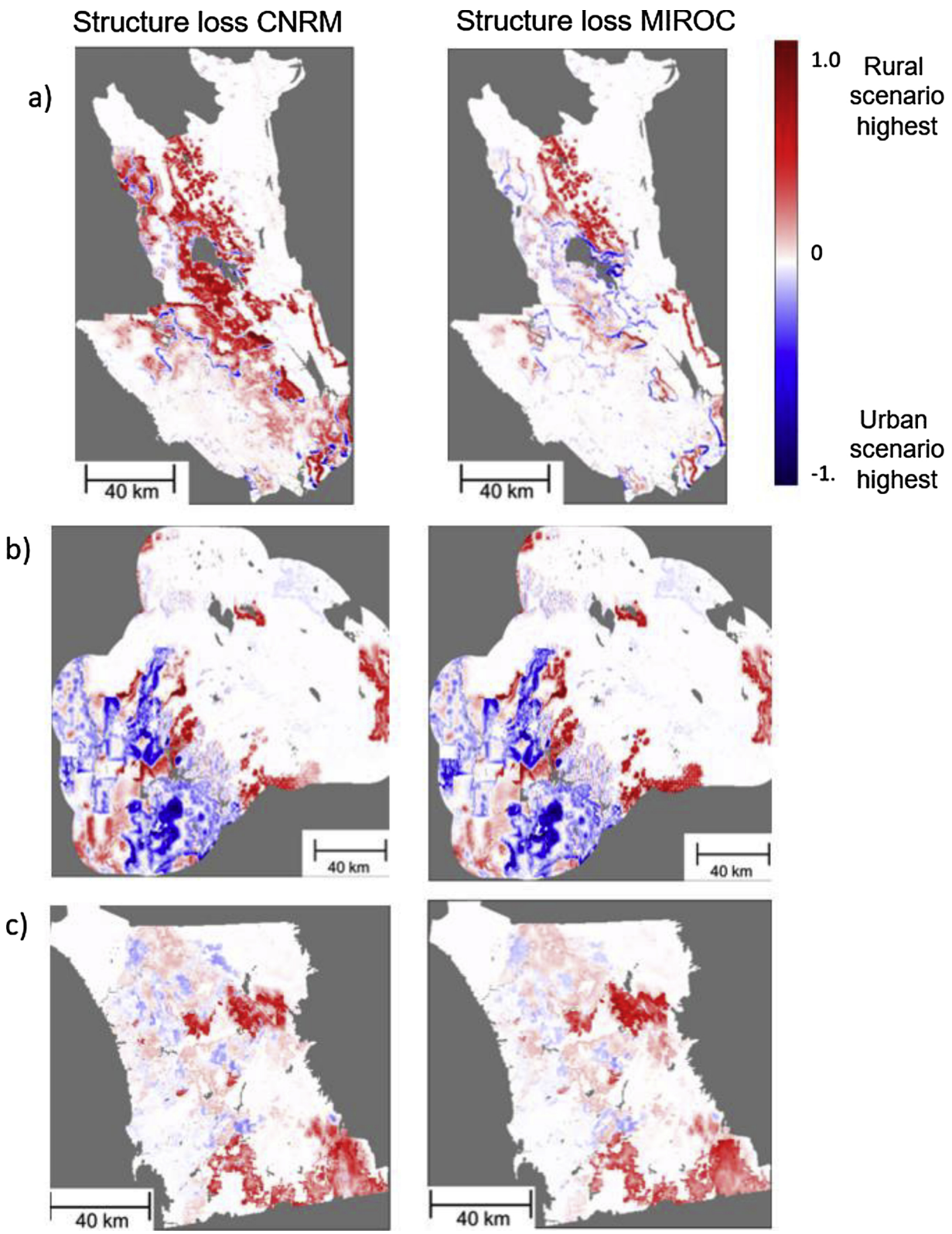


**Fig. 9.** Projected differences in structure loss probability at 2049 between the rural and urban density land use scenarios for CNRM and MIROC in the a) North Coast, b) Butte Plumas, and c) San Diego study areas.

### *4.3. Higher structure loss was seen in low density development*

Regardless of future projections, one of the striking commonalities in the results was that observed structure loss occurred in larger fires and at lower housing densities than the averages for the regions. There are two different statistics related to housing density that are closely related but distinct. The first is the probability of structure loss for any house given its density (i.e., Fig. 6), and the other is the total number of structures lost at different housing densities (i.e., Fig. 3). Our results showed that probability of structure loss is negatively related to

housing density in all regions, and while most destroyed structures were located in lower housing density classes, some structures were also destroyed at high densities. The association between structure loss and housing pattern has been documented in recent studies (Syphard et al., 2012, Alexandre et al. 2016, Kramer et al., 2018), and there has long been an assumption that fire risk is highest at the Wildland-Urban Interface (WUI), where houses meet or intermingle with wildland vegetation, both in the U.S. (e.g., Radeloff et al., 2018, Mell et al., 2010) and internationally (e.g., Lampin-Maillet et al., 2010; Montiel Molina and Galiana-Martín, 2016; Argañaraz et al. (2017)). However, the occurrence of several highly catastrophic wildfire events within high-density developments (e.g., Cohen and Stratton, 2008; Price and Bradstock, 2013; Nauslar et al., 2018), including recent California events, combined with previous lack of data associating changes in fire losses to changes in development patterns (McCaffrey et al. https://fireadaptednetwork.org/fire-narratives-accurate/) have led to questions and debate over which are the most dangerous development patterns.

Thus, one of the most important results of this study is that, even considering the massive numbers of structures that were destroyed in the last two years in wind-driven fire events, the overall mean housing density where houses are most likely to be destroyed (0.08 to 2.01 structures/ha pre-2015 and 1.24–3.61 in recent events) was more than an order of magnitude lower than the average housing density on the landscape for most cases (except the Camp Fire where the destroyed structure density was about 50% lower and the 2017 North Coast Fires, where the destroyed structure density was about 66% lower than total structures). The recent wildfires were uncharacteristic in the sheer number of structures and lives lost relative to historical numbers, in addition to the fact that wildfires did reach and enter parts of high-density urban areas in Coffey Park (Tubbs Fire), Paradise (Camp Fire), and the city of Malibu (Woolsey Fire). Thus, a lot more research is needed to understand how and why so many structures were lost. One clear factor were the wind speeds in these events, in addition to apparently substantial structure-to-structure spread and incendiary ember ignitions in which the houses themselves were more flammable than the nearby vegetation. Nevertheless, the losses in urban areas were still only a portion of the total number of structures destroyed in these fires, and thus they do not change the main conclusions of our study: overall, most structure loss tends to occur in areas of low-density development. One caveat is that we calculated housing density using data from the 2000 Census projected to 2009 as a baseline, and thus housing density has likely changed since then. However, the relative comparisons likely still hold because we consistently used the same housing data. Another recent study reported that the majority of threatened and destroyed structures from the last 30 years in the U.S. were located within the WUI; furthermore, when destroyed houses were not located in the WUI, the most common reason was that the housing density was lower than that in the WUI definition (Kramer et al., 2018).

The most likely explanation for this striking consistency is that housing patterns largely reflect exposure to wildfire. That is, wildfires typically burn through vegetation; and thus, those homes most interspersed with vegetation are most likely to encounter a wildfire in the first place, or be hit by incendiary embers. The reason for occasional catastrophic wildfire losses in high density areas is that, once exposed to a fire, a community with closely spaced homes made of flammable materials can lead to rapid house-to-house spread, particularly during severe weather conditions. In these cases, like the Tubbs fire in 2017 and Camp fire in 2018, the house itself becomes the fuel that propagates the fire.

Therefore, in terms of addressing conflicts between housing and wildfire in the future, the most effective mitigation may be land use and urban planning decisions that reduce the exposure of homes to wildfires (Syphard et al., 2013, 2016, Butsic et al., 2017). However, mitigation measures focused on defensible space and fire-safe construction materials, particularly when houses are closely spaced, are also critical for preventing future losses (Syphard et al., 2015, 2017c), as are other traditional fire management practices such as fire suppression and strategic location of fuel breaks to allow safe firefighter access to defend homes.

### 4.4. Conclusion

Looking at fire ignitions, large fires, and structures burned, we explored the importance of climatic and human variables for explaining fire and structure loss patterns across three diverse California landscapes, under current and future climate (hot-dry or warm-wet) and land use (rural or urban residential growth) scenarios. Across regions, we found that housing and human infrastructure were more responsible for explaining fire ignitions and structure loss probability. Large fires were better explained by climate, topography, and fuel variables. The differing strengths of these relationships interacted with the climate and land use scenarios, resulting in variability across regions in the relative importance of climate and housing patterns on fire and structures burnt. Focusing only on empirical housing density and structures burnt, we found that most structure loss occurred in areas with low housing density (from 0.08 to 2.01 units/ha), and as such, expansion of rural residential land use generally increased projected structure loss probability in the future. Both the historical results and the future projections highlight that future changes are likely to be complex and will result from a range of interacting factors. Climate change will be important to consider for managers and policy makers in some, but not all regions. In all areas, land use change merits increased attention, as local policy decisions can influence future patterns of development and exposure of structures to risk of loss in large wildfires.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.gloenvcha.2019.03.007.

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# AMPHIBIAN UPLAND HABITAT USE AND ITS CONSEQUENCES FOR POPULATION VIABILITY

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*Abstract.* To predict the effects of habitat alteration on population size and viability, data describing the landscape-scale distribution of individuals are needed. Many amphibians breed in wetland habitats and spend the vast majority of their lives in nearby upland habitats. However, for most species, the spatial distribution of individuals in upland habitats is poorly understood. To estimate the upland distribution of subadult and adult California tiger salamanders (*Ambystoma californiense*), we used a novel trapping approach that allowed us to model the spatial variation in capture rates in the landscape surrounding an isolated breeding pond. As expected, we found that captures of adults declined with distance from the breeding pond. However, captures of subadults increased steadily from 10 to 400 m from the breeding site, but there were no captures at 800 m. A negative exponential function fit to the adult capture data suggested that 50%, 90%, and 95% were within 150, 490, and 620 m of the pond, respectively. For subadults, the quadratic function fit to the data similarly suggested that 95% were within 630 m of the pond, but that 85% of this life stage was concentrated between 200 and 600 m from the pond. To investigate the population-level consequences of reducing the amount of suitable upland habitat around breeding ponds, we used a stage-based stochastic population model with subadult and adult survival parameters modified according to our empirical observations of upland distribution. Model simulations suggested that substantial reductions in population size are less likely if upland habitats extending at least 600 m from the pond edge are maintained. Model elasticities indicated that quasi-extinction probabilities are more sensitive to reductions in subadult and adult survivorship than reproductive parameters. These results indicate that understanding the upland ecology of pond-breeding amphibians, especially the distribution and survivorship of subadults, may be critical for designing protective reserves and land use plans.

*Key words:* Ambystoma californiense; *California tiger salamander; declining amphibian; drift fence; matrix simulation model; pitfall trap; population viability analysis; reserve design; terrestrial; upland spatial distribution.*

## INTRODUCTION

In the United States, wetland habitats are protected against draining and filling by state and federal regulations. A few states further require maintenance of a 30–60 m wide upland buffer of undeveloped habitat around some or all wetlands. These buffers capture silt and chemical pollutants before they reach the wetlands, and are generally recognized as effective in protecting water resources (e.g., Phillips 1989, Brosofske et al. 1997). An additional benefit of upland buffers is that they provide essential habitat for a variety of wildlife species. While the contribution of buffers towards the maintenance of viable populations is intuitively obvious, there has been relatively little quantitative evaluation of exactly how buffers may enhance the value of wetlands for wildlife. Recently there have been attempts to estimate the amount of ''core upland habitat'' needed to accommodate populations of semi-aquatic wetland-breeding amphibians (Semlitsch 1998, Semlitsch and Bodie 2003). Summarizing across 32 species, Semlitsch and Bodie (2003) estimated that the core upland habitat used by amphibians extends 159 to 290 m from the wetland edge, revealing that buffers designed to protect water quality encompass only a small fraction of the habitat used by most amphibians. While the Semitsch and Bodie (2003) review provides strong rationale for greater protection of upland habitat around wetlands to enhance habitat values for amphibians, it also emphasizes our rudimentary understanding of amphibian upland ecology.

Losses of wetland and upland habitats are recognized as key contributors to the widespread decline of amphibian populations (Semlitsch 2002, Collins and Storfer 2003). However, experimental research on amphibian declines has continued to focus on the aquatic embryonic and larval stages, while the equally important terrestrial stages are rarely studied (Storfer 2003). This research inequity between aquatic and upland amphibian ecology is not a new phenomenon, and is probably

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PLATE 1. An adult California tiger salamander (*Ambystoma californiense*). Photo credit: Bret Stewart.

due to the relative difficulty of terrestrial studies. Particularly for the diverse array of amphibians that breed in aquatic habitats but spend most of their lives in underground terrestrial retreats, even basic elements of upland ecology have remained essentially a ''black box.'' For example, we know almost nothing about interspecific interactions, density dependent effects on growth and maturation, and how these factors may influence dispersion in the uplands. Further, two recent papers indicate that amphibian population viability is often extremely sensitive to reductions in survivorship of upland stages (Biek et al. 2002, Vonesh and de la Cruz 2002). Clearly, additional experimental and observational studies of upland ecology are warranted (Storfer 2003).

Although population modeling studies have demonstrated that amphibian populations are sensitive to reductions in upland survival parameters, we know of no attempts to estimate the effects of upland habitat loss or modification on populations. For conservation planning, a model reflecting the likely population-level consequences of converting upland habitat to non-habitat or habitat where survival is substantially reduced, would greatly improve our ability to estimate the effects of human modification of landscapes. This would require both a demographic population model and a model describing the spatial distribution of individuals in the uplands. Unfortunately, either of these pieces is available for very few species, mainly due to the rarity of detailed upland distribution data.

The federally threatened California tiger salamander (*Ambystoma californiense*; CTS; see Plate 1) is a species for which there is a pressing need for a realistic analysis of the likely population-level effects of upland habitat conversion. Currently, the best available evidence suggests that this pond-breeding species has declined primarily due to the conversion of its aquatic and upland habitats to intensive land uses (Fisher and Shaffer 1996, U.S. Fish and Wildlife Service 2000, Davidson et al. 2002). In 2004, the U.S. Fish and Wildlife Service listed the CTS as a federally threatened species throughout its range, which includes parts of 22 California counties (U.S. Fish and Wildlife Service 2004*a*). Researchers have characterized many critical aspects of CTS life history, demography, ecology, and genetics (Shaffer et al. 1991, Austin and Shaffer 1992, Fisher and Shaffer 1996, Loredo and Van Vuren 1996, Trenham et al. 2000, 2001, Trenham 2001, Shaffer et al. 2004). We used data from those studies to parameterize a stage-based demographic population model that includes density dependent larval survival and environmental stochasticity. However, our knowledge of upland distribution, based two short-term studies that tracked metamorphosed CTS either visually (Loredo et al. 1996) or with radio transmitters (Trenham 2001), was inadequate to confidently project the population-level impacts of upland habitat loss.

We had two goals for the current study. First, we sought to collect field data that would allow us to derive an empirical model reflecting the distribution of salamanders in the uplands around an isolated breeding pool. Because CTS are usually at least four years old when they breed for the first time (Trenham et al. 2001), we sought to design a study that would yield relevant upland distribution data for adults and subadults. Rather than tracking individuals, we used an upland trap grid to capture salamanders. We modeled trap capture rates as a function of distance from the breeding pond, and based on those relationships estimated the width of surrounding upland habitat needed to encompass

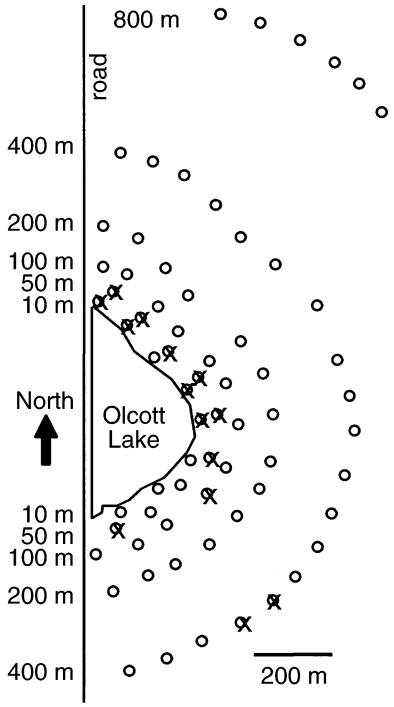


FIG. 1. Map of trap locations east of Olcott Lake, Solano County, California, USA (38.2712° N, 121.8224° W). Small circles indicate the location of each trap. An × is superimposed over traps consistently flooded and thus excluded from analyses.

specific proportions of CTS movements. Second, we used this newly derived model describing upland distribution and our demographic model to simulate the population-level effects of upland habitat loss/conversion around an isolated breeding pond. We explored the behavior of the model across a range of realistic parameter values and conducted an elasticity analysis to determine which parameters had the greatest incremental influence on the probability of quasi-extinction (Morris and Doak 2002). We discuss the implications of our results for the management and recovery of the CTS and other pond-breeding amphibians.

## MATERIAL AND METHODS

### *Field methods*

We collected field data at the Jepson Prairie Preserve, Solano County, California, USA. The site is essentially flat with less than 2.5 m of elevation variation across the entire 625-ha preserve. The uplands are dominated by grassland with a remnant stand of introduced blue gum (*Eucalyptus globulus*). The dominant feature in this landscape is Olcott Lake, a 36-ha playa vernal pool (Fig. 1). This pool fills with winter rainfall and runoff to a maximum depth of ~1 m, and dries every year, typically between May and July. In addition to harboring several endangered crustaceans (U.S. Fish and Wildlife Service 2002), this pool consistently contains large numbers of CTS larvae (H. B. Shaffer, *unpublished data*). Although CTS are known to use the burrows of both California ground squirrels (*Spermophilus beecheyi*) and pocket gophers (*Thomomys bottae*), only gopher burrows were present and abundant in all upland areas of the preserve. The pool is split by a north–south dirt road. We focused our trapping effort east of this road because there are no other suitable breeding pools for several kilometers to the east, whereas there are other breeding pools to the west. Based on prior tracking (Trenham 2001) and interpond movement (Trenham et al. 2001) studies at other sites, we assume that terrestrial salamanders captured east of the road originated exclusively from Olcott Lake.

We installed a total of 68 trap systems around the eastern half of Olcott Lake at locations 10, 50, 100, 200, 400, and 800 m away from the high-water line (hereafter, traps; Fig. 1). The distribution of traps was based on prior observations of CTS movements (Trenham 2001, Trenham et al. 2001). Each trap consisted of a 10 m long section of 0.9 m tall silt fence supported by wooden stakes. The bottom 15–30 cm of the silt cloth was buried in a shallow trench and anchored in place. Fence sections were oriented parallel to the perimeter of Olcott Lake. At both ends of each fence, one 3.8-L plastic bucket with 5 mm diameter drain holes was buried with its lip flush with the ground surface. To allow us to determine the direction of travel of captured animals, a tight-fitting piece of 4 mm thick plywood divided each bucket along the axis of the silt fence. A block of wood was attached to the top side of each bucket lid, such that when the lid was inverted it was supported 3 cm above the bucket lip, providing shade over the entire bucket. To allow the escape of nontarget animals, 15 cm long sections of rope were attached to the lids and hung in each bucket (Karraker 2001). When not in use, the bucket lids were closed to prevent the entry of animals.

Traps were spaced 90 m apart to achieve consistent fence coverage of ~10% at each distance. We shifted the spacing between some traps to avoid low areas subject to flooding. The portion of Olcott Lake east of the road is roughly half-circular with a radius of 240 m and a 754-m perimeter (Fig. 1). An arc 10 m beyond the high-water line has a radius of 250 m and a hemispherical perimeter of 785 m, so the eight 10 m long traps that we installed here encompassed just over 10% of that arc. Along the 50-, 100-, 200-, and 400-m arcs, we installed nine, 12, 14, and 19 traps, respectively, thus keeping coverage between 9.5% and 11.2% of each arc. The six traps installed at 800 m represent 1.8% coverage east of the road at this distance. We did not initially plan for traps at 800 m and only added them after we captured substantial numbers of CTS at 400 m. We constructed the 800 m traps northeast of Olcott Lake because initial captures were generally greater in this direction. We chose the 800 m distance to continue the pattern of doubling distances between

TABLE 1. Demographic information used to construct and parameterize the California tiger salamander population model.

| Parameter | Estimate |
|---|---|
| Age of reproductive females | ≥4 yr |
| Annual subadult survival probability | 0.6†, 0.66 |
| Annual adult survival probability | 0.6†, 0.66 |
| Probability of breeding in typical pond-filling years | 0.5 |
| Probability of breeding in late pond-filling years | 0.1 |
| Probability of late pond-filling years | 0.0, 0.1, 0.3†, 0.5 |
| Probability of complete reproductive failure | 0.0, 0.1†, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 |
| Eggs deposited per breeding female | 814 |
| Survival from egg to metamorphosis | $0.131 \times (\text{no. eggs per m}^2)^{-0.6803}$; maximum = 0.20 |
| Pond areas considered | 700 $m^2$, 3500 $m^2$, 7000 $m^2$ |

*Note:* Where multiple parameter values are listed, daggers (†) indicate best estimates based on Trenham et al. (2000, 2001).

trap lines (Turchin 1998). The decision to construct all six traps in this area was purely for logistical reasons; we wanted to provide a reasonable probability of detection while not dramatically increasing the time to check all traps.

The first appreciable rain of the 2002–2003 season came on 13 December. We began installing traps on 14 December, and captured our first CTS that night. Traps 10 to 400 m from Olcott Lake were installed between 14 December 2002 and 4 January 2003; we added the 800-m traps on 20 January 2003. Beginning on 14 December, traps were opened each day prior to predicted rain, and kept open for several days thereafter. We installed a rain gauge to measure precipitation received between site visits. When open, we checked traps each morning by 07:30. Because we never caught more than one animal if no rain fell during the 24 hours prior, we closed traps after several days without rain or captures. Trapping of subadults and adults was terminated on 21 March 2003.

For each captured CTS, we noted trap number and direction of travel (i.e., moving towards or away from the pond). We also photographed each individual next to a metric ruler, clipped a single toe that was preserved in 70% ethanol, and recorded the sex of adult animals. Animals were immediately released into nearby dense vegetation or pocket gopher burrows. We measured the snout–vent length of each animal from the photographs.

### *Data analysis and modeling*

The dependent variable that we modeled in our analyses was the capture rate of each trap, with the two buckets on each fence considered elements of the same trap. To determine capture rates for each trap we divided the number of adults or subadults captured by the number of nights the trap was open. We took this approach because there was some variability in the number of nights each trap was open. Capture rates were square root transformed prior to further analysis, and traps that were consistently flooded ($n = 14$; Fig. 1) and from which salamanders could easily escape were excluded from these analyses. We used linear and nonlinear regression to fit statistical models relating capture rates to distance from Olcott Lake. Based on these functions we estimated capture rate at 10 m intervals to the point where no further captures were predicted. We summed the capture rates across all distances, and then estimated the cumulative proportion of captures encompassed by upland habitat rings of increasing width.

To investigate the potential effects of increased mortality due to upland habitat loss on adult population size and population persistence, we used a stage-based matrix population model with six stages: new metamorphs, 1-yr-old subadults, 2-yr-old subadults, 3-yr-old subadults, new adults, and older adults (Caswell 2001). We parameterized the basic model with demographic data from our long term study of this species in Monterey County, California, USA (Trenham et al. 2000; P. C. Trenham, *unpublished data*; Table 1, Fig. 2). Because adult males are not presumed to be limiting, the model tracks only females. In the model, salamanders mature at four years old and, in each year, a fraction the surviving adults breed. Each breeding female lays a clutch of 814 eggs, half of which are assumed to be female, and survival from laying to metamorphosis depends on egg density in the pond (Fig. 2). After metamorphosis, upland survival of subadults and adults are fixed, but can be adjusted independently. In reality, subadult survival is poorly characterized. However, assuming that subadults survive at the same rate as adults (0.60) and mature at four years old, approximately 13% would survive to maturity, which matches the available data for this and related species (Scott 1994, Loredo and Van Vuren 1996, Trenham et al. 2000).

At the start of each model run, the population was composed of 100 new metamorphs, 50 1-yr-old subadults, 25 2-yr-old subadults, 13 3-yr-old subadults, seven new adults, and seven older adults. The model included two forms of environmental stochasticity to match observations from our long-term study (Trenham et al. 2000). First, because we found that in years when ponds fill late, females are much more likely to skip breeding, late pond-filling years occurred with a defined probability and the probability that an adult female bred in these years was reduced. Second, in some years model reproduction failed completely, as is com-

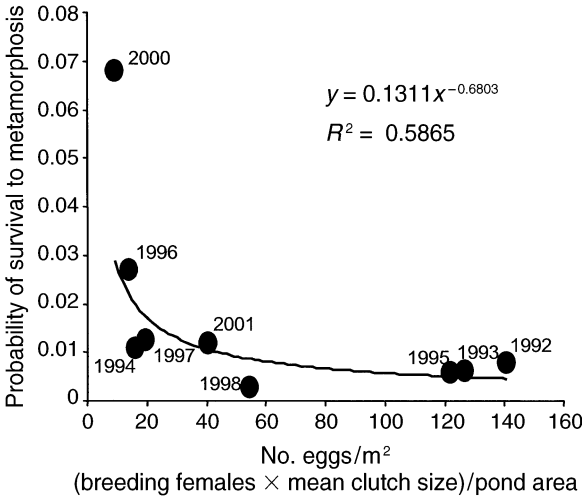


FIG. 2. Data from our long-term study in Monterey County, California, USA, suggest that larval survival is density dependent (Trenham et al. 2000). We fit a negative power function to these data to approximate this relationship. Symbols are labeled with the year for each data point; in 1999 California tiger salamander (CTS) breeding failed completely. Probability of survival to metamorphosis for each year was calculated as the number of newly metamorphosed salamanders emerging from the pond divided by the product of the number of breeding females and the average clutch size. Initial egg density was calculated as product of the number of breeding females and the average clutch size divided by 700 $m^2$, the area of our long-term study pond.

monly observed when ponds dry prior to metamorphosis (Gill et al. 1983, Semlitsch et al. 1996). Each year the program selected one random number to determine if pond-filling was late, and a second random number to determine if reproduction failed. Depending on the random values generated, the program used one of three alternate forms of the transition matrix—the first for typical pond-filling years, the second for late pond-filling years, and the third for years when reproduction failed completely—to project the population at the next time step. We initially evaluated model behavior with the probabilities of late filling and reproductive failure set to zero, and then with these probabilities set at a range of values (Table 1). For each set of parameter values considered we ran the model 100 times, recording for each the mean and variance in the number of adult females at 100 years, and the number of runs that went to zero. Because our model did not include random variation in upland survival probabilities and reproductive output, the probability of extinctions was underestimated.

To determine which parameters had the greatest proportional effect on modeled population viability, we used a simulation approach to estimate the elasticity values for cumulative quasi-extinction probabilities (Morris and Doak 2002). The quasi-extinction threshold was set at five adult females. To obtain elasticities we first ran the model with a baseline set of parameters, and then with each parameter reduced to 95% of its baseline value. For each parameter set, we made 1000 model runs of 100 years each, recording for each run where the adult population dipped to or below the quasi-extinction threshold, the year in which this occurred. Elasticities for each parameter were estimated based on the difference between the baseline and perturbed cumulative quasi-extinction probability at each year (Morris and Doak 2002).

After evaluating model behavior assuming intact upland habitat, we investigated the population-level consequences of maintaining increasingly narrow bands of unaltered upland habitat adjacent to 700-, 3500-, and 7000-$m^2$ breeding ponds. For these simulations, we fixed the probabilities of late pond-filling years and reproductive failures at 0.30 and 0.10, respectively, to match our long-term observations of environmental variation (Trenham et al. 2000; P. C. Trenham, *unpublished data*). We began with the same three alternative forms of the transition matrix described previously. However, based on the estimated cumulative distribution of subadults and adults in the uplands around Olcott Lake, survival parameters were adjusted accordingly. Because actual survival in altered habitat is unknown, we investigated two scenarios for animals moving beyond the protected habitats: (1) no survival and (2) survival reduced by 50%. For example, assuming that 10% of adults remain within 100 m of the breeding pond, an unaltered upland survival probability of 0.60 would be reduced to 0.06 for scenario one, or 0.33 (i.e., 0.06 + [0.54/2]) for scenario two. The first scenario approximates what we imagine occurs with intensive residential development, the second may be representative of some agricultural land uses or low-density housing. We assumed that movement is independent of habitat suitability. Because subadults do not migrate to and from the pond each year, the reduction in survival due to habitat alteration was assessed only once prior to maturity for each cohort. We also compared the effects of basing the cumulative distribution functions on different functional forms of the relationship between density and distance for the Olcott Lake data.

## RESULTS

### *Upland trapping results*

Between 14 December 2002 and 21 March 2003, we captured 74 female, 53 male, and 62 subadult CTS in 2696 trap-nights (see Appendix A for a complete listing of capture data). Only three salamanders were recaptured; for these individuals we used only their initial capture data in the analyses that follow. We captured at least one male, female, and subadult salamander in traps at each distance from 10 to 400 m from Olcott Lake. We captured no CTS in our traps at 800 m. Comparisons of the distributions of adult and subadult captures, however, indicate divergent relationships be-

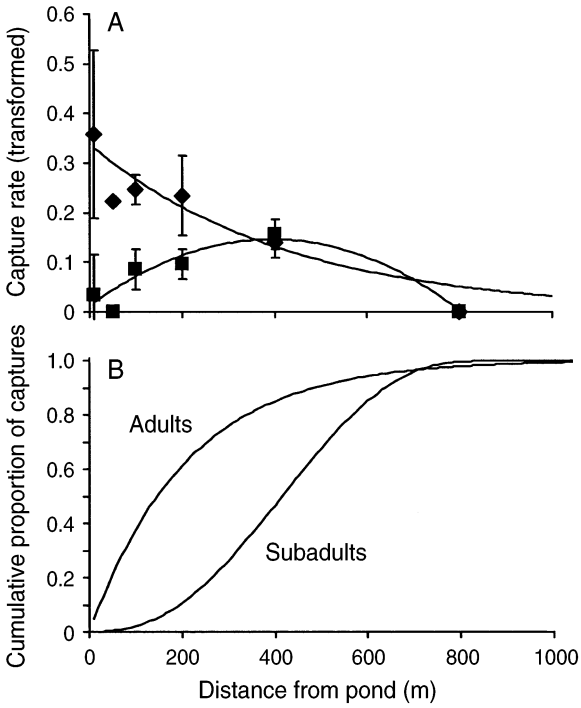


FIG. 3. Spatial distribution of California tiger salamander captures for all non-flooded traps. (A) Square-root-transformed number of adult (diamonds) and subadult (squares) captures per trap-night summarized for each distance (mean ± 2 SE). Lines represent exponential (adults) and second-order polynomial (subadults) regressions fit to the data; parameters are provided in *Upland trapping results.* (B) Using the regression functions represented in Fig. 3A, we estimated the cumulative proportion of subadults and adults encompassed within increasingly wide upland buffers around Olcott Lake.

tween capture rate and distance for these two groups. Adult capture rates declined from a maximum at 10 m, whereas subadult captures increased steadily from 10 to 400 m (Fig. 3A).

To make quantitative predictions about the distribution of adults in the uplands, we fit linear and exponential functions to the full adult data set. Although there was substantial heterogeneity in capture rates among traps at each distance, both the linear ($\sqrt{y} = 0.300 - 0.00039 \cdot x$; $F_{1,52} = 37.7$, $P < 0.0001$, $R^2 = 0.408$) and the exponential ($\sqrt{y} = 0.339 \cdot e^{-0.00236x}$; $F_{2,51} = 104.9$, $P < 0.0001$, $R^2 = 0.402$; Fig. 3A) fits were highly significant and explained roughly 40% of the variance in the data. Because there is a history of biological support for an exponential relationship between density and distance (Turchin 1998), we focus our further investigations on this form. Extrapolating from the exponential fit, we estimate that to encompass 50%, 90%, and 95% of the adults would require upland habitats extending 150, 490, and 620 m from the edge of Olcott Lake, respectively (Fig. 3B). A potential issue of concern with our sampling was the presence of only six traps at 800 m. To assess the influence of our lack of captures at 800 m on the predicted relationship we reanalyzed the data with those traps excluded. Extrapolating from the resulting function ($\sqrt{y} = 0.326 \cdot e^{-0.00205x}$; $F_{2,45} = 96.7$; $P < 0.0001$; $R^2 = 0.235$) the predicted upland habitat areas to encompass the same proportions of adults as above are roughly 13% wider: 170, 550, and 700 m, respectively.

Because subadult captures increased steadily from 10 to 400 m but declined to zero at 800 m we fit a quadratic function to the subadult dataset. Although the true shape of the function between 400 and 800 m cannot be determined from our data, quadratic regression provides a reasonable approximation. Fitting this function to the data resulted in a statistically significant relationship which explained only 18% of the variation ($\sqrt{y} = 0.084 + (1.8 \cdot 10^{-4}x) - (9 \cdot 10^{-7}(x - 290)^2)$; $F_{2,51} = 5.52$, $P = 0.007$, $R^2 = 0.178$; Fig. 3A). Extrapolating from this function the widths of upland habitat to encompass 50%, 90%, and 95% of subadults are 380, 590, 630 m, respectively (Fig. 3B). Upon further inspection, we noticed that very few subadults were captured in the traps south of Olcott Lake; dividing the traps into a northern and southern half there were 53 northern and nine southern captures. Reanalyzing only the northern trap data resulted in a substantially improved fit ($\sqrt{y} = 0.208 + (4.4 \cdot 10^{-5}x) - (1.3 \cdot 10^{-6}(x - 359)^2)$; $F_{2,26} = 10.12$, $P = 0.0006$, $R^2 = 0.438$). However, the predicted upland habitat widths to encompass 50%, 90%, and 95% of subadult CTS were nearly identical at 390, 600, 650 m, respectively.

### *Population model output*

Before attempting to assess the population-level effects of upland habitat alteration for CTS, we investigated the model response to variation in parameters other than upland survival. With no stochastic elements, because larval survival was density dependent the number of adult females in the population rapidly reached an equilibrium determined by upland survival probabilities and pond area. With subadult and adult survival both set at 0.60, half of adult females breeding each year, and no stochastic reproductive failures, the equilibrium adult female population increased by one for each additional 8.1 $m^2$ of pond area.

Next, we investigated how population size and extinction risk responded to a range of stochastic conditions. Fig. 4A shows that, for a given pond area and probability of late pond filling, the average adult population size declines linearly as the probability of reproductive failure increases. Similarly, if the probability of reproductive failure is held constant while the probability of late pond-filling years is increased the mean adult population size declines linearly. Fig. 4B shows that the proportion of model runs going to zero within 100 years accelerates as the probability of reproductive failure increases. Because larvae may survive to metamorphosis in late pond-filling years, but not with reproductive failure, increasing the probability

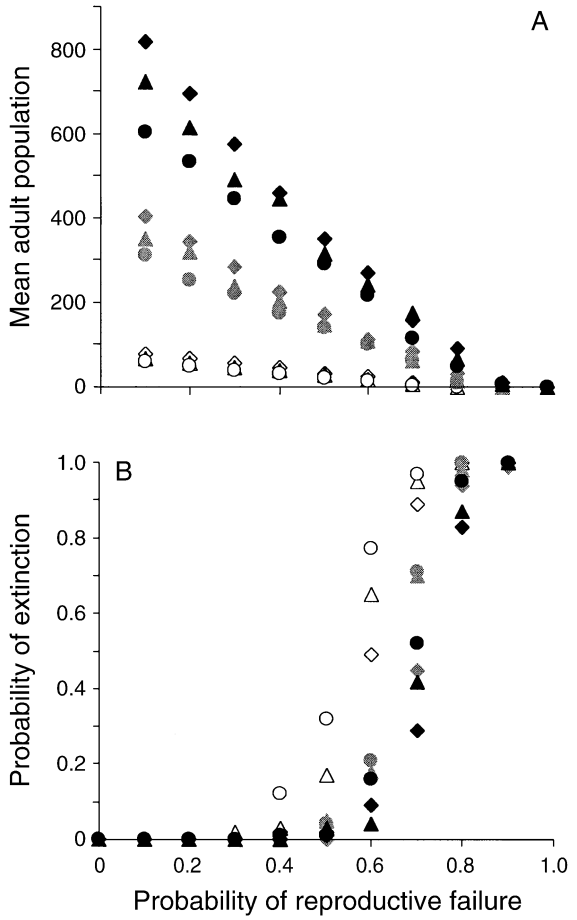


FIG. 4. Using our simulation model, we explored how (A) average California tiger salamander population size and (B) local extinction risk responded to increasing degrees of environmental stochasticity. Environmental stochasticity entered the model as (1) the probability of complete reproductive failure due to early pond drying (range 0–0.9; *x*-axis), and (2) the probability of late pond-filling years when only 10% of surviving females bred (diamonds = 0.1; triangles = 0.3; circles = 0.5). The probabilities of these perturbations were modeled as independent events. Symbol colors indicate the three different pond sizes modeled: 700 $m^2$ (open symbols), 3500 $m^2$ (gray symbols), and 7000 $m^2$ (black symbols). Upland survival of subadults and adults was set to 0.6. Females could breed beginning at four years old, and 50% of surviving females bred in each typical pond-filling year. Probability of survival to metamorphosis declined from a maximum of 0.2 in response to the density of eggs deposited in the pond (Fig. 2).

of the latter produced a larger effect on average population size and the frequency of runs that went to zero.

Fig. 5 summarizes the results of an elasticity analysis of the probability of quasi-extinction in model simulations. This analysis indicated that the probability of quasi-extinction was relatively insensitive to parameters influencing larval survivorship, but highly sensitive to small perturbations of upland survivorship. Of the two upland survivorship parameters, quasi-extinction probability was more than twice as sensitive to shifts in subadult as adult survivorship. Quasi-extinction probability was similarly insensitive to perturbation of each of the two parameters controlling larval survival.

The ultimate goal of this modeling exercise was to investigate the potential population-level consequences of converting upland habitat to nonhabitat or to habitat where survival is substantially reduced. Because there is uncertainty in the model parameters, we conducted simulations for a range of baseline survival parameters, mortality scenarios, and functional relationships between upland distribution and distance (see Table 1). In Fig. 6, we present model results illustrating the estimated effects on adult population size of maintaining increasingly wide areas of undisturbed upland habitat around a 700-$m^2$ pond; the results of model runs for 3500- and 7000-$m^2$ ponds were qualitatively identical (not shown). Consistent with the elasticity analysis results (Fig. 5), increasing annual subadult survivorship from 0.6 to 0.66 resulted in a larger average adult population than did similarly increasing adult survivorship (Fig. 6). Assuming a linear rather than an exponential decline in adult upland densities, resulted in small increases to estimated average population sizes of about 10–20% (Fig. 6).

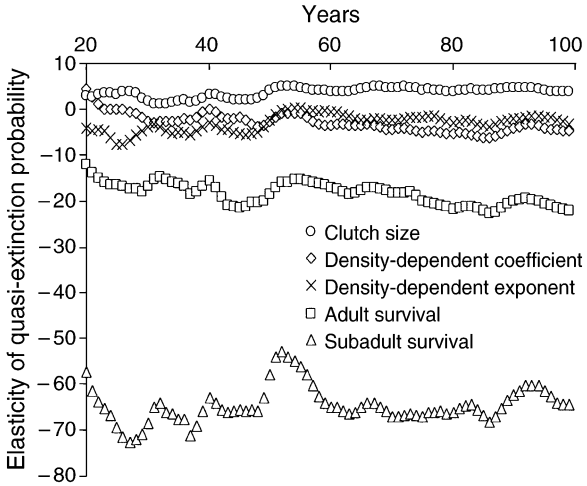


FIG. 5. Estimated elasticity values for cumulative quasi-extinction probabilities in response to perturbations of mean vital rates. Symbols represent elasticity in response to perturbation of various model parameters: subadult survival, adult survival, coefficient and exponent in larval density-dependent survival function, and number of eggs deposited per breeding female. Five adult females was the quasi-extinction threshold. The baseline model parameter values for this analysis were those indicated in Table 1. Elasticities for <20 years are not plotted because few extinctions occurred before this time, and as a result estimates of extinction probabilities and elasticities during this interval are highly variable and unreliable. Methods for elasticity analysis of density-dependent stochastic models are adapted from Morris and Doak (2002).

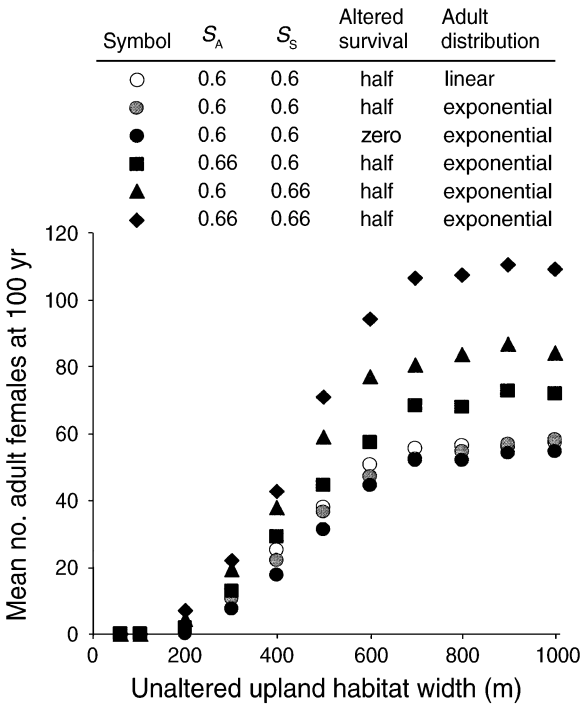


FIG. 6. Simulation model results showing the response of adult population size to the maintenance of increasingly wide bands of unaltered habitat around breeding ponds. Each point represents the mean number of adult females present in the simulated population at time step 100 based on a total of 100 runs with each set of parameter values. Different symbols represent different initial values for upland survival (i.e., with completely intact upland habitat), different mortality scenarios for animals moving into altered habitats (i.e., zero vs. halved survivorship), and adult survivorship ($S_A$) reduced either according to the cumulative distribution function in Fig. 3B (exponential) or a cumulative distribution function based on a linear relationship between adult captures and distance (linear; not shown). Subadult survivorship ($S_S$) was always reduced according to the subadult cumulative distribution function in Fig. 3B. Results shown are for a 700-m$^2$ breeding pond, with late pond-filling years and reproductive failures in 30% and 10% of years, respectively.

In general, as subadult and adult survival were reduced in response to simulated habitat loss, average population sizes declined, with accelerating declines when adjacent habitats extending less than 600 m from the pond edge were maintained (Fig. 6). Although estimated adult population sizes were sensitive to the particular set of parameter values, the proportional effects of a given amount of habitat loss were consistent. For example, under all scenarios considered, maintaining only a 400 m wide ring of upland habitat resulted in population declines of >50% when compared with the unaltered condition. Predicted declines approached 70% when animals moving into altered habitat all died. Leaving 200 m of upland habitat resulted in declines in average population size of 90–100%. Finally, if only 60 m of upland habitat was left intact, populations are generally predicted to go extinct within 100 years, or occasionally persist but at <1% of their estimated capacity in an intact landscape.

## DISCUSSION

To confidently manage wetland habitats for viable populations of semi-aquatic animals requires a more detailed understanding of how these animals use upland habitats (Semlitsch and Bodie 2003). For researchers attempting to understand amphibian population ecology, penetrating the upland ecology of small, secretive, and often fossorial amphibians has remained a daunting empirical challenge (Taub 1961, Semlitsch 1998). While no single method or strategy will provide all of the critical data, our quantitative drift fence analysis of CTS at Jepson Prairie provides at least two novel results. First, adult dispersion appears to be far greater than indicated by earlier projections based on direct observations (Loredo et al. 1996) and radio tracking data (Trenham 2001), and is more in line with estimates based on observations of interpond dispersal over several years (Trenham et al. 2001). Second, the spatial distribution of subadults appears to be very different from that of adults.

To date, radio tracking has been the primary method used to obtain data on the distribution of adult amphibians in the uplands. Semlitsch (1998) and Trenham (2001) used tracking data to estimate the upland distribution ambystomatid salamanders. In a review of six eastern U.S. *Ambystoma* species, adults captured at breeding ponds and tracked directly via radio transmitters or radioactive implants moved an average of 125 ± 73 m (mean ± 1 SD) from ponds (Semlitsch 1998). Similarly, Trenham (2001) documented an average emigration distance of 114 ± 83 m for radio-tracked adult CTS. Assuming that movements are normally distributed, the means approximate the width of upland habitat required to encompass 50% of salamander movements. The means plus 1.645 standard deviations approximate the width of upland habitat needed to encompass 95% of movements (i.e., 245 and 250 m for these two studies). Our trapping results similarly suggest that 50% of adults are within 150 m of Olcott Lake. However, our analyses suggest that to encompass 95% of adults a 620 m wide upland habitat area is needed.

Although direct-tracking data provide valuable information on individual behavior and movements, we place more confidence in our trap-based projections of population distribution in the landscape for several reasons. First, there are always concerns that radio-equipped animals may not behave naturally, which is not an issue with our trap-based approach. Second, rather than assuming a normal distribution for salamander migration distances (Semlitsch 1998, Trenham 2001), we fit statistical models to the spatial distribution of actual capture rates. Finally, whereas radio tracking studies generally follow animals for only a few months after breeding, longer studies suggest that

movement during these initial periods may not be representative of total adult displacement (e.g., Madison 1997, Madison and Farrand 1998). Because CTS adults frequently skip breeding for one or more years (Trenham et al. 2000), following post-breeding movements for just a few months is likely to underestimate overall movement patterns. Trap arrays, in contrast, register upland movements in proportion to their occurrence in the landscape. Interestingly, our projections in the current study closely resemble the spatial distribution of interpond dispersal events in our Monterey County study. In that system we observed adult and subadult dispersal among ponds separated by 60–670 m, but not farther (Trenham et al. 2001).

Because newly metamorphosed and subadult amphibians are generally too small to equip with radio transmitters, almost nothing is known about the upland ecology of these intermediate life stages. Whereas Semlitsch (1998) found tracking data for 265 individual adult *Ambystoma*, he found data for only 18 newly metamorphosed juveniles, and no data on subadults. CTS most commonly require three to five years to reach sexual maturity (Trenham et al. 2000; P. C. Trenham, *unpublished data*), and during this time they are completely terrestrial and rarely encountered. In contrast to the decline in adult capture rates at increasing distances from Olcott Lake, subadult capture rates increased from 10 to 400 m, and then declined to zero at 800 m. The apparent overall greater dispersion of subadults could potentially be a response to size-structured competition, which has been documented in related species (Smyers et al. 2002), or simply a consequence of diffusion-like movement over the lengthy subadult phase compared to the shorter interval between adult breeding events. Regardless of the cause, our data suggest that to encompass 95% of subadults an upland area on the order of 630 m wide would be required.

Although recommending upland habitat protection guidelines to encompass specific proportions of populations is a logical approach (Semlitsch 1998, Faccio 2003), this may not maintain population viability. We used a stochastic population model to evaluate this goal more directly. The results of our model, represented in Fig. 6, suggest that protecting at least 600 m of upland habitat would maintain populations with ~10% reduction in mean population size. Extrapolating from Fig. 3B, this translates to 90% and 92% protection of adults and subadults, respectively, and thus supports the protective value of the 95% protection benchmark. From a management perspective, this is a useful benchmark in situations where the goal is to maintain populations on lands containing one or a few breeding ponds isolated from immigrants. The upper bound on core upland habitat width of 290 m suggested by Semlitsch and Bodie (2003) may adequately protect other species, but our analyses suggest that if it were applied to CTS average population sizes would be reduced by >80% (Fig. 6). Therefore, for long-term preservation of individual CTS populations, the currently best-supported strategy is establishing protected landscapes with breeding ponds buffered by at least 630 m from incompatible upland land uses.

In many situations, due to historic habitat losses, protecting such broad areas of upland habitat will not be possible. Although breeding ponds nested in suboptimal uplands will be more likely to experience local extinctions, if linked to other ponds by dispersal they could contribute to the maintenance of a regional metapopulation (Sjögren-Gulve and Ray 1996, Marsh and Trenham 2001). Experimental metapopulation approaches to conservation may be the only viable option for CTS preservation highly fragmented regions and for the broader recovery of this species. Studies of a wide variety of amphibian species suggest that interpond distances of less than one kilometer should be maintained to avoid isolating breeding ponds (Marsh and Trenham 2001, Semlitsch 2002; but see also Smith and Green 2005). Strategies worth considering may include protecting corridors of marginal upland habitat between breeding sites, pond creation to enhance connectivity among distant sites, and even translocation of individuals to currently isolated unoccupied sites (Trenham and Marsh 2002, Seigel and Dodd 2002).

Ideally, before more detailed guidelines are drawn and predictions made, data from multiple sites and multiple years would be available to evaluate spatial and temporal variation in upland distribution, upland survival, and reproduction. Our model results suggest that obtaining additional data on upland survival should be a priority. In this and similar studies, pond-breeding amphibian populations are sensitive to upland survivorship of adults and subadults (Taylor and Scott 1997, Biek et al. 2002, Vonesh and de la Cruz 2002). Recognizing that upland survivorship of subadults is the parameter in which we have the least confidence and to which model results were most sensitive, this is an important area for additional study. Estimates of survivorship in different land use treatments would be of both basic and applied value (e.g., Rothermel and Semlitsch 2002).

Although we constructed our model as a tool to investigate the effects of upland habitat alteration, the results address some broader patterns of interest. Marsh and Trenham (2001), in reviewing the fit between theoretical metapopulations and pond-breeding amphibians, found little evidence that random extinctions of local populations are common as long as upland habitats were intact. This was also true of our model populations (Fig. 4B), and is due to strong density dependence in larval survivorship. In models where reproduction is enhanced at low densities, there is a strong tendency to recover from stochastic reductions in population size (Taylor and Scott 1997, Vonesh and de la Cruz 2002, Ferrer et al. 2004). From a practical perspective, our model results should also inform attempts

to create breeding habitat for CTS or to assess the value of existing habitats. Our simulations emphasize the value of breeding habitats with large surface areas and those that hold water until metamorphosis in most years. In habitats where the probability of reproductive failure exceeds 0.50, simulations suggest that the result will be frequent local extinctions. However, it is important to note that, due to the potential for the establishment of fishes and other predator populations, reproductive failure is common in both permanent and highly ephemeral pools (Fisher and Shaffer 1996, Semlitsch 2002). Recent work indicates that even pond ''improvement'' that reduces the probability of annual drying, increases invasability by exotic fishes, crayfish and non-native tiger salamanders (*A. tigrinum*) decreasing the biological value of these sites (Fitzpatrick and Shaffer 2004).

The CTS was initially emergency listed as endangered in both Santa Barbara and Sonoma counties due to rapid conversion of its remaining habitat (U.S. Fish and Wildlife Service 2000, 2003). Because habitat loss was the main threat that brought about both of these actions and the statewide listing, a primary recovery objective should be the establishment of preserve areas with sufficient breeding and upland habitat for long-term persistence. To encompass a single isolated breeding pond with a 630 m wide ring of upland habitat (i.e., 95% protection) would require at least 125 ha. In Santa Barbara County, where all known CTS breeding ponds are on privately owned land, the U.S. Fish and Wildlife Service recently determined that about 4500 ha of critical habitat is needed to protect the salamander in perpetuity (U.S. Fish and Wildlife Service 2004*b*). In Sonoma County, confirmed breeding ponds existed on several preserves at the time of the emergency listing, but the largest of these protected areas is just 73 ha, and most are much smaller (U.S. Fish and Wildlife Service 2003). Thus, particularly in Sonoma County, experimental metapopulation approaches may be the only solution to the long-term viability of the remaining populations. Although the study of amphibians in the uplands remains challenging, new approaches are emerging that promise to yield further basic insights and data essential for improved conservation planning and management (Regosin et al. 2003, Rothermel and Semlitsch 2002). The pursuit of guidelines for upland habitat protection around wetlands will benefit from additional quantification of the consequences of habitat loss and appropriate data collection to reduce the assumptions required.

## Acknowledgments

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## APPENDIX A

A table showing raw trapping data is presented in ESA's Electronic Data Archive: *Ecological Archives* A015-031-A1.

## APPENDIX B

A photograph of the study area and some representative traps is presented in ESA's Electronic Data Archive: *Ecological Archives* A015-031-A2.

# Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities

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**Abstract:** *Roads are a widespread and increasing feature of most landscapes. We reviewed the scientific literature on the ecological effects of roads and found support for the general conclusion that they are associated with negative effects on biotic integrity in both terrestrial and aquatic ecosystems. Roads of all kinds have seven general effects: mortality from road construction, mortality from collision with vehicles, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotics, and increased use of areas by humans. Road construction kills sessile and slow-moving organisms, injures organisms adjacent to a road, and alters physical conditions beneath a road. Vehicle collisions affect the demography of many species, both vertebrates and invertebrates; mitigation measures to reduce roadkill have been only partly successful. Roads alter animal behavior by causing changes in home ranges, movement, reproductive success, escape response, and physiological state. Roads change soil density, temperature, soil water content, light levels, dust, surface waters, patterns of runoff, and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments. Roads promote the dispersal of exotic species by altering habitats, stressing native species, and providing movement corridors. Roads also promote increased hunting, fishing, passive harassment of animals, and landscape modifications. Not all species and ecosystems are equally affected by roads, but overall the presence of roads is highly correlated with changes in species composition, population sizes, and hydrologic and geomorphic processes that shape aquatic and riparian systems. More experimental research is needed to complement post-hoc correlative studies. Our review underscores the importance to conservation of avoiding construction of new roads in roadless or sparsely roaded areas and of removal or restoration of existing roads to benefit both terrestrial and aquatic biota.*

Revisión de los Efectos de Carreteras en Comunidades Terrestres y Acuáticas

**Resumen:** *Las carreteras son una característica predominante y en incremento de la mayoría de los paisajes. Revisamos la literatura científica sobre los efectos ecológicos de las carreteras y encontramos sustento para la conclusión general de que las carreteras están asociadas con efectos negativos en la integridad biótica tanto de ecosistemas terrestres como acuáticos. Las carreteras de cualquier tipo ocasionan siete efectos generales: mortalidad ocasionada por la construcción de la carretera; mortalidad debida a la colisión con vehículos; modificaciones en la conducta animal; alteración del ambiente físico; alteración del ambiente químico; dispersión de especies exóticas e incremento en el uso de áreas por humanos. La construcción de carreteras elimina a organismos sésiles y a organismos de lento movimiento, lesiona a organismos adyacentes a la carretera y altera las condiciones físicas debajo ella misma. Las colisiones con vehículos afectan la demografía de muchas especies tanto de vertebrados como invertebrados; las medidas de mitigación para reducir la pérdida de animales por colisiones con vehículos han sido exitosas solo de manera parcial. Las carreteras alteran la conducta animal al ocasionar cambios en el rango de hogar, movimientos, éxito reproductivo, respuesta de escape y estado fisiológico. Las carreteras cambian la densidad del suelo, temperatura, contenido de agua en el suelo, niveles de luz, polvo, aguas superficiales, patrones de escurrimiento y sedimentación, además de agregar metales pesados (especialmente plomo), sales, moléculas orgánicas, ozono y mutrientes a los ambientes que atraviesan. Las carreteras promueven la dispersión de especies exóticas al alterar los hábi-*

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*tats, al estresar a las especies nativas y proveer corredores para movimiento. Las carreteras también promueven el incremento de la caza y la pesca, el hostigamiento pasivo de animales y modificaciones del paisaje. No todas las especies ni todos los ecosistemas son afectados por las carreteras de igual forma, pero en general la presencia de carreteras está altamente correlacionada con cambios en la composición de especies, los tamaños poblacionales y los procesos hidrológicos y geomorfológicos que afectan a la estructura de sistemas acuáticos y reparios. Se necesita más investigación experimental para complementar estudios correlativos post-hoc. Nuestra revisión hace énfasis en que en trabajos de conservación es importante evitar la construcción de nuevas carreteras en áreas carentes de ellas o en áreas con pocas carreteras, además de remover o restaurar carreteras existentes con la finalidad de beneficiar tanto a la biota acuática como la terrestre.*

## Introduction

Among the most widespread forms of modification of the natural landscape during the past century has been the construction and maintenance of roads (Diamondback 1990; Bennett 1991; Noss & Cooperrider 1994). As conservation biologists seek to understand the forces that influence the viability of populations and the overall health of ecosystems, it is important that we understand the scope of the ecological effects of roads of all types, especially important as conservation biologists are asked to participate in the development and implementation of strategies to protect or restore elements of biological diversity and integrity.

Roads of all kinds affect terrestrial and aquatic ecosystems in seven general ways: (1) increased mortality from road construction, (2) increased mortality from collision with vehicles, (3) modification of animal behavior, (4) alteration of the physical environment, (5) alteration of the chemical environment, (6) spread of exotic species, and (7) increased alteration and use of habitats by humans. These general effects overlap somewhat. In some cases animals modify their behavior and avoid roads because of concentrated human activity along roads. Roads may facilitate the spread of invasive species by disrupting native communities and changing physical habitats. Roads may fragment populations through roadkill and road avoidance. Despite the difficulty of categorizing discretely the causal basis in every example, these seven categories provide a useful framework for assessing what is known and unknown about the ecological effects of roads.

Selective road removal, relocation, or remediation may provide ecological benefits in certain situations. Yet, although roads are commonly identified as important correlates or indicators of loss of ecological health (e.g., Noss & Cooperrider 1994), the specific mechanisms by which biota are affected are often complicated or uncertain. Therefore, mitigation or treatment of specific effects, whether during road design or in post-construction remediation, can be costly and fraught with uncertainty.

## Mortality from Road Construction

Road construction kills any sessile or slow-moving organism in the path of the road. The extent to which road construction contributes to direct mortality has not been estimated as has direct mortality from other forms of habitat destruction (e.g., Petranka et al. 1993). The fact that road construction kills individual organisms is obvious, however. The magnitude of such construction is not trivial; the 13,107,812 km of road lanes of all types in the conterminous United States, with an average width of 3.65 m per lane, have destroyed at least 4,784,351 ha of land and water bodies that formerly supported plants, animals, and other organisms (U.S. Department of Transportation 1996). The actual number is likely much higher because this estimate does not include shoulder pavement and land peripheral to the roadbed that is cleared during construction.

Construction may physically injure organisms adjacent to the path of construction. Roads built for extraction of white fir result in damage to trees that is visible up to 30 m from the road (Trafela 1987). Such damage contributes to a decline of up to 30% in forest productivity per rotation, due in part to a decline in growth of damaged trees. Construction also alters the physical conditions of the soil underneath and adjacent to the road. Riley (1984) showed that road construction increases soil compaction up to 200 times relative to undisturbed sites. These changes likely decrease the survival of soil biota that are not killed directly. Direct transfer of sediment and other material to streams and other water bodies at road crossings is an inevitable consequence of road construction (Richardson et al. 1975; Seyedbagheri 1996). High concentrations of suspended sediment may directly kill aquatic organisms and impair aquatic productivity (Newcombe & Jensen 1996).

## Mortality from Collision with Vehicles

Mortality of animals from collision with vehicles is well documented. Many reviews of the taxonomic breadth of the victims of vehicle collision have been published (e.g., Groot Bruinderink & Hazebroek 1996). Few if any terrestrial species of animal are immune. Large mammals ranging in size from moose (*Alces alces*) to armadillos (*Dasypus novemcinctus*) are the best-documented roadkills, probably due to interest in their demography and to their size (Bellis & Graves 1971; Puglisi et al. 1974;

Reilly & Green 1974; Holroyd 1979; Wilkins & Schmidly 1980; Bashore et al. 1985; Davies et al. 1987; Bangs et al. 1989; Palomares & Delibes 1992).

Roadkill among many other species includes American Kestrels (*Falco sparverius*; Varland et al. 1993), Barn Owls (*Tyto alba*; Newton et al. 1991), Northern Sawwhet Owls and Eastern Screech Owls (*Aegolius acadicus and Otis asio*; Loos & Kerlinger 1993), tropical forest birds (Novelli et al. 1988), garter snakes (Dalrymple & Reichenbach 1984), granivorous birds (Dhindsa et al. 1988), American crocodile (*Crocodylus acutus*; Kushlan 1988), green iguanas (*Iguana iguana*; Rodda 1990), desert snakes (Rosen & Lowe 1994), toads (van Gelder 1973), plus a wide range of invertebrates, especially insects (H. C. Seibert & Conover 1991).

This form of mortality can have substantial effects on a population's demography. Vehicle collision is the primary cause of death for moose in the Kenai National Wildlife Refuge in Alaska (Bangs et al. 1989) and for Barn Owls in the United Kingdom (Newton et al. 1991), the second highest form of mortality for Iberian lynx (*Felis pardina*) in southwestern Spain (after hunting; Ferreras et al. 1992), and the third highest form for white-tailed deer (*Odocoileus virginianus*) in New York (Sarbello & Jackson 1985) and wolves (*Canis lupus*) in Minnesota (Fuller 1989). Roadkill is a limiting factor in the recovery of the endangered American crocodile in southern Florida (Kushlan 1988) and is contributing to the endangerment of the prairie garter snake (*Thamnophis radix radix*; Dalrymple & Reichenbach 1984). Roadkill is often nonspecific with respect to age, sex, and condition of the individual animal (e.g., Bangs et al. 1989).

Amphibians may be especially vulnerable to roadkill because their life histories often involve migration between wetland and upland habitats, and individuals are inconspicuous and sometimes slow-moving. Roads can be demographic barriers that cause habitat and population fragmentation (Joly & Morand 1997). In the Netherlands, for example, roads with high traffic volume negatively affect occupancy of ponds by moor frogs (*Rana arvilis*; Vos & Chardon 1998). In Ontario, the local abundance of toads and frogs is inversely related to traffic density on adjacent roads, but the incidence of roadkill relative to abundance is higher on highly trafficked roads (Fahrig et al. 1995). Thus, even though populations in high-traffic areas have apparently already been depressed from cumulative road mortality, they continue to suffer higher proportionate rates of roadkill.

Mitigation measures have been employed in different locations with varying degrees of success (e.g., Yanes et al. 1995). For example, underpasses on Interstate 75 have been only partially successful in reducing roadkill of Florida panthers (*Felis concolor coryi*; Foster & Humphrey 1991). Despite mitigation efforts, roads are likely to be a persistent source of mortality for many species. In general, mortality increases with traffic volume (e.g., Rosen & Lowe 1994; Fahrig et al. 1995). Some species are less likely to be killed on high-speed roads than on medium-speed roads because the former usually have vegetation cleared back further from the road's shoulder, creating less attractive habitat and greater visibility for both animals and drivers. Other species, however, are attracted to the modified habitat alongside and in the meridians of high-speed roads (Cowardin et al. 1985), making them population sinks.

## Modification of Animal Behavior

The presence of a road may modify an animal's behavior either positively or negatively. This can occur through five mechanisms: home range shifts, altered movement patterns, altered reproductive success, altered escape response, and altered physiological state.

Black bears (*Ursus americanus*) in North Carolina shift their home ranges away from areas with high road densities (Brody & Pelton 1989), as do grizzly bears in the Rocky Mountains (*Ursus horribilis*; McLellan & Shackleton 1988). Elk (*Cervus elaphus*) in Montana prefer spring feeding sites away from visible roads (Grover & Thompson 1986), and both elk and mule deer (*Odocoileus hemionus*) in Colorado in winter prefer areas 200 m from roads (Rost & Bailey 1979). Wolves will not establish themselves in areas with road densities greater than a region-specific critical threshold (Jensen et al. 1986; Thurber et al. 1994), probably as a result of a relationship between road density and hunting pressure. Mountain lion (*Felis concolor*) home ranges are situated in areas with lower densities of improved dirt roads and hard-surface roads (Van Dyke et al. 1986), suggesting that either mountain lions avoid these areas or road construction tends to avoid their prime habitat. Elephants (*Loxodonta africana*) in northeastern Gabon preferentially locate in forests away from both roads and villages (Barnes et al. 1991). Both Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*), on the other hand, preferentially establish home ranges in areas with greater road densities (Coleman & Fraser 1989), probably because of the increase in carrion.

Roads may also alter patterns of animal movement. Caribou (*Rangifer tarandus*) in Alaska preferentially travel along cleared winter roads that lead in the direction of their migration (Banfield 1974). Although the road may enhance caribou movement, it results in increased mortality from vehicle collisions and predation by wolves. After calving, female caribou with calves avoid roads (Klein 1991). The land snail *Arianta arbustorum* avoids crossing roads, even those that are unpaved and as narrow as 3 m (Baur & Baur 1990), and extend their movements along road verges. Reluctance to cross roads is also seen in white-footed mice (*Peromyscus*

*leucopus*; Merriam et al. 1989) and many other rodent species (Oxley et al. 1974), even when the road is narrow and covered only with gravel. Cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*) avoid roads as narrow as 3 m (Swihart & Slade 1984). Black bear almost never cross interstate highways in North Carolina (Brody & Pelton 1989) but will cross roads with less traffic volume. Roads act as barriers to gene flow in the common frog (*Rana temporaria*) in Germany, leading to significant genetic differentiation among populations (Reh & Seitz 1990). Other animals that show a reluctance to cross roads include pronghorn antelope (*Antilocapra americana*; Bruns 1977) and mountain lions (Van Dyke et al. 1986).

Some animals seem unaffected by the presence of roads, at least at some spatial scales. Based on a study of 20 wolverines, Hornocker and Hash (1981) concluded that the sizes and shapes of home ranges of wolverines where they are still found in northwestern Montana are independent of the presence of highways. Similarly, the presence of highways explained none of the allelic differentiation among populations of brown hares (*Lepus europaeus*) in Austria (Hartl et al. 1989).

Roads may affect an animal's reproductive success. Productivity of Bald Eagles (*Haliaeetus leucocephalus*) in Oregon (Anthony & Isaacs 1989) and Illinois (Paruk 1987) declines with proximity to roads, and they preferentially nest away from roads. Golden Eagles (*Aquila chrysaetos*) also prefer to nest away from human disturbances, including roads (Fernandez 1993). The reduced nesting success of eagles in proximity to roads may be more a function of the presence of humans than of the road itself; nesting failure by Golden Eagles in Scotland correlates with how easy it is for people to approach but not with proximity to roads themselves (Watson and Dennis 1992). Relative to habitat availability, Sandhill Cranes (*Grus canadensis*) avoid nesting near paved and gravel public roads (Norling et al. 1992); they do not avoid private roads with low-traffic volume (Norling et al. 1992) and can habituate to roads over time (Dwyer & Tanner 1992). Mallards (*Anas platyrhynchos*) in North Dakota, on the other hand, prefer road rights-of-way for nesting (Cowardin et al. 1985), perhaps because of a lower level of predation there.

Roads can also alter escape responses. Pink-footed Geese (*Anser brachyrhynchus*) in Denmark are more easily disturbed when feeding near roads, flying away when humans approach within 500 m, a greater distance than when feeding in areas without roads (Madsen 1985). Both the Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) are more easily disturbed near roads and have disturbance distances of 480–2000 m depending on traffic volume (Van der Zande et al. 1980). Less well known is the effect of roads and vehicles on an animal's physiological state. MacArthur et al. (1979) showed that heart rate and therefore metabolic rate and energy expenditure of female bighorn sheep (*Ovis canadensis*) increase near a road independent of any use of the road. Roads contribute to fragmentation of populations through both increased mortality and modification of behavior that makes animals less likely to cross roads. Fragmentation may be accelerated by roads when spatially critical habitat patches (e.g., "stepping stones") become unoccupied as a result of increased local mortality or reduced recolonization.

## Disruption of the Physical Environment

A road transforms the physical conditions on and adjacent to it, creating edge effects with consequences that extend beyond the time of the road's construction. At least eight physical characteristics of the environment are altered by roads: soil density, temperature, soil water content, light, dust, surface-water flow, pattern of runoff, and sedimentation.

Long-term use of roads leads to soil compaction that persists even after use is discontinued. Soil density on closed forest roads continues to increase, particularly during winter months (Helvey & Kochenderfer 1990). Increased soil density can persist for decades: logging skid trails in northeastern California over 40 years old have soil that is 20% more compacted than soil in nearby areas that have not been used as trails (Vora 1988).

The reduction of water vapor transport on a road with a hard surface increases the surface temperature of a road compared to bare soil, an effect that increases with thickness of the road surface (Asaeda & Ca 1993). The heat stored on the road surface is released into the atmosphere at night, creating heat islands around roads. Animals respond to these heat islands: small birds (Whitford 1985) and snakes, for example, preferentially aggregate on or near warm roads, increasing their risk of being hit by cars and, at their northern range limits, reducing energetic demands for breeding.

During the dry season, the moisture content of soils under roads declines even if the roads are not in use (Helvey & Kochenderfer 1990), probably in response to changes in soil porosity. Roads through forests also increase the amount of light incident on the forest floor. The amount of increase depends on how much of the original canopy and lower strata remain, which depends in turn on the width of the road and roadside verge. The increase in light increases the density of species that preferentially grow where light levels are high, such as early-successional, disturbance-adapted species such as the North American orchid *Isotria medeoloides* (Mehrhoff 1989).

Road traffic mobilizes and spreads dust, which when settled on plants can block photosynthesis, respiration, and transpiration and can cause physical injuries to plants (Farmer 1993). These effects are sufficient to alter

plant community structure, especially in communities dominated by lichens and mosses (Auerbach et al. 1997). Although most sediment enters water bodies through overland flow or mass failure, dust from highly trafficked roads can serve as a source of fine sediments, nutrients, and contaminants to aquatic ecosystems (Gjessing et al. 1984).

Roads and bridges can alter the development of shorelines, stream channels, floodplains, and wetlands. Because of the energy associated with moving water, physical effects often propagate long distances from the site of a direct road incursion (Richardson et al. 1975). Alteration of hydrodynamics and sediment deposition can result in changes in channels or shorelines many kilometers away, both down- and up-gradient of the road crossing. The nature of such responses to channel and shoreline alteration is not always predictable; it may depend on the sequence of flood and sedimentation events after the alteration is made. Roads on floodplains can redirect water, sediment, and nutrients between streams and wetlands and their riparian ecosystems, to the detriment of water quality and ecosystem health. Roads are among the many human endeavors that impair natural habitat development and woody debris dynamics in forested floodplain rivers (Piégay & Landon 1997).

Road crossings commonly act as barriers to the movement of fishes and other aquatic animals (Furniss et al. 1991). Although many headwater populations of salmonid fishes are naturally migratory, they often persist today as fragmented headwater isolates, largely because of migration barriers created by road crossings and other human developments that fail to provide for fish passage (Kershner et al. 1997; Rieman et al. 1997). Salmonids and other riverine fishes actively move into seasonal floodplain wetlands and small valley-floor tributaries to escape the stresses of main-channel flood flows (Copp 1989), but valley-bottom roads can destroy or block access to these seasonally important habitats (Brown & Hartman 1988). Persistent barriers may encourage local selection for behaviors that do not include natural migration patterns, potentially reducing both the distribution and productivity of a population.

Roads directly change the hydrology of slopes and stream channels, resulting in alteration of surface-water habitats that are often detrimental to native biota. Roads intercept shallow groundwater flow paths, diverting the water along the roadway and routing it efficiently to surface-water systems at stream crossings (Megahan 1972; Wemple et al. 1996). This can cause or contribute to changes in the timing and routing of runoff (King & Tennyson 1984; Jones & Grant 1996; Ziemer & Lisle 1998), the effects of which may be more evident in smaller streams than in larger rivers (Jones & Grant 1996). Hydrologic effects are likely to persist for as long as the road remains a physical feature altering flow routing—often long after abandonment and revegetation of the road surface. By altering surface or subsurface flow, roads can destroy and create wetland habitats.

Changes in the routing of shallow groundwater and surface flow may cause unusually high concentrations of runoff on hillslopes that can trigger erosion through channel downcutting, new gully or channel head initiation, or slumping and debris flows (Megahan 1972; Richardson et al. 1975; Wemple et al. 1996; Seyedbagheri 1996). Once such processes occur, they can adversely affect fishes and other biota far downstream for long periods of time (Hagans et al. 1986; Hicks et al. 1991). Roads have been responsible for the majority of hillslope failures and gully erosion in most steep, forested landscapes subject to logging activity (Furniss et al. 1991; Hagans et al. 1986). Because most of these more catastrophic responses are triggered by the response of roads during infrequent, intense storm events, lag times of many years or decades pass before the full effects of road construction are realized.

Chronic effects also occur, however. The surfaces of unpaved roads can route fine sediments to streams, lakes, and wetlands, increasing the turbidity of the waters (Reid & Dunne 1984), reducing productivity and survival or growth of fishes (Newcombe & Jensen 1996), and otherwise impairing fishing (Buck 1956). Existing problem roads can be remediated to reduce future erosion potential (e.g., Weaver et al. 1987; Harr & Nichols 1993). The consequences of past sediment delivery are long-lasting and cumulative, however, and cannot be effectively mitigated (Hagans et al. 1986).

## Alteration of the Chemical Environment

More has been written about the effects of roads on the chemical environment than on all other effects combined. Maintenance and use of roads contribute at least five different general classes of chemicals to the environment: heavy metals, salt, organic molecules, ozone, and nutrients.

A variety of heavy metals derived from gasoline additives and road deicing salts are put into the roadside environment. The most widely documented is lead, but others include aluminum, iron, cadmium, copper, manganese, titanium, nickel, zinc, and boron (Garcia-Miragaya et al. 1981; Clift et al. 1983; Gjessing et al. 1984; Oberts 1986; Araratyan & Zakharyan 1988).

Heavy metal contamination exhibits five patterns. First, the amount of contamination is related to vehicular traffic (Goldsmith et al. 1976; Dale & Freedman 1982; Leharne et al. 1992). Second, contamination of soils, plants, and animals decreases exponentially away from the road (Quarles et al. 1974; Dale & Freedman 1982). Most studies indicate that contamination declines within 20 m but that elevated levels of heavy metals often occur 200 m or more from the road. The pattern of decline is influenced

by prevailing wind patterns (Haqus & Hameed 1986). Once metals reach aquatic environments, transport rates and distances increase substantially (Gjessing et al. 1984).

Third, heavy metals can be localized in the soil, either close to the surface if downward transport has not occurred (Indu & Choudhri 1991) or deep below the surface if pollution levels in the past exceeded those in the present (Byrd et al. 1983). Transportation and localization is largely affected by the physical properties of the soil (Yassoglou et al. 1987). Metals and other persistent chemicals fixed to soils may become remobilized once they are inundated or transported to freshwater environments by wind, water, or gravity.

Fourth, heavy metals accumulate in the tissues of plants (Datta & Ghosh 1985; Beslaneev & Kuchmazokova 1991) and animals (Collins 1984; Birdsall et al. 1986; Grue et al. 1986). As with soil, contamination of plant tissue occurs up to at least 200 m from a road and is greatest for individuals along roads with high traffic volume.

Fifth, heavy metal concentrations in soil decline over time where use of leaded gasoline has been stopped and surface-water flow carries the metal ions away (Byrd et al. 1983; Tong 1990). After they leave the terrestrial environment, however, the mobilized metals may cause additional harm to aquatic biota. Also, some of the processes of metal demobilization may be reversed rapidly if environmental conditions, such as acidity of the soils, sediments, or water, change (Nelson et al. 1991).

Deicing salts, particularly NaCl but also $CaCl_2$, KCl, and $MgCl_2$, contribute ions to the soil, altering pH and the soil's chemical composition (Bogemans et al. 1989). As with lead, discontinuation of the use of deicing salts allows plants damaged by salt stress to recover (Leh 1990). The effects on aquatic biota of temporary surges of salt that often accompany runoff from roads to surface and groundwaters have received little study. Deicing salts on roadways elevate chloride and sodium concentrations in streams (Molles & Gosz 1980; Hoffman et al. 1981; Peters & Turk 1981; Mattson & Godfrey 1994) and in bogs, where road salts can alter patterns of succession in aquatic vegetation (Wilcox 1986). Accumulation of salts from chemicals used for road deicing or dust control can disrupt natural stratification patterns and thus potentially upset the ecological dynamics of meromictic lakes (Hoffman et al. 1981; Kjensmo 1997).

Organic pollutants such as dioxins and polychlorinated biphenyls are present in higher concentrations along roads (Benfenati et al. 1992). Hydrocarbons may accumulate in aquatic ecosystems near roads (Gjessing et al. 1984). In one stream along a British highway, numerous contaminants were present at elevated levels in the water column and sediments, including copper, zinc, and various hydrocarbons, but polycyclic aromatic hydrocarbons associated with stream sediments accounted for most of the observed toxicity to aquatic amphipods (Maltby et al. 1995). Comparatively little research has focused on the questions of the fate and effects of the organic chemicals associated with roads.

Vehicles produce ozone, which increases the concentration of this harmful molecule in the air, especially in areas where vehicle exhaust accumulates (Flueckiger et al. 1984). Roads are also especially important vectors of nutrients and other materials to aquatic ecosystems, because the buffering role normally played by riparian vegetation (Correll et al. 1992) is circumvented through direct runoff of materials in water and sediment where roads abut or cross water bodies. Water moving on and alongside roadways can be charged with high levels of dissolved nitrogen in various forms, and sediment brings a phosphorus subsidy when it reaches surface waters. Road deicing salts are an additional source of phosphorus (Oberts 1986). The degree to which roads directly contribute to eutrophication problems in aquatic ecosystems has been little investigated. Because roads deliver nutrients that originate in the contributing slope area, the nutrient burden is probably largely controlled by surrounding vegetation and land use. An increased density of road crossings of water bodies can be expected to increase delivery of nutrients.

The alteration of the chemical environment by roads results in a number of consequences for living organisms. First, in the terrestrial environment the chemical composition of some woody plants changes in response to pollution. These changes include increased concentrations of chemicals produced by plants, such as terpenoids, which help them resist the toxic effects of pollution (Akimov et al. 1989) and salts (Bogemans et al. 1989), and decreased production of other chemicals, such as soluble protein and chlorophyll *a*, which are necessary for plant function (Banerjee et al. 1983).

Second, organisms may be killed or otherwise displaced as a result of chemical exposure. Virtually all measures of soil biotic diversity and function decline in contaminated soil, including abundance, number of species, species composition, index of species diversity, index of equability, and bulk soil respiration (Muskett & Jones 1981; Guntner & Wilke 1983; Krzysztofiak 1991).

Third, the growth (Petersen et al. 1982) and overall physical health (Flueckiger et al. 1984; Moritz & Breitenstein 1985) of many plants is depressed, even to the point of death (Fleck et al. 1988). The sensitivity of plants to pollutants may change during development; for example, seedlings are more sensitive to salt than are adults (Liem et al. 1984), which influences juvenile recruitment. Pollutants may affect plant health by damaging fine roots, mycorrhizae (Majdi & Persson 1989), and leaves (Simini & Leone 1986) and by changing salt concentrations in plant tissues (Northover 1987). Secondary effects on plant health include decreased resistance to pathogens (Northover 1987), causing further declines. In aquatic environments, plant (and animal) assemblages

may change due to direct and indirect responses to nutrient increases and due to growth suppression or mortality caused by other chemicals introduced by roads.

Fourth, plants (Graham & Kalman 1974; Nasralla & Ali 1985; Dickinson et al. 1987; Guttormsen 1993) and animals (Robel et al. 1981; Collins 1984; Harrison & Dyer 1984; Krzysztofiak 1991; Marino et al. 1992), including those cultivated or raised for agriculture, may accumulate toxins at levels that pose health hazards, including those for humans that consume exposed organisms (Jarosz 1994).

Fifth, increased concentrations near roadsides of some pollutants, particularly salt, attract large mammals, putting them more at risk of being killed by vehicles (Fraser & Thomas 1982). Spills of edible products from trucks and trains also attract wildlife to roadsides. Finally, evolutionary processes may be affected through altered selection pressures that result in local differentiation of populations of both plants (Kiang 1982) and animals (Minoranskii & Kuzina 1984).

## Spread of Exotic Species

Roads provide dispersal of exotic species via three mechanisms: providing habitat by altering conditions, making invasion more likely by stressing or removing native species, and allowing easier movement by wild or human vectors. It is often difficult to distinguish among these factors. Soils modified during road construction can facilitate the spread of exotic plants along roadsides (Greenberg et al. 1997). Some exotic plants establish themselves preferentially along roadsides and in other disturbed habitats (Wester & Juvik 1983; Henderson & Wells 1986; Tyser & Worley 1992; Wein et al. 1992). The spread of exotic diseases (Dawson & Weste 1985; Gad et al. 1986) and insects (Pantaleoni 1989; Schedl 1991) is facilitated by increased density of roads and traffic volume. Road construction that alters the canopy structure of forests promotes invasion by exotic understory plants, which affects animal communities (Gaddy & Kohlsaat 1987). Some roadside verges have been invaded by maritime plants because of their ability to tolerate saline soil (Scott & Davison 1982). Feral fruit trees are found preferentially along roadsides, and some populations are maintained solely by seeds in fruit waste thrown from vehicles (Smith 1986).

Exotic species are sometimes introduced along roadsides for the purpose of erosion control (Niordson 1989). Native species are now more widely preferred for this purpose, but Dunlap (1987) argues that in some cases the need for rapid establishment of plant cover requires the use of exotic species.

In another form of deliberate introduction, roads provide easy access to streams and lakes for fishery managers to stock nonnative hatchery fish (Lee et al. 1997), which adversely affect native biota and disrupt aquatic ecosystems in many ways (Allan & Flecker 1993). Unsanctioned, illegal, and unintentional introductions of fishes, mollusks, plants, and other aquatic organisms also occur frequently (Allan & Flecker 1993), and they are facilitated by public road access to water bodies.

The dispersal of a biological agent such as a pathogen along a roadway can affect both terrestrial and aquatic ecosystems far from the road. In northern California and southwest Oregon, for example, vehicle traffic and roadway drainage along logging and mining roads during the wet season disperse spores of an exotic root disease (*Phythoptera lateralis*) that infects the endemic Port Orford cedar (*Chamaecyparis lawsoniana*; Zobel et al. 1985). Transfer of the water-borne spores from forest roads into headwater stream crossings can result in the infection and nearly complete mortality of Port Orford cedars along a much larger network of downstream channel margins and floodplains, even deep inside otherwise roadless areas. The progressive loss of this important conifer species from riparian ecosystems may engender substantial long-term consequences for the integrity of stream biota, including endangered salmon species, for which the Port Orford cedar provides shade, large and long-lasting coarse woody debris, and stabilization of channels and floodplains.

## Changes in Human Use of Land and Water

Roads facilitate increased use of an area by humans, who themselves often cause diverse and persistent ecological effects. New roads increase ease of access by humans into formerly remote areas. Perhaps more important, roads often increase the efficiency with which natural resources can be exported. At least three different kinds of human use of the landscape, made increasingly possible by roads, can have major ecological effects: hunting and fishing, recreation, and changes in use of land and water.

Roads open up areas to increased poaching and legal hunting. Hunting reduces population sizes of many game species, including brown bear (*Ursus arctos*; Camarra & Parde 1990), Iberian lynx (Ferreras et al. 1992), wolves (Fuller 1989), black bear (Manville 1983), and Egyptian mongooses (*Herpestes ichneumon*; Palomares & Delibes 1992). Roads also increase both legal and illegal fishing in streams and lakes. Native fish populations in previously inaccessible areas are often vulnerable to even small increases in fishing effort. Increased fishing then often gives rise to public demand for fish stocking as an attempt to artificially compensate for the effects of unsustainable harvest, at the further expense of native fishes and other species (e.g., Gresswell & Varley 1988).

Visitors increase when roads make areas more accessible, leading to increased passive harassment of animals—such as elk on Mount St. Helens in Washington State (Czech 1991) and the Oregon Coast Range (Witmer & DeCalesta 1985), brown bear in Europe (Del Campo et al. 1990), and mountain goats (*Oreamnos americanus*) in Montana (Pedevillano & Wright 1987)—and damage to plant communities (Matlack 1993).

Roads are often built into areas to promote logging, agriculture, mining, and development of homes or industrial or commercial projects. Such changes in land cover and land and water use result in major and persistent adverse effects on the native flora and fauna of terrestrial (Van Dyke et al. 1986; Karnefelt & Mattsson 1989; P. Seibert 1993) and freshwater ecosystems (Schlosser 1991; Allan & Flecker 1993; Roth et al. 1996).

Numerous studies have demonstrated declines in stream health associated with roads. Because the nature and extent of land use within a region tend to be highly correlated with road networks, however, it is often difficult or impossible to separate the direct ecological effects of roads from those of the accompanying land-use activities. For example, Eaglin and Hubert (1993) reported that trout biomass and streambed habitat quality in Wyoming streams declined in relation to the number of road crossings and to the proportion of area logged in the contributing catchment. Findlay and Houlahan (1997) found that herptile species diversity in wetlands declined in relation to the density of roads within 2 km of the perimeter. Among streams in the Pacific Northwest, the status or abundance of bull trout populations has been inversely correlated to road density (Rieman et al. 1997; Baxter et al. 1999); these studies used roads as the best available general proxy of cumulative effects associated with land use and human access. On the other hand, some studies (e.g., Roth et al. 1996) have demonstrated correlations of stream biotic integrity with land-use patterns across large catchments but did not investigate the specific roles that roads might play in mediating the causes and effects.

It appears that roads can serve as useful indicators of the magnitude of land-use changes, but it remains unclear to what degree the associated ecological responses result directly from roads themselves. If roads are largely responsible, effects could be ameliorated through altered road design, placement, remediation, or road removal. Strong interactions between roads and land use are likely, however. Forest roads in Idaho, for example, are less prone to erosion when the surrounding landscape remains in natural forest cover (Seyedbagheri 1996).

## Discussion and Conclusions

Roads have diverse and systemic effects on many aspects of terrestrial and aquatic ecosystems. The ecological effects of roads can resonate substantial distances from the road in terrestrial ecosystems, creating habitat fragmentation and facilitating ensuing fragmentation through support of human exploitative activities (Fig. 1a). Habitat deterioration is not widely appreciated as an aspect of ecological fragmentation in aquatic ecosystems. At the scale of an extensive landscape or stream network, however, roads produce a pattern of aquatic habitat loss that differs from the terrestrial pattern yet nevertheless results in the ecological fragmentation of aquatic ecosystems (Fig. 1b). We coin the term *hyperfragmentation* to describe the multidimensional view of ecological fragmentation and habitat loss that emerges when the consequences of roads or any habitat alteration for terrestrial and aquatic ecosystems are considered simultaneously (Fig. 1c). Hyperfragmentation is the result of a spatial footprint of ecological effect that propagates across the landscape differently in freshwater and

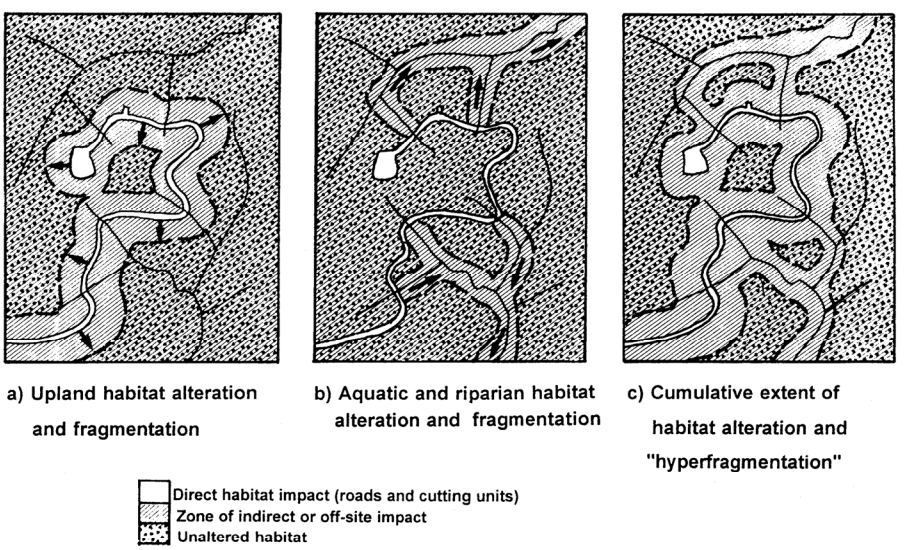


*Figure 1. Spatial pattern of direct and indirect habitat alteration caused by human disturbance in a forested watershed: (a) classical forest edge effects contributing to terrestrial habitat fragmentation, (b) downstream-propagating hydrologic and biotic effects leading to large-scale fragmentation of freshwater habitats and populations, (c) combined terrestrial-aquatic view of landscape alteration that we term* hyperfragmentation *because it considers multiple ecosystem dimensions on the same landscape. Arrows indicate predominant spatial vector of effects.*

aquatic ecosystems than in terrestrial systems. Even where only a small percentage of the land's surface is directly occupied by roads, few corners of the landscape remain untouched by their off-site ecological effects. The breadth of these effects cannot be appreciated unless one takes a broadly transdisciplinary view of ecosystems and biological communities.

Road design, management, and restoration need to be more carefully tailored to address the full range of ecological processes and terrestrial and aquatic species that may be affected. Deliberate monitoring is necessary to ensure that projects have robust ecological benefits and minimal adverse effects and that they are cost-efficient relative to their actual benefits (e.g., Weaver et al. 1987). Of course, such assessments require time and money that are usually unavailable. Most funds used to remediate problem roads are earmarked for actual field operations and are not available to support such assessment and monitoring. Few of the experts building roads or "restoring" them are trained to recognize and address the full spectrum of ecological issues that we have identified. Moreover, by their nature roads have systemic ecological effects that, even if recognized, cannot be overcome.

If a broad view of the ecological effects of roads reveals a multiplicity of effects, it also suggests that it is unlikely that the consequences of roads will ever be completely mitigated or remediated. Thus, it is critical to retain remaining roadless or near-roadless portions of the landscape in their natural state. Because of the increasing rarity of roadless areas, especially roadless watersheds, conservation efforts cannot rely entirely on protection of existing natural areas. But neither can conservation efforts depend entirely on tenuous and unexamined assumptions about the capability of site- and species-specific mitigation and remediation measures to reduce the ecological consequences of existing and proposed roads.

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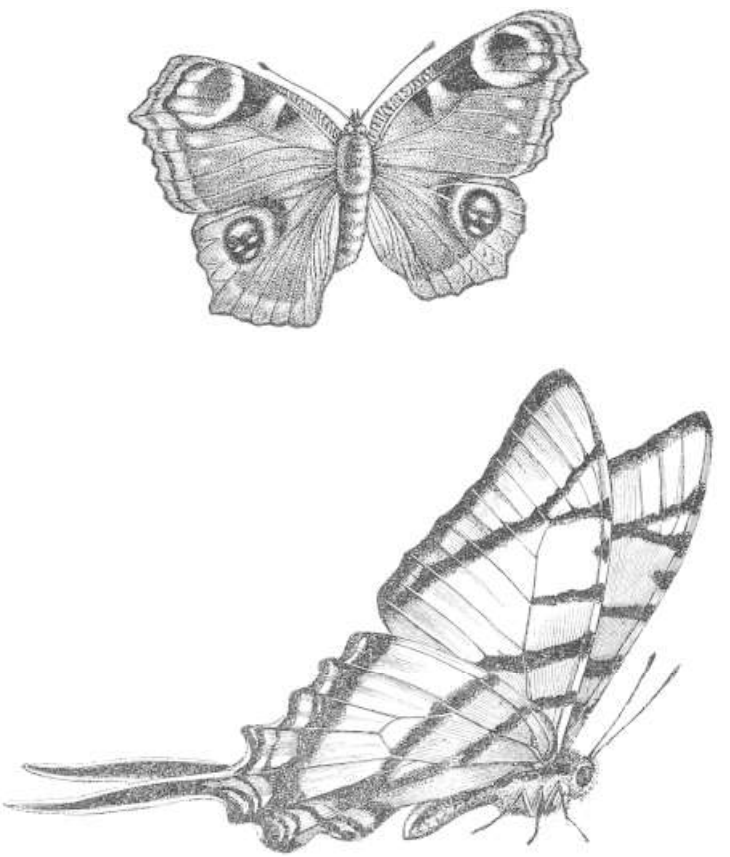

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van der Ree, R., J. A. G. Jaeger, E. A. van der Grift, and A. P. Clevenger. 2011. Effects of roads and traffic on wildlife populations and landscape function: road ecology is moving towards larger scales. *Ecology and Society* **16**(1): 48. [online] URL: http://www.ecologyandsociety.org/vol16/iss1/art48/

*Guest Editorial*, part of a Special Feature on Effects of Roads and Traffic on Wildlife Populations and Landscape Function

# Effects of Roads and Traffic on Wildlife Populations and Landscape Function: Road Ecology is Moving toward Larger Scales

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ABSTRACT. Road ecology has developed into a significant branch of ecology with steady growth in the number of refereed journal articles, books, conferences, symposia, and "best practice" guidelines being produced each year. The main objective of this special issue of *Ecology and Society* is to highlight the need for studies that document the population, community, and ecosystem-level effects of roads and traffic by publishing studies that document these effects. It became apparent when compiling this special issue that there is a paucity of studies that explicitly examined higher order effects of roads and traffic. No papers on landscape function or ecosystem-level effects were submitted, despite being highlighted as a priority for publication. The 17 papers in this issue, from Australia, Canada, the Netherlands, and USA, all deal to some extent with either population or community-level effects of roads and traffic. Nevertheless, many higher order effects remain unquantified, and must become the focus of future studies because the complexity and interactions among the effects of roads and traffic are large and potentially unexpected. An analysis of these complex interrelations requires systematic research, and it is necessary to further establish collaborative links between ecologists and transportation agencies. Many road agencies have "environmental sustainability" as one of their goals and the only way to achieve such goals is for them to support and foster long-term and credible scientific research. The current situation, with numerous small-scale projects being undertaken independently of each other, cannot provide the information required to quantify and mitigate the negative effects of roads and traffic on higher levels. The future of road ecology research will be best enhanced when multiple road projects in different states or countries are combined and studied as part of integrated, well-replicated research projects.

Key Words: *animal movement; animal-vehicle collisions; barrier effect; ecological threshold; gene flow; habitat fragmentation; mitigation; population viability analysis; road ecology; road-effect zone; traffic mortality; traffic noise; traffic volume; transportation planning*

## INTRODUCTION

Humans are responsible for the current unprecedented rate of biodiversity loss across the globe with climate change, pollution, and the loss, fragmentation, and degradation of habitat being the major drivers of extinction (Vitousek et al. 1997). Roads and other linear infrastructure are a major cause of habitat loss, fragmentation, and degradation and are ubiquitous in most landscapes around the world. Worldwide, there are already an estimated 750 million vehicles travelling on approximately 50 million km of public road (T. Langton, *personal communication*), and the road network and traffic volumes are still increasing, particularly in eastern Europe, China, India, and Latin America.

Linear infrastructure is important for society because it provides connectivity for people. However, linear infrastructure also exerts significant negative effects on adjacent habitats, wildlife populations, communities, and ecosystems. Research about the ecological effects of roads and traffic on the natural environment began in 1925 when Dayton Stoner documented the 225 traffic-killed vertebrates from 29 species that he observed during a 632 mile trip in Iowa, USA (Stoner 1925).

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The term "road ecology" was first used in German ("Straßenökologie") in 1981 (Ellenberg et al.), and was later translated into English by Forman et al. (2003) for their book *Road Ecology: Science and Solutions*. Since the mid 1990s, there has been a rapid increase in the number of studies, publications, and symposia, particularly from Europe, North America, and Australia. These include major national and international reports and best practice guidelines (Iuell et al. 2003, Trocmé et al. 2003, National Research Council 2005, Clevenger and Huijser 2009), regular dedicated conferences such as the biennial International Conference on Ecology and Transportation (ICOET), Infra-Eco Network of Europe (IENE), and symposia and special issues of peer-reviewed journals, e.g., *Biological Conservation* (Mader 1990), *Conservation Biology* (Hourdequin 2000), *GAIA* (Jaeger et al. 2005), and *Naturschutz and Landschaftsplanung* (Roedenbeck and Jaeger 2006).

The overall aim of road ecology research is to quantify the ecological effects of roads, with the ultimate aim of avoiding, minimizing, and compensating for their negative impacts on individuals, populations, communities, and ecosystems. This research has demonstrated the numerous and diverse effects of roads and traffic on plants and animals, with most studies focusing at the level of the individual animal. These effects include the loss and fragmentation of habitat, increased rates of wildlife mortality because of collision with vehicles, alterations to light, moisture and wind regimes due to the creation of edges, pollution from traffic, e.g., light, noise, and chemical, and facilitating the spread and dispersal of weeds and feral animals. Roads also affect the aesthetic and recreational quality of landscapes for humans (Di Giulio and Holderegger 2009). Consequently, roads have been described as the single most destructive element in the process of habitat fragmentation (Noss 1993) and their ecological effects are considered "the sleeping giant of biological conservation" (Forman 2002:viii).

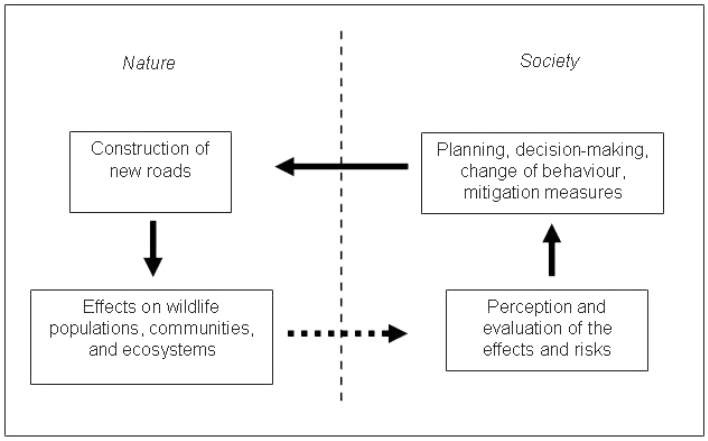
Understanding the impacts of roads and traffic at higher levels is necessary for a number of good reasons. Most governments have agreed that conservation of biodiversity is important and therefore road agencies must endeavor to ensure that they are contributing to achieving this goal. Counting the number of dead animals on the side of the road or measuring the size of the ecological road-effect zone will not, by itself, inform whether roads and vehicles are endangering the existence of populations or species. The important parameter must be the long-term viability of adjacent populations, and this requires data on the sizes of the populations, vital rates, and level of connectivity among subpopulations. Similarly, a critical question when evaluating mitigation works is the extent to which populations have become more viable, and whether they are now sufficiently viable, not simply how many animals pass through an underpass (van der Ree et al. 2007). The extent to which the results from the numerous local studies can be extrapolated to larger spatial and temporal scales is unknown. Therefore, an important next step is to evaluate how the density and configuration of entire road networks affect the functional relationships within and among ecosystems at the landscape scale. Answers to this question will inform cumulative environmental assessments and transportation planning (Roedenbeck et al. 2007). Roads also affect humans in a range of ways but little research on this topic has been completed (Di Giulio and Holderegger 2009).

Reducing the negative effects of roads and traffic will only be possible if more dialogue is achieved between the scientific community and the planners and political decision makers (Fig. 1). The majority of people in the world live in cities and increasingly, their encounters with wildlife involve animals that have died after collision with vehicles. Novel approaches to engage the public, and hence, governments, are required. A recent example was an award-winning exhibition in the Whyte Museum in Banff, Alberta, Canada in 2006 of images of wildlife using the now famous overpasses and underpasses in Banff National Park. A second example was a creative arts competition as part of the IENE 2010 conference for Hungarian school children to portray the conflict, and solutions, between roads and wildlife (Fig. 2).

## ABOUT THIS ISSUE: THE EFFECTS OF ROADS AND TRAFFIC ON POPULATIONS, COMMUNITIES, AND ECOSYSTEMS

The two main objectives of this special issue of *Ecology and Society* were to (1) highlight the need for studies that document the population, community, and ecosystem-level effects of roads and traffic, and (2) publish studies that document

**Fig. 1.** Society's ability to address the negative effects of road networks on wildlife populations and ecosystems depends on the perception of the ecological effects and risks. As the perception of the effects by society has been severely limited (as indicated by the dotted line), alternative approaches may be required that would be based on more indirect indicators of ecological risk and on the precautionary principle.




these effects. The special issue consists of 17 papers from four countries, i.e., Australia, Canada, the Netherlands, and U.S.A., that all deal to some extent with either population or community-level effects of roads and traffic. It became apparent when compiling the special issue that there is a paucity of road ecology studies that explicitly examined higher order effects of roads. No papers on landscape function or ecosystem-level effects were submitted, despite being highlighted as a priority for publication.

The special issue begins with a synthesis paper (Fahrig and Rytwinski 2009) and ends with an insight paper (Simmons et al. 2010). The synthesis is an appropriate first paper because it assesses the widely held assertion that "there are very few studies that assess the population-level effects of roads and traffic." The assertion was found to be partly true and partly false; the authors located 79 studies that provide data on population-level effects (abundance and density) but found that in most cases, the population-level effect was 'hidden' in many of the papers reviewed. Nevertheless, Fahrig and Rytwinski (2009) found that overwhelmingly, roads and traffic had a negative effect on animal abundance, with negative effects outnumbering positive effects by a factor of five. The final paper in the special issue reviews some of the genetic methods used in road ecology and provides an insight into how conservation genetics can be better utilized in future studies. Simmons et al. (2010) argue that conservation genetics is a rapidly evolving field and that many of the widely perceived limitations to the use of genetics are either misconceptions or no longer apply. They conclude with strong recommendations that genetic approaches be combined with field studies to increase the inferential strength of whichever study design is adopted (sensu Roedenbeck et al. 2007).

The road-effect zone is the distance from the edge of the road over which significant ecological effects can be detected (Forman and Alexander 1998). Eigenbrod et al. (2009) quantified threshold effects of a motorway on anuran populations in Canada, and Bissonette and Rosa (2009) investigated the effects of a motorway on the composition and abundance of a small-mammal community in the deserts of Utah, USA. Eigenbrod et al. (2009) were the first to quantify the road-effect zone on the species richness and relative abundance of anurans, and found strong negative effects for four of seven species, extending 250 – 1000 m from the road edge. They conclude that although most anurans are likely to have reduced abundances near motorways, the extent and cause of this relationship will vary among species (Eigenbrod et al. 2009). In contrast, Bissonette and Rosa (2009) found that roadside vegetation in desert environments often provides

**Fig. 2.** Runner up of the "On Dangerous Roads" Competition organized by Varangy Akciócsoport Egyesület for the 2010 Infra-Eco Network of Europe Conference showing an overpass used by wildlife. An ongoing project in the Netherlands is studying the effectiveness of an overpass for amphibians, in combination with fences along the road. This overpass is equipped with a cascading series of small ponds fed with water pumped into the highest pond in the center of the overpass.

suitable habitat for small mammals. Only 2 of 13 species of small mammals were never captured near roads, and the remaining 11 species' numbers were either similar or more abundant near the road than further away.

Vegetation adjacent to roads often provides habitat (e.g., Bissonette and Rosa 2009), and in some landscapes, even the majority of habitat (van der Ree and Bennett 2003). Wildlife that use this habitat will experience traffic noise and may be affected by it. Anthropogenic noise has the potential to severely disrupt the communication of species by acoustic interference or masking. Three studies in this special issue investigate this effect on frogs and birds. Parris and Schneider (2008) found that the Grey Shrike-thrush (*Colluricincla harmonica*) sang at a higher frequency in areas with traffic noise than the Grey Fantail (*Rhipidura fuliginosa*) and that the probability of detecting either species declined substantially with increasing traffic noise and traffic volume. The effects of traffic noise on frogs were assessed by Parris et al. (2009) in an urban landscape in southeast Australia and by Hoskin and Goosem (2010) in tropical rainforest in northeastern Australia. One species of urban frog in and around Melbourne called at a higher pitch in traffic noise, while the second species studied may also call at a higher pitch, but more data is required to be sure (Parris et al. 2009). *Litoria rheocola* in tropical rainforest also called at a higher pitch when closer to the road, as well as calling at a higher rate when near roads (Hoskin and Goosem 2010). The abundance of some species of rainforest frogs was also lower near roads.

A significant proportion of the road ecology literature is focused on evaluating the use and effectiveness of mitigation measures that aim to restore connectivity for wildlife or reduce rates of animal-vehicle collisions. A review presented at the ICOET conference in 2007 concluded that most studies in the scientific and grey literature had focused almost exclusively on documenting rates of use of wildlife passages, and that few had explicitly evaluated the effectiveness of mitigation measures

at enhancing population viability (van der Ree et al. 2007). In this special issue, five papers have addressed the topic of mitigation of road effects on wildlife in differing perspectives. Thorne et al. (2009) highlight the importance of landscape-scale planning to better integrate the needs of wildlife into regional transportation plans. Using two examples from California, USA, they show how road projects can benefit financially and ecologically when road agencies and conservation groups collaborate early in the planning stages. Approximately 1 – 2 million mammal-vehicle collisions occur annually in North America, causing in excess of 200 human fatalities and over one billion U.S. dollars in property damage each year (references in Huijser et al. 2009). Huijser et al. (2009) reviewed the effectiveness and cost of 13 measures considered effective at reducing collisions with large ungulates and found that for many sections of road, the effectiveness, measured as money saved, exceeds the costs to install the mitigation. The results of their cost-benefit model suggests that there must be many locations in North America where the mitigation measures are cost-effective, and thereby would save society money and improve road safety for humans and wildlife if implemented more often. At a smaller spatial scale, Grosman et al. (2009) combined real data on the movement of moose (*Alces alces*) with agent-based computer simulations to investigate if the removal of salt pools or their relocation from adjacent to the highway to 100 – 1500 m away from the road would result in fewer moose-vehicle collisions. Their model predicted that the removal of salt pools from near the edge of the highway would result in an almost 50% reduction in moose-vehicle collisions (Grosman et al. 2009).

The viability of populations adjacent to wildlife crossing structures is one of the fundamental measures of success of mitigation (van der Ree et al. 2007). Two papers in this special issue explicitly investigated the increase in the viability of a population of wildlife after mitigation (Taylor and Goldingay 2009, van der Ree et al. 2009). Taylor and Goldingay (2009) used population modeling to assess the viability of the Greater Glider (*Petauroides volans*) in Brisbane, a rapidly urbanizing area of Australia. They concluded that even a relatively low rate of dispersal across the road was sufficient to substantially reduce the risk of extinction of the smaller subpopulation isolated by the road. Similarly, van der Ree et al. (2009) used population viability modeling to assess the effectiveness of under-road tunnels installed in 1985 to restore connectivity for the critically endangered Mountain Pygmy-possum (*Burramys parvus*; Mansergh and Scotts 1989). They found that the tunnels reduced, but did not completely eliminate the negative effect of the road, with the density of the population affected by the road still 15% lower than a comparable undivided population nearby (van der Ree et al. 2009).

The majority of studies that assess the use of wildlife crossing structures have utilized two primary methods to detect and record wildlife passage, namely remotely triggered cameras, and/or the detection of tracks in a suitable substrate (van der Ree et al. 2007). Clevenger and Sawaya (2010) have used the suggestions of Simmons et al. (2010) and tested the feasibility of a noninvasive genetic sampling approach to identify the species as well as the sex, individual, and relatedness of different individuals using the crossing structure. The technique, if successful, would be applied at a larger scale to determine the level of genetic fragmentation and natural and anthropogenic factors influencing gene flow. They tested their approach on Black Bears (*Ursus americanus*) and Grizzly Bears (*U. arctos*) at two underpasses in Banff National Park. Hair was collected from 90% of crossing events (determined from cameras), and 70% of hair samples had sufficient DNA for extraction, resulting in the identification of five individual bears at each underpass, and highlighting the potential of this method for population-level analysis of the efficacy of wildlife crossing structures (Clevenger and Sawaya 2010).

There is still a paucity of data on the behavior and movement of animals near roads. Bouchard et al. (2009) evaluated the behavioral response of the Northern Leopard Frog (*Rana pipiens*), a species known to be negatively affected by roads and traffic. They studied the movement of frogs during their spring migration and also undertook short distance translocations of migrating frogs and found frogs near roads with more traffic took longer to move and tended to deviate more from straight-line movements when released near roads (Bouchard et al. 2009). The combination of the Northern Leopard Frog's apparent inability to avoid roads and their slow rate of movement make them highly vulnerable to road mortality. The second study in this special issue on the movement behavior of wildlife near roads was for the Squirrel Glider (*Petaurus norfolcensis*) in southeast Australia (van der Ree et al. 2010). The authors found that the size

of the gap in the canopy was the primary determinant of the rate of crossing in their study, with similar rates of crossing across the dual-roadway with tall trees in the median and across single-lane roads. In this study, traffic volume, i.e., approximately 5000 vehicles per day per roadway of which about 25% occurs at night when the gliders are active, did not appear to greatly influence crossing rates.

The traffic volume on minor roads is expected to continue to increase in areas with high human population densities because existing motorways are nearing capacity and the minor roads are expected to accommodate the excess flows (references in van Langevelde and Jaarsma 2009). Traffic calming is a regional planning approach to concentrate these flows onto a few roads, and ensure low-volume and low-speed roads are maintained. The conclusions of population viability modeling suggest that the results are species specific and depend upon the size of the traffic-calmed area as well as the area and quality of habitat (van Langevelde and Jaarsma 2009).

## ROAD ECOLOGY: THE ROAD AHEAD

The research presented in this special feature shows that road ecology is moving toward larger scales. However, it also became evident while compiling this special issue that many higher order, e.g., population, community, ecosystem, or landscape-level, effects remain unquantified. These higher order effects must become the focus of future studies because the complexity and interactions among the effects of roads and traffic are large and potentially unexpected. An analysis of these complex interrelations requires systematic research. Therefore, a promising avenue to further develop the field of road ecology is to establish collaborative links with road and transportation agencies. Experience shows that the level of engagement with each local, state, or national road agency depends largely on the presence of interested people, rather than an institutionalized approach to environmental matters. However, institutional mandates are important as they are often a precondition for interested people to spend their efforts during work hours on these issues. Many road agencies have "environmental sustainability" as one of their goals and the only way to achieve such goals is for them to support and foster long-term and credible scientific research. Every road project is essentially an experiment and when combined with other road projects, they become replicated. The challenge we face as researchers is to (1) use good scientific approaches to design studies that are scientifically robust and maximize the individual value of each road project within a larger experimental scope; (2) ensure our research is applied and has tangible value for road agencies and for ecological outcomes; (3) address the higher order effects of roads, traffic, and mitigation measures.

This special feature demonstrates that the emerging field of road ecology is confronted with many important unanswered questions. Research needs to address large spatial and temporal scales that are not compatible within most postgraduate programs, i.e., single MSc or PhD theses, or short-term research contracts. The synergistic effects of roads and other factors that operate simultaneously, e.g., agricultural intensification and increased urbanization, have rarely been investigated. However, empirical studies are limited by the delayed response of wildlife to many environmental changes, i.e., there is an extinction debt such that wildlife populations will continue to decline for many years, in the order of decades, before they will reach a new equilibrium (Tilman et al. 1994, Findlay and Bourdages 2000). This lack of knowledge is often used as a justification to build more roads by arguing that not enough is known and more research is needed before road construction may slow down. This constitutes a "fragmentation spiral" (Jaeger 2002), because research has been unable to catch up with the ecological effects of the rapid increase in road densities. This situation is contrary to the precautionary principle and flies in the face of the principles of sustainability. The use of computer models may help overcome these limitations. For example, simulation models have demonstrated that there are thresholds in the effects of road density on the viability of wildlife populations above which populations are prone to extinction (Jaeger and Holderegger 2005, Frair et al. 2008). In addition, a research approach is required that will address the remaining uncertainties that to a large degree are irreducible, e.g., through building on the precautionary principle (e.g., Jaeger 2002). This would open up promising new lines of action for landscape management. For example, the German Federal Environment Agency recently suggested that region-specific limits to control landscape fragmentation should be introduced (Penn-Bressel 2005).

With this issue, we hope to contribute to the field of road ecology and to highlight both its appealing theoretical insights and its high practical relevance. Most importantly, we hope that this special issue will inspire further research in road ecology at the scale of populations, communities, and ecosystems. We are looking forward to these exciting research studies to come.

*Responses to this article can be read online at: http://www.ecologyandsociety.org/vol16/iss1/art48/responses/*

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PLOS ONE

RESEARCH ARTICLE

# Survival and Mortality of Pumas (*Puma concolor*) in a Fragmented, Urbanizing Landscape

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## Abstract

Wide-ranging large carnivores pose myriad challenges for conservation, especially in highly fragmented landscapes. Over a 13-year period, we combined monitoring of radio collared pumas (*Puma concolor*) with complementary multi-generational genetic analyses to inform puma conservation in southern California, USA. Our goals were to generate survivorship estimates, determine causes of mortality, identify barriers to movement, and determine the genetic and demographic challenges to puma persistence among >20,000,000 people and extensive urban, suburban, and exurban development. Despite protection from hunting, annual survival for radio collared pumas was surprisingly low (55.8%), and humans caused the majority of puma deaths. The most common sources of mortality were vehicle collisions (28% of deaths), and mortalities resulting from depredation permits issued after pumas killed domestic animals (17% of deaths). Other human-caused mortalities included illegal shootings, public safety removals, and human-caused wildfire. An interstate highway (I-15) bisecting this study area, and associated development, have created a nearly impermeable barrier to puma movements, resulting in severe genetic restriction and demographic isolation of the small puma population (n ~ 17–27 adults) in the Santa Ana Mountains west of I-15. Highways that bisect habitat or divide remaining "conserved" habitat, and associated ongoing development, threaten to further subdivide this already fragmented puma population and increase threats to survival. This study highlights the importance of combining demographic and genetic analyses, and illustrates that in the absence of effective measures to reduce mortality and enhance safe movement across highways, translocation of pumas, such as was done with the endangered Florida panther (*P. c. coryi*), may ultimately be necessary to prevent further genetic decline and ensure persistence of the Santa Ana Mountains population.

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## Introduction

Many large carnivores have been extirpated from substantial portions of their historic range, and extant populations are threatened by habitat loss and fragmentation, and conflict with humans [1]. Human population growth expected over the next century exacerbates these threats [2–5], and exurban development will have substantial impacts on habitat that today is still relatively intact [6]. Because large carnivores pose myriad challenges for conservation in urbanizing landscapes, we began a long-term study of pumas (*Puma concolor*) in 2001 in southern California, USA, to provide quantitative insights and guidance for conservation of pumas and other large carnivores in human-dominated habitats.

Pumas, also known as mountain lions, cougars, or panthers, are wide-ranging carnivores that historically occurred throughout the Americas. Humans have extirpated or greatly reduced puma numbers in much of their former range in the past 200 years [2]. The only documented breeding population of pumas remaining in the eastern United States is in Florida, where a small population of federally endangered pumas (Florida panthers–*Puma concolor coryi*) persists, largely because their endangered status spurred intensive management including translocation and genetic introgression [7, 8]. In the western United States, pumas are hunted for sport in several states, but there is considerable controversy and uncertainty about the long-term consequences of hunting on population persistence. For example, a recent study of heavily-hunted and semi-protected puma populations in Utah [9] did not detect a compensatory decrease in natural mortality in response to heavy hunting pressure, and concluded that uncertainties in the functional relationship between natural and anthropogenic mortality could lead to biased conclusions and mismanagement.

In California, pumas are considered a "specially protected mammal" and hunting is prohibited [10]. Despite these protections, recent genetic studies of pumas in southern California show that the genetic viability and long-term persistence of some populations are in jeopardy [11, 12]. The threats facing pumas in southern California—habitat loss, increased conflict with humans, demographic isolation, and genetic restriction [11–15]—mirror the challenges facing large carnivores in urbanizing landscapes around the world [3], and long-term studies intended to guide conservation and management in these settings are difficult and expensive to conduct. We addressed this information gap by conducting a 13-year study of pumas in the California south coast ecoregion, USA, a biodiversity hotspot [16, 17] with a growing population of >20,000,000 people [18].

Sandwiched between the sprawling metropolitan areas of greater Los Angeles and San Diego, much of the available puma habitat in our study area is not protected from new highways and development, and is subject to ongoing habitat loss and fragmentation [15]. Our goals for this study were to generate survivorship estimates and cause-specific mortality data for pumas in this region, and identify options for improving survivorship and facilitating movement within and among conserved and non-conserved areas. This demographic study builds upon and complements our recent genetic analysis [11], and provides the essential ecological context for understanding the causes and potential solutions to the genetic restriction we found in pumas in the Santa Ana Mountains.

## Materials and Methods

### Statement

We operated under Protocol 10950/PHS, Animal Welfare Assurance number A3433-01, with capture and sampling procedures approved in Protocol number 17233 by the Animal Care and Use Committee at the University of California, Davis, and Memoranda of Understanding and

Scientific Collecting Permits from the California Department of Fish and Wildlife (CDFW). Permits and permissions for access to conserved lands where captures and monitoring were conducted were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (U.S.) Fish and Wildlife Service, U.S. Forest Service, U.S. Bureau of Land Management, U.S. Navy / Marine Corps, U. S. Fish and Wildlife Service, Orange County Parks Department, San Diego County Parks Department, Riverside County Parks Department, San Diego State University, University of California—Riverside, Audubon Starr Ranch, Vista Irrigation District, Rancho Mission Viejo / San Juan Company, Sweetwater Authority, California Department of Transportation, the City of San Diego Water Department and Parks Department, and the Irvine Ranch Conservancy. Anesthetic drug combinations used in capture procedures were either teletamine / zolazapam (Telazol) or medetomidine / ketamine at dosages prescribed in the scientific literature.

## Study Area and Population

The study area encompassed the Santa Ana Mountains (a portion of the Peninsular Ranges) and the remainder of the Peninsular Mountain Ranges and surrounding foothills to the east (hereafter referred to as the eastern Peninsular Range). These areas constitute the majority of occupied puma habitat in southern California south of greater Los Angeles (Fig 1). Pumas are the primary large carnivore remaining in the study area since grizzly bears (*Ursus arctos californicus)* were extirpated in the early 1900s [19, 20].

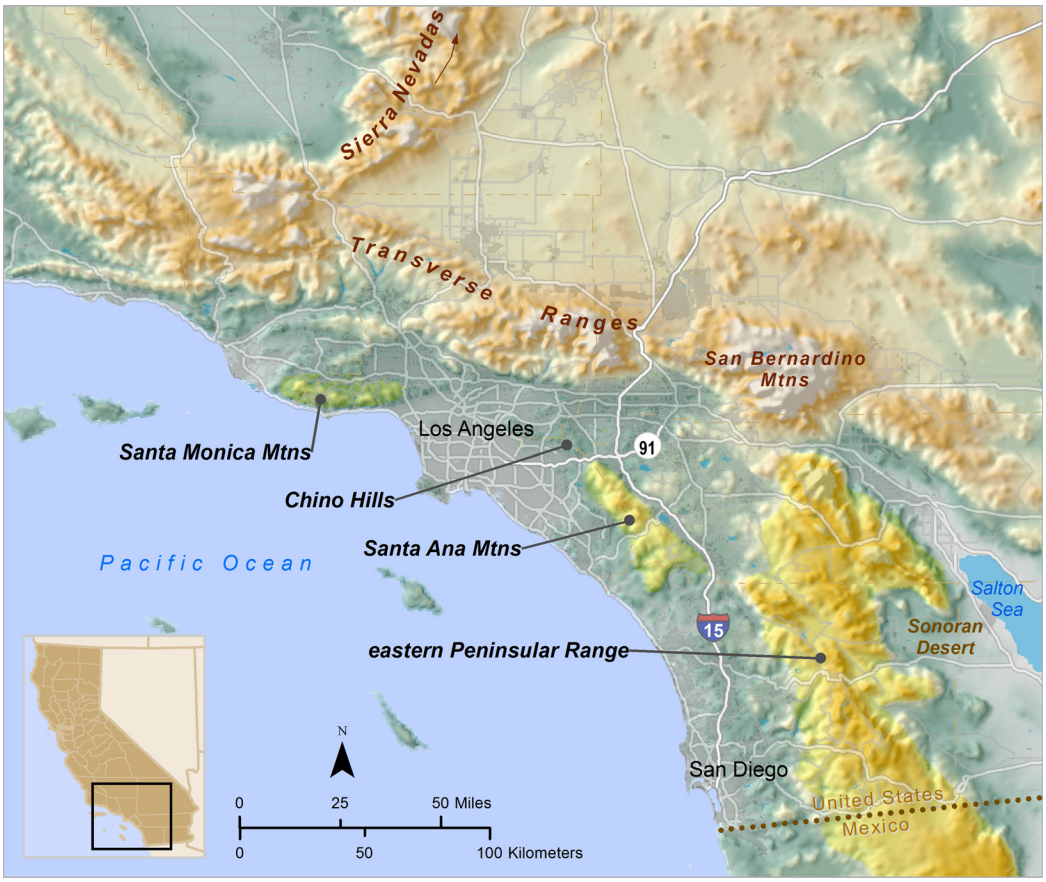


**Fig 1. Puma study area in southern California, USA, and regional context.** The focal area of this study includes the Santa Ana Mountains and the eastern Peninsular Range. Inset shows location within California.

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An extensive and growing network of roads, some carrying more than 250,000 vehicles per day, encircles and fragments the study area [21] (Fig 1). Interstate highway 15 (I-15) connects the greater Los Angeles, Riverside, and San Diego metropolitan areas, and the highway and associated development have been hypothesized to be a barrier to puma movement between the Santa Ana Mountains in the west and the eastern Peninsular Ranges [11, 13, 22, 23]. Therefore, we assigned pumas that were captured or found dead west of I-15 to a putative "Santa Ana Mountains" source population, and those east of I-15 to a putative "eastern Peninsular Range" source population.

Land use varies considerably across the study area, with the eastern Peninsular Ranges generally having less intensive development and more rural, undeveloped, and protected lands. Burdett et al. [15] classified land use and urbanization in the study area into five categories: protected public lands (55% of the study area), private undeveloped (9.5%), rural (14.4%; >16.18 ha per housing unit), exurban (15.7%; 0.68–16.18 ha per housing unit), and suburban/urban (5.4%; <0.68 ha per housing unit). The Santa Ana Mountains have substantial protected public lands, but new highway construction, development, and land use practices tend to be much more intensive immediately adjacent to remaining high quality puma habitat [15].

## Capture and Monitoring Methods

We captured, marked, and monitored radio collared pumas from 2001 through 2013. Pumas were captured primarily using baited cage traps [24], and to a lesser extent using hounds or foothold snares [25, 26]. Each captured animal was tattooed in one ear with a unique numerical identifier ("marked") and a numbered tag was placed in the opposite ear. Age was determined from dental characteristics and body morphometrics as described in Ashman et al. [27] and Laundre et al. [28, 29]. We classified pumas <18 months as kittens, 18–30 months as subadults, and >30 months as adults [30]. We applied Very High Frequency ("VHF"; MOD500 Telonics, Mesa, AZ), and/or Global Positioning System ("GPS"; Simplex P-1D, Televilt, Lindesberg, Sweden; TGW 3580, Telonics, Mesa, AZ; GPS4400S, GPS3300S, and GlobalstarTrack S, Lotek, Ontario, Canada) radio collars to pumas if their body weight exceeded 22.7 kg. GPS locations were collected at varying time intervals from every 5 minutes to every 6 hours depending on specific study objectives.

## Puma Movements

We hypothesized that the Pacific Ocean, Sonoran Desert, major highways, and urban centers would form barriers that constrained pumas in our study area into one or more discrete populations. To test this hypothesis, we examined movements of radio collared pumas from 2001–2013 to determine the degree of interchange within and between the Santa Ana Mountains and eastern Peninsular Range populations, and whether monitored pumas emigrated out of the entire study area. We were particularly interested in determining if ongoing habitat fragmentation had created or hardened existing barriers, and in evaluating puma movements relative to corridors or linkages identified through previous modeling efforts. These included: 1) the east-west "Santa Ana—Palomar Mountains Linkage" across I-15 that connects the Santa Ana Mountains and eastern Peninsular Range puma populations [31]; 2) the "Coal Canyon Corridor" under California State Route 91 (SR-91) linking the Santa Ana Mountains and the Chino Hills to the north [17, 32]; and 3) the "Parque-to-Park Linkage" connecting California and Baja California, Mexico to the south [33].

## Mortality and Survival Analyses

The distribution of radio collared pumas in the populations west and east of the I-15 freeway were compared using the Fisher exact test to determine if they differed by sex or age class,

and a two-sample t-test was used to determine if they differed by average age at entry or exit to the study (in months), or the average number of days monitored (STATA IC 13.0, STATA-Corp, College Station, Texas, USA). A P value of $\leq 0.05$ was used as the cutoff for significance for all analyses.

Deaths of radio collared pumas from 2001–2013 were detected when VHF or GPS data indicated a lack of movement, and the cause of death was determined by field investigation and necropsy. In addition, we combined mortality data for our marked (n = 36) pumas with "unmarked" (n = 218) pumas that were confirmed to have died in the study area from 1981–2013 based on CDFW records. Age determination was less precise for unmarked animals due to conditions of carcasses at discovery or variable experience of reporting parties in the aging of pumas. Therefore, we classified unmarked pumas as either subadults ($\leq$30 months) or adults (>30 months) [30].

We compared long-term trends in the number of pumas being killed under depredation permits in our dataset to the total number of puma mortalities across all of California during the same time period, as reported by CDFW [34], by plotting 5-year simple moving averages for each dataset. For each calendar year, the number of puma mortalities was averaged for the current year and previous 4 years. This allowed us to smooth short-term fluctuations and visualize long-term trends in the data.

Radio collared pumas entered the study on the date they were first captured, and exited on the date of mortality or the last date of detection by radiotelemetry. The number of days each animal was monitored was calculated as the time between entry and exit dates. Cause of death was determined at necropsy for both marked and unmarked animals unless the state of carcass decomposition precluded definitive diagnosis. In those cases, cause of death was classified as "unknown". Because numbers of at-risk individuals varied across the course of the study, a formal cause-specific mortality analysis was not possible [35]. However, source population, sex, and age class (at time of mortality) were evaluated in both marked and unmarked populations for associations with the various causes of mortality using the Fisher exact test (STATA IC 13.0, STATACorp, College Station, Texas, USA).

We estimated survival using the known-fate model in Program MARK (Version 7.1) [36]. We chose a set of 8 models a priori for analysis that included combinations of population, sex, and age class (at the time of collaring) as parameters. Support for each model was assessed using Akaike's Information Criterion (AIC), corrected for small sample size ($AIC_c$). The *sin* link function was used to run all models. If no model was clearly superior to all others (AICc weight >90% and$\Delta$AIC >2) [36–38], we performed model averaging to reduce the uncertainty in our parameter estimates.

We used a Cox proportional hazards model (STATA IC 13.0) to evaluate the relationship of biologically important covariates (source population, sex, age, and year of mortality) to the length of time pumas survived during the study. Adult age class (>30 months old) and mortality years 2007 and 2008 were used as reference categories in the models. Staggered entry into the study was addressed by including the Andersen-Gill formulation [39, 40]. The Breslow approximation method was used to address tied failure times [41], and Schoenfeld residuals were used to test the proportional hazards assumption that relative risk for each variable of interest was the same for the duration of the study.

## Results

### Puma Monitoring and Movements

Our analyses included 74 pumas that were captured, marked, and radio collared between March 2001 and December 2013 (Table 1). The distribution of these marked pumas in the

**Table 1. Demographic characteristics of radio collared pumas in southern California, USA from 2001–2013.**

| Variable | Number of pumas | | |
|---|---|---|---|
| | Total | Santa Ana Mountains | Eastern Peninsular Ranges |
| **Sex** | | | |
| Females | 37 | 17 | 20 |
| Males | 37 | 14 | 23 |
| **Outcome** | | | |
| Survived | 38 | 18 | 20 |
| Died | 36 | 13 | 23 |
| **Age class at entry** | | | |
| <18 months | 19 | 6 | 13 |
| 18 to 30 months | 19 | 9 | 10 |
| >30 months | 36 | 16 | 20 |
| **Age class at exit** | | | |
| <18 months | 2 | 0 | 2 |
| 18 to 30 months | 16 | 7 | 9 |
| >30 months | 56 | 24 | 32 |

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eastern Peninsular Range (n = 43) and Santa Ana Mountains (n = 31) did not differ significantly by sex, age class, average age at entry or exit to the study, or the average number of days monitored.

We detected numerous long distance (>80 km) movements by radio collared pumas from 2001–2013, but only one radio collared puma moved out of the overall study area. In 2009, a young adult male (M53) traveled approximately 150 km south from his capture site in the eastern Peninsular Range, utilizing the Parque-to-Park Linkage to cross the U.S.-Mexico border (Fig 2). He reached a point 70 km south of the border before returning to his original location in the U.S. Several other radio collared pumas were detected near, but not across, the U.S.-Mexico border (Fig 2).

Radio collared puma movements between the eastern Peninsular Range and Santa Ana Mountains were limited, indicating the pumas in these regions formed relatively discrete populations. In 2010, a dispersing sub-adult male (M56) crossed I-15 from west to east several miles south of the proposed Santa Ana Mountains—Palomar Mountains Linkage (Fig 2), but he was killed 25 days later for depredating domestic sheep.

None of the radio collared pumas used the Coal Canyon undercrossing beneath SR-91 at the northern tip of the Santa Ana Mountains to move into the Chino Hills to the north (Fig 2). However, two unmarked pumas were killed from 2001–2013 while attempting to cross this major freeway within 3 km of the Coal Canyon undercrossing.

## Puma Mortality

The number of pumas alive (n = 38) vs. dead (n = 36) by the end of the study did not differ between source populations, sexes, or age class at entrance or exit (Table 1). Though time-at-risk and sample size constraints prevented a formal cause-specific mortality analysis, we report here proportional mortality of both marked and unmarked pumas over the entire study period. Over the course of the entire study period, proportional mortality due to vehicle collisions and depredation permits was greater than for all other causes of mortality. Other known sources of mortality included disease, illegal shooting, arson-caused wildfire, public safety removal, and intraspecific aggression (Table 2). Proportional mortality due to vehicle strikes and

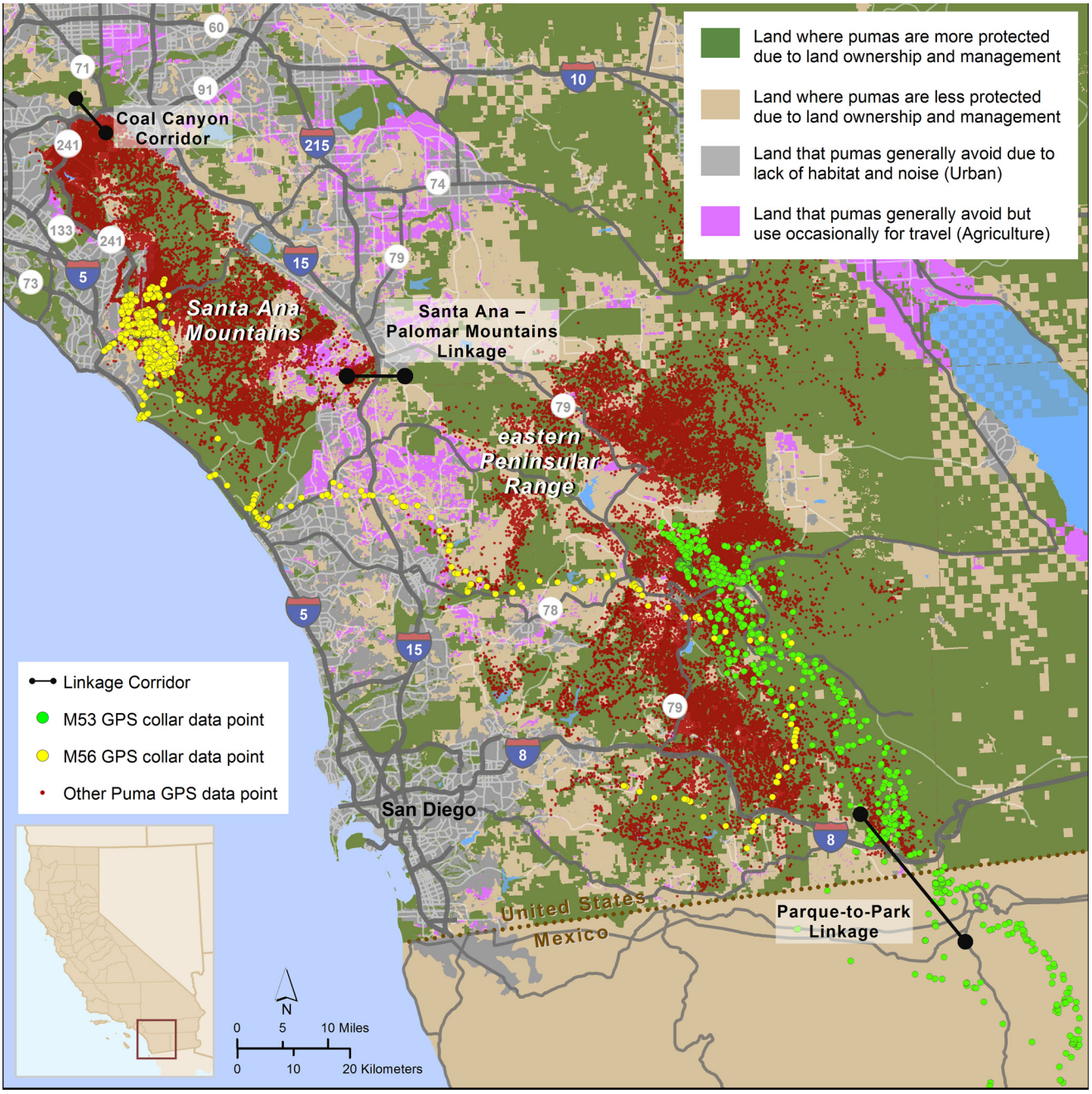


**Fig 2. Puma GPS collar data points collected from 2001–2013 in southern California, USA.** GPS collar data points are overlaid on lands classified (by color) based on their relative levels of puma protection and typical usage. Primary linkages within the study area are noted and GPS collar data points from pumas M53 and M56 are highlighted. Inset shows location within California.

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depredation permits differed between pumas from the eastern Peninsular Range and Santa Ana Mountains populations ($P = 0.034$), but did not differ by sex or age class. In fact, all mortalities of marked pumas due to depredation permits occurred in the eastern Peninsular Range, while 60% of mortalities due to vehicle collisions were in the Santa Ana Mountains (Table 2; Figs 3 and 4). With the exception of vehicle strikes and depredation, the data were too sparse to evaluate relationships between specific causes of mortality and various risk factors.

**Table 2. Proportions and numbers of radio collared pumas that died from different causes in Southern California study areas from 2001–2013.**

| Cause of mortality | Total | Santa Ana Mountains | Eastern Peninsular Ranges |
|---|---|---|---|
| Vehicle Strike[a] | 0.28 (10) | 0.46 (6) | 0.17 (4) |
| Depredation Permit[a] | 0.17 (6) | 0.00 (0) | 0.26 (6) |
| Killed illegally | 0.11 (4) | 0.23 (3) | 0.04 (1) |
| Disease suspected | 0.11 (4) | 0.08 (1) | 0.13 (3) |
| Disease confirmed | 0.06 (2) | 0.00 (0) | 0.09 (2) |
| Fire | 0.06 (2) | 0.08 (1) | 0.04 (1) |
| Public safety | 0.03 (1) | 0.00 (0) | 0.04 (1) |
| Killed by other puma | 0.03 (1) | 0.00 (0) | 0.04 (1) |
| Capture related | 0.03 (1) | 0.00 (0) | 0.04 (1) |
| Unknown | 0.14 (5) | 0.15 (2) | 0.13 (3) |
| Total | 36 | 13 | 23 |

[a] Mortalities secondary to depredation permits and vehicle strikes differed between the two populations (P = 0.034; Fisher's exact test).

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In the combined dataset (marked and unmarked pumas; n = 254), proportional mortality due to depredation permits was approximately 3.4 times higher for males than females (54M:16F; $P = 0.001$), while proportional mortality due to vehicle collisions was equal for both sexes (45M:45F). In the combined dataset, proportional mortality varied between the eastern Peninsular Range and Santa Ana Mountains populations ($P < 0.001$). There were more mortalities due to depredation permits in the eastern Peninsular Range (n = 62, compared to n = 11 in the Santa Ana Mountains), and almost equal numbers of mortalities due to vehicle collisions in the two populations (n = 46 in the eastern Peninsular Range, compared to n = 50 in the Santa Ana Mountains; Fig 5). Mortality varied substantially year by year in the combined dataset, but the trend for mortalities due to depredation permits tended to increase from 1981 to 2004 and then began to decline, before trending upward again through 2013 (Fig 6), a pattern generally similar to that seen in CDFW's graph of statewide depredation data (http://www.dfg.ca.gov/wildlife/lion/depredation.html). In contrast, the trend for deaths due to vehicle collisions increased steadily through 2013, with no decline or downward trend detected after 2004 (Fig 6). Vehicle mortalities occurred throughout the study area (Figs 3 and 4), however the majority of vehicle-related mortalities in the Santa Ana Mountains occurred on California State Highway 241 (SR-241) and SR-74, two highways that traverse puma habitat, and I-15 in the Santa Ana Mountains to Palomar Mountains Linkage area (Fig 3).

## Puma Survival

Survival estimates were calculated using data from the 74 radio collared pumas that were monitored from 2001–2013 for a total of 29,578 puma days (mean = 400, SE = 38 days per animal). Using the known-fate model within Program MARK, the estimated mean annual survival rate was 55.8%, (95% CI = 44.5–65.6%). In the most parsimonious model survival was constant across populations, sexes, and ages ("S(.)"; Table 3). Two models had ΔAIC values <2: model "S(Sex)" which included sex as a parameter (model likelihood = 0.43), and model "S(Population)" which included population as a parameter (model likelihood = 0.37; Table 3). These models yielded annual survival estimates of 58.6% for females and 52.5% for males across the entire study area, and 56.5% for the Santa Ana Mountains population and 55.4% for the eastern Peninsular Range population across all sexes and age groups (Table 3). Due to the distribution of AICc weights among the top models (Table 3), we performed model averaging of similarly

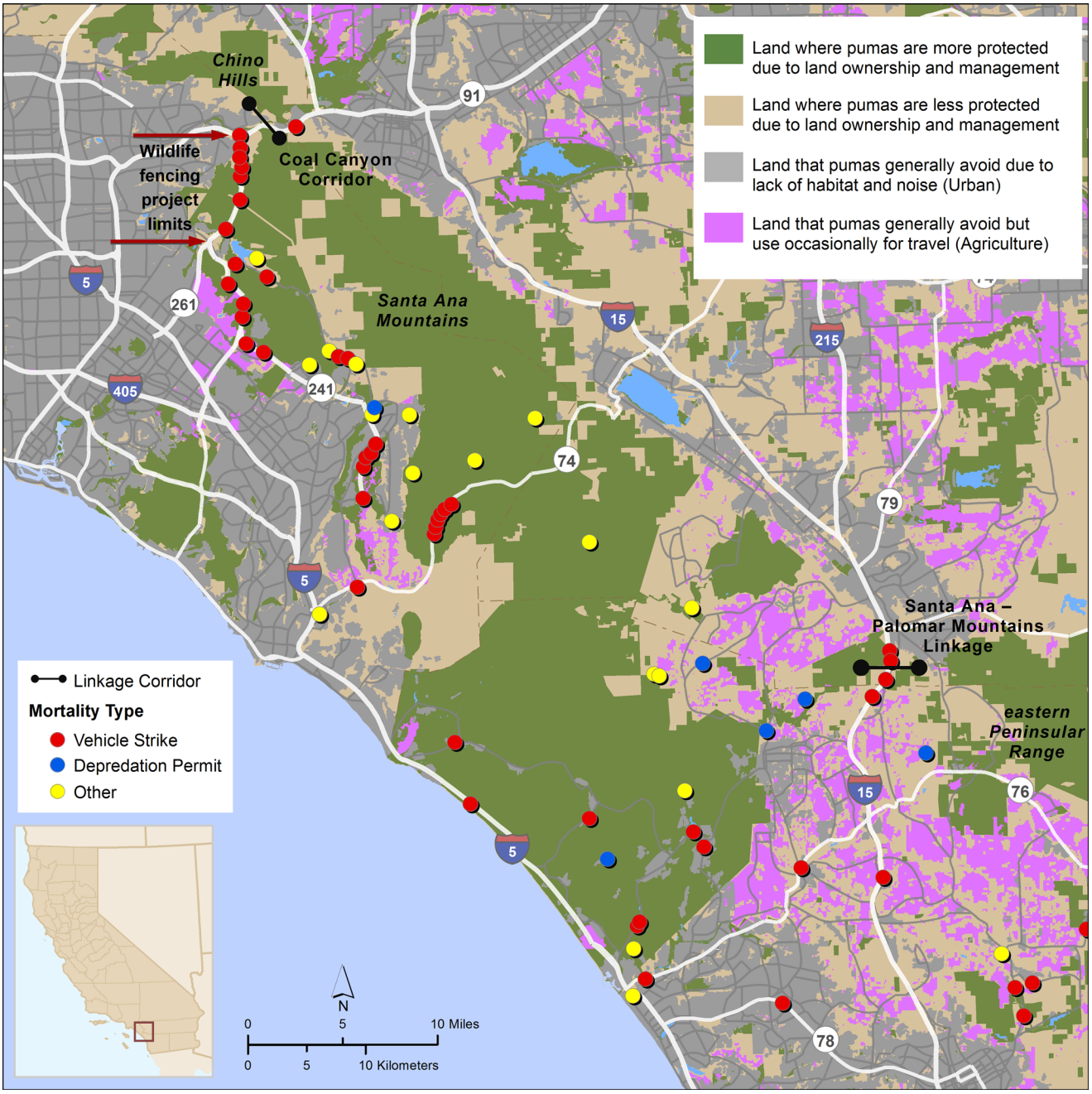


**Fig 3. Sites and causes of puma mortalities in the Santa Ana Mountains, 1981–2013.** The Coal Canyon Corridor and Santa Ana—Palomar Mountains Linkage are noted, as well as the limits of a wildlife fencing project on SR 241. Inset shows location within California.

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parameterized models but did not detect any differences among groups (95% CI of survival estimates overlapped).

Survival rates varied widely among years, and the Cox proportional hazards model identified calendar years 2001, 2003 2005, 2006, and 2009 as having significantly higher hazard ratios compared to years 2007 and 2008 (Table 4). All other covariates, including source population, sex, and age at entry were not significantly associated with time to death. Evaluation of the proportional hazards assumption for the final model based on a test of Schoenfeld residuals

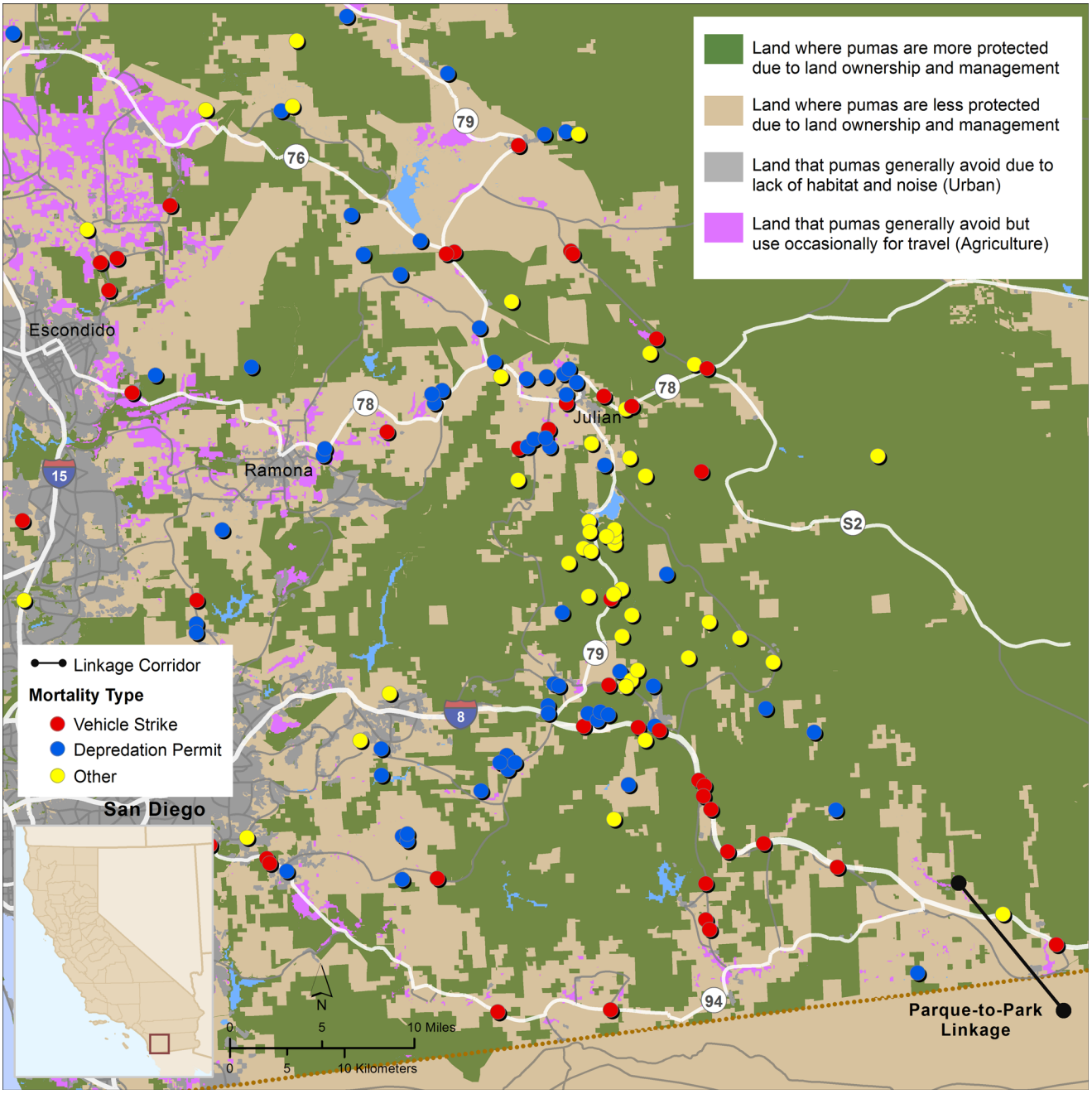


**Fig 4. Sites and causes of puma mortalities in the eastern Peninsular Range, 1981–2013.** Area depicted is generally east of Interstate 15, with the Parque to Park linkage noted. Inset shows location within California.

doi:10.1371/journal.pone.0131490.g004

indicated that the relative risk for each variable of interest, after including year as a variable in the model, did not differ for the duration of the study ($P = 0.99$).

## Discussion

This 13-year study demonstrates the high risk of mortality for pumas associated with fragmentation and urbanization, and coupled with our genetic analyses [12], we conclude that puma

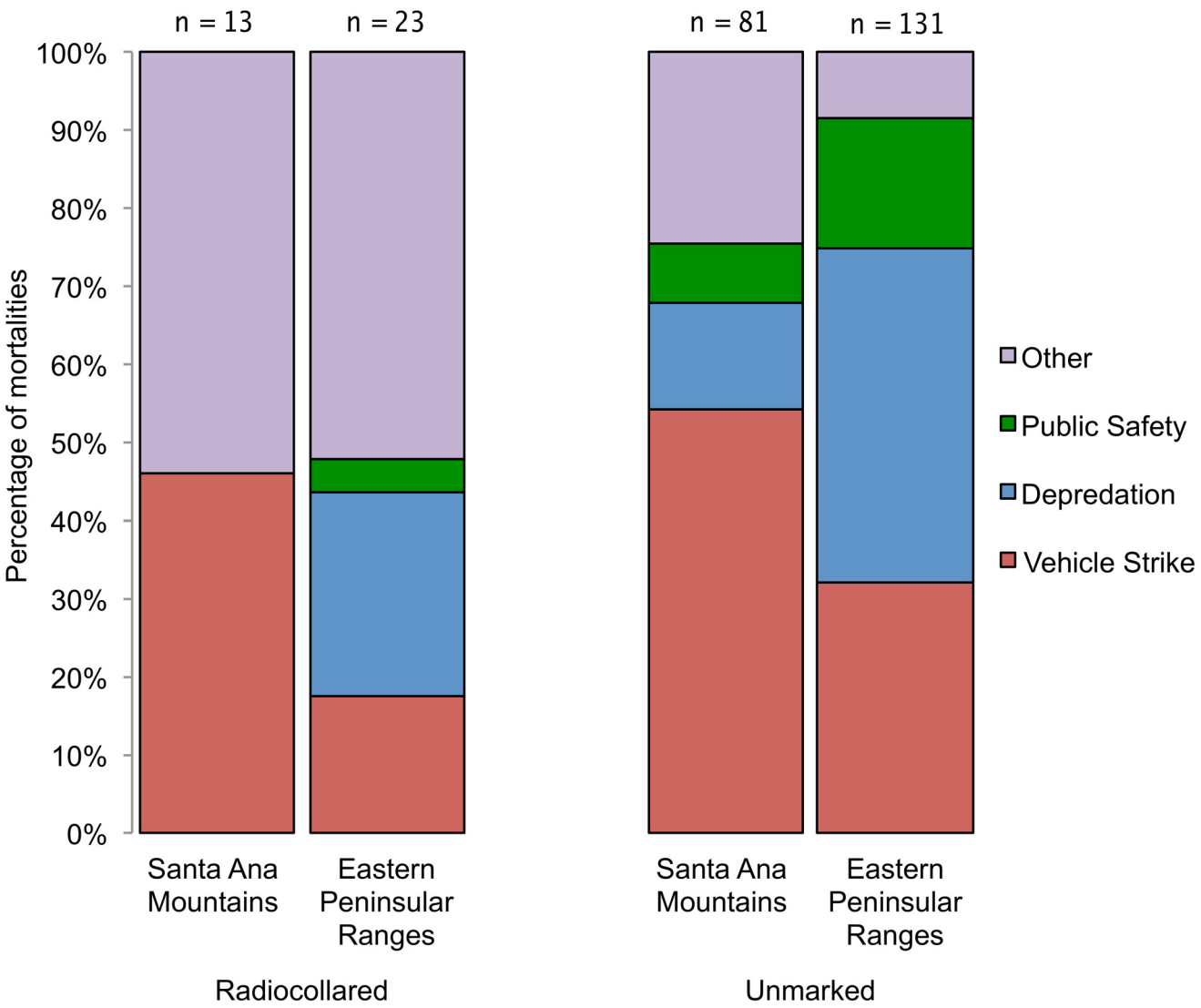


**Fig 5. Percentages of pumas dying from different causes of mortality in southern California, USA.** Mortalities of radiocollared (n = 36; 2001–2013) and unmarked (n = 212; 1981–2013) pumas were assigned to the Santa Ana Mountains or the eastern Peninsular Ranges subpopulation. Six unmarked pumas were not included in this figure because they were found on the I-15 freeway and could not be assigned to a population.

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persistence in this human-dominated landscape is threatened [42–46]. Annual puma survival rates for radio collared pumas in the Santa Ana Mountains (56.5%) and eastern Peninsular Range (55.4%) were very low from 2001–2013, and were similar to those in heavily hunted populations [2, 9, 43]. Indeed, annual survival rates for our study population were lower than rates for pumas in the peri-urban Santa Monica Mountains population northwest of Los Angeles (>75%) [12], and are within the range that is considered a threat to persistence of puma populations [13].

Our movement data (this paper) and our genetic findings [11] support the hypothesis that pumas in the Santa Ana Mountains and eastern Peninsular Range effectively form two subpopulations, bisected by an interstate highway and neighboring development. Our data demonstrate that both subpopulations had low survival; and though proportional mortality is a crude measure of causes of death in a population, the major causes of puma proportional mortality

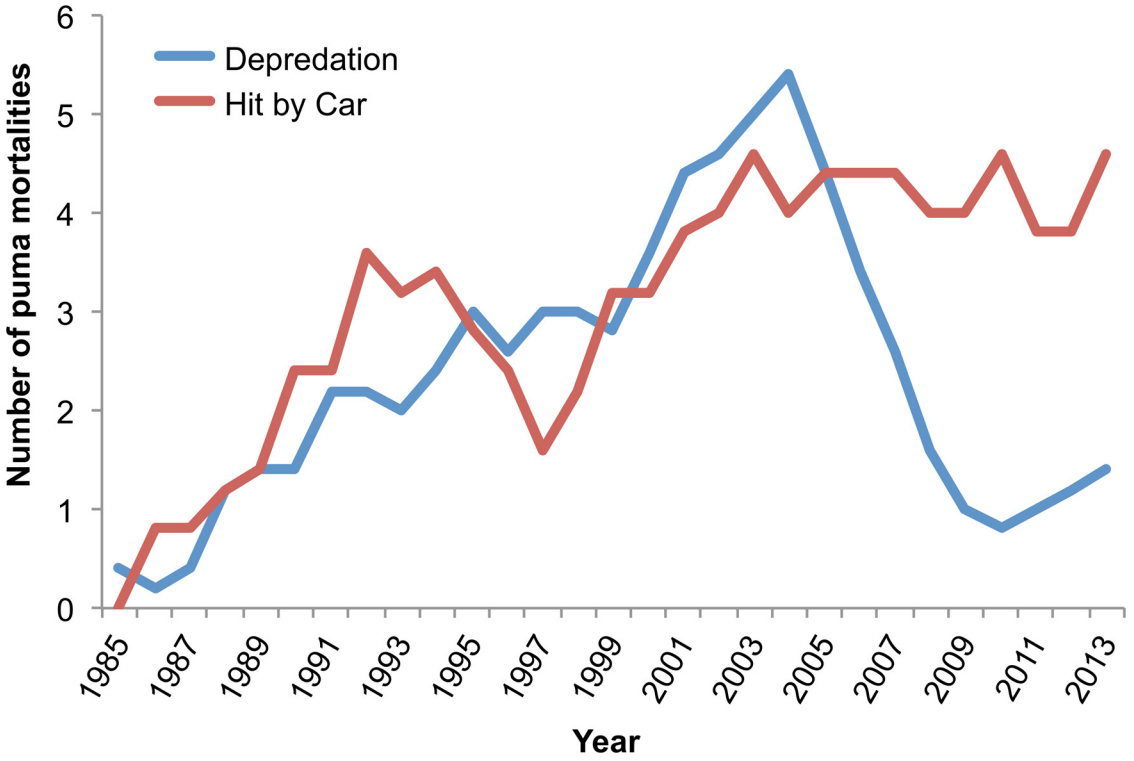


**Fig 6. Pumas killed secondary to vehicle collisions or depredation permits from 1981–2013 in southern California, USA.** Five year moving average of pumas killed secondary to vehicle collisions or depredation permits (n = 174) in the Santa Ana Mountains and eastern Peninsular Ranges.

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differed between these areas. Depredation permits were the most common proportional mortality factor in the eastern Peninsular Range and primarily affected males, whereas vehicle strikes were the main source of proportional mortality in the Santa Ana Mountains, affecting males and females equally. Conservation biologists have long expressed concern about demographic and genetic isolation of pumas in the Santa Ana Mountains [11, 13], and this study, coupled with our companion genetic study [11], provides a comprehensive view of the fractured demographic and genetic connectivity among pumas in this region.

Ernest et al. [11] concluded that Santa Ana Mountains pumas monitored in this study "had high average pairwise relatedness, high individual internal relatedness, a low estimated effective population size, and strong evidence of a bottleneck and isolation from other populations in California." Genetic restriction and isolation were pronounced even though limited gene flow

**Table 3. Results of the known-fate model (Program MARK) for survival (S) for radio collared pumas in southern California, USA.**

| Model | AICc | ΔAICc | AICc Weights | Model Likelihood | Number Parameters | Deviance |
|---|---|---|---|---|---|---|
| S(.) | 397.21 | 0.00 | 0.4668 | 1.00 | 1 | 327.25 |
| S(Sex) | 398.89 | 1.68 | 0.2012 | 0.43 | 2 | 326.93 |
| S(Population) | 399.20 | 1.99 | 0.1724 | 0.37 | 2 | 327.24 |
| S(Age) | 400.24 | 3.03 | 0.1026 | 0.22 | 3 | 326.27 |
| S(Population*Sex) | 402.69 | 5.48 | 0.0301 | 0.06 | 4 | 326.72 |
| S(Population*Age) | 403.68 | 6.48 | 0.0183 | 0.04 | 6 | 323.70 |
| S(Sex*Age) | 405.22 | 8.01 | 0.0085 | 0.02 | 6 | 325.24 |
| S(Population*Sex*Age) | 414.57 | 17.37 | 0.0001 | 0.00 | 12 | 322.52 |

doi:10.1371/journal.pone.0131490.t003

**Table 4. Variables related to time to death in the Cox proportional hazards model of survival of radio collared pumas in southern California, USA.**

| Covariate[a] | Hazard Ratio | SE | Z | P>\|z\| | 95% CI |
|---|---|---|---|---|---|
| **Age at Entry[b]** | | | | | |
| <18 months | 0.53 | 0.28 | -1.21 | 0.23 | 0.19–1.48 |
| 18–30 months | 1.56 | 0.75 | 0.93 | 0.35 | 0.61–3.99 |
| **Year at Exit[c]** | | | | | |
| 2001* | 149.20 | 209.78 | 3.56 | 0.00 | 9.48–2347.27 |
| 2002 | 5.16 | 6.85 | 1.24 | 0.22 | 0.38–69.63 |
| 2003* | 9.86 | 8.34 | 2.71 | 0.01 | 1.88–51.73 |
| 2004 | 5.41 | 6.98 | 1.31 | 0.19 | 0.43–67.91 |
| 2005* | 12.75 | 11.51 | 2.82 | 0.01 | 2.18–74.76 |
| 2006* | 7.10 | 6.82 | 2.04 | 0.04 | 1.08–46.64 |
| 2009* | 8.02 | 7.79 | 2.14 | 0.03 | 1.20–53.77 |
| 2010 | 1.70 | 1.71 | 0.53 | 0.60 | 0.24–12.16 |
| 2011 | 3.03 | 4.03 | 0.84 | 0.40 | 0.23–40.89 |
| 2012 | 6.16 | 6.14 | 1.82 | 0.07 | 0.87–43.44 |
| 2013 | 3.55 | 3.48 | 1.29 | 0.20 | 0.52–24.23 |

*Covariates significant at $P \leq 0.05$.

[a]The final model controlled for population and sex which were not significantly associated with time to mortality

[b]Oldest age class (>30 months old) designated as reference category.

[c]Years 2007 and 2008 designated as reference category

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did occur from the eastern Peninsular Ranges into the Santa Ana Mountains. Genetic analysis showed that a male puma (M86) captured in the Santa Ana Mountains was likely born in the eastern Peninsular Ranges, and successfully migrated into the Santa Ana Mountains during our study. This male, and two females (F61 and F89) captured in the Santa Ana Mountains, were the likely parents of four pumas born in the Santa Ana Mountains in 2010–2011 (M91, F92, M93, and M97) [11]. However, this is the only evidence of successful genetic interchange between the two populations during the study period other than an 8 month old kitten (F102) [11] killed by a car in the Santa Ana Mountains in August 2003. In 13 years, none of the pumas radio collared in the eastern Peninsular Range were observed to move west into the Santa Ana Mountains, and the single radio collared male that did move from the Santa Ana Mountains into the eastern Peninsular Range was killed for depredating domestic sheep within weeks of crossing I-15. This suggests that the estimated 17–27 adult pumas in the Santa Ana Mountains [13] have become an insular population, much like the small population of pumas located in the Santa Monica Mountains [12]. The combination of small population size, limited potential for immigration of new individuals (male and female) into the area, female mortality rates that are similar to males, and negative effects of genetic restriction [11], collectively put the Santa Ana Mountains population at risk for demographic collapse [13, 22, 47].

Southern California has been the focus of multiple regional-scale conservation planning efforts aimed at protecting a network of natural habitats, among extensive urban, suburban, and exurban development and a burgeoning population of >20,000,000 people [48]. Pumas have been a focal species for these efforts because of their ecological value, their inherent value to humans, and their utility as surrogates for other wide-ranging taxa in conservation planning [13, 22, 42, 49–52]. Despite some concerted conservation efforts (e.g. [14]), this study shows that pumas are currently subject to high levels of human-caused mortality, and that wildlife corridors that facilitate safe movement through the landscape are lacking or insufficient. These

threats will only grow worse without further action. For example, additional urban development is underway or proposed on both the east and west sides of I-15 in the Santa Ana–Palomar Mountains Linkage (Figs 2 and 3) [53, 54], and 14,000 new homes and associated highways will be constructed at the south end of SR-241 in the center of puma habitat in the Santa Ana Mountains [55].

Conserving core habitat areas and functional wildlife corridors has been the main focus of conservation efforts for pumas in southern California [15, 31, 32, 56, 57] and coordinated regional action in the form of targeted investment in habitat protection is especially urgent to maintain viability of the Santa Ana Mountains population. However, our analysis highlights that land protection alone will not be sufficient to ensure puma persistence in the region. Also important will be directed focus on improving road infrastructure to facilitate safe wildlife crossings, and reducing depredation conflicts that precipitate puma deaths. Options for enhancing movements across I-15 and other highways include protection of additional lands on both sides of the highway, improving or adding large culverts, adding exclusionary fencing [58] such as that currently being constructed on SR 241 (Fig 3) [59], and possibly constructing vegetated overpasses for wildlife use [60, 61]. Strategies to reduce mortalities stemming from depredation permits include education activities to promote wider use of predator-proof enclosures for their domestic animals during the crepuscular periods and at night [62–65]. A focus on land protection, roadway and wildlife crossing design, and landowner outreach will be critical for persistence of puma in southern California, and may well be a formula for conserving large carnivores in highly populated and fragmented landscapes generally.

The combination of long term field monitoring of radio collared animals coupled with genetic analyses was critical for understanding puma biology and providing directions for conservation efforts in southern California. The movement of puma M86 across I-15 from the eastern Peninsular Ranges may aid in the genetic rescue of the Santa Ana population, but only if his offspring survive and reproduce. To date, only one of his four known offspring are still alive in the wild—a female with two dispersal-age offspring, and evidence points towards pumas being less likely to successfully navigate this human-dominated landscape in the future. In the absence of effective measures to reduce mortality and enhance safe movement across highways, translocation of pumas, such as was done with the Florida panther [66], may ultimately be necessary to prevent further genetic decline and assure persistence of the Santa Ana Mountains population.

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## Author Contributions

Conceived and designed the experiments: TWV WMB RB SAM PRH TS HBE. Performed the experiments: TWV WMB RB HBE JNS. Analyzed the data: TWV WMB JNS CKJ BSC HBE PRH RB. Contributed reagents/materials/analysis tools: JNS CKJ HBE SAM BSC. Wrote the paper: TWV JNS CKJ SAM RB TS BSC PRH HBE WMB.

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**RE: [Federal Register Volume 84, Number 232 (Tuesday, December 3, 2019)]**
**[Notices]**
**[Pages 66268-66269]**
**From the Federal Register Online via the Government Publishing Office [www.gpo.gov]**
**[FR Doc No: 2019-26117]**

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**DEPARTMENT OF TRANSPORTATION**
**Federal Highway Administration**
**Environmental Impact Statement: San Diego and Orange Counties, California**
**AGENCY: Federal Highway Administration, U.S. Department of Transportation.**
**ACTION: Notice of Intent.**

**----------**

**SUMMARY: The Federal Highway Administration (FHWA), on behalf of the California Department of Transportation (Caltrans), is issuing this notice to advise the public that a Draft Environmental Impact Statement (Draft EIS) will be prepared for a proposed highway project in Orange County and San Diego County, California.**

January 8, 2020

To Whom It May Concern

Please accept this letter as comment on the Draft Environmental Impact Statement that will be prepared in relation to the proposed highway project as presented in this publication in the Federal Register. I would request that my comments be considered during the development of the project Draft EIS.

Comments:

As a wildlife veterinarian and researcher who has conducted scientific studies for over a decade in the south Orange County region where the proposed project is planned, I have significant concerns with the negative impacts that several of the proposed alternatives may have on mountain lion (*Puma concolor*) and other wildlife movement and connectivity. My special expertise and knowledge relates to mountain lions in that area, but their movement patterns can illuminate the patterns of numerous other wild species as well.

It is well established by multiple peer reviewed studies and published reports to government agencies (1-4) that mountain lions in the Santa Ana Mountain Range are seriously genetically restricted and have unusually low annual survival rates, with the number one source of mortality being collisions with cars (5). This has resulted in a population under serious threat of extirpation within less than two decades if inbreeding depression begins to reduce reproductive success in the population (3). As a result of the aforementioned studies, the Santa Anas mountain lion population has been petitioned for listing under the California Endangered Species Act, and its status is currently being studied intensively by our research group at the University of California–Davis, as well as by the California Department of Fish and Wildlife. Connectivity across highways has emerged as the most important factor in restriction of

connectivity, and extensive study has been done and is ongoing by our group and collaborators that is related to this issue across the region (4, 6-7, Vickers unpublished data).

The majority of the mountain lion deaths from vehicle collisions in the last two decades have been on the SR 241 Toll Road, but SR 74 and other regional highways that are less busy have also been sites of mountain lion mortalities. The toll road agency has built additional fencing on SR 241 in one 6 mile section to reduce the rate of vehicle collisions, and that has been quite successful in that goal, but other sections of both SR 241, as well as sections of SR 74, remain a danger to mountain lions and other wildlife.

In the area of the proposed project, movement of mountain lions between habitat patches is already compromised in both the north-south and east-west directions by existing housing and roads, with more approved and under construction in Rancho Mission Viejo. Connections between Chiquita Canyon and Bell Canyon habitat areas north of SR 74, and habitat areas to the south of SR 74 are already affected negatively by increasing traffic on SR 74 itself and expanding development in Ranch Mission Viejo, including Los Patrones Parkway. Though passageway structures for wildlife and fencing are present on Los Patrones Parkway, to my knowledge movement studies have not been done with GPS collars to determine if that roadway is having any barrier effect on east-west movement.

Mountain lions must move north and south in the region of the proposed project in order to utilize habitat specifically set aside for conservation. Increasing restriction of access to those habitats is anathema to the effort and expense of conserving those habitat areas originally and maintaining their function for wildlife. Thus any project that is built in that region should be extremely sensitive to negative impacts on mountain lions and other wildlife. Our studies of the impacts of SR's 241, 74, 78, 79, 76, and 67, and large freeways such as SR 91 and I-15, all confirm that essentially any significant highway can be both a barrier and a mortality source. Preliminary results from studies underway by our research team and other UC Davis and University of Southern California researchers, as well as those by other researchers, suggest that the light, noise, and other aspects of highways can have negative impacts on wildlife numbers and diversity near the highways. Thus highways can exert negative effects at some level even when adequate wildlife passageways and fencing are well designed. This should be kept in mind when considering the different alternatives in the Environmental Impact Statement.

As such, all of the Alternatives should be closely evaluated to ascertain that they would not further fragment the mountain lion population in the Santa Ana Mountains and put it at further risk via increased road mortality, or worsen its genetic connectivity.

The Alternatives listed in the Federal Register notice are:

**Alternative 1/No Build Alternative; taking no action.**
**Alternative 13; connect SR 241 to I-5 via a connection from**
**Los Patrones Parkway to La Novia Avenue, I-5 widening and improvements,**
**and the addition of HOT lanes in each direction on I-5**
**Alternative 17; connect SR 241 to I-5 via a connection from**
**Los Patrones Parkway to Avenida Vaquero, I-5 widening and improvements,**

**and the addition of HOT lanes in each direction on I-5**
**Alternative 14; connect SR 241 to I-5 via a connection from**
**Los Patrones Parkway to Avenida Pico, I-5 widening and improvements,**
**and the addition of HOT lanes in each direction on I-5**
**Alternative 11; add I-5 general purpose lanes from I-405 to**
**San Diego County**
**Alternative 12; add I-5 HOT/toll lanes from I-405 to San Diego**
**County**
**Alternative 9; connect Ortega Highway and Antonio Parkway to**
**Avery Parkway and SR 73**
**Alternative 18; connect SR-241 to SR-73 and extend Crown**
**Valley Parkway to SR 241**
**Alternative 21; extend Los Patrones Parkway to Avenida La Pata**
**and add HOT lanes in each direction on I-5**
**Alternative 22; extend Los Patrones Parkway to Avenida La Pata**
**Alternative 23; extend I-5 managed lanes from SR 73 to**
**Basilone Road or from Avenida Pico to Basilone Road (depending on the**
**design option)**

In my view, several of the alternatives would have minimal negative impact on the Santa Ana Mountains mountain lion population. These include Alternatives 1, 11, 12, and 23c and 23d.

In my view, Alternatives 9, 13, 14, 17, 18, 21, and 22 all would potentially disrupt some mountain lion movement through this already fragmented landscape, and further disrupt local gene flow in this imperiled species unless structural plans are such that permeability is assured. All of these alternatives place the highway footprint in lands that currently host many wildlife species including mountain lions and others. Some of the named alternatives would potentially have a negative effect on subsequent major north-south or east-west movement. Alternative 18 for instance would cut a major habitat block (Chiquita Canyon) into 3 pieces, and Alternatives 14, 17, 21, and 22 would all erect another barrier to north-south movement.

In my view, Alternative 21's hot lanes could be added to I-5 without mountain lion habitat disruption, but Alternative 21's extension of Los Patrones Parkway to Avenida La Pata would likely have some detrimental impact on the local mountain lion population.

In my view, of the Alternatives that involve construction of new wide highway segments south of SR 74, Alternative 13 would appear to be least disruptive of large wildlife habitat patches, but like the other Alternatives south of SR 74, some barrier effect on north-south movement of mountain lions may occur unless extraordinary design elements are included that maximize safe travel potential and eliminate mortality potential, but that also eliminate other negative impacts of sound, light, etc from vehicles and infrastructure along the highway. These can include freeway light shielding and design, berms and walls to reflect sound and light away from the habitat, and other measures.

I feel that it is critical that any Alternative that is accepted by the various agencies involved, and the public, keep the interests of wildlife on an even par with transportation improvement in the list of goals of any project.

Thank you,

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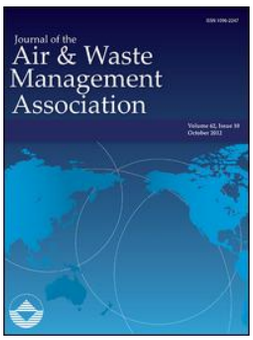

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# An Analysis of Effects of San Diego Wildfire on Ambient Air Quality

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## ABSTRACT

The impact of major gaseous and particulate pollutants emitted by the wildfire of October 2003 on ambient air quality and health of San Diego residents before, during, and after the fire are analyzed using data available from the San Diego County Air Pollution Control District and California Air Resources Board. It was found that fine particulate matter (PM) levels exceeded the federal daily 24-hr average standard during the fire. There was a slight increase in some of the gaseous pollutants, such as carbon monoxide, which exceeded federal standards. Ozone ($O_3$) precursors, such as total hydrocarbons and methane gases, experienced elevated concentration during the fire. Fortunately, the absence of sunlight because of the cloud of thick smoke that covered most of the county during the fire appears to have prevented the photochemical conversion of the precursor gases to harmful concentrations of $O_3$. Statistical analysis of the compiled medical surveillance data has been used to establish correlations between pollutant levels in the region and the resultant health problems experienced by the county citizens. The study shows that the increased PM concentration above the federal standard resulted in a significant increase in hospital emergency room visits for asthma, respiratory problems, eye irritation, and smoke inhalation. On the basis of the findings, it is recommended that hospitals and emergency medical facilities engage in pre-event planning that would ensure a rapid response to an impact on the healthcare system as a result of a large wildfire and appropriate agencies engage in the use of all available meteorological forecasting resources, including real-time satellite imaging assets, to accurately forecast air quality and assist firefighting efforts.

### IMPLICATIONS

The purpose of this research project is to document the amounts and effects of major gaseous pollutants and particulate matter emitted into the ambience of San Diego County by the wildfire of October 2003. In addition, establish correlations between pollutant levels in the region and resultant health problems experienced by the county citizenry using the medical surveillance report compiled in collaboration with area hospitals. Establishing a nexus between the major pollutants emitted and air quality related health problems would be useful in preparing for similar events and developing preventive strategies for the future.

## INTRODUCTION

San Diego, the sixth largest county in the United States, is home to 2.8 million residents, and is the third most populous city in California. The county encompasses 4300 square miles and includes a mixture of urban and rural communities that live in the coast, the mountains, and the desert. It borders Orange and Riverside counties to the North, Mexico to the south, Imperial County to the East, and the Pacific Ocean to the West. San Diego enjoys desirable weather receiving only approximately 20–30 days of rain per year. Around October, this region experiences persistent dry weather and low moisture that create conditions conducive for fire that are reinforced by Santa Ana winds. It was precisely that these conditions that were partially responsible for the 2003 wildfires that besieged Southern California. These turned out to be the most disastrous in the history of the state, as they was characterized by 14 fires in the counties of San Diego, Los Angeles, San Bernardino, and Ventura.

The fires that occurred in San Diego mainly took place in three different locations. The Cedar Fire was the most intense and largest of the fires. The other two were the Paradise and Otay Fires. The Cedar Fire spread ~20 miles to the east of Interstate Route 805, then moved on toward Pine Valley and Julian to the North, and soon spread over the entire area that demarcates the communities of Ramona, Poway, Miramar, Tierrasanta, and Grossmont. The Paradise Fire covered the area of Valley Center, and the Otay Fire burnt the mountainous area close to the U.S.–Mexico border and East Chula Vista. The Santa Ana winds took the fires

toward the west, directly into wild vegetations and the residential areas. The task of fighting the fires was made difficult as local wind patterns sporadically changed the direction of the fire. The whole region was blanketed with clouds of smoke, and ashes were carried over hundreds of miles. The San Diego Air Pollution Control District issued a health advisory recommending that all of the schools in the county be closed and all outdoor activities be limited for over a week. Mass attention was focused, by the increased number of hospital admissions, on what was emitted into the regional atmosphere from the fires.

The wildfire of October 2003 brought residents of San Diego and neighboring cities unprecedented devastating effects far beyond the short-term and long-term harmful suffering done to the environment, flora, and fauna. The San Diego fire consumed an area of >390,000 acres; burned 5597 homes, commercial, and accessory buildings; destroyed 3773 automobiles, trucks, and boats;[1] and caused 16 deaths.[2] The incident became a catalyst for instituting legislations that would ensure that different private and public agencies would be ready to respond to similar catastrophes in the future.

The Cedar Fire released ~300,150 t of PM and other pollutants into the atmosphere.[3] These pollutants are known to cause serious adverse health effects in the human respiratory system. If the government air quality standards are met, a healthy person can expect minimal adverse epidemiological consequences. However, when natural disasters, such as wildfires, occur, they produce such unpredictable, uncontrollable pollutant masses in the atmosphere that no living, breathing creature can escape from its poisonous effects. The purpose of this research project was to document the amounts and effects of major gaseous pollutants and PM emitted into the ambience of San Diego County by the wildfire of October 2003. Another objective was to establish correlations between pollutant levels in the region and resultant health problems experienced by the county residents, by using the medical surveillance report that was compiled in collaboration with area hospitals. It is assumed that establishing a nexus between the major pollutants emitted and air quality-related health problems would help both private and public agencies develop preventive strategies and, thus, be better prepared for similar events in the future.

## Literature Review

Biomass burning and wildfires emit a substantial amount of gaseous pollutants and PM into the environment and cause people to suffer from respiratory illnesses. The seriousness of illness that they may suffer from depends not only on the concentration levels but also on individual sensitivity, physiological characteristics, and susceptibility. Other consequences include nuisance, visibility impairment, ozone ($O_3$) generation, and greenhouse effects. In recent years, air pollution has been considered to be an important cause or risk factor for reproductive health. There have been growing concerns about the adverse effects of air pollution on birth outcomes, such as low birth weight (LBW), intrauterine growth retardation, preterm births, and birth defects.[4–7] Coarse PM ($PM_{10}$) exposure in the second and fourth months has been associated with LBW.[8] Particulate air pollution has been associated with both acute and chronic exacerbation of childhood asthma. More chronic symptoms of bronchitis have been observed in previous cross-sectional studies of children with asthma exposed to PM[9–14].

Wildfire smoke is comprised of a complex mixture of particles, liquids, and gaseous compounds. These include $PM_{10}$, carbon monoxide (CO), nitrogen oxides ($NO_x$), and sulfur dioxide ($SO_2$), oxidants that may include small amounts of $O_3$, polycyclic organic material,[15] and toxic pollutants. These emissions may significantly impact air quality on local, regional, and global scales. Some events are extreme, and the contributions of fires to air pollutant concentrations are readily observable.[16] For instance, the 1997 Indonesia forest fire caused massive transboundary air pollution, producing large amounts of haze in the region and causing visibility and health problems within Southeast Asia. Furthermore, fires of such magnitude have the potential to contribute to global warming and climate change as they emit large amounts of greenhouse gases and other pyrogenic products.[17,18]

PM is the pollutant that has most consistently been associated with short-term effects on mortality.[19] Recent findings tend to relate particulate pollution to an increased plasma viscosity,[20] increased risks of heart rate,[21] electrocardiographic changes in humans,[22–24] and the triggering of myocardial infraction.[25] A high degree of human exposure to concentrated air particles has also been associated with plasma fibrinogen.[26] Several studies have indicated that the smaller particles, which are $<2.5$ μm in diameter, are mainly responsible for the above effects.[19]

Long-term exposure to combustion-related fine particulate and sulfur oxide ($SO_x$)-related air pollution has been identified as an important environmental risk factor for cardiopulmonary and lung cancer mortality. Each 10 $\mu g/m^3$ increase in fine particulate air pollution is associated with an ~4, 6, and 8% increased risk of all cause, cardiopulmonary, and lung cancer mortality, respectively. However, measures of coarse particle fraction and total suspended particles are not consistently associated with mortality.[27]

Time-series and panel studies have shown acute increases in ambient PM to be associated with increases in emergency room visits,[28] hospital admissions for asthma,[29,30] acute symptoms,[31–35] medication use,[31,33] and a decline in peak exploratory flow rates.[31,32,34] There was a 91% increase in asthma and chronic bronchitis incidences during a fire in central Florida in 1998. On average, there was a 1–1.5 day lag between the fire event and the increased emergency room visits and in-patient admissions for asthma.[36]

The most abundant air pollutant from wild land fires is CO. This, coupled with carbon dioxide and methane ($CH_4$), has been found to be a significant source of greenhouse gases. Besides CO, $NO_x$ can also form at lower temperatures, although the amount primarily depends on the nitrogen content of the fires burnt. However, the $SO_x$ produced are in negligible quantities, because forest fires normally contain low sulfur content. Fires also emit a large amount of semivolatile organic compounds (VOCs), which are partitioned between the gaseous and liquid or solid phase at ambient temperatures. Some VOCs are carcinogenic and can condense or absorbed into the surface

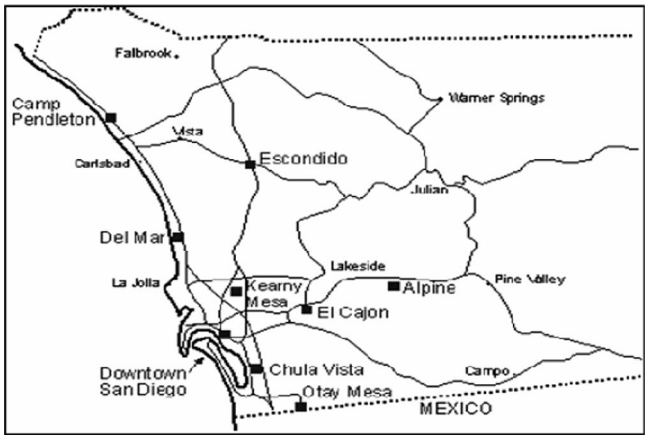


**Figure 1.** San Diego APCD-chosen monitoring stations.

of the particulate. Incomplete combustion produces hydrocarbons, including ethylene, alkynes, aldehydes, furans, and carboxylic acids.[15]

The main health impact is from the exposure to PM. It is a major component of smoke and is comprised of a complex mixture of soot, tars, and volatile substances and, thus, is harmful to human health.[15] In many cases, pollutant gases, such as $SO_x$, $NO_x$, and VOCs, interact with other compounds in the air to form fine particles. Their chemical and physical compositions vary depending on location, time of the year, and weather.[37] Fine PM ($PM_{2.5}$) is becoming more commonly measured during fire-related incidents, because the fine fraction predominates in the smoke and haze, and it is thought to be more responsible than larger particles for the observed health effects.[38,39]

## Methodology

San Diego Air Pollution Control District (APCD) has established nine air monitoring stations that are strategically located to evaluate pollution levels that affect the county residents (Figure 1). Each station monitors specific pollution levels borne by sources pertaining to the area, such as stationary and mobile sources (Table 1).

To assess the impact of the pollutants emitted by the San Diego Wildfire, a 4-week baseline surveillance period before the start of fire (October 25, 2003), a 10-day period during the fire, and a 4-week post-fire surveillance period immediately after the fire were established. For the purpose of analysis, data were primarily obtained from two urban and one remote monitoring locations: Downtown San Diego, Escondido, and Alpine. Downtown San Diego and Escondido are heavily urbanized

**Table 1.** Pollutants monitored by the nine monitoring stations in the San Diego APCD.

| Station | Pollutant Measured |
|---|---|
| Alpine | $O_3$, $NO_2$, NO, $NO_x$, $PM_{10}$ |
| Camp Pendleton | $O_3$, $NO_2$, NO, $NO_x$ |
| Chula Vista | $O_3$, $NO_2$, NO, $NO_x$, $PM_{10}$, $PM_{2.5}$ |
| Del Mar | $O_3$ |
| El Cajon | $O_3$, $NO_2$, NO, $NO_x$, $PM_{10}$, $PM_{2.5}$, $CH_4$, non-$CH_4$ hydrocarbon, THC |
| Escondido | $O_3$, $NO_2$, NO, $NO_x$, CO, $PM_{2.5}$ |
| Otay Mesa | $O_3$, $NO_2$, NO, $NO_x$, CO, $SO_2$, $PM_{10}$ |
| San Diego–Downtown | $O_3$, $NO_2$, NO, $NO_x$, CO, $SO_2$, $PM_{10}$, $PM_{2.5}$ |
| Kearny Mesa | $O_3$, $NO_2$, NO, $NO_x$, $CH_4$, THC, $PM_{10}$, $PM_{2.5}$ |

with a high density of vehicular population. Alpine is a rural town ~25 miles east-northeast of the city of San Diego. It is in the foothill zone, and its western sloping terrain traps air pollutants. For the purpose of this study, average daily, 1-hr maximum and 8-hr maximum readings were referenced to analyze the resultant effects of gaseous pollutants. Standard and local conditions for PM were also noted. Contributions by $O_3$ precursors, such as total hydrocarbons (THC), $CH_4$, and non-$CH_4$ hydrocarbons, were analyzed to determine the behavior of the major pollutants. The conditions for each criteria pollutant of concern in 2002 were recorded by San Diego County as described below.[40]

*$O_3$.* $O_3$ levels were measured in all nine of the locations. The county did not exceed the federal 1-hr concentration of 0.125 ppm. However, the federal 8-hr concentration of 0.085 ppm was exceeded for a total of 13 days. The Alpine station measured the greatest number of days exceeding the 8-hr standard[12] days for $O_3$. This was because emissions from motor vehicles, industry, and anthropogenic activities were blown inland through dense urban areas by the onshore breeze and tended to stay along the west-facing mountain slopes ~2000 ft above sea level. There were also enough pollutant generators in San Diego County to contribute to higher pollution concentrations. The region has adequate conducive atmosphere to produce higher $O_3$ levels, such as persistent light winds, hot temperature, and plenty of sunlight.

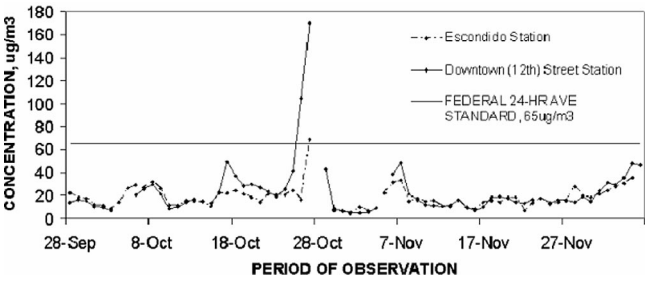


**Figure 2.** $PM_{2.5}$ daily 24-hr average measurements during the surveillance period.

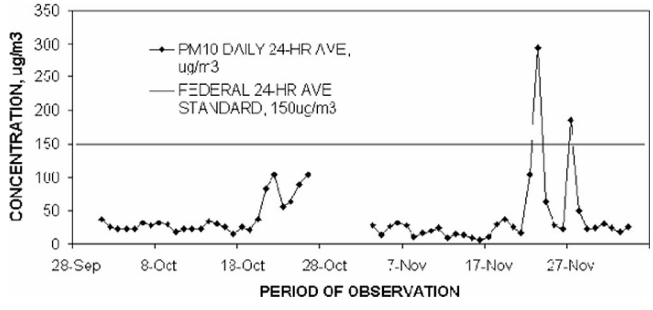


**Figure 3.** $PM_{10}$ measurement in Alpine station during the surveillance period.

*$PM_{10}$.* San Diego APCD measured $PM_{10}$ standards as mandated by both federal and state governments in six locations as shown in Table 1. The stations collected 24-hr samples on specific filters and compared data to air quality standards (annual arithmetic mean: federal –50 $\mu g/m^3$ and state –20 $\mu g/m^3$; and maximum 24-hr, federal –150 $\mu g/m^3$ and state –50 $\mu g/m^3$). The results indicate that the county did not exceed the federal standards except for one location, Otay Mesa, where a high volume of border crossings occurred, and this contributed to a high generation of $PM_{10}$. However, most locations failed to meet state standards, which are more stringent than federal standards.

*$PM_{2.5}$.* $PM_{2.5}$ samples were collected daily in three sites, El Cajon, Escondido, and downtown San Diego. Samples from Kearny Mesa and Chula Vista were taken for measurements every third day. All of the locations met the federal 24-hr standard of 65 $\mu g/m^3$ for $PM_{2.5}$. Three sites exceeded the annual standard, arithmetic mean 15 $\mu g/m^3$, and the more stringent state standard of 12 $\mu g/m^3$.

*CO.* The county attained all of the federal and state standards for CO (maximum 1-hr concentration of 35 ppm for federal and 20 ppm for state, and maximum 8-hr concentrations of 9 ppm for federal and state). The emissions of CO came primarily from automotive vehicles. Strict motor vehicle emission requirements controlled CO emissions formed during combustion.

*$NO_2$.* The annual average federal allowable standard is 0.053 ppm, and the California maximum 1-hr standard is 0.25 ppm. The county has not exceeded either of these limits in more than a decade.

*$SO_2$.* There has never been a violation of $SO_2$ exceeding the standards in San Diego County, although three federal standards and two state standards are in place to limit $SO_2$ pollution. The three federal standards include an annual average of 0.030 ppm, a maximum 24-hr concentration of 0.14 ppm, and a maximum 3-hr concentration of 0.5 ppm. More stringent state standards are a maximum 24-hr concentration of 0.05 ppm and a maximum 1-hr concentration of 0.25 ppm.

The San Diego APCD archives the data on the pollutants, which were measured from the nine monitoring stations. In addition to this source of raw data, similar data are available from the California Air Resources Board (CARB). The meteorological impact on the behavior of pollutant dispersion and movement during the fire was based on the daily forecast generated by San Diego APCD meteorologists. Real-time observations of the meteorologists were also taken into consideration in the analysis of the overall impact to ambient air quality from the fires.

Before October 1, 2003, San Diego County APCD was using the Federal Reference Method (FRM) samplers to collect $PM_{2.5}$ data for data analysis and archiving. The FRM is based on statistical analyses of filter samples collected at the five monitoring stations located throughout the county. These five stations are located in downtown San Diego (Twelfth Avenue), Chula Vista, El Cajon, Kearny Mesa (Overland Avenue), and Escondido. When San Diego APCD became part of the national forecasting program on October 1, 2003, district meteorologists began relying on data collected from the two $PM_{2.5}$ Beta Attenuation Monitor (BAM) samplers for real-time data reporting and forecast verification. Statistical analysis of the FRM data did not show sharp gradients across the county or radical departures from mean conditions. As a result, the two BAM samplers were thought to be adequate for ambient conditions expected in the county. These two BAM samplers are located at downtown San Diego and Escondido monitoring stations. The only real-time $PM_{10}$ Tapered Element Oscillating Microbalance (TEOM) sampler is located at the Alpine monitoring station. Meteorological data were provided by the District Radar Wind Profilers (RWPs) and the Radio-Acoustic Sounding Systems (RASS) located in Miramar and Point Loma.

## Medical Surveillance Methods

Health effects to county residents were assessed through the efforts of San Diego County Health and Human Services Agency, Public Health Services. On Tuesday, October 28, 2003, in response to the fires, smoke, and circulating ashes, a fire-related surveillance process was developed, and by Thursday, October 30, 2003, 15 of the 19 civilian hospital emergency departments in the county (two Navy hospitals were excluded from this surveillance) were asked to participate in this fire-related surveillance. A 3-week surveillance period was established, including 1 week of baseline (pre-event) and 2 weeks following the fires. Because this surveillance was conducted during the fires, the intent was to capture critical information from a limited time period to quickly assess the impact of the fires.

A number of potential fire-related indicators were identified as categories to be monitored. These surveillance categories included the following: asthma, bronchitis, or emphysema; other respiratory conditions with no fever; eye irritation; smoke inhalation; burns; chest pain or cardiac arrests; and diarrhea. The total number of visits made by patients to the hospital was also considered. Each hospital was asked to provide the necessary data to support these surveillance activities.

A standard univariate approach to analysis of the surveillance data using a variety of statistical quality control charts was used in this project. Atypical increases in the number of emergency department (ED) visits, in terms of raw numbers and as a proportion of total ED visits, were monitored with U-charts and P-charts, respectively. Additionally, exponentially weighted moving average (EWMA) charts were generated to detect small shifts in the mean of a variable over time. Time series graphs were generated to evaluate the behavior of the variable over time, and detailed descriptive statistics were inspected to gain insight into the long-term behavior and distributional properties of the variable, including measures of central tendency, dispersion, and degree of normality.

## Estimated Amount of Emissions Computation Method

In a study conducted by the University of California, Berkeley,[3] for the CARB, researchers used the U.S. Department of Agriculture Forest Service First-Order Fire Effects Model

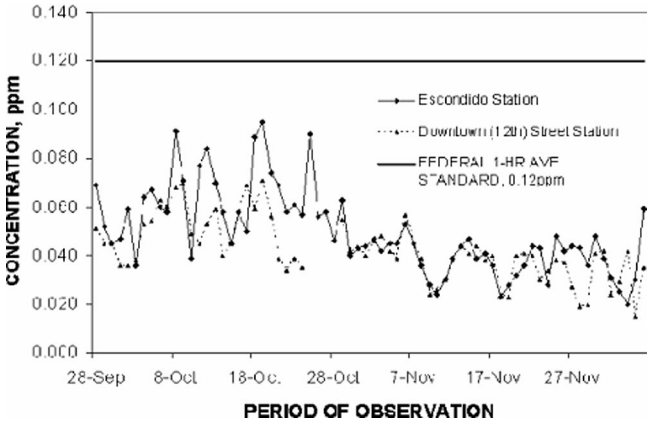


**Figure 4.** $O_3$ daily max. 1-hr average measurements during the surveillance period.

(FOFEM), adapted to run in a Geographic Information System, to assess the fuels that contributed to the fires and the emission amounts and components that resulted from the combustion. The model requires the following inputs: (1) a spatial fuel, vegetation, or land cover map, which should contain vegetation types that can be linked to the FOFEM fuel model library to determine preburn fuel loadings in terms of tons per acre; (2) a fuel model look-up table, which is a relational database table that contains characteristic loadings in several fuel categories and a link to the vegetation-type map that establishes the loadings to be used for each vegetation type; (3) a fire perimeter map, which establishes the spatial extent of the burn area and can be decomposed temporally (into daily perimeters, for example) if those data exist; and (4) user-defined parameters of fuel moisture, seasonality, and fuel loadings.

## RESULTS AND DISCUSSION

Data on pollutants between the period of September 28 and December 6, 2003, from Escondido, downtown (12th Avenue), Kearny Mesa (Overland Avenue), and Alpine monitoring stations were analyzed. The Escondido and downtown stations provided gaseous pollutants and $PM_{2.5}$ data. The $PM_{10}$ data from Alpine station and gaseous pollutant data from Kearny Mesa station, along with meteorological data recorded by San Diego APCD RWPs and RASS located in Miramar and Point Loma were analyzed. Statistical analysis of medical surveillance data compiled by San Diego County Health and Human Services Agency in collaboration with area hospitals was used

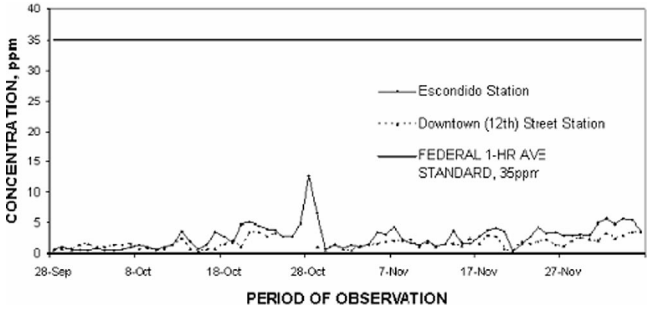


**Figure 5.** CO federal 1-hr average standard measurements during the surveillance period.

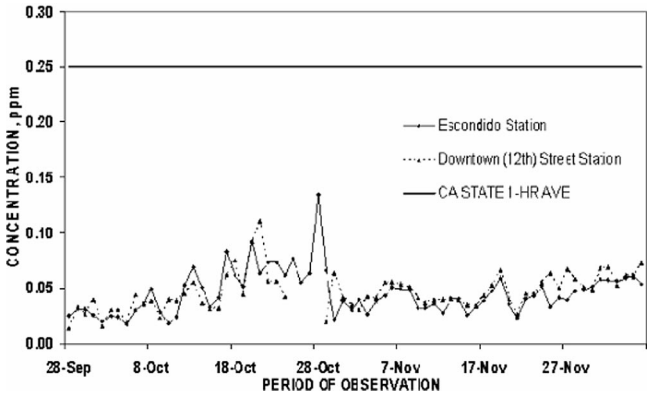


**Figure 6.** $NO_2$ California State 1-hr average standard measurements during the surveillance period.

to establish correlations between pollutant levels in the region and resultant health problems experienced by the county citizens.

### PM

*$PM_{2.5}$.* The $PM_{2.5}$ trend during the observation period is shown in Figure 2. On October 27, 2003, during the fire, the $PM_{2.5}$ U.S. Environmental Protection Agency (EPA) limit of 65 $\mu g/m^3$ was exceeded in the Escondido station. This measurement was recorded by the FRM monitor. The recorded readings during the period before and after the fire episode did not exceed the EPA limit. The data plot before and after the fire episode reveals a consistent trend.

The $PM_{2.5}$ trend during the observation period in the downtown station is shown in Figure 2. During the fire episode on October 26, 2003, the first full day of the fire, $PM_{2.5}$ daily 24-hr average measurement rose sharply to 104.6 $\mu g/m^3$. On October 27, 2003, $PM_{2.5}$ daily 24-hr average measurement recorded was >2.5 times the EPA limit at 170 $\mu g/m^3$. However, similar to the Escondido station, the EPA limit was not exceeded during the surveillance period, the period before and after the fire episode. The data plot revealed a consistent trend before and after the fire episode.

*$PM_{10}$.* The Alpine station monitors real-time $PM_{10}$ using the TEOM monitor. The $PM_{10}$ trend measurement for the

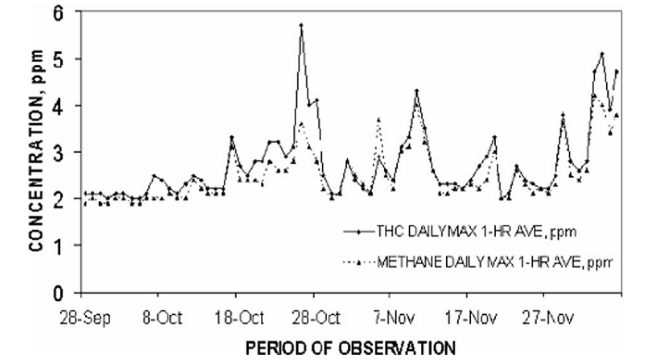


**Figure 7.** $CH_4$ and total THC measurement at the Overland station (Kearny Mesa) during the surveillance period.

**Figure 8.** Photograph of the localized turbulence near the fire.

Alpine station is shown in Figure 3. There was no real-time measurement recorded between October 27 and November 2, 2003, because power supply to the Alpine monitoring station was interrupted by the fire. Just before data recording was lost, the trend showed a steady increase, although it did not reach the maximum 24-hr average federal standard of 150 $\mu g/m^3$. However, the FRM $PM_{10}$ measurement from the Escondido station recorded 179 $\mu g/m^3$ on October 29, 2003. This level exceeded the federal maximum 24-hr average limit. Therefore, it could be inferred that if the Alpine real time monitor was functional at that time, it would have recorded a much higher concentration because of its close proximity to the fire. Real-time measurement indicated an unusually high concentration of $PM_{10}$ on November 23 and 27, 2003, at 294 $\mu g/m^3$ and 184 $\mu g/m^3$, respectively. This was because of the Santa Ana wind condition during that time frame. The strong offshore wind direction stirred and carried the ashes deposited in the burned areas.

## Gaseous Pollutants

Three gaseous pollutants of concern namely $O_3$, CO, and $NO_2$ were analyzed at the Escondido and downtown (Twelfth Avenue) stations based on data recorded by the station monitoring equipment. No data were available between October 25 and October 28, 2003, the period when the fires were burning. The station equipment monitoring these parameters was powered down to support construction efforts of the ballpark nearby.

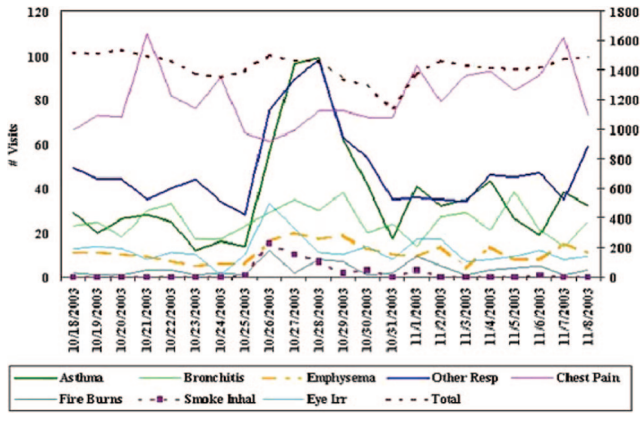


**Figure 9.** Frequency of selected types of visits to San Diego hospital EDs.

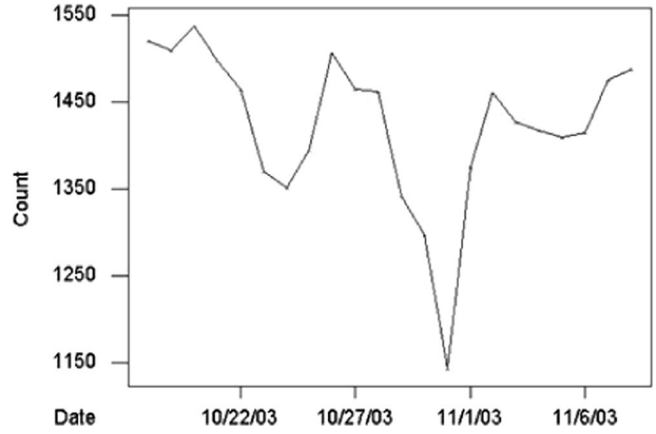


**Figure 10.** Time-series plot for total visits (interval: October 18–November 8, 2003).

*$O_3$.* The $O_3$ trend during the observation period is shown in Figure 4. Throughout the surveillance period, the federal 1-hr $O_3$ concentration of 0.12 ppm was not exceeded on either the Escondido or downtown station. The trend showed a relative decrease in concentration after the start of the fire and continued until the end of the surveillance period.

*CO.* The CO trend during the surveillance period at the Escondido and downtown stations is shown in Figure 5. Recorded data showed that CO concentrations before, during, and after the fire were well below and did not exceed the federal 1-hr standard of 35 ppm. However, on October 28, 2003, the state and federal 8-hr standard was exceeded by 1.6 ppm over the 9-ppm maximum.

*$NO_2$.* The $NO_2$ trend during the surveillance period in Escondido station is shown in Figure 6. There is no federal 1-hr maximum concentration for $NO_2$. However, the state of California mandates a 1-hr maximum concentration

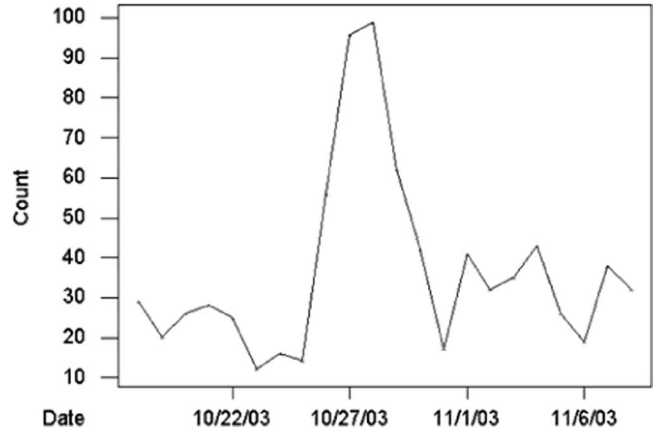


**Figure 11.** Time-series plot for asthma. (interval: October 18–November 8, 2005)

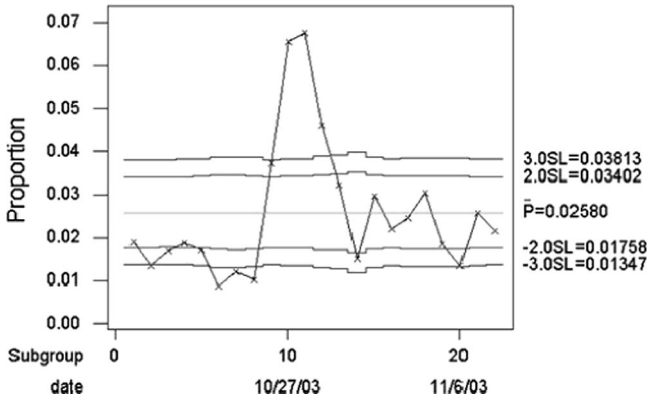


**Figure 12.** P-chart plot for asthma (interval: October 18–November 8, 2003).

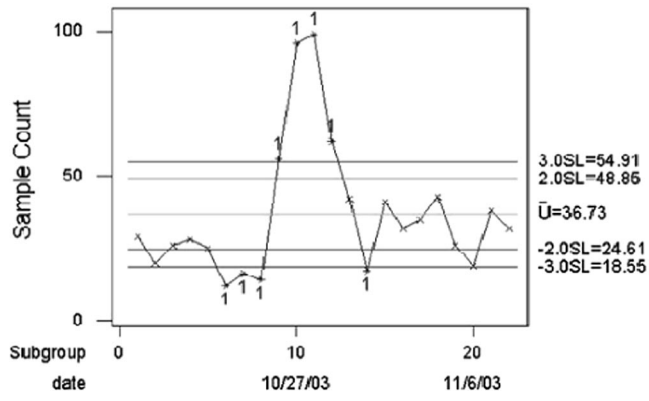


**Figure 13.** U-chart plot for asthma (interval: October 18–November 8, 2003).

level for $NO_2$ of 0.25 ppm. Recorded data showed that $NO_2$ concentrations before, during, and after the fire did not exceed the California state 1-hr standard of 0.25 ppm in both the Escondido and downtown stations.

*$CH_4$ and THC.* The $CH_4$ and THC trend during the surveillance period is shown in Figure 7. The Overland Avenue station is the station closest to the Cedar Fire in which $CH_4$ and THC were measured.

## Meteorological Influence

The San Diego APCD forecasted for a moderate level of $PM_{2.5}$ throughout the county from Saturday, October 25, 2003, through Sunday, October 26, 2003, because of the Santa Ana winds. Santa Ana winds are warm, dry winds that blow from the east (offshore) and have wind speeds >25 knots (12.9 m/sec). The Cedar Fire began at ~5:30 p.m. on Saturday, October 25, 2003. On Saturday evening, at ~7:30 p.m., data recorded by the San Diego APCD RWP indicated a wind direction shift that was consistent with Santa Ana condition.

Although on October 26, 2003, the fire was driven in the southwest direction by the Santa Ana winds, there was no significant surface smoke impact except in the areas immediately around the fire. The wind condition near the coast was not strong. The Point Loma RASS recorded a shallow mixed layer during the morning followed by a weak neutral atmosphere later in the day. These conditions were not conducive to heavy smoke impacts at the surface level from a lofted plume of smoke.

As the first full day of the fire progressed on October 26, 2003, conditions in the close proximity of the fire recorded a different result. Throughout the morning, the fire advanced rapidly in a southwesterly direction and burned the heavily populated communities of Poway, Miramar, and Tierrasanta. Flames and a vortex of heavy smoke prevailed in the vicinity of the fires, particularly downwind and on the leading edge of the fire. Figure 8 shows the localized turbulent condition as the wind fanned the fire. In addition, the intense fire produced its own circulation, an indication of a firestorm.

The Santa Ana wind condition decreased in strength toward the end of the day on October 26, 2003. Consequently, the westward progression of the fire was either stopped or was put under control. At dawn of October 27, 2003, the fire progression was shifted toward the east, away from major population centers and into the mountain communities. Data recorded on October 27, 2003, showed offshore winds aloft during the first half of the day followed by a turning of the winds to weak onshore in the early afternoon and then general stagnation conditions during the evening and nighttime. At the same time, the recorded data showed an isothermal atmosphere during the early morning with surface-based inversion forming later in the day. These meteorological conditions were more conducive to trapping smoke in the surface layer.

On October 28, 2003, the data recorded showed wind conditions becoming stagnant during the day with low-level winds becoming southerly in the evening. The data also showed a surface-based inversion during most of the day. These stable conditions were conducive for trapping the smoke in the surface layer. Even as the fires continued burning eastward into the more rural areas of the county, satellite imaging taken by the National Oceanographic and Atmospheric Administration showed an abrupt stop and slow smoke movement offshore.

Data recorded on Wednesday, October 29, 2003, showed southerly winds in the low levels during the early morning hours, turning to offshore during the day and south-southwest and southerly winds at night. For the same day, the recorded data showed a shallow marine layer capped by an inversion that lifted during the day and dissipated at night. These conditions were consistent with air mass change and improved air quality conditions. Although the fires continued to burn in the inland, mountain areas of the county, similar meteorological conditions continued until the fire was out on November 4, 2003.

## Medical Surveillance

During the surveillance period, 15 of the 19 hospitals (79%) participated by providing the following surveillance information from October 18 through November 8, 2003: (1) number of patients admitted to the hospital; (2) date of admission; and (3) type of medical problems encountered (asthma, bronchitis, emphysema, other respiratory problems, and/or chest pain).

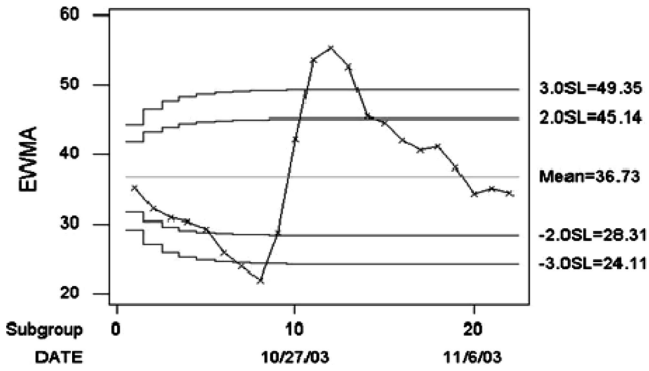


**Figure 14.** EWMA plot for asthma (interval: October 18–November 8, 2003).

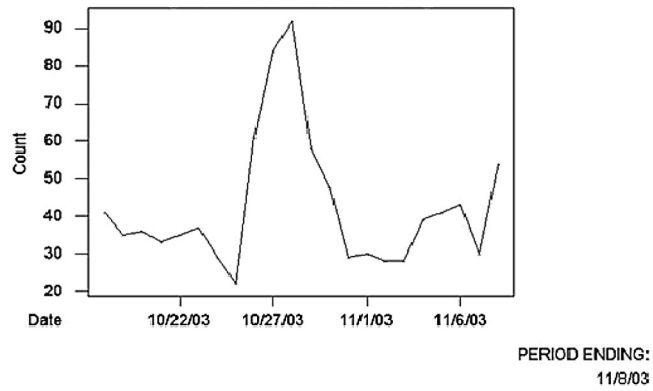


**Figure 15.** Time-series plot for other respiratory conditions with no fever (interval October 18–November 8, 2003).

The participating hospitals represented geographic diverse locations and included several hospitals near the fire-impacted areas. As seen in Figure 9, several of the surveillance indicators increased significantly during the periods of the fire. The most dramatic increase was asthma and other respiratory complaints with no fever. Each of the surveillance indicators is additionally described below.

*Total Visits*. The impact of the fires on area ED visits varied across hospitals. In total, information on 31,321 visits was recorded and analyzed. For the surveillance time period, the mean number of cases was 1423 visits per day among 15 hospitals. In general, the total number of ED visits declined (Figure 10) during selected periods of the fire. The day with the minimum number of total visits was October 31, 2003. The period of greatest decrease in total volume of patients corresponds with the days that the schools and employees were asked to remain at home (October 27–31, 2003). When the total visits were analyzed using the EWMA method, the mean number of total visits continued to remain lower for over a week after the fires began. During this period, the moving average decreased substantially.

*Asthma*. Several respiratory indicators were monitored at EDs throughout the county, and related visits were assessed. In general, each of the respiratory indicators demonstrated significant increases during the fire period with expected postfire levels approaching prefire levels with the decline in the fires and subsequent improvement in air quality.

Asthma-related visits increased significantly, particularly during the days of greatest fire burn and unhealthy air quality. Both the total number of asthma visits and the proportion of asthma visits increased. These increases correspond well with the increases in the air quality index. Figure 11 displays the number of asthma-related visits over time with the days of greatest number of asthma-related visits occurring on Tuesday, October 28. Controlling for the total number of visits, Figure 12 includes the proportion of asthma-related visits during the surveillance period. Additional information about the asthma-related results are detailed in Figures 13 and 14.

*Bronchitis*. Bronchitis-related visits were monitored, and they showed a slight increase during the surveillance period when they were measured using the same methodology as the one used for asthma-related cases. The mean number of cases across all of the participating hospitals was 25 per day. Although a slight increase in bronchitis-related visits was noted in each of the analyses, the increase was neither significant nor sustained.

*Other Respiratory with No Fever*. The surveillance category for other respiratory illness/problems with no fever-related visits were analyzed. The intention of this indicator was to track people with a multitude of respiratory-related symptoms not previously identified as asthma, bronchitis, or respiratory illness that occur along with fever, such as influenza and pneumonia. A dramatic increase in visits with complaints primarily associated with the other respiratory illnesses without fever observed after the beginning of fires on October 25 is likely a direct result of the increasingly poor air quality. Analysis of this indicator reveals that both the total number of visits and the proportion of visits increased significantly, particularly during the days of greatest fire burn and ash fallout (Figures 15 and 16, respectively).

*Smoke Inhalation*. Because of the large area of fire burn in both densely and rural populated areas, it was expected

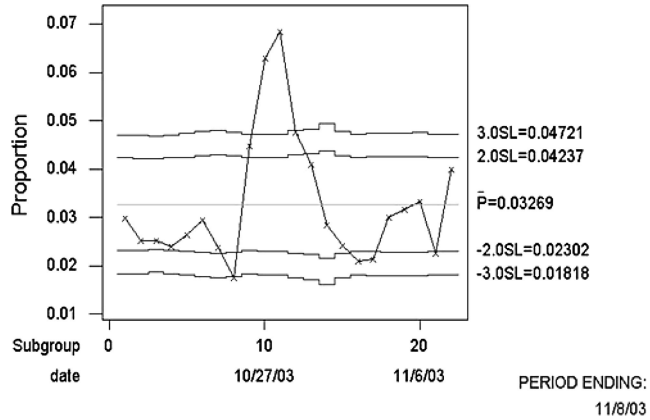


**Figure 16.** P-chart plot for other respiratory conditions with no fever.

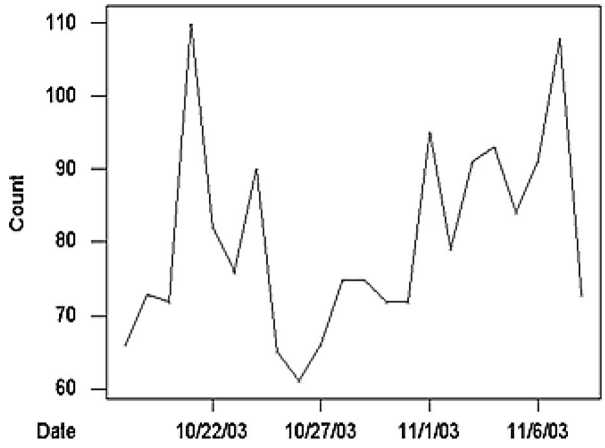


**Figure 17.** Time series plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

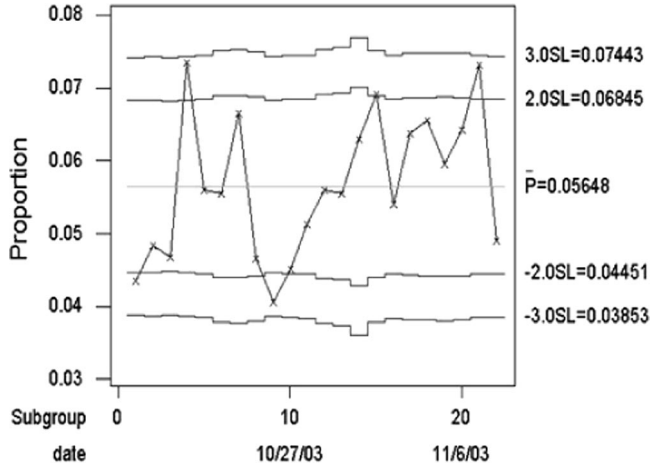


**Figure 18.** P-chart plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

that hospitals would experience a number of patients with smoke inhalation. Although the overall number of smoke inhalation-related visits across participating hospitals was small each day during the surveillance period, smoke inhalation-related visits increased markedly. Both the total number of smoke inhalation visits and the proportion of visits increased for a brief period during the periods of greatest fire burn.

*Eye Irritation.* Because of several days of large ash fall throughout San Diego County, it was expected that a number of patients would seek treatment for eye irritation at EDs. The indicator for eye irritation was analyzed. Although very few patients experiencing eye irritation problems were reported during the prefire period, a brief increase in those with eye irritation occurred during the days of greatest fire burn and ash fallout.

*Chest Pain/Cardiac Arrest.* Because of the uncertainty of determining how the fire and air quality would impact patients suffering from chest pain or cardiac arrest, an indicator was selected to assess the same during the surveillance period. The indicator for chest pain was analyzed. As seen in Figures 17 and 18, the number of chest pain and cardiac arrest visits does not appear to have noticeably increased as a result of the fire. Figure 19 describes the U-chart and Figure 20 describes the EWMA during this time. Although the time period is limited to ~3 weeks, it is difficult to determine whether this pattern is typical during nonfire periods.

*Diarrhea/Gastroenteritis.* During the fires, selected parts of the county were without power for several days. Because of the increased chance of people consuming spoiled food or contaminated water, an indicator for diarrhea/gastroenteritis was monitored. This indicator was analyzed using the same criteria explained before. In general, diarrhea-related visits during this surveillance period did not increase or decrease from the usual trend.

### Sources and Estimated Amount of Emissions

The estimated prefire fuel loading for the Cedar and Paradise fires, the predominant fires that occurred about the same time, is shown in Table 2. Table 3 shows the estimated emission amounts of selected pollutants. The data

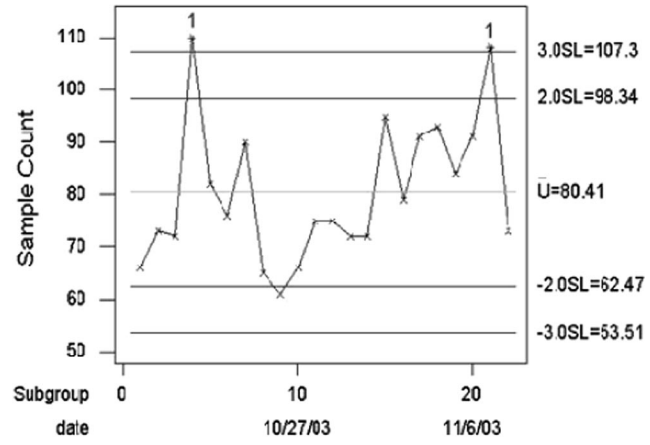


**Figure 19.** U-chart plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

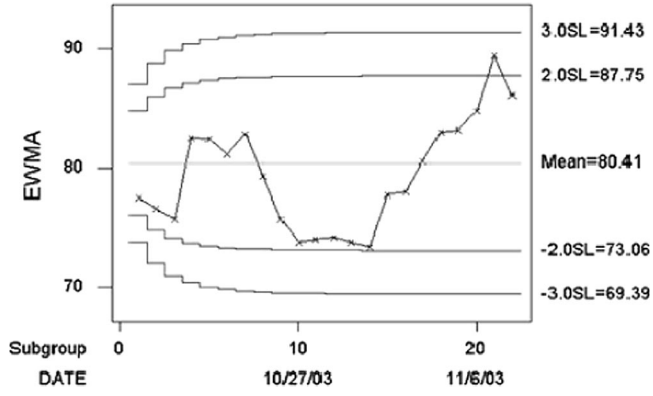


**Figure 20.** EWMA plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

**Table 2.** Estimated prefire fuel loading in tons.

| Fuel Component | Paradise Fire | Cedar Fire | Total Both Fires |
|---|---|---|---|
| Canopy branch wood | 0 | 12,104 | 12,104 |
| Canopy foliage | 0 | 85,399 | 85,399 |
| Duff | 86,059 | 509,287 | 595,346 |
| Herbs | 6562 | 43,983 | 50,545 |
| Litter | 27,458 | 151,329 | 178,814 |
| Regen | 286 | 3447 | 3733 |
| Shrubs | 321,020 | 1,585,703 | 1,906,723 |
| Wood 0–1 inch | 2861 | 23,483 | 26,344 |
| Wood 1–3 inch | 0 | 12,115 | 12,115 |
| Wood >3 inches | 0 | 87,059 | 87,059 |
| Total all fuel types | 444,246 | 2,513,909 | 2,958,155 |

output for preburn conditions and emissions tabulated in Tables 2 and 3 was based on the Cedar and Paradise fire perimeter input and processed by the FOFEM. The model determined the emissions based on the moisture content of the fuel and the moisture in the burning environment and the preburn fuel loading from the fuel models.[3]

## CONCLUSIONS

On the first full day of the San Diego Wildfire on October 26, 2003, the Overland Avenue station recorded the highest THC concentration level, about twice the average concentration of the period before the fire. THC is a precursor to the formation of ground-level $O_3$. However, the meteorological condition during this phase of the fire progression was such that the heavy smoke produced by the fire was allowed to rise and blanket the entire county. Photochemical reaction provided by sunlight did not happen. Therefore, $O_3$ levels on this day and subsequent days during the fire remained below the allowable levels set by EPA at 0.12 ppm.

The CO concentration level rose by 250% on October 28, 2003, at the Escondido station, the highest recorded level during the fire and during the surveillance period, which slightly exceeded the state and federal 8-hr average. There was a 100% increase in the $NO_2$ level recorded on October 28, 2003, at the Escondido station. However, this level is within the allowable limit of 0.25 ppm according to the California state daily maximum 1-hr average standard. Although there were no data available on $O_3$, CO, and $NO_2$ at the downtown station on October 25–28, 2003, other stations that monitor these pollutants of concern did not record concentrations that exceeded the allowable limits during the entire period that the downtown station was offline.

**Table 3.** Emissions mass estimate totals, in tons.

| Pollutant | Paradise Fire | Cedar Fire | Total Both Fires |
|---|---|---|---|
| $PM_{10}$ | 3951 | 22,610 | 26,561 |
| $PM_{2.5}$ | 3,354 | 19,188 | 22,542 |
| CO | 38,963 | 222,190 | 261,153 |
| $CH_4$ | 1558 | 8886 | 10,444 |
| TNMHC | 2727 | 15,549 | 18,276 |
| $NH_3$ | 388 | 2221 | 2609 |
| $N_2O$ | 69 | 399 | 468 |
| $NO_x$ | 1198 | 6958 | 8156 |
| $SO_2$ | 371 | 2147 | 2518 |

TNMHC = total non-$CH_4$ hydrocarbon.

The meteorological condition that allowed the heavy smoke to lift and create a thick blanket that turned day almost into night let the PMs settle over most of the county. Consequently, the downtown and Escondido stations recorded the highest level of $PM_{2.5}$ concentration. The downtown station recorded a $PM_{2.5}$ concentration of 104.6 $\mu g/m^3$ on the first full day of the fire on October 26, 2003, and 170.1 $\mu g/m^3$ on October 27, 2003. The Escondido station recorded a 69.2 $\mu g/m^3$ $PM_{2.5}$ concentration on October 27, 2003. All of these readings exceeded the federal daily maximum 24-hr average.

The ability of the fire to create a localized weather condition, such as a different wind pattern from the general prevailing condition, suggests that actual levels of pollutants in random points within the surveillance area may vary from measured levels recorded by the monitoring stations. During the fire, actual air quality depended on where one was located in the affected areas of the county. This also accounted for the variance in the concentration levels above the allowable range for those pollutants that exceeded established standards as recorded in different monitoring stations.

Meteorological conditions that allowed for massive air mass change, such as that which began to prevail on October 29, 2003, during the fire, helped mitigate the effects of pollutants to affected areas. This was indicated by the decrease in concentration of pollutants to allowable levels and the decrease in ED admissions during the surveillance period.

The total number of ED visits declined during the period of the fire, and these correspond with the days that the school children and employees were asked to remain at home. In addition, many roads and freeways were closed because of the fires. Each of these is likely to have influenced the behavior of people seeking treatment or refuge at local EDs. These results presented in the medical surveillance demonstrated that selected increases in certain types of ED visits did occur during this period. Particularly, selected respiratory-related conditions increased significantly. Communication with various medical providers during the fires indicated that the ash, smoke, and unhealthy air quality resulted in an increase in asthma-related medical visits and inquiries.

There are a number of limitations associated with an assessment related to the disaster. The medical surveillance was primarily based on the chief complaint of the patient on arrival at the ED. Because this is not the final diagnosis of the patient's reason for visit, it is possible, although unlikely, that the final results may have been slightly different from that presented by this study. Additional studies are needed to additionally assess the impact of the fire on ED utilization trends, long-term impact of the fire on health outcomes, and the effect of a local disaster on health service options.

The results indicated that there was a direct correlation between the increase in PM, specifically $PM_{2.5}$, concentration level and the significant increase in ED visits for asthma, other respiratory with no fever, eye irritation,

and smoke inhalation. The pattern for increase in emergency visits for asthma was consistent with documented studies from previous wildfires[36] in which there was a 1–1.5-day lag between the periods of exposure to high concentrations of PM from wildfires to the actual time of admission.

The FOFEM results indicated that shrubs and duff were the predominant sources of combustion, totaling ~2.5 million t or ~85% of the fuel components of the San Diego wildfire. Clearly, these were catastrophic fire events that burned, for the most part, in chaparral and other shrub-dominated ecosystems.[3]

## RECOMMENDATIONS

The following recommendations are made in the event a similar catastrophe occurs in the future: (1) improve the capability of accurate real-time monitoring of PMs, because it is the pollutant of concern that has an immediate impact on the health of county residents; mobile monitoring capability is an added resource, because it can better assess the actual condition independent of prevailing meteorological condition; (2) encourage hospitals and emergency medical facilities to engage in preevent planning that would ensure a rapid response to an impact on the healthcare system as a result of a large wildfire; and (3) use all available meteorological forecasting resources, including real-time satellite imaging assets to accurately forecast air quality, assist firefighting efforts, and mobilize emergency service providers.

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PLOS ONE

RESEARCH ARTICLE

# Residential development alters behavior, movement, and energetics in an apex predator, the puma

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## Abstract

Human development strongly influences large carnivore survival and persistence globally. Behavior changes are often the first measureable responses to human disturbances, and can have ramifications on animal populations and ecological communities. We investigated how a large carnivore responds to anthropogenic disturbances by measuring activity, movement behavior, and energetics in pumas along a housing density gradient. We used log-linear analyses to examine how habitat, time of day, and proximity to housing influenced the activity patterns of both male and female pumas in the Santa Cruz Mountains. We used spatial GPS location data in combination with Overall Dynamic Body Acceleration measurements recorded by onboard accelerometers to quantify how development density affected the average distances traveled and energy expended by pumas. Pumas responded to development differently depending on the time of day; at night, they were generally more active and moved further when they were in developed areas, but these relationships were not consistent during the day. Higher nighttime activity in developed areas increased daily caloric expenditure by 10.1% for females and 11.6% for males, resulting in increases of 3.4 and 4.0 deer prey required annually by females and males respectively. Our results support that pumas have higher energetic costs and resource requirements in human-dominated habitats due to human-induced behavioral change. Increased energetic costs for pumas are likely to have ramifications on prey species and exacerbate human-wildlife conflict, especially as exurban growth continues. Future conservation work should consider the consequences of behavioral shifts on animal energetics, individual fitness, and population viability.

## Introduction

Habitat conversion is a primary driver of species extinctions and increases exposure of wildlife to anthropogenic disturbances [1]. These disturbances influence many integral animal behaviors (e.g., foraging, mating, and movement) [2] and transform species interactions [3–4].

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Conversion to low-density development at the wildland-urban interface is the fastest growing type of land use change in the continental United States [5] and is expected to continue expanding in the coming decades [6]. Although many species, including mammalian apex predators, continue to live at the wildland-urban interface [7], these regions may prove to be population sinks due to the increased risk of human-caused mortality or from the costs of adopting behavioral adaptations in response to human disturbances [8].

Behavioral changes by animals often provide the first measurable indication that individuals are responding to anthropogenic disturbance [9–11]. These behavioral responses can alter energetic budgets with important effects on individual fitness that may lead to population and community level changes. Movement behavior in particular carries rich information about where, when, and how an animal interacts with its surroundings, providing insight into the relationship between internal state and environmental factors [12]. Technological advances with GPS and accelerometer tracking devices now allow scientists to link animal movement behavior to caloric expenditure, which greatly increases our understanding of how animal energetics are impacted by human development at the landscape level. With the integration of accelerometers and traditional biologgers, we can monitor how natural and anthropogenic landscape structures change behavioral patterns and energy allocation in wild animals [13], with far ranging conservation implications for species living at the wildland-urban interface.

Large carnivores are frequently the first species to be lost from ecosystems as humans transform and develop landscapes [14]. Despite this, comparatively little is known about the behavioral and energetic responses of predators to development that could eventually lead to their local extirpation [15]. Large carnivores often respond to human disturbance and persecution through behavioral modifications much like prey species respond to predators [10]. Pumas (*Puma concolor*) have demonstrated behavioral responses to human developments by avoiding roads, moving quickly through developed areas, and changing temporal feeding patterns [8,16]. As human development continues to fragment previously intact landscapes, it becomes increasingly vital to understand how large carnivores adjust their behavior and energetic responses to anthropogenic perturbations. Only by better understanding these relationships can we implement protective policies that reduce human-wildlife conflict and promote their continued co-existence with humans [17].

Here we examined how human development alters daily behavior and energetics of pumas in the Santa Cruz Mountains of central California. We investigated the extent to which proximity to houses affected puma movements and daily activity budgets. These behavioral differences translate into differential energetic costs that progressively accumulate over time, which may have lasting repercussions on individual fitness[18]. We also investigated whether habitat type and time of day influenced how pumas responded to human development. In order to link behavior change to energetic impacts, we evaluated how human development affected the daily movement patterns and caloric expenditures of pumas using GPS tracks, which we calibrated using accelerometer data from a much finer temporal scale. Lastly, we explored the extent to which puma prey demands are altered in human-modified habitats and discuss potential consequences for recruitment of future generations.

## Methods

### Study species and area

Pumas are territorial, apex predators which live throughout diverse habitats in the Americas [19]. Individuals are primarily nocturnal and solitary, although females will typically raise and accompany cubs for up to 15–21 months after birth. In our study area in the Santa Cruz Mountains of California, pumas predominantly feed on black-tailed deer (*Odocoileus*

*hemionus columbianus*, 90% by biomass), but occasionally on other species, including wild boars (*Sus scrofa*), raccoons (*Procyon lotor*) and house cats (*Felis catus*) [20].

Our 1,700 $km^2$ study area encompasses a diverse landscape ranging from dense, urban development to large tracts of intact and relatively undisturbed native vegetation. Puma home ranges contain both protected and developed lands, with an average home range housing density of 21.7 ± 3.0 SE houses/$km^2$ (range 4.6–51.5) [8]. Even pumas that regularly move through or near residential areas also use nearby protected areas, allowing for comparison of movement behavior across a disturbance gradient within individual pumas. The vegetation is primarily forested (e.g., woodlands, hardwood and conifer forests) and shrubland (e.g., scrub and chaparral) habitats. It is bisected by a large freeway and further crisscrossed by numerous other smaller roads providing access to rural houses and developments. The climate is Mediterranean, with precipitation concentrated between November and April, and elevation ranges from sea level to 1155m.

## Data collection

We captured 22 wild pumas (11 males, 11 females) from June 2010—March 2013 using trailing hounds, cage traps, or leg hold snares. Each animal was tranquilized using Telazol at a concentration of 100mg/mL (3.3–6.0 mg/kg estimated body weight) and outfitted with a GPS/VHF collar (3.7 kg; Model GPS Plus 1D, Vectronics Aerospace, Berlin, Germany). Six of the 22 animals were also equipped with a custom-built archival 3-axis accelerometer sampling continuously at 64Hz when activated [21]. The tri-axial accelerometer was mounted such that the x-axis was parallel to the anterior-posterior plane of the animal, the y-axis to the transverse plane, and the z-axis to the dorsal-ventral plane.

Accelerometers on pumas were programmed to record at a duty-cycle of 2 days on and five days off to maximize battery life. The GPS was programmed to acquire locations every 15 minutes during a 24-hour intense sampling period starting from noon one day each week. The Animal Care and Use Committee at UC Santa Cruz approved all animal-handling procedures (Protocols Wilmc0709 and Wilmc1101).

## Data processing

During each 15-minute GPS sampling interval, we assigned one behavioral state (active or inactive) to each collared individual and considered these states to be mutually exclusive. We considered any distance greater than 70m between successive 15 minute GPS fixes to be an active period, and a distance smaller than 70m to be an inactive period. We used accelerometer measurements to determine the distance cutoff between activity states as follows. We used a random forest algorithm described in Wang et al. [22] to categorize 2-second increments of accelerometer measurements into mobile or non-mobile behaviors. These were then aggregated into 15-minute observation periods to match the GPS sampling periods. After inspecting the data visually, we identified 10% activity (i.e., 10% of accelerometer measurements categorized as mobile out of 15 minutes) as the cutoff between active and inactive periods. Because of the strong linear relationship ($r = 0.89$) between accelerometer defined activity and the distance traveled between GPS fixes, 10% activity recorded by accelerometers corresponded to 70 meters between GPS fixes.

## Environmental and anthropogenic measurements

Our study animals inhabit a landscape primarily comprised of forested or shrubland habitats interspersed with developed areas. To examine how human development and habitat type affected puma behavior, we collected spatial information on buildings and habitat types

surrounding each puma GPS location. Using the Geographic Information Systems program ArcGIS (v.10, ESRI, 2010), we digitized house and building locations manually from high-resolution ESRI World Imagery basemaps for rural areas and with a street address layer provided by the local counties for urban areas. For each puma GPS position recorded, we calculated the distance in meters to the nearest house. We placed circular buffers with 150m radii around each GPS location and used the California GAP analysis data [23] to categorize the local habitat as either predominantly forested or shrubland. We chose a buffer size of 150m based on a previous analysis of puma movement responses to development [24].We also classified the time each GPS location was recorded as diurnal or nocturnal based on sunset and sunrise times.

## Markov chains

We modeled puma behavior sequences as discrete-time Markov chains, which are used to describe activity states that depend on previous ones [25]. Here, we used first-order Markov chains to model a dependent relationship between the succeeding behavior and the preceding behavior. First-order Markov chains have been successfully used to describe animal behavioral states in a variety of systems, including sex differences in beaver behavior [26], behavioral responses to predators by dugongs [27], and impacts of tourism on cetacean behavior [28–29]. Because we were modeling behavior transitions with respect to spatial characteristics, we recorded the states of the puma (active or inactive) in the 15 minutes prior to and succeeding each GPS acquisition. We populated a transition matrix using these preceding and succeeding behaviors and examined whether proximity to houses influenced the transition frequencies between preceding and succeeding behavior states. Transition matrices are the probabilities that pumas remain in a behavioral state (active or inactive) or transition from one behavior state to another.

We built multi-way contingency tables to evaluate how sex (*S*), time of day (*T*), proximity to house (*H*), and habitat type (*L*) affected the transition frequency between preceding (*B*) and succeeding behaviors (*A*). Because high-dimensional contingency tables become increasingly difficult to interpret, we first used log linear analyses to evaluate whether sex and habitat type influenced puma behavior patterns using two three-way contingency tables (Before × After × Sex, abbreviated as BAS). Log linear analyses specifically test how the response variable is influenced by independent variables (e.g., sex and habitat) by using Likelihood Ratio Tests to compare hierarchical models with and without the independent variable [25]. We found that there were strong sex differences in activity patterns because adding *S* to the model greatly increased the goodness-of-fit ($G^2$) compared to the null model ($\Delta G^2 = 159.8$, d.f. = 1, $P<0.0001$), which assumed that succeeding behaviors only depend on preceding ones. Therefore, we evaluated data from male pumas separately from those of female pumas.

We then used another three-way contingency table for each sex to evaluate whether behavior patterns differed between habitats (*L*). We found that including habitat type significantly improved model fit for male ($\Delta G^2 = 7.9$, df = 1, $P<0.005$) but not female pumas ($\Delta G^2 = 3.18$, df = 1, $P = 0.0744$). Thus we evaluated three sets of data: all females, males in forests, and males in shrublands. For each dataset, we created four-way contingency tables (Before × After × House × Time) to evaluate how development and time of day affected behavioral transitions using the likelihood ratio methods described above.

Our null model (*BA*, *BHT*) is built such that succeeding behaviors (*A*) are only affected by behaviors in the previous time steps (*B*) and independent of proximity to houses and time of day. We tested whether including additional factors (proximity to house and time of day) improved model fit by comparing the null model with hierarchically more complex models. For example, the effects of proximity to housing on succeeding behaviors are evaluated by

comparing the goodness-of-fit ($G^2$) values for the null model and the model containing an interaction between succeeding behaviors and houses (*BAH*, *BHL*). We also tested the interaction between proximity to houses and time of day by comparing the saturated model (*BAHT*), which fits the data fully, to a less complex model without the interaction term (*BAH*, *BAT*, *BHT)*. Finally, we selected the best fitting model by minimizing the Akaike Information Crtierion (AIC) estimate.

## Behavioral budgets

We tested whether transition matrices differed when pumas were close to houses or roads using the Z test for proportions [30]. We also estimated the amount of time pumas spent in each behavioral state by conducting an eigenanalysis on the transition matrix. Because Markov chains are ergodic matrices, we used the left eigenvector of the transition matrix to estimate the proportion of time pumas spent in each state [25]. We compared these values using a Z test of proportions and calculated 95% confidence intervals using the Wilson's score test [31].

## Puma travel and energetic costs

For each puma, we identified all 24-hour intensive sampling periods during which GPS points were recorded every 15 minutes. At a fix rate of 4 times an hour, up to 96 GPS points are recorded throughout the day, equating to a total of 95 travel segments (straight lines between consecutive points). We removed any days from analyses that were missing more than 10% (i.e., 9 points) of potential GPS fixes. We determined the linear length of all travel segments and calculated the total daily distance (*D*) in km traveled by pumas by summing all travel segments and correcting for any missing GPS fixes using the formula:

$$D_{total} = D_{summed} \times 95/n \tag{1}$$

in which n represents number of actual recorded segments. Next, we calculated the minimum cost of transport (*COT*, W/kg) expended daily for each puma by adapting the equation developed by Taylor et al. [32]:

$$\mathrm{COT} = \sum_{\mathrm{i}}^{\mathrm{n}} 10.7(\mathrm{wt})^{-0.316} \times \mathrm{v_i} + 6.03(\mathrm{wt})^{-0.303} \tag{2}$$

in which *wt* is the weight (kg) of the animal when captured and $v_i$ is the velocity of travel (m/s) between consecutive GPS points. *COT* has the units Watts/kg, which we converted to kcal/kg by applying the conversion factor 4.1868 Watt = 1 cal/s.

Lastly, we estimated the minimum number of black-tailed deer, the primary prey of pumas in our area, needed to sustain each puma given their daily minimum *COT*. We calculated the daily deer biomass (*DB*) needed to fulfill each puma's prey requirements using Eq 3 [33]:

$$DB\left(\frac{kg}{day}\right) = \frac{COT\ (kcal)}{1890\left(\frac{kcal}{kg}\right) \times 0.86 \times 0.88} \tag{3}$$

in which 1890 kcal represents the caloric content in each kg of wet deer tissue [34], and this value is then modified by multiplying it by the conversion efficiency (0.86) and the proportion of deer in a puma's diet—here estimated as 88% [20]. Finally, we used Eq 4 to convert the daily deer biomass into an estimate of the yearly deer requirements [33]:

$$\frac{Deer}{year} = \frac{DB\left(\frac{kg}{day}\right) \times 365\ days}{36.5\ kg \times 0.79} \tag{4}$$

in which 36.5 kg is the average weight of a black-tailed deer doe [35] and 0.79 is the edible proportion of the deer [34].

It is broadly understood that the energetic estimates generated using the equation developed by Taylor et al. [32] are the minimum estimates for *COT*. Even at 15-minute GPS sampling intervals, animals can deviate greatly from straight-line travel paths, thus expending many more kcals than estimated. In contrast, Overall Dynamic Body Acceleration (ODBA) measurements recorded by accelerometer collars, which sums the dynamic acceleration of the subject across three dimensions, provide a more precise measurement of energetic expenditure because it takes measurements at a rate of 64Hz [36]. Not all pumas were outfitted with accelerometer collars and we were unable to use ODBA alone to estimate energetic budgets. Instead we recorded ODBA values from two wild pumas whose accelerometers were active concurrent to the GPS intensive sampling periods. Using those values, we calculated the correlation between COT estimates from ODBA measurements and those estimated using velocities generated from intensive GPS sampling by Eq 2. This resulted in a correction factor that we applied to the energetic estimates of each puma in the study.

## Development influences on puma movement

To quantify puma exposure to human development, we used ArcGIS (v. 10.1, ESRI, 2012) to create buffers of 150m around all GPS points within each 24-hour intensive GPS sampling period. We then calculated the number of houses encompassed within each buffer polygon and also recorded the time of day. For each day, we recorded the average housing density individual pumas were exposed to and the average distance pumas traveled between successive GPS locations during both nocturnal and diel periods. We hypothesized that pumas would use more calories by moving faster and further through areas with more houses in order to minimize their exposure to development [24,37]. However we also predicted that this relationship might be affected by time of day because pumas may prefer to stay hidden if they are in more developed areas during the day.

We used linear mixed effects models using restricted maximum likelihood estimation with the average diurnal and nocturnal calories burned between successive GPS points as the dependent variable. To select the best model, we used a top-down model selection approach to compare models with no random terms, with random intercepts, and with both random intercepts and slopes [38]. We started by fitting a linear model that included the full complement of fixed effects terms: sex of the puma (male coded as 1 and female as 0), time of day (day coded as 1 and night as 0), the average number of houses (log-transformed to account for all distributions being bound at zero), the interactions between sex and time of day, and the interaction between time of day and housing. In a second model, puma identity was included as a factor in the model to allow for random intercepts. For the third model, we also tested whether individual pumas responded to time of day, the log average number of houses, and their interaction differently by including random slopes for those terms. We used AIC to compare the three models to determine the optimal model structure. We examined the residuals for our final model visually to identify any obvious deviations from normality.

To quantify the difference in puma energetic expenditure between areas with low and high housing density, we calculated the average caloric expenditure by individual pumas in the top and bottom housing density quartiles of their home range for both days and nights. To maximize statistical power, only pumas with a minimum of 20 day and 20 night measurements were included in this analysis. We added day and night averages to get total daily difference in caloric expenditure. We calculated the percentage increase in calories used as the total daily difference between caloric expenditure for high and low housing density divided by the

average daily caloric expenditure for the individual puma. In order to conceptualize variation of human disturbances for individual pumas, we classified average housing density in the top and bottom quartiles into the following categories described by Theobald [5]: rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to1.236 houses per hectare), suburban (greater than 1.236 and up to 9.884 houses/hectare), or no housing. We used the package *nlme* [39] in R (v. 3.0.2, R Core Team, 2013) for all analyses.

## Results

### Log linear analyses

We recorded 78,242 GPS locations for 22 pumas, comprised of 6,967 behavioral transitions (e.g. active to inactive) for males in shrubland habitats, 11,379 transitions for males in forested habitats, and 21,977 transitions for females in all habitats. Log linear analyses revealed that both proximity to houses and time of day influenced puma activity levels, but this effect differed by sex, and by habitat type for males. Proximity to houses and time of day had a significant positive effect on the number of behavior transitions of male pumas in forests (Table 1). However, for males in forests, support for the interaction term (proximity to houses × time of day) was ambiguous because the two models had a ΔAIC of less than 0.2, indicating that they were statistically indistinguishable [40]. AIC comparison revealed that the best models for all female pumas and males in shrublands included the proximity to houses, time of day, and an interaction between the two (Table 1). This indicates that the time of day determined how pumas altered their movement patterns near development, which we discuss next.

**Table 1. Results of log-linear analysis for all puma behavioral transition models.**

| Study Group | Model[ab] | ΔAIC[c] | Components added[a] | $\Delta G^2$, *df*, *P*-value |
|---|---|---|---|---|
| Males, Forests | Null (BA, BHT) | 72.0 | | 84, 6, — |
| | Previous Location × House (BAH, BHT) | 63.8 | BAH | 71.8, 4, 0.002 |
| | Previous location × Time (BAT, BHT) | 2.2 | BAT | 10.2, 4, <0.001 |
| | Previous location × Time + Previous location × House (BAT, BAH, BHT) | 0.01 | BAT | 4.01, 2, 0.001 |
| | | | BAH | 4.01, 2, 0.045 |
| | Time × House (BAHT) | 0.00 | TH | 0, 0, 0.135 |
| Males, Shrubland | Null (BA, BHT) | 53.4 | | 65.4, 6, — |
| | Previous Location × House (BAH, BHT) | 54.0 | BAH | 62, 4, 0.002 |
| | Previous location × Time (BAT, BHT) | 8.4 | BAT | 16.4, 4, <0.001 |
| | Previous location × Time + Previous location × House (BAT, BAH, BHT) | 11.5 | BAT | 15.5, 2, <0.001 |
| | | | BAH | 15.5, 2, 0.64 |
| | Time × House (BAHT) | 0.00 | TH | 0, 0, < 0.001 |
| Females, All habitat | Null (BA, BHT) | 90.8 | | 102.8, 6, — |
| | Previous Location × House (BAH, BHT) | 66.6 | BAH | 76.4, 4, <0.001 |
| | Previous Location × Time (BAT, BHT) | 41.3 | BAT | 49.3, 4, <0.001 |
| | Previous Location × Time + Previous location × House (BAT, BAH, BHT) | 24.5 | BAT | 28.5, 2, <0.001 |
| | | | BAH | 28.5, 2, <0.001 |
| | Time × House (BAHT) | 0.00 | TH | 0, 0, < 0.001 |

[a] A: Succeeding behavior; B: Previous behavior; T: Time; and H: Number of Houses.

[b] In null models, effects of time and number of houses were assumed to be independent of behavioral transitions. Succeeding behaviors (A) are only dependent upon preceding behaviors (B), and not on time of day (T) or proximity to housing (H). Subsequent models which incorporate the housing and time covariates and their interactions are listed below the null.

[c] ΔAIC values are in comparison to the top model for each study group.

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## Behavioral budgets

All puma behavioral transitions showed contrasting responses to housing depending on the time of day (Fig 1). At night, all pumas regardless of sex or habitat were less likely to remain inactive, more likely to remain active, and more likely to transition between behavioral states near houses. In contrast, male and female pumas were more likely to stay inactive near houses during the daytime. However, male pumas in forests were also less likely to remain active near houses in the forest during the day whereas male pumas in shrublands were unaffected.

Both male and female pumas were generally more active at night than during the day. Male pumas near houses at night were active 26.9% and 21.1% of the time in forested and shrubland habitats, respectively, compared with 17.2% and 13.2% when they weren't close to human structures (Fig 2). Females were active 13.3% of the time when near houses at night, compared with only 7.5% when further away (Fig 2). In the daytime, puma activity was generally low, with females and males in forests exhibiting no difference in activity level in relation to proximity to houses (Fig 2). However, males in shrubland habitats were less likely to be active near houses (2.8%) than when far from houses (8%) during the day.

## Energetic costs

Our COT estimates based on ODBA measurements from accelerometers for pumas 16M and 28F showed that our energetic expenditure estimates from GPS movement data greatly underestimated caloric intake. Applying the COT formula from Taylor et al. [32] to the intensive GPS sampling period, we estimated that 16M expended 2,492 and 2,296 kcals over two days and that 28F expended 1,793 kcals. In contrast, our COT estimates from ODBA for the same three days were about 2–2.5 times higher at 6,079 and 5,492 kcals, and 3,608 kcal, respectively. We used the results from a linear regression between the COT values calculated using 15 min GPS and ODBA measurements (intercept = 8.21, slope = 1.88; $r = 0.75$) to apply corrections factor to all puma energetic calculations.

We used 19 pumas (10 males and 9 females) to evaluate movement activities and energetics over 369 24-hour intense sampling periods (216 for females and 153 for males) (Table 2). Male pumas, averaging 53.3 kg ± 7.82kg (SD), traveled a mean of 7.43 km ± 2.2 km daily and expended 5,145 kcal ± 542 kcal (after factoring the correction factor). Females, averaging 39.8 kg ± 2.73 kg, were more sedentary and traveled a mean of 4.12 km ± 0.5 km daily and expended 4,760 kcal ± 555 kcal. If a puma only subsisted on a diet of black-tailed deer, we calculated that a male puma would need to kill a minimum average of 45.5 doe equivalents/year and that a female puma would need to kill 42 doe equivalents/year.

## Development influences on puma energetics

We found that the model structure that included random intercepts and slopes for Puma ID minimized AIC values and fit the data better compared to a fixed-effects model (ΔAIC = 632) and the model with random intercepts only (ΔAIC = 23.4). The final model included all original fixed effects terms for sex, time, the log-transformed number of houses, the interaction between sex and time, and the interaction between time and number of houses (Table 3). As expected, males burned more calories than females during both nocturnal and diurnal hours (Fig 3). However, the influence of increased housing density on puma energetic expenditures differed depending on time of day, with pumas burning more calories between GPS points in more developed areas during nocturnal hours but not during diurnal hours.

Average daily caloric expenditure for individual pumas was consistently higher on days when pumas were in high housing density areas than in low housing density areas, constituting a 434.3 ± 130.3 SE kcal increase for females and a 513.3 ± 83.1 SE kcal increase for males

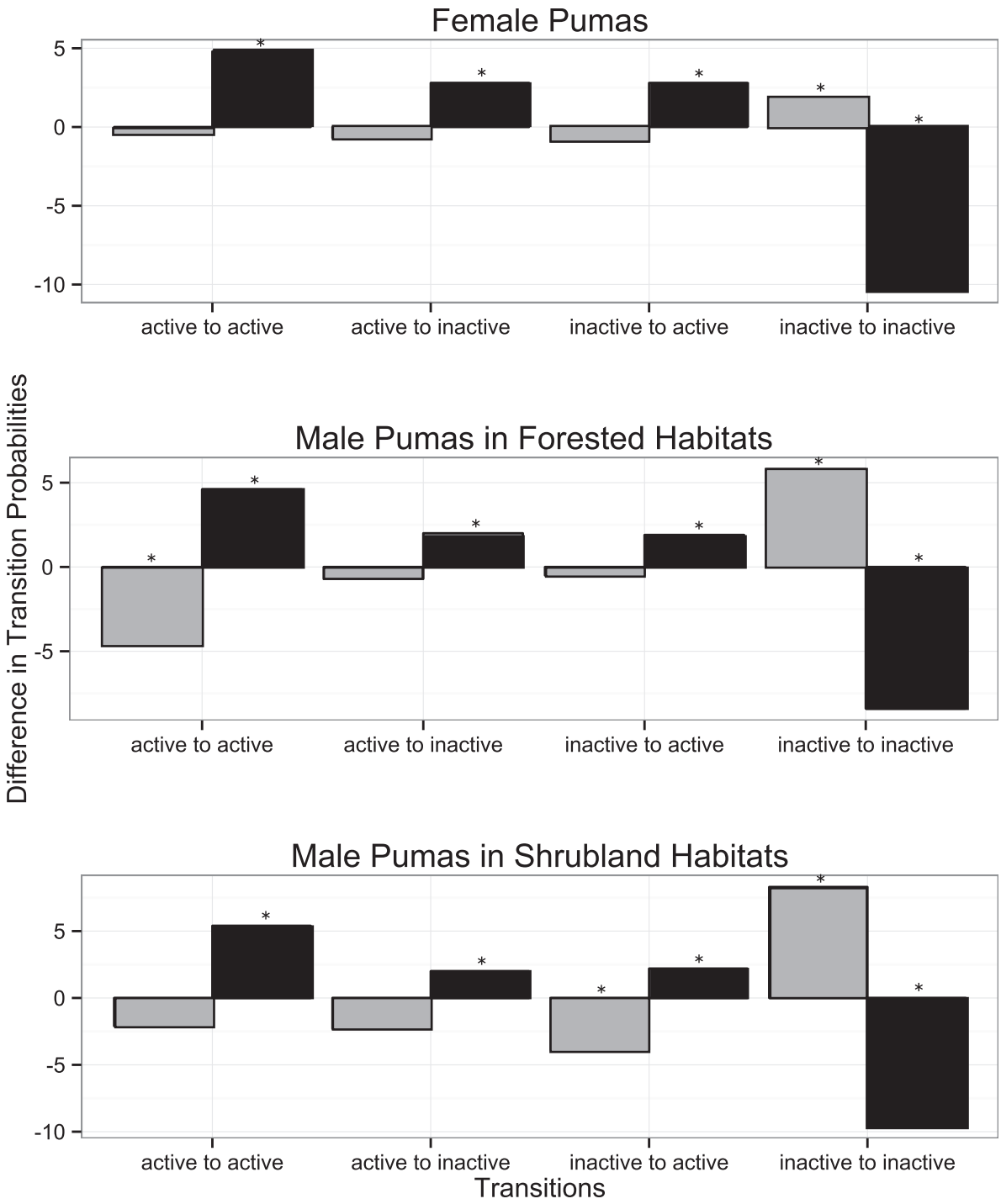


**Fig 1. The effect of proximity to houses on the daytime (gray) and nighttime (black) transition probabilities between activity states for female pumas, male pumas in forested areas, and male pumas in shrubland habitats.** Difference in transition probabilities is calculated as probability of transitioning between states when pumas are ≤150m from buildings subtracted by the probabillity of transitioning between states when pumas are >150m from buildings. A positive value means pumas are more likely to engage in those transitions when close to buildings than when further away. Asterisks above columns represent significant differences between transition probabilities close and far from houses ($P < 0.05$).

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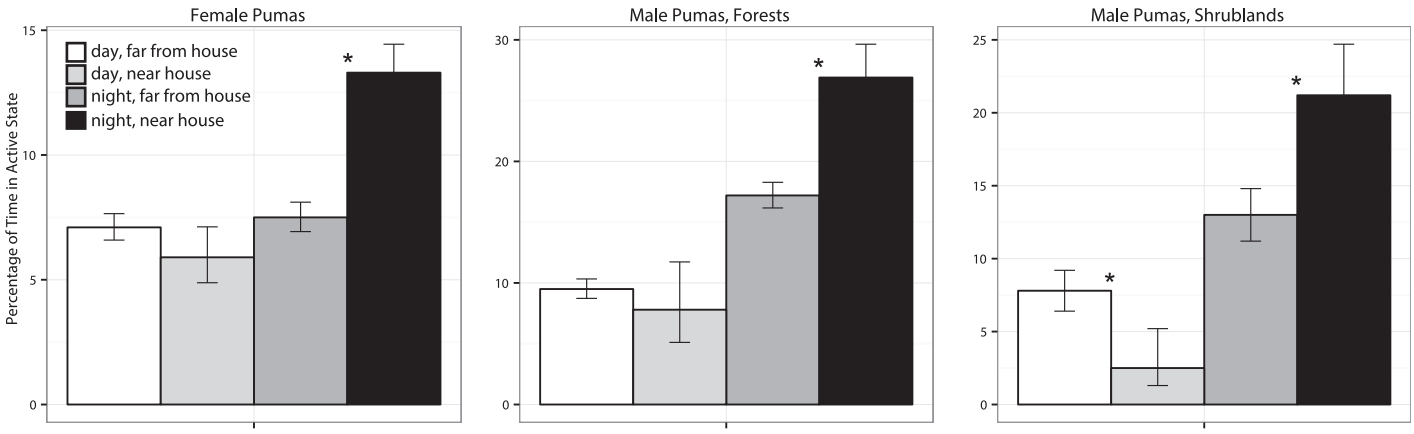


**Fig 2. Proportion of time spent active for female pumas,male pumas in forests, and male pumas in shrublands ≤150m from buildings during the day (light gray) or night (black bars) and >150m from buildings during the day (white) or night (dark grey bars).** Asterisks between paired columns represent significant differences between activity levels near houses and far from houses ($P < 0.05$). Error bars represent 95% confidence intervals.

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(Table 4). These differences in average daily caloric expenditure were equivalent to a mean total percentage increase of 10.1 ± 3.1 SE% of daily kcals used by individual females and 11.6 ± 1.8 SE% of daily kcals used by males. When the increase in daily calories is converted to the extra number of deer required annually by each puma, females would need to kill an additional 3.4 deer annually to meet higher energetic requirements, and males would need to kill 4.0 more deer.

**Table 2. Mean (± standard error) of daily distanced traveled, daily caloric expenditure, and projected annual deer requirements of 9 female (F) and 10 male (M) pumas.**

| Puma ID | Days monitored | Daily distance (m) | Daily kcal/kg | Deer/year |
|---|---|---|---|---|
| 7F | 42 | 3236 ± 378 | 97.8 ± 0.6 | 36.3 ± 0.2 |
| 11F | 22 | 3935 ± 489 | 104.5 ± 0.8 | 35.2 ± 0.3 |
| 18F | 8 | 4001 ± 939 | 119.3 ± 1.7 | 40.0 ± 0.6 |
| 19F | 35 | 3927 ± 495 | 107.9 ± 0.8 | 39.9 ± 0.3 |
| 23F | 38 | 4389 ± 373 | 133.3 ± 0.8 | 48.0 ± 0.3 |
| 24F | 15 | 3966 ± 462 | 145.0 ± 1.0 | 47.7 ± 0.3 |
| 25F | 14 | 4493 ± 941 | 138.2 ± 2.0 | 48.1 ± 0.7 |
| 28F | 24 | 4111 ± 606 | 129.9 ± 1.2 | 41.6 ± 0.4 |
| 29F | 18 | 5060 ± 511 | 124.8 ± 1.0 | 42.2 ± 0.3 |
| Female total | 216 | 4132 ± 176 | 118.9 ± 1.1 | 41.6 ± 0.3 |
| 16M | 12 | 10760 ± 1140 | 96.2 ± 1.5 | 50.4 ± 0.8 |
| 17M | 8 | 4297 ± 706 | 95.0 ± 1.0 | 40.2 ± 0.4 |
| 22M | 29 | 9830 ± 1091 | 91.2 ± 1.4 | 52.0 ± 0.8 |
| 26M | 28 | 6743 ± 810 | 103.0 ±1.2 | 39.6 ± 0.5 |
| 27M | 22 | 6853 ± 1000 | 99.5 ± 1.4 | 43.4 ± 0.6 |
| 31M | 10 | 7047 ± 1298 | 94.8 ±1.8 | 46.1 ± 0.9 |
| 34M | 17 | 6504 ± 727 | 90.1 ± 1.0 | 47.1 ±0.5 |
| 35M | 19 | 4215 ± 484 | 97.3 ±0.7 | 38.8 ±0.3 |
| 36M | 6 | 9192 ± 1874 | 96.4 ± 2.6 | 49.4 ± 1.3 |
| 37M | 2 | 8877 ± 3 | 98.23 ± 0.1 | 48.4 ± 0.0 |
| Male total | 153 | 7334 ± 373 | 96.3 ± 0.6 | 45.0 ± 0.5 |

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**Table 3. Results of final mixed effects model to predict puma activity.**

| Model Parameter | β | SE | t | *P* |
|---|---|---|---|---|
| Sex | 5.50 | 2.84 | 1.94 | 0.069 |
| Time | - 0.66 | 0.78 | -0.85 | 0.395 |
| Number of Houses (log-transformed) | 1.21 | 0.28 | 4.26 | < 0.001 |
| Sex X Time | -3.10 | 0.97 | -3.21 | 0.001 |
| Time X Number of Houses | - 1.45 | 0.49 | -2.95 | 0.003 |

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## Discussion

This study explores how housing development influences puma behavior and energetics in a fragmented landscape. Our results suggest a clear relationship between proximity to houses and puma movement activity. This effect was modulated by the time of day, whereby pumas were more likely to be active and remain active when within 150m of development at night. We also found that pumas were more likely to transition between behavioral states when close to houses. These activity shifts may reflect discomfort with being in close proximity to humans and domestic animals or reaction to other abiotic disturbances from these sources, such as light pollution or human-associated sounds [41].

As we predicted, there was a significant positive relationship between distance traveled and the number of houses surrounding each puma's travel path. This pattern resulted in greater metabolic demand associated with higher densities of residential development. Both male and female pumas moved further and expended more calories in developed areas at night but not during the day, providing evidence that puma response to development was strongly influenced by the time of day. Although pumas only increased their movement activity near houses at night, we found that this still resulted in increased net energetic expenditure. Increases in distance traveled are unlikely to be influenced by deer availability, as occupancy of deer is ubiquitous across our study site in both developed and protected areas [20].

The increases in caloric expenditure we observed could in part explain observed increases in puma kill rate in developed areas [8]. To compensate for the higher energetic costs of living in developed areas alone, we found that pumas would need to kill on average a minimum of 3.4 and 4.0 more deer annually for female and male pumas, respectively. This estimated increase is likely conservative, as we have previously found that pumas in the most developed parts of our study area kill over 20 more deer per year than pumas in less disturbed areas [8]. Higher kill requirements based on increased movement may exacerbate other behavioral influences on energetics, including changes in feeding rates and handling time of prey [8] and altered diet composition [20].

Although pumas in our study area are not legally harvested, human-caused mortality is the leading cause of death for collared pumas. Hence, even in the absence of puma hunting, which is illegal in California, high human-induced mortality rates due to depredations give pumas strong incentive to alter their behaviors to minimize contact with people. Pumas fear humans in this human-dominated ecosystem, demonstrated by immediate responses to human stimuli [41], altered feeding behavior [8,24,41], reduced occupancy of developed areas [7], and strong avoidance of development when engaged in reproductive behaviors [24]. As large tracts of land increasingly transition from undeveloped to exurban development, non-lethal human disturbances will likely continue to alter puma behavior. As demonstrated here, changes in puma movement behavior has energetic consequences. The cumulative energetic cost of all behavior change in human-dominated systems is likely to exceed even the substantial estimated energetic requirements reported here.

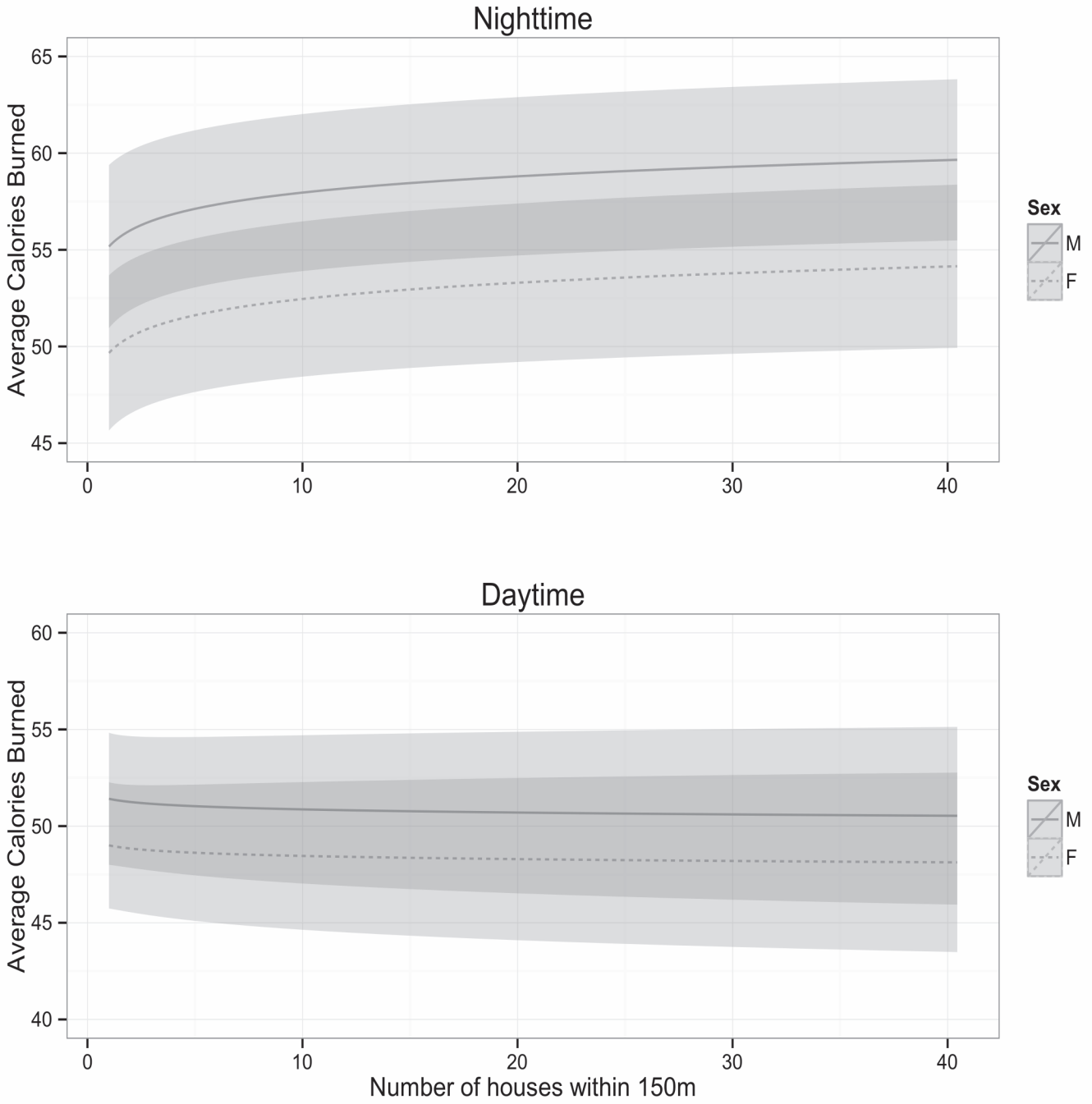


**Fig 3. Predicted curves bounded by 95% confidence intervals relating the average calories expended between 15-minute GPS points and the average number of houses in a 150m radius around locations in nighttime and daytime.** Predictions for males are indicated by the solid line and females are indicated by the dashed line.

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Increased energetic requirements are likely to disproportionalty impact females with kittens, given their higher energetic demands [34]. Kittens older than 6 months follow their mothers to kill sites to feed [42]; if these locations are close to development, their feeding times

**Table 4. Caloric difference between time spent in high and low housing density areas relative to each puma.**

| Puma Sex | Puma ID | Difference in kcals (day)[a] | Difference in kcals (night)[a] | Total Difference (kcal) | Increase in Daily Calories (%)[b] | Change in annual deer consumption | Bottom 25% Housing Density[c] | Top 25% Housing Density[c] |
|---|---|---|---|---|---|---|---|---|
| Female | 23F | -754.5 | 809.5 | 55.1 | 1.1 | 0.4 | Rural | Suburban |
| | 11F | 94.1 | 19.8 | 113.9 | 2.9 | 0.9 | No Housing | Exurban |
| | 28F | 128.7 | 128.3 | 256.9 | 5.7 | 2.0 | No Housing | Exurban |
| | 7F | 124.9 | 206.3 | 331.2 | 8.3 | 2.6 | No Housing | Exurban |
| | 19F | 509.1 | 10.5 | 519.6 | 12.3 | 4.0 | No Housing | Rural |
| | 25F | 54.7 | 736.1 | 790.9 | 16.2 | 6.2 | No Housing | Exurban |
| | 29F | 21.2 | 951.3 | 972.6 | 24.4 | 7.6 | No Housing | Exurban |
| Male | 26M | -23.5 | 328.6 | 305.1 | 7.2 | 2.4 | No Housing | Exurban |
| | 22M | 114.9 | 288.1 | 403.0 | 7.5 | 3.1 | No Housing | Rural |
| | 17M | 418.8 | 40.2 | 459.0 | 11.8 | 3.6 | No Housing | Exurban |
| | 27M | 63.0 | 408.4 | 471.4 | 10.9 | 3.7 | No Housing | Rural |
| | 35M | 2.8 | 543.6 | 546.3 | 12.9 | 4.3 | No Housing | Exurban |
| | 16M | 343.1 | 551.9 | 895.0 | 19.3 | 7.0 | Rural | Exurban |

[a] Differences are calculated from average caloric expendature during days and nights spent in the top and bottom quartiles of housing density per puma.

[b] Increase in daily calories are measured as the total increase in caloric expendature divided by individual average daily caloric expendature.

[c] Housing density classifications are derived using categories described in Theobald (2005).

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may decline in response to disturbances [8]. Additionally, females may choose daytime resting locations further away from kill sites in developed areas, thus reducing the energetic gains kittens receive from carcasses. Although we could not track kitten survival during our study, most female pumas we tracked had kittens and lived in home ranges that encompassed developed areas. Future studies that measure kitten recruitment will shed light on the added energetic and survival costs of raising kittens in human-modified landscapes.

Our approach of using GPS and accelerometer data allowed us to obtain more accurate estamates of energetic use and requirements, which were likely underestimated in previous studies using GPS or telemetry data alone. The average activity levels of our study animals (20.8%) was relatively low compared to Beier et al.'s [37] estimates of 25% diel activity for pumas in southern California. This discrepancy may be due to methodological differences; Beier et al. [37] used the radio-telemetry to estimate the locations of animals, which is characterized by lower precision and sampling in comparison to GPS data. Pumas tracked in our study have some of the lowest travel distances (4–7 km/day) of any pumas studied, traveling less than half as far as those monitored by other studies [34,43]. However, despite their relatively short travel distances, our corrected estimates of puma energetic expenditures (average of 4,760 kcal for females and 5,145 kcal for males) was nearly twice as high as those of Laundré [34] (average of 2,420 kcal for females and 3,144 kcal for males), which suggests that previous estimates of puma energetics from GPS or radio-tracked animals have considerably underestimated true field energetics. Metabolic costs derived soley from mimimum COT equations or telemetry-only tracking studies may woefully underestimate true large predator hunting costs due to their inability to account for additional energy demand associated with topographic complexity, substrate type, intermittent locomotion, maneuvering, feeding and weather [13,44,45].

Incorporating calibrated accelerometer datasets alongside GPS locations, as demonstrated here for pumas, allows for significantly finer-scale reconstruction of behavioral and energy budgets. Our accelerometer-corrected estimates for minimum annual deer consumption (42

deer/yr for females without kittens and 45.5 deer/yr for males) are likewise much higher than those predicted by Laundré [34] (14.9 deer/yr for females and 19.4 deer/yr for males). Instead, our estimates are similar to the field-estimated kill rates of 25–84 deer/yr for pumas in our population [8].

Our study provides evidence that behavioral responses to human disturbance have energetic consequences to individuals. While previous research had focused primarily on how urbanization and development affect the persistence or declines in wildlife populations, more studies now examine the behavioral responses of these species as they adapt to increased human presence [8,46]. Understanding how animal motivations and behaviors are altered by human influences can shed light on why some species can continue to persist in human dominated landscapes while others become extirpated [47,48]. New technologies such as accelerometers can reveal much more than whether or not an animal is in an area, but elucidate how successfully the individual is able to move, feed, and reproduce [49]. Increasing awareness of the consequences of human-induced behavioral change in wildlife can contribute to more robust wildland-urban interface planning and reductions in human-wildlife conflict.

Currently, exurban or low density development is the fastest growing type of land-use change in the United States [50]. As low density development fragments previously intact landscapes, it could pose significant challenges to survival for wildlife due to cummulative effects of increased non-lethal human disturbance. By incorporating energetic measurements from accelerometers, we showed the substantial consequences of these changes in behavior on energetic costs and requirements. Changes in movement activity and behavior can provide the first indications of predator energetic responses to development. Large carnivores such as pumas occupy pivotal roles in ecosystems, and changes to their behaviors can lead to demographic effects that reverberate throughout the ecological community. In addition, as energetic needs increase with development, large carnivores may switch to domestic or synanthropic prey sources, exacerbating conflict with humans and threatening carnivore survival and population persistence. For all large carnivores, accounting for human-induced behavioral change should play a larger role in any conservation management strategy.

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**Writing – original draft:** Yiwei Wang, Justine A. Smith.

**Writing – review & editing:** Yiwei Wang, Justine A. Smith, Christopher C. Wilmers.

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OPINION

# Op-Ed: There's a quick way to help prevent wildfires: Shut off the power grid

Flames burn near power lines in Montecito, Calif. on Dec. 16, 2017. (Mike Eliason / Associated Press)

By MICHAEL W. WARA

DEC. 10, 2018
3:05 AM

The challenge created by wildfires in California — and our need to adapt to a hotter, drier climate — cannot be overstated. The state, which leads the nation on environmental issues, must call upon the creativity of its innovators and the adaptability of its citizens to secure its future. The reality of climate change means we need to make urgent big investments in infrastructure that will keep us safe.

The Legislature began to implement wildfire solutions last session that, over time, will make California safer. Gov. Jerry Brown added more than $250 million to this year's budget, doubling the state's forest-thinning efforts and increasing prescribed burns, which could make parts of the state less combustible. Stricter building codes are also under discussion, along with limiting new construction and rebuilding in the likely path of fires. There are also calls to put power lines underground — at tremendous cost.

But these strategies will take time — probably a decade or more. And we cannot afford more firestorms like the ones that swept through Santa Rosa and Ventura in 2017, and Paradise and Malibu in November.

The most destructive fires in recent California history have been traced, to a high degree of probability, to downed utility power lines or electrical equipment malfunctions. (The causes of last month's Camp fire and Woolsey fire have yet to be determined, but electrical infrastructure problems are the suspected cause.) In the fires' terrible wake, California residents are also faced with bailing out utilities when they are found liable for the conflagrations.

*Deploying clean "distributed energy" — individualized power generation and storage — could be a kind of green New Deal.*

There is a simple and effective way to reduce the risk of utility-caused wildfire, and it doesn't take decades to implement: Shut the power off when and where wind and drought create wildfire risk. All other options for preventing these fires — such as putting power lines underground or trimming trees that threaten power infrastructure — will take too long or are too prone to error to adequately address the crisis we're facing.

To make it acceptable to turn off whole sections of the electricity grid, the state will have to start a crash program to build a backup power supply for households and businesses in high-risk wildfire areas. The logical choices are individual solar and battery setups for households, and "microgrids" linking business districts. We need to make it OK for the utilities to take decisive action to avoid wildfire threats: When the main grid has to go down for safety, backup power must be available to keep medical devices, refrigerators and the internet up and running.

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Deploying clean "distributed energy" — individualized power generation and storage — could be a kind of green New Deal. It would not only cut down on destructive wildfires, it could create enormous numbers of new jobs all over the state. And it could speed up our pursuit of statewide emissions-free energy. Establishing an alternative to the massive, interconnected grid that delivers power would also add security to a system vulnerable to other natural disasters as well as cyber threats. It might expand over time to include areas not threatened by wildfire.

Setting up off-the-grid power sources would be costly, but it's a much smarter investment than repeatedly bailing out utilities after fires. As massive as the project would be, it compares in scale and cost to wildfire losses in just the last two years.

By my back-of-the-envelope calculation, it would cost something like $30 billion to install individualized backup power for 1 million of the highest-risk homes if the costs were fully funded by the state. But the state wouldn't have to foot the whole bill; it could provide very low-cost financing, paid back over many years on customer utility bills, while providing additional assistance to low- and moderate-income customers.

California can't afford to have more towns and neighborhoods destroyed or hollowed out by fire. Spending billions on alternatives to utility-delivered power might have seemed like an unaffordable luxury once, but now it's clear what doing nothing will mean: more lives, livelihoods and communities lost in what the governor calls the "new abnormal."

*Michael W. Wara is the director of the Climate and Energy Policy Program at the Woods Institute for the Environment at Stanford University.*

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# Increasing impacts of climate change upon ecosystems with increasing global mean temperature rise

**Rachel Warren · Jeff Price · Andreas Fischlin · Santiago de la Nava Santos · Guy Midgley**

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**Abstract** In a meta-analysis we integrate peer-reviewed studies that provide quantified estimates of future projected ecosystem changes related to quantified projected local or global climate changes. In an advance on previous analyses, we reference all studies to a common pre-industrial base-line for temperature, employing up-scaling techniques where necessary, detailing how impacts have been projected on every continent, in the oceans, and for the globe, for a wide range of ecosystem types and taxa. Dramatic and substantive projected increases of climate change impacts upon ecosystems are revealed with increasing annual global mean temperature rise above the pre-industrial mean ($\Delta T_g$). Substantial negative impacts are commonly projected as $\Delta T_g$ reaches and exceeds 2°C, especially in biodiversity hotspots. Compliance with the ultimate objective of the United Nations Framework Convention

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on Climate Change (Article 2) requires that greenhouse gas concentrations be stabilized within a time frame "sufficient to allow ecosystems to adapt naturally to climate change". Unless $\Delta T_g$ is constrained to below 2°C at most, results here imply that it will be difficult to achieve compliance. This underscores the need to limit greenhouse gas emissions by accelerating mitigation efforts and by protecting existing ecosystems from greenhouse-gas producing land use change processes such as deforestation.

## 1 Introduction

Effects of climate change are already being observed on a wide range of ecosystems and species in all regions of the world (Rosenzweig et al. 2007), in response to the 0.74°C rise ($\Delta T_g$) in global mean temperature (GMT) that has been experienced since pre-industrial times (Solomon et al. 2007). Such responses include changes in phenology and shifts in species ranges (e.g. Walther et al. 2002; Root et al. 2003), whilst the first extinctions which are likely to be attributable to climate change—acting synergistically with disease—have already occurred in amphibians (Pounds et al. 2006; Bosch et al. 2006). Coral reef bleaching is expected to increase strongly with rising sea surface temperatures (Hughes et al. 2003). At the same time, the ocean has already acidified by 0.1 pH units since pre-industrial times (Solomon et al. 2007) due to the direct effects of increasing atmospheric concentrations of carbon dioxide from the pre-industrial level of 280 ppm to the 2005 level of 379 ppm $CO_2$ (Solomon et al. 2007).

The literature contains a growing number of studies that project for the future increasingly severe impacts that further anthropogenic climate change would have on ecosystems and species around the world (see the 71 studies referenced in Tables 2, 3, 4 and 5). Such studies typically identify the onset of some positive, but predominantly negative, impacts upon a species or ecosystem as the climate changes. However, these studies have largely been carried out independently from each other and have used a wide range of future climate scenarios. This makes it difficult to compare results and obtain a clear and aggregated picture of how impacts accrue with increasing global mean temperature rise. Such an aggregated picture is important for two reasons: firstly it addresses climate change at the appropriate scale, i.e. as a global phenomenon; and secondly it enables the evaluation of major policy recommendations, such as the much discussed 2°C limit suggested by the EU as both a "safe" and achievable level of global temperature increase. Existing reviews (Houghton et al. 2001; Thomas et al. 2004a; Hare 2006; Warren 2006) have not included the full range of recent literature and have not estimated uncertainties. Similarly to the summary given in Fischlin et al. (2007), this paper integrates the dispersed and fragmented literature on ecosystem impacts of projected climate change, often expressed at a regional level, into a set of tables of projected impacts for different levels of global mean temperature rise with respect to pre-industrial times, $\Delta T_g$, providing an estimate of uncertainty in these levels. The tables report the main findings in terms of: range losses for species, habitats or entire ecosystems; extinction risks; and other biodiversity impacts caused by ecosystem degradations or declines in key populations due to anticipated climate changes.

## 2 Materials and methods

### 2.1 Literature search

A literature search was made to assess pertinent impacts of climate change on both terrestrial and marine ecosystems across the globe (Fischlin et al. 2007). Search engines were first used to identify references in the peer reviewed literature, and further references were then derived from information provided within these. Existing reviews (Gitay et al. 2001; Thomas et al. 2004a; Hare 2006; Warren 2006) were particularly useful in identifying additional references. All references were then reviewed for specific information about thresholds in local or global temperature change/sea level rise above which adverse consequences could be expected, and also for quantified projections of ecosystem or species changes associated with quantified local or global climate changes, taking note of the climate scenario and any general circulation model (GCM) used, and the treatment of dispersal and migration. Thus studies that contained insufficient detail about the climate scenario used, or that did not provide quantitative estimates of the resultant ecosystem or species changes, could not be included in the analysis. In particular, studies which reported only the general direction of trends in response to changing temperature or precipitation were deliberately excluded. In cases where more than one study addressed similar species or ecosystems, each study was included separately in the summary table, since it may be projecting different sensitivities due to the use of other climate change scenarios and/or assessing other kinds of impact responses.

### 2.2 Converting to a pre-industrial reference point for global mean temperature change

Information on the climate change scenario simulated by each original study was converted to a common pre-industrial reference point for temperature. Studies often refer to baselines of pre-industrial (<1850), 1960–1990 mean, 1990, or "present day" (e.g. 1980–1999). In this study the temperature rise between pre-industrial and the 1960–1990 mean is taken as 0.3°C and the temperature rise between pre-industrial and 1990 is taken as 0.6°C (Houghton et al. 2001); whilst that from the mid 1970s to 1990 is taken as 0.2°C (Houghton et al. 2001). Where studies report impacts as caused by a particular GCM simulation using the HadCM3 model, Table 7 of Arnell et al. (2004) was used to convert the temperatures to a common pre-industrial baseline.

While some of the literature relates impacts directly to global mean temperature increases, many studies refer only to local temperature rise, and hence upscaling from a local to a global scale is required. Upscaling was carried out as detailed below for the different classes of studies identified (Table 1) and also provided an opportunity to estimate the uncertainties arising from the use of different GCMs in climate projection. Whenever possible it was also considered whether the impact had been estimated based only on temperature change, or also on associated precipitation change.

When studies gave minimal detail about GCM scenarios, such as referring to them only as "$CO_2$ doubling scenarios", the original literature publishing that scenario was traced, and/or the model authors were contacted, in order to verify the global mean

**Table 1** Detail of the upscaling methodology used to derive global mean temperature (GMT) change ($\Delta T_g$) for the eight study classes a–h

| Class | Description of study | Derivation of central estimate of GMT change $\Delta T_g$ | Derivation of range of GMT change |
|---|---|---|---|
| a | Relates global impacts directly to $\Delta T_g$ | $\Delta T_g$ by definition already provided: harmonised if necessary to pre-industrial | Not derived unless provided in original study |
| b | Relates local impact (e.g. x% species at risk of extinction) to regional temperature change without using GCM output | $\Delta T_g$ is the mean of values derived via upscaling procedure, using the cited regional temperature change | Range of values derived via upscaling procedure using the cited regional temperature change |
| c | Relates a local impact (e.g. y% species at risk of extinction) to regional temperature change while using the output of specific GCM(s)[2] | As not all studies provide the regional temperature change this may need to be derived by first downscaling for the appropriate timeslice (e.g. Gyalistras and Fischlin 1999). $\Delta T_g$ is then the mean of values derived via a subsequent upscaling of the downscaled regional temperature change | Range of values derived via upscaling procedure, using the downscaled regional temperature change |
| d | As b but regional precipitation change also used | As b | As b |
| e | As c but study uses also GCM simulated precipitation as well as temperature | Upscaling is not applicable, as procedure is based on temperature only. $\Delta T_g$ is derived from published values simulated by the used GCM(s) | Not derivable |
| f | Cases where upscaling is not possible because regional temperature changes are out of range of the GCM patterns available | Estimated from maps in Meehl et al. (2007) relating local and global temperature change | Not derivable |
| g | As c or e but GCM output comes from 3 or more different GCM models | Mean of values as simulated by the used GCM(s) | Range derived from published values simulated by the used GCM(s) |
| h | Cases where the key variable is sea surface temperature | Estimated from maps in Meehl et al. (2007) relating local surface air temperature over the sea to $\Delta T_g$, since maps of SST were not readily available, and increases in surface air temperature over the ocean were assumed to approximate increases in SST | Not derivable |

temperature increase corresponding to $CO_2$ doubling, taking into account the control $CO_2$ concentration as necessary.

### 2.3 Dynamics

Many reviewed studies do not consider a temporal dimension. There are two issues here (1) whether the climate scenario a study considers relates to transient or equilibrium climate change and (2) whether the projected ecological response is considered a steady state. Studies in class b project impacts without distinguishing between transient and equilibrium temperature change. However, most studies use models, which project the future long-term ecological response to a changed climate (i.e. a new steady state) while the climate scenario is a transient one: studies in classes c and e are typically based on transient climate change scenarios produced by GCMs, although there are a few which also include equilibrium temperature change scenarios. Hence, the ecological projections are *not* mere snapshots of a transient climate change and its concomitant response, rather do these studies artificially hold the transient climate constant and assume the ecosystem response to equilibrate, regardless of the time the system may need to actually reach such an equilibrium. Thus an important question is the time lag between the forcing temperature change, be it transient or equilibrium, and the ecosystem response (see Section 4). The upscaling procedure described below is based on transient GCM scenario outputs throughout.

### 2.4 Upscaling procedure

The upscaling procedure involved the use of $0.5 \times 0.5°$ resolution outputs produced from original $5 \times 5°$ resolution outputs of five GCM models HadCM3, ECHAM4, CSIRO2, PCM, and CGCM2, by using pattern scaling and downscaling methods (Christensen et al. 2007). These climate projections based on transient GCM outputs were available for the entire global land area at a resolution of $0.5 \times 0.5°$. They were produced from up to four IPCC SRES emission scenarios (Nakicenovic et al. 2000) providing 13 different GCM patterns on which to base the upscaling (available at http://ipcc-ddc.cru.uea.ac.uk). In each $0.5 \times 0.5°$ grid cell, 13 alternative twenty-first century time series of regional annual (or if required seasonal) temperature were thus available, each one expressed as the running 30-year mean temperature increase since 1961–1990 mean climate, to smooth inter-annual variability.

For each study in Table 1 of type b or c, the location was then related to a grid cell or to grid cells depending on how large an area the study covered. For each grid cell, all 13 upscaling calculations were carried out, to encompass the full range of inter-GCM and inter-scenario pattern variability as an uncertainty surrogate. The upscaling calculation was simply performed by examining any one of the 13 time series for a grid cell. A computer program calculated the date at which the regional temperature reached the temperature threshold which is referred to in the study of type b or c and therein associated with some particular impact on an ecological system. The program then used this derived date to identify the associated global temperature rise $\Delta T_g$ in the transient GCM runs, matching this same date, using if available the global temperature time series from the exact same GCM scenario as

**Table 2** Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise $\Delta T_g$, relative to pre-industrial climate (mean and range), showing also regional temperature change $\Delta T_{reg}$ relative to 1990 if provided by the literature: range losses for species, habitats or whole ecosystems

| No. | $\Delta T_g$ above pre-ind °C | $\Delta T_g$ (range) | $\Delta T_{reg}$ above 1990 °C (range) | Impacts to unique or widespread ecosystems or population systems | Region | Taxa | Source |
|---|---|---|---|---|---|---|---|
| 1 | 1.3 | 1.1–1.6 | 1 | 8% loss freshwater fish habitat, 15% loss in Rocky Mountains, 9% loss of salmon | N America | Fish | 13 |
| 2 | 1.6 | | | Bioclimatic envelopes eventually exceeded leading to 10% transformation of global ecosystems; loss of 47% wooded tundra, 23% cool conifer forest, 21% scrubland, 15% grassland/steppe, 14% savannah, 13% tundra and 12% temperate deciduous forest. Ecosystems variously lose 2–47% areal extent | Globe | | 6 |
| 3 | 1.6 | 1.1–2.1 | 1 | Suitable climates for 25% of eucalypts exceeded | Australia | Plants | 12 |
| 4 | 1.7 | 1.3–2.4 | 2 | 16% freshwater fish habitat loss, 28% loss in Rocky Mountains, 18% loss of salmon | N America | Fish | 13 |
| 5 | 1.8 | | | Mean latitude of range of *Aloe dichotoma* shifts S by 1.1° of latitude causing range loss | Namibia | Plants | 68 |
| 6 | <1.9 | <1.6–2.4 | <1 | Range loss begins for Golden Bowerbird | Australia | Birds | 4 |
| 7 | 1.9 | 1.6–2.4 | 1 | Range loss of 40–60% for Golden Bowerbird | Australia | Birds | 4 |
| 8 | 2.1 | | | Without dispersal 17 common European deciduous trees variously lose 1–100% of their range (2 sp. lose 100%); whilst full dispersal could reduce this to 11 losing between 1–99% (2 sp. lose 99%) and 6 increasing their range by 42–303% | Europe | Plants | 67 |
| 9 | 2.3 | 1.6–3.2 | 3 | 24% loss freshwater fish habitat, 40% loss in Rocky Mountains, 27% loss of salmon | N America | Fish | 13 |
| 10 | 2.4 | | | 63 of 165 rivers studied lose >10% of their fish species | Globe | Fish | 19 |
| 11 | 2.5 | 1.9–4.3 | | 42% of UK land area with bioclimate unlike any currently found there; in Hampshire, declines in climate suitability space for curlew and hawfinch and gain for yellow-necked mouse; loss of montane habitat in Scotland; potential bracken invasion of Snowdonia montane areas | UK, Europe | Birds, mammals, plants | 57 |
| 12 | 2.5 | | | 20–70% loss (mean 44%) of coastal bird habitat at 4 sites | USA | Birds | 29 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 13 | 2.5 | 1.9–3.5 | | 20% loss of coastal migratory bird habitat | Delaware, USA | Birds | 36 |
| 14 | 2.7 | | | 32–70% of 111 European mammals studied lose >30% of current distribution whilst 24–35% undergo range expansions | Europe | Mammals | 71 |
| 15 | 2.7 | | | Bioclimatic envelopes exceeded leading to eventual transformation of 16% of global ecosystems: loss of 58% wooded tundra, 31% cool conifer forest, 25% scrubland, 20% grassland/steppe, 21% tundra, 21% temperate deciduous forest, 19% savanna. Ecosystems variously lose 5–66% of their areal extent | Globe | | 6 |
| 16 | 2.8 | 2.3–4.6 | 2.1–2.5 | Cloud forest regions lose hundreds of metres of elevational extent, potential extinctions $\Delta T_{reg}$ 2.1°C for C America and $\Delta T_{reg}$ 2.5°C for Africa | C. America, Tropical Africa, Indonesia | | 17 |
| 17 | 2.8 | 2.1–3.1 | 3 | Eventual loss of 9–62% of the mammal species from Great Basin montane areas | USA | Mammals | 32 |
| 18 | 2.8 | | | Most European bird distributions are reduced in area by 81% and displaced from 38–53% of their present location; 25% have ranges reduced by > = 90%. Avian species richness reduced by 9–60% depending on dispersal assumptions | Europe | Birds | 65 |
| 19 | 2.8 | 1.9–3.8 | 3 | 38–54% loss of waterfowl habitat in prairie pothole region | USA | Birds | 37, 38 |
| 20 | 2.9 | | 3.2–6.6 | 50% loss existing tundra offset by only 5% eventual gain; millions of Arctic nesting shorebirds species variously lose up to 5–57% of breeding area; high Arctic species most at risk; geese species variously lose 5–56% of breeding area | Arctic | Birds | 14 |
| 21 | 2.9 | | | Lat. of N forest limits shifts N by 0.5° latitude in W Europe, 1.5° in Alaska, 2.5° in Chukotka and 4° in Greenland | Arctic | Plants | 40 |
| 22 | 2.9 | | | Substantial loss of boreal forest | China | Plants | 15 |
| 23 | 3.0 | | | 66 of 165 rivers studied lose >10% of their fish species | Globe | Fish | 19 |

**Table 2** (continued)

| No. | $\Delta T_g$ above pre-ind °C | $\Delta T_g$ (range) | $\Delta T_{reg}$ above 1990 °C (range) | Impacts to unique or widespread ecosystems or population systems | Region | Taxa | Source |
|---|---|---|---|---|---|---|---|
| 24 | 2.4–4.0 | | | 431 bird species lose on average 76–89% of their present range, with new potential ranges overlapping original ones by 31–47% so that species richness declines locally by a mean of 9–56% depending on dispersal assumptions | Europe | Birds | 73 |
| 25 | 3.3 | 2.3–3.9 | 2.6–2.9 | Substantial loss of alpine zone, and its assoc. flora and fauna (e.g., alpine sky lily, and mountain pygmy possum) | Australia | Plants, marsupials | 45 |
| 26 | 3.4 | | | 6–22% loss of coastal wetlands; large loss migratory bird habitat particularly in USA, Baltic and Mediterranean | Globe | Birds | 35, 36 |
| 27 | 3.5 | 2.3–4.1 | 2.5–3.5 | Loss of temperate forest wintering habitat of Monarch butterfly | Mexico | Insects | 28 |
| 28 | 3.6 | 2.6–4.3 | 3 | Bioclimatic limits of 50% of eucalypts exceeded | Australia | Plants | 12 |
| 29 | 3.6 | 3.0–3.9 | | Parts of the USA lose 30–57% neotropical migratory bird species richness | USA | Birds | 43 |
| 30 | 3.7 | | | Bioclimatic envelopes exceeded leading to eventual transformation of 22% of global ecosystems; loss of 68% wooded tundra, 44% cool conifer forest, 34% scrubland, 28% grassland/steppe, 27% savannah, 38% tundra and 26% temperate deciduous forest. Ecosystems variously lose 7–74% areal extent | Globe | | 6 |
| 31 | 3.7 | 2.6–4.8 | 3 | Up to 60% loss in upland stream macro-invertebrate abundance; local extinction of 4 taxa; 25% of mean species richness at risk of local extinction | UK | Invertebrates | 62 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 32 | 4.0 | 3.3 | 47–78% of 111 European mammals studied lose >30% of current distribution whilst 13–33% undergo range expansions | Europe | Mammals | 71 |
| 33 | >>4.0 | 5 | Bioclimatic limits of 73% of eucalypts exceeded | Australia | Plants | 12 |
| 34 | 4.9 | | Without dispersal 17 common European deciduous tree species variously lose 15–100% of their range; full instantaneous dispersal could reduce this to 11 losing between 13% and 100% and 6 increasing their range by 3–320% | Europe | Plants | 67 |
| 35 | 5.0 | | 92–97% of 100 *Banksia* species studied experience range contraction, 9% expand | W Australia | Plants | 74 |
| 36 | 5.2 | | 62–100% loss of bird habitat at 4 major coastal sites | USA | Birds | 29 |

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

**Table 3** Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise $\Delta T_g$, relative to pre-industrial climate (mean and range), showing also regional temperature change $\Delta T_{reg}$ relative to 1990 if provided by the literature: extinction risks

| No. | $\Delta T_g$ above pre-ind °C | $\Delta T_g$ above pre-ind °C (range) | $\Delta T_{reg}$ above 1990 °C (range) | Impacts to unique or widespread ecosystems or population systems | Region | Taxa | Source |
|---|---|---|---|---|---|---|---|
| 37 | 0.6 | | | Amphibian extinctions/extinction risks on mountains due to climate-change induced disease outbreaks | Costa Rica, Spain, Australia | Amphibians | 52, 54 |
| 38 | 1.6 | 1.2–2.0 | 0.7–1.5 | 9–31% (mean 18%) of species committed to extinction | Globe (20% terrestrial surface) | Plants, vertebrates and insects | 1 |
| 39[a] | 1.6 | | | 23–25% of bird species at risk of extinction, and 1–2% projected extinct | Western Hemisphere | Birds | 70 |
| 40 | 1.7 | 1.2–2.6 | | 38–45% of the plants in the Cerrado committed to extinction | Brazil | Plants | 1, 44 |
| 41 | 1.7 | 1.3–3 | | 2–18% of the mammals, 2–8% of the birds and 1–11% of the butterflies committed to extinction | Mexico | Mammals, birds, insects | 1, 26 |
| 42 | 1.75 | 1.5–2.0 | | 2–4% loss of global vascular plant diversity | Globe | Plants | 64 |
| 43 | 1.9 | 1.6–2.4 | 1 | 7–14% of reptiles, 8–18% of frogs, 7–10% of birds, and 10–15% of mammals committed to extinction as 47% of appropriate habitat in Queensland lost | Australia | Reptiles, amphibians, birds, mammals | 1, 7 |
| 44 | 2.1 | | | 41–51% loss in plant endemic species richness | S Africa, Namibia | Plants | 39 |
| 45 | 2.1 | | 1.4–2.6 | 13–23% of butterflies committed to extinction | Australia | Insects | 1, 30 |
| 46 | 2.1 | 1.4–2.6 | | Bioclimatic envelopes of 2–10% plants exceeded leading to endangerment or extinction; mean species turnover of 48% (spatial range 17–75%); mean species loss of 27% (spatial range 1–68%) | Europe | Plants | 22 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 47 | 2.2 | | | 3–16% of plants committed to extinction | Europe | Plants | 1 |
| 48 | 2.2 | 2.1–2.3 | 1.6–1.8 | 15–37% (mean 24%) of species committed to extinction | Globe (20% terrestrial surface) | Plants, vertebrates and insects | 1 |
| 49 | 2.2 | 1.7–3.2 | | 8–12% of 277 medium/large mammals in 141 national parks critically endangered or extinct; 22–25% endangered | Africa | Mammals | 23 |
| 50 | 2.3 | 1.5–2.7 | 2°C SST | Loss of Antarctic bivalves and limpets | Southern Ocean | Molluscs | 51 |
| 51 | 2.3 | 1.5–2.7 | 2.5–3.0 | Extinctions (100% potential range loss) of 10% endemics; 51–65% loss of Fynbos; including 21–40% of *Proteaceae* committed to extinction; Succulent Karoo area reduced by 80%, threatening 2800 plant species with extinction; 5 parks lose >40% of plant species | S Africa | Plants | 1, 5, 24, 25 |
| 52 | 2.3 | 2.3–4.0 | 2.5–3.0 | 24–59% of mammals, 28–40% of birds, 13–70% of butterflies, 18–80% of other invertebrates, 21–45% of reptiles committed to extinction; 66% of animal species potentially lost from Kruger National Park | S Africa | Mammals, birds, reptiles, insects, other invertebrates | 1, 27 |
| 53 | 2.3 | 2.2–4.0 | | 2–20% of mammals, 3–8% of birds and 3–15% of butterflies committed to extinction | Mexico | Mammals, birds, insects | 1, 26 |
| 54 | 2.3 | 1.6–3.2 | | 48–57% of Cerrado plants committed to extinction | Brazil | Plants | 1 |
| 55[a] | 2.3 | | | 27–28% of bird species at risk of extinction, and 2–3% projected extinct | Western Hemisphere | Birds | 70 |
| 56 | 2.3 | | | Changes in ecosystem composition, 32% of plants move from 44% of area with potential extinction of endemics | Europe | | 16 |

**Table 3** (continued)

| No. | $\Delta T_g$ above pre-ind °C | $\Delta T_g$ above pre-ind °C (range) | $\Delta T_{reg}$ above 1990 °C (range) | Impacts to unique or widespread ecosystems or population systems | Region | Taxa | Source |
|---|---|---|---|---|---|---|---|
| 57 | 2.4 | | | Bioclimatic range of 25–57% (full dispersal) or 34–76% (no dispersal) of 5,197 plant species exceeded leading to extinction risks | Subsaharan Africa | | 60 |
| 58 | 2.5 | | 2°C SST | Functional extinction of coral reef ecosystems (overgrown by algae) | Indian Ocean | Corals, fish | 9 |
| 59 | 2.6 | | | 4–21% of plants committed to extinction | Europe | Plants | 1 |
| 60 | 2.7 | | | 1–6 rodent species (1–5% of 111 mammals studied) committed to extinction | Europe | Mammals | 71 |
| 61 | 2.8 | 2.5–3.0 | | Multimodel mean 62% (range 40–100%) loss Arctic summer ice extent, high risk of extinction of polar bears, walrus, seals; Arctic ecosystem stressed | Arctic | Mammals | 11, 53 |
| 62 | 2.8 | | | 65 species at increased risk of extinction with high risk for endemic Scottish Crossbill, Imperial Eagle and Marmora's warbler | Europe | Birds | 65 |
| 63 | 2.9 | | 2.1–3.9 | 21–36% of butterflies committed to extinction; >50% range loss for 83% of 24 lat. restricted species | Australia | Insects | 1, 30 |
| 64 | 2.9 | 2.6–3.3 | 2.1–2.8 | 21–52% (mean 35%) of species committed to extinction | Globe (20% terrestrial surface) | Plants, vertebrates and insects | 1 |
| 65 | 3.1 | 2.3–3.7 | 2°C SST | Functional extinction of remaining coral reef ecosystems (overgrown by algae) | Globe | Corals, fish | 2 |
| 66 | 3.1 | 2.5–4.0 | 2 | High risk of extinction of Golden Bowerbird as habitat reduced by 90% | Australia | Birds | 4 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 67 | 3.1 | 1.8–4.2 | 3–4 | Risk of extinction of Alpine species | Europe | Plants | 41 |
| 68 | 2.4–4.0 | | | Of 40 endemic/near endemic species studied, 5–8 are threatened with extinction losing 90–100% of their original range | Europe | Birds | 73 |
| 69 | 3.3 | 2.8–3.8 | 2 | Risk of extinction of Hawaiian honeycreepers as suitable habitat reduced by 62–89% | Hawaii | Birds | 18 |
| 70 | 3.3 | | 3.7 | 4–38% of birds committed to extinction | Europe | Birds | 1 |
| 71[a] | 3.3 | | | 32–34% of bird species at risk of extinction, and 6–8% projected extinct | Western Hemisphere | Birds | 70 |
| 72 | 3.5 | 2.0–5.5 | | Projected extinction of 15–40% endemic species in global biodiversity hotspots (narrow specificity) | Globe | | 50 |
| 73 | 3.6 | 2.6–3.7 | | 30–40% of 277 mammals in 141 parks critically endangered/extinct; 15–20% endangered | Africa | Mammals | 23 |
| 74 | 3.9 | | | 4–24% plants critically endangered/extinct; mean species turnover of 63% (spatial range 22–90%); mean species loss of 42% (spatial range 2.5–86%) | Europe | Plants | 22 |
| 75 | 4.0 | 3.0–5.1 | 3 | Likely extinctions of 200–300 species (32–63%) of alpine flora | New Zealand | Plants | 33 |
| 76 | 4.0 | | | 1–10 species (1–9.% of 111 mammals studied) committed to extinction | Europe | Mammals | 71 |
| 77 | >4.0 | | 3.5 | 38–67% of frogs, 48–80% of mammals, 43–64% of reptiles and 49–72% of birds committed to extinction in Queensland as 85–90% of suitable habitat lost | Australia | Reptiles, amphibians, birds, mammals | 1, 7 |
| 78[a] | 4.5 | | | 39–42% of bird species at risk of extinction, and 10–15% projected extinct | Western Hemisphere | Birds | 70 |
| 79 | >>4.0 | | 5 | 57 endemic frogs/mammals eventually extinct, 8 endangered | Australia | Amphibians, mammals | 7 |

**Table 3** (continued)

| No. | $\Delta T_g$ above pre-ind °C | $\Delta T_g$ above pre-ind °C (range) | $\Delta T_{reg}$ above 1990 °C (range) | Impacts to unique or widespread ecosystems or population systems | Region | Taxa | Source |
|---|---|---|---|---|---|---|---|
| 80 | >>4.0 | | 7 | Eventual total extinction of all endemic species of Queensland rainforest | Australia | Reptiles, amphibians, birds, mammals | 7 |
| 81 | 5.0 | | | 22–24% of 100 *Banksia* species studied projected extinct | W. Australia | Plants | 74 |
| 82[a] | 6.9 | | | 50–57% of bird species at risk of extinction, and 19–30% projected extinct | Western Hemisphere | Birds | 70 |

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)
[a] Uniquely in this table, these five entries originate from a study which considers impacts by 2100 through a combination of climate change and land use change

**Table 4** Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise $\Delta T_g$, relative to pre-industrial climate (mean and range), showing also regional temperature change $\Delta T_{reg}$ relative to 1990 if provided by the literature: large-scale ecosystem collapse

| No. | $\Delta T_g$ above pre-ind °C | $\Delta T_g$ above pre-ind °C (range) | $\Delta T_{reg}$ above 1990 °C (range) | Impacts to unique or widespread ecosystems or population systems | Region | Taxa | Source |
|---|---|---|---|---|---|---|---|
| 83 | 2.5 | | 2°C SST | Functional extinction of coral reef ecosystems (overgrown by algae) | Indian Ocean | Corals, fish | 9 |
| 84 | 2.5 | 2.0–3.0 | | Major loss of Amazon rainforest with large losses of biodiversity | S America, Globe | | 21, 46 |
| 85 | >2.5 | | | Sink service of terrestrial biosphere saturates and begins turning into a net carbon source | Globe | Land ecosystems | 58, 59 |
| 86 | 3.1 | 2.3–3.7 | 2°C SST | Functional extinction of remaining coral reef ecosystems (overgrown by algae) | Globe | Corals, fish | 2 |
| 87 | 3.7 | | | Few ecosystems can adapt | Globe | | 6 |
| 88 | 3.7 | | | 50% of nature reserves cannot fulfil conservation objectives | Globe | | 6 |

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

**Table 5** Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise $\Delta T_g$, relative to pre-industrial climate (mean and range), showing also regional temperature change $\Delta T_{reg}$ relative to 1990 if provided by the literature: miscellaneous impacts

| No. | $\Delta T_g$ above pre-ind °C | $\Delta T_g$ above pre-ind °C (range) | $\Delta T_{reg}$ above 1990 °C (range) | Impacts to unique or widespread ecosystems or population systems | Region | Taxa | Source |
|---|---|---|---|---|---|---|---|
| 89 | 0.6 | | | Increased coral bleaching | Caribbean, Indian Ocean, Great Barrier Reef | Corals | 2 |
| 90 | <1 | | | Marine ecosystems affected by continued reductions in krill possibly impacting Adelie and chinstrap penguin populations; Arctic ecosystems increasingly damaged | Antarctica, Arctic | Crustaceans | 42, 11, 14 |
| 91 | 1.7 | 1–2.3 | 1°C SST | All coral reefs bleached | Great Barrier Reef, SE Asia, Caribbean | Corals | 2 |
| 92 | 1.9 | 1.0–2.8 | | Most areas experience 8–20% increase in number ≥7 day periods with Forest Fire Weather Index > 45: increased fire frequency converts forest and Macquis to scrub, leads to more pest outbreaks | Mediterranean | | 34 |
| 93 | 2.0 | 1.3–2.3 | 1 | 21% decline in spring macro-invertebrate abundance in upland streams | UK | Invertebrates | 62 |
| 94 | 2.1 | 1.0–3.2 | 1–2 | Alpine systems in Alps can tolerate local temperature rise of 1–2°C, tolerance likely negated by land use change | Europe | | 8 |
| 95 | 2.2 | – | | Net primary production rises from 45–60 (pre-industrial) to 60–75 Pg C/year; net ecosystem production from zero (pre-industrial) to 2.5–7.5 Pg C/year | Globe | | 69 |
| 96 | 2.3 | 2.0–2.5 | | Fish populations decline, wetland ecosystems dry and disappear | Malawi (Africa), Great Lakes | Fish | 20 |
| 97 | 2.4 | 2.0–3.5 | | 4–20% of the earth's terrestrial surface experiences novel climate; 4–20% experiences disappearing climate | Globe | | 61 |
| 98 | 2.4 | 1.8–3.2 | 3 | Extreme levels of mortality in loggerhead sea turtle | Southern US | Reptiles | 63 |
| 99 | 2.6 | 1.6–3.5 | | Most areas experience 20–34% increase in number ≥7 day periods with Forest Fire Weather Index > 45: increased fire frequency converts forest and Macquis to scrub, causes more pest outbreaks | Mediterranean | | 34 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 100 | 2.8 | 1.2–4.5 | 1–3 | Extensive loss/conversion of habitat in Kakadu wetland due to sea level rise and saltwater intrusion | Australia | | 10 |
| 101 | 2.8 | 2.5–3.0 | | Multimodel mean 62% (range 40–100%) loss Arctic summer ice extent, high risk of extinction of polar bears, walrus, seals; Arctic ecosystem stressed | Arctic | Mammals | 11, 53 |
| 102 | 2.9 | 1.6–4.1 | | Threat of marine ecosystem disruption through loss of aragonitic pteropods | S Ocean | Crustaceans | 49 |
| 103 | 2.9 | 1.6–4.1 | | 70% reduction in deep-sea cold-water aragonitic corals | Ocean Basins | Corals | 48 |
| 104 | 3.0 | | | In a study of 1420 pollinator species feeding on 429 plant species, 17–50% experience disruption in food supply | Illinois, USA | Plants, insects | 72 |
| 105 | 3.1 | 1.9–4.1 | 3–4 | Alpine systems in Alps degraded | Europe | | 8 |
| 106 | 3.2 | – | | Net primary production rises from 45–60 (pre-industrial) to 72–93 Pg C/year; net ecosystem production from zero (pre-industrial) to 0–7 Pg C/year | Globe | | 69 |
| 107 | 3.3 | 2.0–4.5 | | Reduced growth in warm water aragonitic corals by 20–60%; 5% decrease in global phytoplankton productivity | Globe | Corals | 2, 47, 48 |
| 108 | 4.0 | 2.5–4.5 | | 12–39% earth's surface experiencing novel climate; 10–48% disappearing climate | Globe | | 61 |

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

used originally by the study to assess the impact. The process was repeated (1) for the other 12 GCM/emission scenarios and (2) for eight surrounding adjacent grid cells to test the sensitivity of the results in terms of spatial coherence when using a group of grid cells versus a single grid cell. For each GCM scenario, the average $\Delta T$ for the nine (central plus eight adjacent) grid cells was computed. The resultant collection of up to 13 global $\Delta T$ values gave the range of global annual mean temperature rise as listed in Tables 2, 3, 4 and 5. In cases where a study has referred to an area larger than a group of nine grid cells, either a cluster of disjunct groups or contiguous orographic features, such as a mountain range or a plain, were aggregated into several clusters of grid cell groups across the region. The entries in the tables reflect also the average and range of outputs over the appropriate clusters of groups of grid cells.

Large local temperature increases can lie outside the range of the outputs of the GCMs held in the database. If this was the case, the study was not included in the upscaling calculations. GCMs with temperature changes that were too low to reach the study value(s) were excluded. Table 6 in the Appendix details which GCMs were used in the upscaling. If more than two GCMs were thus out of range, we assumed case f (Table 1) to avoid underestimating $\Delta T_g$. Note that the GCM time series for $\Delta T_g$ are provided with respect to an observed mean over the period 1961–1990, ensuring that correct temperature reference points were maintained in all upscaling.

## 3 Results

Tables 2, 3, 4 and 5 provide the resultant summary of key impacts on various ecological systems, ranging from the global level to that of individual, endemic species. The supplementary information in Table 6 in the Appendix provides for each entry from Table 2a–d information on the GCM runs used in upscaling, the climate variables considered by the impact study, and the category of the upscaling method we applied (a–h, see Table 1). 71 studies were found to provide sufficient quantitative climatic and ecological information for inclusion in Table 2a–d. Projected impacts were found for all major world regions, but only one study focused on Asia. Most studies were on terrestrial systems, whilst relatively few covered changes in the marine environment. Range losses and extinctions (Tables 2 and 3) were projected for many important taxa with vascular plants, birds, and mammals being particularly well represented. A significant number of studies also projected impacts on amphibians, reptiles, fish, butterflies, and freshwater or marine invertebrates. Table 2 also shows many projections for major losses of regional ecosystems as climate changes. Table 4 shows projections for large scale collapse in ecosystems, i.e. thresholds at which major components of the world's ecosystems become irreversibly damaged, positive feedbacks emerge, or their functioning, collapse. As global temperatures rise, many of these thresholds start to be crossed at around $\Delta T_g = 2.5°C$ above the pre-industrial level.

A key finding is that some significant negative impacts for range losses and extinctions (Tables 2 and 3), and also damages to marine ecosystems (Table 4), were projected to occur for values of $\Delta T_g$ below 2°C, especially in some biodiversity hotspots, and also globally for the diversity rich coral reef ecosystems ($\Delta T_g = 1.7°C$). However, it is also noticeable that, given the analyzed literature, projected impacts

increase in magnitude, numbers and geographic spread once a 2°C rise in global mean temperature is reached. Beyond this temperature rise the level of impacts and the transformation of the Earth's ecosystems become steadily more severe, with the potential collapse of some entire ecosystems, and extinction risks accelerating and becoming widespread. Additional positive feed-backs emerge causing land ecosystems to transition from their current status as a net carbon sink to a net carbon source.

## 4 Discussion

### 4.1 General

A large body of literature exists discussing the potential future impacts of climate change upon ecosystems, as reviewed in Fischlin et al. (2007). Much of this literature does contain only qualitative or no directly comparable quantitative projections of change or does not relate any quantitative estimates of change to quantitative changes in global climate. Previous integrating summaries of climate change impacts on wild species and ecosystems have suggested substantial ecosystem disruption with projected anthropogenic climate changes, and particularly the increased risk of species extinction (e.g. Thomas et al. 2004a, b). Such findings have been criticised partly because they did not reference the projected impacts to a consistent measure of climate change. In order to provide robust findings in a policy relevant manner, it is critical to reduce the uncertainty created by this lack of a common reference. Hence Warren (2006) and Hare (2006) both took steps to do so. The results reported here, through use of a common temperature reference point, confirm the likelihood of significant negative impacts of climate change first mooted in studies such as Thomas et al. (2004a, b), but provide a far clearer picture of the likely increase in scale of impacts with increasing levels of climate change, together with an indication of uncertainty associated with $\Delta T_g$.

With our common referencing system, we can also address the question as to what extent the literature has sampled the range of climate change forcings of the next few centuries adequately for the observations made by this study to be valid. The likely range of temperature increase in 2100 is 1.1°C to 6.4°C above the 1980–1999 average (i.e. 1.6°C to 6.9°C above the pre-industrial level), showing that the literature currently does not sample the upper end of this range, with most studies considering only the range between 1.5°C and 4°C above pre-industrial). Within these limits however, a broad range of global annual mean temperature rises is sampled, owing to the many different scenarios and GCMs used. This is the case for those studies that are based on GCM scenario outputs as well as the many other regional scenarios based only upon potential local, non-GCM-scenario based climate changes. A small subset of the studies considers the effects of doubling $CO_2$ concentrations, whilst another subset is based on transient climate change simulations. Because different GCMs are used in these subsets, the resultant global mean temperature, and concomitantly precipitation, values vary considerably among climate models, in particular in cases where regional scenarios of climate change were derived. We believe the small subset of table entries referring only to $CO_2$ concentration doubling has not introduced a bias. Owing to a sampling of a relatively comprehensive temperature

range similar to that covered by many scenarios (0.3–6.4°C, IPCC 2007), the overall interpretation of the results is not biased by any artificial clustering of data around a particular global mean temperature rise.

The majority of the impacts found in the literature are negative, with the exception of those projecting increases in primary production. Whilst a higher productivity may indeed increase vegetation growth, this in itself can disrupt species assemblages and thereby degrade ecosystems. For example, in tropical forests increased concentrations of $CO_2$ are stimulating rapid growth by vines (Granados and Körner 2002), which can strangle large trees (Phillips et al. 2002); and increasing growth rate and turnover of trees could even result in lower carbon storage rates, thus reducing the forest's service as a carbon sink (Feeley et al. 2007). Hence, with the exception of enhanced growth at moderate climate change we have rarely identified definitively positive impacts of climate change upon ecosystems. Whilst some authors consider transitions from desert to grassland or grassland to forest as "positive" in terms of gains in net primary production, this often neglects the issue of transient dynamics between previous and new equilibrium, and threats to endemic and specialist organisms of the replaced environments. Some studies indicate transitionally an even lower productivity (e.g., Fischlin and Gyalistras 1997).

### 4.2 Uncertainties in the analysis

This study has considered the role of uncertainty only in a limited manner, as it is difficult to quantify. The uncertainty analysis carried out is limited by its dependency on downscaling and upscaling of pattern-scaled transient temperature outputs of GCMs, and thus is contingent on the assumptions of pattern regularity as assumed in most down-scaling procedures (e.g., Gyalistras et al. 1994), in particular that the patterns are constant over a particular temperature range. It is also assumed that the patterns are independent of the history of greenhouse gas forcing, whereas in actuality an equilibrium climate change pattern may differ from transient ones. Equilibrium patterns were not available for this analysis, but would be more suitable for use with studies of type b, or studies of type c or d which actually use outputs of equilibrium runs of GCMs. The uncertainty analysis also reflects only the different relationships between global and local temperature displayed by various GCMs, and not the relationship between global temperature and local precipitation changes. In some cases where impacts are strongly driven by precipitation and models differ widely for the location in question, for example entry 41, the loss of forest cover in the Amazon basin (Cox et al. 2004), this could be important.

Much of the literature reviewed here is based on a biogeographical or bioclimatic approach. Whilst this approach has been criticised for its shortcomings in largely ignoring some mechanisms such as physiological responses, the treatment of species–species interactions, the limited accounting for population processes or migration (Pearson and Dawson 2003; Pearson 2006), or the common assumption that current species distributions are in equilibrium with current climate, the approach has nevertheless proved capable of simulating known species range shifts in the distant and the recent past (Martinez-Meyer et al. 2004, Araujo et al. 2005), and furthermore, is generally corroborated by the observed responses of many species to recent climatic changes (e.g. Walther et al. 2002; Root et al. 2003; Rosenzweig et al. 2007) and climate-change induced changes in geographical species ranges, which are starting to

be reported (Thomas et al. 2006; Foden et al. 2007). However the approach remains nevertheless to be comprehensively and explicitly tested against the observational record (Midgley and Thuiller 2005), an opportunity that should be taken as soon as possible. Most of the studies reported in Tables 2 and 3 result from detailed analysis of well-studied species and ecosystems in a given locality. In the case of the global extinction rate estimates (Thomas et al. 2004a) there has been a debate as to the validity of the particular species–area relationship used to estimate extinction rates (Thuiller et al. 2004; Thomas et al. 2004b; Buckley and Roughgarden 2004; Harte et al. 2004; Lewis 2006). Whilst these estimates are based on extrapolation of studies of endemics, Thomas et al. (2004b) argue that this creates only a small bias because such a large percentage of global species are in fact endemics. The study of Malcolm et al. (2006) provides an overall estimate of extinctions of endemics in biodiversity hotspots that does not rely on bioclimatic modelling of individual species, and generally supports the findings of Thomas et al. (2004a), though the use of endemic–area relationships rather than simple species–area relationships indicates some reduced impacts.

Responses of species to changing climate will also be affected by biotic interactions, which affect the levels of space occupancy and dispersal; e.g. in alpine plant communities, mutualists are expected to be able to tolerate greater climate change than competitors at slow rates of climate change, whereas at faster rates they may be excluded by competitors if these can easily disperse into newly climatically suitable areas (Brooker et al. 2007).

## 4.3 Factors omitted or partly considered in this study and the underlying literature

### *4.3.1 Direct effects from raising atmospheric $CO_2$ concentrations*

In Tables 2, 3, 4 and 5, the temperature column is essentially used as a proxy for the accompanying other changes, which will occur concurrently, such as precipitation change or elevated $CO_2$ concentrations. However, only a limited number of studies that project climate change impacts upon ecosystems consider concurrent changes such as the direct effects of elevated ambient $CO_2$ concentrations associated with local or global scenarios of temperature rise. This is particularly true of studies based on bioclimatic modeling, or niche-based modelling techniques that simulate species geographic range shifts. Despite increasing evidence that $CO_2$ fertilization effects on crop species have been somewhat overestimated in the past (Fischlin et al. 2007), those on wild plant species and particularly trees are corroborated by strong evidence (e.g., Ainsworth and Long 2005). This may remain a significant omission in the modeling of some ecosystem types. For example, $CO_2$ fertilization may differentially affect woody and herbaceous species, affecting the dynamics of forest–savanna–grassland conversions with major implications for biodiversity (Bond et al. 2003). Whilst a small number of entries in the tables derive from consideration of ocean acidification, the literature in this area is in its infancy. As oceans continue to acidify as atmospheric $CO_2$ concentrations rise concurrently with warming, there is significant potential for changes in marine food webs and hence the valuable ecosystem services that the oceans provide for humankind (Orr et al. 2005; Haugan et al. 2006).

*4.3.2 Indirect effects of climate change*

Tables 2, 3, 4 and 5, and the literature upon which they are based, largely document only the projected impacts on ecological systems resulting directly from climate changes such as changes in temperature and precipitation, the most commonly considered variables. However, there are a number of other impacts on ecosystems to be expected, that result from non climatic causes or indirectly via climatic changes. For example (1) wildfires and certain defoliating insects are projected to increase with warming (for example in boreal forests and the Mediterranean, e.g., Fischlin et al. 2007; Kurz et al. 2008), and decomposition rates will change by large percentages as rainfall changes (for example in deciduous forests in the USA, e.g. Lensing and Wise 2007) both of which is likely to have further impacts on forest and grassland ecosystems as well as causing substantive biotic feedbacks to the climate system; (2) secondary succession may last several centuries (Fischlin and Gyalistras 1997), thus delaying actual impacts and causing additional effects in other communities; (3) surprising ecological changes may also occur in marine and terrestrial communities with climate change if predators and prey become decoupled, or newly engage with each other, which could occur if they have differing phenological, geographical, and/or physiological responses to climate change (Price 2002; Burkett et al. 2005); (4) indirect impacts from sea ice melting, for example reductions in sea ice in the Antarctic are likely to have contributed to the dramatic 80% declines in krill observed since 1970 (Atkinson et al. 2004) with penguin populations already affected, and particularly if climate change shifts the Antarctic Circumpolar Current, krill could suffer further and the ecosystem could be severely impacted; (5) climate change is also projected to cause deglaciations, e.g. of the Himalayan region, which would adversely affect the hydrology of the downstream regions, e.g. of the Indian region including its ecosystems; (6) increases in the magnitude and/frequency of (intra-annual) extreme weather events are projected with climate change as climate variability increases (e.g. Schär et al. 2004; Meehl et al. 2007), all of which have a significant potential to affect ecosystems further (e.g. Fuhrer et al. 2006). Many impact models consider such effects only in a limited manner, e.g. because of a too coarse temporal resolution; (7) climate change may affect major modes of inter-annual cyclic variability such as El Nino, the North Atlantic Oscillation, or the Pacific Decadal Oscillation. GCMs do not capture such changes to a realistic extent and many impact models have only captured such climate variability effects to a limited extent if at all. Changes to these cycles are likely to affect ecosystems through for example, changed rainfall patterns and/or drought and fire incidence (e.g. Holmgren et al. 2001).

*4.3.3 Land-use change*

This meta-analysis focuses on the impacts of climate change and does not account for the effects of land-use change. More realistic impacts, notably those of species extinctions in 2100 and beyond, are likely to be greater than Tables 2, 3, 4 and 5 indicate, since land-use change is included in only one study (Sekercioglu et al. 2008), and is known to negatively impact biodiversity. These additional negative impacts from land-use change would only be avoided if effective stringent policies would soon be put into place that avoid further conversion of natural and semi-natural ecosystems to agriculture, landscape fragmentation, and/or other degradations within a

given type of land use as for instance also caused by intensification of agricultural practices. Owing to the development of human systems and their adaptation to climate change, including the potential use of biofuels as a mitigation measure, both of which may force new areas into cultivation, and the projected increases in global human populations, there are in fact rather to be expected increased pressures on extant land uses than the reverse. Some scenarios of future land uses have been developed for and reviewed in the Millennium Ecosystem Assessment (2005) and evince this overall trend.

Since land-use change is well known to be of critical relevance for biodiversity conservation, Lewis (2006) raised the concern that recent literature on potential extinctions due to climate change could distract conservationist's efforts in preventing land-use change in existing ecosystems, in particular with respect to avoiding deforestation. Jetz et al. (2008) projects losses of current ranges for 21–26% of the world's approximately 8,750 bird species by 2050, and for 29–35% by 2100, due to the combination of climate change scenarios from Solomon et al. (2007) and land-use change scenarios from the Millennium Ecosystem Assessment (MEA 2005). The need to provide for species to disperse successfully to reach areas that become newly climatically suitable increases the need for protecting existing ecosystems from land-use change. These findings suggest that avoided deforestation policies offer a crucial double benefit of reducing both climate change and land-use change impacts upon biodiversity. Thus, for these reasons we consider evidence that climate change can have severe impacts on biodiversity as presented in this analysis rather to provide an additional strong incentive for preserving existing ecosystems, including their protection from land-use changes, than an invitation to neglect conservation policies.

#### *4.3.4 Dynamics*

There are very few studies in the literature, which take into account the effect that the rate of climate change exerts upon ecosystems. This is also likely to be a key factor, since the slower the rate of change the greater is the potential for adaptation by dispersal or through natural selection for physical or behavioural characteristics better suited to a changed climate (for a recent review see Fischlin et al. 2007, notably Section 4.4.5). For very small amounts of warming there may be benefits in terms of increased productivity in ecosystems which are below their thermal optimum, for example in boreal forests. However, as temperature increases further the thermal optimum is passed, and the ecosystem begins to decline. It is the passing of such thresholds or "tipping points", the onset of negative impacts, which are the focus of the literature underlying this paper.

Some such "tipping points" are breached when a certain magnitude of climate change is reached. Regional features of the earth's climate system might also be disrupted, with concurrent un-quantified impacts upon ecosystems. For example, the Indian Monsoon might be disrupted (Zickfield et al. 2005). At the Earth system scale, as temperature continues to rise, additional positive feedback mechanisms may be activated. Examples are the saturation of the net carbon sink land ecosystems currently provide, the transition to a net source (Fischlin et al. 2007, Fig. 4.2), or the risk for the potential release of methane from tundra yedoma and permafrost (Fischlin et al. 2007) and perhaps beyond 2100 even clathrates from shallow seas. The weakening of the land sink, let alone the turning into a source, as well as a

release of substantive amounts of methane would cause a strong amplification of the greenhouse effect, greatly exacerbating the ongoing climate change.

Some such "tipping points" are breached when a certain rate of climate change surpasses the rate by which ecosystems can adapt naturally. During past phases of large climate changes, species have typically responded by shifting range rather than by evolving in situ (Davis and Shaw 2001). Ecosystems have been estimated to be able to withstand a temperature increase of only 0.05–0.1°C/decade (van Vliet and Leemans 2006), much slower than the current rate of 0.13°C/decade (Solomon et al. 2007) and hugely slower than the current rate near the poles of 0.46°C/decade, considered sufficient to cause serious ecosystem disruption. Foden et al. (2007) show how the currently observed migration rate of *Aloe dichotoma* (quiver tree), a Namib desert plant, in response to observed climate change, would be insufficient to keep pace with a moderate climate change scenario for 2050. Based on a comprehensive review of these issues Fischlin et al. (2007) concluded that "The resilience of many ecosystems is likely to be exceeded this century" for business-as-usual emissions scenarios (e.g. IS92a, A1FI, A2). Resilience is here understood as the capacity of ecosystems to adapt naturally and sufficiently fast to their changing environment without altering their mode of operation entirely.

This meta-analysis is based on impact studies that assume in many cases a new hypothetical equilibrium between the projected climate change and the impacted ecosystems. Typically the forcing climate change is then assumed to have remained constant indefinitely at the $\Delta T_g$ for which the impact was assessed and that the ecosystems are given sufficient time to adapt till the new estimated equilibrium has been reached. Most of the literature used in this analysis does not explicitly discuss the time dimension, but it can nevertheless be assumed in most cases that the ecosystem impacts in Table 5 might also occur if the temperature thresholds are breached transiently (i.e. local or regional temperature "overshoots") as simulated in various studies of the dynamics of climate change (O'Neill and Oppenheimer 2004).

Den Elzen and Meinshausen (2006) show that transient probabilities of exceeding various temperature thresholds might either be higher, or lower, than the equilibrium probabilities of exceedance of that threshold. Similarly Mastrandrea and Schneider (2006) show how probability of exceedance of temperature thresholds in stabilisation scenarios is a strong function of the pathway to stabilisation. Thus, one may argue that our assessment may indeed be questioned as the evolution of temperature and other concomitant climate change variables differ. However, the advantage of our approach is that the ranking of the impacts relative to the temperature increase as an indicator of climate change is unlikely to be affected even if the absolute values might have to be corrected as our understanding of these relationships progresses. In this respect our results can be viewed as being quite robust and conservative.

The question remains whether the impact models used have realistic sensitivities. Otherwise overestimations or underestimations of the impacts would have to be expected. The majority of the impact models we used here have considered changes in temperature as well as precipitation and many have also considered the beneficial effects from $CO_2$ fertilisation, in particular at the global level. This makes the models more likely to exhibit realistic responses to climate change than this was the case for many earlier studies, which followed less integrative approaches.

Nevertheless, the particular approach that many current state-of-the-art impact models follow may lead to biases. First in cases where the climate change was assumed to remain constant after having reached $\Delta T_g$, the impact models that have

not yet reached the new equilibrium tend to underestimate the impacts. Secondly, if the magnitude of climate change exceeds rapidly certain tolerances, i.e. the fundamental niches, of impacted species, even long-lived species such as trees are likely to suffer mortalities before they are replaced by newly arriving, other species for which the new, climatic situations are more benevolent. Thus, in general the more rapid climate change, the more likely such transient ecosystem degradations become. Indeed, the modelling approaches generally followed do incompletely mimic such effects and for these reasons tend to rather underestimate than overestimate impacts. Finally, for other processes such as coral bleaching and local extinction of sensitive species, which can occur within a relatively short time span of a few years, transient temperature peaks might be very critical. If emissions are reduced in a manner such that there is transient overshooting of the final equilibrium temperature, impacts may then be considerably greater than indicated in Tables 2, 3, 4 and 5.

Therefore we consider the results from our meta-analysis to be in general rather conservative and it appears to be unlikely that they are biased towards overestimating the severity of the consequences of climate change for ecosystems. However, critical uncertainties remain, in particular because most impact models depend to a large extent on knowledge about the realized niches only. Should fundamental niches be significantly larger than the realized ones, overestimations of climate change impacts are bound to result. Indeed, the difficulties to assess the true fundamental niches of most species remain a relevant source of uncertainty (Kirschbaum and Fischlin 1996), a fact that still significantly constrains the ability of most currently used kinds of ecological models to assess climate change impacts.

## 5 Conclusions

A literature-based integrated assessment of the effects of climate change upon a wide range of ecological systems has shown that the negative impacts accrue as annual global mean temperature rise as little as 1.6°C (low end of the likely range of IPCC scenarios,[1] IPCC 2007) above the pre-industrial level, already with several examples of projected severe damages, range losses, and extinctions. As global temperatures reach and exceed 2°C above pre-industrial levels, negative impacts rapidly increase. This includes increases in range losses and extinctions and increasing damage to some critical ecosystem structure and functioning. As global temperatures increase further beyond 2°C above pre-industrial, the literature and models increasingly project impacts accruing to entire systems and becoming more widespread across a range of different species groups and regions. Several critical aspects of ecosystem functioning are projected to begin to collapse at a temperature of 2.5°C (Table 4). These represent either the potential collapse of entire ecosystems e.g. wide-spread impoverishment of coral reefs, or comprise impacts, which are in our judgement dangerous, because they likely imply irreversible damages, such as extinctions of key species, or the onset of positive feedbacks, such as $CO_2$ emissions, accelerating climate change. In our judgement, risking the widespread collapse of multiple global

[1]This value considers the multi-model projected lower end of the likely range of the IPCC SRES B1 scenario (IPCC 2007, Table SPM.3) of +1.1°C warming by 2100 relative to 1980–1999 and adding +0.5°C already realized global warming for period 1980–1999 relative to preindustrial climate.

ecosystems (Table 4) represents "dangerous anthropogenic interference" and would comprise a breach of compliance with Article 2 of the United Nations Framework Convention on Climate Change.

This meta-analysis confirms and expands upon the results of other assessments (Houghton et al. 2001; Hare 2006; Warren 2006; Fischlin et al. 2007), which have shown that climate change is a threat to ecosystems and species worldwide, with coral reef, Arctic, Mediterranean, and mountain ecosystems including many biodiversity hotspots being particularly at risk. Hare (2006) also identified substantial increases in risks to ecosystems and species beyond the EU 2°C target using "burning ember" diagrams. We consider that our study, with a more extensive literature review, using a tabular approach and including some uncertainty analysis, provides further strong justification for policies constraining annual global mean temperature change relative to preindustrial climate to no more than 2°C—at least from an ecosystem preservation point of view. This temperature would avoid the projected breaching of the aforementioned large-scale ecosystem collapses, as well as a large proportion of the onset of many of the projected negative impacts such as range losses, extinctions, ecosystem damages including disruptions of their structure and functioning. Since we identified some significant impacts in biodiversity hotspots such as amphibian extinctions in tropical forests and wide spread coral bleaching in reefs below a 2°C warming, protection of the majority of ecosystems would however require a more stringent target, as argued by Rosentrater (2005) for the Arctic.

Many of the impacts tabulated here appear to be clearly in conflict with Article 2 of the United Nations Framework Convention on Climate Change in not allowing ecosystems to adapt naturally. Minimising the rate of climate change is expected to also reduce the risks of climate change for ecosystems, although this aspect can not yet be well analysed with current techniques available to assess impacts. According to the precautionary principle it appears that a reduction in current and future land use change will give ecosystems and species the best chance to adapt to the climate changes that are projected to occur in the twenty-first century even under stringent mitigation policy. In particular, avoided deforestation is a policy which meets both these goals, although alone this policy is of course not sufficient to constrain climate change to 2°C above pre-industrial levels. Further analyses of many of the findings from this study made in an even broader context of climate change impacts on ecosystems can be found in Fischlin et al. (2007).

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## Appendix

The Table 6 below contains detailed information concerning the underlying studies used in each entry of Tables 2–5, where column 1 is identical to column 1 of Tables 2–5, and the following abbreviations are used: **E** indicates an empirical derivation, **M** indicates a modelling study, a **number** refers to how many GCMs were used in the original literature. Other codes indicate if model projections included precipitation (**P**), ocean acidification (**pH**), sea ice (**SI**), sea level rise (**SLR**), sea

surface temperature (**SST**) or anthropogenic water use (**W**); dispersal assumptions from the literature. **D**—estimate assumes dispersal; **ND**—estimate assumes no dispersal; **NR**—not relevant since species/ecosystem has nowhere to disperse to in order to escape warming (e.g. habitat is at top of isolated mountain or at southern extremity of austral landmass). **IMAGE**, **BIOME4**, **LPJ**, **MAPSS** refer to specific models as used in the study, to assess climate change impacts, e.g. LPJ denotes the Lund–Potsdam–Jena dynamic global vegetation model (Sitch et al. 2003). **DVGM** refers to dynamic global vegetation model. GCM abbreviations used here: **H2**—HadCM2, **H3**—HadCM3, **GF**—GFDL, **EC**—ECHAM4, **CS**—CSIRO, **CG**—CG, **PCM**—NCAR PCM. Lower case a–h refers to how the literature was addressed in terms of up/downscaling and these are defined in Table 1. The GCM outputs used in the upscaling calculations are those used in the IPCC Third Assessment Report (TAR IPCC 2001) and are at 5° resolution: HadCM3 A1FI, A2, B1, B2 where A2 is an ensemble of 3 runs and B2 is an ensemble of 2 runs; ECHAM4 A2 and B2 (not ensemble runs); CSIRO mark 2 A2, B1, B2; NCAR PCM A2 B2; CGCM2 A2 B2 (each an ensemble of 2 runs). Where GCM scenario names only were provided further details were taken from: HadCM2/3 (Mitchell et al. 1995; Hulme et al. 1999; Arnell et al. 2004), http://ipcc-ddc.cru.uea.ac.uk.

**Table 6** Supplementary to Tables 2, 3, 4 and 5: the table below contains detailed information on models and how the upscaling and downscaling were performed for each entry in Tables 2, 3, 4 and 5 and uses the same numbering scheme

| Table no. | Entry no. | Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry |
|---|---|---|
| 2 | 1, 4, 9 | M, 5, ND, c; ref. quotes 13.8% loss in Rocky Mountains for each 1°C rise in JJA temperature, upscaled with CS, PCM, CG |
| 2 | 2, 15 | M, 5, IMAGE, a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990 |
| 2 | 3 | M, D, b; no GCM used in ref.; upscaled with H3, EC, CS, PCM, CG |
| 2 | 14, 32 | M, P, GDD, D&ND, a; ref uses B1 and A2 of H3 with ΔT rise of 2.4°C and 3.7°C respectively compared to the 1961–1990 mean |
| 2 | 6, 7 | M, P, NR, e; upscaled at several sites using H3, EC, CS, PCM, CG |
| 2 | 5 | M, H3, E4, P, D&ND, a; GFDL based estimates omitted due to lack of access to global temperature time series |
| 2 | 10 | M, H3, W, a; ref. uses B2 of H3 in 2070 that has a ΔT rise of 2.1°C with respect to the 1961–1990 mean |
| 2 | 11 | M, P, D, d; UKCIP02 high emission scenario used as central value; upscaled for Hampshire from UKCIP02 (Hulme et al. 2002) regional maps using H3, EC, CS |
| 2 | 12 | M, SLR, a; analysis based on transient 50% probability of sea level rise using the US EPA scenarios for ΔT of 2°C above 1990 baseline |

**Table 6** (continued)

| Table no. | Entry no. | Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry |
|---|---|---|
| 2 | 13 | M, H3, SLR, a; IS92a median ΔT 2.0°C above 1990 (Kattenberg et al. 1996, Fig. 6.20) and range 1.4–3.0°C |
| 2 | 16 | M, GE, P, NR, d; GENESIS GCM with 2.5°C rise for $CO_2$ doubling from 345 to 690ppm, 345 ppm corresponds quite closely to the 1961–1990 mean; upscaling then gives the range; across locations variously used H3, EC, CS, CG |
| 2 | 17 | M, NR, b; upscaled with H3, EC, CS, and CG |
| 2 | 18 | M, P, D, HadCM3, ECHAM4, GFDL, a; Huntley et al. (2006) give 2.5°C relative to 1961–1990 mean |
| 2 | 19 | M, 2, P, d, g; range is due to importance of ΔP, GFDL $CO_2$ doubling is from 300 ppm which is close to 1900 climate sensitivity in ref of 3.7; UKMO in 2050 is 1.6°C above 1961–1990 mean, 1.9°C above preindustrial |
| 2 | 20, 21 | M, H2, BIOME4, P, NR, c; A1 scenario of H2GS has ΔT of 2.6°C relative to 1961–1990 mean |
| 2 | 22 | M, BIOME3, P, d, f; H2 2080s has global ΔT of 2.6°C above 1961–1990 mean |
| 2 | 23 | M, H3, W, a; ref. uses A2 of H3 in 2070 that has a ΔT of 2.7°C with respect to the 1961–1990 mean and hence 2.5°C with respect to 1990 |
| 2 | 24 | M, H3, GF, EC, P, D&ND, a |
| 2 | 25 | M, CS, P, d; upscaled with H3, EC, CS, CG |
| 2 | 26 | M, H2, SLR, NR, a; H2 2080s without aerosols has global ΔT of 3.4°C above pre-industrial (Hulme et al. 1999) |
| 2 | 27 | M, 2, P, D, d; study used $CO_2$ doubling scenarios—CCC ΔT at doubling is 3.5°C relative to 1900 whilst GFDL R30 is 3.3°C relative to 1900; upscaling gives range H3, EC, CG |
| 2 | 28 | M, D, b; upscaled with H3, EC, CS |
| 2 | 29 | M, CCC, P, D, d; $CO_2$ equilibrium doubling scenario has ΔT of 3.5°C relative to 1900; downscaled with CGCM and upscaled with H3, EC, CS, CG |
| 2 | 30 | M, 5, IMAGE, P,a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990 |
| 2 | 31 | M, P, D (based on empirical calibration), d; upscaled with H3, EC, CS, PCM, CG |
| 2 | 33 | M, D, f; Meehl et al. (2007), Fig. 10.3.5 shows this occurs for ΔT ≥3.5°C above 1990 |
| 2 | 12, 34 | M, D&ND, P, HadCM3, a; Ohlemüller et al. (2006) use HadCM3 projections quoted as '2.0, 4.8°C above 1931–1960 mean for entries 12, 34 respectively, add 0.1°C to convert to pre-industrial |

**Table 6** (continued)

| Table no. | Entry no. | Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry |
|---|---|---|
| 2 | 35 | M, 3, P, a |
| 2 | 36 | M, SLR, a; US EPA scenario of 4.7°C above 1990. |
| 3 | 37 | E |
| 3 | 38 | M, D&ND, a; 18% matches minimum expected climate change scenarios which Table 3 of Thomas et al. (2004a) lists as ΔT of 0.9°–1.7°C (mean 1.3°C) above 1961–1990 mean; 8 of 9 sub-studies used H2 |
| 3 | 39, 55, 71, 78, 82 | M, D, a; |
| 3 | 40 | M, H2, P, ND, d; table 3 of Thomas et al. (2004a) gives global ΔT of 1.35°C above 1961–1990; HHGSDX of H3; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG |
| 3 | 41 | M, H2, P, D&ND, d; Beaumont and Hughes (2002) give global mean temperature rise of 1.8°C relative to the 1961–1990 mean |
| 3 | 42 | M, D, P, a |
| 3 | 43 | M, D, b; upscaled using H3, EC, CS, PCM, CG |
| 3 | 44 | M, H3, P, D, d; H3 2050 SRES mean |
| 3 | 45 | M, H2, P, D, d, g; table 3 of Thomas et al. (2004a) gives global ΔT of 1.35°C above 1961–1990; upscaled with H3, EC, CS, PCM, CG; uses a local ΔT range across Australia |
| 3 | 46 | M, H3, P, D&ND, d; ref. uses B1 of H3 in 2050 with a ΔT of 1.8°C above the 1961–1990 baseline; downscaled with H3 and then upscaled with H3, EC, CG |
| 3 | 47 | M, H2, P, D&ND, d; studies used global annual mean ΔT of 1.7–2.0°C above 1961–1990 mean |
| 3 | 48 | M, P, D&ND, a; table 3 of Thomas et al. (2004a) mid-range climate scenarios have a mean ΔT of 1.9°C above 1961–1990 |
| 3 | 49 | M, H2, P, D&ND, d; ref. refers to A2 of H3 in 2050 that has a ΔT of gives as 1.9°C above 1961–1990 (Arnell et al. 2004); downscaled with H3 then upscaled with H3, EC, CS, PCM, CG |
| 3 | 50 | H; upscaled using maps from WGI, chapter 10 |
| 3 | 51 | M, 2, P, NR, d; scenarios on CRU website used with ΔT of 2.0°C above 1961–1990, agrees with Table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG |
| 3 | 52 | M, H2, P, D, d; the 66% is from a suite of 179 representative species, table 3 of Thomas et al. (2004a) lists global ΔT of 2.0°C above 1961–1990 mean, upscaled with H3, EC, CS, CG |
| 3 | 53 | M, H2, P, D&ND, d; table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean using HHGGAX; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG |

**Table 6** (continued)

| Table no. | Entry no. | Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry |
|---|---|---|
| 3 | 54 | M, H2, P, ND, d; table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean using HHGGAX; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG |
| 3 | 56 | M, IMAGE, P, D&ND; Bakkenes et al. (2002) gives the global temperature change relative to 1990 |
| 3 | 57 | M, P, D&ND; ref. uses B1 in H3 in 2080s from (Arnell et al. 2004) |
| 3 | 58 | M, SST, h |
| 3 | 59 | M, H2, D&ND, d; ref. uses global ΔT of 2.3°C above 1961–1990 mean; downscaled with H3 and upscaled with H3, EC, CG |
| 3 | 60, 76 | M, P, D & ND, a |
| 3 | 61 | M, 15, SI, a; Arzel et al. (2006) uses 15 GCMs with A1B for 2080s, ΔT A1B 2080s multi-model from WGI, chapter 10, Fig. 10.3.2 is 2.5°C above 1990; ACIA uses 4 GCMs with B2, multi-model ΔT is 2.2°C over 1961–1990 or 2.0°C above 1990 |
| 3 | 62 | M, P, D, HadCM3, ECHAM4, GFDL, a; Huntley et al. (2006) give 2.5°C relative to 1961–1990 mean |
| 3 | 63 | M, 10, P, D, d, g; Beaumont and Hughes (2002) give global mean temperature rise of 2.6°C relative to the 1961–1990 mean |
| 3 | 64 | M, P, D, ND, a; Table 3 of Thomas et al. (2004a) maximum climate scenarios have a mean ΔT of 2.6°C above 1961–1990 or 2.3°C above 1990 |
| 3 | 65 | M, SST, h |
| 3 | 66 | M, P, NR, e; upscaled for several sites taken from maps in ref., using H3, EC, CS, CG |
| 3 | 67 | M, NR |
| 3 | 68 | M, 3, a, P, cloudiness, D & ND |
| 3 | 69 | M, NR, b; % derived from Table 1 in Benning et al. (2002) for all forest areas combined on the 3 islands studied; upscaling considers changes averaged over 3 islands and uses H3, EC, CS, CG |
| 3 | 70 | M, H3, P, D&ND, d, f; table 3 of Benning et al. (2002) lists global ΔT of 3°C above 1961–1990 mean |
| 3 | 72 | M, 7, BIOME3, MAPSS, P, D&ND, a; uses $CO_2$ doubling scenarios from Neilson and Drapek (1998) Table 2; control concentrations were obtained directly from modellers; thus deduced mean global mean ΔT for this study |
| 3 | 73 | M, H3, P, D&ND, d; ref. uses A2 in H3 in 2080 that has a ΔT of 3.3°C above 1961–1990 (Arnell et al. 2004) |
| 3 | 74 | M, H3, P, D, d, f; ref. lists ΔT of 3.6°C for A1 in H3 in 2080 relative to 1961–1990, downscaled with H3 and upscaled with H3, EC, CG |

**Table 6** (continued)

| Table no. | Entry no. | Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry |
|---|---|---|
| 3 | 75 | M, NR, b; upscaled with H3, EC, CG |
| 3 | 77 | M, NR, b, f; Meehl et al. (2007), Figs. 10.3.5 and 10.3.2 suggest global ΔT of 3.5°C relative to 1990 |
| 3 | 79 | M, NR, b, f; Meehl et al. (2007), Fig. 10.3.5 shows this occurs for ΔT ≥3.5°C above 1990 |
| 3 | 80 | M, NR, b, f |
| 3 | 81 | M, 3, P, a |
| 4 | 83 | M, SST, h |
| 4 | 84 | M, a |
| 4 | 85 | M, 2, P, LPJ; upscaled with H3, EC5 |
| 4 | 86 | M, SST, h |
| 4 | 87, 88 | M, 5, IMAGE, a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990 |
| 5 | 89 | M, 4, SST |
| 5 | 90 | E, SI |
| 5 | 91 | M, SST, h |
| 5 | 92 | M, P, NR, d; HadRM3PA2 in 2050, Fig. 13 in Moriondo et al. (2006) shows ΔT matching B2 of H3 of 1.6°C above 1961–1990 mean; downscaled with H3 and upscaled with H3, EC, CS, PCM, CG |
| 5 | 93 | M, P, D (based on empirical calibration), d, upscaled with H3, EC, CS, PCM, CG |
| 5 | 94 | E, P, D, b; upscaled using H3, EC, CS, PCM, CG |
| 5 | 95 | M, H2 with aerosols in 2050, a, 6 DVGMs, global temperature taken from Raper et al. (2001). |
| 5 | 96 | E, P, NR, a |
| 5 | 97 | M, a; Williams et al. (2007) use the B1 scenario from a mean of 9 GCM simulations used in IPCC (2007) which have a global temperature increase of 1–2.5°C averaging approximately 1.9°C above 1990 (hence 2.4 above pre-industrial) |
| 5 | 98 | M, d; upscaled using H3, EC, CS, PCM, CG |
| 5 | 99 | M, P, NR, d; HadRM3PA2 in 2050, taken from Fig. 13 of Moriondo et al. (2006) |
| 5 | 100 | M, CS, b; upscaled with H3, EC, CS, PCM, CG |
| 5 | 101 | M, 15, SI, a; Arzel et al. (2006) uses 15 GCMs with A1B for 2080s, ΔT A1B 2080s multi-model from WGI, chapter 10, Fig. 10.3.2 is 2.5°C above 1990; ACIA uses 4 GCMs with B2, multi-model ΔT is 2.2°C over 1961–1990 or 2.0°C above 1990 |
| 5 | 102, 103 | pH, g; IS92a in 2100 has 788 ppm $CO_2$ and ΔT of 1.1–3.6°C above 1990 |
| 5 | 104 | M, a; |
| 5 | 105 | E, P, D, e; upscaled with H3, EC, CS |
| 5 | 106 | M, H2 with aerosols in 2100, a, 6 DVGMs, global temperature taken from Raper et al. (2001) |

**Table 6** (continued)

| Table no. | Entry no. | Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry |
|---|---|---|
| 5 | 107 | pH, a; impact is at $CO_2$ doubling, T range given by IPCC (2007) for equilibrium climate sensitivity |
| 5 | 108 | M, a; Williams et al. (2007) use the A2 scenario from a mean of 9 GCM simulations used in IPCC (2007) which have a global temperature increase of 2–4°C averaging approximately 3.5°C above 1990 (hence 4°C above pre-industrial) |

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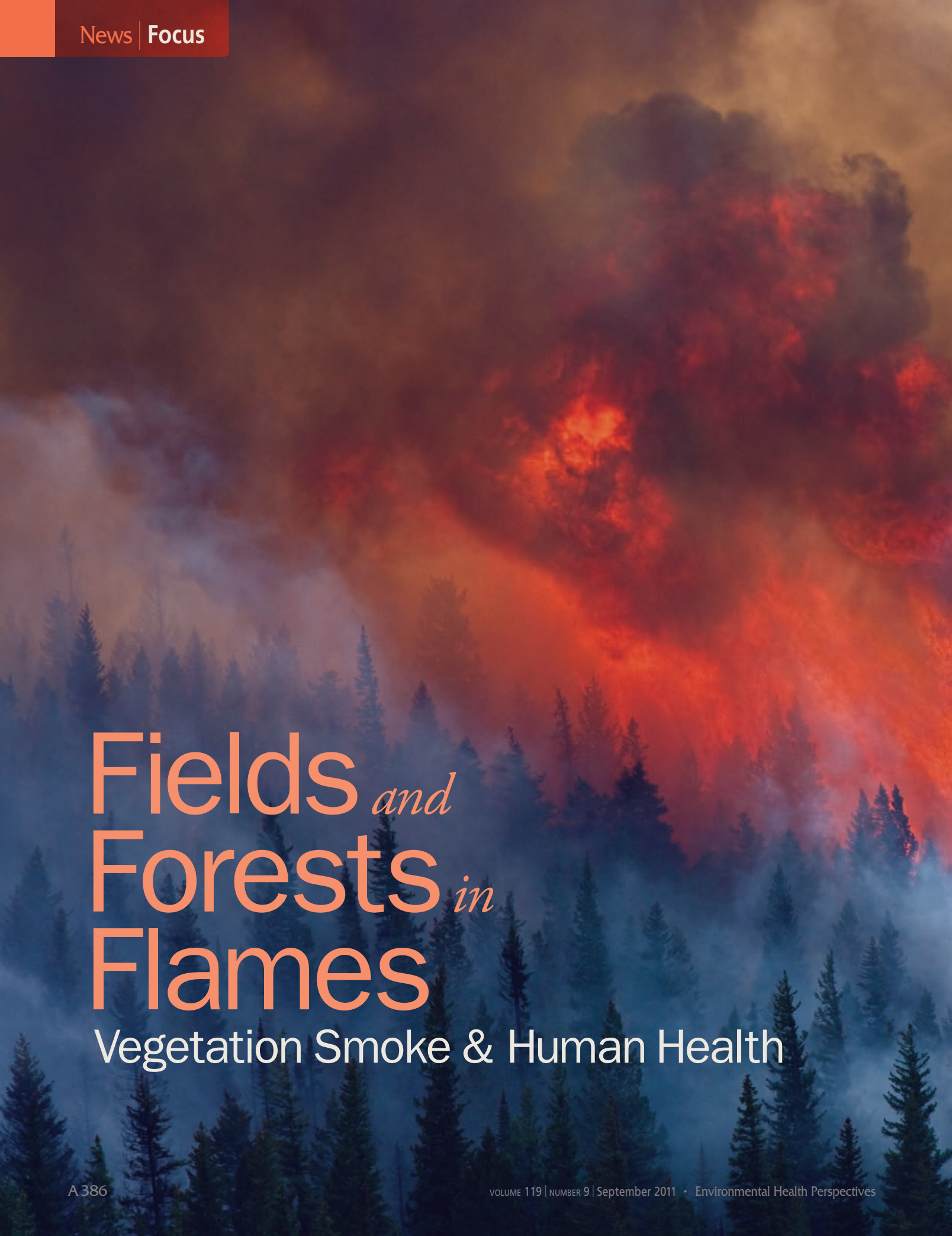

# Fields *and* Forests *in* Flames

## Vegetation Smoke & Human Health

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*Author Bob Weinhold lived this article this summer as the area where he lives was regularly swathed in smoke from wildfires nearby and in New Mexico and Arizona, each of which had the largest wildfire in its history. The smell of the fumes reminded him of his days fighting and patrolling for wildfires while working for the U.S. Forest Service in Oregon.*

People have lived for tens of thousands of years in the presence of smoke from fires. That long period of adaptation tends to allow healthy younger adults in today's environments to be generally resistant to serious adverse health effects from smoke from sources such as wildfires, prescribed forest burns, agricultural field burns, and peat bog fires, says Wayne Cascio, director of the U.S. Environmental Protection Agency (EPA) Environmental Public Health Division.

But a high percentage of people aren't young, healthy adults. In the United States, nearly half the population suffers from at least one chronic illness,[1] potentially placing them at risk for adverse effects from exposure to fire smoke. Children and older adults also are considered more vulnerable to smoke's effects.[2] The limited health research that's been done on smoke from large-scale fires has provided some refinements to these general categories of vulnerable people, and new information occasionally emerges. There also has been a trickle of information identifying the toxic substances that characterize smoke from various kinds of fires, and pinning down the specific body systems that are vulnerable and the pathways through which damage occurs.

**The Red Eagle Fire of 2006 burned more than 34,000 acres across Glacier National Park and adjacent Blackfeet Tribal Land.**

But much remains unknown about the varying toxicity of emissions from different types of vegetation fires and the vulnerability of specific groups of people, although a good deal of research has examined the adverse health effects of smoke related to heating and cooking with wood.[3] Filling these voids is essential, Cascio says. "It is critically important to define who is at highest risk so that individual and community-based intervention strategies can be developed to specifically mitigate the health risks associated with smoke exposure," he says. "The goal, of course, is to provide education or intervention to the most sensitive individuals in the most cost-effective way without needlessly worrying or interfering with the daily activities of [others]."

Such information can also help organizations and individuals who deal with fire threats as they work to integrate health concerns with many other factors, such as land management practices and programs, cultural mores, political influences, and funding.

## Conflagrations in the Woods

In the United States there has been an irregular but generally upward trend in the occurrence and severity of forest wildfires in the last 50 years. Each year between 1960 and 2010, some 1.1–9.9 million acres burned, with the highest acreage burned in 2006.[4] At least 7 million acres burned in each of 7 of those 50 years; 6 such years occurred in the period 2000–2010.[4] At least 5 million acres burned in each of 14 years, 10 of which fell in the period 1996–2010.

The annual acreage burned is expected to increase to about 10–12 million acres within just a few years.[5] One of the forces expected to drive this projected increase in fires is climate change, which is expected to usher in increased drought, spreads in insect damage, and longer fire seasons, according to the U.S. Forest Service, Bureau of Land Management, U.S. Fish and Wildlife Service, National Park Service, Bureau of Indian Affairs, and National Association of State Foresters, and a growing body of independent studies.[5,6,7] Among the areas expected to face the greatest increase in fire threats are the Southeast, Southwest, and West, although the Midwest and East also are expected to experience some increases.

However, some experts remain cautious, saying the science on wildfires and future impacts of climate change is still a work in progress. Brian Schwind, director of the U.S. Forest Service's Remote Sensing Applications Center, says, "It's a really complicated picture with a lot of variables. We're early in the analytical phases. Sometimes we jump to conclusions a little fast."

**Clockwise from top left:** The Station Fire burns north of Los Angeles, California, 30 August 2009. A wall of smoke from the fire rises over the city that same day; by the next day the Los Angeles skyline was obscured. The Station Fire was considered a "megafire," meaning it could not be extinguished without the aid of natural forces such as rain.

Clockwise from top left: © Gene Blevins/Reuters, © AP Photo/Jon Vidar, © Fred Prouser/Reuters

Historically, people have caused most wildfires. Of the 63,591–96,386 fires that occurred each year from 2001 to 2010, 80–90% were human-caused in any given year.[8] For acreage burned, lightning often plays a much bigger role—when lightning fires strike backcountry areas, they are more often allowed to burn. But people still were the ignition source for 12–65% of the acreage burned in any of those years.[8] Among the human causes of fires are arson, accidents, carelessness, and intentional prescribed fires designed to reduce acute threats or remove vegetation for planting, wildlife management, or other purposes.

More people have the opportunity to accidentally or intentionally start a fire as they increasingly move into the so-called wildland–urban interface, where residential areas butt up against and mingle with forests.[5] That settlement pattern puts more people into close proximity to major fire sources, increasing the odds they'll receive significant smoke exposures. It also results in an increase in man-made structures being burned by forest fires, says Stephen Mueller, a senior specialist in atmospheric science for the Tennessee Valley Authority. "Buildings and other structures usually contain plastic materials and various stored chemicals—pesticides, insecticides, paint, solvents, cleaning solutions, etc.—that release extremely toxic substances when burned," he says. "This can represent a significant source of toxic air pollutants in certain areas."

Globally, forest wildfire statistics are very scarce, says Pieter van Lierop, forestry officer with the Food and Agriculture Organization (FAO) of the United Nations. In 2010 hard data were available for less than half the world's countries and only about three-fourths of the world's forests.[9] Inconsistent methods and reporting make it impossible to determine realistic total numbers of fires and acreage burned for any given year, or to detect trends. But it's clear from global satellite images that significant fires in all types of vegetation occur multiple times every year on all continents except Antarctica.[10] The percentage of these fires that are caused by humans is considered to be roughly 90–95%, van Lierop says.

Although hard global data aren't available, researchers have used models and satellite images to calculate that fires in grasslands and savannas account for 44% of fire-derived carbon emissions, with 20% from tropical deforestation and degradation fires, 16% from tropical woodland fires, 15% from fires in forests outside the tropics, 3% from agricultural field burning, and 2% from peat fires.[11] These estimates don't necessarily reflect emissions of toxic substances, though, because emissions vary according to factors such as the type of vegetation burned, moisture content, fire temperature, wind conditions, how "aged" the smoke is, and time of year.

A global picture is also emerging for what are being termed "megafires," according to a report sponsored by the FAO.[12] The authors say the megafire label applies when a burn can't be controlled by people without the help of natural forces such as rain, and it causes significant, long-lasting effects on an area's environment and social and economic structure. Prime examples covered in some detail in the report include fires in Australia (2009), Botswana (2008), Brazil (1998), Greece (2007), Indonesia (1997/1998), Israel (2010), Russia (2010), and the United States (2003).

Other megafires have occurred in other years in some of these countries as well as in countries such as Canada, China, South Africa, Portugal, Spain, and Turkey. All were fueled in part by overzealous fire suppression or land practices that substantially altered the more fire-resistant natural vegetation mosaic and allowed fuels[13] to accumulate.[12] Drought and "extreme fire weather" (i.e., low humidity and high temperature combined with high winds) increased the hazard, and people almost always were the final straw, acting as the match in one way or another. Should these preventable fires increase as projected,[9] their size and inability to be controlled will escalate the number of people exposed to toxic smoke and the length of time they are at risk.

## Who's Affected by Wildfire Smoke?

The general health threat posed by smoke close to a fire has been widely recognized in the past decade by organizations such as the EPA,[14] the U.S. Centers for Disease Control and Prevention,[2] the California Department of Public Health,[15] and the Pediatric Environmental Health Specialty Units, a network of academically based children's environmental health experts.[16] But people some distance away also are exposed. For instance, on many days in June 2011 the smoke plume from Arizona and New Mexico's Wallow Fire extended as far as 1,000 miles.[17]

However, one of the large deficits in knowledge about the toxicity of smoke is the distance from a fire at which the smoke still poses a significant health threat, according to many experts. "Smoke changes as it travels, and the PM [particulate matter] might pose greater risk when it is closer to the source," says Sarah Henderson, an environmental epidemiologist at the British Columbia Centre for Disease Control. However, she adds, "Anytime that smoke results in elevated PM, it has health effects."

Smoke can contain thousands of individual compounds, in categories such as PM, hydrocarbons and other organic chemicals, nitrogen oxides, trace minerals, carbon monoxide, carbon dioxide, and water vapor.[15] As just one example of elements in a complex mix, a 2009 fire in a mixed-evergreen forest in central Portugal generated emissions that included degradation products from biopolymers (such as levoglucosan from cellulose and methoxyphenols from lignin), *n*-alkanes, *n*-alkenes, *n*-alkanoic acids, *n*-alkanols, monosaccharide derivatives from cellulose, steroid and terpenoid biomarkers, polycyclic aromatic hydrocarbons (with retene being the most abundant), and even-carbon-number homologs of monoglycerides (which the authors say were identified for the first time as biomarkers in biomass burning aerosols).[18]

The health effects widely considered to be linked with wildfire smoke include exacerbation of preexisting respiratory conditions such as asthma and chronic obstructive pulmonary disease (COPD), reduced lung function, chest pain, and general symptoms such as eye irritation, fatigue, headache, dizziness, and stress.[15] Woodsmoke exposure may depress the respiratory immune defenses[19] and has been linked with emergency department visits for upper and lower respiratory effects.[20] The evidence regarding cardiovascular effects has been mixed, but recent research is reinforcing these health issues as a possible area of concern, though sometimes only for certain categories of people in any given study.[21,22,23,24,25,26]

Based on the limited research conducted so far, public health officials generally consider children, older people, pregnant women, smokers, and people with chronic respiratory problems to be especially vulnerable to health effects from outdoor fires.[2,15,16] Cascio says other populations that might be vulnerable and deserve greater study include diabetics, fetuses, people with cystic fibrosis and primary pulmonary hypertension, and those carrying certain genetic polymorphisms.

Refinements to this information are surfacing as studies trickle out. For instance, a study of bushfires in the Darwin, Australia, area in 2000, 2004, and 2005 found indigenous people were significantly more vulnerable to a range of respiratory disorders and had a statistically significant increase in hospital emissions for ischemic heart disease 3 days after initial exposure to smoke in relation to each 10-μg/m$^3$ increase in $PM_{10}$.[22] The patients may have been at greater risk than others in the area because of greater underlying cardiorespiratory problems, the authors say.

This finding may be broadly applicable around the world. "Many other indigenous populations have a similar spectrum of social disadvantage and ill health as those from Australia, so the higher risk we saw in indigenous Australians is likely to be similar for those groups," says Fay Johnston, lead author of the study and a public health physician and research fellow at the University of Tasmania's Menzies Research Institute. This kind of knowledge can help refine local responses

**Top to bottom: The Las Conchas Fire burns in the Jemez Mountains of New Mexico southwest of Los Alamos National Laboratory, June 2011. If the fire had reached the nuclear waste stored at the laboratory, the result could have been a plume of radioactive smoke; extensive thinning around the facility reportedly averted such a disaster. October 2003 wildfires in San Diego County, California, destroyed more than 900 homes. The burning of buildings, vehicles, and other trappings of human society can add more toxic substances to wildfire smoke.**

to fires. "If a severe smoke pollution event were to affect an indigenous community," Johnston says, "the health outcomes are likely to be more serious, and public health officials would need to consider this when planning their responses."

Another line of research involves the toxicologic differences between wildfire smoke and other types of particulate pollution. In an investigation of wildfires in central and northern California in 2008, researchers found that PM collected in the city of Tracy over 2 days at the peak of the fires was about 10 times more damaging to alveolar macrophages than ambient PM collected in the area under normal conditions, on an equal-dose basis.[27] In California's Central Valley, another team of researchers investigated differences between air in an urban area, Fresno, and near a wildfire about 100 miles to the northwest near Escalon.[28] PM from each area induced very different inflammatory, oxidative stress, and xenobiotic responses in human bronchial epithelial cells, providing further evidence that it's probably inappropriate to simply extrapolate findings on urban pollution to wildfire pollution.

However, urban air and wildfire smoke can have one thing in common—isocyanic acid, which was recently identified for the first time in outdoor air in each of these settings.[26] The limited information available indicates the acid could plausibly contribute to cardiovascular problems and inflammation, although effects at the concentrations present in wildfire smoke have yet to be observed.

Much more is generally known about the health risks posed by ground-level ozone, and a recent study indicates wildfires in the western United States can help spark the formation of the toxic substance, increasing ambient ozone by up to 50 ppb for a short period of time and potentially traveling long distances.[29] Such bursts of ozone could cause affected areas to exceed the current federal 8-hour ozone standard of 75 ppb.[30]

In addition to polluting the air, wildfires can affect soil and water quality. In a study following fires in 2005 and 2006 in three watersheds in Southern California, researchers found organic or particulate-bound mercury in surface soils can be more readily deposited in waterways after a fire.[31] Awareness of that tendency could lead to actions such as better testing of fish in affected waterways or improved sampling for water quality if the waterways are a drinking water source. However, it appears this phenomenon may depend on local soils, vegetation, waterways, and weather, because an analysis of 146 sites in Minnesota that had burned some time between 1759 and 2004 found intense fires had reduced soil mercury concentrations for tens, even hundreds, of years.[32] In contrast, such reductions lasted only a year or so in the California settings.[31]

## Prescriptions for Fires

Wildfires are not the only large-scale fires humans encounter; in many areas around the world, people are exposed for substantial periods of time each year to smoke from prescribed (or controlled) fires, which are commonly used to preclude out-of-control wildfire threats. Experts attempt to do these on days with suitable weather (i.e., higher humidity, lower temperature, and low wind), when atmospheric conditions allow optimal smoke dispersion. They also try to restrict how the fire will spread, for instance by scraping out a perimeter line or setting fires from an outside boundary where terrain or winds will force the burn inward. But such fires still generate considerable smoke

Top to bottom: NASA; © Mark Avery/Orange County Register/Corbis

of varying compositions. In addition, they occasionally escape their intended boundaries and turn into wildfires.

U.S. federal, state, and other agencies have conducted prescribed burns on about 2.2 million acres per year in the past decade.[33] Prescribed fires also are widely used globally, though hard data is scant.

Research on the health effects of prescribed burns is very limited. In a study of South Carolina prescribed fires, researchers found that plots in which the vegetation had been mechanically chipped in advance of burning emitted significantly less PM and carbon monoxide than nonchipped plots.[34] The authors say this has implications for both firefighters and nearby communities. In Georgia, another team found emissions of most volatile organic compounds were much higher during the smoldering phase of prescribed fires in pine forests compared with the flaming phase.[35] They also found emissions of several pinene compounds from prescribed fires were much higher than those from fireplace wood burning.

A study of prescribed burns in Arizona ponderosa pine forests found the emissions, which included PM, polycyclic aromatic hydrocarbons, organic carbon, elemental carbon, potassium, chlorine, sulfur, and silicon, were characteristic of smoldering, low-intensity burns.[36] On the basis of the information in this and other studies, Marin Robinson, chairwoman of the Department of Chemistry and Biochemistry at Northern Arizona University, says, "I would argue that the biggest health effects associated with prescribed burns are short-term and involve susceptible individuals living in neighboring communities."

Problems could be significant in some settings, though. In another study of the Darwin, Australia, area, researchers found that when $PM_{10}$ from fires (many of which were prescribed burns) exceeded 40 μg/m$^3$, emergency department admissions for asthma increased sharply.[37] That concentration is far below the current 24-hour standard of 150 μg/m$^3$ established by the U.S. EPA[38] and even the level of 65–75 μg/m$^3$ recommended in September 2010 by the agency's Clean Air Scientific Advisory Committee.[39] Other researchers report that smoke from prescribed fires in Australian bushlands contained acrolein, formaldehyde, and carbon monoxide at levels of concern.[40]

## Other Types of Fires: Bogs and Cropland

Although wildfires in peat bogs are the source of just a small fraction of the world's smoke emissions, they can have a major impact on air quality in the areas where they burn. For instance, they were an important fuel in the megafires in Russia and Indonesia, and they occur widely in boreal forests. Since they become more flammable in normally moist areas that are undergoing extended drought, they could become an increasingly important smoke source if drought becomes more common in some areas.

A large June 2008 peat bog fire in North Carolina that burned about 6 weeks generated smoke affecting significant portions of the state. The fire, smoldering in peat 3–15 ft deep, had a poor oxygen supply and generated extensive smoke due to incomplete combustion. There were periods of $PM_{2.5}$ concentration greater than 200 μg/m$^3$ at ground-based monitors 200 km from the fire.[21] The composition of peat fire emissions is known to differ substantially from forest fires, but the relative toxicity of these emissions is unknown. However, Mueller points out that low-temperature or smoldering combustion such as that associated with peat fires (and fireplaces) is notorious for emitting high amounts of carbon monoxide.

Moscow, Russia, during wildfires of the summer of 2010. Record-breaking high temperatures and drought conditions across Russia set the stage for these 2010 fires. These "extreme fire weather" factors are expected to occur more frequently in more locales in coming years.

Whatever the specific toxic substances were, researchers studying cardiopulmonary-related emergency department visits associated with the 2008 peat bog fire found a 37% relative increase in heart failure (traits of the population studied, such as low income and high prevalence of health problems such as hypertension, diabetes, ischemic heart disease, and heart failure, may have contributed to susceptibility).[21] They also reported increases in emergency department visits for COPD (73% increase), asthma (65% increase), and pneumonia and acute bronchitis (59% increase).[21] Major peat fires were burning once again in North Carolina throughout late spring and summer of 2011.[41,42,43]

In agricultural fields, burning residue is a common practice worldwide. It's done to kill pests, improve fertilization (by increasing nitrogen availability), and make planting easier, often at a lower cost than some other options such as mechanical tilling. As with forest wildfires, global data on field burning is limited. However, an analysis of satellite images from 2001 through 2003 indicated that about 1.5–1.6 million agricultural field burns occurred each year, accounting for an average 8–11% of annual global fire activity.[44] Regions with the highest activity included the Russian Federation, Eastern Europe, and Central Asia.

In the United States, field burning averaged 43% of the equivalent area burned by wildfires from 2003 to 2007 and peaked at 79% of the equivalent area in 2003.[45] Field burning is a source of pollutants such as fine and coarse PM, nitrogen dioxide, sulfur dioxide, carbon monoxide, and methane.[46] The states with the highest emissions (largely from sugarcane, wheat, rice, and bluegrass fields) are Arkansas, California, Florida, Idaho, Texas, and Washington. In those six states alone, about 15.5 million people live in "source" counties (that is, counties with crop burning

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areas), although it's uncertain how many had significant smoke exposures.[46] The percentage of a state's population that lives in source counties can be quite high, such as 47% in Idaho and 25% in Arkansas.[46]

Field burning can occur for extended periods of time in any given area, leading to chronic exposures to the emissions.[46] Smoke can readily waft beyond the source counties, although as with forest fires, the distance at which toxic effects occur remains largely unknown.

The limited research on health effects of field burning has found some significant respiratory and cardiopulmonary problems, says Jessica McCarty, a research scientist at Michigan Tech Research Institute. "The threat is highly variable, based on [local farming] laws, air quality laws, crop type, and cultural practices of burning," she says.

## Few Studies, Many Possibilities

All together, there have been several dozen studies of health effects related to wildfires, prescribed forest burns, peat bog fires, and agricultural field burning. That's a relatively small number given the huge variation in source material that can burn, the various underlying conditions of people who can be affected, and other variables (by comparison, more than 1,700 health studies have been conducted for ground-level ozone). One reason for that dearth is that the research is hard to do.

Johnston explains that fires often are short-term events, and appropriate individual health data are often lacking, as are data on possible confounders. Sometimes the available study population isn't large enough to generate clear associations. Another major limitation is the lack of monitoring data in burn areas. More recent studies are beginning to circumvent this issue by using tools such as pollution models and satellite data. But those approaches still have limitations that often don't allow them the precision of ground monitors.

Despite the difficulties, "it is clear that more research must be done to fully characterize the chemical composition of the particulate matter arising from these various sources," Cascio says. Ralph Delfino, vice chair for research and graduate studies at the University of California, Irvine, Department of Epidemiology, says more information is needed about the mechanisms through which fire emissions cause harm. "It would also be useful from a public health perspective to have better information for health advisories such as data to forecast the locations of smoke plumes and data on the clinical characteristics of potentially susceptible populations to enable targeted alerts. There is sufficient evidence to warn people with persistent asthma who may benefit from the use of preventive antiinflammatory medications," he says. He adds that improved application of satellite imagery plus ground-level air monitoring could help in forecasting smoke movements.

Despite the potential public health benefits to be had from these types of studies, Delfino says he has repeatedly found little support for this kind of research, possibly because decision makers and funders are rarely exposed to significant smoke. "People change their minds when they are in the middle of it, though," he says.

North Carolina Forest Service

**The Pains Bay peat fire in Dare County, North Carolina, was started 5 May 2011 by a lightning strike. The peat that feeds smoldering fires like this one can extend more than a dozen feet underground. These fires are notoriously hard to extinguish.**

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**Clockwise from top left: a sweet potato field in Indonesia; a sugarcane field in Cuba; a bluegrass field in Rathdrum, Idaho. Agricultural field burning is practiced around the world as a relatively inexpensive way to prepare fields for crops. Some jurisdictions around the world require permits prior to an agricultural burn, addressing issues such as extent and timing, in an effort to reduce health risks to area residents.**

Clockwise from top left: © Rob Huibers/Panos Pictures; © Chris de Bode/Panos Pictures; © Jerome A. Pollos/AP Photo

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RESEARCH ARTICLE

# Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species

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## Abstract

Current climate change may be a major threat to global biodiversity, but the extent of species loss will depend on the details of how species respond to changing climates. For example, if most species can undergo rapid change in their climatic niches, then extinctions may be limited. Numerous studies have now documented shifts in the geographic ranges of species that were inferred to be related to climate change, especially shifts towards higher mean elevations and latitudes. Many of these studies contain valuable data on extinctions of local populations that have not yet been thoroughly explored. Specifically, overall range shifts can include range contractions at the "warm edges" of species' ranges (i.e., lower latitudes and elevations), contractions which occur through local extinctions. Here, data on climate-related range shifts were used to test the frequency of local extinctions related to recent climate change. The results show that climate-related local extinctions have already occurred in hundreds of species, including 47% of the 976 species surveyed. This frequency of local extinctions was broadly similar across climatic zones, clades, and habitats but was significantly higher in tropical species than in temperate species (55% versus 39%), in animals than in plants (50% versus 39%), and in freshwater habitats relative to terrestrial and marine habitats (74% versus 46% versus 51%). Overall, these results suggest that local extinctions related to climate change are already widespread, even though levels of climate change so far are modest relative to those predicted in the next 100 years. These extinctions will presumably become much more prevalent as global warming increases further by roughly 2-fold to 5-fold over the coming decades.

## Author Summary

Climate change is an important threat to the world's plant and animal species, including species on which humans depend. However, predicting how species will respond to future climate change is very difficult. In this study, I analyze the extinctions caused by the climate change that has already occurred. Numerous studies find that species are shifting their geographic ranges in response to climate change, typically moving to higher elevations and latitudes. These studies also contain valuable data on local extinctions, as they document the loss of populations at the "warm edge" of species' ranges (lower elevations

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and latitudes). Here, I use these data to show that recent local extinctions related to climate change have already occurred in hundreds of species around the world. Specifically, among 976 species surveyed, local extinctions occurred in 47%. These extinctions are common across climatic zones, habitats, and groups of organisms but are especially common in tropical regions (which contain most of Earth's species), in animals (relative to plants), and in freshwater habitats. In summary, this study reveals local extinctions in hundreds of species related to the limited global warming that has already occurred. These extinctions will almost certainly increase as global climate continues to warm in the coming decades.

## Introduction

Anthropogenic climate change may be a major driver of biodiversity loss in the next 100 years, but the possible impacts of climate change on species survival remain highly uncertain [1–3]. Global mean annual temperatures increased by ~0.85˚C between 1880 and 2012 and are likely to rise by an additional 1˚C to 4˚C by 2100 [4]. Modeling studies have predicted that various levels of species loss will result from this future climate change, ranging from 0% to >50% of all species currently known [3]. This uncertainty has many sources (e.g., different climate models and different hypotheses about species dispersal). One of the most important sources of uncertainty hinges on the details of how species respond to climate change. For example, if species can evolve rapidly enough in response to changing climate, then species extinctions due to climate change might actually be limited [5,6].

Species can potentially respond to climate change in several ways. The most important case to consider may be that when the species' present-day (realized) climatic niche no longer occurs within the species' current geographic range (because of the potential for global extinction of the species under these conditions). In this case, the possible responses of the species include the following: (i) undergoing niche shifts, such that the species' realized niche changes to incorporate these new climatic conditions (e.g., through plastic changes and/or by evolutionary adaptation to the modified abiotic and/or biotic conditions), (ii) dispersing to track the original climatic conditions over space (e.g., moving to higher latitudes or elevations), and (iii) going extinct [5–8]. While each of these responses has been shown in some cases (at least in local populations), the relative frequency of each is still unclear [7,8]. However, changes in species' geographic ranges have been especially well documented [9–11].

These data on geographic range shifts contain important but underutilized information on how species respond to climate change. Range shifts observed under climate change typically involve an overall shift towards higher latitudes and higher elevations [9–11]. These shifts can be composed of one (or both) of two types of changes (Fig 1): (i) range expansions at the cool edge of the species range (higher latitudes and elevations) and (ii) range contractions at the warm edge (lower latitudes and elevations). The presence of warm-edge contractions is critically important. A warm-edge contraction occurs when populations from one or more localities at the lowest latitudes or elevations of a species' regional distribution disappear (i.e., are inferred to no longer occur at those localities), leading to an overall shift in the species range towards higher latitudes or elevations. These contractions indicate that species are failing to shift their niches sufficiently to tolerate these new conditions and that these populations are instead going extinct (referred to as "local extinction" hereafter). This must be true regardless of the specific mechanism of local extinction (e.g., elevated death rates, increased emigration, or declining recruitment). The many papers that have assessed range shifts and that have included surveys of warm-edge populations can therefore provide a wealth of data about

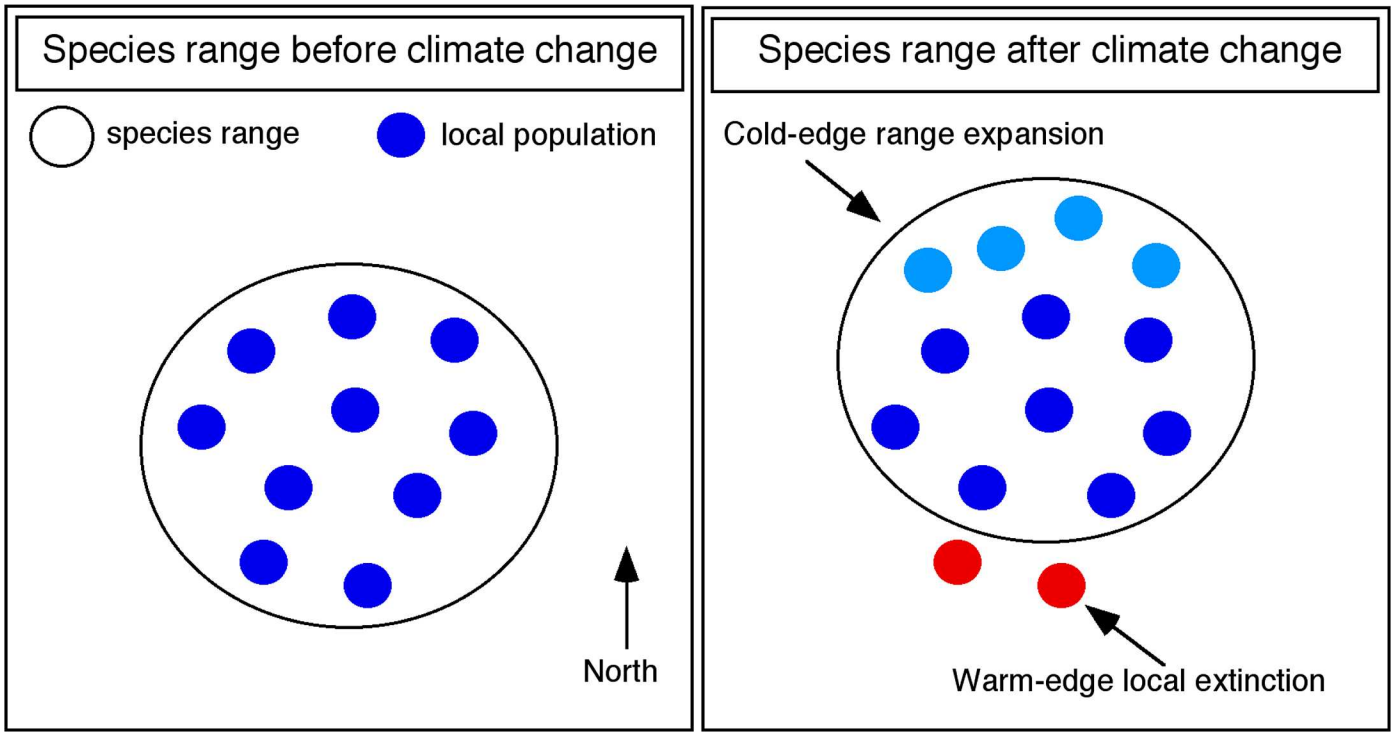


**Fig 1. Hypothetical example illustrating the two components of a geographic range shift associated with climate change.** The large open circle indicates the species' overall geographic range. Small dark blue circles indicate populations before climate change. After climate change, the overall geographic range is shifted northward (large open circle), both through the range expansion (new populations; small light blue circles) added at the northern, "cold" edge of the species range and range contraction (local extinction of original populations; small red circles) at the southern, "warm" edge of the species range. Similar patterns occur for range shifts along an elevational gradient. Modified from Cahill et al. [12].

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which species have (and have not) undergone local extinctions potentially related to climate change. These data are particularly useful because published papers on range shifts need not be strongly biased towards documenting warm-edge contractions, given that many studies that included data on warm edges also surveyed the cool edge. Thus, even though studies that failed to find any range shifts might go unpublished (a potential source of bias), studies that documented an overall range shift need not show a warm-edge contraction.

Here, I analyze the extensive data on range shifts to examine the prevalence of local extinctions related to modern climate change. I also provide a synthesis of inferred local extinction across habitats, climatic zones, and taxonomic groups. I systematically searched the literature for studies that examined shifts in species' ranges at their warm edges, shifts that were considered (in the original studies) to be related to current climate change. Hundreds of examples of local extinctions were found across diverse climatic zones, habitats, and taxonomic groups. Not all species exhibiting range shifts showed warm-edge contractions, but ~50% of the species surveyed had local extinctions inferred to be related to climate change. These results suggest that even the relatively small changes in climate that have already occurred are sufficient to cause widespread local extinctions and that many species may be unable respond to climate change fast enough to avoid extinction as global climate warms even further.

## Results

The Web of Science was searched repeatedly between December 2014 and March 2016 using keywords related to climate change, range shifts, and local extinctions (see Materials and

Methods). All studies that monitored the warm edge of at least one species' range and that tied their results to climate change with explicit statistical analyses were included. Importantly, studies can document overall range shifts but need not find that the warm-edge populations that they examined had local extinctions.

A total of 27 studies (Table 1; [13–39]) met all the necessary criteria to address potential climate-associated warm-edge range shifts (see Materials and Methods). The sampled species were broadly distributed across clades (e.g., animals = 716; plants = 260) and regions (e.g., Asia = 332; Europe = 268; Madagascar = 30; Oceania = 58; North America = 233; South America = 55). Among the 976 unique species surveyed, 460 species had warm-edge contractions, and 516 did not (S1 Appendix). Therefore, local extinctions related to climate change are already very common (47.1% of species examined), even given the relatively modest rise in global temperatures that has occurred so far (less than 1˚C increase in global mean annual temperature; [4]).

These 976 species spanned many clades, habitats, and regions (Table 1; S1 Appendix). Comparison between those species that showed warm-edge contractions and those that did not provides potential insights into which species may be most sensitive to climate change, in terms of the climatic zones and habitats that they occur in and the clades that they belong to. Furthermore, there is no evidence that there were more species with local extinctions in studies that ended more recently, were of longer duration, or began earlier (based on midpoints for ranges of values; Table 1). Specifically, regression analyses of the proportion of species with local extinctions against (i) the study end date, (ii) the duration of the study, and (iii) the study start date all yielded nonsignificant results (end date: $r^2 = 0.001$, $p = 0.8910$; duration: $r^2 = 0.045$, $p = 0.2896$; start date $r^2 = 0.047$, $p = 0.2788$; after removing nine studies with four or fewer species: end date: $r^2 = 0.146$, $p = 0.1181$; duration: $r^2 = 0.132$, $p = 0.1376$, but unexpectedly trending towards fewer extinctions in studies with longer durations; start date $r^2 = 0.177$, $p = 0.0821$, with more extinctions in studies beginning more recently, not earlier). Therefore, the frequency of local extinctions was initially compared across species in different studies, regardless of differences in the duration, beginning, or end date of the study in which they were surveyed.

Overall, the frequency of local extinctions was similar (close to 50%) across most climatic zones, habitats, gradients, and clades. Nevertheless, there were some significant differences. First, local extinctions were significantly more common in species from tropical and subtropical regions (combined and referred to as tropical hereafter for brevity) than in those from temperate regions ($p < 0.0001$; Chi-squared test, testing the assumption of equal frequencies of local extinction among species between regions; subsequent $p$-values are also from Chi-squared tests). Specifically, 54.6% of the 504 included tropical species had local extinctions, whereas only 39.2% of the 472 temperate species did (Fig 2A). The pattern was even stronger when only considering terrestrial species on elevational gradients (54.6% of 504 tropical species versus 28.2% of 301 temperate species), which applied to all plants and most animals. In part, this pattern of more frequent tropical extinction arose from a much lower frequency of extinctions for temperate plants (59.4% of 155 tropical species versus 8.6% of 105 temperate species; $p < 0.0001$). The very low frequency of temperate extinctions in plants was based on a single study from very high latitudes [19]. Nevertheless, there were also significantly more local extinctions in tropical animals (52.4% of 349 tropical species versus 38.8% of 196 temperate species; $p = 0.0022$), if one compares terrestrial species on elevational gradients. This restriction also made them more comparable to the sampled plants (all from terrestrial, elevational gradients) and still encompassed most sampled animal species (76.1%; 545 of 716 species). Across all animals, the difference was not significant ($p = 0.2309$), possibly because of the influence of temperate marine and freshwater species (see below). Among the most well-

**Table 1. Summary information on the 27 range-shift studies used to document local extinctions related to climate change.** Studies are listed alphabetically by first author. The major taxonomic group surveyed is given (Taxon, all groups are animals except for "Plant"), along with the total number of species surveyed (Total Species), the percentage of those species with one or more local extinctions (% Local Extinction), the general habitat type (Habitat; including terrestrial, freshwater, and marine), the climatic region (tropical-subtropical versus temperate), the geographic region where the study was conducted (note that North America here extends to Central America), the type of range shift (latitudinal, elevational), the dates of the initial survey and the resurvey, and the duration in between (for surveys and/or resurveys spanning multiple years, the midpoint of each was used to calculate the duration).

| Reference | Taxon | Total Species | % Local Extinction | Habitat | Climatic Region | Geographic Region | Range Shift | Initial Survey | Resurvey Date | Duration |
|---|---|---|---|---|---|---|---|---|---|---|
| Angelo and Daehler [13] | Plant | 4 | 50 | Terrestrial | Tropical | Oceania (Hawaii) | Elevational | 1966–1967 | 2008 | 41.5 |
| Beever et al. [14] | Mammal | 1 | 100 | Terrestrial | Temperate | North America | Elevational | 1898–1956 | 2003–2006 | 77.5 |
| Brusca et al. [15] | Plant | 27 | 56 | Terrestrial | Tropical | North America | Elevational | 1963 | 2011 | 48 |
| Chen et al. [16] | Insect | 208 | 56 | Terrestrial | Tropical | Asia | Elevational | 1965 | 2007 | 42 |
| Comte and Grenouillet [17] | Fish | 31 | 74 | Fresh. | Temperate | Europe | Elevational | 1980–1992 | 2003–2009 | 20 |
| Dieker et al. [18] | Insect | 2 | 50 | Terrestrial | Temperate | Europe | Elevational | 1958–1986 | 2008–2009 | 36.5 |
| Felde et al. [19] | Plant | 105 | 9 | Terrestrial | Temperate | Europe | Elevational | 1900 | 2008 | 108 |
| Forero-Medina et al. [20] | Bird | 55 | 29 | Terrestrial | Tropical | South America | Elevational | 1969 | 2010 | 41 |
| Franco et al. [21] | Insect | 3 | 100 | Terrestrial | Temperate | Europe | Latitudinal | 1970–1999 | 2004–2005 | 20 |
| Freeman and Freeman [22] | Bird | 54 | 74 | Terrestrial | Tropical | Oceania (New Guinea) | Elevational | 1965 | 2012 | 47 |
| Hiddick et al. [23] | Marine invertebrates | 65 | 55 | Marine | Temperate | Europe | Latitudinal | 1986 | 2000 | 14 |
| Hitch and Leberg [24] | Bird | 1 | 100 | Terrestrial | Temperate | North America | Latitudinal | 1967–1971 | 1998–2002 | 31 |
| Menendez et al. [25] | Insect | 39 | 54 | Terrestrial | Temperate | Europe | Elevational | 1981–1993 | 2006–2007 | 24 |
| Moritz et al. [26] | Mammal | 27 | 41 | Terrestrial | Temperate | North America | Elevational | 1914–1920 | 2003–2006 | 87.5 |
| Myers et al. [27] | Mammal | 8 | 12 | Terrestrial | Temperate | North America | Latitudinal | 1883–1980 | 1981–2006 | 62 |
| Nye et al. [28] | Fish | 28 | 50 | Marine | Temperate | North America | Latitudinal | 1968 | 2008 | 40 |
| Perry et al. [29] | Fish | 10 | 40 | Marine | Temperate | North America | Latitudinal | 1997 | 2001 | 24 |
| Ploquin et al. [30] | Insect | 16 | 69 | Terrestrial | Temperate | Europe | Elevational | 1988–1989 | 2007–2009 | 19.5 |
| Pomara et al. [31] | Squamate | 1 | 100 | Terrestrial | Temperate | North America | Elevational | 1965 | 2008 | 43 |
| Raxworthy et al. [32] | Amphibian-Squamate | 30 | 37 | Terrestrial | Tropical | Madagascar | Elevational | 1993 | 2003 | 10 |
| Rowe et al. [33] | Mammal | 4 | 25 | Terrestrial | Temperate | North America | Elevational | 1927–1929 | 2006–2008 | 79 |
| Rubal et al. [34] | Mollusca | 7 | 29 | Marine | Temperate | Europe | Latitudinal | 1917, 1940 | 2011 | 94 |
| Sheldon [35] | Insect | 1 | 0 | Terrestrial | Temperate | North America | Elevational | 1977–1978 | 2006 | 28.5 |
| Telwala et al. [36] | Plant | 124 | 60 | Terrestrial | Tropical | Asia | Elevational | 1849–1850 | 2007–2010 | 159 |
| Tingley et al. [37] | Bird | 92 | 25 | Terrestrial | Temperate | North America | Elevational | 1900–1930 | 1980–2006 | 78 |
| Warren and Chick [38] | Insect | 2 | 0 | Terrestrial | Tropical | North America | Elevational | 1973–1974 | 2012 | 38.5 |

(*Continued*)

**Table 1.** (*Continued*)

| Reference | Taxon | Total Species | % Local Extinction | Habitat | Climatic Region | Geographic Region | Range Shift | Initial Survey | Resurvey Date | Duration |
|---|---|---|---|---|---|---|---|---|---|---|
| Zuckerberg et al. [39] | Bird | 31 | 71 | Terrestrial | Temperate | North America | Both | 1980–1985 | 2000–2005 | 20 |

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sampled groups of animals, tropical extinction was significantly more common in birds (51.4% of 109 tropical species versus 37.1% of 124 temperate species; $p = 0.0284$), but not in insects (local extinctions in 55.2% of 210 tropical species versus 59.0% of 61 temperate species; $p = 0.6007$). For other animal groups, the species sampled here were either predominantly temperate (mammals, fish, and marine invertebrates) or tropical (squamate reptiles and amphibians), and so did not allow for similar within-clade comparisons.

Overall, the frequency of climate-related local extinctions (Fig 2B) was similar in terrestrial (45.6% of 835 species) and marine environments (50.9% of 110; $p = 0.2964$). In contrast, the frequency in freshwater species was substantially higher (74.2% of 31; $p = 0.0053$ across all three habitats). However, the estimate for freshwater species was based on a single study of European fishes [17]. Comparing fish only (all temperate) also supported a significantly higher frequency of extinction in freshwater environments relative to marine environments ($p = 0.0240$; local extinctions in 47.4% of 38 marine species versus 74.2% of 31 freshwater species). All marine species included here were temperate animals, but there was no significant difference in extinction frequencies between marine and terrestrial environments when only temperate animals were compared ($p = 0.1676$; marine: 50.9% of 110 species, terrestrial: 42.9% of 226 species). Terrestrial and freshwater species remained significantly different in this more restricted comparison ($p = 0.0011$).

The frequency of local extinctions (Fig 2C) was somewhat lower for species surveyed along elevational gradients relative to those on latitudinal gradients (elevational: 45.8% of 836 species; latitudinal: 55.0% of 140 species; $p = 0.0439$). Most (78.6%) species measured along latitudinal gradients were marine (and all marine studies focused on latitudinal gradients), and all were temperate. Again, most species included here were based on studies of elevational gradients in terrestrial environments.

Local extinctions were also broadly similar in frequency across taxonomic groups (Fig 3). Nevertheless, local extinctions were significantly more common ($p = 0.0018$) in animals (50.1% of 716) than plants (38.8% of 260). This difference was reduced when comparing only animals and plants on terrestrial, elevational gradients (47.3% of 556 animal species versus 38.8% of 260 plant species; $p = 0.0236$). Among these latter species, the plant–animal difference was nonsignificant for tropical species (and was actually reversed: local extinctions in 52.4% of 349 tropical animal species versus 59.4% of 155 tropical plants; $p = 0.1500$) but was strong for temperate species (38.6% of 207 temperate animal species versus 8.6% of 105 temperate plants; $p < 0.0001$).

The frequencies of local extinctions across different animal groups (Fig 3) were broadly similar to the overall value for animals (50.1%), but with higher values in insects (56.1% of 271 species; based on six studies; Table 1) and fish (59.4% of 69 species; three studies) relative to mammals (35.0% of 40 species; four studies), birds (43.8% of 233 species; five studies), amphibians (36.8% of 19 species; one study), and squamate reptiles (lizards and snakes; 41.7% of 12 species; two studies). Local extinctions were also broadly similar in frequency in various groups of marine invertebrates, including crustaceans (46.7% of 15; one study), annelids (64.5% of 31; one study), and molluscs (45.4% of 22; two studies). The frequency in echinoderms was lower (25.0%; one study) but was based on a very small sample size (4 species).

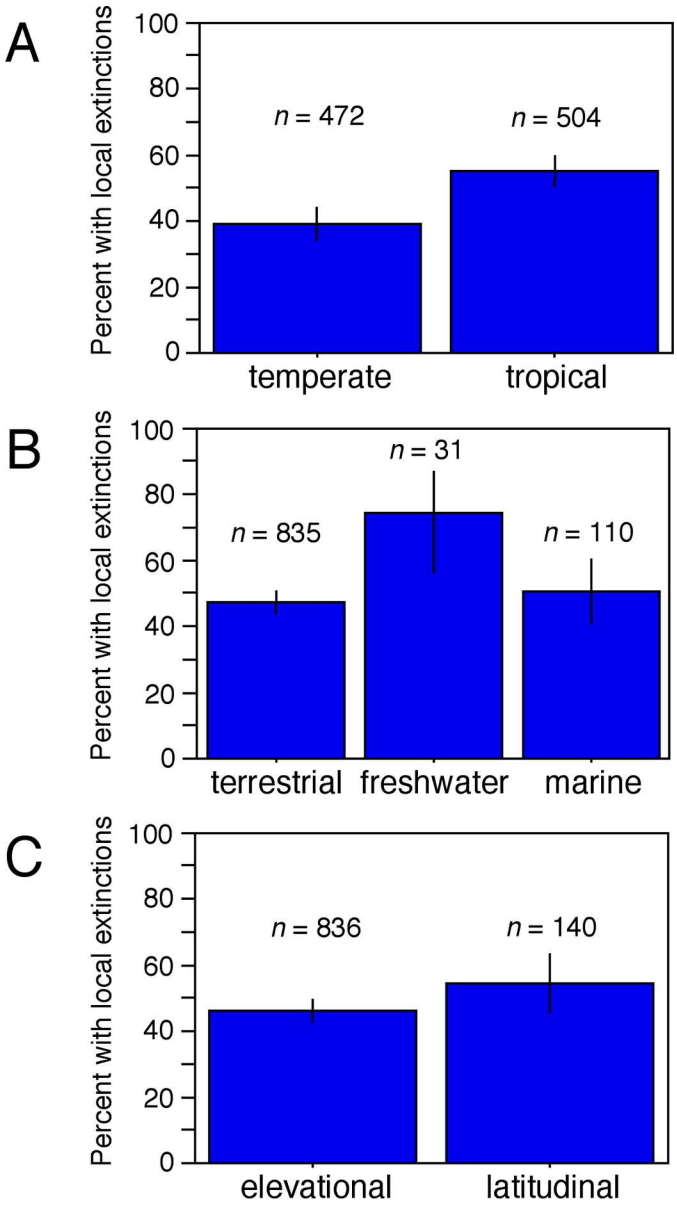


**Fig 2. The frequency of local extinctions related to climate change across different climatic regions, habitats, and gradients.** (A) Species are categorized as temperate or tropical (based on the location of the study), and the percentage of species with one or more local extinctions is shown, along with the sample sizes of species in each region. (B) Species are categorized as terrestrial, freshwater, or marine, and the frequency of species with local extinctions is shown (along with total species per habitat). (C) Species are categorized based on whether they were surveyed along elevational or latitudinal transects. Vertical lines indicate 95% confidence intervals on the estimated frequency of species with local extinctions.

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Results were generally similar using both general linear models (GLMs; see below) and general linear mixed models (GLMMs; see next paragraph). GLM results are given in full in S2 Appendix and are summarized here. Simultaneously including all 976 species and most variables (habitat [terrestrial versus freshwater versus marine], climatic regions [tropical versus temperate], taxonomic group [plants versus animals], survey type [latitudinal versus elevational], and study dates [start date, end date, and duration in between]) showed that most

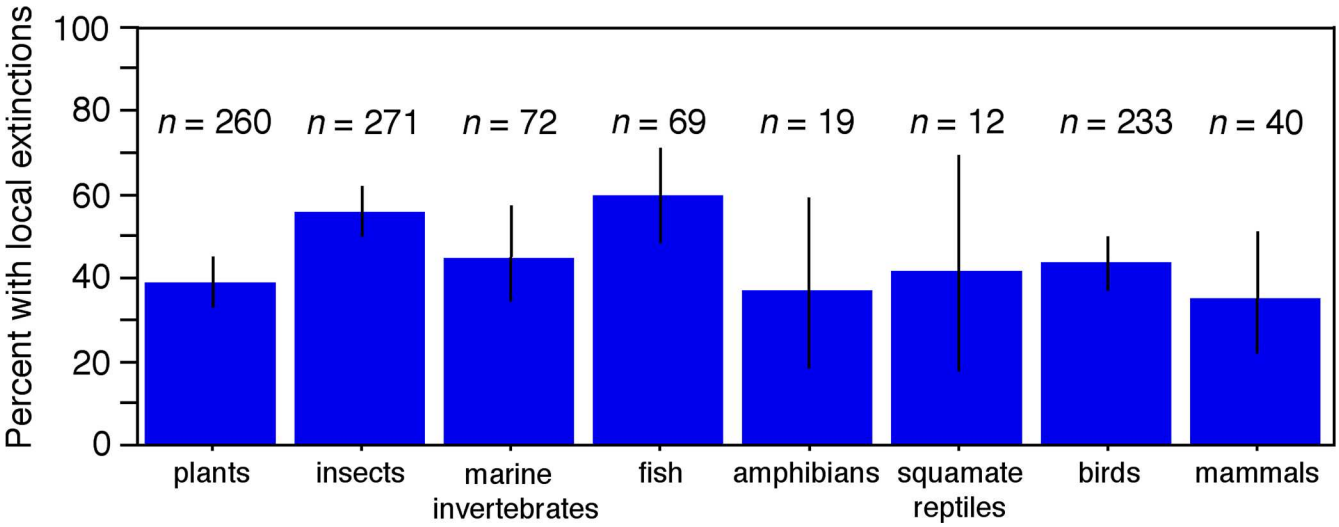


**Fig 3. The frequency of local extinctions related to climate change across different taxonomic groups**. The percentage of species with one or more local extinctions in each taxonomic group is shown, along with the total sample size of species surveyed in that group. For ease of presentation, four different groups of marine invertebrates (annelids, crustaceans, molluscs, and echinoderms) are shown together. Frequencies for these four groups were averaged to obtain a single value, and sample sizes of species across groups were summed. Squamate reptiles include lizards and snakes. Vertical lines indicate 95% confidence intervals on the estimated frequency of species with local extinctions.

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variables had significant effects on the frequency of extinction, except for the study dates. There were strong effects of habitat and climate ($p < 0.00001$) but weaker effects of taxonomic group ($p = 0.0246$). Results were similar when excluding study dates and taxonomic group. Including geographic regions showed that most regions had no significant effect (except for Madagascar and South America). Given that Madagascar and South America were represented by one study each, these region effects were not considered further. Furthermore, the effects of climatic region, habitat, taxonomic group, and survey type remained significant when geographic regions were included. Comparing species only on terrestrial elevational gradients (805 species in total) further confirmed the significant effects of climate and taxonomic group. Similarly, considering plants only (260 species) also confirmed the significant effects of climatic region. Considering only terrestrial animals on elevational gradients (545 species) showed a significant effect of climate ($p = 0.0023$) after removing study dates, which had no significant effect. Considering birds alone (233 species) and including climatic region, survey type, and study dates showed that climatic region, survey type, start date, and end date had significant effects. For insects (271 species), when including climatic region, study dates, and survey type, no variables were significant. For fish (69 species), a model including habitat (freshwater versus marine), study dates, and survey type showed that no variables were significant. However, habitat was significant if other variables were removed. Similarly, for temperate animals (367 species), a model including habitat, survey type, and study dates showed that only habitat and survey type were significant. Comparison of plants and animals on terrestrial elevational gradients (including study dates) showed that extinction is significantly different between temperate plants and animals (more common in animals), but not between tropical ones. Across animals, the effects of taxonomic group were limited and depended on the other variables included. If only taxonomic groups and study dates were included, then annelids, fish, and insects showed significantly more extinction ($p = 0.03$–$0.05$). Including habitat and survey type (and removing study dates) showed stronger effects in fish and annelids (as well as in crustaceans and molluscs), but not in insects.

Results were also broadly similar using GLMMs, with study identity included as a random effect. Results are summarized below and given in full in S3 Appendix. The impacts of study dates were somewhat counterintuitive (and rarely significant), and analyses including them sometimes failed. When most variables were included (habitat, climatic region, taxonomic group [plant versus animal], survey type, and study dates), all variables were significant except for study dates and taxonomic group, with strong effects of habitat, climatic region, and survey type. When study dates were removed, only habitat and survey type were significant. When geographic regions were included (and study dates excluded), only South America had a significant effect, and habitat, taxonomic group, and climatic region were significant or marginally significant. Comparing tropical and temperate species on terrestrial, elevational gradients showed significant effects of climatic region ($p = 0.0017$) and taxonomic group ($p = 0.0119$), but not of study dates. When study dates were removed, no variables were significant. Plants alone showed a significant effect of climatic region ($p < 0.0001$), but analyses failed if study dates were included. Animals on terrestrial, elevational gradients showed no significant effect of climatic region (again, study dates had to be excluded). Considering birds alone showed no significant effect of climate but a significant effect of survey type (excluding study dates). Insects showed no significant effects of climate or survey type, regardless of whether study dates were included. Analyses of fish failed unless study dates and survey type were excluded, but habitat alone (marine versus freshwater) had a significant effect ($p = 0.0265$). Analyses of temperate animals (367 species) including habitat, survey type, and study dates showed only habitat type as significant ($p = 0.0307$), but excluding study dates showed significant effects of habitat and survey type. Comparing only temperate plants and animals showed a significant effect of taxonomic group, when study dates were included ($p = 0.0116$) or excluded ($p = 0.0005$; study dates had no significant effect). In contrast, there was no significant effect of taxonomic group when comparing tropical plants and animals (504 species total; excluding study dates). Analyses of animals alone showed no significant effect of taxonomic group.

In summary, several patterns emerged as significant across all (or most) analyses. First, there were significant effects of climatic region overall, with extinction more common in tropical regions. This was present in plants across all analyses and generally present in animals. Animals showed significantly more extinction than plants overall and when comparing temperate, but not tropical, species. There were significant effects of habitat on animals overall (higher extinction in freshwater), even when considering fish alone. Finally, GLM analyses showed some effects of taxonomic groups across animals (with higher extinction in fish and annelids) and possibly in insects, molluscs, and crustaceans. The GLMM analyses did not show these group effects, possibly because many animal groups are included based on a single study.

## Discussion

The results of this study show that local extinctions (inferred to be related to climate change) are already widespread and have occurred in hundreds of species. Roughly half of the 976 species that were surveyed for range shifts showed evidence of local extinctions (47%). This proportion was surprisingly similar across diverse climatic regions, habitats, and taxonomic groups. The results here suggest that even the modest changes in climate that have occurred so far are enough to drive local populations in many species to extinction. The results here also suggest that local populations in many species cannot shift their climatic niches rapidly enough to prevent extinction. This pattern of widespread local extinction seems likely to become even more prevalent as the global climate warms further (by roughly 2 to 5-fold [4]) in the next several decades.

The results here showed generally similar patterns of local extinction across climatic zones, habitats, and clades. Nevertheless, most analyses showed that local extinctions were

significantly more common in tropical species (Fig 2A), in freshwater species (Fig 2B), and in animals. A greater impact of climate change on tropical species has been predicted by several authors (e.g., [40–42]). This prediction is related to the narrower climatic niche widths for temperature-related variables in tropical species that are associated with reduced temperature seasonality in the tropics (e.g., [43,44]) and lower rates of temperature-related climatic niche change in tropical species (e.g., [42]). The results here provide support for this prediction based on documented local extinctions that have already occurred: species in tropical regions had local extinctions more frequently than those in temperate regions (54.6% versus 39.2%), especially when species were compared on terrestrial, elevational gradients (54.6% versus 28.2%). This pattern was strongest in plants and when animals were compared on terrestrial elevational gradients. Overall, these results further support the idea that the negative impacts of climate change on biodiversity are more frequent (per species) in tropical regions [40–42], where biodiversity is highest.

Climate-related local extinctions were also similar in frequency in marine and terrestrial species (Fig 2B) but were more common in freshwater species (although freshwater habitats were represented by a single study). Freshwater species may be especially susceptible to changes in precipitation patterns (e.g., drought), which can substantially alter or eliminate their habitats (e.g., [45]), quickly resulting in local extinction. In contrast, marine species may experience less impact from changes in precipitation. Furthermore, they may be buffered from temperature changes because they can potentially adjust the temperatures that they experience by movement within the water column (more so than is possible for most freshwater species; [46,47]).

The frequency of local extinctions was also broadly similar across diverse taxonomic groups (~35%–60%; Fig 3), including plants, insects, fish, amphibians, squamate reptiles, endothermic vertebrates (birds and mammals), and many marine invertebrates (annelids, crustaceans, and molluscs). However, local extinctions were significantly more common in animals than plants (and animals are far more species-rich than plants). They were also relatively common in insects (the most species-rich group of animals) and fish (the most species-rich group of vertebrates). Local extinctions were not particularly common in amphibians (36.7%) or squamate reptiles (41.7%), although both groups were included here based primarily on one study [32]. Nevertheless, both groups appear to have been strongly impacted by climate change overall. For example, many amphibian species have undergone sharp declines and global extinctions, many of which are thought to be caused by an interaction between climate change and an infectious disease (chytrid fungus; [48]). However, these chytrid studies were not included here because they were not focused on surveying warm-edge populations over time. Similarly, local extinctions related to climate change have been documented in many lizard species [49]. Again, these were not included here because they were not based on a systematic survey of warm-edge populations. Nevertheless, if the species studied by Sinervo et al. [49] were included here, the frequency of local extinctions in squamates would go from 41.7% (of 12 species) to 77.4% (of 124 species), but with the caveat that their study focused on documenting local extinctions and so might overestimate this frequency. It should also be noted that the well-publicized declines in amphibian populations globally are not necessarily inconsistent with the frequency of local extinction observed here. For example, a global assessment of amphibian populations [50] noted declines in 43% of amphibian species (compare to the 47% of all species here with local extinctions and the 37% for amphibians), but these declines also included those unrelated to climate change (e.g., habitat destruction and overexploitation). Thus, the frequency of climate-related declines here is not necessarily an underestimation relative to the declines documented by the global amphibian assessment [50].

A major conclusion of this study is that populations of many species are already unable to undergo niche shifts that are fast enough to prevent local extinction from climate change. The

rate is emphasized here because even if the absolute amount of niche change needed to avoid extinction might be attainable, it might require more time to achieve than is allowed by the rapid pace of anthropogenic climate change. Given this result, and that climate is predicted to change even further in the near future, the persistence of many species might depend largely on their ability to successfully shift their geographic ranges to higher latitudes or elevations and remain within their original climatic niche. Indeed, the summary here shows numerous instances of cool-edge expansions (in 367 of 904 species, with cool edges that were stable in 371 others and contracted in 166 others).

Unfortunately, these movements may be impeded for many species by one or more factors. First, human impacts may prevent species from successfully dispersing (including agriculture, roads, and urbanization), or these human impacts may simply leave them no habitat to disperse to (e.g., [51,52]). Second, many species are already confined to islands, peninsulas, and mountaintops, where dispersal to higher latitudes or elevations may not be possible (e.g., [53]). Third, even if dispersal is unimpeded by human or natural barriers, it may simply occur too slowly to allow species to remain within their climatic niche (e.g., [54,55]).

The combination of these potential limits to dispersal and the widespread local extinctions documented here is troubling. However, the results here do not rule out the possibility that rapid niche shifts will occur in some populations of many species in the future, preventing global extinctions. Indeed, roughly half of the species surveyed showed no local extinctions, and most species had some populations that persisted locally (but again, this is under the limited climate change that has already occurred). The future persistence of species will depend on many factors [6,8], including rates and patterns of climate change at each location, dispersal, niche shifts, local climatic microrefugia [56], and the contribution of population-level niche width to species-level niche width (e.g., whether species are broadly tolerant or locally specialized to different climatic conditions across their ranges [44]). Most importantly, I suggest that the patterns of present-day local extinctions obtained from range-shift studies should be part of the evidence used to predict species persistence in the future.

There are several potential sources of bias that may have influenced some aspects of these results but should not overturn the major conclusions. First, "local extinction" means that individuals of a given species are entirely absent from a location that they previously occupied. However, it can be difficult to distinguish between extinction and a substantial decline in abundance that causes the species to go undetected at a given location (e.g., [57]), and studies did not necessarily provide statistical evidence for the absence of a species at a site. Here, the estimates of previous researchers were used, and it was assumed that they adequately documented local absences (otherwise, their estimates of range shifts would also be erroneous). Furthermore, strong declines that make a species undetectable at a given site might soon lead to local extinction. Second, there may be a bias in terms of unpublished results. Specifically, some researchers who monitored the warm edge of a population but failed to find any changes associated with climate change may not have published their negative results. Such a reporting bias would lead to overestimating the proportion of species experiencing local extinction in this study. Nevertheless, local extinctions were still documented in hundreds of species across regions and clades, even if there are hundreds of additional species in which these local extinctions did not occur. Additionally, numerous species ($n$ = 171) showed evidence of a cool-edge expansion without a corresponding contraction in the warm edge. Thus, a species can undergo a range shift but without local extinction, which should limit this source of publication bias. Third, it was assumed that previous researchers correctly associated the patterns that they observed with climate change. In theory, other factors such as overharvesting or habitat destruction may have contributed to the observed local extinctions in some cases (e.g., [21]).

Again, the analyses here primarily assume that the main conclusions of these previous studies were not erroneous.

Finally, despite the widespread pattern of warm-edge contractions and local extinctions, 521 species showed no local extinctions at the warm edge, indicating that they have successfully persisted in the face of the climate change that has occurred so far. However, even these species might still go globally extinct when global climate changes further. Additionally, contrary to the overall trend, 54 species were documented here as having expansions at both their warm edge and their cool edge (6.0% of 904 species with data on both cool and warm edges). One scenario by which this may occur is if cool-edge limits are set by colder temperatures (allowing expansion as global climate warms) and warm-edge limits are set by low precipitation (allowing warm-edge expansion), given that precipitation may increase in some areas because of climate change [4]. Indeed, some studies have found evidence for warm-edge expansions through this mechanism [58]. It is also important to note that local extinctions related to climate change need not be confined to the warm edge of the species range and so might actually be underestimated here. For example, there could be climate-related local extinctions far from the warm edge that are associated with certain microclimates (e.g., equatorially facing slopes at the cool edge of a species range; [59]).

In summary, the results here show that widespread local extinctions (seemingly related to climate change) have already occurred in hundreds of species, with broadly similar patterns of extinction across diverse clades, habitats, and climatic regions. Importantly, levels of climate change so far are limited relative to those generally predicted for the next 100 years [4]. The results here suggest that many species are unable to shift their niches rapidly enough to prevent local extinction. This inference of climate change outpacing niche change supports predictions from other sources, including transplant experiments in plants [60], phylogenetic analyses of rates of niche change in plants and animals [42,61,62], and projections based on selection, heritability, and temperature tolerances in lizards [49]. Local extinctions from climate change might also impact species that many human populations depend on for food, such as grasses (e.g., wheat, rice, and corn [62]). More generally, this study demonstrates that analyses of range shifts can provide extensive data on local extinctions related to climate change that have already occurred. These local extinctions offer a potentially important but underutilized source of information for the challenging task of predicting patterns of species survival and extinction in the future.

## Materials and Methods

### Selection of Studies

Web of Science searches were initially conducted from December 2014 to April 2015 using the Boolean search terms Topic = (global warming OR climate change) AND Topic = (local extinction OR range contraction OR range shift). A second Web of Science search was conducted between April 2015 and May 2015 to identify additional studies potentially missed by the first set of keywords, using the search terms TS = (global warm* OR climate change) AND TS = (extinction* OR contraction* OR range shift*), excluding results from TS = (global warming OR climate change) AND TS = (local extinction OR range contraction OR range shift). Each set of Web of Science results was sorted by relevance and then binned into subsets of 50. Searching was ceased when less than 1 in 50 studies per subset was relevant (see below for criteria). Finally, a third Web of Science search was performed on 1 March 2016 to find more recently published studies. This third search used the keywords TS = (global warm* OR climate change) AND TS = (extinction* OR contraction* OR range shift*). A total of 1,530 results were found in this third search. Results were sorted by relevance, and the first 300 (~20%) were examined. The last 40 of these 300 included no relevant studies.

Some additional studies were also found that were listed as references in the papers identified by these initial Web of Science searches. The reference list was also checked against a recent review study [11], which also conducted thorough searches of the literature on climate-related range shifts. Three studies were added from that survey which were not initially included here. Finally, several relevant studies were also found in the survey of Gibson-Renemer et al. [63], which had similar rules for inclusion of studies. Although those authors did not conduct a systematic search of the literature (as done here), they nevertheless included five studies not found in the searches described above. These were also added here.

In theory, the fact that "extinction" and "contraction" were included as keywords might have biased the results to include more papers documenting local extinctions and range contractions than would be obtained from a search of range-shift studies that excluded these as keywords (possibly leading to overestimation of the frequency of local extinctions). However, this seems unlikely in practice. First, these were included as "or" keywords, along with "range shifts." Examining the keywords and titles of the 27 selected papers showed that most were focused on overall range shifts, with no mention of local extinction (extinction or extirpation are mentioned in the titles of only 4 of 27 studies and as keywords in only 4 of the 21 studies with keywords; "contraction" is mentioned in only 1). Furthermore, the fact that the survey results here were checked against another recent review on range shifts [11], and that three missing studies were added, also makes this potential bias seem unlikely. In other words, if many range-shift studies were missed because of this bias, they should have been added at that point.

Overall, these searches were extensive but may not be truly exhaustive. Regardless, many studies were found that documented local extinctions, and finding more studies that did so would not overturn this main conclusion.

Studies were included that monitored one or more populations at the warm edge of a species' range (the edge that is lower in elevation or closer to the equator) over a relatively long time span. Studies were only included that spanned an interval of at least 10 years. The mean study duration was ~50 years (range = 14 to 159; Table 1). Studies were included that related their findings on range shifts to climate change through an explicit statistical analysis (but noting that these inferences could still be incorrect, for example, if other factors instead of climate change caused local extinctions of a particular species). The included studies all documented populations along elevational or latitudinal transects at two or more discrete time points.

Some recent studies have inferred climate-related range shifts based on overall trends in latitudinal and elevational distributions across a large number of localities over time, rather than systematically resurveying specific localities at different time points (e.g., [64]). These studies are valuable for documenting range shifts in general but were excluded here, since they do not unambiguously represent local extinctions (because the overall patterns described might be driven solely by range expansions instead).

## Categorizing Species

Studies that documented warm-edge range contractions (and that were linked to climate change by the authors of the original studies) were considered evidence of climate-associated local extinction, regardless of changes at the cool edge. Studies differed in whether they reported changes at the population level (e.g., [28,37]) or species level (e.g., [33]). The analysis here was conducted at the species level. Therefore, if populations of the same species differed in the pattern of their range shifts, the species was categorized as showing evidence of local extinction if at least one population did so.

Most species were included in only one study. However, the plant species *Anthoxanthum odoratum* was included by both Angelo and Daehler [13] (in Hawaii) and Felde et al. [19] (in

Europe). However, since this species is not native to Hawaii, it was excluded from the dataset of Angelo and Daehler [13], along with all other nonnative species in that study.

For each study, it was noted whether the range shifts were elevational or latitudinal, as well as the general habitat of the organisms (i.e., terrestrial, freshwater, or marine), the higher taxa to which they belonged, the specific geographic location of the study, and whether the species occurred in a tropical or subtropical region (arbitrarily defined as within 35˚ of the equator) or in a temperate region (>35˚). Species were assigned to these climatic regions based solely on the location where they were surveyed, rather than on their overall geographic range. Species were also assigned to taxonomic categories, including plants, insects, fish, amphibians, birds, mammals, and squamate reptiles (i.e., lizards and snakes), as well as marine annelids, crustaceans, echinoderms, and molluscs. The beginning and end dates of the study were also noted (e.g., the date of the initial survey and the subsequent resurvey) and were used to estimate the duration of the study. Some studies provided a range of dates for the start and/or end date. In these cases, the midpoint of each range of dates was used to estimate the start, end, and duration (Table 1). Data for all species are provided in S1 Appendix.

The studies included (Table 1) spanned many geographic regions (e.g., North America, South America, Europe, Asia, and Oceania). Many studies were conducted in North America ($n$ = 13; here extending to Central America) and Europe ($n$ = 8), but the actual number of species sampled was more broadly distributed among regions (e.g., Asia = 332; Europe = 268; Madagascar = 30; Oceania = 58; North America = 233; and South America = 55). Africa and Australia were not represented, although nearby Madagascar and New Guinea were. The numbers of temperate and tropical species included were nearly equal. Further, there was no clear hypothesis for why particular continents alone should be an important factor influencing the frequency of local extinctions (e.g., separate from temperate versus tropical effects).

## Statistical Analyses

Chi-squared analyses were initially used to compare the proportion of climate-associated local extinctions across some categories (i.e., tropical versus temperate; freshwater versus marine versus terrestrial; and latitudinal versus elevational gradients), testing the null hypothesis that frequencies of local extinction were equal between these categories. A series of analyses were conducted to assess whether frequencies of local extinction were higher in tropical regions relative to temperate regions, after accounting for the potential influence of different habitats, gradients, and clades (see Results). Similar analyses were conducted to assess the impacts of different habitats and clades (i.e., plants versus animals). However, potential analyses were restricted by the available data. For example, it was not possible to compare the effect of tropical versus temperate climates on marine or freshwater organisms, since only temperate marine and freshwater species were included here. For this reason, different sets of analyses were conducted for each question.

These analyses were then repeated using GLMs and GLMMs, both in R. These analyses were implemented treating the presence of warm-edge local extinction in a species as the binomial, dependent variable. GLMM analyses were conducted using the R package *lme4* [65]. GLMM analyses treated the study (from which the species data were obtained) as the random variable and the other variables as the fixed variables. GLM and GLMM analyses initially included all species and all or most variables and were then restricted to smaller sets of species (and variables) to test additional hypotheses and reduce potentially confounding effects (as in the Chi-squared analyses).

Phylogenetic information was not incorporated here, since phylogenies and comparable branch lengths spanning all the included species were not available (especially species-level

phylogenies for fish, insects, plants, and marine invertebrates). Nevertheless, some analyses were conducted to assess patterns within and between clades (see Results).

## Supporting Information

**S1 Appendix. Data for the 976 species used in this study.**
(XLSX)

**S2 Appendix. Results of GLM analyses, showing variable coefficients.**
(DOC)

**S3 Appendix. Results of GLMM analyses, showing variable coefficients.**
(DOC)

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## Author Contributions

**Conceptualization:** John J. Wiens.

**Investigation:** John J. Wiens.

**Writing – original draft:** John J. Wiens.

**Writing – review & editing:** John J. Wiens.

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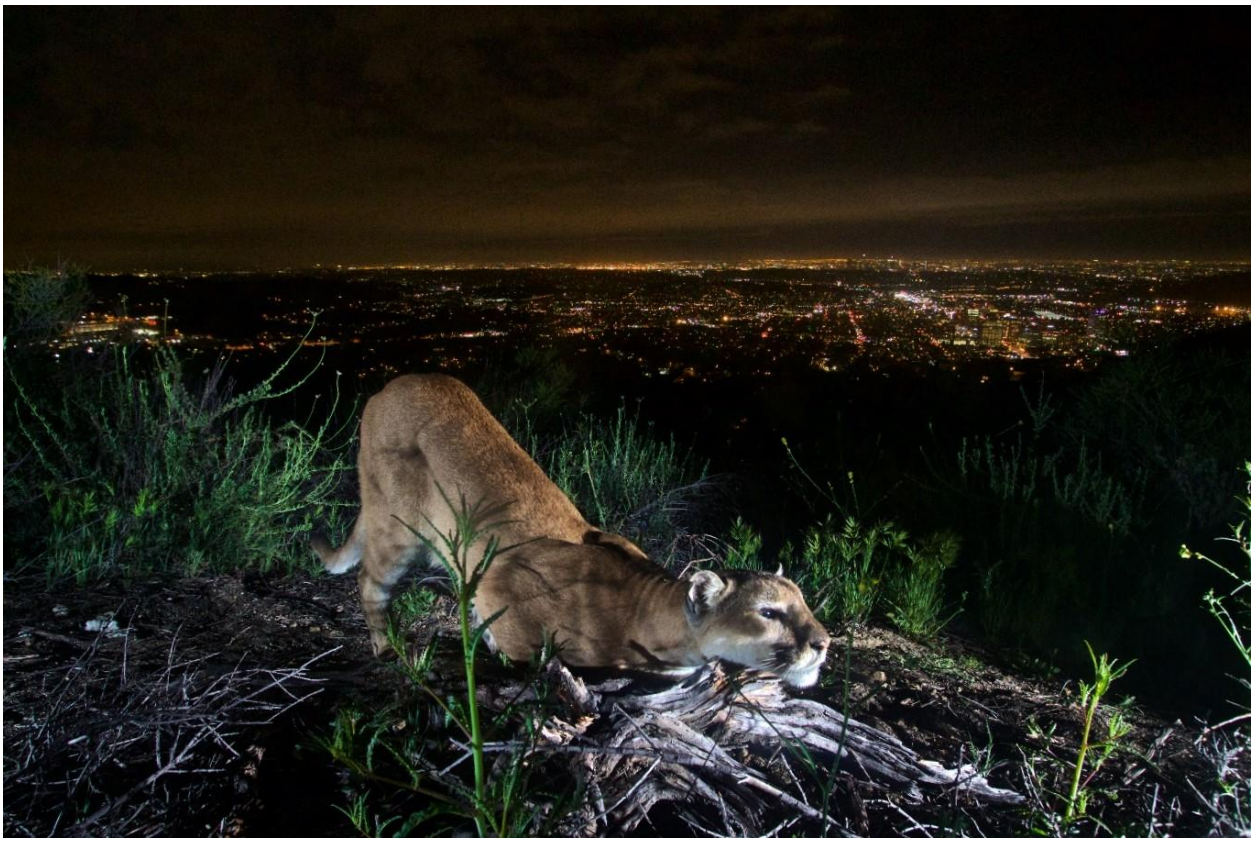
# BEFORE THE CALIFORNIA FISH AND GAME COMMISSION

## A Petition to List the Southern California/Central Coast Evolutionarily Significant Unit (ESU) of Mountain Lions as Threatened under the California Endangered Species Act (CESA)



A Mountain Lion in the Verdugo Mountains with Glendale and Los Angeles in the background. Photo: NPS

Center for Biological Diversity and the Mountain Lion Foundation

June 25, 2019

Notice of Petition

For action pursuant to Section 670.1, Title 14, California Code of Regulations (CCR) and Division 3, Chapter 1.5, Article 2 of the California Fish and Game Code (Sections 2070 *et seq*.) relating to listing and delisting endangered and threatened species of plants and animals.

I. SPECIES BEING PETITIONED:

Species Name: Mountain Lion (*Puma concolor*). Southern California/Central Coast Evolutionarily Significant Unit (ESU)

II. RECOMMENDED ACTION: Listing as Threatened or Endangered

The Center for Biological Diversity and the Mountain Lion Foundation submit this petition to list mountain lions (*Puma concolor*) in Southern and Central California as Threatened or Endangered pursuant to the California Endangered Species Act (California Fish and Game Code §§ 2050 et seq., "CESA"). This petition demonstrates that Southern and Central California mountain lions are eligible for and warrant listing under CESA based on the factors specified in the statute and implementing regulations. Specifically, petitioners request listing as Threatened an Evolutionarily Significant Unit (ESU) comprised of the following recognized mountain lion subpopulations:

1. Santa Ana Mountains
2. Eastern Peninsular Range
3. San Gabriel/San Bernardino Mountains
4. Central Coast South (Santa Monica Mountains)
5. Central Coast North (Santa Cruz Mountains)
6. Central Coast Central

Alternatively, as detailed in the petition, in the event the Commission determines that these six populations collectively either do not comprise a single Southern California/Central Coast ESU or otherwise do not meet the criteria for listing as Threatened, petitioners request the Commission consider whether any of these populations, singularly or in combination, comprise one or more ESUs and meet the criteria for listing as Threatened or Endangered pursuant to CESA.

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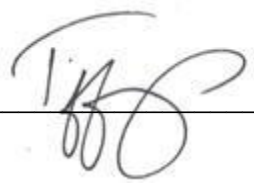
I hereby certify that, to the best of my knowledge, all statements made in this petition are true and complete.

Signature:  Date: 6/25/19

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**Executive Summary**

The Center for Biological Diversity and the Mountain Lion Foundation submit this petition to list mountain lions (*Puma concolor;* cougar, puma) in Southern and Central Coastal California as "threatened" or "endangered" pursuant to the California Endangered Species Act (CESA) (California Fish and Game Code §§ 2050 et seq.). Following Section 670.1, Title 14, California Code of Regulations, petitioners present scientific information regarding life history, population trend, range, distribution, abundance, kind of habitat necessary for survival, factors affecting the ability to survive and reproduce, degree and immediacy of threat, impact of existing management efforts, suggestions for future management, availability of sources and information, and a detailed distribution map.

Specifically, petitioners request listing as a "threatened species" an evolutionarily significant unit (ESU) comprised of the following recognized mountain lion subpopulations:

1. Santa Ana Mountains
2. Eastern Peninsular Range
3. San Gabriel/San Bernardino Mountains
4. Central Coast South (Santa Monica Mountains)
5. Central Coast North (Santa Cruz Mountains)
6. Central Coast Central

As demonstrated in this petition, mountain lions in these areas comprise an ESU (referred to as the "Southern California/Central Coast ESU") and meet the statutory definition of a "threatened species."

The California Fish and Game Commission has long recognized that ESUs can be designated and listed under CESA, and this interpretation of CESA has been upheld by the courts. *See California Forestry Assn. v. California Fish & Game Com.* (2007) 156 Cal.App.4th 1535, 1540 ("Consistent with the policy of the CESA, we will hold that the term 'species or subspecies' includes evolutionarily significant units"); *Central Coast Forest Assn. v. Fish & Game Com.* (2018) 18 Cal.App.5th 1191, 1197, fn. 4 [*"CCFA II*"] ("An ESU is included within the term 'species or subspecies' in sections 2062 and 2067."). While the ESU concept has primarily been applied to fish, the Commission recently listed an ESU of a mammal, the Pacific Fisher, as a "threatened species." *See* 14 C.C.R. 670.5(b)(6)(J) ("Fisher (*Pekania pennant*) Southern Sierra Nevada Evolutionarily Significant Unit").

Under CESA, a "threatened species" is "a native species or subspecies of a … mammal… that, although not presently threatened with extinction, is likely to become an endangered species in the foreseeable future in the absence of the special protection and management efforts . . . ." Cal. Fish & Game Code § 2067. An animal is an "endangered species" when it is "in serious danger of becoming extinct throughout all, or a significant portion, of its range due to one or more causes, including loss of habitat, change in habitat, overexploitation, predation, competition, or disease." Cal. Fish & Game § 2062.

Certain populations of the Southern California/Central Coast mountain lion ESU are already "in serious danger of becoming extinct" (*e.g.* Santa Ana and Santa Monica mountains), and if assessed separately, would individually meet the definition of an "endangered species." When considered as a whole, the Southern California/Central Coast ESU is not at imminent risk of extinction but still faces significant and growing threats that ultimately threaten the viability of the entire ESU; it consequently meets the definition of a "threatened species."

Currently, there is no reliable estimate of mountain lion abundance in California. In 1984 the California Department of Fish and Wildlife (CDFW) estimated between 4,000-6,000 adult mountain lions in the state (Mansfield and Weaver 1984). However, CDFW acknowledges that this estimate is outdated and likely overestimates mountain lion abundance. CDFW is currently undertaking a large-scale research effort to estimate mountain lion numbers throughout California.

While reliable absolute abundance estimates are unavailable, recent genetic research has led to estimates of effective population size for California mountain lion populations.[1] These estimates highlight the genetic isolation among California mountain lion populations and raise significant concerns for the continued viability of mountain lions in Southern California and along the Central Coast.

Researchers have recently identified 10 genetically distinct mountain lion populations in California (Figure ES-1) (derived from Gustafson et al. 2018). Nine of these populations occur almost exclusively in California, while one is centered in Nevada but extends into the northeastern corner of California.

The abundance of mountain lions in the North Coast and inland populations (Western Sierra Nevada, Eastern Sierra Nevada, and the genetic cluster centered in the state of Nevada) is not well established; however, these populations are better connected than Southern California and Central Coast mountain lions, and they show relatively high levels of genetic diversity. Gustafson et al. (2018) suggest that these four populations may comprise an ESU. While these populations should be monitored and managed to ensure their continued viability, petitioners do not seek protection of these populations as an ESU under CESA at this time.

Considering the genetic source-sink dynamics among the remaining six populations, petitioners demonstrate that the populations along the Central Coast and in Southern California collectively comprise an ESU that warrants protection under CESA.[2] The Southern California/Central Coast ESU is comprised of six genetically distinct mountain lion populations: Central Coast North (CC-N, which includes mountain lions in the Santa Cruz Mountains and East Bay), Central Coast

[1] At its simplest, effective population size is the number of animals contributing offspring to the next generation. It is an important measure of the genetic health of a population.

[2] As explained *infra* at Section 3.0, these remaining populations can be grouped into one or several potential ESUs. Petitioners believe that for purposes of listing under CESA, treating them as a single ESU is supported by the best available science. Moreover, a single ESU also is the most pragmatic from a management perspective, as recovery of the individual populations ultimately depends upon maintaining and/or reestablishing connectivity between them. *See CCFA II,* 18 Cal.App.5th 1191, 1237 ("[T]he nature of the ESU designation is such that genetics alone are not determinative: One must look beyond genetics to questions of policy to determine which populations to include in an ESU.")(quotations omitted).

Central (CC-C), Central Coast South (CC-S, which includes the mountain lions in the Santa Monica Mountains), San Gabriel/San Bernardino Mountains (SGSB), Santa Ana Mountains (SAM), and Eastern Peninsular Range (EPR) (Gustafson et al. 2018).

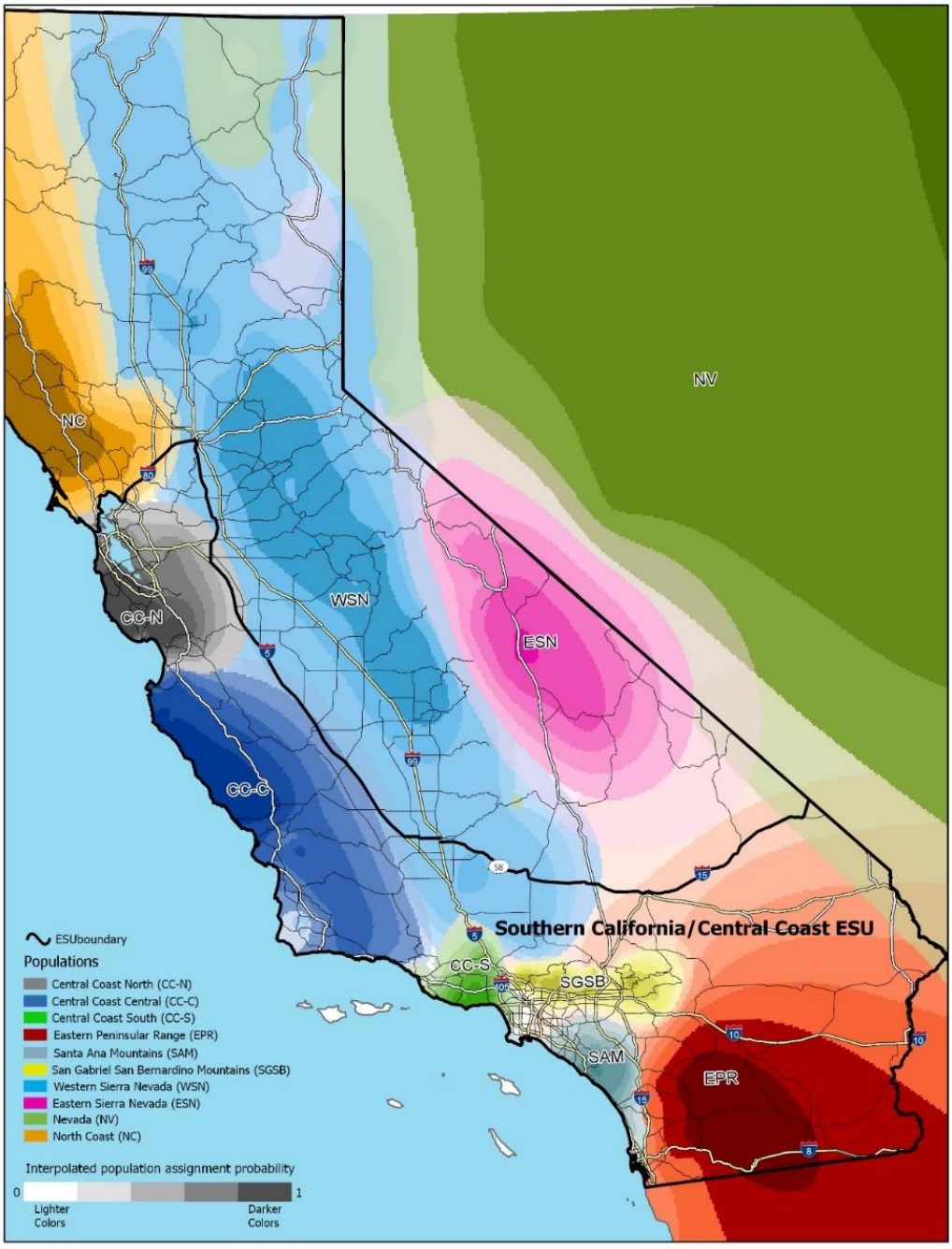


**Figure ES-1**. Map of genetically distinct mountain lion populations and major roadways in California based on data collected from 1992-2016 (the division and status of these populations could change over time and with further research). The black lines show the proposed Southern California/Central Coast ESU boundary. Derived from Gustafson et al. (2018). Genetics data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie. Roads data source: ESRI.

The boundary of the Southern California/Central Coast ESU is proposed in Figure ES-1, and includes mountain lions that occur south of the San Francisco Bay and I-80, west of I-5 to the intersection of I-5 and SR-58, south of SR-58 to I-15, south of the I-15 from the SR-58 intersection to the California-Nevada border, and, for the purposes of CESA, as far south as the California-Mexico border. These boundaries are recommended as they include virtually all mountain lions associated with the six populations comprising the ESU and are also unambiguous and readily discernable for purposes of management. We recommend including mountain lions in the Tehachapi and Sierra Pelona Mountains south of SR-58 in this ESU. While most mountain lions sampled from this region share some genetic affinities with Western Sierra Nevada (WSN) animals, many also show genetic connections with CC-S, SAM, EPR and SGSB mountain lions. This area serves not just as a connecting link between mountain lion populations comprising the Southern California/Central Coast ESU, but also between this ESU and all other California mountain lions and is therefore essential for the overall genetic health of mountain lions in the state.

While Southern California and Central Coast mountain lions face a multitude of threats, the greatest challenges stem from habitat loss and fragmentation and the consequent impact on their genetic health. Most of the populations comprising the ESU have low genetic diversity and effective population sizes, which puts them at increased risk of extinction (Ernest et al. 2003; Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016; Gustafson et al. 2018; Benson et al. 2019). The populations most at risk are the SAM, CC-S, SGSB, and CC-N populations. Due to extreme isolation caused by roads and development, the SAM and CC-S, populations exhibit high levels of inbreeding, and, with the exception of the endangered Florida panther, have the lowest genetic diversity observed for the species globally (Ernest et al. 2014; Riley et al. 2014; Gustafson et al. 2018; Benson et al. 2019). The SGSB and CC-N similarly have low observed genetic diversity and effective population sizes, and they reside in areas of significant isolation and habitat fragmentation, which also puts them at increased risk (Gustafson et al. 2018). And although the CC-C and EPR populations have slightly higher levels of genetic diversity and effective population sizes, high rates of development, habitat loss and fragmentation, and human-caused mortalities in both areas could lead to a similar fate of isolation, genetic drift, low effective population size, and increased risk of extinction in the foreseeable future.

Although minimum viable effective population size has been found to vary depending on the species (Frankham 1995; Traill et al. 2010), general conservation management practice over the past few decades has followed a 50/500 rule, under which an effective population size of 50 is assumed sufficient to prevent inbreeding depression in the short term (over the duration of five generations) and an effective population size of 500 is sufficient to retain evolutionary potential in perpetuity (Traill et al. 2010; Frankham et al. 2014). It is clear that Central Coast and Southern California mountain lion populations are genetically compromised and face significant risk of extinction in both the short- and long-term. Five of the six populations have effective population sizes well below 50 (from lowest to highest: CC-S, SGSB, SAM, CC-N, EPR), and one population (CC-C) is just barely above that threshold at $N_e = 56.6$ (Table ES-1) (Gustafson et al. 2018).

**Table ES-1.** Effective population size from Gustafson et al. (2018) and estimated total adult population of Central Coast and Southern California Mountain Lion Populations.

| Population | Effective Population Size ($N_e$) | Estimated Total (Adult) Population (N)[1] |
|---|---|---|
| Central Coast North (CC-N) | 16.6 | 33-66 |
| Central Coast Central (CC-C) | 56.6 | 113-226 |
| Central Coast South (CC-S) | 2.7[2] | 5-10 |
| Santa Ana Mountains (SAM) | 15.6[3] | 31-62 |
| San Gabriel/ San Bernardino Mountains (SGSB) | 5 | 10-20 |
| Eastern Peninsular Range (EPR) | 31.6 | 63-126 |
| **Total** | | 255-510 |

[1]Calculations are based on the estimated ratio of effective to total adult population size ($N_e$/N) of Florida panthers being 0.25 to 0.5 (Ballou et al. 1989). This ratio was used in the USFWS Florida Panther Recovery Plan (USFWS 2008). Petitioners recognize that these derived population estimates, while informative, are not definitive and will likely be superseded by new population estimates being developed by CDFW.
[2]Benson et al. (2019) calculated an $N_e$ of 4 for the Santa Monica Mountains population within the CC-S. Applying the Ballou et al. (1989) factors would lead to an estimate of 8-16 mountain lions in this area, which is roughly consistent with current estimates of this well-monitored population.
[3]Several studies provide $N_e$ calculation for the SAM population. Ernest et al. (2014) calculated an $N_e$ of 5.1 and Benson et al. (2019) calculated an $N_e$ of 6. Applying the Ballou et al. (1989) factors to the most recent calculation would lead to an estimate of 12-24 mountain lions in the SAM, which is roughly consistent with current estimates.

Although low effective population sizes standing alone are cause for conservation concern for Southern California and Central Coast mountain lion populations, there are other human-caused factors that further limit their long-term persistence. Habitat loss and fragmentation due to roads and development have led to extreme levels of isolation and high mortality rates. With low genetic diversity and high risk of inbreeding depression due to genetic isolation, vehicle strikes on roads, increased conflicts with humans that lead to depredation kills, high levels of intraspecific strife likely due to limited space and lack of connectivity, rodenticide and other environmental toxicant poisoning, and impacts of more frequent human-caused wildfires and climate change, the small isolated mountain lion populations of Southern California and the Central Coast will likely not persist without the restoration and enhancement of functional connectivity between populations and large blocks of heterogeneous habitats**.**

Loss of mountain lions in Southern California and the Central Coast would be devastating not just for the mountain lions themselves but also the many species that directly and indirectly rely on them. These top predators are important ecosystem engineers that facilitate healthy ecosystems and allow biodiversity to thrive (Ripple and Beschta 2006; Ripple and Beschta 2008;

Ripple et al. 2014; Ruth and Elbroch 2014; Barry et al. 2019; Elbroch and Quigley 2019). As keystone species mountain lions help support plant recruitment in riparian areas, stabilize stream banks, and sustain healthy habitats for a myriad of aquatic and terrestrial species, including plants, invertebrates, fish, amphibians, reptiles, birds, and mammals (Ripple and Beschta 2006; Ripple and Beschta 2008; Ripple et al. 2014). Their kills are also an important source of food for multiple terrestrial and avian scavengers (Ruth and Elbroch 2014; Barry et al. 2019; Elbroch and Quigley 2019).

Existing laws and regulations have proven to be inadequate to protect Southern California and Central Coast mountain lions. Although the California Wildlife Protection Act of 1990 (Proposition 117) prohibits hunting of mountain lions and has funded the acquisition of important habitat for preservation, the Act alone does not ensure that core habitats and connectivity are protected from development, highways, or other threats. Moreover, numerous mountain lions are killed each year pursuant to depredation authorizations issued under this regime, and there is no limit to the number of depredation permits a property owner can request or any limit to the number of depredation permits which can be issued for any population. And while CDFW has proactively issued a bulletin detailing a new depredation policy for mountain lions in the CC-S and SAM that requires property owners to first implement non-lethal measures prior to being issued a kill permit, this policy does not apply to other vulnerable populations.

Other environmental laws also are insufficient. State and local agencies continue to interpret the California Environmental Quality Act (CEQA) as allowing for the construction of highways and other development in mountain lion habitat and essential corridor areas without adequate mitigation despite severe impacts of such projects on mountain lions. Agencies likewise have generally interpreted CEQA and the federal National Environmental Policy Act as not requiring implementation of connectivity measures when projects fragment or destroy mountain lion habitat. And perhaps most importantly, Caltrans lacks a clear affirmative mandate to design, build, or improve crossings for mountain lions on existing highways, despite the undisputed role of transportation infrastructure in preventing connectivity and gene flow.

Future human population growth and associated development will further diminish and fragment remaining mountain lion habitat, driving Southern California and Central Coast mountain lions closer to extinction and undermining any chance of recovery. Should state and local agencies continue to build and expand roads and highways and permit construction in wildlife habitat and corridors without ensuring adequate habitat connectivity, the genetic health of mountain lion populations will continue to decline while the number of mountain lions killed by vehicle strikes and other human activity will increase.

Ultimately, without a reversal of these trends, mountain lions will disappear from Southern and Central Coastal California in the coming decades, representing a loss of the species from a significant portion of its range in the state. Nevertheless, most of the threats facing mountain lions can be halted or sufficiently reduced if CDFW is provided with adequate resources and all relevant state and local agencies sufficiently prioritize mountain lion conservation in their decision-making. Legal protection of mountain lions under CESA, along with the attention and resources that such listing will generate, can help ensure the long-term survival of this iconic and ecologically significant species in Southern and Central Coastal California.

**The Southern California/Central Coast Evolutionarily Significant Unit (ESU) of Mountain Lions Warrants Listing as Threatened under the California Endangered Species Act (CESA)**

# 1 Introduction

This petition summarizes available scientific information regarding the natural history of mountain lions, their distribution and abundance in California, population trends and threats, describes the proposed ESU, and discusses the limitations of existing management measures in protecting the species. As demonstrated below, mountain lions in Southern California and along the Central Coast meet the criteria for protection as a threatened species under the California Endangered Species Act (CESA), and would benefit greatly from such protection.

# 2 Life History

## *2.1 Species Description*

Adult female mountain lion (left) and kittens (right). Photos: NPS.

The mountain lion (*Puma concolor*) is also commonly called a puma (from the Inca language Quechua) or cougar (corrupted from cuguacuarana from the indigenous Guarani people in Paraguay, Argentina, Bolivia, and Brazil). Adults are large, slender cats with short, muscular limbs and a long tail that is about one third of the animal's total length. Their hind limbs are longer than their fore limbs, which makes them highly adapted for jumping through rugged terrain or pouncing on their prey. They have tawny pelage that can be lighter/whitish on their belly and the undersides of their legs and they have areas of white around the muzzle, throat and chest. They have black fur on the backs of their rounded ears, the tip of their tail, and outlining their muzzle. Their eyes are a grayish brown to golden color, and the nose is pink with a black outline.

Adult body size and weight can vary depending on the geographic range (Iriarte et al. 1990). Mountain lions are smaller and weigh less near the equator and are larger and heavier towards the poles, which likely reflects the size of available prey and the presence of sympatric carnivores (Iriarte et al. 1990). Males are typically larger than females. Males generally weigh 55-65kg with a length of 2.2-2.3m from the nose to the tip of the tail, and females generally weigh 35-45kg with a length of 2.0-2.1m (Currier 1983).

Mountain lion kittens are born weighing approximately 400g, and their eyes and ear canals remain closed for one to two weeks after birth (Currier 1983). They have light coats with dark spots and a white muzzle, chest, and belly. Like the adults, they have black fur on the backs of their rounded ears, the tip of their tail, and outlining their muzzle. Their eyes are initially blue, change to mostly brown within four months, and then change to a golden color at around nine months (Currier 1983). The dark spots on their coat start to fade at 12-14 weeks of age, presumably when a kitten starts to accompany its mother on hunts, but the spots are still distinguishable until the animal is about one year old (Currier 1983). Adult weight is typically reached between the second and fourth year.

### *2.2 Taxonomy and Population Genetics*

The mountain lion is in the order Carnivora and is a member of the cat family Felidae. Unlike the large, roaring cats of the subfamily Pantherinae (*e.g*., lions, tigers, and leopards), mountain lions are categorized with small, purring cats in the subfamily Felinae (*e.g*., bobcats, lynxes, ocelots, cheetahs, and jaguarundi). Their scientific name is *Puma concolor*, formerly called *Felis concolor*. Based on molecular and morphological features, it is thought that mountain lions share a common ancestor with cheetahs (*Acinonyx jubatus*) and jaguarundi (*Puma yaguaroundi*).

Mountain lion fossil records in North America date back 300,000 years (Pierce and Bleich 2003); however, they were likely extirpated during a massive extinction event at the end of the Pleistocene, which eliminated about 80% of large vertebrates in North America (Culver et al. 2000; Caragiulo et al. 2013). Genetic studies suggest that after this extinction event, a small number of Central and South American mountain lions migrated north and repopulated North America (Culver et al. 2000; Caragiulo et al. 2013). As a result, existing North American mountain lions exhibit founder effects and have less genetic diversity compared to mountain lions in Central and South America (Culver et al. 2000; Caragiulo et al. 2013).

There is some debate regarding the number of subspecies of mountain lions. Two subspecies are “tentatively” recognized by the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Cat Specialist Group: *Puma concolor concolor* (Linnaeus, 1771) in South America and *Puma concolor couguar* (Kerr, 1792) in North and Central America and possibly northern South America west of the Andes Mountains (Kitchener et al. 2017). However, there are various studies that suggest the divergence of multiple subspecies of mountain lions. About 30 subspecies of mountain lions throughout the Americas have been referenced in the literature, with about 15 subspecies in North America (Young and Goldman 1946; Currier 1983; Pierce and Bleich 2003).

Based on more recent genetic analyses of mitochondrial DNA (mtDNA) from mountain lions throughout the Americas, Caragiulo et al. (2013) found that the mountain lions they sampled could be separated into three broad groupings: North America, Central America, and South America, with North American mountain lions having the least variation in mtDNA compared to populations in Central and South America. Although that study genotyped 601 specimens, the distribution of sampling within the broad geographic range was limited compared

to a study conducted by Culver et al. (2000), which analyzed mtDNA from 315 mountain lions sampled from more locations throughout the species' geographic distribution. Culver et al. (2000) found six phylogeographic groupings or subspecies throughout the Americas.

Despite this ongoing debate, the United States Fish and Wildlife Services (USFWS) has long recognized mountain lion subspecies under the federal Endangered Species Act (ESA). Two of these subspecies have been protected under the ESA due to low population sizes: the eastern cougar (*Puma concolor couguar*), which was listed as endangered and is now thought to be extinct, with the last recorded occurrence in 1938 (USFWS 2018), and the endangered Florida panther (*Puma concolor coryi*), which is an isolated population that is now restricted primarily to the cypress swamps of southern Florida. In addition, the California mountain lion (*Puma concolor californica*) was recognized by USFWS in response to a 1994 petition by the Mountain Lion Foundation to list the population of California mountain lions in the Santa Ana Mountains as endangered, as those populations that occur within most of California, southern Oregon, western Nevada, and northern Baja California, Mexico (USFWS 1994). Additionally, the California Department of Fish and Wildlife (CDFW) recognizes the Yuma Puma (*Puma concolor browni*) as a (sub)species of special concern that occurs in the desert plains and low mountains along the Colorado River in southeastern California, southwestern Arizona, northeastern Baja California, Mexico, and northwestern Sonora, Mexico (CDFW 1990).

In California, researchers have recently identified 10 genetically distinct mountain lion populations in California and Nevada, nine of which have core areas in California (Figure 1) (Gustafson et al. 2018). In the study, 992 mountain lions from throughout California and Nevada were genotyped using 42 microsatellite loci to identify regional populations and evaluate functional connectedness between the populations (Gustafson et al. 2018). The divergence of these populations is likely the result of habitat fragmentation caused by roads and development (Ernest et al. 2003; Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). According to Gustafson et al. (2018), mountain lions in the North Coast and inland populations (Nevada, Eastern Sierra Nevada, Western Sierra Nevada) appear to be better-connected than those in the south and along the central coast, with relatively larger effective population sizes and higher levels of genetic diversity. The authors suggest that these populations may comprise an evolutionarily significant unit (ESU). Considering the genetic source-sink dynamics among the remaining populations (Gustafson et al. 2018), petitioners demonstrate that the populations in Southern California and along the Central Coast collectively comprise an ESU (referred to as the "Southern California/Central Coast ESU"). See *Section 3.0 Southern California and Central Coast Mountain Lions Comprise and Evolutionarily Significant Unit* for more discussion.

The Southern California/Central Coast ESU is comprised of six genetically distinct mountain lion populations: Central Coast North (CC-N, which includes mountain lions in the Santa Cruz Mountains), Central Coast Central (CC-C), Central Coast South (CC-S, which includes mountain lions in the Santa Monica Mountains), San Gabriel/San Bernardino Mountains (SGSB), Santa Ana Mountains (SAM), and Eastern Peninsular Range (EPR) (Figure 1) (Gustafson et al. 2018). Most of these populations appear to be struggling with low genetic diversity and effective population sizes, which puts them at increased risk of extinction (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2018;

Benson et al. 2019). The populations struggling the most include the SAM, CC-S, SGSB, and CC-N populations. Although the CC-C and EPR have slightly higher levels of genetic diversity and effective population sizes, high rates of development in both areas could lead to a similar fate of isolation, genetic drift, low effective population size, and increased risk of extinction in the foreseeable future.

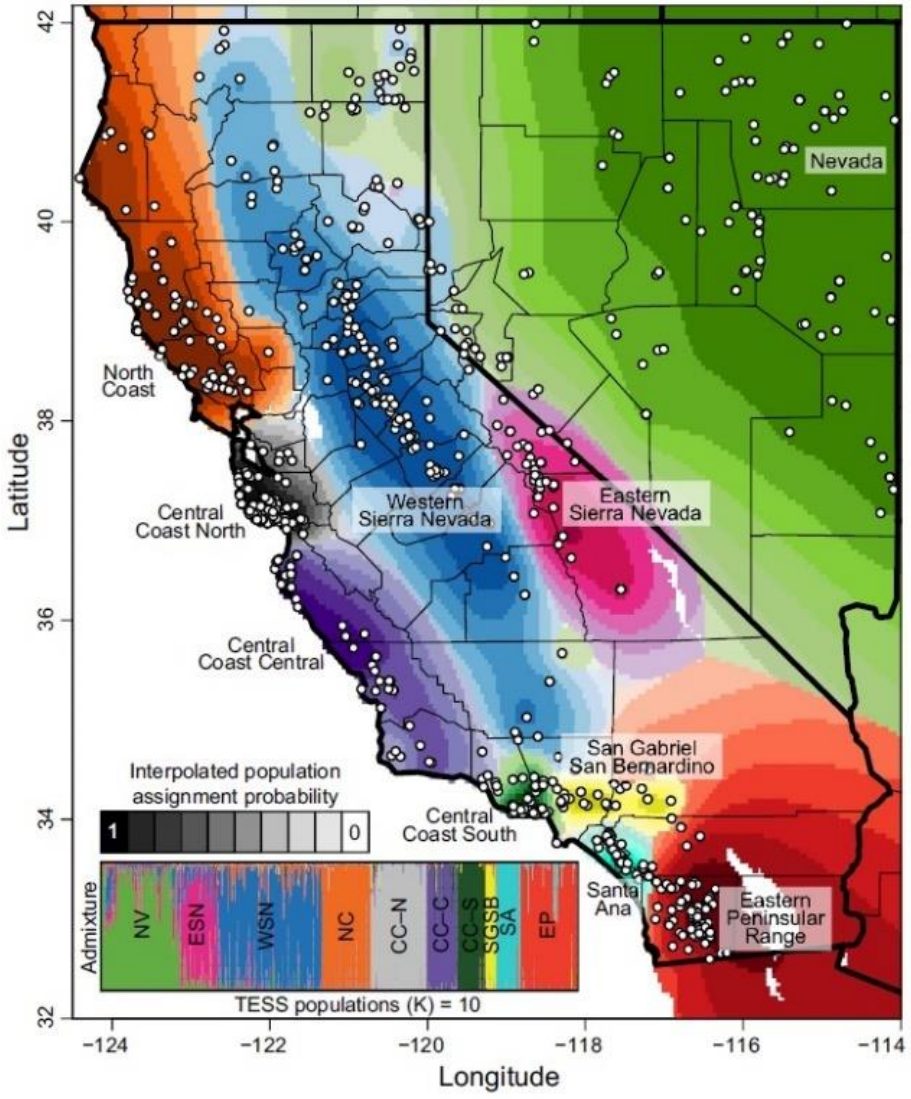


**Figure 1**. Map of genetically distinct mountain lion populations in California. The Central Coast North (CC-N), Central Coast Central (CC-C), Central Coast South (CC-S), San Gabriel/San Bernardino (SGSB), Santa Ana Mountains (SAM), and Eastern Peninsular Range (EPR) mountain lion populations should be considered an evolutionarily significant unit (ESU). Each color represents a genetically distinct mountain lion population. White dots are individual animals sampled. Source: Gustafson et al. (2018).

Although discrete populations have been identified in Southern California mountain ranges, other mountain lions have been regularly observed outside of the CC-S, SAM, SGSB, and EPR core areas, including transient and resident mountain lions in the Mojave and Colorado deserts and along the Lower Colorado River (*i.e.*, Yuma mountain lion [*Puma concolor browni*], a recognized subspecies of special concern). These populations presumably occur in low

densities due to limited resources, such as lower prey abundance/vulnerability or less suitable habitat. In fact, Kucera (1998) states that habitat within the Yuma mountain lion range is generally considered to be of low or no suitability for mountain lions. Relatively low density populations are inferred by the larger ranges of mountain lions in desert environments; four individual Yuma mountain lions had home ranges of 389km$^2$ to 1621km$^2$, which is much larger than other California mountain lion home ranges (Grigione et al. 2002; Riley et al. 2014; Zeller et al. 2017; see *Section 2.5 Habitat Requirements* for more details) but similar to those estimated for other desert mountain lions (Kucera 1998). This petition considers these low-density transients and resident lions as included within the Southern California/Central Coast ESU.

### 2.2.1 Effective Population Size and Extinction Risk

It has been established that genetic factors play a critical role in extinction risk. Inbreeding depression, loss of genetic diversity, and accumulation of deleterious mutations can lead to elevated extinction risk due to reduced reproductive fitness and evolutionary potential (*i.e.*, the ability to adapt to change) (Spielman et al. 2004; Frankham 2005; Traill et al. 2010). Effective population size ($N_e$) is a key metric used to assess a population's genetic viability and its chances of long-term persistence. Effective population size is an estimate of the size of an idealized population that would lose heterozygosity (*i.e.*, genetic diversity) at the same rate as the observed population; it indicates a population's rates of inbreeding and genetic drift (changes in allele frequencies over generations based purely on chance). A lower effective population size indicates a higher risk of inbreeding depression. Factors that affect effective population size include census population size (*i.e.*, the total number of individuals within a population), breeding sex ratio, variance in reproductive success, and population density. Several characteristics of these mountain lion populations, including small census population size, low density, female-biased sex ratios, and skewed male reproductive success, reduce effective population size, which suggests that these populations have an increased risk of inbreeding depression and extinction (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019).

The minimum effective population size for a population to persist has been debated (*e.g.*, Jamieson and Allendorf 2012; Frankham et al. 2014). Although minimum viable effective population size has been found to vary depending on the species (Frankham 1995), general conservation management practice over the past few decades has followed a 50/500 rule, which purports that an effective population size of 50 is sufficient to prevent inbreeding depression in the short term (over the duration of five generations) and an effective population size of 500 is sufficient to retain evolutionary potential in perpetuity (Frankham et al. 2014). In a 2012 review, Jamieson and Allendorf (2012) concluded that the 50/500 rule is a useful guiding principle in conservation management when genetic concerns are likely to affect the short- and long-term viability of populations. However, Frankham et al. (2014) later revised the 50/500 rule and recommended an effective population size of 100 to limit the loss of total fitness to <10% in the short-term and an effective population size of 1,000 to retain evolutionary potential for fitness in perpetuity, while recognizing that fragmented populations should be evaluated on a case-by-case basis.

Whether the 50/500 or 100/1,000 rule is considered, it is clear that Central Coast and Southern California mountain lion populations are genetically imperiled and face extinction in both the short- and long-term. Five of the six populations have effective population sizes well below 50 (from lowest to highest, according to Gustafson et al. 2018: CC-S, SGSB, SAM, CC-N, EPR), and the remaining population (CC-C) is just barely above that threshold at $N_e$ = 56.6 (Table 1) (Ernest et al. 2014; Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). Although the ratio of effective to total adult population size ($N_e$/N) varies by species, the effective population size is often much lower than the total adult population size (Frankham 1995). Several studies indicate that the $N_e$/N in wild vertebrate populations ranges from 0.2 to 0.5 (Ballou et al. 1989; Mace and Lande 1991; Spong et al. 2000; Laundré and Clark 2003). Ballou et al. (1989) estimated the $N_e$/N to be 0.25-0.5 in their population viability assessment of the Florida Panther, which aligns with other studies on big cats (Frankham 1995; Spong et al. 2000). This range was used in the USFWS's Florida Panther Recovery Plan (USFWS 2008), and, if applied to the Central Coast and Southern California mountain lion populations, the total number of mountain lions in the areas combined would be 255 to 510 individuals (Table 1). This is well below the recommended minimum viable population size of at least 5,000 adult individuals for the long-term persistence of a population (Frankham 1995; Reed et al. 2003; Traill et al. 2010).

**Table 1.** Effective population size and estimated total adult population of Central Coast and Southern California Mountain Lion Populations from Gustafson et al. (2018).

| Population | Effective Population Size ($N_e$) | Estimated Total (Adult) Population (N)[1] |
|---|---|---|
| Central Coast North (CC-N) | 16.6 | 33-66 |
| Central Coast Central (CC-C) | 56.6 | 113-226 |
| Central Coast South (CC-S) | 2.7[2] | 5-10 |
| Santa Ana Mountains (SAM) | 15.6[3] | 31-62 |
| San Gabriel/ San Bernardino Mountains (SGSB) | 5 | 10-20 |
| Eastern Peninsular Range (EPR) | 31.6 | 63-126 |
| **Total** | | 255-510 |

[1]Calculations are based on the estimated ratio of effective to total adult population size ($N_e$/N) of Florida panthers being 0.25 to 0.5 (Ballou et al. 1989). This ratio was used in the USFWS Florida Panther Recovery Plan (USFWS 2008). Petitioners recognize that these derived population estimates, while informative, are not definitive and will likely be superseded by new population estimates being developed by CDFW.

[2]Benson et al. (2019) calculate an $N_e$ of 4 for the Santa Monica Mountains population within the CC-S. Applying the Ballou et al. (1989) factors would lead to an estimate of 8-16 mountain lions in this area, which is roughly consistent with current estimates of this well-monitored population.

[3]Several studies provide $N_e$ calculation for the SAM population. Ernest et al. (2014) calculated an $N_e$ of 5.1 and Benson et al. (2019) calculated an $N_e$ of 6. Applying the Ballou et al. (1989) factors to the most recent calculation would lead to an estimate of 12-24 mountain lions in the SAM, which is roughly consistent with current estimates

Habitat loss and fragmentation due to roads and development have led to extreme levels of isolation in these populations, which have lowered their effective population sizes and, ultimately, their ability to survive and reproduce with a diverse gene pool (Ernest et al. 2014; Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). However, re-establishing gene flow among isolated subpopulations of a species can increase effective population size and reduce extinction risk (Frankham et al. 2014). Thus, the implementation of wildlife crossing infrastructure at existing barriers along with the preservation of intact, heterogeneous habitats would facilitate connectivity among Central Coast and Southern California mountain lion populations and significantly improve their chances of long-term survival.

### 2.2.2 Central Coast North (CC-N) Mountain Lion Population

In a statewide study, Gustafson et al. (2018) found that the CC-N population clustered genetically with the CC-C and CC-S populations. The population exhibited evidence of a previous genetic bottleneck and was found to have low genetic diversity and a low effective population size ($N_e$ = 16.6). There is some evidence, though weak, that suggests the CC-N population is a source population, with limited gene flow with the other Central Coast populations and the Western and Eastern Sierra Nevada populations (Gustafson et al. 2018). CDFW has identified that the Santa Cruz Mountains population, which occurs within the CC-N area, is struggling due to fragmentation from roads and development as well as lack of protected habitat (Dellinger 2019). The low genetic diversity and effective population size threaten both the short- and long-term survival of the CC-N population.

### 2.2.3 Central Coast Central (CC-C) Mountain Lion Population

The CC-C mountain lion population has been found to exhibit a previous genetic bottleneck (Gustafson et al. 2018). It has intermediate levels of genetic diversity and the highest effective population size ($N_e$ = 56.6) among the Central Coast and Southern California populations (Gustafson et al. 2018). Although this effective population size exceeds the older standard of 50 to prevent in-breeding depression in the short-term, it falls well below the recommended newer standard of 100 and is insufficient for the long-term persistence of the population. This population was found to be clustered genetically with the CC-N and CC-S populations and identified as a source population with limited gene flow with other Central Coast populations, the Western and Eastern Sierra Nevada populations, and the SGSB population (Gustafson et al. 2018). Although the CC-C population appears to be the healthiest population in the Central Coast and Southern California, the lack of sufficient protected lands and high rates of development and habitat fragmentation in the area threaten the persistence of this population (Dellinger 2019).

### 2.2.4 Central Coast South (CC-S) Mountain Lion Population

The CC-S mountain lion population has been found to exhibit a prior genetic bottleneck, with low genetic diversity and an extremely low effective population size ($N_e$ = 2.7 to 4) (Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). This population was

found to be clustered genetically with the CC-N and CC-C populations and identified as a genetic sink population, with limited gene flow from mountain lions along the Central Coast and in the Sierra Nevada (Gustafson et al. 2018).

A recent population viability analysis focused on the Santa Monica Mountains population, a subpopulation within the CC-S that has been severely isolated due to roads and development, found that if the population remains isolated with little or no immigration (similar to what is currently being observed in the area), the population could experience high levels of genetic erosion, with 40-57% loss of predicted heterozygosity within 50 years (Benson et al. 2016a). When considering just demographic processes with little or no immigration and no inbreeding depression, the population was predicted to have a 15-22% chance of extinction within 50 years (Benson et al. 2016a; Benson et al. 2019). However, if inbreeding depression occurs, which is a strong possibility given the predicted substantial loss of genetic diversity and the documentation of father-daughter, grandfather-granddaughter, and grandmother-grandson inbreeding within the population (*e.g.*, Riley et al. 2014)[3], population growth will likely decline and chances of extinction within 50 years is predicted to be 99.7%, with a median time to extinction of 15.1 years (Benson et al. 2016a; Benson et al. 2019).

### 2.2.5 Santa Ana Mountains (SAM) Mountain Lion Population

The SAM mountain lion population has been found to have the lowest genetic diversity of all populations in California, with levels nearly as low as the endangered Florida panther (Ernest et al. 2014; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). This population is also estimated to have a low effective population size ($N_e$ = 5.1 to 15.6) and high levels of relatedness and inbreeding (Ernest et al. 2014; Gustafson et al. 2018; Benson et al. 2019). The SAM population was found to be a genetic sink population, with limited gene flow with the EPR population (Gustafson et al. 2018). In a 16-year study (2001-2016) seven migrants (out of 146 sampled animals), were detected via genetics and GPS collar tracking to have crossed the I-15 between the EPR and SAM (three males from the EPR to SAM, four males from the SAM to the EPR); only one migrant is known to have reproduced (Gustafson et al. 2017). Low genetic diversity and effective population size in the SAM are indicative of a genetic bottleneck that is estimated to have occurred 40-80 years ago, around the time when urban development and multi-lane highway construction boomed in Southern California (Ernest et al. 2014; Gustafson et al. 2018). This population was also found to be largely disconnected from all the other California populations, along with the EPR population.

A recent population viability analysis found that if the population remains isolated with little or no immigration (similar to what is currently being observed in the area), the population could experience further genetic erosion, with 28-49% loss of predicted heterozygosity within 50 years (Benson et al. 2019). When considering just demographic processes with little or no immigration and no inbreeding depression, the population was predicted to have a 16-21% chance of extinction within 50 years. However, to avoid inbreeding depression in wild populations, loss in heterozygosity should be less than 5-10% over 100-200 years (Soule et al. 1986; Benson et al. 2016a), which suggests that inbreeding depression in the SAM population is

[3] Inbreeding has been documented in the SMM population in Riley et al. 2014 and in ongoing studies by the NPS. More information from the NPS is available here: https://www.nps.gov/samo/learn/nature/puma-profiles.htm

a strong possibility. In addition, evidence of potential inbreeding depression has been observed in the population (*e.g.*, kinked tails coupled with low genetic diversity, Figure 2, Ernest et al. 2014). When inbreeding depression was considered in the population viability analysis, population growth will likely decline and chances of extinction within 50 years is predicted to be 100%, with a median time to extinction of 11.7 years (Benson et al. 2019).

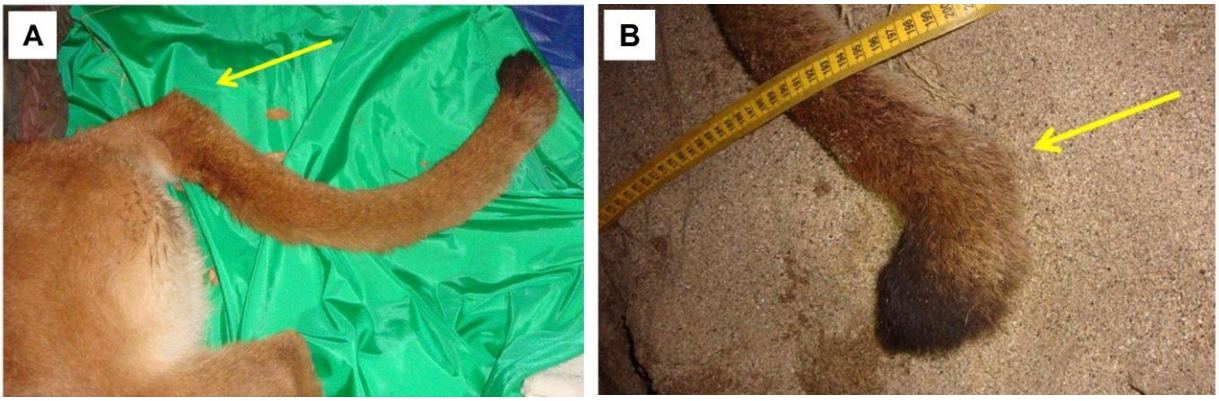


**Figure 2.** Two SAM mountain lions with a kink at the base of the tail (A) and near the tip of the tail (B). These individuals had among the lowest genetic diversity measured in the study. Source: Ernest et al. 2014.

### 2.2.6 San Gabriel/San Bernardino Mountains (SGSB) Mountain Lion Population

According to Gustafson et al. (2018), the SGSB mountain lion population exhibits extremely low genetic diversity and effective population size ($N_e$ = 5), though the sample size from SGSB was low. They were also found to be a sink population, with limited gene flow with populations in the Western Sierra Nevada, CC-C, and the EPR (Gustafson et al. 2018). Although genetic studies on this population are limited, patterns of isolation, loss of genetic diversity, and low effective population size are similar to those of the SAM and CC-S populations and likely indicate a high risk of extinction. Not only is the population's long-term survival at stake, but the geographic location of the SGSB population is paramount. Despite only limited gene flow between the SGSB population and the Western Sierra Nevada, CC-C, and EPR, this population represents a critical linkage between mountain lion populations in the northern, central coast, and southern mountain ranges of California (Gustafson et al. 2018). Restoration and enhancement of connectivity is key for the continued survival of the SGSB population as well as the Central Coast and Southern California mountain lion populations.

### 2.2.7 Eastern Peninsular Range (EPR) Mountain Lion Population

Gustafson et al. (2018) found that the EPR population exhibits a prior genetic bottleneck. Although the population was found to have a higher effective population size than the other Southern California mountain lion populations ($N_e$ = 31.6), this is still well below the older standard of 50 to prevent in-breeding depression in the short-term and is insufficient for the long-term persistence of the population. In addition, the EPR population was found to be largely disconnected from all the other California populations, with limited gene flow and low connectivity with the SAM and SGSB populations (Gustafson et al. 2018). With continued development in San Diego, Riverside, and Imperial Counties, the EPR population could have a

similar fate of isolation, genetic drift and inbreeding, and risk of extinction as the other Central Coast and Southern California populations.

As mentioned previously, there are records for mountain lions outside of the core mountain ranges in Southern California, which are likely transients or residents of smaller populations. For example, the Yuma mountain lion has been recognized by CDFW as a subspecies of special concern, and likely occurs in low density in the desert plains and low mountains of the Colorado River Valley. Genetic studies on the Yuma mountain lion are limited, and no samples were obtained from that area for the study conducted by Gustafson et al. (2018). However, the low densities of transients and smaller populations in areas where roads and development threaten connectivity make them part of the EPR and larger Southern California population, and as such, they are considered a conservation concern and are included in this petition.

### *2.3 Reproduction and Growth*

Dens are often in rocky outcrops (left) or in dense vegetation (right). Photos: NPS.

Mountain lions are polygamous breeders, and mates likely locate each other with auditory and olfactory signals (Currier 1983). They may reproduce at any time of year, though seasonal pulses have been documented and the timing of reproduction may be affected by prey abundance or climate (Pierce and Bleich 2003). In North America, kitten births are most common between April and September (Currier 1983; Beier 1995; Pierce and Bleich 2003).

Pairs generally mate for about 2-5 days (Beier et al. 1995), though there are instances in which pairs have been recorded traveling together for up to 16 days (Seidensticker et al. 1973). During this time they vocalize frequently, travel little, will sometimes share a kill, and copulate up to 70 times per day (Seidensticker et al. 1973; Beier et al. 1995; Pierce and Bleich 2003). Female estrous cycles last an estimated 4-12 days, and it is hypothesized that numerous acts of copulation stimulate ovulation and improve chances of successful fertilization (Pierce and Bleich 2003, Kitchener 1991). If the litter is born dead or removed within 24 hours of birth, females will go into estrous within a few weeks (Currier 1983). In addition, competing males have been

known to commit infanticide[4], presumably to trigger estrous in females, though scientists are still investigating what drives this behavior.

Gestation lasts 82-96 days (Young and Goldman 1946; Currier 1983). Litter size ranges from 1-6, though 2-4 kittens per litter are typical (Pierce and Bleich 2003; Beier et al 2010; Riley et al. 2014). Females average larger litters during their first year of reproduction and tend towards smaller litters when they are older (Pierce and Bleich 2003). The sex ratio of litters has generally been found to be equal (Pierce and Bleich 2003). Females keep their kittens in dens located in rocky terrain or in dense vegetation that provide cover (Young and Goldman 1946), and they may move their young to several different dens until the young are weaned at about 2-3 months old (Pierce and Bleich 2003). Denning mountain lions have been found to avoid roads and stay at a distance from human disturbance four times greater (~600m) than non-reproductive mountain lions (~150m) (Wilmers et al. 2013).

Females care for their young for 1-2 years, at which point the mother comes into estrous and either abandons the cubs or acts aggressively towards them to prevent them from following her, as older males will kill cubs (Young and Goldman 1946; Seidensticker et al. 1973; Currier 1983; Beier 1995; Pierce and Bleich 2003). Newly independent young have been found to stay in the area where the mother leaves them for 2-3 weeks, and then disperse away from the direction their mother left (Beier 1995). Typically 50% of females stay in their natal range and 50% disperse while all males disperse, and siblings sometimes travel for a short time together (Pierce and Bleich 2003; Logan and Sweanor 2010). Subadult mountain lions may disperse up to 500km from their natal home ranges as they explore and establish their own territories (Pierce and Bleich 2003).

Mountain lions reach sexual maturity at 2-4 years of age. Although they are rarely known to mate until they have an established home range, transient males may occasionally breed with resident females (Hornocker 1970; Seidensticker et al. 1973; Currier 1983).

### *2.4 Diet and Foraging Ecology*

Mountain lion cub feasting on a deer kill in the Santa Monica Mountains. Photo: NPS.

[4] Infanticide has been documented in the Santa Monica Mountains mountain lion population. More information from the NPS is available here: https://www.nps.gov/samo/learn/nature/puma-profiles.htm

Large ungulates, especially deer, are the preferred prey of mountain lions, making up about 70% of their diet (Currier 1983; Iriarte et al. 1990). Hornocker (1970) estimated that the average adult mountain lion consumes 860-1,300kg of large prey annually. However, mountain lions are opportunistic predators, and they have been documented eating a wide variety of other large and smaller prey, including moose, elk, wild horses, burros, pronghorn, bighorn sheep, mountain goats, wild hogs, coyotes, bobcats, porcupines, badgers, rabbits, raccoons, rodents, turkeys, and livestock (Currier 1983; Iriarte et al. 1990; Garcelon unpublished data).

Their diet can vary by prey availability, prey vulnerability, the presence of sympatric carnivores, the season, and the age and sex of the mountain lion (Currier 1983; Iriarte et al. 1990; Knopff et al. 2010; Allen et al. 2014a). For example, deer have been found to make up >90% of the diet in mountain lions in the Santa Monica Mountains and in Northern California (Allen et al. 2014a; Riley et al. 2014), while in Florida wild hogs were found to be the most common prey (Maehr et al. 1990), and in northwestern Sonora, Mexico bighorn sheep were found to be the primary prey (Rosas-Rosas et al. 2003). These observed patterns were likely due to the availability of different prey in different geographic regions. A study conducted in Alberta, Canada, Knopff et al. (2010) found that while adult females were more likely to kill small ungulates (*e.g.*, deer), adult males were more likely to kill larger ungulates (*e.g.*, elk), and subadults relied on both small ungulates and nonungulate prey (*e.g.*, beavers, snow hares). A similar pattern was found in a mountain lion population in the Greater Yellowstone Ecosystem, in which older, larger individuals hunted larger prey and younger, smaller individuals hunted smaller prey (Elbroch and Quigley 2019). In addition, mountain lions were found to prey upon female ungulates in the spring before and during the birthing period, and they would more often prey upon male ungulates in the fall during the rut, highlighting that prey vulnerability may play a role in mountain lion predation (Knopff et al. 2010).

Mountain lion preying on a coyote in Joshua Tree, California. Photo: Brendan Cummings

Mountain lions roam through expansive home ranges in search of prey, often hunting between dusk and dawn. Although they are generally most active at dusk and dawn, their peak activities have been observed to shift to more nocturnal patterns when they are closer to human

disturbance (Van Dyke et al. 1986). Mountain lions are primarily solitary animals and will repeatedly move and wait as they stalk and ambush their prey (Beier et al. 1995). Once within close proximity, mountain lions will lunge at their prey and kill the animal by crushing the trachea and suffocating it or by breaking its neck at the base of the skull with a bite (Currier 1983; Pierce and Bleich 2003). Instead of eating their kill right away, mountain lions drag their kill to a secluded spot to feed. They cover it with brush and other debris and return to feed at night for up to five days (Currier 1983; Beier et al. 1995). However, the presence or perceived presence of humans has been found to reduce overall feeding time (Smith et al. 2015; Smith et al. 2017).

Deer kill rates vary depending on the sex of the mountain lion, whether or not the female has cubs, and surrounding human land use. Male kill rates have been found to range from 35 to 47 ungulates per year, regardless of housing density (Anderson , Jr . and Lindzey 2003; Cooley et al. 2008; Knopff et al. 2010; Smith et al. 2015). However, kill rates for females differ depending on human disturbance. In lower density housing areas, kill rates of solitary females and females with kittens have been found to be 52-60 and 57-68 ungulates per year, respectively, while females in high density housing areas were found to have a kill rate of 81 ungulates per year (Anderson , Jr . and Lindzey 2003; Cooley et al. 2008; Knopff et al. 2010; Smith et al. 2015). This pattern could be driven by reduced time spent at kill sites in more developed areas, indicating that females are not consuming as much of each carcass and therefore need to kill more prey (Smith et al. 2015). This may reflect a trade-off made by females to choose feeding sites closer to human-disturbed areas and expend more energy killing prey in order to reduce potential encounters with males that pose a threat to themselves or their kittens (Benson et al. 2016b). Another factor that may be contributing to higher kill rates in developed areas is that mountain lions expend more energy traveling faster and farther in human-dominated landscapes and therefore require increased caloric intake compared to mountain lions away from developed areas (Wang et al. 2017).

### *2.5 Habitat Requirements*

Mountain lions are primarily solitary (except in certain situations, such as when breeding, when females are rearing cubs, or when dispersing with siblings), territorial cats that occur in low density. They require large areas of relatively undisturbed habitats with adequate connectivity to allow for dispersal and gene flow. They have large home ranges that include heterogenous habitats. In the United States these often consist of pine forests, riparian and oak woodlands, streams, chaparral, and grasslands, though they are also known to occur in desert habitats (*e.g.*, Figure 3).

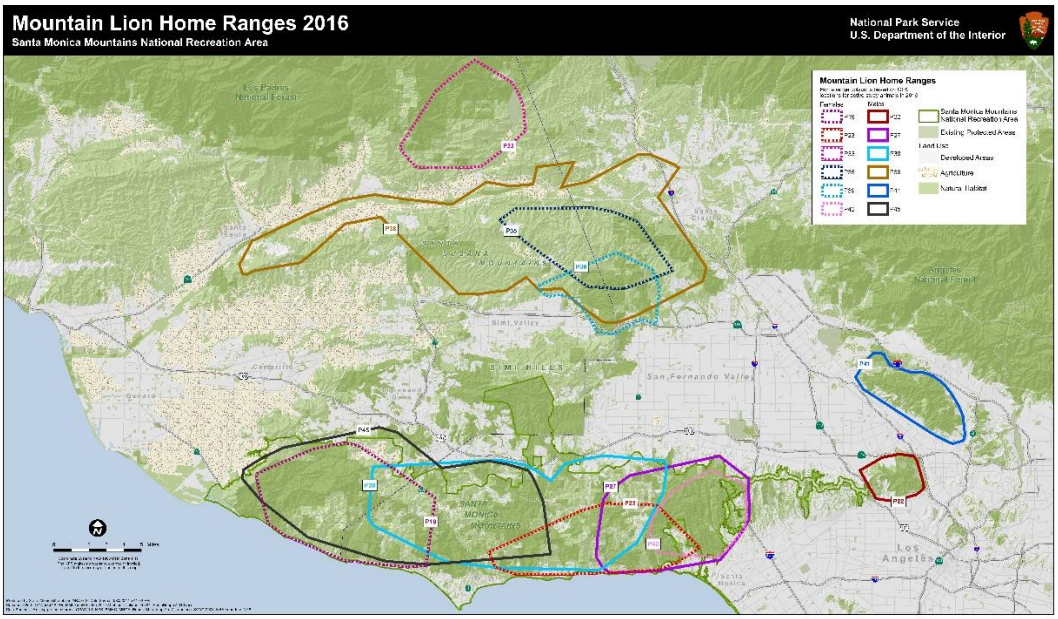


**Figure 3.** Home ranges of mountain lions being actively studied in 2016 by NPS in and near the Santa Monica Mountains. Source: NPS.

Mountain lions have been found to utilize different habitats within a 24-hour period (Dickson and Beier 2002; Dickson et al. 2005; Dickson and Beier 2006; Kertson et al. 2011; Zeller et al. 2017). Riparian habitats were found to be preferred over grasslands and human-disturbed areas during the day, which likely represents the animals resting in areas with understory vegetation for cover (Dickson and Beier 2002; Dickson et al. 2005). However, nocturnal movement patterns showed that mountain lions utilize a broad range of habitats as they travel through their home ranges and hunt (Dickson et al. 2005). Although riparian vegetation was the highest ranked habitat for nocturnal use, usage of riparian areas was not statistically different from the use of scrub, chaparral, grasslands, or woodlands (Dickson et al. 2005).

Nocturnal patterns of movement and stasis suggest that mountain lions generally avoid areas with human disturbance (*i.e.*, residential developments and two-lane paved roads) and use a variety of habitats to stalk and pursue their prey (Dickson and Beier 2002; Dickson et al. 2005). In addition, Dickson and Beier (2006) found that when mountain lions were traveling or hunting, they preferred canyon bottoms and gentle slopes and used steeper slopes and ridgelines to a lesser extent. And Benson et al. (2016b) found that mountain lions tend to choose feeding sites on steeper slopes in habitats with dense understory vegetation, such as chaparral, scrub, and upland forest. Although mountain lions will use moderately disturbed areas as they travel and hunt (Wilmers et al. 2013; Gray et al. 2016), occupancy is lower in developed areas and they are more likely to use developed areas if they border open spaces (Wang et al. 2015). Thus, mountain lions require a habitat mosaic that provides sufficient room to roam away from human-disturbed areas and connected to expansive, intact, heterogeneous habitats (Beier 1995; Dickson and Beier 2002; Dickson et al. 2005; Kertson et al. 2011; Zeller et al. 2017).

Home range size can vary depending on geographic area, season, sex, reproductive status, and prey density (Currier 1983; Grigione et al. 2002; Riley et al. 2014). Males generally have

much larger home ranges than females, and females with cubs tend to have even smaller home ranges (Beier et al. 1995; Grigione et al. 2002). Male home ranges tend to include partially or entirely overlapping female home ranges, and to a limited extent, they may partially overlap with other male home ranges (Figure 3) (Seidensticker et al. 1973; Currier 1983; Pierce and Bleich 2003). Mountain lions mark their home ranges with scrapings in the ground, often containing urine or feces (Seidensticker et al. 1973). Males make scrapings more often than females (Allen et al. 2014b), and females may only make scrapings when they are in estrous (Seidensticker et al. 1973; Currier 1983; Pierce and Bleich 2003).

Seasonal variation in home range size can differ depending on geographic area. Grigione et al. (2002), found strong influences of seasonality in average mountain lion home ranges in the Sierra Nevada mountains, with much larger home ranges in the summer (541km$^2$ for females, 723km$^2$ for males) compared to those in the winter (349km$^2$ for females, 569km$^2$ for males). These patterns likely reflect the abundance and distribution of deer – during the winter deer would be concentrated at lower elevations, which allowed mountain lions to reduce their home ranges, while in the summer deer could disperse to higher elevations and the mountain lions would expand their ranges accordingly (Grigione et al. 2002). However, seasonal variation was not as pronounced and had the reverse trend in Coastal California mountain ranges, including in the SAM, where the average area of winter home ranges was slightly larger (100km$^2$ for females, 350km$^2$ for males) than summer home ranges (90km$^2$ for females, 300km$^2$ for males) (Grigione et al. 2002). These differences were not statistically significant, and this pattern is likely due to the moderate year-round climate in the coastal ranges, where prey abundance and distribution does not exhibit as extreme shifts as those in the Sierra Nevada (Grigione et al. 2002). This generally aligns with Zeller et al. (2017), who found that mountain lion home ranges in the SAM and EPR ranged from 41-497 km$^2$, with mean home range sizes of 188km$^2$ for females and 316 km$^2$ for males. And Riley et al. (2014) found that CC-S mountain lions had home ranges similar in size to the SAM and EPR mountain lions, with female home ranges being 100-200km$^2$ and male home ranges being 300-500 km$^2$. According to the Santa Cruz Puma Project, in the Santa Cruz Mountains female home ranges are on average about 100 km$^2$ and male home ranges are about 230 km$^2$ (Santa Cruz Puma Project 2015). Although studies are limited regarding the home range size of the CC-C and SGSB mountain lions, given their close proximity and similar seasonality to other Central Coast and Southern California populations, they are likely similar.

### *2.6 Survivorship and Mortality*

According to the National Park Service (NPS), mountain lions can live up to 13 years in the wild. As a top carnivore with no natural predators, conspecifics and humans are the main drivers of mountain lion survivorship and mortality. Although studies regarding kitten (<18 months), subadult (18-30 months), and adult (>30 months) survivorship are limited, some long-term studies of radio-collared mountain lions on the CC-S, SAM, and EPR provide valuable insights for these Central Coast and Southern California populations (Beier and Barrett 1993; Riley et al. 2014; Vickers et al. 2015).

In a study conducted in the CC-S area (which encompasses the Santa Monica Mountains, Simi Hills, and Santa Susana Mountains) that included 42 mountain lions from 2002 to 2012, Riley et al. (2014) found an annual adult survival of ≥ 75%, though Benson et al. (2016a) found

lower subadult survival rates. Although adult survival in the CC-S is similar to previous studies conducted in California and the southwestern US (Beier 1993; Logan and Sweanor 2001), it is higher than what was found in the SAM and EPR populations during the same time period. From following 74 radio-collared mountain lions from 2001 to 2013, Vickers et al. (2015) found an annual survival rate across all age groups of 56.5% and 55.4% in the SAM and EPR, respectively.

In the Santa Monica Mountains: Female mountain lion P-23 hunted down a deer on Mulholland Drive (left). In 2018 she was killed by a vehicle strike on Malibu Canyon Road. An uncollared mountain lion killed by a vehicle strike on Malibu Canyon Road in 2004 (right). Photos: NPS

Vehicle strikes, depredation kills, and intraspecific strife (including male aggression towards conspecifics and infanticide) are the primary causes of mortality in the Central Coast and Southern California populations (Beier 1993; Riley et al. 2014; Vickers et al. 2015). Other known causes of death in California mountain lion populations include rodenticide poisoning, disease, poaching/illegally killing, starvation/abandonment, public safety removal, and human-caused wildfires (Beier 1993; Riley et al. 2014; Vickers et al. 2015). Causes of mortality will be discussed more in depth in *Section 5.0 Abundance and Population Trends* and *Section 6.0 Factors Affecting Ability to Survive and Reproduce*.

## 3 Southern California and Central Coast Mountain Lions Comprise an Evolutionarily Significant Unit

### *3.1 CESA Provides for Listing of ESUs*

CESA defines an "endangered species" as a species or subspecies of animal or plant that is in serious danger of becoming extinct through either all or "a significant portion" of its range. (Cal. Fish & Game Code § 2062.) A "threatened species" is likely to become an endangered species in the foreseeable future in the absence of special protection and management efforts. (Cal. Fish & Game Code § 2067.) CDFW has concluded—and appellate courts have upheld—that the term "range" is construed to refer to the range of a species or subspecies *within* California, not the worldwide range of the species or subspecies. (*California Forestry Assn. v. California Fish & Game Com.* (2007) 156 Cal.App.4th 1535, 1550-551.) This means that a species or subspecies which may not be endangered in other states or countries may still be endangered within California. Courts also have confirmed that the phrase "significant portion" of

a range authorizes CDFW to designate certain populations of a species or subspecies as "evolutionarily significant units" or "ESUs" and list such populations as endangered under CESA. (*Id.* at 1549; *Central Coast Forest Assn. v. Fish & Game Com.* (2018) 18 Cal.App.5th 1191, 1236-37 [*"CCFA II*"].) In other words, ESUs are a population of a species or subspecies "that is considered distinct for purposes of conservation." (*Central Coast Forest Assn. v. Fish & Game Com*. (2012) 211 Cal.App.4th 1433, 1439 fn 5 [depublished] ["*CCFA I*"].)

CDFW has confirmed that the use of ESUs to evaluate the status of species pursuant to CESA is appropriate.[5] In the *Status Review of Fisher,* CDFW designated fishers in northern California and the southern Sierra Nevada as two separate ESUs based upon the reproductive isolation of these fisher populations and the degree of genetic differentiation between them. In designating these ESUs, CDFW highlighted the need to maintain "geographically widespread and genetically diverse" populations of the species.

### *3.2 Southern California and Central Coast Mountain Lions are Significantly Reproductively Isolated from Other Populations and Form an ESU*

Southern California and Central Coast mountain lion populations could be grouped into one or several potential ESUs. However, petitioners believe that for purposes of listing under CESA, treating the CC-N, CC-C, CC-S, SAM, SGSB, and EPR populations as a single Southern California/Central Coast ESU is both supported by the best available science and makes sense from a management perspective. Gustafson et al. (2018) suggest that the North Coast and inland populations (Nevada, Eastern Sierra Nevada, and Western Sierra Nevada) may form an ESU (hereinafter "North Coast/Inland ESU") given that they were found to be genetically diverse and well-connected. Due to extreme isolation and high levels of human-caused mortalities, functional connectivity between Southern California and Central Coast mountain lion populations and the healthier North Coast/Inland ESU has become severely impaired (Gustafson et al. 2018, see further discussion in *Section 2.2 Taxonomy and Population Genetics* and *Section 6.0 Factors Affecting Ability to Survive and Reproduce*). There is a tenuous link made up of small mountain ranges (*i.e*., Tehachapi and Sierra Pelona Mountains) that connect the North Coast/Inland ESU with the proposed Southern California/Central Coast ESU. Thus, although there is some (limited) connectivity between the North Coast/Inland ESU and the proposed ESU, as a practical matter under current management the two ESUs are functionally isolated.

Southern California and Central Coast populations have lower levels of genetic diversity and are relatively disconnected from each other compared to North Coast and inland populations. The Central Coast populations form a genetic cluster while the SAM and EPR populations form a second, less connected genetic cluster (Figure 4) (Gustafson et al. 2018). The SGSB population, though isolated, is most genetically similar to the Western Sierra Nevada, CC-C, and EPR populations, which indicates that it is an important intersection for statewide genetic connectivity (Figure 4) (Gustafson et al. 2018).

Genetic source-sink dynamics are informative in determining gene flow among the populations and how they are connected. Five genetic source populations were identified: the

[5] California Department of Fish and Wildlife, *Status Review of Fisher* (June 10, 2015), available at https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=101470.

Eastern and Western Sierra Nevada populations, CC-N, CC-C, and EPR (Gustafson et al. 2018). The Sierra Nevada populations were the greatest genetic source populations and the CC-N population had only weak evidence of being a source population (Gustafson et al. 2018). The CC-S, SGSB, and SAM were identified as genetic sink populations with limited connectivity to source populations (Figure 4) (Gustafson et al. 2018). Maintaining and reestablishing genetic connectivity with source populations like the CC-C, EPR, and Western Sierra Nevada populations are important for the long-term viability of Southern California and Central Coast populations (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gray et al. 2016; Gustafson et al. 2017). This underscores the importance of the Tehachapi and Sierra Pelona Mountains as the key remaining linkage, though tenuous, for statewide genetic connectivity.

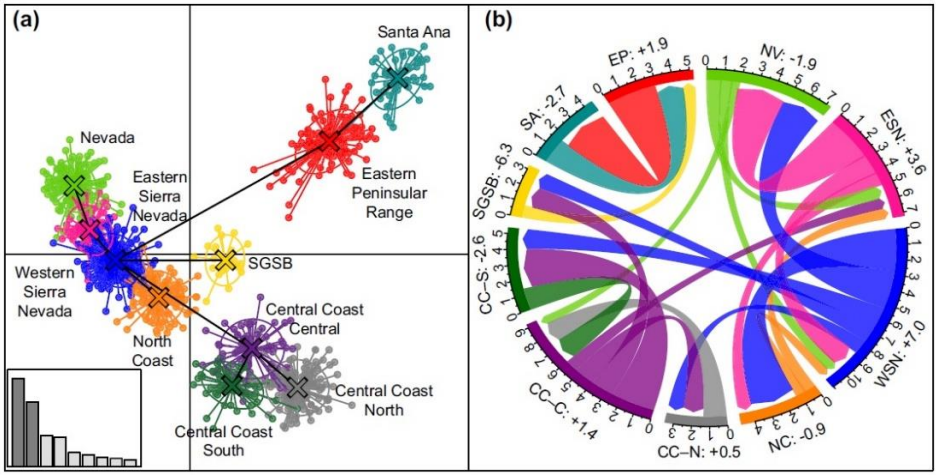


**Figure 4.** Functional connectedness of California mountain lion populations. Each color represents a genetically distinct population. In (a), the results of the discriminant analysis of principal components shows connectivity among California mountain lions. The x-axis represents latitude with north to the left and south to the right. The y-axis represents longitude, separating the Central Coast populations from Southern California populations. In (b), estimated migration rates between populations are shown. Source-sink dynamics are indicated by positive (source) or negative (sink) net migration rates. Source: Gustafson et al. (2018).

While genetics as currently understood could support several different ESU formulations, petitioners believe a single Southern California/Central Coast ESU is the most pragmatic from a management perspective, as recovery of the individual subpopulations ultimately depends upon maintaining and/or reestablishing connectivity between them. *See CCFA II*, 18 Cal.App.5th 1191, 1237 ("[T]he nature of the ESU designation is such that genetics alone are not determinative: One must look beyond genetics to questions of policy to determine which populations to include in an ESU.") (quotations omitted). Designating Southern California and Central Coast mountain lions as an ESU would help ensure "geographically widespread and genetically diverse" populations of mountain lions in California.

While petitioners believe that listing of a single Southern California/Central Coast ESU as threatened is both a permissible and prudent course of action for the Commission, petitioners also request that as additional data become available over the course of CDFW conducting its status review that the agency also assess other possible ESU formulations for Southern California and Central Coast mountain lions. One such formulation would be to group all three Central Coast populations (CC-N, CC-C and CC-S) into one ESU, with the remaining three

populations placed into a second ESU (SAM, EPR and SGSB). Alternatively, the Central Coast populations could be treated as one ESU, SAM and EPR as a second ESU, and SGSB separately listed as a third ESU. Petitioners believe the genetic data in Gustafson et al. (2018) could support each of these alternative formulations. Lastly, given each of the six populations at issue are themselves already genetically distinguishable and occupy significant portions of the range of mountain lions in California, each could be separately treated as an ESU. Under this formulation, the SAM and CC-S populations would clearly warrant endangered listing, the CC-C and EPR populations would warrant threatened listing, and the CC-N and SGSB populations would warrant at least threatened and likely endangered listing.

### *3.3 Proposed Boundary of the Southern California/Central Coast ESU*

We propose the Southern California/Central Coast ESU to include mountain lions that occur in areas east of the Pacific Ocean, south of the San Francisco Bay Area waters and I-80, west of I-5 to the intersection of I-5 and SR-58 at Bowerbank/Buttonwillow, south of SR-58 to I-15, south of the I-15 from the SR-58 intersection to the California-Nevada border, and, for the purposes of CESA, north of the California-Mexico border (Figure 5). These boundaries are recommended as they include virtually all mountain lions associated with the six populations comprising the ESU and are also unambiguous and readily discernable for purposes of management.[6]

[6] In the event the Commission determines that the proposed ESU should instead be treated as separate Southern California (SAM, EPR, SGSB) and Central Coast (CS-N, CS-C, CS-S) ESUs, we propose the boundary between them to be delimited by I-5 and I-710.

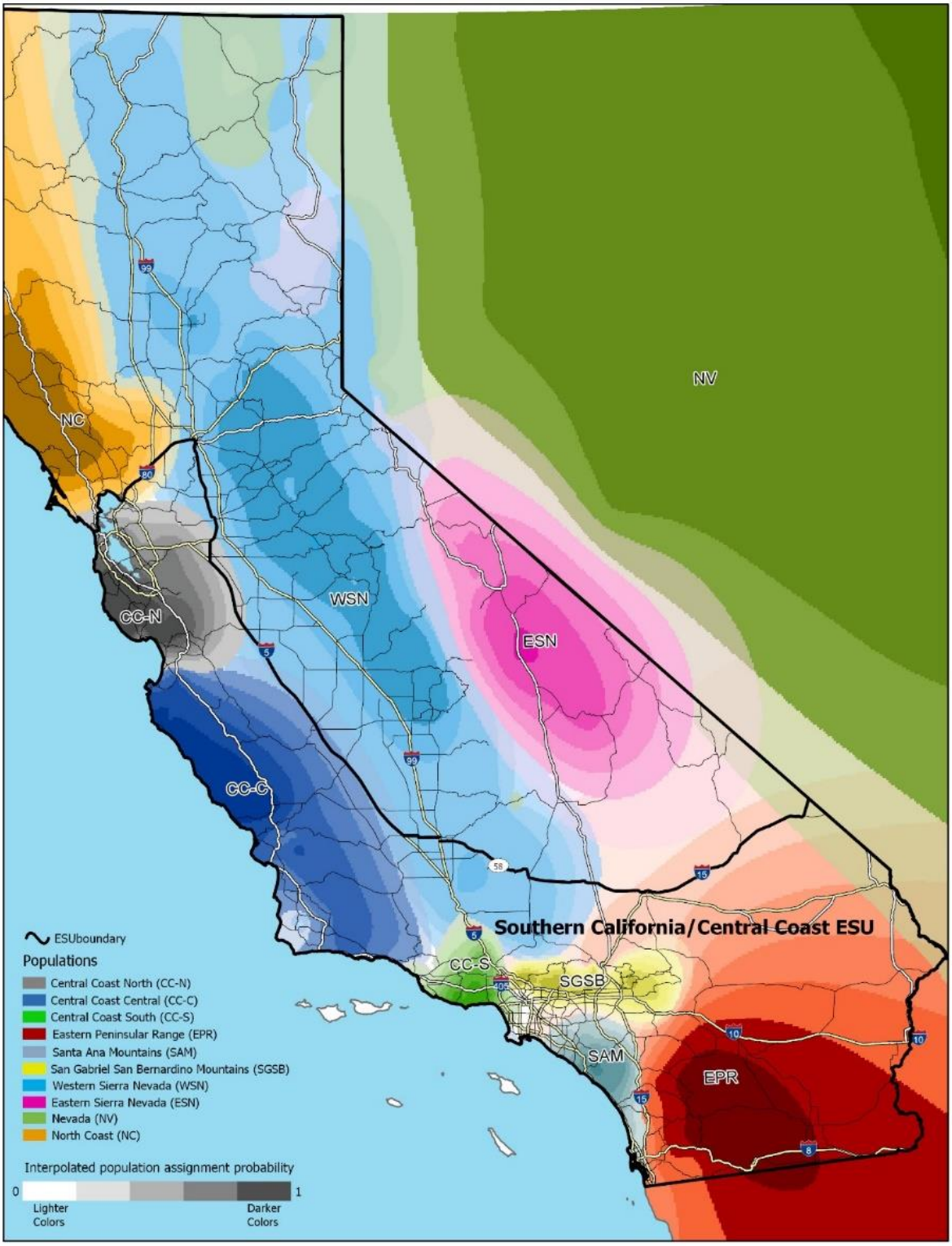


**Figure 5.** Map of the Southern California/Central Coast ESU boundary. Derived from Gustafson et al. (2018). Genetics data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie. Roads data source: ESRI.

We recommend including mountain lions in the Tehachapi and Sierra Pelona Mountains south of SR-58 in the Southern California/Central Coast ESU. While most mountain lions sampled from this region share some genetic affinities with Western Sierra Nevada (WSN) animals, individuals sampled in the Tehachapi Mountains and surrounding areas, including the Sierra Pelona Mountains in the Angeles National Forest and the Los Padres National Forest, had genetic structures made up of multiple genetic populations from the northern, central coastal, and southern populations (Figure 6). This area serves not just as a connecting link between mountain lion populations comprising the Southern California/Central Coast ESU, but also between this ESU and all other California mountain lions. The Tehachapi and Sierra Pelona Mountains are the last remaining linkages for statewide genetic connectivity and are critical for the overall genetic health of Southern California and Central Coast mountain lions. Consequently, mountain lions in these areas should be considered part of the listed entity.

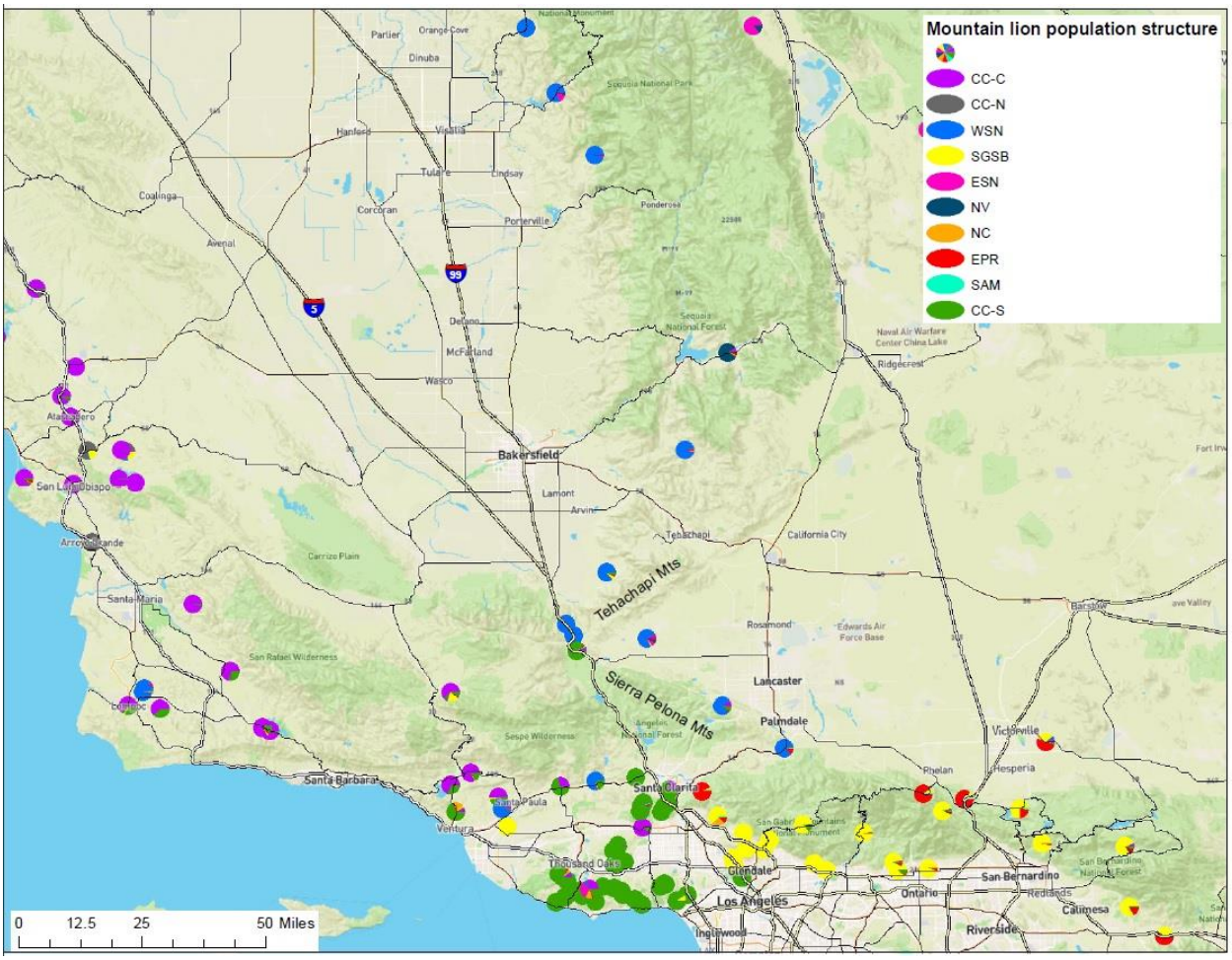


**Figure 6.** Map of mountain lion genetic structure in and surrounding the Tehachapi and Sierra Pelona Mountains, the last remaining linkage between the coastal, southern, and northern populations. Data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie.

### *3.4 Southern California and Central Coast Mountains Lions are Essential to the Region's Biodiversity*

Additional support for designation of a Southern California/Central Coast ESU is provided by the fact that mountain lions are a keystone species critical to maintaining biodiversity in coastal California's ecosystems. The loss of these mountain lions—which are the only remaining large predator in the region—would lead to a trophic cascade wherein deer populations would increase and overgraze vegetation due to the lack of predation and lack of risk of predation, causing other repercussions to other species and habitats (Ripple and Beschta 2006; Ripple and Beschta 2008; Ripple et al. 2014). In addition, their kills are an important source of food for multiple terrestrial and avian scavengers (Ruth and Elbroch 2014; Elbroch et al. 2017; Barry et al. 2019).

Ripple and Beschta (2006) highlighted the critical role of mountain lions in western ecosystems by comparing habitat quality and the levels of biodiversity in two separate areas of Zion National Park – Zion Canyon, which mountain lions generally avoid due to high human presence, and North Creek, which mountain lions inhabit due to less human presence. The sustained lack of mountain lions in Zion Canyon has led to an unnaturally high density of deer, which has had profound impacts on Zion Canyon ecosystems. Ripple and Beschta (2006) observed Zion Canyon had low numbers of hydrophytic plants, wildflowers, amphibians, lizards, and butterflies while North Creek had significantly higher numbers in each of these categories.

North Creek riparian areas had well vegetated and stable banks while Zion Canyon lacked bank vegetation and its banks were continuing to erode (Ripple and Beschta 2006). The study noted that such geomorphic transformation of stream channels where mountain lions were absent were caused by plant loss on stream banks, which led to high levels of erosion and sedimentation, less shading and higher water temperatures, a larger width:depth ratio in streams, loss of hydrologic connectivity with historical floodplains, and loss of a wide variety of species, including native plants, benthic invertebrates, butterflies, fish, amphibians, and reptiles (Ripple and Beschta 2006).

The study concluded that removing a large carnivore from an ecosystem "appears to have [] profound effects on lower trophic levels, as well as multiple indicators of ecosystem status and native species abundance." (Ripple and Beschta 2006.) A similar study found that in Yosemite Valley—where mountain lions are largely absent due to high human presence—deer populations have expanded leading to a lack of oak recruitment and a decrease in biodiversity (Ripple and Beschta 2008). And their kills support disproportionately high levels of mammal, bird, and invertebrate diversity (Ruth and Elbroch 2014; Elbroch et al. 2017; Barry et al. 2019) and may even play a role in tree and other vegetation growth (Ruth and Elbroch 2014). In sum, extinction of Southern California and Central Coast mountain lions would result in degraded habitats and reduced abundance and diversity of other species, likely undermining the biological diversity, ecosystem function, and resilience of California's coastal regions.

### *3.5 Californians Derive Aesthetic, Recreational, and Economic Value from Southern California and Central Coast Mountain Lions*

The people of California derive aesthetic, recreational, economic, spiritual, scientific, educational, and emotional value from Southern California and Central Coast mountain lions. For instance, the City of Los Angeles has designated October 22 as "P-22 day" to honor a young (and mate-less) male mountain lion that lives in Griffith Park and to acknowledge the importance of Southern California mountain lions to the region. Many people view mountain lions as a symbol of wildness and cherish landscapes that still are home to these predators. People from within and beyond the region choose to recreate, hike, bike, camp, fish, and hunt in California's wildlands in part because they enjoy exploring and sharing landscapes with mountain lions. And these activities are a significant economic driver for the state: A report commissioned for California State Parks found that direct outdoor recreation expenditures for Los Angeles, Southern California, the Central Coast and the San Francisco Bay Area totaled nearly $15 billion per year.[7] The Outdoor Industry Association concluded that outdoor recreation in California generates $92 billion of consumer spending annually and directly employs 691,000 Californians—more jobs than the wine and television industry combined.[8]

Mountain lions also provide an economic and social benefit because, by controlling deer populations, they reduce collisions between deer and automobiles. There are 1.2 million deer-vehicle collisions in the United States per year, incurring an estimated $1.66 billion in damages, 29,000 injuries, and 200 deaths (Gilbert et al. 2016). Impacts of deer-vehicle collisions are particularly severe in the eastern United States where white-tailed deer are overabundant. Gilbert et al. (2016) determined that if mountain lions recolonized the eastern United States, their presence would result in a 22 percent decline in deer-vehicle collisions over thirty years.

It is estimated that 7,000 to 23,000 wildlife vehicle collisions have occurred annually on California roads (Shilling et al. 2017; Shilling et al. 2018; State Farm Insurance Company 2016, 2018). These crashes result in human loss of life, injuries, emotional trauma, and property damages that can add up to $300-600 million per year (Shilling et al. 2018). If Southern California and Central Coast mountain lions became extinct, there would likely be a significant increase in deer-vehicle collisions in the region, along with associated human fatalities, injuries, and property damage.

An overabundance of deer in the eastern United States is also linked to an increase in ticks, which has led to increased incidences of Lyme disease among humans (Telford 2017; Côté et al. 2004). Lyme disease is now the most common vector-borne illness in the United States, with over 30,000 cases per year, primarily in the eastern United States.[9] Increases in deer abundance and attendant increases in ticks and tick-borne disease among humans would be

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[7] BBC Research & Consulting, *California Outdoor Recreation Economic Study: Statewide Contribution and Benefits* (2010), available at https://www.parks.ca.gov/pages/795/files/ca%20outdoor%20rec%20econ%20study-statewide%2011-10-11%20for%20posting.pdf.

[8] Outdoor Industry Association, *California Recreation Report*, available at https://outdoorindustry.org/wp-content/uploads/2017/07/OIA_RecEcoState_CA.pdf.

[9] Centers for Disease Control and Prevention, *Lyme Disease Data and Surveillance*, available at https://www.cdc.gov/lyme/datasurveillance/index.html?CDC_AA_refVal=https%3A%2F%2Fwww.cdc.gov%2Flyme%2Fstats%2Findex.html.

expected if Southern California and Central Coast mountain lions became extinct. Loss of Southern California and Central Coast mountain lions would have far-reaching effects not only on California's ecology, but also on public health and the region's economy.

Protection of Southern California and Central Coast mountain lions under CESA would confirm that this species is a vital member of our ecosystems which is worthy of protection. Conservation of these mountain lions would provide compelling evidence that large carnivores and abundant human populations can co-exist, even in densely populated landscapes (Benson et al. 2019).

## 4 Historical and Current Distribution

Mountain lions once had the most expansive range of any New World terrestrial mammal (Seidensticker 1991). They roamed most of the Americas (excluding most of Alaska and the northern areas of Canada) from approximately 50º N to 50ºS latitude and could be found from sea level to about 4,000m elevation (Young and Goldman 1946, Pierce and Bleich 2003) in habitats varying from dense forests, to dry deserts, savannahs, and swamp lands.

Due to habitat loss and hunting after the arrival of European colonists, the mountain lion's current range has been reduced to one third of its historical range in North America (Figure 7) (Culver et al. 2000; Pierce and Bleich 2003). In the United States, the species' range has been reduced to 15 western states and a small remnant population in Florida (endangered Florida panthers [*Puma concolor coryi*]), with isolated animals occasionally appearing in additional states. Continued hunting pressure and changes in land management practices have pushed most populations into mountainous, relatively unpopulated areas, though isolated populations are known to occur in more urban areas (Currier 1983; Gustafson et al. 2018).

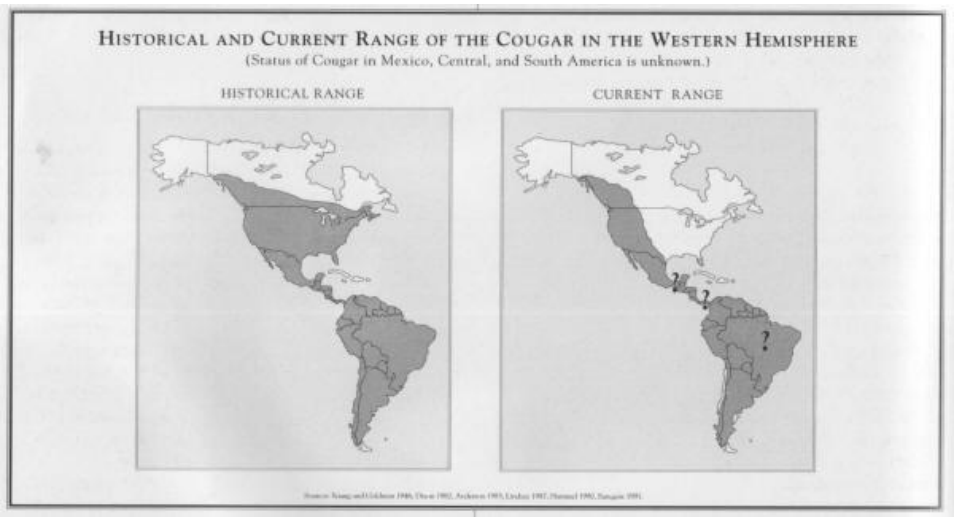


**Figure 7**. Historical and current range of mountain lions. Source: Hansen 1992.

In California, habitat fragmentation from roads and development has led to highly fragmented, divergent populations (Ernest et al. 2003; Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Gustafson et al. 2018). As mentioned in *Section 2.2 Taxonomy and Population Genetics*, nine genetically distinct populations have been identified within California

(Gustafson et al. 2018), with Southern California and Central Coast populations being the most constrained populations (and a tenth population centered in Nevada but extending slightly into California). Those located in highly urbanized areas of Southern California coastal mountain ranges, including the CC-S, SAM, and SGSB populations are especially restricted (Figure 8) (Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019).

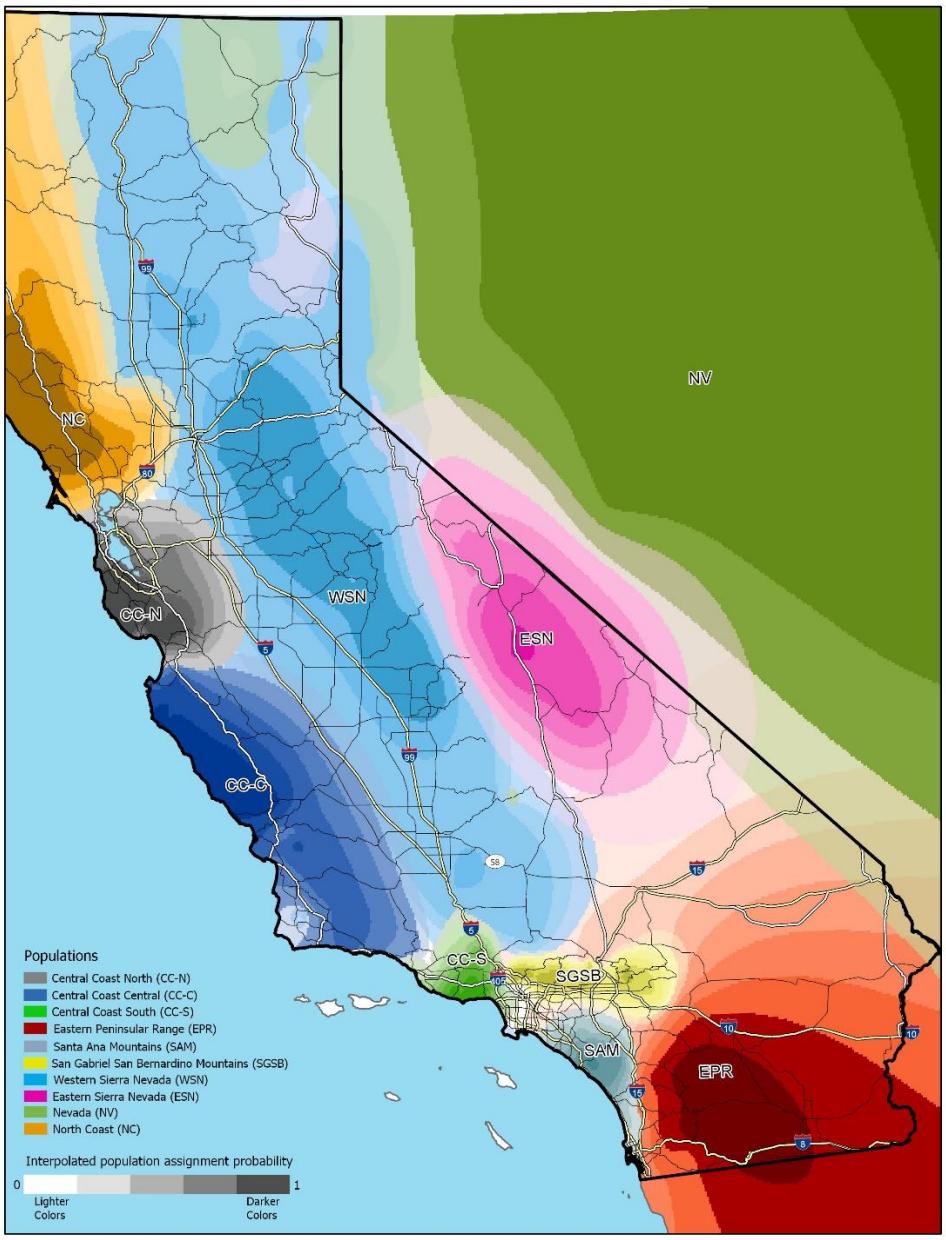


***Figure 8.*** Map of genetically distinct mountain lion populations and major roads in California. The CC-S (which includes the Santa Monica Mountains), SGSB, and SAM populations are exceptionally constrained. The map is based on data collected from 1992-2016 (the division and status of these populations could change over time and with further research. Derived from Gustafson et al. (2018). Genetics data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie. Roads data source: ESRI.

### *4.1 Central Coast North (CC-N) Mountain Lion Population*

The CC-N mountain lion population occurs mostly within the counties of Alameda, Contra Costa, San Mateo, Santa Clara, and Santa Cruz (Figure 8). The area is almost divided into two portions: an eastern half and a western half. The Santa Cruz Mountains make up the core area of the CC-N, bound by the Pacific Coast to the west, development lining the San Francisco Bay to the north and north west, and Highway 101 to the south. The eastern portion of the CC-N consists of various open space and nature preserves in the Berkeley Hills and Diablo Range bound by development lining the San Francisco Bay and Highway 101 and associated developments to the west, San Pablo Bay and Suisun Bay and associated developments to the north, I-5 to the east, and State Route 130 (SR-130) to the south. Interestingly, the CC-N seems almost bisected by the San Francisco Bay and Highway 101 and associated developments.

### *4.2 Central Coast Central (CC-C) Mountain Lion Population*

The CC-C mountain lion population occurs mostly within the counties of Monterey, San Benito, San Luis Obispo, and Santa Barbara. The area encompasses the central and southern portions of the Southern Coast Ranges, including the Santa Lucia Range, Sierra de Salinas, the Temblor Range, and the Sierra Madre Mountains. It is bound by the Pacific Ocean to the west, Highway 101 and SR-156 and associated development to the north, the I-5 and San Joaquin Valley to the east, and SR-126 and associated developments to the south (Figure 8).

### *4.3 Central Coast South (CC-S) Mountain Lion Population*

The CC-S mountain lion population is limited to the Santa Monica Mountains, Simi Hills, and the Santa Susana Mountains in Ventura and Los Angeles Counties (Figure 8). The Santa Monica Mountains population has the isolated area with about 660 $km^2$ within the Santa Monica Mountains National Recreation Area (Riley et al. 2014). The Pacific Ocean lies to the south while the cities of Oxnard, Thousand Oaks, San Fernando Valley, Los Angeles, and Santa Monica and major freeways including Highway 101, Interstate 5 (I-5) and Interstate 405 surround the area and create major movement barriers.

The Simi Hills is a smaller area of open space located north of the Santa Monica Mountains; the areas are bisected by Highway 101. This open space is mostly surrounded by development, including Simi Valley to the northwest, Thousand Oaks to the west, Agoura Hills to the southwest, Calabasas to the southeast, and Woodland Hills, Canoga Park, and Chatsworth to the east.

The Santa Susana Mountains are located north of the Santa Monica Mountains and Simi Hills. The area is generally bordered by freeways and the edges of development and agriculture. SR-118 borders the south and southwest, SR-126 borders the north and northwest, and I-5 borders the east.

### *4.4 San Gabriel/San Bernardino Mountains (SGSB) Mountain Lion Population*

The SGSB mountain lion population occurs within the Transverse Ranges located northwest of the City of Los Angeles within Los Angeles, Kern, and San Bernardino Counties (Figure 8). The western and southern boundaries of the San Gabriel and San Bernardino Mountains are lined with urban developments and major freeways, including the San Fernando Valley, cities of San Bernardino, Rancho Cucamonga, and West Covina, and the I-5, I-210, and I-10 freeways. The northern and eastern boundaries of the area are abutted by agriculture, suburban development, high desert, and roads.

### *4.5 Santa Ana Mountains (SAM) Mountain Lion Population*

The SAM mountain lion population inhabits about 1,533km$^2$ of undeveloped areas of the SAM within Orange, Riverside, and San Diego Counties (Beier and Barrett 1993; Benson et al. 2019). The area is mostly bound by major freeways and development (Figure 8). SR-241 creates the western boundary, SR-91 borders the northwest boundary, I-5 creates the eastern boundary, and agriculture and development border the southern extent. The closest intact habitat known to be used by other mountain lions is to the east/southeast, in the Peninsular Ranges.

### *4.6 Eastern Peninsular Range (EPR) Mountain Lion Population*

The EPR mountain lion population occurs in mountain ranges east of the SAM and south of the San Bernardino Mountains. The EPR is a predominantly north to south range that runs through San Diego, Riverside, and Imperial Counties and the California-Mexico border. They include the San Jacinto, Laguna, and San Ysidro Mountains in California and continue south into the mountain ranges of Baja California, Mexico. The western boundary of the EPR population is lined with roads and urban development, including areas around the cities of Escondido, San Diego, and Chula Vista. Studies regarding the northern, southern, and eastern extent of the population are limited; however, movement patterns documented by Vickers et al. (2015) and Vickers et al. (2017) between 2001 and 2016 suggest that EPR mountain lions generally stay north of the U.S. – Mexico border, along the edges of the desert that borders the east side of the EPR, and south of I-10. Although the EPR population has been found to be largely disconnected from all other California populations, some mountain lion movement was documented traversing between the EPR and SGSB (Vickers et al. 2015), which would have occurred at the northern boundary of the EPR, and there is evidence of limited genetic exchange between the two populations (Gustafson et al. 2018). In addition, one young male mountain lion was documented to the south using the Parque-to-Park Linkage to cross the US-Mexico border several times (where the terrain is too rugged to install a border wall), but he was eventually killed in Mexico in a collision with a vehicle (Vickers et al. 2015; W. Vickers *unpublished data*). Little is known about the mountain lions south of the border, but the movement patterns of EPR mountain lions suggest that they may form a discrete population within the EPR north of the US-Mexico border (Vickers et al. 2015; Vickers et al. 2017).

## 5 Abundance and Population Trends

According to the International Union for Conservation of Nature (IUCN), mountain lion populations are decreasing throughout their remaining range (Nielsen et al. 2015). Mountain lion population densities are generally low, which may be driven by prey density, competition between males for access to females, and mutual avoidance (Pierce and Bleich 2003). In the United States, population densities for mountain lions have been found to range from 0.4 to 4.3 resident adults per 100km$^2$ and 0.4 to 7.1 total mountain lions per 100km$^2$, though it varies by population and the presence of human-induced pressures (*e.g.*, hunting) (Pierce and Bleich 2003). In California, where hunting has been outlawed but other anthropogenic pressures such as roads and development are present, resident adult and total population densities have been found to be 1.1 and 3.6 per 100 km$^2$, respectively (Pierce and Bleich 2003). Adult sex ratio has been reported to be about 2-3:1 in favor of females (Hornocker 1970; Seidensticker et al. 1973; Beier 1993; Santa Cruz Puma Project 2015). These low population densities and female-biased sex ratios further highlight the species' need for expansive, connected, heterogeneous habitats to support viable populations.

It has been estimated that 4,000 to 6,000 adult mountain lions roam California (Mansfield and Weaver 1989). However, CDFW acknowledges that this estimate from 1984 is outdated and relied on density estimates from regional studies to derive a statewide abundance. The agency has since declared that the number of mountain lions throughout the state is unknown, and they have embarked on an intensive statewide research project to better understand mountain lion numbers regionally and throughout the state.[10] Working with other agencies, academic institutions, and non-profits, CDFW plans to have statewide and region-specific mountain lion population estimates by 2022 (Vaughan 2018).

As mentioned in *Section 2.2 Taxonomy and Population Genetics*, one way in which the abundance of mountain lions can be estimated is with the ratio of effective to total adult population size ($N_e/N$) of 0.25 to 0.5, as was used by USFWS to generate an abundance estimate for the endangered Florida panther (Ballou et al. 1989; USFWS 2008). Using this method with the estimated effective population sizes of the nine genetically distinct mountain lion populations centered in California from Gustafson et al. (2018) and Benson et al. (2019), the statewide total population would be 818 to 1,634 individuals (255 to 510 in the Central Coast and Southern California populations [Table 1], and 563 to 1,124 in the remaining Eastern Sierra Nevada, Western Sierra Nevada, and North Coast populations), which is much lower than the 4,000 to 6,000 estimate. This is also well below the recommended minimum viable population size of at least 5,000 adult individuals for the long-term persistence of a population (Frankham 1995; Reed et al. 2003; Traill et al. 2010). Petitioners recognize that the $N_e/N$ methodology has limitations and is but one method of generating an overall abundance estimate. More studies are needed to determine regional and statewide mountain lion abundance, including CDFW's ongoing efforts which should produce a more scientifically robust statewide abundance estimate.

[10] CDFW 2018 - Commonly Asked Questions About Mountain Lions. Accessed on 11 April 2019 at: https://www.wildlife.ca.gov/Conservation/Mammals/Mountain-Lion/FAQ#359951241-how-many-mountain-lions-are-in-california

Despite unknown statewide population estimates, researchers have been closely tracking several of the Central Coast and Southern California populations. Through their published studies and reports they provide some insights regarding abundance and population trends for these populations.

### *5.1 Central Coast North (CC-N) Mountain Lion Population*

Studies on the CC-N mountain lion population are limited, and abundance and population trends are unknown. However, with an effective population size of 16.6 (Gustafson et al. 2018), and an $N_e/N$ of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult population would be 33 to 66 individuals (see Table 1). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, these numbers are grossly insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014).

Gustafson et al. (2018) found that this population has low genetic diversity and a low effective population size, which suggests that it is at increased risk of inbreeding depression within five generations and eventual extinction. Ongoing studies in the Santa Cruz Mountains highlight high levels of human-caused mortalities. Depredation kills are the leading cause of death in collared mountain lions in the Santa Cruz Mountains (Wang et al. 2017), and CDFW reported 34 depredation kills between 2010 and 2016 in the CC-N counties of Alameda, Contra Costa, San Mateo, Santa Clara, and Santa Cruz (see Appendix A[11]). In addition, at least six mountain lions have been killed by vehicle strikes on Highway 17 in the Santa Cruz Mountains between 2008 and 2018 (Midpensinsula Regional Open Space 2017; Slade 2018) and news outlets reported at least three mountain lions killed by vehicle strikes on the I-280 in San Mateo County between 2014 and 2016 (Wilmers 2014, CBS SF 2015, Kamala 2016). The poor genetic health of the CC-N population is likely due to habitat fragmentation and isolation caused by roads and development combined with high levels of human-caused mortalities. CDFW has identified the Santa Cruz Mountains population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019). Poor connectivity and continued development in the CC-N will likely lead to further isolation, increased human-caused mortalities, decreased genetic diversity, and increased risk of extinction in the foreseeable future.

### *5.2 Central Coast Central (CC-C) Mountain Lion Population*

Studies on the CC-C mountain lion population are limited, and abundance and population trends are unknown. However, with an effective population size of 56.6 (Gustafson et al. 2018), and an $N_e/N$ of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult population would be 113 to 226 individuals (see Table 1).

Although Gustafson et al. (2018) found that this population has intermediate levels of genetic diversity and the highest effective population size among the Central Coast and Southern

[11] These data were downloaded from the CDFW website; however, they no longer appear to be available online. These numbers have been shown to be low by a factor of two in some areas, likely due to incomplete reporting, and therefore should be considered absolute minimums (W. Vickers, *pers comm*).

California mountain lion populations, with an effective population size of 56.6, it just barely exceeds the older standard of 50 to prevent inbreeding depression in the short-term (Frankham et al. 2014; Gustafson et al. 2018). In addition, it falls well below the recommended newer standard of 100 and is insufficient for the long-term viability of the population (Frankham et al. 2014). And the lack of sufficient protected lands and high rates of development in the area threaten the persistence of this population (Dellinger 2019). Thus, although the CC-C population appears to be the healthiest population in the Central Coast and Southern California, it is still at increased risk of inbreeding depression and extinction, and connectivity to smaller adjacent areas should be improved (Dellinger 2019).

### *5.3 Central Coast South (CC-S) Mountain Lion Population*

The NPS has been studying the CC-S population since 2002, though most studies regarding population dynamics focus on the Santa Monica Mountains mountain lions (Riley et al. 2014; Benson et al. 2019). Since 2002, NPS has collected data from 55 mountain lions within the Santa Monica Mountains and 19 mountain lions from the Simi Hills and Santa Susana Mountains.[12] There are currently 20-25 live mountain lions being tracked in the Santa Monica Mountains, 7-12 of which are adults (born in 2014 or earlier, the status of 5 adults are unknown) and 13 of which are juveniles or subadults (born in 2015 or later).[13] Given that the Santa Monica Mountains area is relatively small, adult survival rate is high (≥ 75%), and juvenile/subadult survival is low due to intraspecific strife and the inability to disperse, the Santa Monica Mountains population is likely space-limited and these numbers may represent the Santa Monica Mountains' carrying capacity (Riley et al. 2014; Benson et al. 2019). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, the extremely low effective population size and total adult population size are grossly insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014). And CDFW has identified the CC-S population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019).

The long-term survival of the Santa Monica Mountains population is severely threatened due to extreme habitat fragmentation and isolation caused by surrounding roads and development that impede movement in or out of the area (Riley et al. 2014). Limited space and lack of connectivity with suitable mountain lion habitat inhibit dispersal for subadults and likely drive unusually high levels of intraspecific strife, which is the most common cause of mortalities in the

[12] The NPS provides puma profiles (last updated August-November 2018) of the marked animals (*i.e.*, tagged or radio-collared) they have been studying in the CC-S, which includes those studied in Riley et al. (2014). Some data presented in this section take these data into account. Accessed on 3 April 2019 at: https://www.nps.gov/samo/learn/nature/puma-profiles.htm.

[13] The adult population in the Santa Monica Mountains is generally consistent with the estimated 0.25 to 0.5 $N_e/N$; the Santa Monica Mountains was estimated to have an effective population size of four (Benson et al. 2019), which would suggest a total adult population size of 8 to 16. Interestingly, Gustafson et al. (2018) estimated an effective population size of 2.7 for the greater CC-S population, which would indicate a total adult population of 5 to 10 individuals throughout the Santa Monica Mountains, Simi Hills, and Santa Susana Mountains (see Table 1). There are currently 10 to 17 adult mountain lions being tracked throughout the CC-S area, which would put their $N_e/N$ ratio at 0.16 to 0.27, which is still within the range of other species' $N_e/N$ ratios (Frankham et al. 1995; Ballou et al. 1989; Mace and Lande 1991; Spong et al. 2000; Laundré and Clark 2003).

area (Riley et al. 2014). Although intraspecific strife is known to occur among mountain lions, there have been multiple cases of aggressive adult males killing their siblings, female offspring, and previous mates documented in the Santa Monica Mountains population, and researchers noted that "clearly this is rarely a sound evolutionary strategy as the survivorship of offspring or siblings is traded against the probability of future reproduction" (Riley et al. 2014). For 23 radio-collared individuals within the Santa Monica Mountains for which the cause of death is known, nine deaths were the result of instraspecific strife. Eight of the nine deaths (89%) were of animals less than four years old. In addition, three uncollared mountain lions in the Santa Monica Mountains less than four years old were found dead by intraspecific strife, which brings the total to 12 deaths by intraspecific strife documented in the Santa Monica Mountains between 2002 and 2018.

Although all subadult males and half of subadult females typically disperse from their natal areas (Logan and Sweanor 2010), only one subadult successfully dispersed from the Santa Monica Mountains between 2002 to 2012 – P-22, the famous male mountain lion who successfully crossed Highway 101 and I-405 freeways and established his home range in Griffith Park (Riley et al. 2014). Unfortunately, P-22 is extremely isolated with the smallest home range ever reported for an adult male ($26km^2$), and he has not had any opportunities to mate (Riley et al. 2014). In addition, vehicle strikes account for 17% (4/23) of known radio-collared mountain lion deaths in the Santa Monica Mountains. According to the NPS, most males in the Santa Monica Mountains do not live past the age of two. Thus, many healthy, young animals are not able to disperse from the Santa Monica Mountains, establish their own home ranges, and successfully reproduce.

Conversely, lack of connectivity also inhibits migrants coming from outside the Santa Monica Mountains and contributing to the population's gene pool. Only two outside mountain lions have been known to immigrate into the Santa Monica Mountains since 2002: P12 (from Simi Hills, alive as of August 2018, age 12) and P45 (from north of Highway 101, status unknown, age would be 6-7 if alive). While there has been no sign of P-45 since February, 2019 and no offspring from him have been detected, P-12 has been fairly prolific in the Santa Monica Mountains, fathering at least eight litters. Although P-12's appearance initially improved genetic diversity in the Santa Monica Mountains population, consistent immigration in small populations is needed so that the genetic diversity gains of immigrant mountain lions are not lost (Riley et al. 2014; Benson et al. 2016a; Benson et al. 2019). Subsequent inbreeding by P-12 with his daughters and granddaughters and inbreeding already occurring with other breeding adults in the Santa Monica Mountains have led to dangerously low genetic diversity (Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). With continued isolation, inbreeding, and loss of genetic diversity, there is increasing risk of inbreeding depression and extinction. With inbreeding depression, the probability of extinction within 50 years is predicted to be 99.7 %, with a median time to extinction of 15.1 years (Benson et al. 2016a; Benson et al. 2019).

### *5.4 Santa Ana Mountains (SAM) Population*

Restricted habitat availability and high mortality rates in the SAM likely limits population size, and Benson et al. (2019) estimated that the SAM population is likely comprised of 16 adults and 13 juveniles (kittens and subadults). These numbers are slightly lower than the 31 to 62 adult mountain lions estimated from the SAM population's effective population size of 15.6 (Gustafson et al. 2018) (see Table 1). According to (Benson et al. 2019), high levels of human-caused adult mortalities may limit growth potential in the SAM, and it is uncertain if the population could be larger without as many anthropogenic pressures. In fact, although hunting is illegal in California, mountain lions in Southern California have a lower annual survival than many hunted populations (Vickers 2014). Interestingly, other studies calculated a much lower effective population size of 5.1 (Ernest et al. 2014) and four (Benson et al. 2019), which would align with the suggested carrying capacity. Regardless of which effective population size is used, they are all well below the frequently-used threshold of 50 and insufficient to prevent inbreeding depression in the short-term.

Although population trends are unclear, two long-term studies on radio-collared mountain lions in the SAM provide some insight (Beier 1993; Vickers et al. 2015). In a study that consisted of 32 radio-collared animals in the SAM from 1988 to 1993, researchers found a 75% adult survival rate (Beier and Barrett 1993), which is similar to adult survival rates in other populations, like the CC-S population (Riley et al. 2014). However, in a second, more recent study conducted in the area consisting of 31 marked mountain lions from 2001 to 2013, researchers found a 56.5% survival rate across all sexes and age groups (Vickers et al. 2015). The marked decrease in adult survival rate between the two studies coincides with an increase in the proportion of mortalities caused by vehicle strikes, with the 1988-1993 and the 2001-2013 studies resulting in 32% (10/31) and 46% (6/13) of deaths caused by vehicle strikes, respectively (Beier 1993; Vickers et al. 2015). It also parallels an upward trend of mountain lion mortalities caused by vehicle strikes throughout Southern California over time (Vickers et al. 2015). Other causes of death in the SAM population included depredation kills, illegal killing, disease, intraspecific strife, and human-caused wildfires (Beier and Barrett 1993; Vickers et al. 2015). Depredation kills were found to be 3.4 times more likely with males compared to females (Vickers et al. 2015).

The SAM mountain lion population's high adult mortality rates combined with isolation, small size, low genetic diversity, low effective population size, and limited immigration of new individuals cause demographic instability and put the population at high risk of extinction (Beier 1993; Beier and Barrett 1993; Ernest et al. 2014; Vickers et al. 2015; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, the extremely low effective population size and total adult population size are insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014). Roads and development prevent dispersal and sustained immigration in the SAM, and lack of consistent gene flow has led to high levels of inter-relatedness and inbreeding (Ernest et al. 2014; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). Further genetic erosion is likely without improved connectivity to facilitate immigration (Benson et al. 2019). CDFW has identified the SAM population as at risk due to current habitat and genetic concerns, at-risk internal habitat and

connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019). If inbreeding depression occurs within this population, population growth will likely decline and the probability of extinction within 50 years is predicted to be 100%, with a median time to extinction of 11.7 years (Benson et al. 2019).

In 13 years, only one radio-collared individual crossed I-15, the major barrier between the SAM and the EPR, and that animal was killed 25 days after his crossing for depredating domestic sheep (Vickers et al. 2015). And although Gustafson et al. (2017) documented three males immigrating into the SAM from the EPR and four males emigrating from the SAM to the EPR over a 15-year period, only one of the males (M86, an immigrant to the SAM) is known to have successfully bred. While M86 improved the SAM population's genetic diversity (Gustafson et al. 2017), high levels of mortalities due to vehicle strikes and depredation/illegal killings likely reduce the number of immigrants that can successfully establish as breeding adults (Vickers et al. 2015). With high levels of adult mortalities due to vehicle strikes, depredation kills affecting 3.4 times more males than females, and a small population with a female-biased adult sex ratio, there is potential for occasional male extinction in the SAM, which could severely limit the short- and long-term viability of the population (Beier and Barrett 1993; Benson et al. 2019).

### *5.5 San Gabriel/San Bernardino Mountains (SGSB) Population*

Studies on the SGSB mountain lion population are limited, and the abundance and population trends are unknown. However, with an effective population size of 5 (Gustafson et al. 2018), and an $N_e/N$ of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult population would be 10 to 20 individuals (see Table 1). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, these numbers are grossly insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014). And CDFW has identified the SGSB population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019).

Although a population viability study has not been conducted for the SGSB population, given its low genetic diversity, low effective population size, and patterns of isolation due to roads and development creating movement barriers (Gustafson et al. 2018), the SGSB mountain lion population likely has high risk of inbreeding depression and extinction. The loss of this population could undermine genetic connectivity for mountain lions statewide because the SGSB population, along with the Tehachapi and Sierra Pelona Mountains, represents a critical linkage between mountain lion populations in the northern and southern mountain ranges of California (Gustafson et al. 2018). Restoration and enhancement of connectivity in the SGSB and surrounding mountain ranges are key for the continued survival of the SGSB population as well as all of the Central Coast and Southern California mountain lion populations.

### *5.6 Eastern Peninsular Range (EPR) Population*

Studies on the EPR mountain lion population are limited and the abundance and population trends are unknown. However, with an effective population size of 31.6 (Benson et al. 2019), and an $N_e/N$ of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult

population would be 63 to 126 individuals (see Table 1). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, these numbers are insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014).

Vickers et al. (2015) followed 43 marked mountain lions in the EPR from 2001 to 2013, and their study provides some insight regarding survival rate and causes of mortality. Annual survival rate was found to be 55.4% in the EPR, which is similar to the SAM population (Vickers et al. 2015). The primary causes of death of marked mountain lions were depredation kills (26% [6/23]) and vehicle strikes (17% [4/23]). When assessing mountain lion death data from CDFW from 1981 to 2013, depredation and vehicle strikes accounted for about 70% of mountain lion deaths in the EPR: 40% (62/154) by depredation kills and 30% (46/154) by vehicle strikes (Vickers et al. 2015).

Although the EPR population was found to have the highest genetic diversity and effective population size among the Southern California mountain lion populations (Gustafson et al. 2018), movement and genetic studies have shown that the EPR population is largely disconnected from all other California populations (Ernest et al. 2014; Vickers et al. 2015; Vickers et al. 2017; Gustafson et al. 2018). And CDFW has identified the EPR population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019). Thus, high human-caused mortality rates combined with continued development in San Diego, Riverside, and Imperial Counties could lead to further isolation, decreased genetic diversity, increased inbreeding depression, and increased risk of extinction.

## 6 Factors Affecting Ability to Survive and Reproduce

Female mountain lion, P-23, crossing a road in the Santa Monica Mountains. She was struck by a vehicle and found dead near Malibu Canyon Road in January 2018. Photo: NPS

Most, if not all, factors affecting the ability of the Southern California and Central Coast mountain lion populations to survive and reproduce are caused by humans. Lack of wildlife connectivity is the primary driver of their potential demise. Habitat loss and fragmentation due to roads and development have led to extreme levels of isolation and high mortality rates, which are driving these populations towards extinction. Continued development in current suitable

mountain lion habitat further threatens these populations. With low genetic diversity and high risk of inbreeding depression due to genetic isolation, vehicle strikes on roads, increased conflicts with humans that lead to depredation kills, high levels of intraspecific strife likely due to limited space and lack of connectivity, rodenticide and other environmental toxicant poisoning, and impacts of more frequent wildfires and climate change, Southern California and Central Coast mountain lions will likely not persist unless there is a concerted effort to restore and enhance functional connectivity between populations and large blocks of heterogeneous habitats.

The populations in Southern California are especially vulnerable to extinction, which is reflected in a 2005 review conducted by the US Forest Service regarding Land Management Plans in the National Forests of Southern California that states the "greatest concern for the long-term health of mountain lion populations on the national forests of southern California is loss of landscape connectivity between mountain ranges and large blocks of open space on private land." [14] The review emphasizes that continued development along with new and wider roads degrade habitat linkages and create movement barriers, and "[w]ithout the national forests and linkages between the mountain ranges and other large habitat preserves, there is not much long term potential for mountain lions in southern California."

Ultimately, the persistence of mountain lions in the Central Coast and Southern California requires maintenance and restoration of connectivity between subpopulations and adequate habitat. The extreme isolation, dangerously low genetic diversity, high levels of inbreeding, and high rates of human-caused mortalities (*e.g.*, vehicle strikes, depredation kills, intra-specific strife due to limited space, rodenticide poisoning, etc.) underscore the urgent need for proactive measures to enhance connectivity (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2017; Benson et al. 2019).

Male mountain lion M110 in San Diego County was euthanized by a CDFW warden because he was severely injured and for stated public safety concerns (he was found in a neighborhood close to homes). This occurred days after he was illegally shot by a livestock owner (open wound on right flank). Necropsy results indicated he had two broken legs consistent with a vehicle strike and four different compounds of anticoagulant rodenticides in his blood. Had he not been euthanized, he likely would have died from starvation due to his injuries. Source: Vickers (2014).

[14] Forest Service, U.S. Department of Agriculture, *Final Environmental Impact Statement, Land Management Plans, Angeles National Forest Cleveland National Forest Los Padres National Forest San Bernardino National Forest* (Sept. 2005), available at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5166889.pdf.

Measures to conserve core habitat areas and functional wildlife corridors, like the recently adopted Habitat Connectivity and Wildlife Movement Ordinances in Ventura County,[15] are vital to the preservation of Central Coast and Southern California mountain lion populations, but just protecting land is not enough to ensure their survival. Conserving natural habitats on both sides of freeways and constructing effective crossing infrastructure (*e.g.*, culverts, underpasses, vegetated overpasses, and exclusionary fencing) at existing roads and barriers would facilitate movement and gene flow while reducing mortalities due to vehicle strikes (Riley et al. 2014; Vickers et al. 2015; Benson et al. 2019). Promoting wider implementation of predator-proof enclosures for domestic animals would further reduce human-caused mortalities by limiting opportunities for potential conflict and reducing the use of depredation permits (Vickers et al. 2015). In addition, changes in depredation permit policy could further reduce mortalities. For example, CDFW adopted a new depredation permit policy based on a 2017 bulletin for mountain lions in the CC-S and SAM areas, which requires affirmative non-lethal alternatives and improved husbandry before kill permits are issued when mountain lion depredations occur in those areas (CDFW 2017; see *Section 8.1.1 CDFW Departmental Bulletins*). Expanding these policies in conjunction with enforceable implementation and reporting requirements across the state, or at least into the SGSB, EPR, CC-N, and CC-C, population areas, would reduce mortalities from this source. Prohibiting the use of second-generation anticoagulants, rodenticides, and other environmental toxicants in California (*i.e.*, with AB 1788, sponsored by Assembly Member Richard Bloom in 2019) would even further reduce human-caused mortalities of mountain lions, as toxicants bioaccumulate up the food chain and can kill mountain lions or weaken their immune systems and make them more susceptible to disease or more vulnerable to conspecifics (Riley et al. 2003; Riley et al. 2007; Serieys et al. 2015). A combination of habitat conservation, implementation of effective road/barrier crossing infrastructure, and outreach and education to property owners and owners of domestic animals combined with depredation permit policy change could save these populations from extinction (Vickers et al. 2015).

### *6.1 Low Genetic Diversity and Inbreeding Depression*

As detailed in *Section 2.2 Taxonomy and Population Genetics* and *Section 5.0 Abundance and Population Trends*, inbreeding is a serious threat to the persistence of the Central Coast and Southern California mountain lion populations. Inbreeding depression, loss of genetic diversity, and accumulation of deleterious mutations can lead to elevated extinction risk due to reduced reproductive fitness and evolutionary potential (*i.e.*, the ability to adapt to change) (Spielman et al. 2004; Frankham 2005; Traill et al. 2010). Decades of isolation due to roads and development fragmenting habitat and limiting connectivity has led to low genetic diversity and effective population sizes, high levels of inter-relatedness, and dangerous levels of inbreeding, especially in the CC-S, SAM, SGSB, and CC-N populations (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). Although demographic and environmental stochasticity (*e.g.*, a disease outbreak, wildfire, drought or flooding) can increase risk of extinction, especially in small populations, inbreeding has also been shown to be an indicator of extinction risk and may impact how populations are able to respond to stochastic events (Frankham and Ralls 1998). In addition, endangered species

[15] More information regarding the Habitat Connectivity and Wildlife Movement Ordinances available at: https://vcrma.org/habitat-connectivity-and-wildlife-movement-corridors

tend to have lower genetic diversity than non-endangered species, which suggests that inbreeding and low genetic variation may have an important role in a species' risk of extinction (Frankham and Ralls 1998). Thus, genetic factors should be considered when assessing the status of these populations.

The CC-S, SAM, SGSB, and CC-N populations have been found to have low genetic diversity, with the SAM population's genetic variation nearly as low as the endangered Florida panther's (*Puma concolor coryi*) (Ernest et al. 2014; Riley et al. 2014; Gustafson et al. 2017). And, as mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, the CC-S, SGSB, SAM, CC-N, and EPR populations have effective population sizes well below the older and less conservative threshold of 50, while the CC-C population's effective population size is just barely above that threshold at $N_e = 56.6$ (Ernest et al. 2014; Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). These numbers suggest that inbreeding depression could occur within the short-term (over the duration of five generations) and these populations are at increased risk of extinction.

Without improved connectivity, the SAM and Santa Monica Mountains (within the CC-S) populations are predicted to experience continued genetic erosion and losses in heterozygosity of 28-49% and 40-57%, respectively, within 50 years (Benson et al. 2016a; Benson et al. 2019). This could lead to inbreeding depression, which could cause reduced fitness in a variety of ways. In Florida panthers, inbreeding depression led to reproductive issues (*e.g.*, poor sperm quality, low testosterone levels, poor fecundity and recruitment, failure of testes to descend), increased susceptibility to parasites and disease, and physical issues (*e.g.*, atrial septal defect, a deadly congenital heart defect; kinked tails) (Roelke et al. 1993; Johnson et al. 2010). Suffering from shrinking, fragmented habitats, high mortality rates from hunting, and inbreeding depression, the Florida panther population declined to less than 30 individuals, and genetic restoration via the translocation of eight female mountain lions from Texas (*Puma concolor stanleyana*) was needed to prevent their extinction (Johnson et al. 2010).

The SAM and CC-S populations are severely constrained in fragmented habitats with similar numbers as the Florida panther population prior to genetic rescue (Beier and Barrett 1993; Johnson et al. 2010; Riley et al. 2014; Vickers et al. 2015). Although the fragmented populations appear to be stable, high levels of inbreeding have been documented in the Santa Monica Mountains (Riley et al. 2014) and evidence of inbreeding depression (*i.e.*, low genetic diversity and kinked tails) has been observed in the SAM (Ernest et al. 2014). If these populations remain isolated, they will inevitably have the same fate as the Florida panthers. Researchers predict that with inbreeding depression, the SAM and Santa Monica Mountains populations have a 100% and 99.7% chance of becoming extinct within 50 years, with median time to extinction of 11.7 and 15.1 years, respectively (Benson et al. 2019).

The SGSB population was also found to have low genetic diversity and effective population size (Gustafson et al. 2018), which suggests that the population experienced a prior genetic bottleneck and inbreeding is likely. Although genetic studies on this population are limited, it is clear that continued development in and around the SGSB will further isolate the population and lead to more inbreeding and even lower genetic diversity, which will drive the population faster towards extinction. It is important to note that despite only limited gene flow

between the SGSB population and the Western Sierra Nevada, CC-C, and the EPR (Gustafson et al. 2018), this population represents a critical linkage between mountain lion populations in the northern and southern mountain ranges of California. Restoration and enhancement of connectivity is key for the continued survival of the SGSB population as well as all of the other the Central Coast and Southern California mountain lion populations.

Gustafson et al. (2018) found that the EPR population also exhibits a prior genetic bottleneck. The EPR population was found to be largely disconnected from all the other California populations, with limited gene flow and low connectivity with the SAM and SGSB populations (Gustafson et al. 2018). Movement patterns and genetics indicate potential isolation from other populations (Vickers et al. 2015; Gustafson et al. 2017; Gustafson et al. 2018), and continued development in these areas will likely lead to further isolation, genetic drift, and risk of extinction similar to what is being observed in the CC-S, SAM, and SGSB populations.

Although genetic studies are limited for the CC-N population, it was found to have low genetic diversity and low effective population size (Gustafson et al. 2018), which forewarns of inbreeding depression and increased risk of extinction. CDFW has identified the Santa Cruz Mountains mountain lion population, which occurs within the CC-N area, as vulnerable to decline and extinction due to fragmentation from roads and development as well as lack of protected habitat (Dellinger 2019).

Studies suggest that one immigrant every 1-2 years would reduce extinction risk in the SAM and Santa Monica Mountains populations (Beier and Barrett 1993; Gustafson et al. 2017; Benson et al. 2019). This may apply to the other populations with low genetic diversity and effective population size (Gustafson et al. 2018). Increasing connectivity throughout the Central Coast and Southern California would address issues of inbreeding by facilitating movement between populations, increasing effective population size, and reducing high mortality rates driven by vehicle strikes and depredation. Thus, proactive measures to effectively restore and enhance connectivity are needed to minimize risk of inbreeding depression and extinction in Central Coast and Southern California populations.

### *6.2 Vehicle Strikes*

In California, an estimated 100 mountain lions are killed every year by vehicle strikes (Pollard 2016). In the Central Coast and Southern California, vehicle strikes represent a significant threat to the persistence of mountain lion populations, though Southern California has more documentation regarding this issue. The number of mortalities caused by vehicle strikes has been increasing in Southern California since the 1980s, and vehicle strikes account for a high proportion of deaths in mountain lions in the SAM, CC-S, and EPR (Beier and Barrett 1993; Riley et al. 2014; Vickers et al. 2015:Vickers et al. 2017). From 1981 to 2013 vehicle strikes accounted for 53% (50/94) of mountain lion deaths in the SAM and 30% of mountain lion deaths in the EPR (46/154) (Vickers et al. 2015). Riley reported that 14% (2/14) of collared mountain lion deaths from 2002 to 2012 were due to vehicle strikes, and the NPS reported that 18 mortalities from vehicle strikes occurred between July 2002 and January 2018 in the CC-S (Figure 9). Although the CC-N population is less studied, there is evidence that vehicle strikes are a significant cause of mortalities in this population; at least six mountain lions have been

killed by vehicle strikes on Highway 17 in the Santa Cruz Mountains between 2008 and 2018 (Midpeninsula Regional Open Space 2017; Slade 2018) and news outlets reported at least three vehicle strikes killing mountain lions on the I-280 in San Mateo County between 2014 and 2016 (Wilmers 2014; CBS San Francisco 2015; Kamala 2016). Similarly, in 2018 at least two mountain lions were reported to have been killed by vehicle strikes in San Luis Obispo County in the CC-C (Tanner 2018). Clearly, vehicle strikes are an important cause of mortality for the Central Coast and Southern California mountain lion populations.

**Figure 9.** Locations of 18 mountain lion vehicle strikes in the Santa Monica Mountains and surrounding areas from July 2002 to January 2018. Source: NPS

High adult mortality rates can have severe consequences, particularly for small populations with female-biased adult sex ratios and low effective population sizes (Beier and Barrett 1993; Benson et al. 2019). Vehicle strikes have been found to affect males and females equally, regardless of age, which can result in relatively high adult male mortalities (Vickers et al. 2015). Low male adult survival increases the risk of extinction, as it could result in occasional extinctions of breeding males and therefore reduced reproductivity (Benson et al. 2019), which has been previously observed in the SAM (Beier and Barrett 1993). In the Santa Monica Mountains, where adult survival is high, vehicle strikes (along with intraspecific strife) make it more difficult for subadults to successfully disperse, which limits breeding opportunities for mountain lions born in the Santa Monica Mountains (Riley et al. 2014; Benson et al. 2019). Freeways and vehicle strikes also limit the ability for immigrants to enter the Santa Monica Mountains and contribute to the population's gene pool (Riley et al. 2014; Benson et al. 2019). These patterns highlight the dire outlook for Central Coast and Southern California mountain lion populations due to lack of connectivity between populations and suitable habitat. The continued construction of roads and development and inaction to enhance connectivity threatens the survival of these struggling populations.

### *6.3 Depredation and Illegal Kills*

Mountain lions killed on depredation permits (and one killed by vehicle strike) in San Diego County in 2015. Source: Vickers et al. (2017).

In 1990 California voters passed The California Wildlife Protection Act (Proposition 117), making the mountain lion a "specially protected species" and outlawing mountain lion sport-hunting in California. However, the law requires CDFW to issue depredation permits that allow people to "take" mountain lions when a mountain lion kills or injures domestic animals such as livestock or pets or damages property. The legal definition of "take" is to "hunt, pursue, catch, capture, or kill, or attempt to hunt, pursue, catch, capture, or kill" (Cal Fish & Game Code, *§86*), and the vast majority of permits to take in the three decades since the passage of Proposition 117 have authorized killing one or more mountain lions. The number of depredation permits issued and the number of reported kills has varied over time, and on average over 40% of permits result in reported kills. Since 1990 there has been an average of 97 reported depredation kills every year; however, these estimates are likely low due to underreporting and incomplete records (W. Vickers, *pers comm*). Depredation kills (along with vehicle strikes) account for the majority of mountain lion mortalities in the SAM and EPR (Vickers et al. 2015; Vickers et al. 2017). Although less is known about depredation kill impacts in the CC-N and CC-C, there is evidence that suggests depredation kills could be a significant source of mortality in these populations. In the Santa Cruz Mountains in the CC-N, depredation kills are the leading cause of death in collared mountain lions (Wang et al. 2017), and CDFW reported 34 depredation kills between 2010 and 2016 in the CC-N counties of Alameda, Contra Costa, San Mateo, Santa Clara, and Santa Cruz (see Appendix A[16]). Although population dynamics are even less studied in the CC-C, between 2010 and 2016 there were 46 reported depredation kills in the counties of Monterey, San Benito, San Luis Obispo, and Santa Barbara (See Appendix A*[Id.]*).

[16] These data were downloaded from the CDFW website; however, they no longer appear to be available online. These numbers have been shown to be low by a factor of two in some areas, likely due to incomplete reporting, and therefore should be considered absolute minimums (W. Vickers, *pers comm*).

An illegally killed mountain lion in San Mateo County. Photo: Tiffany Yap

Depredation kills result in more deaths in male mountain lions compared to female mountain lions. Statewide, of mountain lions killed for depredation in 2017, 68% were males (CDFW 2018), and from 1981 to 2013, there were 3.4 times more male than female mountain lions killed for depredating in the SAM and EPR (Vickers et al. 2015). The majority of lions reported killed for depredating were of subadult (1-2 years old) and adult mountain lions (>2 years old) (CDFW 2018), many of which were likely dispersers that may have not yet established home ranges. Dispersing lions often come up against roads and development as they search to establish home ranges (Beier 1995, Vickers 2015, Riley 2014). This suggests that even if individuals are able to navigate across roads and freeways without being struck by vehicles, they often come into conflict with humans, which threatens their survival. This was reflected in the EPR, when the only GPS collared immigrant to have crossed I-15 from 2001 to 2013 arrived from the SAM only to be killed on a depredation permit 25 days after his arrival for depredating a sheep (Vickers et al. 2015). Not only do lions killed for depredating diminish the total abundance of these populations, but because males are predominantly killed, the number of animals that are the primary gene dispersers are also greatly reduced, which further inhibits adequate genetic connectivity (Vickers et al. 2017).

Reported depredation kills do not include mountain lions that are illegally poached or killed, many of which likely go undocumented (Beier and Barrett 1993; Vickers et al. 2015). Illegal kills have been observed in the CC-S, SAM, and EPR (Beier and Barrett 1993; Riley et al. 2014; Vickers et al. 2015) as well as in the CC-N (Yap 2018 *pers observation* ), and although 80 mountain lions were reported as being killed under depredation permits in 2017, 89 deaths were being investigated (CDFW 2018).

As mentioned in *Section 6.2 Vehicle Strikes*, high levels of mortalities among male breeders or potential male breeders (*i.e*., dispersers) can have severe impacts on small, isolated mountain lion populations with female-biased adult sex ratios and low effective population sizes (Beier and Barrett 1993; Benson et al. 2019). Low survival of breeding males increases extinction risk, as occasional breeding male extinctions can occur and therefore reduce reproductivity throughout the population (Beier and Barrett 1993; Benson et al. 2019). And low survival of subadults and adults may limit both dispersers and immigrants from successfully

breeding and increasing genetic diversity (Vickers et al. 2015; Benson et al. 2019). Thus, depredation and illegal kills in conjunction with lack of connectivity between populations and suitable habitat in the Central Coast and Southern California severely limit the potential for these populations to survive and reproduce. Continued development and lack of connectivity will likely push mountain lions into more conflicts with humans, which could increase depredation and retributory kills and further drive these populations towards extinction.

### *6.4 Intraspecific Strife*

Intraspecific strife: a female mountain lion, P-7, was killed by her father, P-1. Photo: NPS

As detailed in *Section 5 Abundance and Population Trends*, intraspecific strife is the leading cause of mortality in the Santa Monica Mountains (Riley et al. 2014). Although intraspecific strife is a common source of mortality in mountain lion populations, (Beier and Barrett 1993; Logan and Sweanor 2001; Allen 2014), unusually high levels of intraspecific strife have been observed in this population (Riley et al. 2014). About 41% (9/22) of deaths in radio-collared mountain lions being tracked from 2002 to 2018 were from intraspecific strife,[17] with multiple cases of aggressive adult males killing their siblings, offspring (male and female), and previous mates (Riley et al. 2014). While males are likely to have larger home ranges to protect food resources and access to females, killing offspring or potential mates has no apparent evolutionary benefit, as it reduces chances of future reproduction (Riley et al. 2014). In addition, infanticide has been documented in the Santa Monica Mountains (Riley et al. 2014), perhaps to trigger the female to come into estrous. These high levels of intraspecific strife are likely due to limited space in the Santa Monica Mountains caused by dispersal barriers (Riley et al. 2014; Benson et al. 2019). As roads and development further encroach on Central Coast and Southern California mountain lion populations, intraspecific strife could become more common; this was

[17] The NPS provides puma profiles (last updated August-November 2018) of the marked animals (*i.e.*, tagged or radio-collared) they have been studying in the CC-S, which includes those studied in Riley et al. (2014). Some data presented in this section take these data into account. Accessed on 3 April 2019 at: https://www.nps.gov/samo/learn/nature/puma-profiles.htm.

documented in the SAM on two occasions (one GPS-collared, one previously GPS-collared) since the publication of Vickers et al. (2015) (W. Vickers *unpublished data*). Enhanced connectivity between populations and suitable habitat would facilitate dispersal, which would reduce and/or prevent high levels of intraspecific strife (Riley et al. 2014; Benson et al. 2019) and improve the survival and reproduction rates, especially for the most struggling populations.

### *6.5 Abandonment*

Santa Monica Mountains mountain lion kittens P-57 and P-58 were abandoned by their mother, P-42, a first-time mother who left with male P-27 and never returned. Photo: NPS

Abandonment of kittens is fairly common in the Santa Monica Mountains and accounts for about 23% (5/22) of the known causes of death for marked/collared animals.[18] Although this likely occurs in other mountain lion populations, the causes of abandonment are unclear. There are various reasons why females might abandon their cubs. The cubs could be sick, the female may not be able to take care of them, or perhaps the female was initially protecting them from a mature male. Unfortunately, there is a lack of data regarding why and how often cubs get abandoned. Yet this is one of the main causes of death for mountain lions in the Santa Monica Mountains, which likely affects this already-small population.

Mountain lion cubs can also become orphaned if the mother is killed before they have dispersed. If they are too young to fend for themselves, they likely starve to death or are preyed upon by other predators. If the young are more mobile, they may come up against areas where they are more likely to encounter humans as they search for food. This was seen in November 2017, when a mother mountain lion was killed by a vehicle strike in the SAM and two of her cubs were found roaming near human establishments – one in a backyard and the other along a road (Veklerov 2018). Both were too young to survive on their own and were placed in the Oakland Zoo.

[18] Id.

### *6.6 Poisoning from Rodenticides and Other Environmental Toxicants*

The famous mountain lion of Griffith Park, P-22, suffering from notoedric mange, a parasitic skin disease that has been linked with the ingestion of rodenticide poisoning (left) and mountain lion P-34 found dead on a trail due to rodenticide poisoning (right). Photos: NPS

Although mountain lions are not the primary target of environmental toxicants, such as rodenticides and other pesticides and herbicides, secondary poisoning has been documented in many non-target animals, especially predators (e.g., coyotes (Riley et al. 2003), bobcats (Riley et al. 2007; Serieys et al. 2015), San Joaquin kit fox (McMillin et al. 2008), California fishers (Gabriel et al. 2012), raptors (Lima and Salmon 2010), and many more). Data regarding pesticide poisoning in mountain lions are limited; however, there is evidence that these big cats are likely vulnerable to similar negative impacts that other predators experience, including direct death, weakened immune systems, and vulnerability to predators or conspecifics (Riley et al. 2003; Riley et al. 2007; Serieys et al. 2015; Rudd et al. 2019).

While poisoning can sometimes lead to direct death, rodenticide exposure has also been associated with notoedric mange, a parasitic skin disease that has led to high levels of mortalities, population declines, and even local extirpations in Southern California bobcats (Riley et al. 2007; Serieys et al. 2015). Although the link between rodenticide poisoning and mange is not as clear in mountain lions, since 2002 five mountain lions in the CC-S have been found suffering from mange, and researchers suspect that rodenticide poisoning may have played a role (Reyes-Velarde 2019a). In addition, of four dead mountain lions in the Santa Monica Mountains that were found to have rodenticides in their systems, two died from poisoning and two died from intraspecific strife, and it is possible that indirect effects of poisoning may have prevented the mountain lions from escaping conflict or fighting back (Riley et al. 2007). And rodenticide poisoning is suspected to be the cause of death in mountain lion P-47, who was recently found dead in Santa Monica Mountains (Reyes-Velarde 2019b), and CC-N mountain lion 36m, who was found dead in the Santa Cruz Mountains in 2015 (Wilmers 2015).

The Department of Pesticide Regulation (DPR) analyzed data provided by CDFW and found that 92% (59/64) of tested mountain lions from throughout the state had detectable levels of anticoagulant rodenticides, which indicates alarmingly high exposure rates (DPR 2018). This has been found to be true in the CC-S as well, where researchers have found that 94% (17/18) of mountain lions tested had traces of rodenticides in their systems (Reyes-Velarde 2019a).

Rodenticides have been implicated in mountain lion mortalities in the CC-S, and in the SAM anticoagulant rodenticide residues were detected in the livers of 100% of deceased animals tested, with up to five different compounds being detected in some animals (Riley et al. 2007; Riley et al. 2014; W. Vickers, *pers comm*). And a study conducted by CDFW and the Integral Ecology Research Center (IERC) has found that mountain lions are being exposed to dangerously high levels of illegal pesticides, such as carbofuran, being used on illegal marijuana grow sites, which can also bioaccumulate and cause health issues (Rudd et al. 2019). Furthermore, it is possible that herbicide exposure from deer could be detrimental to mountain lions as well. Although poisoning from environmental toxicants may not constitute a large proportion of direct deaths (that we are aware of), it is possible that high exposure levels influence other causes of mortalities. Any additional mortalities in the small, isolated Central Coast and Southern California populations suffering from other anthropogenic pressures could impact the short- and long-term survival of these mountain lions.

### *6.7 Wildfires*

After the Woolsey Fire, the body of mountain lion P-64, known to use culverts to cross the Hwy-101 and SR-118 freeways a total of 41 times, was found dead with severely burned paws. Photos: NPS

Although fire is a natural disturbance in California ecosystems, sprawl development with low/intermediate densities extending into habitats that are prone to fire have led to more frequent wildfires that burn larger areas (Syphard et al. 2007; Syphard et al. 2009). Most wildfires in California are caused by human ignitions, like power lines, arson, improperly disposed cigarette butts, debris burning, fireworks, campfires, or sparks from cars or equipment (Keeley and Fotheringham 2003; Syphard et al. 2007; Syphard et al. 2012; Bistinas et al. 2013; Balch et al. 2017; Radeloff et al. 2018; Syphard et al. 2019). In fact, human-caused fires account for 95-97% of all fires in California's Mediterranean habitats (Syphard et al. 2007, Balch et al. 2017). In addition, climate change is leading to hotter, drier conditions that make fires more likely to burn. At least 29 fires throughout California in the last two years were caused by electric power and distribution lines, and transmission lines are suspected to be the cause of last year's Camp Fire and Woolsey Fire (Atkinson 2018; Chandler 2019).

Increased frequency of wildfires poses a threat to the survival of Central Coast and Southern California mountain lions. Although mountain lions are highly mobile and generally able to move away from wildfires, in severe weather conditions wind-driven fires can spread quickly – they can cover 10,000 hectares in one to two days, as embers are blown ahead of the

fires and towards adjacent fuels (*e.g*., flammable vegetation, structures) (Syphard et al. 2011). If their movement is constrained by roads and development and they are unable to access escape routes, then their chances of surviving wildfires are greatly reduced. Vickers et al. (2015) documented one death of a collared mountain lion in the SAM and one in the EPR due to human-caused wildfires, and the deaths of two collared mountain lions in the CC-S in 2018 have been attributed to the Woolsey Fire.[19] Environmentally stochastic events (*e.g*., wildfires, flooding) could destabilize small mountain lion populations and make them vulnerable to extinction (Benson et al. 2016a; Benson et al. 2019). In addition, increased frequency of fire ignitions can cause shifts in natural fire regimes, which can lead to large-scale landscape changes, such as vegetation-type conversion or habitat fragmentation, which can impact wide-ranging species like the mountain lion (Jennings 2018).

Increasing landscape connectivity (*e.g*., by designing corridors, removing barriers, and preserving habitats that are close to each other) is important for resilience to environmentally stochastic events and climate change adaptation (Heller and Zavaleta 2009). Enhanced connectivity that incorporates corridor redundancy (*i.e*. the availability of alternative pathways for movement) would allow for improved functional connectivity and resilience. Compared to a single pathway, multiple connections between habitat patches increase the probability of movement across landscapes by a wider variety of species, and they provide more habitat for low-mobility species while still allowing for their dispersal (Mcrae et al., 2012; Olson & Burnett, 2008; Pinto & Keitt, 2008). In addition, corridor redundancy provides resilience to uncertainty, impacts of climate change, and extreme events, including wildfires, by providing alternate escape routes or refugia for animals seeking safety (Cushman et al., 2013; Mcrae et al., 2008; Mcrae et al., 2012; Olson & Burnett, 2008; Pinto & Keitt, 2008).

### *6.8 Climate Change*

A strong, international scientific consensus has established that human-caused climate change is causing widespread harms to human society and natural systems, and climate change threats are becoming increasingly dangerous. In a 2018 *Special Report on Global Warming of 1.5°C* from the Intergovernmental Panel on Climate Change (IPCC), the leading international scientific body for the assessment of climate change describes the devastating harms that would occur at 2°C warming, highlighting the necessity of limiting warming to 1.5°C to avoid catastrophic impacts to people and life on Earth (IPCC 2018). In addition to warming, many other aspects of global climate are changing. Thousands of studies conducted by researchers around the world have documented changes in surface, atmospheric, and oceanic temperatures; melting glaciers; diminishing snow cover; shrinking sea ice; rising sea levels; ocean acidification; and increasing atmospheric water vapor (USGCRP, 2017).

Climate change is increasing stress on species and ecosystems, causing changes in distribution, phenology, physiology, vital rates, genetics, ecosystem structure and processes, and increasing species extinction risk (Warren et al., 2011). A 2016 analysis found that climate-related local extinctions are already widespread and have occurred in hundreds of species, including almost half of the 976 species surveyed (Wiens 2016). A separate study estimated that nearly half of terrestrial non-flying threatened mammals and nearly one-quarter of threatened

[19] Id.

birds may have already been negatively impacted by climate change in at least part of their distribution (Pacifici et al. 2017). A 2016 meta-analysis reported that climate change is already impacting 82% of key ecological processes that form the foundation of healthy ecosystems and on which humans depend for basic needs (Scheffers et al. 2016). Genes are changing, species' physiology and physical features such as body size are changing, species are moving to try to keep pace with suitable climate space, species are shifting their timing of breeding and migration, and entire ecosystems are under stress (Cahill et al., 2012; Chen et al., 2011; Maclean & Wilson, 2011; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Warren et al., 2011).

Improving landscape connectivity is a key factor for climate change resilience and adaptation (Heller and Zavaleta 2009). Without functional connectivity that provides multiple pathways for mountain lion movement, isolated Central Coast and Southern California mountain lion populations and the prey they depend on may not be able to shift their ranges as available resources shift. Enhanced connectivity that provides redundant corridors for safe passage between suitable habitats would improve chances of survival and reproduction in the face of climate change by increasing the probability of movement across landscapes by a wider variety of species and providing alternate escape routes or refugia for animals seeking safety (Mcrae et al. 2008; Pinto and Keitt 2008; Mcrae et al. 2012; Cushman et al. 2013; Olson and Burnett 2013).

## 7 Degree and Immediacy of Threat

As demonstrated in the previous sections, Central Coast and Southern California mountain lions are at risk of extirpation under current conditions. Roads and development have fractured connectivity, which has led to the separation of at least six isolated, genetically distinct populations in the CC-N, CC-C, CC-S, SAM, SGSB, and EPR (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Benson et al. 2019). Due to extreme isolation and high levels of human-caused mortalities, the SAM and CC-S mountain lions have low genetic diversity, low effective population sizes, and high levels of inbreeding (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Benson et al. 2019). Benson et al. (2019) predicted high losses of heterozygosity in the SAM and Santa Monica Mountains populations, which suggests that inbreeding depression is imminent. If inbreeding depression occurs, the SAM and Santa Monica Mountains/CC-S populations will likely go extinct within 50 years, with median times to extinction of 11.7 years and 15.1 years, respectively (Benson et al. 2019). With similarly low genetic diversity and effective population size, the SGSB and CC-N populations likely have a similar fate. And although the CC-C and EPR populations appear to be slightly healthier with more genetic diversity and a higher effective population size, these populations have effective population sizes that are still well below the most recent recommended threshold to prevent inbreeding depression in the short-term (Frankham et al. 2014; Gustafson et al. 2018); continued development in these areas could propel these populations towards extinction more quickly. Clearly, Central Coast and Southern California mountain lion populations are succumbing to anthropogenic pressures, and without immediate action to restore and enhance connectivity between the populations and suitable habitat, they will be lost, potentially within our lifetimes.

Immediate action is critical for the long-term persistence of Central Coast and Southern California mountain lions and the health of Central Coast and Southern California ecosystems. Connectivity between the populations and suitable habitat must be restored and enhanced to facilitate movement and gene flow while reducing human-caused mortalities. Anthropogenic pressures, especially vehicle strikes and depredation kills, should be minimized to help the recovery of these populations. Although translocation of outbred animals has been shown to be effective to increase genetic diversity (Johnson et al. 2010), this would only be a short-term, unsustainable solution given the current level of isolation of these populations (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Benson et al. 2019). Strategically-placed road/barrier crossing infrastructure that allows for dispersal and gene flow and reduces mortalities would be a more comprehensive, long-term solution to save these populations in perpetuity. And the preservation of intact linkages, especially the Tehachapi and Sierra Pelona Mountains, is essential to maintain statewide genetic connectivity. Immediate regulatory action under the CESA is needed to enhance connectivity among Central Coast and Southern California mountain lion populations and suitable habitat to ensure the conservation of these iconic big cats.

## 8 Inadequacy of Existing Regulatory Mechanisms

### *8.1 State Regulatory Mechanisms*

Proposition 117

The California Wildlife Protection Act of 1990 (Proposition 117) declared that the mountain lion is a "specially protected mammal under the laws of this state." (Cal. Fish & Game Code § 4800(a).) Proposition 117 acknowledged that mountain lion habitat in the Santa Monica Mountains, Santa Ana Mountains, Santa Susana Mountains, and Simi Hills is disappearing rapidly and that "[s]mall and often isolated wildlife populations are forced to depend upon these shrinking habitat areas within the heavily urbanizing areas of this state." (Cal. Fish & Game Code § 2780(d).) Proposition 117 further found that "[c]orridors of natural habitat must be preserved to maintain the genetic integrity of California's wildlife." (*Id*.)

In order to preserve mountain lion populations in California, Proposition 117 mandated that mountain lions are not to be considered a "game mammal," such that hunting is generally prohibited. (Cal. Fish & Game Code § 3950.1(a).) Subject to certain exceptions, Proposition 117 makes it unlawful to take, injure, possess, transport, import, or sell a mountain lion. (Cal. Fish & Game Code § 4800(b).) Nonetheless, a mountain lion may still be removed or killed if it is "perceived to be an imminent threat to public health or safety" or is perceived by CDFW to be "an imminent threat to the survival of any threatened, endangered, candidate, or fully protected sheep species." (Cal. Fish & Game Code § 4801.) Mountain lions that have not been designated an "imminent threat to public health or safety" may still be removed via nonlethal means. (Cal. Fish & Game Code § 4801.5(a).)

A person whose livestock or other property has been damaged or destroyed by a mountain lion may request a permit to "take" the mountain lion. (Cal. Fish & Game Code § 4802.) CDFW is required to immediately take action to confirm that there has been a

depredation. (Cal. Fish & Game Code § 4803.) If CDFW is satisfied that there has been a depredation, CDFW "shall promptly issue a permit to take the depredating mountain lion." (*Id*.) There is no limit to the number of depredation permits a property owner can request from CDFW. In addition, mountain lions that are encountered while pursuing or inflicting injury on livestock or domestic animals may be taken immediately without the need for a permit. (Cal. Fish & Game Code § 4807.)

While Proposition 117 prohibits all hunting of mountain lions as well as the purposeful killing of mountain lions in most circumstances, it does not contain provisions to ensure that connectivity between core habitats for the Southern California or Central Coast mountain lions will be protected. As discussed above in *Section 6.0 Factors Affecting the Ability to Survive and Reproduce*, the primary threat to Southern California and Central Coast mountain lions is not hunting—it is habitat fragmentation and the lack of crossing infrastructure, which has led to major declines in genetic diversity, high levels of inbreeding, and high levels of human-caused mortalities via vehicle strikes, depredation kills, and intraspecific strife due to limited space and the inability for young mountain lions to disperse.

#### 8.1.1 CDFW Departmental Bulletins

CDFW has issued "Departmental Bulletins" relating to mountain lions. The most recent bulletin was issued in December 2017 and applied specifically to the Santa Monica Mountains and SAM mountain lion populations (the "2017 Bulletin") (CDFW 2017).[20] The 2017 Bulletin acknowledged (1) the lack of genetic diversity in the Santa Monica Mountains and SAM mountain lion populations and (2) that human population growth and anthropogenic barriers are restricting connectivity with other mountain lion populations. In order to reduce unnecessary killings of mountain lions in the Santa Monica Mountains and SAM populations, the 2017 Bulletin provides that any person reporting a depredation (a "reporting party") may be issued a first permit to employ non-lethal measures to deter mountain lions from further depredation, and a second permit to "haze" a depredating mountain lion. In the first instance, the reporting party would institute economically feasible measures designed to reduce the potential for attracting mountain lions such as removing the carcasses of depredated animals, installing or repairing and consistently using enclosures to exclude mountain lions, or employing guardian animals in the immediate vicinity of livestock or other domestic animals. The 2017 Bulletin provides that CDFW would not be required to issue a lethal depredation permit until (1) a third depredation event has occurred, and (2) CDFW has confirmed that the reporting party has already implemented all reasonable preventative measures.

In January of 2018, CDFW adopted the 2017 Bulletin's new depredation permit policy. Although this provides some additional protections and will likely reduce lethal take of mountain lions in the Santa Monica Mountains and the SAM, researchers have documented instances wherein domestic animal owners killed mountain lions in these areas without complying with CDFW instructions under the new policy (W. Vickers, *pers comm*). The 2017 Bulletin does not apply to other vulnerable populations, like the SGSB, EPR, CC-N, and CC-C mountain lions. In

[20] California Department of Fish and Wildlife, *Human/Wildlife Interactions in California: Mountain Lion Depredation, Public Safety, and Animal Welfare – Amendment to Department Bulletin 2013-02* (Dec. 15, 2017), available at https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=153021.

addition, the new policy is not designed to ensure protection of habitat or connectivity necessary for the continued survival of the Santa Monica Mountains and SAM mountain lion populations and is insufficient to ameliorate the anthropogenic mortalities related to potential extirpation.

### 8.1.2 California Environmental Quality Act

The California Environmental Quality Act ("CEQA") is California's landmark environmental law and establishes a state policy to prevent the "elimination of fish or wildlife species due to man's activities, ensure that fish and wildlife populations do not drop below self-perpetuating levels, and preserve for future generations representations of all plant and animal communities...." (Cal. Pub. Res. Code § 21001(c)). Towards this end, state and local agencies are required to analyze and disclose the impacts of any discretionary decision or activity. CEQA contains a substantive mandate that agencies should not approve projects as proposed if there are feasible alternatives or mitigation measures which would substantially lessen the significant environmental effects of such projects. (Cal. Pub. Res. Code § 21002.)

CEQA requires a "mandatory finding of significance" if a project may "substantially reduce the number or restrict the range of an endangered, rare or threatened species." (Cal. Code Regs., tit. 14, § 15065(a)(1).) CDFW has interpreted this provision to apply to species of special concern, which are species that are "experiencing, or formerly experienced, serious (noncyclical) population declines or range retractions (not reversed) that, if continued or resumed, could qualify it for State threatened or endangered status."[21] CDFW further provides that species of special concern "should be considered during the environmental review process." (*Id.*; Cal. Code Regs., tit. 14, § 15380.) Thus, a potentially substantial impact on a species of special concern, threatened species, or endangered species could be construed as "per se" significant under CEQA. (*Vineyard Area Citizens for Responsible Growth, Inc. v. City of Rancho Cordova* (2007) 40 Cal.4th 412, 449.) And under CEQA, when an effect is "significant," the lead agency approving the project must make a finding that changes or alterations have been incorporated into the project to avoid or mitigate its significant impacts, or that such changes are within the responsibility of another agency, or that mitigation is infeasible. (Cal. Pub. Res. Code § 21081(a).) These provisions therefore provide some protections to species that are listed as species of special concern, threatened, or endangered.

However, Southern California and Central Coast mountain lions are not listed as a species of special concern or as threatened or endangered, such that a project that has the potential to significantly impact one of these populations would not necessarily qualify as a "significant effect" under a lead agency's interpretation of CEQA. In such case, CEQA's substantive mandate to adopt all feasible alternatives or mitigation measures might not be triggered.

CEQA also requires a "mandatory finding of significance" if a project may "substantially reduce the habitat of a fish or wildlife species; cause a fish or wildlife population to drop below self-sustaining levels; threaten to eliminate a plant or animal community." (Cal. Code Regs., tit. 14, § 15065.) Moreover, CEQA's "Environmental Checklist" in Appendix G of the CEQA

[21] California Department of Fish and Wildlife, *Species of Special Concern* , available at https://www.wildlife.ca.gov/Conservation/SSC.

Guidelines characterizes a project's effects as "significant" if the project would "interfere substantially with the movement of any native [] wildlife species or with established native resident or migratory wildlife corridors...."

While these provisions might theoretically offer some protection for Southern California or Central Coast mountain lions, in practice they have not provided sufficient protection. Under CEQA, lead agencies have discretion to develop their own thresholds of significance. (*East Sacramento Partnerships for a Livable City v. City of Sacramento* (2016) 5 Cal.App.5th 281, 300; Cal. Code Regs., tit. 14, § 15064(d)). This allows local agencies—who are often under pressure from developers to approve projects—to make significance determinations that are inconsistent with independent scientific analysis, including CDFW's analysis. For instance, in December 2017, the City of Temecula approved a 200-acre mixed use project called the Altair Specific Plan that would allow development in the last remaining viable linkage for the SAM mountain lion population between the Santa Ana Mountains and Peninsular Ranges. The City determined that impacts to mountain lions were not significant despite strong disagreement by CDFW, USFWS, and independent mountain lion experts.[22] CDFW warned the City of Temecula that the SAM population has "extremely low genetic diversity which is attributed to low gene flow between the small Santa Ana Mountains population and the larger population in the Peninsular Ranges" and that development is contributing to this genetic decay. (*Id*.) CDFW concluded that "increased human activity associated with the proposed Civic Site at this sensitive location would [] be detrimental to facilitating the movement of mountain lions across Interstate Highway 15 (I-15) to the Peninsular Range." (*Id*.)

Even when a lead agency acknowledges that an effect is "significant," CEQA allows a lead agency to adopt a "statement of overriding considerations" and approve a project if the agency finds that other factors outweigh the environmental costs of the project or that further mitigation is infeasible. (Cal. Code Regs., tit. 14, § 15093(b); Cal. Pub. Res. Code § 21081.) This means that even if a project may have a significant effect on a "wildlife population" like the CC-S, SAM, SGSB, or EPR mountain lions, an agency could interpret CEQA as still allowing approval of the project. CEQA in practice is therefore inadequate to protect the Southern California and Central Coast mountain lions.

Finally, as noted above, the lack of adequate wildlife connectivity and wildlife crossings is the primary factor driving Southern California and Central Coast mountain lions closer to extinction. Yet, agencies have not interpreted CEQA (or the National Environmental Policy Act, discussed further below) as including a clear legal mechanism for mitigation for impacts on wildlife connectivity. For example, in the Final Environmental Impact Report/Final Environmental Impact Statement for the Northwest 138 Corridor Improvement Project (the "Northwest 138 EIR"), Caltrans and the Los Angeles County Metropolitan Transportation Authority wrote: "The proposed project has the potential to directly or indirectly impact wildlife movement throughout the project limits. However, with the inclusion of the proposed avoidance and minimization measures, impact levels area expected to be relatively low. Exact acres of impacts to wildlife corridors are unable to be quantified, and currently there is no real

[22] City of Temecula, *Altair Specific Plan Final Environmental Impact Report* (Oct. 2017), available at https://temeculaca.gov/DocumentCenter/View/4513/Altair-Specific-Plan-Final-Environmental-Impact-Report-FEIR.

mechanism for compensatory mitigation for these types of impacts."[23] The Northwest 138 EIR also contained no analysis of the highway's impacts on mountain lions, given that they are not presently listed as threatened or endangered.

Indeed, CDFW has urged lead agencies to consider wildlife connectivity in CEQA planning documents, without success. For instance, the Los Angeles County General Plan Draft EIR concluded that the buildout of the General Plan "will impact regional wildlife linkages" and have a "significant adverse effect on wildlife movement."[24] The Draft EIR concluded that policies proposed in the General Plan "do not provide for mitigation for loss of wildlife movement opportunities. If development impacts regional wildlife linkages and impedes wildlife movement, connectivity will be lost on a regional scale in these vital landscape corridors and linkages. Thus impacts to wildlife movement remain significant at the General Plan level." (*Id*.) In commenting on the Draft EIR, CDFW specifically objected to this conclusion:

> The Department does not concur with the conclusion in the DPEIR that unavoidable loss of wildlife movement opportunities or nursery sites within or outside of an SEA does not warrant mitigation. Without mitigation, the Project and subsequent projects would result in direct and cumulative loss of biological diversity. Mitigation opportunities for wildlife corridors and nursery sites are best established during large scale planning efforts such as this General Plan. Wildlife corridor areas can be delineated and set aside in the General Plan for current and future conservation efforts. An assessment could be placed on development within the Project area to secure the acquisition of these critical linkages and sites, therefore reducing impacts to wildlife corridors and nursery sites and ensuring biological diversity.[25]

In responding to this comment, Los Angeles County refused to implement CDFW's recommendations, claiming "it cannot be assumed that wildlife corridor areas for future conservation that can be set aside because those properties may not become publicly owned." (*Id*.) Los Angeles County's responses to CDFW's recommendations underscore that lead agencies have not interpreted CEQA to include a clear legal mechanism for mitigation for impacts on wildlife connectivity, even though such connectivity is critical to the survival of Southern California and Central Coast mountain lions.

### 8.1.3 Significant Natural Areas Program

The Significant Natural Areas Program ("SNAP") requires CDFW to develop and maintain a spatial data system that identifies those areas in the state that are most essential for maintaining habitat connectivity, including wildlife corridors and habitat linkages. (Cal. Fish & Game Code § 1932(b).) SNAP also requires CDFW to consult with other government agencies and stakeholders to identify natural areas deemed to be most significant. (Cal. Fish & Game

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[23] State of California Department of Transportation, *Northwest State Route 138 Corridor Improvement Project Final Environmental Impact Report / Environmental Impact State and Section 4(f) Evaluation* (June 2017), available at https://www.metro.net/projects/nw138/nw138-FEIR-FEIS/.

[24] County of Los Angeles, *Los Angeles County General Plan Update Draft Environmental Impact Report* (June 2014), available at http://planning.lacounty.gov/assets/upl/project/gp_2035_deir.pdf.

[25] County of Los Angeles, *Los Angeles County General Plan Update Final Environmental Impact Report* (March 2015), available at http://planning.lacounty.gov/assets/upl/project/gp_2035_lac-gpu-final-eir-final.pdf.

Code § 1932(f).) SNAP further requires CDFW to seek maintenance and perpetuation of the state's most significant natural areas for present and future generations in the most feasible manner. (Cal. Fish & Game Code § 1932(g).)

However, SNAP does not require or authorize any particular land use action or decision. (Cal. Fish & Game Code § 1932.5.) Likewise, SNAP does not change or prevent the change of use of any area identified pursuant to the program. (Cal. Fish & Game Code § 1933.) It therefore does not *require* any particular natural areas to be conserved. Because of this, it is insufficient to protection wildlife connectivity essential to the survival of Southern California and Central Coast mountain lions.

#### 8.1.4 Natural Community Conservation Planning Act

The Natural Community Conservation Planning Act is a voluntary conservation planning mechanism for proposed development projects within a planning area to avoid or minimize impacts to wildlife. (Cal. Fish & Game Code § 2801(f).) The NCCP Act is designed to promote coordination among agencies and landowners to conserve unfragmented habitat areas and multihabitat management. (Cal. Fish & Game Code § 2801(d).)[26]

There are no Natural Community Conservation Plans ("NCCPs") that cover the Santa Monica Mountains or San Gabriel Mountains. There are a few NCCPs that cover portions of the Santa Ana Mountains and Eastern Peninsular Ranges, some of which also act as "habitat conservation plans" or "HCPs" pursuant to the Federal Endangered Species Act (16 U.S.C. § 1539). These include the County of Orange (Central Coastal) NCCP/HCP, the Orange County Transportation Authority NCCP/HCP, Western Riverside County Multiple Species HCP, San Diego Multiple Habitat Conservation Program, San Diego Multiple Species Conservation Program, and the San Diego North County Multiple Species Conservation Plan. There also is an NCCP that covers the Coachella Valley and portions of the San Bernardino Mountains called the Coachella Valley NCCP/HCP.

Of these NCCPs, only four "cover" portions of the Southern California mountain lion populations: (1) Western Riverside County Multiple Species HCP; (2) San Diego Multiple Habitat Conservation Program; (3) San Diego County Multiple Species Conservation Program; and (4) San Diego North County Multiple Species Conservation Plan.[27] Below is a discussion of each as they relate to mountain lions:

(1) The Western Riverside County Multiple Species HCP acknowledges that the SAM mountain lion population is at high risk of extirpation due to demographical instability unless there is a "movement connection between the Santa Ana Mountains

[26] The NCCP Act also is described on CDFW's website at https://www.wildlife.ca.gov/conservation/planning/NCCP.

[27] California Department of Fish and Wildlife, *Conservation Plans By Species*, available at https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=108719&inline. Both San Diego Gas & Electric and San Diego County Water Authority are permittees of HCPs/NCCPs covering mountain lions, but these only apply to activities undertaken by these entities.

and the Palomar Mountains."[28] However, mountain lions are considered to be "adequately conserved."[29] As such, the Western Riverside County Multiple Species HCP offers little protection for the SAM mountain lion population. While this HCP does identify linkages designed to ensure connectivity for mountain lions, the Western Riverside County Regional Conservation Authority has failed to enforce the HCP to protect such linkages when permittees such as the City of Temecula approve development that would severely constrict or impair such linkages.

(2) The San Diego Multiple Habitat Conservation Program is an NCCP and HCP that purportedly covers mountain lions, but the program readily concedes that mountain lions (as well as deer) "were not a major consideration in linkage design."[30] In addition, the EIR/EIS states that "[d]ue to the limited availability of habitat in the study area, implementation of the MHCP is not expected to substantially increase or decrease the population viability of the mountain lion."[31] The EIR/EIS likewise concludes there are no major populations or critical locations for the mountain lion within the plan area, and concludes it is "adequately conserved" under the plan. (*Id*.)

(3) The San Diego Multiple Species Conservation Program is an NCCP and HCP that covers 900 square miles in the southwestern portion of the San Diego. The Program lists mountain lions as "conserved" and states that mountain lions "will be covered by the MSCP because 81% of the core areas (105,000± acres) that support its habitat will be conserved."[32] While the Program generally notes that linkage areas were designed to accommodate "large animal movement," the Program does not identify any linkages designed for mountain lions or any specific measures designed to protect them. Likewise, while the Program states that "[s]pecific design criteria for linkages and road crossings/undercrossings are included in subarea plans," not all subarea plans are complete.

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[28] Western Riverside County Regional Conservation Authority, *Western Riverside County MSHCP Species Accounts*, available at http://wrcrca.conserveriverside.com/wrcrca/Permit_Docs/MSHCP_Docs/volume2/vol2-secb_Mammals.pdf.

[29] Western Riverside County Regional Conservation Authority, *Western Riverside County Multiple Species Habitat Conservation Plan*, available at http://wrcrca.conserveriverside.com/wrcrca/Permit_Docs/MSHCP_Docs/volume1/Vol1-sec2.pdf.

[30] San Diego Association of Governments, *San Diego Multiple Habitat Conservation Program Biological Monitoring and Management Plan (Volume III)* (Mar. 2003), available at https://www.sandag.org/programs/environment/habitat_preservation/mhcp_vol3.pdf.

[31] San Diego Association of Governments, *Final Environmental Impact Statement/Environmental Impact Report for Threatened and Endangered Species Due to Urban Growth within the Multiple Habitat Conservation Program Planning Area* (Mar. 2003), available at https://www.sandag.org/programs/environment/habitat_preservation/mhcp_eir_vol1.pdf.

[32] County of San Diego, *Final Multiple Species Conservation Program* (Aug. 1998), available at https://www.sandiegocounty.gov/content/dam/sdc/pds/mscp/docs/SCMSCP/FinalMSCPProgramPlan.pdf.

(4) The San Diego North County Multiple Species Conservation Plan is one of the "subarea" plans anticipated by San Diego Multiple Species Conservation Program. However, it has not been completed and is still "in development."[33]

(5) The Orange County Transportation Authority NCCP/HCP ("OCTA Plan") lists the mountain lion as a covered species for purposes of the federal HCP, but not for purposes of the NCCP permit. The OCTA Plan acknowledges that despite protection from hunting, annual survival for radio-collared lions is "surprisingly low" at 55.8 percent and that vehicle collisions and depredation permits are primary sources of mortality. The OCTA Plan states that targeted investment in habitat protection is "especially urgent to maintain viability of the Santa Ana Mountains populations."[34] The OCTA Plan does contain four "Species Goals" for mountain lions, including (1) acquiring 1,013 acres of suitable habitat; (2) fencing realignment near the Highway 241 toll road; (3) funding of the North Coal Canyon Restoration Project; and (4) a "wildlife crossing policy" requiring pre-construction surveys to ensure existing crossings "maintain or improve functionality" if modified by new freeway projects. However, despite allowing the expansion of two highways in lion habitat (Projects G and J), the OCTA Plan does not require the construction of any specific wildlife crossings. The OCTA Plan nonetheless claims that impacts on the mountain lion will be offset through these "Species Goals."

There are no NCCPs that cover the Central Coast. In addition, there are no NCCPs that cover portions of the Santa Cruz Mountains except the Santa Clara Valley Habitat Plan. However, this Plan does not cover mountain lions.

## *8.2 Federal Regulatory Mechanisms*

### 8.2.1 National Environmental Policy Act

The National Environmental Policy Act ("NEPA") is the nation's charter for protection of the environment. (40 C.F.R. § 1500.1(a).) NEPA is designed to ensure that environmental information is available to the public *before* decisions are made or actions taken and to help public officials make decisions based on an understanding of the environmental consequences. (40 C.F.R. § 1500.1(b)-(c).) Federal agencies must prepare an environmental impact statement ("EIS") if it is known that an action will significantly affect the environment, or an environmental assessment ("EA") if the extent of effects are unknown. (42 U.S.C§ 4332; 40 C.F.R. §§ 1502.3 & 1508.9.) NEPA further requires federal agencies to analyze reasonable alternatives to the proposed project. (40 C.F.R. § 1502.14(a)-(c).) NEPA requires the federal agency to consider the degree of adverse effect on a species or its critical habitat designated pursuant to the Federal Endangered Species Act. (*Conservation Cong. v. United States Forest Serv*. (E.D.Cal. 2017) 235 F.Supp.3d 1189, 1207.)

[33] County of San Diego, *Multiple Species Conservation Program*, available at https://www.sandiegocounty.gov/pds/mscp/.
[34] Orange County Transportation Authority, *Natural Community Conservation Plan/Habitat Conservation Plan* (Nov. 2016), available at https://www.octa.net/pdf/NCCP%20HCP%20FINAL.pdf.

However, agencies have not interpreted NEPA as requiring analysis of impacts to populations that are not currently listed as threatened or endangered, such as the Southern California or Central Coast mountain lions. For instance, Caltrans prepared an Initial Study with Proposed Mitigated Negative Declaration/Environmental Assessment for the State Route 118 Widening Project (the "State Route 118 EA") in October 2017 pursuant to NEPA and CEQA. The State Route 118 EA contains no analysis of whether adding more traffic lanes to State Route 118 will impact mountain lions or degrade wildlife connectivity even though multiple mountain lions have died recently attempting to cross State Route 118.[35]

NEPA also is insufficient to protect Southern California and Central Coast mountain lions because courts have interpreted NEPA as primarily a "procedural" statute. While NEPA does require federal agencies to consider detailed information regarding a project's environmental effects, "NEPA itself does not mandate particular results." (*Winter v. NRDC, Inc.* (2008) 555 U.S. 7, 23.)

### *8.3 Regional and Local Plans and Policies*

#### 8.3.1 Santa Monica Mountains National Recreation Area General Management Plan

The Santa Monica Mountains National Recreation Area General Management Plan ("GMP") was prepared pursuant to NEPA and provides a framework for the management of the Santa Monica Mountains National Recreation Area ("SMMNRA"), which is administered by the National Park Service, California State Parks, and the Santa Monica Mountains Conservancy. The GMP recognizes that the Santa Monica Mountains mountain lion population's ability to survive in the face of large-scale habitat fragmentation and destruction is uncertain.[36] (GMP at 154.) The GMP states that "it is likely that their persistence [] would depend upon their capability of dispersing to and from other habitat areas beyond the Santa Monica Mountains." (GMP at 154; see also GMP at 157.) The GMP identifies the "greatest threat" to natural resource preservation in the SMMNRA as "loss of habitat connectivity from increased development and urban encroachment." (*Id*. at 157.) The GMP concedes that "the situation is especially serious for mountain lions" and lists mountain lions as a "park species of concern." (*Id*. at 157 & 161.) The GMP agrees that improvements to facilitate wildlife movement across freeways or through developments may be necessary, but does not propose or require any specific actions to improve wildlife movement across freeways or through development.

The preferred alternative in the GMP provides for enhancing connectivity of undisturbed habitats in the SMMNRA by creating large expanses of open space. (*Id*. at 292.) In addition, the Las Virgenes Canyon and Liberty Canyon areas are included within the SMMNRA boundary to help provide wildlife connectivity for mountain lions and other large species. (*Id*. at 293.) Even though the GMP recognizes the threats facing the Santa Monica Mountains mountain lion

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[35] National Parks Traveler, *Another Mountain Lion Killed Near Santa Monica Mountains National Recreation Area* (Jan. 27, 2017), available at https://www.nationalparkstraveler.org/2017/01/another-mountain-lion-killed-near-santa-monica-mountains-national-recreation-area.

[36] National Park Service, U.S. Department of Interior, *Santa Monica Mountains National Recreation Area General Management Plan Environmental Impact Statement* (July 2002), available at https://www.nps.gov/samo/learn/management/loader.cfm?csModule=security/getfile&PageID=383979.

population and takes steps to protect this population, the GMP does not apply to lands outside of the SMMNRA and thus is insufficient to address the regional connectivity issues facing the population. Nor does the GMP apply to roads and highways under Caltrans' jurisdiction.

### 8.3.2 Ventura County Wildlife Connectivity Ordinance

The Ventura County Board of Supervisors adopted an ordinance on March 12, 2019 (the "Connectivity Ordinance") to help facilitate wildlife connectivity and minimize habitat fragmentation for mountain lions, mule deer, California gnatcatchers, bobcats, least bell's vireos, California red-legged frogs, and other species. The Connectivity Ordinance establishes overlay zones called "habitat connectivity and wildlife corridors" ("HCWCs") and "critical wildlife passage areas" ("CWPAs") in which development standards and permitting requirements apply. Development standards include 200-foot setbacks from surface water features such as streams and wetlands, limits on certain wildlife impermeable fencing, encouraging compact siting of development, and prohibiting non-commercial planting of invasive plants. Two of the linkages targeted in the Connectivity Ordinance are the Santa Monica Mountains – Sierra Madre Mountains connection and the Sierra Madre Mountains – Castaic Connection, which connect wildlife habitat in the Santa Monica Mountains, Santa Susana Mountains, Simi Hills, and Los Padres National Forest.

While the Connectivity Ordinance should help allow wildlife to move more easily through private lands between core habitat areas, it would do little to ensure connectivity across major roads and highways because Ventura County does not have jurisdiction over these areas. The ordinance would, however, establish 200-foot setbacks from the exit and entry points of 25 existing road crossings in order to facilitate wildlife movement through the crossings. Caltrans and its road maintenance and improvement activities are not regulated by the Connectivity Ordinance. The Connectivity Ordinance is therefore a step in the right direction but insufficient on its own to address the threats facing the CC-S mountain lion population.

### 8.3.3 Los Angeles County Significant Ecological Areas Program

Los Angeles County is currently in the process of updating the Significant Ecological Areas ("SEAs") Ordinance. The draft ordinance is intended to protect biodiversity in SEAs from incompatible development and ensure that projects reduce habitat fragmentation and edge effects by providing technical review of impacts and requiring mitigation.[37] Like the Ventura County ordinance, the SEAs designations can lead to compact development and allow wildlife to more easily move across private lands between core habitat areas. However, the SEA ordinance is not specifically designed to protect mountain lions and would not regulate Caltrans and its road maintenance and expansion activities.

[37] Los Angeles County Department of Regional Planning, *Significant Ecological Areas Ordinance Update, Public Hearing Draft* (Feb. 14, 2019), available at http://planning.lacounty.gov/site/sea/wp-content/uploads/2019/02/EX-C-SEA-Ordinance-Public-hearing-Draft-2-14-2019.pdf

### *8.4 Future Development Will Further Threaten the Survival of Southern California Mountain Lions*

Continued development in Southern California is expected to further impair connectivity between core habitat areas, leading to further decreases in genetic diversity for Southern California mountain lions. In the environmental review for Southern California national forest land management plans, the U.S. Forest Service found that impaired connectivity poses a serious threat to Southern California mountain lions: the "greatest concern for the long-term health of mountain lion populations on the national forests of southern California is loss of landscape connectivity between mountain ranges and large blocks of open space on private land."[38] The review warned that private land development in Southern California is "steadily reducing the habitat linkages that wildlife species need to connect large blocks of national forest land with other public and private natural spaces and habitat reserves." The review observed that the "widening of the existing highway system and new highways" are a threat to mountain lions because they create barriers to movement. The review concluded that "[w]ithout the national forests and linkages between the mountain ranges and other large habitat preserves, *there is not much long term potential for mountain lions in southern California*." The review noted that maintenance and restoration of corridors between large wildlands is essential to conserving mountain lions in Southern California

As anticipated by the U.S. Forest Service's environmental review, private land development is currently being approved on linkage areas without sufficient mitigation for Southern California mountain lions or wildlife connectivity. For instance, the 1,000-acre Northlake Specific Plan ("Northlake") was approved by the Los Angeles County Board of Supervisors on April 2, 2019. The Santa Monica Mountains Conservancy ("SMMC") formally objected to the Board's approval of Northlake, noting that the development would degrade a known wildlife linkage between the Angeles National Forest and Los Padres National Forest.[39] CDFW raised similar concerns about the development because it would impair a linkage that is "highly suitable for regional wildlife movement and connectivity" for mountain lions and other species.[40] The Board of Supervisors approved Northlake notwithstanding the objections and concerns of SMMC and CDFW.

Likewise, the Los Angeles County Board of Supervisors approved the 12,000-acre Centennial Specific Plan ("Centennial") on April 30, 2019, despite SMMC warning the Board that Centennial "would sever the most optimal five-mile-wide habitat linkage across Highway 138 between I-5 and State Route 14."[41]

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[38] Forest Service, U.S. Department of Agriculture, *Final Environmental Impact Statement, Land Management Plans, Angeles National Forest Cleveland National Forest Los Padres National Forest San Bernardino National Forest* (Sept. 2005), available at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5166889.pdf.

[39] Santa Monica Mountains Conservancy, *Draft Supplemental Environmental Impact Report Comments on Northlake Specific Plan Project*, May 22, 2017.

[40] California Department of Fish and Wildlife, *Draft Supplemental Environmental Impact Report Comments on Northlake Specific Plan*, June 12, 2017.

[41] Santa Monica Mountains Conservancy, *Centennial Project Draft Environmental Impact Report Comments County Project No. 02-232*, July 17, 2017.

In the SAM, key linkage and habitat areas remain unprotected and subject to potential or actual development. The Altair Specific Plan discussed in *Section 8 Inadequacy of Existing Regulatory Mechanisms* exemplifies this trend. Other lands in the Santa Ana-Palomar Mountain linkage have been subject to development proposals such as the Temecula Creek Inn (Vickers 2015). The Orange County Board of Supervisors also approved a 6,000-acre development in the Santa Ana Mountains in the "center of puma habitat" (Vickers 2015).[42]

Development in wildlands and linkages will intensify as Southern California's population increases. The Southern California Association of Governments ("SCAG") Program EIR estimates that between 2016 and 2040 the Southern California region will grow by 3.8 million residents and 1.5 million households.[43] The SCAG Program EIR concludes that transportation projects within the SCAG region such as "mixed flow lane projects" and "grade separation projects" may result in significant impacts on wildlife movement, including direct habitat removal and fragmentation that would disrupt corridor functionality. The SCAG Program EIR also acknowledges that "an increase in wildlife-roadway interactions as a result of the development of new transportation projects may increase wildlife injury and fatalities."

The SCAG Program EIR recognizes that "[b]arriers to wildlife movement exist throughout the SCAG region, including large areas of urban development and multilane freeways that cut off regional movement corridors for large migratory species such as mountain lions (*Puma concolor*)." SCAG Program EIR further notes that "wildlife crossings serve to alleviate these barriers and facilitate wildlife movement through the region" and references the planned Liberty Canyon Crossing. However, the Program EIR does not identify any other planned crossings or identify funding for the Liberty Canyon Crossing.

The SCAG Program EIR also confirms that only portions of the lands in the Santa Monica Mountains, SAM, SGSB, and EPR are designated as "open space and recreation" or "undevelopable and protected." Indeed, much of these lands are designated for single family residential or mixed residential. At this time, there are also "vast areas" in Southern California that are undeveloped but are not designated as open space or are otherwise protected, according to SCAG. In addition, agricultural lands are rapidly being converted to urban development throughout Southern California with an estimated 230,000 acres converted between 1996 and 2004 and up to 700,000 acres may be converted by 2030. In short, SCAG recognizes that wildlife connectivity will become even more impaired in the Southern California region due to anticipated growth, but SCAG does not offer any solutions to address the effects of this impaired connectivity on Southern California mountain lions.

Other studies confirm that much of the remaining mountain lion habitat in Southern California is on unprotected lands and at risk of development. According to Burdett et al. (2010), almost half of suitable mountain lion habitat in Southern California (since 1970) is on private lands, of which 35% will be developed by 2030, and other currently contiguous habitat will

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[42] See also Chris Boucly, "New community coming to South County," *The Orange County Register* (Mar. 24, 2012), available at https://www.ocregister.com/2012/03/24/new-community-coming-to-south-county/

[43] Southern California Association of Governments, *Draft Program Environmental Impact Report* (Dec. 2015), available at http://scagrtpscs.net/Documents/2016/peir/draft/2016dPEIR_Complete.pdf.

become fragmented. Hunter et al. (2003) similarly found that 30% of high suitability mountain lion habitat and 76% of medium suitability mountain lion habitat in Southern California is not protected from development. In addition, Zeller et al. (2017) found that only 35% of resource-use patches and 47% of corridors identified in their study area, which encompassed much of the SAM and EPR, were fully protected. Given the extreme isolation, low genetic diversity, and high adult mortality rates from vehicle strikes and depredation kills, increased efforts to protect the species and their habitat are warranted.

Within Riverside County, which covers a significant portion of the Santa Ana Mountains, population growth is expected to be especially high; the Riverside County General Plan predicts that the County's population and housing stock will increase to 3.6 million people and 1.3 million dwelling units by 2035, which constitutes a 65 percent increase.[44] Within San Bernardino County, which encompasses portions of the San Bernardino and San Gabriel Mountains, more than 630,000 people will be added to the County along with 230,000 homes.[45] As urban development overtakes mountain lion habitat and linkage areas throughout the region, conflict with mountain lions, and consequent killing of lions under depredation permits will likely increase. Similarly, use of anticoagulant rodenticides and other environmental toxicants in these areas will likely increase, leading to increased illness and fatalities to "non-target organisms" such as Southern California mountain lions.

Caltrans and local transportation agencies are expected to continue building and expanding roads and highways in Southern California to accommodate actual and anticipated vehicles and development. Caltrans' 2018 State Transportation Improvement Program ("STIP") lists many large-scale road and highway projects planned for Southern California.[46] These include converting SR-71 to a four- and six-lane freeway as well as adding more lanes to the I-15 Freeway adjacent to the SAM,[47] which already acts as a nearly impenetrable barrier to the SAM and EPR mountain lion populations. As noted in *Section 8 Inadequacy of Existing Regulatory Mechanisms*, Caltrans has certified an EIR/EIS to convert the existing two-lane SR-138 into a four or six-lane highway, which will create major barrier between the Tehachapi Mountains and Angeles National Forest. Caltrans also intends to widen SR-118, which will further impair connectivity between the Santa Monica Mountains and Santa Susana Mountains to the detriment of the Santa Monica Mountains mountain lions. There are numerous other road and highway projects planned for Southern California in the next few years.[48] These projects will be funded in part by SB 1, which will raise approximately $52 billion over 10 years.

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[44] County of Riverside, *Riverside County General Plan Environmental Impact Report No. 521* (March 2014), available at https://planning.rctlma.org/Portals/14/genplan/general_plan_2014/EnvironmentalImpactReport/03-0_ProjectDescription_2014-04-07.pdf.

[45] San Bernardino County, *Countywide Plan Growth Forecast*, available at http://countywideplan.com/wp-content/uploads/2018/08/CWP_OH_GrowthForecast_FINAL_20180809.pdf.

[46] California Department of Transportation, *2018 Report on STIP Balances County and Interregional Shares* (Aug. 1, 2018), available at http://www.catc.ca.gov/programs/stip/2018-stip/2018_ORANGE_BOOK.pdf.

[47] Riverside County Transportation Commission, *I-15 Express Lanes Project Southern Extension*, https://www.rctc.org/i15-express-southern-extension/

[48] Kurt Snibbe, "Here are the major highway improvement projects happening in Southern California through 2023," *Orange County Register* (Jan. 23, 2018), https://www.ocregister.com/2018/01/23/here-are-maps-and-a-list-of-the-major-highway-improvement-projects-in-southern-california/; Jeong Park, "2019 will be a busy year for big road construction projects in Orange County," *Orange County Register* (Dec. 31, 2018),

Along with this expansion in roads and highways will come an increase in automobile use: SCAG predicts that the number of vehicle miles travelled ("VMT") in the region is expected to increase 13.3 percent by 2040 (from 448 million VMT per day to 504 million VMT per day). This significant increase in automobile use will further impair connectivity and lead to more collisions between automobiles and lions.

*8.5 Future Development Will Further Threaten the Survival of Central Coast Mountain Lions*

Future development and highway expansion in the San Francisco Bay Area and Central Coast is anticipated to further fragment habitat for Central Coast mountain lion populations and will increase threats to their survival.

The Association of Bay Area Governments' Plan Bay Area projects that the population of the San Francisco Bay Area is expected to increase from 7.2 million to 9.3 million by 2040—a 30 percent increase.[49] This includes a 26 percent increase in San Mateo County and a 36 percent increase in Santa Clara County, both of which encompass significant portions of the Santa Cruz Mountains. The Plan Bay Area also envisions a 25 percent increase in housing units in San Mateo County, and a 31 percent increase in Santa Clara County.

The Greenbelt Alliance's "At Risk" Report ("Greenbelt Report") estimates that 22,700 acres in San Mateo County are at medium or high risk for development, significant portions of which are in the Santa Cruz Mountains.[50] The Greenbelt Report shows that only 113,000 acres of the Santa Cruz Mountains are permanently protected and warns that San Mateo County has planned to develop housing in remote areas on the eastern slope of the Santa Cruz Mountains. The Greenbelt Report estimates that Santa Clara County has 54,100 acres at high or medium risk of development, significant portions of which are in the Santa Cruz Mountains and eastern foothills. The Greenbelt Report further shows that while large swaths of the eastern Santa Cruz Mountains are currently at "low risk" for development, only fragmented portions enjoy permanent protection.

Similarly, the EIR for the Plan Bay Area 2040 notes that land use growth footprints overlap with approximately 1,040 acres of "Essential Connectivity Areas" or "ECAs."[51] The EIR claims these growth footprints are in already urbanized corridors that are degraded so that their function as linkages is limited. The EIR acknowledges that development projects may directly encroach on wildlife corridors, but does not provide any plan to address the effects of

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https://www.ocregister.com/2018/12/31/2019-will-be-a-busy-year-for-big-road-construction-projects-in-orange-county/.

[49] Metropolitan Transportation Commission and Association of Bay Area Governments, *Bay Area Plan*: *A Strategy for A Sustainable Region* (July 18, 2013), available at http://files.mtc.ca.gov/pdf/Plan_Bay_Area_FINAL/Plan_Bay_Area.pdf.

[50] Greenbelt Alliance, *At Risk 2017* (May 2017), available at https://www.greenbelt.org/at-risk-2017/.

[51] Metropolitan Transportation Commission and Association of Bay Area Governments, *Draft Environmental Impact Report for Plan Bay Area 2040* (April 2017), available at http://2040.planbayarea.org/cdn/farfuture/JHbwWZgw24OSpVBL0b8cJ5_2KHOdckVexpxYp5McOkI/1499352691/sites/default/files/2017-07/PBA%202040%20DEIR_0_1.pdf.

such encroachment. In addition, Caltrans has a number of highway improvement projects planned in Santa Clara and San Mateo counties.[52]

There also is development pressure on the Pajaro Hills linkage, which is important to the Central Coast North mountain lion population and connects the Santa Cruz Mountains and Gabilan Range.[53] The Land Trust of Santa Cruz County notes that while a few large ranches cover most of the Pajaro Hills, many of the properties are parcelized, creating the potential for development which would fragment the landscape. Only 8 percent of the Pajaro Hills is permanently protected.

Growth is expected to increase in the Monterey Bay Area, leading to further fragmentation of natural habitats by urban or exurban development. The Association of Monterey Bay Area Governments predicts that the population in the Monterey Bay Area will rise from 755,403 in 2015 to 883,300 in 2040.[54] The Land Trust of Santa Cruz County notes that while high rates of conversion of forests, rangeland and farmland has largely been prevented in Santa Cruz County, exurban development, roads and mining are fragmenting wildlife habitat. Vineyard conversion adjacent to Zayante, Beer Creek, and Summit roads is causing habitat fragmentation in one of the largest intact habitat patches connecting Santa Cruz and Santa Clara counties. The Land Trust of Santa Cruz County estimates that only 44 percent of the large patches of intact habitat are protected. The Conservation Lands Network likewise confirms that much of the Santa Cruz Mountains do not currently qualify as protected areas.[55]

In San Luis Obispo County, the population is expected to increase by 41,650 between 2015 and 2045.[56] The sparsely populated North Coast region of San Luis Obispo County is currently characterized by ranchlands, rural development, and open space. However, the San Luis Obispo Council of Governments ("SLOCOG") predicts more population growth in this region as compared to other regions. SLOCOG also predicts significant increases in traffic volumes on Highway 101 throughout San Luis Obispo County. The US 101 Corridor Mobility Master Plan also contains various proposals to expand the Interstate 101 freeway in San Luis Obispo County, including adding more lanes to the freeway.[57] There are also proposals to widen portions of State Route 46, the western portions of which bisect mountain lion habitat. The Caltrans State Route 46 Corridor System Management Plan concedes that widening segments 2 and 3 of State Route 46 "could present additional barriers to animal movements by further

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[52] Caltrans District 4, *Projects By County*, available at http://www.dot.ca.gov/d4/projects_list.htm.
[53] Land Trust of Santa Cruz County, *A Conservation Blueprint* (May 2011), available at https://landtrustsantacruz.org/blueprint/conservation-blueprint_low-res_110522.pdf.
[54] Association of Monterey Bay Area Governments, *2040 Metropolitan Transportation Plan/Sustainable Communities Strategy* (June 2018), available at http://ambag.org/programs/met_transp_plann/documents/Final_2040_MTP_SCS/AMBAG_MTP-SCS_Final_EntireDocument.pdf.
[55] Conservation Lands Network, *1.0 Progress Report* (2014), available at https://www.bayarealands.org/wp-content/uploads/2017/07/CLN-1.0-Progress-Report.pdf.
[56] San Luis Obispo Council of Governments, *2019 Regional Transportation Plan Public Review Draft* (Feb. 2019), available at https://www.dropbox.com/s/6pysudp1g36n4a5/__Public%20Rev%20draft.pdf?dl=0 .
[57] San Luis Obispo County of Governments, *US 101Corridor Mobility Master Plan* (Sept. 2014), available at http://www.dot.ca.gov/hq/tpp/offices/ocp/5_SLOCOG%20101_executive_summary_draft_9%2019%2014.pdf.

dividing large, contiguous wildlife habitat areas."[58] There are numerous other road and highway expansion projects planned for Santa Cruz, Monterey, San Luis Obispo, and Santa Barbara counties.[59] The expansion of existing roads and highways along with increased numbers of automobiles will further impair connectivity in the Central Coast region.

## 9 CESA Listing for Southern California and Central Coast Mountain Lions Would Supplement Proposition 117's Protections.

### *9.1 CESA Listing is Consistent with Proposition 117.*

CESA protections for Southern California and Central Coast mountain lions are consistent with and supplemental to those established by Proposition 117. Both CESA and Proposition 117 include "take prohibitions"—CESA makes it unlawful for any person or agency to import, export, take, possess, or purchase a listed species. (Cal. Fish & Game Code § 2080.) By the same token, Proposition 117 makes it unlawful to take, injure, possess, transport, import, or sell a mountain lion. (Cal. Fish & Game Code § 4800(b).)

Both CESA and Proposition 117's take prohibitions are subject to certain exceptions. Under CESA, CDFW may authorize that a person, agency, or institution take a listed species "for scientific, educational, or management purposes." (Cal. Fish & Game Code § 2081(a).) CESA defines scientific resources management activities to include "research, census, law enforcement, habitat acquisition, restoration and maintenance, propagation, live trapping, and, transplantation, and, in the extraordinary case where population pressures within a given ecosystem cannot be otherwise relieved, [] regulated taking." (*San Bernardino Valley Audubon Society v. City of Moreno Valley* (1996) 44 Cal.App.4th 593, 604, quoting Cal. Fish & Game Code § 2061.) The regulations implementing CESA also allow for the take of a listed species for management or law enforcement purposes: "Department wildlife management activities. The possession or take of endangered, threatened, or candidate species by employees and agents of the Department for scientific, educational and management purposes, and for law enforcement purposes, is not prohibited." (Cal. Code Regs., tit. 14, § 783.1(c).) As discussed above in *Section 8 Inadequacy of Existing Regulatory Mechanisms*, Proposition 117 also contains exceptions which allow for the take of mountain lions in certain circumstances. These exceptions are sufficiently similar that in most cases take of mountain lions properly authorized by Proposition 117 could be consistent with CESA's exceptions for wildlife management activities or law enforcement purposes. (Cal. Code Regs., tit. 14, § 783.1(c).)

### *9.2 CESA Listing Would Further the Goals of Proposition 117.*

CESA listing would further Proposition 117's goals of protecting and restoring wildlife habitat as human populations increase. (Cal. Fish & Game Code § 2780(a).) CESA listing would also help preserve "corridors of natural habitat [] to maintain the genetic integrity" of mountain lions in the Santa Monica Mountains, Santa Ana Mountains, Santa Susana Mountains, Simi Hills, and Coast Range. (Cal. Fish & Game Code § 2780(a).)

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[58] Caltrans, *State Route 46 Corridor System Management Plan* (June 2009), available at http://www.dot.ca.gov/hq/tpp/corridor-mobility/CSMPs/d5_CSMPs/SR%2046/SR-46%20CSMPo100.pdf.
[59] Caltrans District 5, *Projects By County*, available at http://www.dot.ca.gov/d5/.

Likewise, CESA requires that "reasonable and prudent alternatives" that will not jeopardize the existence of a listed species be developed in coordination with the project proponent and state lead agency consistent with conserving the listed species and maintaining the project purpose to the greatest extent feasible. (Cal. Fish & Game Code § 2053(b).) In the event that such alternatives are infeasible, individual projects may still be approved if appropriate mitigation measures are implemented. (Cal. Fish & Game Code § 2054.) CESA envisions these mandates will be incorporated into the CEQA process. (Cal. Fish & Game Code §§ 2064-2065; Cal. Code Regs., tit. 14, §§ 783.3 & 783.5.)

Consistent with Proposition 117, CESA further provides that it is the policy of the state to conserve and protect listed species and their habitat, including through acquiring lands for habitat. (Cal. Fish & Game Code § 2052.) Towards this end, CESA directs state agencies to utilize their authority to conserve listed species. (Cal. Fish & Game Code § 2055.) If the Southern California and Central Coast mountain lions were listed under CESA, this mandate would apply to, for example, Caltrans, which currently lacks a clear mandate to conserve these lions or habitat connectivity necessary for their continued survival.

CESA authorizes CDFW to develop and implement "nonregulatory recovery plans" for listed species with priority given to species that are or may be "significantly affected by anticipated land use changes, climate change, or changes in aquatic conditions." (Cal. Fish & Game Code §§ 2079.1(a) & (b).) Given the strong evidence that land use changes will significantly affect (and have already significantly affected) Southern California and Central Coast mountain lions, CDFW could develop and implement a recovery plan for these lions pursuant to this provision.

In sum, CESA listing would build upon the protections in Proposition 117 by establishing an affirmative duty to ensure the survival and recovery of the Southern California and Central Coast mountain lions by, *inter alia*, (1) prohibiting the approval of projects that could jeopardize their continued existence or result in destruction of essential habitat (Cal. Fish & Game Code § 2053(a)); (2) requiring state agencies such as Caltrans to utilize their authority to conserve listed species (Cal. Fish & Game Code § 2055); and (3) requiring appropriate mitigation measures be implemented for projects that could destroy mountain lion habitat or impair connectivity (Cal. Fish & Game Code § 2054).

To the extent there is any tension between the provisions in Proposition 117 and CESA, Proposition 117 is to be "liberally construed to further its purposes." (Prop. 117 § 9.) Because Proposition 117 and CESA both have similar purposes, Proposition 117 should be construed to be consistent with CESA.

## 10 Recommended Management and Recovery Actions

Recommendations for the management and recovery of Southern California and Central Coast mountain lion populations are as follows:

1. Design and build crossing infrastructure in strategic locations to improve wildlife connectivity and permeability at existing roads and highways. Crossing infrastructure should include but is not limited to overcrossings, underpasses, culverts, and exclusionary fencing that guides animals to safer crossing areas. The following crossing locations have been identified by mountain lion experts and should be prioritized for the implementation of crossing infrastructure: 1) I-15 Freeway at Temecula Creek Bridge to enhance the Palomar Linkage and connect the Santa Ana and Eastern Peninsular Mountain Ranges (Gustafson et al. 2017; Zeller et al. 2017; Ernest et al. 2014; Riley et al. 2018); 2) I-15 Freeway at "Site 5" as described in Riley et al. (2018); 3) Hwy-101 at West Liberty Canyon. (Riley et al. 2018.)

2. Improve or add large culverts to existing freeways in areas suitable for mountain lion crossing. (Vickers 2015).

3. Dedicate sufficient Wildlife Conservation Board, Habitat Conservation Fund and other state funding sources towards acquiring key mountain lion habitat and for establishment of highway crossing infrastructure.

4. Ensure that suitable habitat exists (through preservation or restoration/enhancement) on both sides of crossing structures and culverts (South Coast Wildlands 2008). Restrict human activity near crossing structures and relocate foot trails away from these structures (South Coast Wildlands 2008).

5. Fully protect mountain lion habitat, including resource-use patches and corridors (Zeller et al. 2017; Vickers et al. 2015). Prohibit large-scale development in primary travel corridors and habitat linkages, such as in and around the last remaining linkage for statewide genetic connectivity in the Tehachapi and Sierra Pelona Mountains (Gustafson et al. 2018) and in corridor areas between the SAM and EPR (Gustafson et al. 2017).

6. Require analysis of region-wide wildlife connectivity in all new development proposals (Gustafson et al. 2018).

7. Reduce depredation conflicts that precipitate mountain lion deaths (Vickers et al. 2015). Develop and implement outreach and education activities to promote use of predator-proof enclosures for domestic animals. (Vickers et al. 2015.) Expand CDFW's new three-step depredation permit policy in the CC-S and SAM areas to include all mountain lions across the state, or at a minimum, within the SGSB, EPR, CC-N, and CC-C population areas. Enhance the policy with enforceable implementation of non-lethal protective measures and reporting requirements.

8. Prohibit the use of second-generation anticoagulant rodenticides ("SGARs"), such as brodifacoum, bromadiolone, difenacoum, and difethialone in Southern California and Central Coast mountain lions' core habitat areas and linkages. Limit the use of other pesticides and herbicides that may have negative effects on mountain lion populations in Southern California and the Central Coast.

9. Identify “priority areas” for establishing wildlife passage features for the Southern California and Central Coast mountain lions using the best available science, including data collected by various agencies, academic institutions, and organizations, including but not limited to the National Park Service, the Karen C. Drayer Wildlife Health Center at UC Davis, the Road Ecology Center at UC Davis, and the Santa Cruz Puma Project at UC Santa Cruz.

10. Require Caltrans to analyze how projects in the State Highway Operation Protection Program and State Transportation Improvement Program can be designed to facilitate wildlife connectivity through wildlife passage features such as culverts, undercrossings, overcrossings, bridges, directional fencing, scuppers, barrier breaks, roadside animal detection systems, etc. Require Caltrans to collect and analyze roadkill data to identify hotspots where mountain lions are killed. Require Caltrans to implement wildlife passage features to the greatest extent feasible and as expeditiously as possible.

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