CITY COUNCIL MEETING
MEMORANDUM

TO: Mayor and Councilmembers
Gary Halbert, Interim City Manager
Shawn Hagerty, City Attorney

FROM: James Jeffries, City Clerk

DATE: June 11, 2025

SUBJ: Updated Council Meeting Materials – June 11, 2025

PUBLIC HEARING:

(6) Public Hearing for the Development of Fanita Ranch, to Consider Certifying Final Recirculated Revised Environmental Impact Report Including Second Recirculated Sections (ENV-2025-0003, AEIS 2022-4, AEIS 2017-11), and Approving the Fanita Ranch Development Plan and Development Review Permit (DR-2025-0001), Vesting Tentative Map (TM-2025-0001), and Conditional Use Permits for Public Parks (CUP2025-0001 and CUP-2025-0002), and a Fire Station (CUP-2025-0003). (Planning and Building – Sawa)

The attached correspondence for above mentioned Item was received and is provided for your consideration.

Monday June 9th 2025

NO Fanita Ranch Project

Do you work for us or for out of town developers?

Attn Sandi Sawa AICP
Planner
City Council members
Mayor Minto

We did not all hear about this quick slick move to approve this project on Strathmore Drive!
Some received e-mails, I heard, of the public notice—

We the people said NO to this project and voted against it — and still the corruption continues!

This huge project is a disaster to our city—destroying and over-taxing our community!—plus increasing CRIME!

Thousands of vehicles will be on our surface roads and arteries every day and night.

On Strathmore Dr we have poor access to get out on our back hills with a gate at Ganley closed, presently.
→ our cell phones do not work!
→ In the event of a massive wildfire or mass shooting or any danger, the people will not get out!
Emergency vehicles will not get there in time to help the elderly or sick or injured. Our emergency personnel can not do everything and be everywhere.

NO FANITA RANCH DEVELOPMENT! pg 2 Sandys

Problems not mitigated

No new access rds with thousands of homes

CURRENT TRAFFIC CONGESTION WILL BE MULTIPLIED
MAST MISSION GORGE CUYAMACA Hwy 67
FANITA PKWY CARLTON ~~HILLS~~ /
and all surface streets Hwy 52 / already a nightmare!

NOISE DIRT AIR QUALITY UTILITIES WILL BE IGNORED ?!
Destruction of birds wildlife habitat trees plants
Danger to children travelling to and from school dodging traffic (elementary high school daycare and preschool)

Fanita Pkwy and Cuyamaca st can not process thousands of extra trips day and night with additional construction, dirt moving, cement, day workers. It will be a huge, huge disaster to our community and the lives we live and enjoy here in Santee.

We already have the pollution from the landfill, construction everywhere dirt dust debris creeping into our lungs and homes

SMELL
NOISE
DUST
SICKNESS

I find commercial use up to 80,000 sq ft questionable! (what kind of? businesses?)

This is not essential housing and most will be unaffordable to most citizens.

STOP THE LIES!
STOP THE DEVELOPMENT!

S

From: RANDY AVERY [redacted]
Sent: Monday, June 9, 2025 5:41:07 PM
To: Sandi Sawa <SSawa@CityofSanteeCa.gov>
Subject: Fanita Ranch Project

I am totally against the Fanita Ranch Project. We are in a fire zone, and will have limited access to roads leaving our homes if there is another fire in our area.
The traffic is already unbearable and congested in every direction, adding 3000 more homes in the area is totally ludacris!
Why do we have to continue to try to protect our neighborhood?

Betty Avery
on [redacted]

From: C COSTANTINO JR [redacted]
Sent: Monday, June 9, 2025 12:53 PM
To: Sandi Sawa <SSawa@CityofSanteeCa.gov>
Cc: John Minto <JMinto@CityofSanteeCa.gov>; Ronn Hall <RonnHall@CityofSanteeCa.gov>; Dustin Trotter <DTrotter@CityofSanteeCa.gov>; rmcnellis@cityofsanteeca.gov; Laura Koval <LKoval@CityofSanteeCa.gov>
Subject: Citizen Response & Objections to Fanita Ranch Final EIR

Please see the attached letter denoting various concerns & objections to the Fanita Ranch Development project, submitted for the scheduled Public Hearing during the June 11th, 2025 City Council Meeting.

Please provide confirmation of receipt of this email / letter.

Thank You,
Carl Costantino

City of Santee

Attn: Sandi Sawa, Director of Planning, Mayor John Minto, & the City Council of Santee,

Re: Fanita Ranch Development, upcoming June 11^{th}, 2025 Public Hearing

As a concerned, long term (45+ years) resident of the City of Santee, this letter serves to voice my strong opposition to the proposed Fanita Ranch project, for the following reasons:

1) This project is fundamentally incompatible with the current and projected capacity of Santee's infrastructure. Santee is already experiencing the consequences of rapid, dense development without concurrent Infrastructure.
   - 1.1. This development plans to add nearly 3,000 additional housing units, along with commercial spaces, parks, trails, and community facilities, on approximately over 2,600 acres of land north of the city.
   - 1.2. City Street Traffic congestion has worsened considerably, especially along Mission Gorge Rd, Cuyamaca Rd, Mast Blvd, & Magnolia Ave, with Cuyamaca & Magnolia being 2 of the 3 planned roadways into Fanita Ranch.
   - 1.3. State Route 52, which is over capacity (effectively the day it opened), is in gridlock mornings & afternoons, on a daily basis.
   - 1.4. Adding an influx of thousands of new residents and vehicles from this development can only exacerbate these issues, & will fundamentally alter the character of our community, shifting away from a livable, open-space town into another traffic-clogged, overextended suburban grid.
   - 1.5. The Fanita Ranch proposal indicates three distinct "villages", yet the necessary road extensions (Fanita Parkway, Cuyamaca Street, & Magnolia Avenue) at this time remain largely theoretical. There is no funding plans nor evidence that the city or county is prepared to expand and maintain the road network, utilities, and emergency response services at the scale required to support such an expansion.
   - 1.6. Simply put, we do not have the infrastructure, nor the funding, to accommodate this magnitude of growth without significant, long-term negative consequences for current residents.

2) Construction in this project's location would also risk irreversible damage to area watershed, sensitive ecological preserves, including Mission Trails, Sycamore Canyon, & other nearby natural resources & wildlife habitats.

3) Most importantly, **<u>100% of the proposed development area is designated by CalFire as a "Very High Fire Hazard Severity Zone".</u>** ***<u>(Please See Page 3)</u>***

3.1. I can vividly recall watching the flames of the 2003 Cedar Fire traverse this area's hillsides from Hwy 67 all the way into Kearny Mesa, and now Home Fed & Santee want to put 3000 homes, etc. into this very same High Fire-risk pathway?!?

3.2. We all saw the horrific destruction of the Palisades & Eaton Fires in Los Angeles. Over 16,000 Structures burned. The Fanita Ranch development would simply be tinder for a repeat of this disastrous Fire.

3.3. We have seen the consequences of poor wildfire planning in other parts of California — <u>Santee must not follow that path.</u>

<u>Finally, & above all else . . .</u>

4) The Fanita Ranch development has been repeatedly voted down by the citizens of Santee, as well as ruled against by the Court.

4.1. This revised proposal continues to fail to address the very real limitations of Santee's Infrastructure, and the "Very High" Fire Hazards, & Environmental risks involved.

4.2. To approve this project would demonstrate an utter lack of respect & consideration for the citizens of Santee, for whom you are sworn to represent.

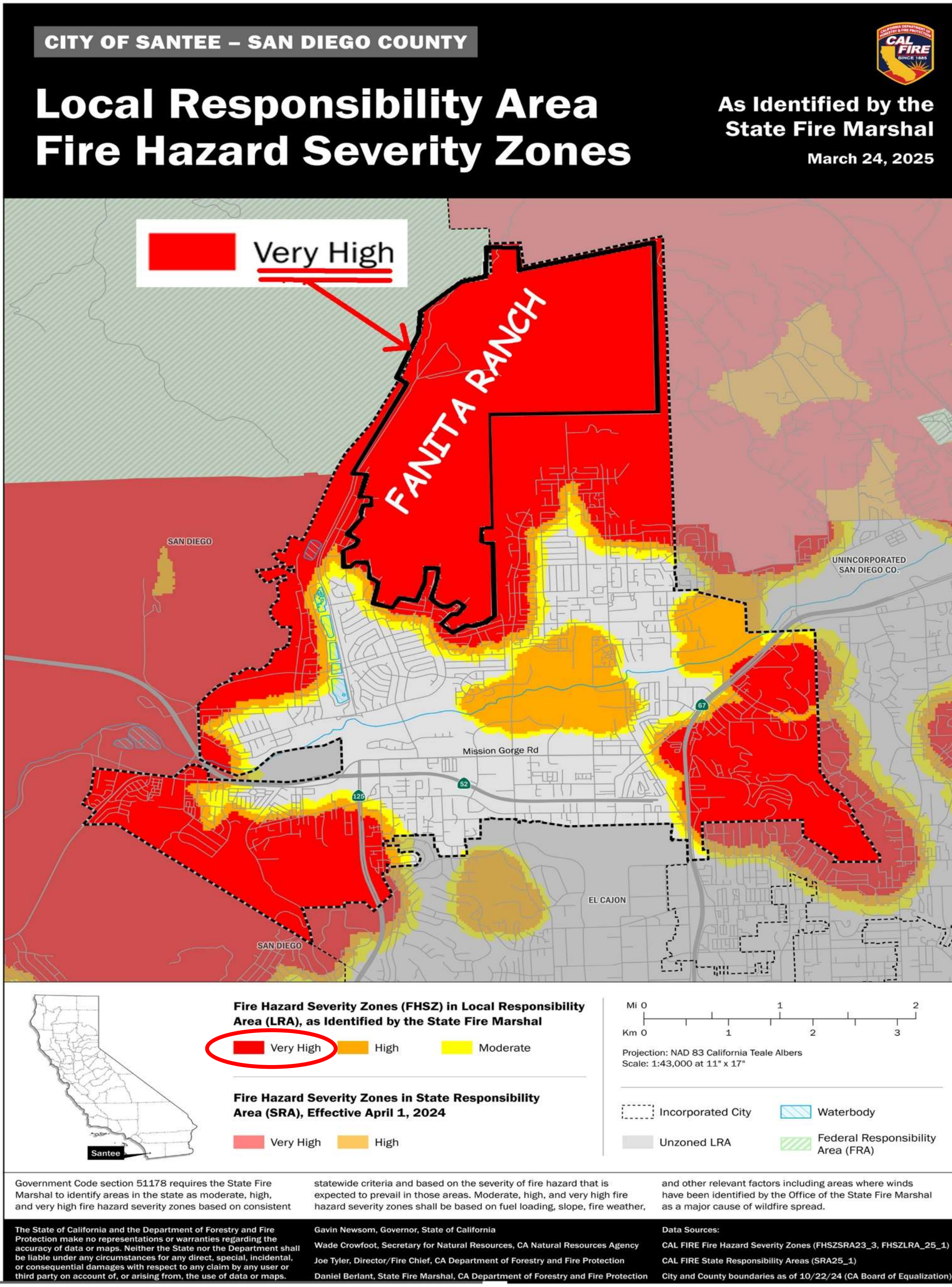
4.3. The City of Santee must prioritize the well-being, safety, & stability of its current citizens over the greed & ambitions of large-scale developers. Santee should not bear the burden of Home Fed's bad investment.

Development does NOT inherently equal progress. True progress lies in improving the quality of life for the residents who already call Santee home.

I respectfully urge your office & the City Council of Santee to do what is best for the citizens of Santee, and <u>reject the Fanita Ranch Housing Development</u>.

Thank you for your time and consideration.

Sincerely,
Carl & Mary Costantino,
Santee Residents for 45+ years


CITY OF SANTEE – SAN DIEGO COUNTY
Local Responsibility Area
Fire Hazard Severity Zones
As Identified by the State Fire Marshal
March 24, 2025
CAL FIRE
Very High
FANITA RANCH
SAN DIEGO
UNINCORPORATED SAN DIEGO CO.
67
Mission Gorge Rd
52
125
EL CAJON
SAN DIEGO
Santee
Fire Hazard Severity Zones (FHSZ) in Local Responsibility Area (LRA), as Identified by the State Fire Marshal
Very High
High
Moderate
Fire Hazard Severity Zones in State Responsibility Area (SRA), Effective April 1, 2024
Very High
High
Mi 0 1 2
Km 0 1 2 3
Projection: NAD 83 California Teale Albers
Scale: 1:43,000 at 11" x 17"
Incorporated City
Waterbody
Unzoned LRA
Federal Responsibility Area (FRA)
Government Code section 51178 requires the State Fire Marshal to identify areas in the state as moderate, high, and very high fire hazard severity zones based on consistent statewide criteria and based on the severity of fire hazard that is expected to prevail in those areas. Moderate, high, and very high fire hazard severity zones shall be based on fuel loading, slope, fire weather, and other relevant factors including areas where winds have been identified by the Office of the State Fire Marshal as a major cause of wildfire spread.
The State of California and the Department of Forestry and Fire Protection make no representations or warranties regarding the accuracy of data or maps. Neither the State nor the Department shall be liable under any circumstances for any direct, special, incidental, or consequential damages with respect to any claim by any user or third party on account of, or arising from, the use of data or maps.
Gavin Newsom, Governor, State of California
Wade Crowfoot, Secretary for Natural Resources, CA Natural Resources Agency
Joe Tyler, Director/Fire Chief, CA Department of Forestry and Fire Protection
Daniel Berlant, State Fire Marshal, CA Department of Forestry and Fire Protection
Data Sources:
CAL FIRE Fire Hazard Severity Zones (FHSZSRA23_3, FHSZLRA_25_1)
CAL FIRE State Responsibility Areas (SRA25_1)
City and County boundaries as of 10/22/24 (CA Board of Equalization)

From: [redacted]
To: Sandi Sawa
Subject: Comments IRT Fanita Ranch EIR
Date: Wednesday, June 11, 2025 1:48:09 PM

Greetings,

I urge the Santee City Council to vote against approval of the Fanita Ranch Housing development. Approving residential development that is located solely within a Very High Fire Hazard Severity Zone with very limited emergency egress is irresponsible and reckless. It would put the new residents, and the residents of existing surrounding neighborhoods at increased risk in event that large scale evacuations become necessary to escape a fast approaching fire storm.

The fire evacuation plan, dated 2022, included in the latest circulated EIR appears to assume evacuation times based on best case scenarios. It does not adequately consider that the only available routes must pass through existing established neighborhood on small side streets that are not designed to handle large volumes of vehicle traffic, such as would be encountered during a mass evacuation during a fast approaching fire storm. Such a firestorm occurred during the Cedar fire in 2003, the axis of which burned through the proposed Fanita Ranch development site at a very fast rate of spread. The fire EIR does not adequately account for traffic complications during a large scale evacuation, such as a disabled vehicle incident at one of the choke points which would severely obstruct evacuating traffic flow. Blocked and impassable streets during the recent Pacific Palisades fire illustrates how such an incident is a very real risk.

The City Councils continuous attempts to circumvent court rulings and block a citizen vote on the development give the appearance that the City is working exclusively on behalf of the developer, not for the citizens who elected them, and reflects negatively on the City.

Very respectfully,

David Kramer

Santee resident

From: Eleanor Aylesworth-Warsh
To: Sandi Sawa
Subject: I am opposed to the Fanita Ranch project. Santee does not have the infrastructure for this project.
Date: Tuesday, June 10, 2025 4:04:09 PM

The site for this project is in a fire zone and will add too much traffic to Magnolia and the access to the 52 Hwy.

Eleanor Aylesworth-Warsh
Realtor
license#01365373
Balboa Real Estate, Inc.
[redacted]
Cell: [redacted]

From: GLORIA GERAK
To: Sandi Sawa; ssawa@cityofsantee.gov
Subject: Fanita Ranch Final EIR
Date: Tuesday, June 10, 2025 1:03:24 PM

S. Sawa

We fell that your response to the citizen comments in the final EIR is not adequate. We are concerned about fire mitigation as an example: the Los Angeles Fires. Should there be a fire - there is no way the Citizens can exit safely due to the traffic on Mast Blvd. Additionally, not enough attention is being given to Air Quality and Noise. As a person who lives along Mast Blvd, the sound wall were built to mitigate the increased noise and the DB's were to be lower than 60 DB during waking hours. We had meters in our yard, placed by the City and the sound was never at 60 DB - always higher. In other words, the sound walls failed from their initial installment. How will you mitigate this additional traffic noise?
ENVIRONMENTAL STATUS: A Final Recirculated Revised EIR (State Clearinghouse Number SCH#2005061118), including Second Recirculated Sections of the Final Revised EIR will be presented to the City Council for certification in compliance with the California Environmental Quality Act (CEQA). **Areas of significant and unmitigable impact that require a Statement of Overriding Considerations include Air Quality, Noise, Recreation, Transportation, and Utilities and Service Systems. T**he purpose of this notice is to give property owners in the vicinity of the subject property and other interested parties an opportunity to be informed of the proposal prior to action by the City Council. The time within which judicial review of a City Council decision must be sought is governed by Section 1094.6 of the California Code of Civil Procedure. A right to appeal a City Council decision is governed by the Code of Civil Procedure Section 1094.5. At the subject hearing any interested party may appear and be heard. The meeting will be broadcast live on public access channels 117 on Cox Cable and 99 on AT&T/U-verse, live streamed online, and recorded.

Respectfully:

Gloria Valenti Gerak
Ronald Gerak
Alexander Gerak

[redacted]
Santee, CA 92071
Office [redacted]
Mobile [redacted]

From: CPB [redacted]
Sent: Monday, June 9, 2025 8:08:56 PM
To: Sandi Sawa <SSawa@CityofSanteeCa.gov>
Subject: Fanita Ranch

> Dear Ms Sawa,
> I am against building in the Area under consideration for several reasons . Air Quality,
> Noise, Our famous Santee Lakes Recreation area will also be affected a place our
> Citizens enjoy would be destroyed by thousands of cars each day roaring bye and not to mention the danger of fires . Your own fire expert advised that the city and Home Fed hired said it would take me 2 hours to get to Mission Gorge Rd in event of a
> Fire. I have lived in Santee for 41 years and the disregard of this City Representatives
> Is alarming and they ignore our concerns for our safety . This is a working class area we drive to work and the thought of thousands of more cars trying to drive to the 52 not to
> Mention getting to West Hills High School and Sycamore School is not safe for us
> And our children . The proposed routes Fanita and Cuyamaca and Mast and your map
> Attachment shows tentative - - - - marks for Magnolia is this because the
> Representive for that area doesn’t want Magnolia involved ?
>
> Sincerely
> Janis Barnhart
> [redacted]
>
>
>
> Sent from my iPad

From: Yvonne Young
To: Sandi Sawa
Subject: Fanita Ranch Project
Date: Wednesday, June 11, 2025 8:42:40 AM

Good Afternoon,
Pushing through the Fanita Ranch project when the voters have already voted against it is ridiculous. You are not listening to the parties that elected you. You have already wasted a lot of money going against your voters. I think this is irresponsible and is going to end up costing all of Santee's residents more money for unnecessary lawsuit's.
Calling this an Essential Housing Project is just ridiculous. It's just another way to get around the will of the people. If it was really essential housing every house built would lie in the median income of all the residents of Santee. But this is not about essential housing it's all about money!!!!!!!!!!!!!
No wonder why people no longer have any belief in Government. They vote against something and the politicians disagree with the voters so they find some way to get around the voters, doesn't sound like democracy to me.
Thanks
Jeff Young
[redacted]

From: Marie Weber [redacted]
Sent: Friday, June 6, 2025 4:46:54 PM
To: Sandi Sawa <SSawa@CityofSanteeCa.gov>
Subject: Fanita Ranch

Sandi Sawa,
I have a question about the Fanita Ranch project which I would like included with the challenge to approve the development. I believe the judge ordered Santee city council to remove their past approval of this project. When I look at the Active Projects map, however, it is still listed as approved. https://www.cityofsanteeca.gov/documents/planning-building/active-projects/active-projects-map.pdf So, did council ever rescind their approval? It's clearly listed as "Approved - Not Built". The map is not old, as I see projects listed from the current year (2025). I also question how this project fits Califormia's definition of Essential Housing. It seems as though Santee City Council has created it's own definition to avoid a vote of the citizens due to the overwhelming majority against Fanita Ranch.
Sincerely,
Marie Weber

From: Mary Fujimoto
To: Sandi Sawa
Cc: Dustin Trotter; John Minto
Subject: Fanita Ranch
Date: Wednesday, June 11, 2025 8:07:21 AM

Dear City of Santee,

It is rather frustrating that Fanita Ranch continues to appear as a done deal in the City of Santee's eyes.

This project has fire risks to those residents that should buy there and traffic in the community will not be mitigated. I have not been a fan of Fanita Ranch because of those hazardous (in the case of fire - look at Paradise- look at LA (Palisades and Alta Dena) issues and traffic but could learn to accept this project if the project came to a vote to residents as was supposed to happen as a result of Prop N. However, the City has done all it could do to circumvent and obstruct a vote of residents. Frankly, myself and others should not have to continually correspond on this project because our elected officials do not want to put the project on a ballot for residents to vote on.

Please just put the Fanita Ranch project up to a vote and let the chips fall where they will. At least it would be a decision of the residents.

Thank you,

Mary Fujimoto
[redacted]

From:	Maureen Wallace
To:	Sandi Sawa
Subject:	Fanita Ranch
Date:	Tuesday, June 10, 2025 2:35:00 PM

Sandi Sawa,
My name is Maureen Wallace and I live at the end of the current Fanita Ranch on Cadwell Road. I am opposed to any further development of the Fanita Ranch area.
First, the citizens of Santee continue to vote down the expansion of Fanita Ranch. I do not understand how the mayor and our city council can continue to support Fanita Ranch expansion. Aren't they supposed to support the opinions of their citizens? Having lived here for 39 years, every time Fanita Ranch is voted down, somehow the council and Mayor manage to bring it back up. I thought once you voted something down, that ended the discussion on it.
Second, homeowners living along the hillsides in Fanita Ranch have seen their homeowners insurance continually rise. Building more homes in this area is only going to make it harder for new homeowners to afford the insurance. In the last 2 years I have stood in my yard to see smoke coming from 3 fires that were "accidentally " started from Miramar. Always during warm weather and one fire we could see the fire burning up the hillside.
I am unable to attend the meeting tomorrow night but I hope my views will be shared. I know I am one of many who share these same feelings.
Sincerely,
Maureen Walllace

-----Original Message-----
From: Mike Leathers [redacted]
Sent: Monday, June 9, 2025 4:02 PM
To: Sandi Sawa <SSawa@CityofSanteeCa.gov>
Subject: Fanita Ranch

I have lived in the City of Santee since 1964 . Went to Grade and High School here. Worked for the City for over 20 years. I have seen quite a few City Councils come and go. However I have never seen a City Council work so hard to go against the wishes of the people as this one. How many times do the people have to say no to Fanita Ranch. The city traffic is horrendous and the traffic enforcement of the Sheriff's Office has been cut over the last 10 years. We have little to no electric grid in this county, water resources are limited and you want to build more homes in a box canyon. Money from Home Fed that made it way thru Political Action Committees should not play a part in decisions to build and destroy Santee's last bit of open space. The city has NOT taken care of the infrastructure we have, we don't even have cellular service throughout Santee. Let's take care of what we have now!! No on Fanita Ranch!!!!
Sent from Mike's iPhone

From: Tina Deesen [redacted]
Sent: Saturday, June 7, 2025 5:42 PM
To: Sandi Sawa <SSawa@CityofSanteeCa.gov>
Subject: Fanita Ranch Final 2nd Recirculated Sections FREIR

Dear Director Sawa and City Council,

Please respect the Democratic process and allow the citizens of Santee to make a final vote on the project.

Even though the proposed new homes are built with fire protections in mind, the older homes like mine are not. A fire in that area puts my home, which is very close to the proposed Fanita Ranch community, at huge risk. It's only right you take that into consideration as I am a current voting Santee citizen.

We deserve our vote to be heard.

Sincerely,

Tina Deesen

From: SS DD
To: James Jeffries
Subject: Submitted Public Comments
Date: Tuesday, June 10, 2025 5:24:36 PM

Hello again. As I may not be able to attend tomorrow's meeting in person, I am requesting that the following comments are submitted both into the record, as well as distributed to each Council Member under the name "Truth", thank you.

Each comment is following each item number. There are a total of 4 separate comments (items: #2, #6, #8, #9).

If you have any questions, feel free to email me back.

Item 6: (Fanita)

Why did "…the Final Recirculated REIR [fail] to adequately Disclose the proposed project's Inconsistency with the Santee General Plan…"?

What lead to issues to begin with: "…On August 25, 2021, the City of Santee adopted Urgency Ordinance No. 592, declaring the need for an Essential Housing Program…"

What makes a Project "a Certified Essential Housing Project" versus any Other housing? Is it just because it contains a Ton of Units?

The item says: "The Density Bonus Law is to be 'interpreted liberally'…" – That's Questionable. Everything must be Specified in Law. Does Density Bonus apply to so-called Sprawl developments like this? What about to Major developments that have 3 sub-developments within like this one?

For Air Quality, it says the Fanita Ranch project:

It Conflicts with applicable Air Quality Plans… – What plans?
And there will be a Significant Increase in traffic at intersections located Outside Santee's jurisdiction, or no funding mechanism is currently available, or no feasible mitigation is available… – Which is it? And there will be an Increase in Vehicle Miles Traveled Above the calculated threshold… – Will that come back to SANDAG and their Regional Plan to Reduce VMT?"

"Under State CEQA Guidelines…, a public agency may Approve a project even though the project would cause a Significant effect on the

Environment if the agency makes a fully informed and publicly disclosed decision that there is no feasible way to lessen or avoid the significant effect…, and Specifically Identified expected benefits from the project Outweigh…Reducing or Avoiding significant environmental impacts of the project…

The proposed Resolution…[finds] that economic, legal, social, technological or other benefits, including Region-Wide benefits, of the project Outweigh the Unavoidable adverse environmental effects, rendering adverse environmental effects 'Acceptable.'" – Who is Region-Wide? – SANDAG or the State? Care to Specifically Identify the expected Benefits that Outweigh the Unavoidable adverse effects, as Required? Is the benefit the $105 million in Development Impact Fees? Is it to meet the State's RHNA Housing Quota numbers? What's the point of CEQA if Environmental Protection can be Waived?

This project will have businesses, a school (or 59 units), parks, farm, orchards and vineyards – How many?
Also a fire station – Who would build it? Who would own it?
Also a potential solar farm – Why can't that be a community farm or dog park for all of these future people?

Question: How do the Developers Not know if they need a school or not? Taking almost 30% of the land of the City – It's kind of obvious they need a school and a Whole City to meet their needs. Has anyone considered the adverse effect of adding an entire village will include Changing the Character of the neighborhood?

How does this project fit in with CalFire's new Fire Maps? Is Fire Safety another adverse effect the State is willing to Waive?

From:	Zachary Billot
To:	Sandi Sawa
Subject:	Public Comment Submission for Fanita Ranch Public Hearing
Date:	Wednesday, June 11, 2025 11:13:47 AM
Attachments:	Public Comment Fanita Ranch_06112025.docx

Hello,

Please see attached for written public comment submission for this evening public hearing on the Fanita Ranch Development. Thank you!

Sincerely,

Zach Billot (He/Him)
CA Climate Action Corps Fellow

858.273.7800

sandiegobirdalliance.org

June 11, 2025

Public Comment Fanita Ranch Development

To the Santee City Councilmembers and Mayor:

I write to express my deep concern with the revival of the Fanita Ranch Development project and urge the council to vote no for three distinct reasons:

1. Precedent setting development that disregards statutory requirements for citizen approval of new zoning through Measure N. Through the passage of this Measure, citizens must be allowed the right to vote on approval of projects if they are outside of the constraints of the General Plan. Increased capacity of this development, while baked in saving housing costs and providing affordable living, do not change the fact that the zoning should have been a consultation process. I'm concerned that habitat conserved lands seem to be a priority, but the fragmentation of this area into smaller pieces, with now more extensive trail system, and the accommodating vehicular and foot traffic, lead to serious concerns about the development and the way it should have been approved.
2. Serious habitat fragmentation that damages the livelihood and little remaining habitat for dense sage scrub animals like the Bell's Sparrow. Sycamore Canyon and the surrounding protected lands around this new development are some of the last deep coastal sage scrub habitats in the County. Numerous species, including those protected under law like the California Gnatcatcher, will be harmed by the damage to this ecosystem. Bell's Sparrow, a regional endemic also relies on these deep sage scrub habitats and with more encroachment, species like these two which DO NOT adapt well to manmade infrastructure, will be left with increasingly smaller habitats that will be even more susceptible to fire damage. Fragmentation from this development only speeds up the rate at which these species will struggle to survive in a changing world.
3. Hazardous construction into dangerous high fire risk zones. With this development, the City of Santee sets a precedent that it is willing to build housing into areas with extreme fire risk, knowing that families likely will not be able to insure and will suffer the consequences of fire damage wholly. San Diego is expected at minimum to experience equal or greater fire damage in the coming decades, and given the severity of fires in Los Angeles County, it's possible San Diego experiences something that large too. Building into this habitat, which is at extreme fire risk, regardless of the preparatory steps, is an unwise choice for the safety and security of San Diegans that will move to the area. With increased fire mitigation strategies, more land will be damaged that vulnerable species rely on.

Please consider voting no on this motion, due to the dangerous consequences of this development.

Sincerely,

Zach Billot

San Diego Bird Alliance

From: Meredith Stevenson <mstevenson@biologicaldiversity.org>
Sent: Tuesday, June 10, 2025 4:59 PM
To: Sandi Sawa <SSawa@CityofSanteeCa.gov>
Subject: Comment Letter on FREIR for Fanita Ranch

Good afternoon,
Attached please find a letter from the Center for Biological Diversity regarding the FREIR for Fanita Ranch. We will also send the letter via FedEx. The references are available here and on a flash drive we will send tomorrow. Please confirm that you received the letter and were able to download the references.

Thank you,

Meredith Stevenson
Staff Attorney
Center for Biological Diversity
574-309-5620
mstevenson@biologicaldiversity.org

June 10, 2025

Sent via email, with references via FTP and FedEx

Sandi Sawa, AICP Director of Planning & Building
Department of Development Services
City Hall, Building 4
10601 Magnolia Avenue
Santee, California 92071
Telephone: (619) 258-4100, extension 167
Email: ssawa@cityofsanteeca.gov

Re: Second Recirculated Sections of the Final Revised Environmental Impact Report for Fanita Ranch, SCH# 2005061118

Dear Ms. Sawa:

This letter is submitted on behalf of the Center for Biological Diversity (the "Center") regarding the Second Recirculated Final Revised Environmental Impact Report ("2025 FREIR") for Fanita Ranch (the "Project") (State Clearinghouse No. 2005061118). This FREIR is the latest environmental document prepared pursuant to the California Environmental Quality Act ("CEQA"), intended to address the deficiencies the San Diego County Superior Court noted in the 2022 First Recirculated REIR for the Project ("2022 REIR").

The Center is a non-profit, public interest environmental organization dedicated to the protection of native species and their habitats through science, policy, and environmental law. The Center has over 1.7 million members and online activists throughout California and the United States. The Center has worked for many years to protect imperiled plants and wildlife, open space, air and water quality, and overall quality of life for people in Santee and throughout San Diego County.

I. The 2025 FREIR Still Lacks an Adequate Analysis of the Project's Impacts Relating to Wildfire and Emergency Evacuation.

CalFire's updated 2025 maps and the FREIR confirm that a Very High FHSZ now covers the entire Project site (Cal Fire, 2025), yet the FREIR fails to adequately assess the Project's wildfire ignition and public safety risks and adopt feasible mitigation measures to reduce or avoid the Project's fire safety impacts. Among other things, the City failed to fully consider new information from the recent Eaton and Palisades Fires (LA Fires), which indicates an increased likelihood that the Project will increase ignition risk and pose safety risks to residents.

As stated in the Center's prior comments, the Project site has historically been extremely susceptible to wildfire. As the 2022 REIR acknowledges, "wildfire has occurred and would likely occur in the Project vicinity again." (2022 REIR, EIR Appendix P-1.) The Project fire map further indicates that virtually the entire Project site has been burned at least once, with the vast majority having burned numerous times. (*Id*., Figure 5.) Additionally, the High FHSZ landscapes surrounding the Project area further increase the site's wildfire risk. (Cal Fire, 2025.)

Given the extremely high risk of wildfire in the area, and the past history of repeated burnings at the Project site, it remains critical that the City prepare a revised EIR that adequately discloses and analyzes the Project's wildfire impacts in light of the recent LA Fires under similar conditions, as well as difficulties in evacuation during those fires.

A. The FREIR Fails to Acknowledge or Adequately Analyze the Increase in Fire Risk Resulting from the Project in Light of the Recent LA Fires.

The FREIR remains deficient because it fails to acknowledge or adequately analyze conditions on the Project site similar to the conditions that contributed to the 2025 LA Fires. CEQA requires a revised EIR or subsequent EIR when significant new information indicates (1) "[a] new significant environmental impact would result from the project"; or (2) "[a] substantial increase in the severity of an environmental impact would result unless mitigation measures are adopted that reduce the impact to a level of insignificance." (Pub. Res. Code § 21166; CEQA Guidelines § 15088.5(a); CEQA Guidelines, § 15162(a)(2), (a)(3)(A), (B).) But here, the FREIR dismisses pertinent new information from the LA Fires because the Los Angeles wildfires occurred 150 miles from the City with "different fuel types, weather, and terrain." (2025 FREIR at 1-9.)

This conclusion is unsupported. As explained in prior comments, the Project site has similar fire conditions to those that gave rise to the 2025 Eaton and Palisades Fires. For example, chaparral, one of the most widespread vegetation communities on the Project site, fueled both the Eaton and Palisades fires and poses a similar threat on the Project site. (McKenzie, 2025; 2020 DREIR at 4.3-6.) Specifically, chamise is prominent in both the Santa Monica Mountains where the Palisades Fire began and on the Project site. (2020 DREIR at 4.3-6; Bland, 2025.) Additionally, similar weather poses a risk, as the Santa Ana winds that fueled the Los Angeles Fires threaten to fuel fires at the Project site. (2022 REIR at 4.18-15; Laskowski, 2025.) And terrain also bears similarities: the Project site encompasses "steep topography that can facilitate fire spread" (2022 REIR at 4.18-15), while the steep slopes, canyons and valleys along the Santa Monica and San Gabriel Mountains added to dangerous fire conditions and contributed to the LA Fires' severity. (Top 20, 2025; Graff, 2025.)

B. The FREIR Improperly Relies on Project Features to Avoid Assessing Relevant New Information.

Instead of analyzing the significance of these similar conditions, the FREIR relies on project features to keep wildfire ignition risks below the significance threshold. Specifically, the FREIR emphasizes that the Project is "a new, master-planned, and ignition-resistant community" that utilizes project features such as "fuel modification zones, fire-hardened structures, code-compliant access, fire flow and hydrants, automatic interior fire sprinklers, flying ember protections, and ongoing maintenance, among others." (2025 FREIR at 1-9.) The FREIR explains that the Project's features render the Project so different than the LA Fire communities that the FREIR need not consider new information from the LA Fires. (2025 FREIR at 1-9.) This is incorrect for several reasons.

<u>First</u>, longstanding case law provides that substituting mitigating design features for impact analysis violates CEQA. (*People ex rel. Bonta v. County of Lake* (2024) 105 Cal.App.5th 1222, 1234 [county could not avoid analyzing wildfire risk and effectiveness of measures to reduce wildfire risk reduction by deeming them "design features"]; *Lotus v. Department of Transportation* (2014) 223 Cal.App.4th 645, 658 ["The failure of the EIR to separately identify and analyze the significance of the impacts . . . before proposing mitigation measures . . . precludes both identification of potential environmental consequences arising from the project and also thoughtful analysis of the sufficiency of measures to mitigate"]; *San Joaquin Raptor Rescue Center v. County of Merced* (2007) 149 Cal.App.4th 645, 663 ["A mitigation measure cannot be used as a

device to avoid disclosing project impacts"].) This makes sense, considering an EIR must first inform the public and decisionmakers of a project's significant impacts, and *then* propose mitigation measures and project features to eliminate them, supported by substantial evidence. In other words, relying on project features to mitigate potential impacts of fast-moving fires like the recent LA Fires does not eliminate the requirement to first analyze the significance of the potential impacts.

The FREIR touts the Orchard Hills development, in Irvine, CA as an example of how Fanita Ranch's project features will perform in a wildfire. (2025 FREIR at 1-9.) However, unlike this Project, Orchard Hills includes nearly 200-foot fuel modification zones, fire walls to protect the development from embers, and perimeter roads in consideration of Santa Ana wind direction. (Flemming, 2025.) As a result, the FREIR fails to provide adequate support for its conclusion that this Project will perform the same as Orchard Hills.

<u>Second</u>, even if effective, the project features do not address other reasonably foreseeable impacts of a fire similar to the recent LA Fires on the Project site. Fires, especially the hotter and longer-burning variety that have overtaken California in recent decades, can prove disastrous for plant and animal life. If native habitat fire regimes are disrupted, the habitats they provide can become degraded. (Keeley 2005; Keeley 2006.) When fires occur too frequently, type conversion occurs, and 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; Keeley 2006; Syphard et al. 2009.) Wildfires can have a long-lasting negative effect on habitat, and can impair animals' movement (Jennings 2018), mating ability, foraging, and reproductive success. (See Syphard et al. 2007 ["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."].) This could have serious consequences for special-status species in the project area such as mountain lions (Blakey et al., 2022; Jennings, 2018), whose populations are already struggling in much of the state due to lack of connectivity and genetic isolation. (Benson et al., 2019; Gustafson et al., 2021.) As a result, the City must take into account new information on the LA Fires' impacts on biological resources and mitigate accordingly.

<u>Third</u>, the project features do not address the evacuation concerns the Center raised in prior comments. The FREIR claims that new information on evacuation difficulties from the LA Fires is irrelevant due to several project features that were not

present in all LA Fire evacuation zones: automatic sprinkler systems (Appendix U at 3), on-site sheltering, primary and secondary access points (Appendix U at 2), and less vulnerable structures. (Appendix U at 4.) However, while potentially helpful, these project features do not consider or address older residents' unwillingness to evacuate the LA Fires, their difficulties due to physical constraints, logistical challenges for older residents, immediate health risks to older evacuees, and new information regarding health risks of wildfire smoke. (See Center DREIR Comments at 7-11.) Instead, to address these concerns, the FREIR offers only reassurances that "for Fanita Ranch, there *could be* evacuation, or temporary relocation into other parts of the community or into Santee with a short duration." (Appendix U at 4 [emphasis added].) Appendix U also suggests that "transportation or other special requirements can be provided during an emergency evacuation"; however, this is not required. (Appendix P2 at 21 [stating that "[t]ransportation should be accessible to all populations, including people with disabilities and other access and functional needs" not that it *must*].)

The FREIR also fails to address the Center's concerns regarding new information on impacts from smoke inhalation and particularly its impact on older residents. Appendix U states only: "Regarding smoke-related health issues, wildfires occurring in and around Fanita Ranch would be short duration as the fuels burned and the fire was driven around the project, further downwind." (Appendix U at 4.) However, even short periods of smoke inhalation can impact residents' health and is associated with increased risk of exacerbation of pre-existing respiratory and cardiovascular disease, as well as premature mortality. (Melton, 2023.) A revised EIR must take into account new information on smoke inhalation and mitigate accordingly.

The FREIR also fails to adequately address the Center's concerns regarding evacuation alerts. Instead, Appendix U incorrectly states that Emergency Alerts of evacuation areas in Santee requires a "layered approach," including wireless emergency alerts (text/email), Alert San Diego (Reverse 911), Television, Radio, social media, and in the field law enforcement and fire personnel. (Appendix U at 3.) As noted in prior comments, the Project's Wildland Fire Evacuation Plan relies only on text message/email alerts and does *not* require other methods that likely saved many residents during the Los Angeles fires such as police cruisers and helicopters with blowhorns, door-to-door notifications, television notifications, and changeable message signs. (2022 REIR, Appendix P2 at 9.) Considering new information from the LA Fires, electronic notifications are not sufficient: not only are they prone to error, but they also may not be suited to the Project's older population, which is less likely to receive disaster warnings

(Melton, 2023) and may lack access to critical internet communications to monitor fire conditions, preparedness, and evacuation notices. (Center DREIR Comments at 7-8; Melton, 2023; Lin, 2025; Lee et al., 2021; Courtin & Knapp, 2017.)

In short, a project built in a location known to have very high or high wildfire risk cannot compensate for wildfire hazards simply through a fire-resistant design. Because the FREIR fails to acknowledge significant wildfire impacts based on new information, the FREIR also fails to mitigate them to reduce these impacts. The public—including future residents of the Project and existing residents nearby—have a right to know the full extent of the Project's impacts on wildfire ignition and evacuation. "Omission of material necessary to informed decision-making and informed public participation is prejudicial." (*Sierra Club v. County of Fresno*, (2018) 6 Cal.5th 502, 515.)

II. Conclusion

Thank you for the opportunity to submit comments on the 2025 FREIR for Fanita Ranch. We urge the City to prepare a new EIR for the Project that fully complies with CEQA and recirculate the revised EIR. Because significant new information has become available, the City must reevaluate and incorporate this information, as well as new research and studies on the Project's impacts that have become available in the last few years.

Given the possibility that the Center will be required to pursue legal remedies in order to ensure that the City complies with its legal obligations including those arising under CEQA, we would like to remind the City of its statutory duty to maintain and preserve all documents and communications that may constitute part of the "administrative record" of this proceeding. (§ 21167.6(e); *Golden Door Properties, LLC v. Superior Court* (2020) 53 Cal.App.5th 733, 762.) The administrative record encompasses any and all documents and communications that relate to any and all actions taken by the City with respect to the Project, and includes "pretty much everything that ever came near a proposed [project] or [] the agency's compliance with CEQA . . . ." (*County of Orange v. Superior Court* (2003) 113 Cal.App.4th 1, 8.) The administrative record further includes all correspondence, emails, and text messages sent to or received by the City's representatives or employees, that relate to the Project, including any correspondence, emails, and text messages sent between the City's representatives or employees and the Applicant's representatives or employees. Maintenance and preservation of the administrative record requires that, *inter alia*, the City (1) suspend all data destruction policies; and (2) preserve all relevant hardware unless an exact replica of each file is made.

Please add the Center to your notice list for all future updates to the Project and do not hesitate to contact the Center with any questions at the email listed below.

Sincerely,

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Extinction vortex dynamics of top predators isolated by urbanization

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Abstract. Extinction risk is elevated in small, isolated populations due to demographic and genetic interactions. Therefore, it is critical to model these processes realistically in population viability analyses (PVA) to inform local management and contribute to a greater understanding of mechanisms within the extinction vortex. We conducted PVA's for two small mountain lion populations isolated by urbanization in southern California to predict population growth, extinction probability, and loss of genetic diversity with empirical data. Specifically, we (1) provide the first PVA for isolated mountain lions in the Santa Ana Mountains (SAM) that considers both demographic and genetic risk factors and (2) test the hypothesis that variation in abundance and mortality between the SAM and Santa Monica Mountains (SMM) result in differences in population growth, loss of heterozygosity, and extinction probability. Our models predicted 16–21% probability of local extinction in the SAM due purely to demographic processes over 50 yr with current low levels or no immigration. Our models also predicted that genetic diversity will further erode in the SAM such that concern regarding inbreeding depression is warranted unless gene flow is increased, and that if inbreeding depression occurs, rapid local extinction will be highly likely. Dynamics of the two populations were broadly similar, but they also exhibited differences driven by larger population size and higher mortality in the SAM. Density-independent scenarios predicted a rapidly increasing population in the SMM, whereas growth potential did not differ from a stable trend in the SAM. Demographic extinction probability and loss of heterozygosity were greater in the SMM for density-dependent scenarios without immigration. However, higher levels of immigration had stronger, positive influences on both demographic viability and retention of genetic diversity in the SMM driven by lower abundance and higher adult survival. Our results elucidate demographic and genetic threats to small populations within the extinction vortex, and how these vary relative to demographic structure. Importantly, simulating seemingly attainable increases in connectivity was sufficient to greatly reduce extinction probability. Our work highlights that conservation of large carnivores is achievable within urbanized landscapes, but requires land protection, connectivity, and strategies to promote coexistence with humans.

Key words: demographic stochasticity; extinction; heterozygosity; inbreeding; mortality; population viability analysis; Puma concolor; *urbanization.*

Introduction

Demographic and genetic processes, and interactions between them, influence probability of extinction for small, isolated populations (Saccheri et al. 1998, O'Grady et al. 2006). Specifically, deterministic stressors, demographic and environmental stochasticity, and inbreeding depression can all contribute to increased extinction probability (Mills and Smouse 1994, Beissinger et al. 2008). However, the relative influence of these processes in different wildlife populations remains difficult to predict and empirical demonstrations are rare (Palomares et al. 2012, Wootton and Pfister 2013). The predicted decline to extinction of small populations from these interacting processes is referred to as the extinction vortex (Gilpin and Soulé 1986). Modeling dynamics of small, isolated populations provides critical information to local conservation efforts and also

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contributes to a more general understanding of the forces influencing extinction.

All populations with small numbers of breeding individuals are likely to be destabilized by demographic stochasticity (Lande 1993, Morris and Doak 2002) and are also the most likely to suffer from inbreeding depression (Mills and Smouse 1994). However, variation in local environmental conditions, and resulting differences in demographic structure, can influence population growth, the rate at which genetic diversity is lost, and extinction probability (Stacey and Taper 1992, Reed 2005). Prior to the onset of inbreeding depression, some small populations continue to exhibit strong survival and reproduction (Benson et al. 2016a), while others suffer from poor demographic performance due to ongoing deterministic stressors (Caughley 1994). Comparing dynamics of isolated populations of the same species but of varying abundance, and with different vital rates and associated deterministic stressors, will increase our understanding of demographic and genetic processes of small populations.

Mountain lions (*Puma concolor*) exist at low density, have female-biased sex ratios, and often exhibit highly skewed male reproductive success (Johnson et al. 2010, Riley et al. 2014). These traits reduce effective population size (Mills and Smouse 1994) and have made mountain lions important study species for investigating small population dynamics (Johnson et al. 2010, Benson et al. 2016a). Indeed, one of the clearest demonstrations of inbreeding depression driving a population to the brink of extinction was with endangered Florida panthers (a subspecies of mountain lions, *Puma concolor coryi*; Johnson et al. 2010). Panthers exhibited reduced fitness from inbreeding depression and declined to fewer than 30 individuals; however, extinction was avoided and the population rapidly increased following genetic restoration (Johnson et al. 2010).

Small, isolated populations of mountain lions have also persisted within the highly urbanized landscape of southern California in the Santa Monica Mountains (SMM) and Santa Ana Mountains (SAM) northwest and southeast of Los Angeles. These two populations exhibit the lowest genetic diversity documented for the species aside from Florida panthers (Ernest et al. 2014, Riley et al. 2014). Recently, a population viability analysis (PVA) indicated that mountain lions in the SMM population exhibited strong survival and reproduction and predicted generally stable population growth for the next 50 yr (Benson et al. 2016a). However, this PVA also predicted potential for extinction due purely to demographic factors, as well as rapid loss of genetic diversity that raised concern about inbreeding depression (Benson et al. 2016a). An earlier PVA for mountain lions occupying the SAM indicated that the population was demographically unstable and that additional habitat loss would lead to a high risk of extinction (Beier 1993). This PVA explicitly considered the influence of corridors and habitat loss on extinction probability due to demographic processes, but ignored potential effects of inbreeding depression. Furthermore, most of the demographic rates came from the literature rather than from empirical data collected within the SAM (Beier 1993). Given the isolation and low genetic diversity documented for this population (Ernest et al. 2014, Gustafson et al. 2017), as well as additional fragmentation of the available habitat that has occurred (Burdett et al. 2010), an updated PVA constructed with empirical genetic and demographic data is needed for mountain lions in the SAM to evaluate the influence of interactions between genetics, demography, and landscape connectivity in this heavily human-dominated landscape.

The SMM and SAM are both occupied by small populations of mountain lions in similar habitats isolated by anthropogenic barriers and exhibiting low levels of genetic diversity (Ernest et al. 2014, Riley et al. 2014). However, there are notable differences in demographic structure of the two populations that could have consequences for population dynamics and viability. First, the estimated number of breeding adults in the SAM was approximately twice that estimated for the SMMs (Beier 1993, Ernest et al. 2014, Riley et al. 2014, Benson et al. 2016a). Differences in abundance were clearly related to the smaller patch of available habitat within the SMM relative to the SAM (Beier 1993, Benson et al. 2016a). Importantly, smaller population and habitat island size are strong predictors of reduced genetic diversity (Frankham 1995). Second, survival rate of radiocollared adult mountain lions in the SAM, where the main cause of death was collisions with vehicles, was lower than other unhunted populations (Vickers et al. 2015). In contrast, adult survival in the SMM was as high or higher than most unhunted populations and the main cause of death was intraspecific strife (Riley et al. 2014, Benson et al. 2016a). This could have important implications because mountain lion population growth is most strongly influenced by adult female survival (Lambert et al. 2006, Benson et al. 2016a). Thus, comparing the dynamics of these populations will inform conservation efforts and provide empirical insight into the influence of variation in demographic structure (i.e., abundance and survival rate) on the relative influence of demographic and genetic processes, and how they interact to influence extinction risk. Such research would represent an important case study for understanding the dynamics of isolated populations and provide insight into management strategies for maintaining viable populations of top predators within human-dominated landscapes.

We used the individual-based population model of Benson et al. (2016a) parametrized with empirical demographic and genetic data collected during long-term studies of mountain lions in our focal populations to model dynamics and viability. We constructed starting populations with empirical, multi-locus genotypes that reflected the age, sex, and genetic structure of the current populations and projected models forward to estimate stochastic population growth, extinction probability, and measures of genetic diversity over the next 50 yr. We used these model projections to address multiple questions regarding the viability of populations of top predators in isolated mountain ranges within highly urbanized landscapes. First, we investigated the dynamics and viability of mountain lions in the SAM to evaluate the influence of demographic and genetic processes on probability of extinction. Second, we hypothesized that variation in population abundance and mortality patterns in small, isolated mountain lion populations would result in differences in population growth, the rate of loss of genetic diversity, and extinction probability. We predicted that reduced adult survival would result in lower population growth and greater extinction probability due purely to demographic processes (P1a). We also tested the alternative prediction that the greater number of breeding adults and carrying capacity in the SAM would offset the lower survival and result in similar growth and extinction probability between the two populations (P1b). Next, we predicted that genetic diversity would erode more quickly in the SMM population given the smaller number of individuals and smaller amount of available habitat (P2). Finally, we predicted that reductions in vital rates due to inbreeding depression would result in high probability of extinction for both populations (P3). We provide the first PVA for mountain lions in the SAM that explicitly models both demographic and genetic processes. More broadly, our results elucidate how variation in abundance, carrying capacity, vital rates, and sources of mortality influence mechanisms underlying the extinction vortex for isolated populations in fragmented landscapes. Thus, our work provides a case study that will help to inform conservation of isolated wildlife populations in human-dominated landscapes.

Materials and Methods

Study area

We studied mountain lions in two isolated mountain lion populations occupying mountain ranges southeast (SAM: Orange, Riverside, and San Diego Counties) and northwest (SMM: Los Angeles and Ventura Counties; Fig. 1) of the city of Los Angeles. The SAM population

Fig. 1. Greater Los Angeles, southern California, USA showing the location of the Santa Monica (blue polygon) and Santa Ana (red polygon) Mountains within which we studied population dynamics of mountain lions. Also shown are other nearby mountain ranges, major (white lines) and more minor (gray lines) roads, and areas where natural habitat has been replaced by urbanization (dark gray) and agriculture (lighter gray).

inhabited approximately 1,533 km^2 in the SAM, a portion of the Peninsular Ranges including federal, state, county, and private lands. The SMM population inhabited approximately 600 km^2 in the Santa Monica Mountains, part of the Santa Monica Mountains National Recreation Area, a unit of the National Park Service that included an assemblage of federal, state, and privately owned lands. The areas occupied by both populations were bordered by a combination of anthropogenic (freeways, development, agriculture) and natural (Pacific Ocean) barriers that have drastically restricted movement of mountain lions between the populations and surrounding areas. Both were characterized by a Mediterranean climate, with cool, wet winters and hot, dry summers. Vegetation consisted mainly of mixed chaparral, coastal sage scrub, oak woodlands and savannahs, riparian woodlands, and nonnative annual grasslands. Mountain lions were the only remaining large carnivore and the only wild ungulates were mule deer (*Odocoileus hemionus*). Both study areas have been described extensively elsewhere (Burdett et al. 2010, Riley et al. 2014, Vickers et al. 2015, Benson et al. 2016b).

Capture and monitoring

We captured mountain lions using Aldrich foot-snares or cable restraints, baited cage-traps, or by treeing them with trained hounds. We deployed global positioning system (GPS) or very high frequency (VHF) radio-collars on adult and subadult mountain lions. In the SMM, we also captured 3–5 week old kittens at natal dens by hand and implanted VHF transmitters in their peritoneal cavities (Moriarty et al. 2012). We monitored survival and determined causes of mortality of radio-instrumented mountain lions as described previously (Beier and Barrett 1993, Vickers et al. 2015, Benson et al. 2016a). We monitored reproduction of all collared females in the SMM using GPS telemetry to locate natal dens and count kittens (Moriarty et al. 2012). In the SAM, all capture and handling was conducted 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). In the SMM, animal capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee under protocol PWR_SAMO_Riley_M-t.Lion_2014.A3.

Genotyping

We genotyped all captured mountain lions at 44 (SAM) or 54 (SMM) microsatellite loci using laboratory methods and markers described previously (Ernest et al. 2014, Riley et al. 2014). Briefly, we extracted DNA from blood or tissue using DNeasy Blood & Tissue Kit (QUIAGEN, Valencia, California, USA). The loci used for genotyping mountain lions in both populations conformed to expectations for Hardy-Weinberg and linkage equilibria (Ernest et al. 2014, Riley et al. 2014). We used many of the same genotypes analyzed by Ernest et al. (2014) and Riley et al. (2014) to parameterize our model but also included genotypes from mountain lions captured more recently. We also genotyped mountain lions from samples obtained from areas adjacent to our focal populations to simulate immigration in our models.

Demographic parameters

We separated mountain lions into three age classes for parameter estimation. Kittens were dependent offspring with their mother (0–14 months), subadults were independent animals prior to reproduction (females, 14–25 months; males, 14–42 months), and adults were breeding animals (females, >25 months; males, >42 months; Benson et al. 2016a). We estimated sex and age-class specific survival rates using the Kaplan-Meier estimator generalized for staggered entry (Pollock et al. 1989) implemented in R version 3.1.3 (R Development Core Team 2015) with the package “survival”. We estimated survival for adults and subadults separately for the SMM and SAM using empirical data from each population. We used survival data collected during 1987–1993 (Beier and Barrett 1993) and 2003–2016 (Vickers et al. 2015; T. W. Vickers et al., *unpublished data*) for the SAM, and during 2002–2015 for the SMM (Riley et al. 2014, Benson et al. 2016a). Females in the model bred in the first month after reaching adulthood and again following loss or independence of kittens, consistent with documentation in our field study (Benson et al. 2016a). We estimated the probability of females having two, three, or four kittens in a litter based on the proportion of these litter sizes documented in the SMM during 2004–2017 (all input demographic parameters are shown in Appendix S1: Table S1). Although the samples sizes used to estimate demographic parameters were relatively small numerically, they should be representative given the small size of the populations.

Model overview

We used the individual-based population model for mountain lions of Benson et al. (2016a) that incorporated demographic and environmental stochasticity, as well as a simple form of density dependence. We did not have data to understand the influence of catastrophes on vital rates of mountain lions in these populations, so our model assumes these unpredictable events do not occur during our projections. We began models with starting populations of individuals that reflected the sex, age, and genetic structure of the populations and projected the models forward to estimate the demographic and genetic structure of future populations. In the SAM, we combined information from published estimates of population density and available habitat, as well as information from our ongoing 15-yr field study to assemble the starting population. Beier and Barrett (1993) and Beier (1993) estimated 2,070 km^2 of available habitat for the SAM population. We adjusted this estimate by subtracting 506 km^2 to remove the Chino Hills that are now isolated from the SAM by highway 91 and no longer occupied by mountain lions (Fig. 1). We further reduced the available habitat by 2% to reflect habitat loss during 1993–2017 based on estimates of Burdett et al. (2010). Thus, our estimate of available habitat for mountain lions in the SAMs was 1,533 km^2. Beier and Barrett (1993) estimated mountain lion density to be 0.7 females and 0.35 males/100 km^2. We applied estimates of mountain lion density (0.7 females and 0.35 males/100 km^2; Beier and Barrett 1993) to our habitat area estimate, which yielded 11 adult females and 5 adult males. We also included 9 kittens and 4 subadults. Although we did not formally estimate population density in our study, the abundance:habitat area ratios we used from Beier and Barrett (1993) agreed with observations made using telemetry, genetic analysis, and camera trapping during our intensive 15-yr study. We assigned empirical genotypes at 44 loci to all starting individuals in the SAM. The starting population for the SMM population was 15 mountain lions (including 5 adult females and 2 adult males) with empirical genotypes at 54 loci as described by Benson et al. (2016a).

We ran simulations consisting of 5,000 population projections of 50 yr unless noted otherwise. Although researchers sometimes attempt to predict extinction probability farther into the future (e.g., 100 yr), we followed the recommendation of Morris and Doak (2002:452) to avoid projecting population viability far into the future because of the increased uncertainty of predictions made over longer time periods. The population dynamics simulated by the model were a reflection of individual-based demographic processes specified by empirical probability distributions estimated with data collected in both populations. We imposed mortality (survival senescence) on all mountain lions of both sexes in the model that reached 15 yr of age (Benson et al. 2016a). We incorporated density dependence by imposing a maximum number of adult, breeding males (SMM, n = 2; SAM, n = 5) and females (SMM, n = 6; SAM, n = 11) that could exist in the population at any given time. For the SMM, we felt confident that our estimates were the maximum numbers of breeding individuals that could occupy the available habitat. The greater area and size of the SAM population contributed to uncertainty in our carrying capacity estimates; thus, we also explored an alternate scenario with a greater carrying capacity of 7 adult males and 14 adult females. For all scenarios, when all the adult slots of a given sex were occupied, we eliminated individuals of that sex that would have otherwise transitioned from sub-adults to adults. This process simulated density-dependent population regulation through death or dispersal. Although the upper limits for adult males and females were fixed, the number of adults varied stochastically during model projections due to variation in survival and reproduction. When breeding occurred within the model, we assigned genotypes to resulting offspring based on principles of Mendelian genetics (i.e. 1 allele randomly inherited from each parent at each loci). Additional details of the model and submodels are provided by Benson et al. (2016a).

Submodels

Survival.—We incorporated environmental and demographic stochasticity into age-class-specific survival rates as in Benson et al. (2016a). Specifically, we generated environmentally stochastic monthly survival probabilities by transforming survival rates and their standard deviations estimated from each study population into beta shape parameters using the betaval function in the R package popbio. At each monthly time step, we drew a random survival value from this beta distribution, which was used as the environmentally stochastic survival probability for all individuals of the same sex and age class during that time step. We then assessed demographically stochastic survival of each individual using a Bernoulli trial with the monthly survival probability as the threshold between survival and mortality.

Reproduction.—We designated reproductive males and females in the starting population and, thereafter, randomly selected breeding animals from subadults eligible to transition to adults when openings became available. Female age at first reproduction varied stochastically between 25 and 33 months in our model. Males reaching breeding status remained reproductive until death. If no adult males were present in our simulated populations, males were allowed to begin breeding at 36 months as the reason for delayed breeding in males is presumably due to social constraints imposed by dominant adult males. Breeding females were eligible to become pregnant until death whenever they did not have dependent offspring. Litter size varied stochastically by generating a random, uniform value between 0 and 1 for each reproductive female and comparing the value to a cumulative probability distribution for litter sizes we documented. We determined the sex of each offspring using a Bernoulli trial with a probability of 0.5.

Immigration.—We assigned a fixed annual immigration rate prior to starting a simulation. We transformed this into a monthly probability and assessed immigration stochastically using Bernoulli trials during each monthly time step. We restricted immigration to subadult males. Subadult males are more likely to disperse and to undertake longer and riskier dispersal events than females (Sweanor et al. 2000). Indeed, all immigration documented into the SMM and SAM populations has involved subadult males (Riley et al. 2014, Gustafson et al. 2017). We assigned genotypes to immigrants from mountain lions genotyped in adjacent areas north and east of the SMMs (n = 18) and east of the SAM (n = 83). We modeled different immigration scenarios ranging from no immigration to a rate of one immigrant per year for our main analyses. We also modeled immigration rates for both populations based on immigration observed with radio-tracking and genetic analysis of mountain lions within and adjacent to our focal populations. Specifically, we observed two immigrants in 15 yr in the SMM (Riley et al. 2014; S. Riley et al., *unpublished data*) and three immigrants in 15 yr in the SAM (Gustafson et al. 2017). We were conservative with respect to modeling how much additional immigration could occur in our main analyses so we limited these to 1 immigrant per year. However, we also conducted additional scenarios to explore the hypothetical influence of two immigrants per year. For additional details of all submodels see Benson et al. (2016a).

Model outputs

Demography and extinction.—We estimated λ_t (Lambda [population growth] at time t) as N_t/N_{t-1}, where N_t is total population size at time t. We estimated λ_s (stochastic lambda) across time periods of interest with the formula:

$$\frac{[\sum^{N_{\text{years}}} \ln(\lambda_t)]}{N_{\text{years}}}$$

We report median λ_s from the distribution of values across all projections for simulations of interest. We estimated credible intervals for λ_s using the highest posterior density (HPD) derived using the R package coda (v. 0.17-1). We estimated probability of extinction as the proportion of projections that went extinct during a given simulation and derived estimates of variability by conducting a nonparametric bootstrapping procedure implemented in the R package boot (v. 1.3-17). We ran 1,000 bootstraps of 5,000 population projections to estimate uncertainty regarding extinction probability with 95% HPD intervals. We estimated the effective population size based on a census of the breeding animals in simulated populations using the formula: $N_e = (4 \times N_{BF} \times N_{BM})/(N_{BF} + N_{BM})$ (Crow and Kimura 1970), where N_e is the effective population size, N_{BF} is the number of breeding females, and N_{BM} is the number of breeding males.

Genetic parameters.—We estimated measures of genetic diversity from genotypes of mountain lions in populations simulated by our models 1–50 yr in the future using mean values across all projections. Specifically, we estimated expected (H_e) and observed (H_o) heterozygosity, individual inbreeding coefficient (F_{is}), the mean number of alleles per loci (N_A), and the proportion of polymorphic loci using the R package adegenet v. 2.0.0. Our genetic predictions varied stochastically because they were realistically linked to the stochastic demographic processes we modeled. Thus, by running 5,000 projections for each scenario, our models captured considerable environmental, demographic, and genetic stochasticity.

Elasticity analysis.—We investigated proportional sensitivity (elasticity) of λ_s to small (5%) increases in vital rates (Morris and Doak 2002). We conducted these analyses with the density-independent model to investigate which demographic parameters had the greatest influence on λ_s in the absence of density-dependent limitations. We calculated sensitivity values (S) for each demographic parameter:

$$S = \frac{\text{Log}\lambda_s(\text{increased}) - \text{Log}\lambda_s(\text{original})}{\text{parameter}(\text{increased}) - \text{parameter}(\text{original})}$$

and elasticity (E) for each demographic parameter following Morris and Doak (2002):

$$E = S \times \left(\frac{\text{parameter}_{\text{original}}}{\text{parameter}_{\text{adjusted}}}\right).$$

Inbreeding depression.—We simulated inbreeding depression by running population projections with input parameters reduced to reflect proportional changes in age- and sex-specific survival rates documented between inbred and outbred Florida panthers following the genetic restoration program (Hostetler et al. 2010, Benson et al. 2011; see Appendix S2: Table S1).

Results

Population viability in Santa Ana Mountains

Density-dependent simulations predicted stable median stochastic population growth over the next 50 yr in the SAM, regardless of the level of immigration (Table 1). However, there was an 11–21% probability of extinction across all immigration scenarios in the density-dependent simulations, inversely related to the level of immigration (Table 1, Fig. 2). The scenarios without immigration, or with the low level observed in our study, resulted in substantial loss of genetic diversity (e.g., 28–49% of expected heterozygosity) over 50 yr (Fig. 3; Appendix S3, S4). Predicted loss of heterozygosity decreased with higher levels of immigration, and heterozygosity was largely maintained with one immigrant per year (Fig. 3; Appendix S3: Table S1, Appendix S4: Fig. S1). Other measures of genetic diversity including percent polymorphism, inbreeding coefficient, and the number of alleles per loci responded to varying degrees of isolation and immigration similarly over time (Appendix S3: Table S1). When we explored the influence of a larger carrying capacity in the SAM (7 adult males and 14 adult females), population growth

Table 1. Demographic results predicted by individual-based population model for mountain lions in the Santa Ana and Santa Monica Mountain, Southern California, USA.

	No immigration		Observed immigration		1 immigrant/2 yr		1 immigrant/1 yr	
Parameter	Estimate	95% HPD†	Estimate	95% HPD†	Estimate	95% HPD†	Estimate	95% HPD†
Santa Anas								
λ_s‡	1.00	0.89, 1.01	1.00	0.95, 1.01	1.01	0.93, 1.02	1.01	0.95, 1.02
Extinction probability	0.22	0.20, 0.23	0.16	0.15, 0.17	0.11	0.10, 0.11	0.08	0.07, 0.09
Time to extinction (yr)	31	12, 50	31	11, 50	33	13, 50	33	13, 50
Adults (n)§	8	0, 11	9	0, 15	9	0, 15	10	0, 15
N_E§	6	0, 11	6	0, 12	6	0, 12	7	3, 14
Santa Monicas								
λ_s‡	1.00	0.89, 1.02	1.01	0.93, 1.02	1.01	0.98, 1.02	1.01	1.00, 1.02
Extinction probability	0.29	0.28, 0.30	0.16	0.15, 0.17	0.04	0.04, 0.05	0.02	0.01, 0.02
Time to extinction (yr)	31	13, 50	31	13, 49	33	12, 50	32	11, 48
Adults (n)§	5	0, 8	5	0, 8	6	0, 8	7	4, 8
N_E§	4	0, 6	4	0, 6	4	0, 6	5	3, 6

Notes: Estimates are median or mean estimates at year 50 based on 5,000 population projections.
HPD, highest posterior density; λ_s, stochastic population growth.
† 95% highest posterior density credible intervals.
‡ Median value.
§ Effective population size (mean value).

rate was similar (λ_s = 1.01 [0.92, 1.02], but extinction probability was reduced (10% with observed level of immigration; Appendix S5: Table S1). All immigration scenarios with higher carrying capacity yielded lower probability of extinction, ranging from 12% with no immigration to 5% with one immigrant per year (Appendix S5: Table S1). Loss of genetic diversity slowed slightly and effective population size increased with greater carrying capacity, although diversity still declined substantially with no immigration or the observed level (Appendix S5: Table S2). Simulating inbreeding depression in the SAM by reducing age-specific survival rates proportional to reductions documented in inbred Florida panthers, resulted in rapidly declining population growth (λ_s = 0.84, [0.61, 0.96]), 100% probability of extinction over fifty years, and median time to extinction of 11.7 yr (5.2, 23.5; Fig. 4).

Comparing dynamics of SAM and SMM

Median stochastic population growth rate predicted by the density-dependent scenarios was similarly stable in the two populations (Table 1, Fig. 2). However, the density-dependent scenarios for both populations also predicted extinction probabilities of 16–28% over 50 yr with no or observed immigration (Table 1, Fig. 2). Extinction probability due purely to demographic processes was reduced for both populations with higher levels of immigration, but more so for the SMM (Table 1, Fig. 2). Density-independent scenarios predicted a rapidly increasing population in the SMM (λ_s = 1.17 [1.11, 1.22]), whereas the predicted trend in the SAM did not differ from stable (λ_s = 1.06 [0.89, 1.12]; Fig. 5). Sensitivity and elasticity analysis showed that adult female survival had the strongest influence on density-independent population growth in both populations (Appendix S6: Table S1). Female subadult survival, female kitten survival, and litter size had moderate influence on population growth for both populations, whereas male survival parameters had little influence (Appendix S6: Table S1). When we explored the influence of two immigrants per year, extinction probability was further reduced and genetic diversity increased beyond the starting values in 50 yr (Appendix S7: Tables S1, S2).

Genetic diversity declined rapidly in both populations with no or observed immigration (Fig. 3; Appendix S3, S4). No immigration resulted in a greater loss of genetic diversity for SMM (57% loss expected heterozygosity) compared with SAM (49% loss; Fig. 3; Appendix S3, S4). However, the SMM population responded more strongly to increased levels of immigration as with one immigrant every 1–2 yr, the SMM retained more of its genetic diversity over 50 yr relative to the SAM (Fig. 3; Appendix S3, S4). Similar to the SAM, simulating inbreeding depression in the SMM resulted in predictions of declining population growth (λ_s = 0.89, [0.75, 0.96]), high probability of extinction (>99%) over 50 yr, and rapid median time to extinction (15.1 yr; Fig. 4).

Discussion

Our modeling predicted a 16–21% probability of local extinction for mountain lions in the SAM over the next 50 yr with the low level of immigration observed in our study or no immigration. Thus, demographic and environmental stochasticity leave the SAM population vulnerable to extinction even before considering inbreeding depression, consistent with earlier predictions for this population (Beier 1993). Furthermore, our results

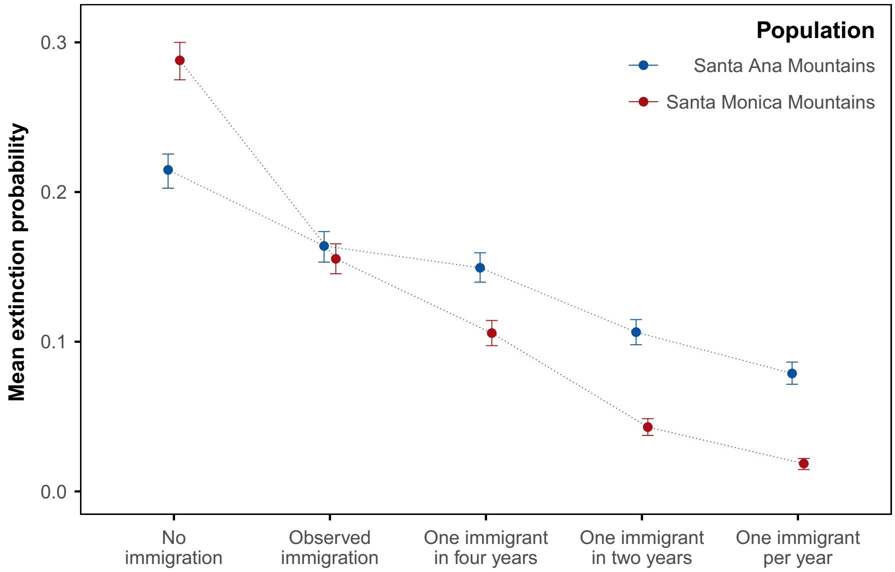

FIG. 2. Estimated extinction probability (without considering potential inbreeding effects) in 50 yr for mountain lion populations in the Santa Ana and Santa Monica Mountains from an individual-based population model based on 5,000 projections and varying levels of immigration.

suggest that, unless gene flow is increased, genetic diversity will rapidly erode in the SAM, and that, if inbreeding depression occurs rapidly, local extinction will be highly likely. We acknowledge that it is impossible to predict exactly when inbreeding depression will occur in a wild population, but our predictions with respect to genetic diversity are alarming and far surpass proportional losses of heterozygosity suggested by previous researchers to warrant concern regarding inbreeding depression (e.g., 5–10% loss in 100 yr; Soulé et al. 1986, Allendorf and Ryman 2002). Importantly, our predictions suggest that the loss of genetic diversity in SAM mountain lions in the next 50 yr will approach proportional losses experienced in another population of the same species (Florida panthers) that nearly went extinct due to poor demographic performance associated with inbreeding depression (Johnson et al. 2010; Appendix S4). Simulating a higher carrying capacity of 7 adult males and 14 adult females resulted in reduced extinction probability and slowed the loss of heterozygosity, highlighting benefits of even small increases in additional habitat and number of breeding adults (Frankham 1995). However, even with higher carrying capacity and abundance, the model predicted a 10% probability of extinction and 24% loss of expected heterozygosity over 50 yr.

Dynamics of the SAM and SMM populations were broadly similar, but our simulations revealed differences in their dynamics caused by variation in deterministic stressors, survival rates, and population abundance. The density-independent scenarios provided partial support for our prediction that lower survival in the SAM would negatively influence growth rate (P1a). Clearly, density independence is unrealistic given the space limitations experienced by both populations; however, these scenarios were instructive to compare growth potential and dynamics. Density-independent models predicted a rapidly increasing population for the SMM, whereas density-independent λ_s in the SAM did not differ significantly from a stable trend. Extinction probability was approximately three times greater (5.6%) in the SAM compared to the SMM (1.8%) in the absence of density dependence. Furthermore, in our density-dependent scenarios, higher levels of immigration (1–2 per year) in the SMM raised the credible interval of λ_s above 1, predicting a slightly increasing trend, whereas credible intervals overlapped 1 for all predictions of λ_s in the SAM, even with similarly high levels of immigration (Table 1; Appendix S7: Tables S1, S2). Clearly, realized population growth is limited by available habitat in both populations, but growth potential also appears to be limited by high human-caused mortality in the SAM. The leading cause of death for radiocollared mountain lions in the SAM was vehicle strikes, which did not differ in frequency by age or sex class, and resulted in high mortality of adults (Vickers et al. 2015). Although poor adult male survival had relatively little influence on density-dependent population growth, it influenced extinction probability by causing male extinction in some simulations for this small population with a female-biased adult sex ratio. These dynamics appear to be realistic as there was evidence of occasional male extinction in the SAM during previous research (Beier 1993). Conversely, adult survival of both sexes was high in the SMM where population growth appears to be mainly limited by the lack of additional habitat. Subadults survive poorly in the SMM due to the difficulty of successfully

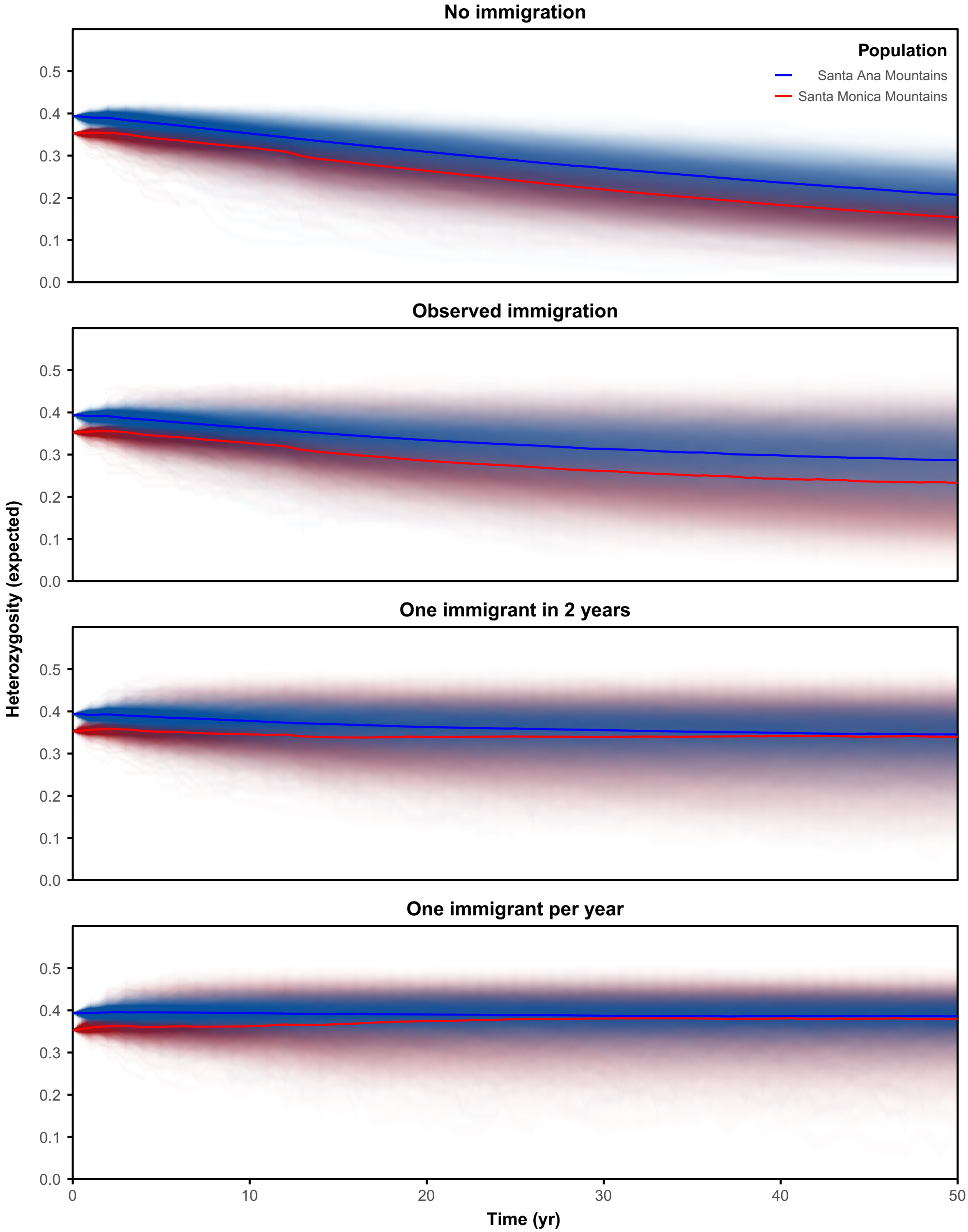

FIG. 3. Estimated expected heterozygosity over 50 yr for mountain lion populations in the Santa Ana and Santa Monica Mountains from and individual-based population model based on 5,000 projections and varying levels of immigration.

dispersing, as many young animals are killed by breeding males or hit by vehicles before or during dispersal (Riley et al. 2014). The difficulty of dispersal, combined with high survivalof breeding adults in a space-limited population provides few opportunities for mountain lions born in the SMM to breed.

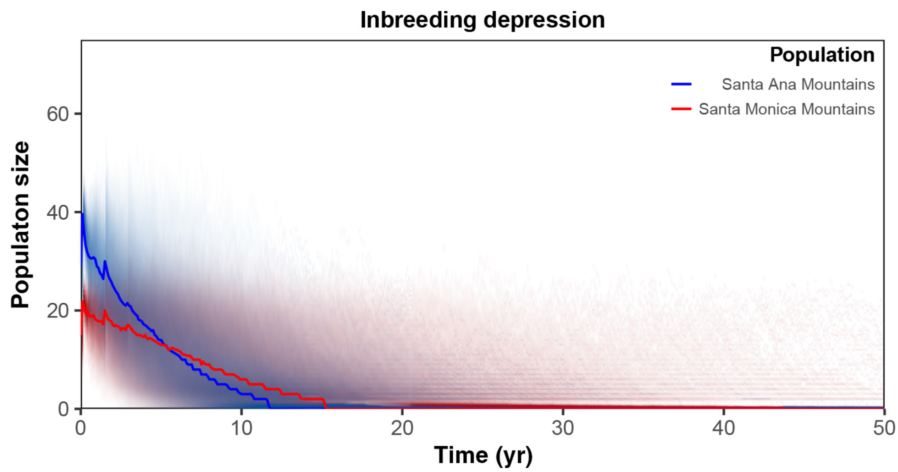

FIG. 4. Density-dependent demographic projections from individual-based population model showing predicted population sizes for mountain lions in the Santa Ana and Santa Monica Mountains over 50 yr based on 5,000 projections when we simulated inbreeding depression with the observed level of immigration.

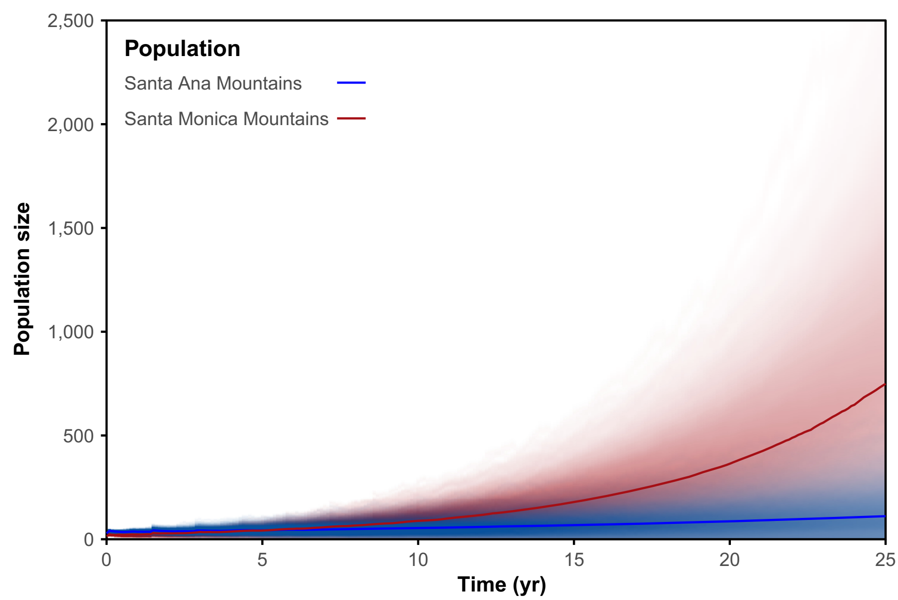

FIG. 5. Density-independent demographic projections from individual-based population model showing predicted mountain lion population size in the Santa Ana and Santa Monica Mountains over 25 yr based on 5,000 projections.

The SMM population had a slightly higher probability of extinction with no immigration than the SAM in our density-dependent scenarios, but increasing immigration resulted in a more pronounced reduction in extinction probability for the SMM. In fact, with one immigrant per year, extinction probability in the SMM did not differ from that predicted by the density-independent model suggesting that increased connectivity could largely mitigate the effects of isolation and limited habitat in the SMM, at least with respect to demographic extinction risk. The lesser positive impact of immigration on demographic extinction probability in the SAM was likely associated with the lower survival of adult males, which meant that tenure of immigrants successfully establishing as breeding adults was often short-lived. Although these comparisons were useful for evaluating the influence of variation in demographic structure on the dynamics of small populations, we recommend cautious interpretation of these differences for practical purposes. Indeed, predictions regarding extinction probability from PVA are probably best viewed as relative assessments (Morris and Doak 2002).

The greatest long-term threat to both populations appears to be the rapid loss of genetic diversity associated with their isolation from mountain lions in surrounding areas. With no immigration, the predicted rate of loss of expected heterozygosity over 50 yr was greater for the smaller SMM population relative to the SAM population. This provided support for our prediction (P2) and is consistent with theoretical and empirical work indicating that population abundance and habitat island size are strong, positive predictors of genetic diversity (Crow and Kimura 1970, Frankham 1995). However, with immigration rates observed during the last 15 yr, predicted loss of heterozygosity was similar in the two populations. Importantly, simulating increased immigration and gene flow had a stronger positive influence on heterozygosity in the smaller SMM population. Thus, although heterozygosity is lost more rapidly in smaller populations, immigration events can also more quickly reverse these losses and restore diversity. In the SMM, only one or two males generally breed at any one time, such that when a radiocollared male immigrant entered the population in 2009 and began breeding it resulted in a rapid increase in population-level genetic diversity (Riley et al. 2014). A single breeding immigrant also positively influenced genetic diversity in the SAM (Gustafson et al. 2017), and relatively few immigrants have similarly influenced small populations of other large mammals (Vilà et al. 2003, Hogg et al. 2006, Adams et al. 2011). However, the key to maintaining diversity in small populations is to ensure that immigration occurs consistently (Mills and Allendorf 1996), to prevent reversal of short-term diversity gains as immigrants begin breeding with their offspring (Riley et al. 2014, Benson et al. 2016a). In addition to the larger population size, lower adult survival likely contributed to a reduced positive influence of immigration on genetic diversity in the SAM by limiting the reproductive success of immigrants. This finding further highlights the link between demographic and genetic factors in terms of influencing extinction in small populations. Despite interesting differences, we stress that our models predict rapid loss of diversity in both populations, indicating that viability will likely be compromised by interactions between genetics and demography unless gene flow is increased.

Mountain lions are not endangered in southern California and genetically diverse populations of mountain lions exist in areas such as the Sierra Nevada Mountains and other mountain ranges in southern California (Ernest et al. 2014, Riley et al. 2014). However, there is value to conserving viable populations of a native top predator within the SAM and SMM to maintain stable predator–prey dynamics and naturally functioning ecosystems within these isolated mountain ranges. This contention echoes growing recognition among ecologists and managers that conservation efforts should prioritize ecological function and maintaining ecosystem processes across extensive geographic areas, rather than simply preserving minimum viable populations somewhere across the range of a species (Soulé et al. 2003, Ritchie et al. 2012). Predators and other highly interactive species may be especially important to conserve in as many places as feasible to maintain important species interactions and ecosystem functions (Soulé et al. 2003, Lindenmayer et al. 2008, Cadotte et al. 2011). Indeed, research from around the world has begun to highlight the potential for conserving large predators within human-dominated landscapes (Athreya et al. 2013, Chapron et al. 2014, Riley et al. 2014). Our work suggests that conserving mountain lions in isolated mountain ranges in greater Los Angeles is feasible with relatively modest increases in landscape connectivity. If achieved over the long-term, this would be an important step toward maintaining intact, functioning ecosystems in these mountain ranges that lie within one of the most human-impacted landscapes in the world.

Our results suggest mitigation strategies for mountain lions in SAM and SMM should target two main threats: isolation and mortality. Increasing connectivity between both populations and the areas across the freeways should (1) decrease extinction probability due purely to demographic processes, and (2) maintain genetic diversity and prevent the onset of inbreeding depression. Translocation of outbred animals can be effective to quickly increase genetic diversity in threatened mountain lion populations (Johnson et al. 2010), but strategically located highway crossing structures (Gloyne and Clevenger 2001) allowing for dispersal and gene flow could be a more comprehensive long-term strategy. Our results suggest that maintaining genetic diversity in these populations would require at least one migrant every 1–2 yr. Given the expense of erecting highway crossing structures, translocation would certainly be a less expensive strategy, especially in the short-term. Indeed, the estimated cost for a bridge to connect the SMM population with habitat north of the 101 Freeway (Fig. 1) is approximately US$60 million. However, our results indicate that animals would need to be translocated frequently and indefinitely if connectivity is not improved, whereas a highway crossing structure would provide long-term connectivity once erected. Furthermore, populations of other species are also isolated by the freeways and other barriers surrounding these habitat islands (Delaney et al. 2010, Riley et al. 2006). Thus, construction of highway crossing structures, although unquestionably an expensive initial investment, would likely provide regular, consistent immigration of mountain lions and many other species that should increase the likelihood of maintaining healthy populations and intact ecosystems within these isolated mountain ranges. However, we certainly do not discount the value of translocation as a management tool. Translocation may be an especially valuable option if proposed development further degrades or prevents improvement of currently available passageways, and if the significant financial challenges delay construction of new crossing structures. As a specific example, extensive residential and resort development projects have been proposed for construction in the primary corridor area that has facilitated some movement of mountain lions between the SAM and habitat east of the

Interstate Highway 15 (Gustafson et al. 2017). Our results show that further reduction in immigration and gene flow, which are likely to occur with new development in corridor areas, would increase demographic extinction probability and hasten the loss of genetic diversity.

Our sensitivity analyses and inbreeding simulations show that increased mortality could have rapid, negative consequences for population growth and extinction probability in both populations, supporting our prediction (P3). Despite the smaller population size, predicted demographic extinction probability in the SMM was generally similar to that in SAM under the current levels of immigration largely because of the strong growth potential afforded by higher adult female survival. If female mortality increases in future years from the multitude of mortality agents documented in the SMMs (e.g., aggression from males, vehicle strikes, rodenticide poisoning) this could destabilize the population and increase extinction probability. Thus, reducing mortality in both populations is important and should decrease probability of extinction due to environmental and demographic stochasticity. In addition to highway crossing structures, exclusionary fencing strategically implemented along roadways where mountain lions are killed can be effective at reducing mortality (Foster and Humphrey 1995), such as that recently constructed along SR 241 in the SAM (Vickers et al. 2015). Strategies to promote best practices for housing domestic animals could reduce mortality from depredation permits issued to kill mountain lions threatening livestock (Vickers et al. 2015). To reduce mortality in the SAM and SMM from depredation mortality, the California Department of Fish and Wildlife (CDFW) has recently changed policies regarding depredation permit issuance in these two populations such that non-lethal deterrence methods must be attempted before lethal removal can occur (CDFW 2017).

Differences in demographic structure between the two populations revealed important aspects that have contributed to their persistence and highlighted management priorities for both populations. The greater demographic vigor of the SMM population is critical to its persistence, as a population with six to eight adults would clearly be at much higher risk of local extinction if survival and reproduction declined. Thus, in addition to management efforts to reduce mortality from documented causes such as vehicle strikes and rodenticide (Riley et al. 2014), it would be prudent to evaluate and monitor population dynamics of their main prey (mule deer) in the SMM to ensure the prey base remains adequate to support strong survival and reproduction. Greater population abundance in the SAM reduced demographic extinction probability and slowed the erosion of genetic diversity in simulations without immigration. Thus, the larger population size is beneficial to the persistence of mountain lions in the SAM, especially during periods when no immigration occurs. If additional habitat loss or fragmentation reduced the number of breeding adults that could occupy the SAM, this would have negative consequences for both demographic extinction risk and loss of genetic diversity. For instance, a population as small as the SMM population, but with the poor survival of the SAM would have a higher probability of extinction than we documented for either population. As noted above (see *Model overview*), both habitat loss and isolation appear to have reduced the population size over the last 25 yr. Our model results suggest it is critical to ensure that future habitat loss in the SAM is prevented and that fragmentation does not isolate portions of the current population.

Although our model realistically models demographic and genetic processes in these small populations with empirical data, we acknowledge that our model and data have limitations. For instance, although we were able to account for demographic and genetic processes, density dependence, and varying levels of immigration, we did not have sufficient data to understand the influence of catastrophes on the vital rates and viability of these populations. Two unpredictable forces that could potentially cause catastrophes include wildfires and disease outbreaks. Wildfires have become larger and more frequent in southern California shrubland ecosystems, and increasingly destructive wildfires appear to be linked to expansion of the urban–wildland interface (Keeley et al. 1999). Wildfires have directly caused mortality of mountain lions within our study populations (Vickers et al. 2015) and can also temporarily displace mountain lions (Jennings et al. 2016; S. P. D. Riley and J. A. Sikich *unpublished data*). Previous research on Iberian lynx (*Lynx pardinus*) has noted the potential that outbreaks of disease such as feline leukemia and reduced immune response associated with low genetic diversity could negatively affect population viability (Millán et al. 2009, Palomares et al. 2012). We note that catastrophic mortality associated with wildfires, disease, or other unpredictable events could substantially increase extinction probability above the predictions generated by our model.

Our results demonstrate that small populations isolated by freeways and urbanization are subjected to elevated extinction risk due to interactions between demography and genetics. We agree with previous authors that demographic and genetic risk factors for small populations should not be considered in isolation (Mills and Smouse 1994, Soulé and Mills 1998) and that both must be addressed in any comprehensive wildlife conservation strategy within urbanized landscapes (Benson et al. 2016a). Indeed, other small, isolated populations of felids are threatened by a combination of limited habitat and mortality, such as the highly endangered Iberian lynx (Ferreras et al. 2001). Inbreeding depression and extinction vortex dynamics are also concerns for Iberian lynx, and their conservation will require restoring habitat and improving demographic parameters (Palomares et al. 2012). As urbanization increases globally, it will be necessary to (1) protect habitat patches large enough to facilitate persistence of populations of large carnivores, (2) mitigate anthropogenic deterministic stressors, and (3) restore and maintain connectivity within and between habitat patches if we are to maintain populations and ecosystem processes (e.g., predator–prey interactions) within urban landscapes (Crooks 2002). Our results also show that relatively small changes in abundance and key demographic parameters can influence loss of genetic diversity as well as extinction probability due to non-genetic processes. The difficulty of conserving top predators in the modern world are well documented (Woodroffe 2000, Ripple et al. 2014) and our work further details the demographic and genetic challenges facing large carnivores in human-dominated landscapes. Yet our results also provide reason for optimism, as seemingly realistic increases in gene flow appear sufficient to substantially reduce probability of extinction of top predators due to combined demographic and genetic threats within the second largest metropolitan area in the United States. Long-term conservation of mountain lions in greater Los Angeles would provide compelling evidence that large carnivores and abundant human populations are compatible, even within the most intensely developed landscapes.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1868/full

Data Availability

Data are available on Zenodo: https://doi.org/10.5281/zenodo.2548917

Report

Current Biology

Mountain lions avoid burned areas and increase risky behavior after wildfire in a fragmented urban landscape

Highlights

- After the wildfire, mountain lions avoided burned areas and increased risky behavior
- Post-fire risky behavior included increased road crossings and daytime activity
- Altered movement and space use post-fire increased risk of intraspecific conflict
- Risky behavior may increase mortality risk for animals in urban fire-prone regions

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In brief

When wildfires and urbanization coincide, animals trade off risks of burned landscapes with those of anthropogenic environments. Blakey et al. find that after an exceptionally large wildfire in an urbanized region, mountain lions avoided burned areas and increased activities that elevated their risk of negative interactions with humans and conspecifics.

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Report

Mountain lions avoid burned areas and increase risky behavior after wildfire in a fragmented urban landscape

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SUMMARY

Urban environments are high risk areas for large carnivores, where anthropogenic disturbances can reduce fitness and increase mortality risk.[1] When catastrophic events like large wildfires occur, trade-offs between acquiring resources and avoiding risks of the urban environment are intensified. This landscape context could lead to an increase in risk-taking behavior by carnivores if burned areas do not allow them to meet their energetic needs, potentially leading to human-wildlife conflict.[2,3] We studied mountain lion behavior using GPS location and accelerometer data from 17 individuals tracked before and after a large wildfire (the 2018 Woolsey Fire) within a highly urbanized area (Los Angeles, California, USA). After the wildfire, mountain lions avoided burned areas and increased behaviors associated with anthropogenic risk, including more frequent road and freeway crossings (mean crossings increased from 3 to 5 per month) and greater activity during the daytime (means from increased 10% to 16% of daytime active), a time when they are most likely to encounter humans. Mountain lions also increased their amount of space used, distance traveled (mean distances increased from 250 to 390 km per month), and intrasexual overlap, potentially putting them at risk of intraspecific conflict. Joint pressures from urbanization and severe wildfire, alongside resulting risk-taking, could thus increase mortality and extinction risk for populations already suffering from low genetic diversity, necessitating increased connectivity in fire-prone areas.

RESULTS

Direct effects of wildfire on mountain lions

Direct and immediate effects of wildfire on mountain lions can include injury and mortality. Of the 11 individual mountain lions being tracked at the time of the Woolsey Fire that had the potential to be affected by it, two died or were presumed to have died during or soon after the fire.

Do mountain lions avoid burned areas after a large wildfire?

At the population level, mountain lions avoided burned areas after the wildfire (Figures 1 and 2) and no individual animal showed significant selection for them. Males avoided burned areas more than females, as indicated by their generally larger and more negative effect sizes (Figure 1). Proportions of locations within burned areas compared before and after the fire showed the same trend as selection analyses (Table S1), specifically, much lower proportions of locations in burned areas post-fire. Excluding the two males that had less than 10% of their pre-fire locations within the burn perimeter (P56 and P61, Table S1), all 3 males showed strong and significant avoidance (effect size −0.63 to −1.45). The response of females to the fire was more variable (Figure 1). The post-fire burned area use that did occur was concentrated (61%) in the patchily burned region in the southeast corner of the outer burn perimeter, and within the Simi Hills (north of the US-101 freeway) where the majority of the landscape (66%) burned (Figure 2).

Do mountain lions increase behaviors that put them at anthropogenic risk after a large wildfire?

While there was support for mountain lions increasing use of urban areas after the wildfire, the magnitude of this increase was negligible (Figure 3A). The probability of urban use was low before the fire (∼4.3%), and while this increased after the fire, it remained low (∼5.4%); this 1% change was much lower than

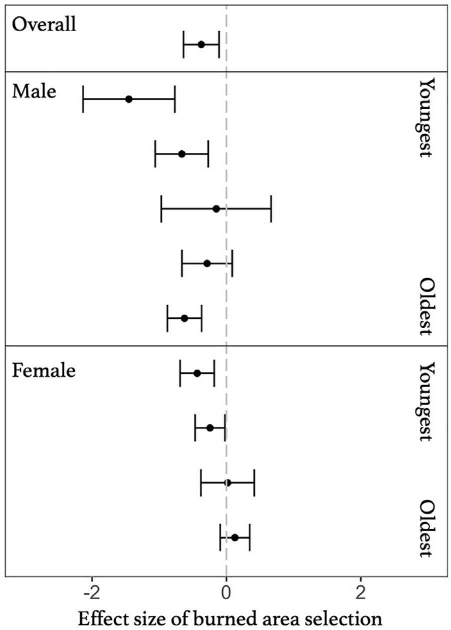

Figure 1. Results of resource selection analysis for burned areas after the fire by the 9 individual mountain lions who were tracked both before and after the fire

The two individuals assumed to have perished during or soon after the fire were excluded. Each point shows the effect size comparing selection for burned areas before and after the fire using step selection functions, for each individual mountain lion. The overall effect size was calculated using a meta-analytic approach and all error bars show 95% confidence intervals. Negative effect sizes indicate selection against burned areas while positive effect sizes indicate selection for burned areas following fire.

See also Table S1.

the range of variability in proportion of urban use by mountain lions across the population (0%–15%) (Table S2). Regardless of fire, mountain lions used urban areas rarely (mean for study animals was 5% of the time, including time periods before and after the fire) and use of urban areas was variable among individuals ranging from one female who used urban areas less than 1% of the time to two females who used urban areas > 10% of the time. All sex and age classes were variable in urban area use.

Consistent with our predictions, mountain lions tended to increase road crossings after the wildfire, with the fitted relationship indicating an increase from ~3 crossings per month before the fire to ~5 crossings per month 15 months after the fire (Figure 3B). Mountain lions also increased their daytime activity after the fire from 10% of the day to 16% of the day, although the continuous response model indicated a potential slight increase prior to the wildfire event (Figure 3C). Our analysis pooled all major road crossings (major roads shown in Figure 4), though mortality risk (both perceived and actual) is likely to vary with the size and traffic volume of roads. California has the busiest roads in the USA and the busiest interstate in any USA city runs through our study area (I-405).[4] The first successful crossing of the I-405 freeway over the 16 years of the broader study was recorded in the months after the fire; comparing crossing frequencies of the busy US-101 freeway, we observed roughly one crossing every 2 years before the fire, compared to one crossing every 4 months after the fire.

Do mountain lions increase behaviors that could increase the risk of conflict with conspecifics after a large wildfire?

Mountain lions increased both their distance traveled and the amount of space used after the fire (Figures 3D and 3E). Distance travelled increased from ~250 ± 48 (predicted 95 % confidence interval [CI]) km per month to ~ 390 ± 48 km per month, a more than 50% increase from pre-fire distances. Although adult males either decreased or retained similar amount of space used after the fire, subadult males and all females, the groups most at risk in intraspecific encounters, increased their amount of space used by ~15%–24%. Results of the age-sex class analyses should be interpreted cautiously due to the low number of individuals per class and wide confidence intervals (Figure 3E and Table S3).

Where analyzed, trends towards increases in spatial overlap in mountain lion landscape use after the fire did not perform better than the null model (Table S4), potentially due to the relatively low sample size and the confounding factor of two males perishing in the fire and an additional three males perishing of anticoagulant rodenticide poisoning and vehicular collision during the 15 months post-fire. However, we saw a trend towards an increase in spatial overlap after the fire between the dominant male and other males in the study area after the fire (Figure 4). Additionally, mean observed overlap was greater for all age-sex classes after the fire across all iterations of the model validation expressed as a proportion of male and female home ranges, though this difference was negligible for male-female overlap (Figure S1). Specifically, important components of intrasexual overlap in this territorial species more than doubled: overlap of the dominant male on other males increased from 10% to 23% post-fire (Figure 4C) and overlap between females increased from 7% to 18% post-fire (Figure S1).

DISCUSSION

In an urban landscape after the wildfire, we found support for the prediction that mountain lions avoided burned areas post-fire, and increased behavior that could expose them to risk. Changes in behavior by mountain lions post-fire are likely due to a complex trade-off balancing the necessity to acquire food and breed, while avoiding conspecific conflict and encounters with humans in a transformed and fragmented landscape. These kinds of trade-offs between anthropogenic disturbances and other major disturbance events are an increasing reality for carnivores persisting in human-dominated landscapes worldwide.[5–7]

Carnivores have varying responses to fire, and this is likely to be strongly influenced by how fire changes the structure of vegetation, and with it, the ability to capture prey.[8,9] In the case of cursorial carnivores, such as wolves and coyotes, fire may increase their abilities to capture prey.[10,11] Whereas ambush predators such as mountain lions, lynx, and African lions may require more heterogeneity, including retained vegetation cover, in post-fire landscapes in order to successfully stalk prey.[12–15] The mountain lions in our study mostly avoided burned areas in the 15 months after the fire. This contrasted with studies that indicate opportunistic use of burned landscapes by carnivores,[7,16,17] but was consistent with Eby et al.,[13] who found that despite abundant prey in burned areas, African lions (*Panthera leo*) avoided the burned landscape, likely due to reduced

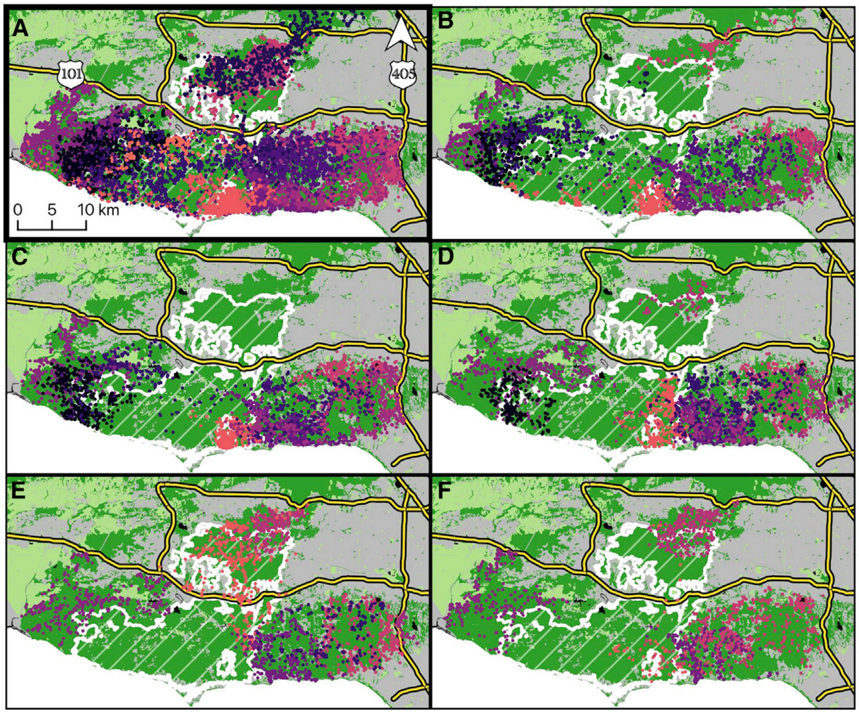

Figure 2. Study area within the Los Angeles and Ventura County areas of California, USA, showing locations of 17 individual mountain lions in periods before and after the 2018 Woolsey Fire

The study area includes the Santa Monica Mountains (south of the 101 freeway) and Simi Hills (north of the 101 freeway).

(A–F) Locations of 17 individual mountain lions studied within the periods from 15 months prior the fire (A) and 15 months after the fire (B)–(F) (in 3-month intervals) are shown in different colors for each individual. Time periods shown include 15 months pre-fire to time of fire (A); time of fire to 3 months post-fire (B); 3–6 months post-fire (C); 6–9 months post-fire (D); 9–12 months post-fire (E); and 12–15 months post-fire (F). Of the 17 individuals, 12 were tracked both pre- and post-fire (though of these, 1 individual was suspected to have perished in the fire and 1 individual died soon after) and 5 individuals were tracked only after the fire (Figure S3). Land use is shown by dark green (natural areas), light green (altered open areas) and gray (urban areas). The area burned by the Woolsey Fire (2018) is shown in white outline with white hatching. Freeways are shown in yellow.
See also Table S1.

cover decreasing ambush hunting success. In the Santa Monica Mountains, the most intensive use of burned areas in our study occurred in areas surrounding a patchily burned area in the southeastern part of the outer burn perimeter of the Woolsey Fire (Figure 3), an area that was more heterogeneously burned and that included some sizable unburned patches. Use of these areas could be due to hunting advantages and prey availability in landscapes where burned areas are patchy, and near the edges of burns.[14,18] We did not account for differences in burn severity across the landscape, which can be an important predictor of wildlife post-fire habitat use, because fires within Southern Californian shrubby vegetation tend to burn with uniformly high-intensity, stand-replacing fire.[19] Our findings are overall consistent with the reduction in predator-prey interactions for ambush predators after the fire proposed by Doherty et al. [9], and the need to find suitable habitat to capture prey is likely one of the drivers of the risk-taking behaviors we observed.[2]

There is extensive evidence globally that large carnivores avoid areas of high human footprint (areas of relatively greater human population and infrastructural development) in space and time.[20,21] Our study indicated that even after a considerable disturbance that transformed the structure of over half the landscape used by the resident population, urban areas remained a strong deterrent. However, mountain lions did increase their exposure to anthropogenic risk by increasing road and freeway crossings and by increasing activity during the day when human activity is greatest. Human killings of mountain lions (in response to depredation of livestock) may be more likely in areas of intermediate housing density than in more urban areas,[22] and vehicle strikes are also a very high cause of mountain lion mortality[23] in this population. Therefore, mountain lions in our study area may be experiencing an assessment risk-response mismatch, whereby the animals' assessment of risk does not accurately reflect mortality risk.[24]

Reduction of suitable habitat after fire has the potential to result in greater risk of intraspecific conflict in carnivore populations within urban environments, where dispersal is constrained by multiple barriers. Though carnivore home ranges tend to be smaller and population densities higher in urban areas,[25] during the study period, the population we studied presented a relatively extreme example, given that the Santa Monica Mountains, south of the 101 freeway, were being used by at least eight males (most being subadults), though its size is the equivalent of 1 to 2 home ranges for adult males.[26,27] In this context, multiple behavioral changes by the mountain lions in our study, including a 50% increase in distance traveled, use of 15%–24% larger areas by females and subadults, and a trend towards greater intrasexual overlap, have the potential to increase the risk of intraspecific conflict, especially between males. In our study area, intraspecific conflict, specifically being killed by an adult male, is the biggest cause of mortality for subadult mountain lions, and adult males have also been recorded to kill adult females and kittens, including their own offspring and past mates.[23,26] Intraspecific conflict (fatal or otherwise) is likely to be exacerbated in urban areas where barriers prevent subadults from dispersing into new territories.[23,26,28] Therefore, after a severe wildfire, when space available for hunting and moving within cover is reduced, animals must trade-off energetic demand with perceived risk of encountering adult males, weighing behaviors that put them at greater risk of conflict against greater flexibility in space use and, potentially, diet.[29]

The increases in amount of space used and distance traveled that we observed could be influenced by multiple factors. A severe wildfire like the Woolsey Fire could allow mountain lions to move more efficiently by removing dense cover in the landscape and

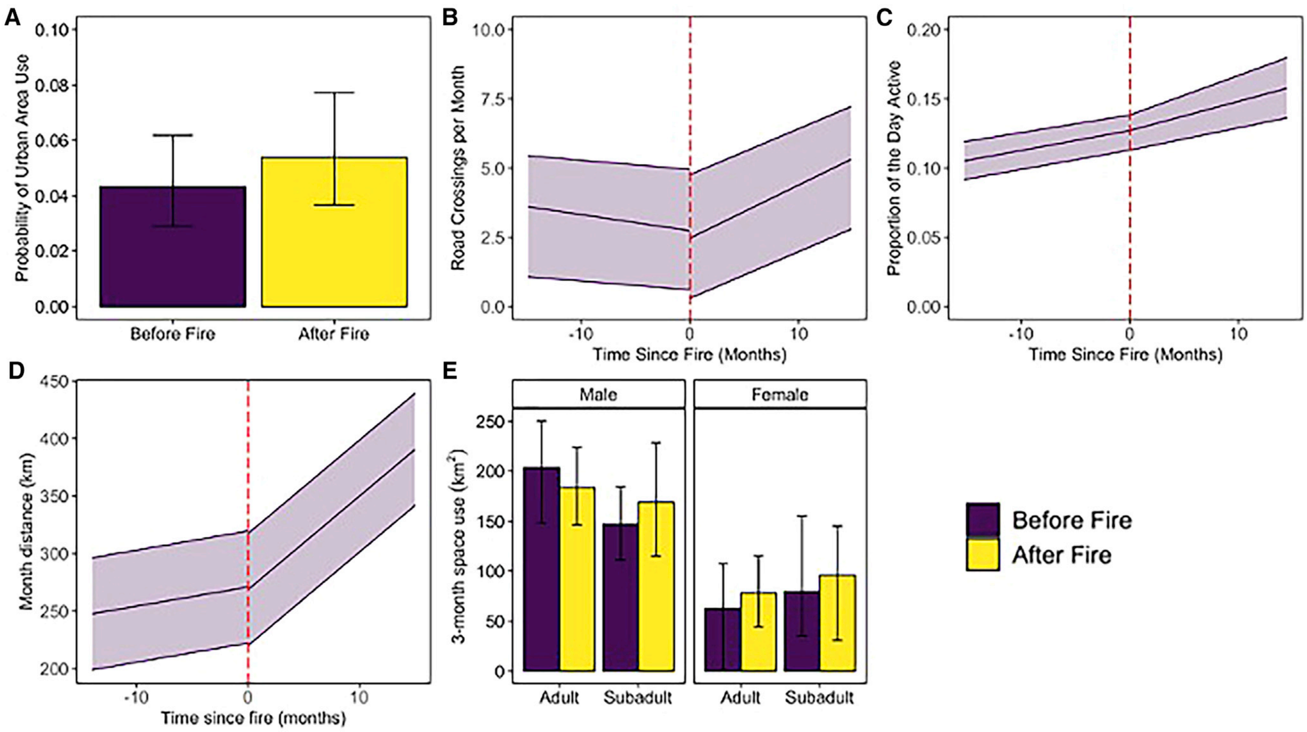

Figure 3. Predicted changes in risky behaviors by mountain lions after the 2018 Woolsey Fire, based on mixed effects models comparing probability of mountain lion use of urban areas

(A–D) Comparing probability of mountain lion use of urban areas (A), frequency of road crossings per month (B), proportion of day spent active (C), monthly distance traveled (D), and mean area of amount of space used over 3-month periods separated by sex and age class before and after the 2018 Woolsey Fire (E). The periods before and after fire were defined by the 15 months prior to and following the Woolsey Fire.

Models used to predict relationships included a mixed effects logistic regression model (A), segmented linear mixed effects models (B) and (C), segmented mixed effects meta-regression (D), and a linear mixed effects model (E).

Error bars and bands show 95% confidence intervals around fitted relationships.

See also Table S2.

due to the reduction in human recreational use in the short-term after fire.[30,31] Alternatively, increased space use could indicate an increase in avoidance of either humans or adult males, in the more sparse landscape where concealment is more challenging, given that mountain lions generally avoid open areas.[27] Alternatively, or perhaps concurrently, hunting could be more difficult for mountain lions due to the lack of cover on the landscape to ambush deer, as observed for African lions in savanna habitats.[13] All of these scenarios are likely to influence energy expenditure, indicating that a major disturbance, such as the wildfire in this study, could lead to energy deficits in carnivore populations.[32]

Our study was an opportunistic study of a population of mountain lions who were tracked before, during, and after a wildfire. The limited number of individuals who were not impacted by the wildfire precluded a natural experiment (such as a BACI design), therefore we must consider the possibility of other factors that could have influenced the behavior of mountain lions in our system over the 30 months of the study. Variability in human activity is unlikely to have contributed to changes in mountain lion behavior because our study ended (March 2, 2020) prior to local and statewide restrictions on public movement due to COVID-19 in the state and county (beginning March 19, 2020). Over the study period, rainfall varied, with greater rainfall after the fire than before, and two and a half mule deer (*Odocoileus hemionus*) calving seasons (important periods for mountain lion hunting) occurred, with one and a half prior to the fire and one after the fire (Figure S2). We cannot rule out the possibility that fluctuations in, and interactions between, weather and mule deer abundance influenced mountain lion behavior during our study. However, it is unlikely that these variables resulted in the findings we report here. The greater rainfall after the fire would be expected to increase deer forage and subsequently decrease, rather than increase, mountain lion space use and therefore reduce road crossings.[33,34] Further, given that mule deer tend to be crepuscular, the increase in daytime activity is unlikely to be explained by variability in environmental conditions changing deer abundance.[35,36]

Conservation implications

Our findings have important implications for the conservation of large carnivore populations living near urban areas, showing that wildfire can not only result in direct mortality, but could also influence carnivore behavior in ways that increase anthropogenic risks, like vehicular collisions and encounters with humans, as well as increase the risk of intraspecific conflict. These risks can interact. For example, one subadult male in this study was hit and killed by a vehicle on a freeway immediately after an altercation with an uncollared adult male. Behavioral changes observed in this study (e.g., variable usage of burned areas, increased activity

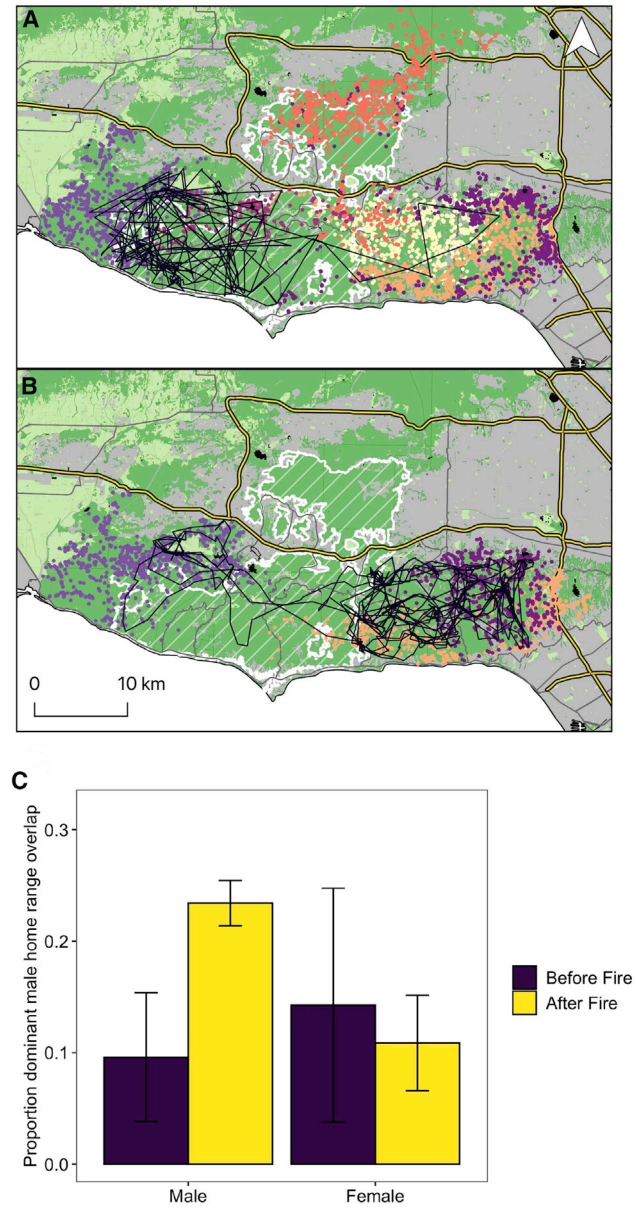

Figure 4. Observed overlap between the dominant adult male and subadult males before and after the 2018 Woolsey Fire

The dominant male (P30) is shown by a black line and subadult males are shown in colored points, different colors signify different individuals. Time periods include two ~6-month periods before (8th May 2018–8th November 2018) and after (21st March 2019–10th September 2019) the 2018 Woolsey Fire.

(A–C) (A) indicates the period before the fire until the Woolsey fire, when P30 was dominant (8th May 2018–8th November 2018), and (B) shows a similar period of time ending with P30's death (21st March 2019–10th September 2019). Before the fire, P30 regularly used the area within the fire perimeter and was rarely in the eastern half of the Santa Monica Mountains (A), whereas post-fire, he occasionally moved through the burned area and largely relocated to the eastern end, overlapping extensively with multiple subadult males. (C) shows the mean (± SE) proportion of P30's space use that overlaps with six other individual mountain lions (3 males and 3 females), tracked concurrently with him, before and after the fire. We defined P30 as the dominant male since he showed behaviors including territorial marking through scraping, breeding, and regular use of core natural areas.

Land use is shown by dark green (natural areas), light green (altered open areas), and gray (urban areas) and the extent of the Woolsey Fire (2018) is shown in white outline with white hatching. Primary and secondary roads are shown with gray lines with freeways in yellow (both were used in the road crossing analysis).

See also Figure S1.

during the day, and increased distance traveled) could be indicative of increased hunting challenges or hunting flexibility. If the fire-transformed landscape reduces the ability of mountain lions to ambush deer, they might rely on other prey items, including smaller carnivores, which in turn put them at greater risk of poisoning from toxicants such as anticoagulant rodenticides.[37]

Greater risk-taking behaviors by carnivores living near urban areas could lead to increased mortality in populations already suffering from low genetic diversity, leading to increased extinction risk.[38–40] As the world continues to urbanize and as we see increasing frequency of high severity fires in many of the world's fire-prone landscapes,[41] we are likely to see similar challenges for carnivore conservation in a broader range of global regions and taxa. Increasing the connectivity among urban habitat patches through a system of wildlife overpasses or underpasses,[42] already known to be important for increasing genetic exchange, could be particularly critical in fire-prone areas when the quantity of already limited suitable habitat can be greatly reduced post-fire.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.08.082.

A video abstract is available at https://doi.org/10.1016/j.cub.2022.08.082#mmc3.

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AUTHOR CONTRIBUTIONS

R.V.B., S.P.D.R, D.T.B, and J.A.S. conceived the ideas, J.A.S. and S.P.D.R collected the data, R.V.B. conducted the analysis, wrote the paper and made graphs. J.A.S, S.P.D.R., and D.T.B. edited and provided feedback on the manuscript throughout development.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We worked to ensure sex balance in the selection of non-human subjects. One or more of the authors of this paper self-identifies as a member of the LGBTQ+ community. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and code	Dryad data repository	Data and code are available at Dryad: https://doi.org/10.5068/D1M97D
Software and algorithms		
R v 3.6.1	R Development Core Team	https://www.r-project.org/
Rstudio v. 1.3.1093	Rstudio Team	https://www.rstudio.com/
adehabitatHR v. 0.4.16	The Comprehensive R Archive Network (CRAN)	https://cran.r-project.org/web/packages/adehabitatHR
adehabitatLT v 0.3.25	CRAN	https://cran.r-project.org/web/packages/adehabitatLT
amt v. 0.1.4	CRAN	https://cran.r-project.org/web/packages/amt
ctmm v. 0.5.11	CRAN	https://cran.r-project.org/web/packages/ctmm
ggplot2 v. 3.3.0	CRAN	https://cran.r-project.org/web/packages/ggplot2
lme4 v 1.1-23	CRAN	https://cran.r-project.org/web/packages/lme4
metafor v. 2.4-0	CRAN	https://cran.r-project.org/web/packages/metafor
momentuHMM v. 1.5.1	CRAN	https://cran.r-project.org/web/packages/momentuHMM
QGIS v. 3.4	QGIS Development Team	https://qgis.org

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources or reagents should be directed to and will be fulfilled by the lead contact, Rachel Blakey (rvblakey@cpp.edu).

Materials availability

The study did not generate new unique reagents.

Data and code availability

The data and code generated during this study are available at Dryad: https://doi.org/10.5068/D1M97D.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We captured and tracked mountain lions using global positioning system (GPS) collars (*Puma concolor*) as part of a long-term study conducted by the National Park Service (2002–present).[26,27,43] Mountain lions were captured using foot cable-restraints, baited cage-traps, or by treeing them with trained hounds; and immobilized with ketamine hydrochloride combined with medetomidine hydrochloride, administered intramuscularly. All animals were monitored throughout the time they were immobilized, during which time we estimated age, based on body size and tooth wear measurements. Age classes were: kittens (dependent offspring with their mother, 0-14 months), subadults (independent animals prior to reproduction: females 14-25 months, males 14-42 months), and adults (breeding animals: females >25 months, males >42 months).[44] We fitted adult and subadult animals with Vectronic Aerospace GPS collars (Berlin, Germany; Vertex Plus and Vertex Lite models) equipped with VHF beacons. Animal capture and handling procedures were permitted through a scientific collecting permit with the California Department of Fish and Wildlife (SCP # 05636) and the National Park Service Institutional Animal Care and Use Committee (Protocol PWR_SAMO_Riley_Mt.Lion_2014.A3). For this study, we used locational and accelerometer data for 17 individual mountain lions, collected over a 2.5-year period between 2017 and 2020, encompassing a large wildfire event, the 2018 Woolsey Fire. Individuals tracked for the study included 9 females (5 adult, 2 subadults, and 2 subadults that became adults during the study period) and 8 males (2 adult, 1 subadult, 1 kitten, and 4 subadults that became adults during the study period). Age was calculated for each three-month period, and the male kitten was treated as a subadult for the purposes of the study, given that he was estimated to be close to subadult age ($\sim$ 1 year old) and his mother was not observed during his capture.

We programmed collars to collect 8 locations per 24-hour period (7 at night, 1 during the day). The seven fixes at night were at 2 h intervals beginning at 5:00pm Pacific Standard Time (PST), while the day location was collected at 1:00pm PST. On average, 90% of programmed fixes for periods used in this study were successful, with individual mountain lion fix rates ranging from 69% to 98%. Collars also collected activity data on two axes (X: anterior-posterior/surge, Y: lateral/sway), averaged across every 5 minute period. A third axis (Z: dorso-ventral/heave) was only available for two of the seventeen individuals, so these data were not used in the analysis. Accelerometer measurements were 99% successful on average, with all individuals recording > 96% of expected measurements.

METHOD DETAILS

Study area

We studied an urban population of mountain lions within Los Angeles and Ventura counties, California, in the Santa Monica Mountains and Simi Hills (34°05'N, 118°46'W) (Figure 2). All patches of natural habitat were bordered by major freeways, urbanization, agricultural development, or the Pacific Ocean. The study population in the Santa Monica Mountains, in particular, has been genetically isolated from nearby populations by roads and urbanization,[26,38] leading to high extinction risk.[44] Land-use was variable across the study area, and included federal, state, and local parklands, as well as urban areas consisting of high-density residential, commercial, and industrial areas, low-density rural or suburban residential areas, and agricultural areas. Natural vegetation in the study area consisted of mixed chaparral, coastal sage scrub, oak woodlands and savannas, riparian woodlands, and non-native annual grasslands. The only wild, large ungulates were mule deer, which are the predominant prey for mountain lions in the region,[43] and two-and-a-half mule deer (*Odocoileus hemionus*) calving seasons occurred during the study period (Figure S2). The climate of the study area was Mediterranean, with cool, wet winters and hot, dry summers. Rainfall varied over the study period, with greater rainfall after the fire than before.,. The area is prone to drought and wildfire,[45] with two major wildfires occurring within less than a decade prior to this study, the Springs Fire in 2013, 9,814 ha, and the Woolsey Fire in 2018, 39,234 ha. The Woolsey Fire was the largest fire on record to have affected the Santa Monica Mountains and burned > 40% of the natural area in the Santa Monica Mountains and > 66% of the natural area in the Simi Hills (Figure 3).

QUANTIFICATION AND STATISTICAL ANALYSIS

Study design

We included locational data for 17 individual lions during 15 months leading up to and 15 months following the Woolsey Fire (2018). Mountain lion tracking periods varied (Figure S3), and more individuals were tracked after the fire (F: 9; M: 6) compared to before the fire (F: 5; M: 7). We therefore used resampling methods that balanced numbers of individuals among age classes to validate our findings (Table S3).

Do mountain lions avoid burned areas after a large wildfire?

To evaluate whether mountain lions decreased use of areas after they were burned in the Woolsey Fire, we compared selection coefficients for individual mountain lions derived from step selection functions before and after the fire using a meta-analytic approach.[46] Individual mountain lions were excluded from this analysis if an adaptive Local Convex Hull (LoCoH), calculated from every location recorded during the study period (the period spanning 15 months before and after the focal fire), overlapped with the burned area from the focal fire by less than 10%, or if they were not tracked during both periods (both before and after fire). We used the *adehabitatHR v0.4.16* package[47] within the *R v3.6.1* environment[48] to fit LoCoH home ranges and used the maximum number of nearest neighbors as all those points which were within the maximum distance between any 2 points recorded for animals in this analysis.

We first fitted a separate step selection function to each individual mountain lion during the periods before and after the fire separately using the *amt v 0.1.4* package.[49] These functions compared observed "steps" (movements connecting successive locations) with random possible steps generated from distributions of turning angles and step lengths from the broader population. We used only night locations for the step selection analysis, defined as locations collected between one hour after sunset and one hour before sunrise. The observed and random (i.e., "available") steps were compared to estimate selection coefficients using a conditional logistic regression to match observed to related randomly selected steps as strata. We used a sample rate of 2 h with a tolerance of 1 h and generated 1000 random steps for each observed step. The high tolerance level was not necessary and unlikely to have influenced the analysis, given > 99.96 of steps were within ± 5 minutes of the 2 h interval. Steps were separated into "bursts" for each night, to ensure sample intervals were regular (2 h intervals between each step). We then calculated effect sizes (yi) representing the change in selection of areas within the fire perimeter before and after they were burned by subtracting the "before fire" coefficient ($coef_{before}$) from the "after fire" coefficient ($coef_{after}$) for each individual. This meant that positive coefficients indicated selection for burned areas was higher after the fire, and negative values indicated that selection for burned areas was lower after the fire. We calculated the sampling standard error (sei) using the following approach recommended by Senn, Gavini, Magrez, & Scheen, [50] where se_{before} and se_{after} are the standard errors of the selection coefficients before and after the fire for each individual and ri is the correlation between the coefficients before and after the fire.

$$yi = coef_{after} - coef_{before}$$

$$sei = \sqrt{se_{after}^2 + se_{before}^2 - (2 \times ri \times se_{after} \times se_{before})}$$

Our sample size was small (5 males and 4 females tracked both before and after the fire), so we were chiefly interested in population-level selection for or against burned areas. We therefore estimated a population-level effect size using random effects meta-analysis[46] using the *metafor v. 2.4-0* package.[46] Along with the step-selection analyses and for comparison with them, we calculated mountain lion use of areas within the burn perimeter before and after the fire as the number of point locations whose 10 m radius intersected with the burned area (to allow for some variability in GPS location and fire layer accuracy).

Do mountain lions increase behaviors that put them at anthropogenic risk after a large wildfire?

We calculated three metrics associated with behaviors that may place mountain lions at additional risk from humans and anthropogenic threats: use of urban areas; number of road crossings; and proportion of daytime period active. We defined urban areas as commercial, and industrial areas and residential areas with $\geq$ 2.5 houses/hectare identified within the Southern California Association of Governments land use map.[51] This map was the most accurate available land-use data for the region, because later versions classified land uses at the parcel scale, rather than based on observed boundaries between different land uses. The dataset we used was reflective of the landscape throughout the study period from 2017–2020 for the broad development and altered-open classifications that we used in these analyses. The geographic information system (GIS) program for the park monitors land use in and around SMMNRA as part of the National Park Service Inventory and Monitoring Program. We defined mountain lion use of urban areas before and after the fire as a binary variable where point locations whose 10 m radius intersected urban areas were recorded as used (1), and those locations whose buffer did not intersect with urban areas were unused (0). We compared use of urban areas before and after the fire using a mixed effects logistic regression with period (before and after fire) as a fixed effect and individual mountain lion as a random intercept using *lme4 v 1.1-23*[52] (see Tables S3 and S5 for details of all analyses). We compared 3 models to investigate how the probability of mountain lion use of urban areas changed after the fire including: null (no effect of fire); step response (an abrupt change in urban use after the fire compared to before the fire); continuous response (a change in the relationship between urban use and time after the fire) (Table S5). We compared models using Akaike's Information Criterion adjusted for small sample size (AICc) and identified the most parsimonious model as the model with the lowest AICc, that was separated from a less complex nested model by ΔAIC > 2. Modelled coefficients and fitted relationships are presented with 95% confidence intervals, and confidence intervals around the fixed effects were calculated for fitted relationships using parametric bootstrapping.

To quantify road crossing behavior, we first exported each month of locations for each mountain lion into a movement trajectory using the *adehabitatLT v0.3.25* package.[47] We classified a major road as all freeways and secondary roads using road data from the U.S. Census Bureau, ([53]), adding roads that had similar amount and speed of traffic based on observations by National Park Service biologists. Specific roads included are shown in Figure 4. We added a 50 m buffer (50 m either side) to each road, to allow for road width and spatial uncertainty in road and mountain lion datasets. Road crossings were identified manually as "minimum road crossings", using lines between two consecutive points that traversed any buffered road, using QGIS v. 3.4.[54] When the line drawn between two consecutive point locations traversed a single road more than once, and the starting point was on one side of the road, whereas the ending point was on the other side, this was counted as one crossing. When the line drawn between two consecutive point locations traversed a road any number of times, but both starting and ending points were on the same side of the road, this was counted conservatively as zero crossings. As point locations were separated by a minimum of 2 h, we cannot discount the possibility of the animal taking an alternative (rather than the shortest) route to traverse between the two points. However, in all cases where we have recorded a crossing, the alternative route would have resulted in at least one road crossing, so our measure of "minimum road crossings" remains consistent with these possibilities.

We analyzed the relationship between road crossings and fire in a similar way to the urban use analyses (Tables S3 and S5). We used linear mixed effects models with the number of road crossings per individual per month as the response variable and individual mountain lion as a random intercept, and we used model selection to assess support for either an abrupt (step) response or a gradual (continuous) response to fire (Table S5). To account for unequal fix rates among months and individuals, we included fix rate (the number of locations recorded for an individual mountain lion during the month when road crossings were counted) as a fixed effect in all road crossings models.

To estimate the proportion of the daytime period spent active, we analyzed accelerometer data for lions where it was available (Figure S3 & Table S3). Given that we did not have field observations to inform our estimations of behavioral state, we used unsupervised Hidden Markov Models (HMMs) to estimate two states approximating "resting" and "active" behavior.[55] The HMM method explicitly models temporal dependence which is inherent in accelerometer data and assumes that the observed acceleration data time series is driven by an unobserved (hidden) behavioral state process.[55] We split the data into separate individuals.[55] We fitted a 2-state HMM using two data streams (activity of the X and Y axes), for which we assumed Gaussian distributions. We estimated starting values for our two states by examining distributions of the two data streams. We also fitted HMMs considering time of day as a covariate (cosine(2*pi*(hour of day/24)) using starting values extracted from the simpler models. These models did not improve fit compared to the simpler models based on AICc, so we retained the simpler models. Prior to analysis we standardized activity measurements by dividing all values for separate individuals and collars by the maximum recorded value during the period the collar was worn by the animal, given collar tightness can affect acceleration values measured by the sensor.[56] We fitted HMMs using the *momentuHMM v1.5.1* package.[57]

Next, we separated daytime activity data, including all data collected from one hour after sunrise to one hour before sunset to avoid crepuscular periods.[27] We removed 24 h periods from the dataset if they had < 95% of expected recordings. We then calculated the proportion of daytime active as the proportion of time that was classified as "active" using the HMM method. We used logit-transformed proportion of daytime active as the response variable in linear mixed effects models (LMM) with individual as a random intercept to account for variability in activity levels among individuals (Tables S3 and S5). Consistent with the urban use and road crossings analyses, we used model selection to assess support for either an abrupt (step) response or a gradual (continuous) response to fire (Table S5).

Do mountain lions increase behaviors that could increase risk of conflict with conspecifics after a large wildfire?

We calculated three metrics to quantify behaviors that could place mountain lions at additional risk due to increased chance of conspecific interactions: distance travelled, amount of space used, and spatial overlap with other mountain lions.

We quantified distance travelled using a continuous time movement modelling (CTMM) approach.[58] The continuous time approach aims to separate the sampling processes from the animal's underlying movement processes by fitting a model accounting for the positional and velocity autocorrelation properties inherent in movement data, and then simulating multiple possible trajectories based on this model.[59] We used model selection to fit a movement model to each monthly period for each individual mountain lion that best described the positional and velocity autocorrelation of the animal's movement for that period. For 38 out of 257 individual-months analyzed, the movement showed no statistically significant evidence for velocity autocorrelation, so we were unable to estimate distance for these months. We estimated monthly distance travelled and variance of these estimates for the remaining 219 months. Given that the CTMM approach allows for estimation of uncertainty, we used a mixed effects meta-regression approach, fitted via restricted maximum likelihood, using estimated distance as the effect sizes and variance of distance as the sampling variances, with individual mountain lion as a random effect (Tables S3 and S5). Our estimated values of distance travelled were normally distributed around a mean of 330 ± 120 km (SD) per month. Moderators (covariates) were defined in the same way as fixed effects for the models of urban use, road crossings, and daytime activity (Table S5). We compared 3 models to investigate whether mountain lions changed their distance travelled after the fire including: null (no effect of fire on distance travelled); step response to fire (abrupt change in distance travelled after the fire); and continuous response (a change in the relationship between distance travelled and time after the fire) (Table S5). We fitted continuous time movement models and estimated distance travelled using the *ctmm v 0.5.11* package.[58]

We quantified the amount of space used and estimated home range overlap using adaptive local convex hulls (LoCoH),[60] implemented within *the adehabitatHR v0.4.18*. While we recognize that this method can underestimate the amount of space used and is sensitive to sampling rates,[61] it performs well when animal movement is constrained by barriers like roads and urban areas,[60] and our sampling rate was generally consistent among individuals. Since we were more interested in comparative space use (before and after fire), rather than absolute measurements of area, we believe this approach is robust.

We quantified the amount of space used by calculating the adaptive LoCoH for every individual mountain lion and every 3-month period which contained a $\geq$ 75% fix rate (Table S3). We analyzed the relationship between amount of space used and fire using linear mixed effects models with individual mountain lion as a random intercept (Table S5). We used model selection to assess support for an abrupt (step) response to fire and did not investigate a gradual response to fire as space use was calculated for 3-month periods (Table S5). We also fitted models including the interaction between period (before and after fire) and age-sex class, given the known disparities between amount of space used across age-sex classes,[27] though we interpret these results cautiously due to the low number of individuals in each group (Table S3).

We took two approaches to investigating changes in home range overlap before and after the fire. For the first approach, we focused on an adult male who held the largest territory within the Santa Monica mountains prior to the Woolsey Fire, P30, which we refer to as the "dominant male". We examined all animals that had the potential to overlap with P30 (individuals that used the Santa Monica Mountains area as part or all of their home range) and that were tracked at the same time as P30 for at least 3 months both before and after the fire. This resulted in a dataset of 6 mountain lions (3 males and 3 females), who were tracked for periods ranging from 5 to 11 months (both before and after fire) concurrently with P30. For space use calculations, we limited tracking periods to the same period of time before and after the fire for each individual. For each individual we calculated amount of space used over the period they were tracked concurrently with P30 using adaptive LoCoHs. We then calculated areal overlap of the LoCoH with the corresponding LoCoH for P30 during the same period. Given the small sample size (6 individuals with one measure of overlap per period for a total of 12 measures of overlap), we interpreted the results graphically rather than conducting a formal analysis. Our second approach to quantifying overlap involved calculating the overlap between every pair of mountain lions that were tracked during concurrent 3-month periods (Table S3). We restricted this to animals that used the same region (e.g., animals that exclusively used the Simi Hills portion of the study area were only compared to other animals that used this part of the study area). We analyzed the overlap data in the same way as the first overlap analysis, but separated into two datasets, one expressing overlap as proportions of female home ranges overlapped and the other expressing overlap as proportions of male home ranges overlapped. We fitted linear mixed effects models to each of those two datasets using pair category (male-male, male-female, female-female) as a fixed effect and overlap pair (pair of individual mountain lions for which overlap was calculated) as a random intercept (Table S5). Similar to the space use analysis, we used model selection to assess support for an abrupt (step) response to fire (Table S5).

All analyses were conducted within *R v3.6.1*[48] using *Rstudio v. 1.3.1093*,[62] all plots were made using *ggplot2 v. 3.3.0*[63] and all map figures were made using QGIS v. 3.4.[54]

Resampling for model validation

In order to account for the variability in sampling across individuals and age-sex classes, we resampled observations in each dataset 100 times to provide equal numbers of locations across sex and age classes and re-ran the model selection analysis. The specific approaches for each analysis are listed in Table S3. We recorded the percentage of iterations for which the most parsimonious models from the full dataset were selected as well as the proportion of models that resulted in fitted relationships in the same direction (e.g. greater or lower magnitude after compared to before fire) as the full-data model for all analyses. Where the majority of the relationships were in the same direction as the full dataset and the majority of iterations showed the same direction in relationships, we classified the relationships as robust. An additional validation step was performed for the urban use analysis. Given the female who used urban areas the most frequently (P75 — 15% of use was urban) was only sampled after the wildfire, we performed an additional check and removed her from the dataset and re-fit the models. We found that the strength and direction of the relationships were similar and that the same model type was found to be the most parsimonious, so we retained the full dataset.

Most of our analyses showed that the most parsimonious model and the direction of relationships were consistent across 100% of iterations, and we report only the exceptions below. In the analysis of urban use, models predicting abrupt changes were selected as the most parsimonious 76% of the time, with continuous responses to fire 24% of the time. In the road crossings analysis, 78% of model iterations showed an increase in road crossings after fire with 25% of models showing an abrupt change and 62% showing a continuous response. For the space-use analysis, direction of the relationships (increase in space use after fire) was consistent across 83 % of iterations. When space use was separated into sex and age classes, model selection was consistent across all iterations, but the consistency of relationship directions (increase or decrease after fire) varied among sex and age classes (adult male: 63 %, subadult male: 100 %, adult female: 81 %, subadult female: 92 %).

CALIFORNIA WILDFIRES

‘Literally off the charts’: LA’s critically dry conditions stun scientists as fires rage

BY ALASTAIR BLAND
JANUARY 15, 2025

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Smoke from the Eaton Fire fills the sky in La Cañada Flintridge on Jan. 8, 2025. Hills and canyons are critically dry. Photo by Jules Hotz for CalMatters

IN SUMMARY

Key moisture measurements are only 2% to 5% of average, leaving dusty soils. And the recent swing from wet to dry is among the most extreme on record. This combination of climatic conditions crossed into a danger zone, priming much of Southern California for wind-whipped fires.

Lea esta historia en ***Español***

As much of Los Angeles smolders, wind warnings return and fire crews stand guard, scientists say almost unprecedented climatic conditions throughout Southern California led up to the disaster.

Last summer was one of the hottest on record, and the extreme swings between wet and dry conditions over the past two years have been unusually severe. Two rainy winters — which promoted heavy growth of brush — have been followed by **near-zero rainfall** for the past eight months and counting.

This pattern of weather whiplash, likely exacerbated by climate change, hasn't been seen in Southern California since 1992-1993, and before that, 1907-1908. "We find only three instances where an anomalously dry start to the wet season follows back-to-back wet water years," a team of UCLA researchers wrote in a **report** released on Monday.

Soil moisture levels across much of the region from Santa Barbara to San Diego hover between just 2% and 5% of average — leaving dust where there should be mud.

Also, an important measure called "vapor pressure deficit" has exceeded norms. Calculated from a combination of temperature and relative humidity, it reflects the ability of air to draw moisture from the landscape.

“The way to think about vapor pressure deficit is that it is the drying power of the air,” said John Battles, a UC Berkeley forest ecology professor.

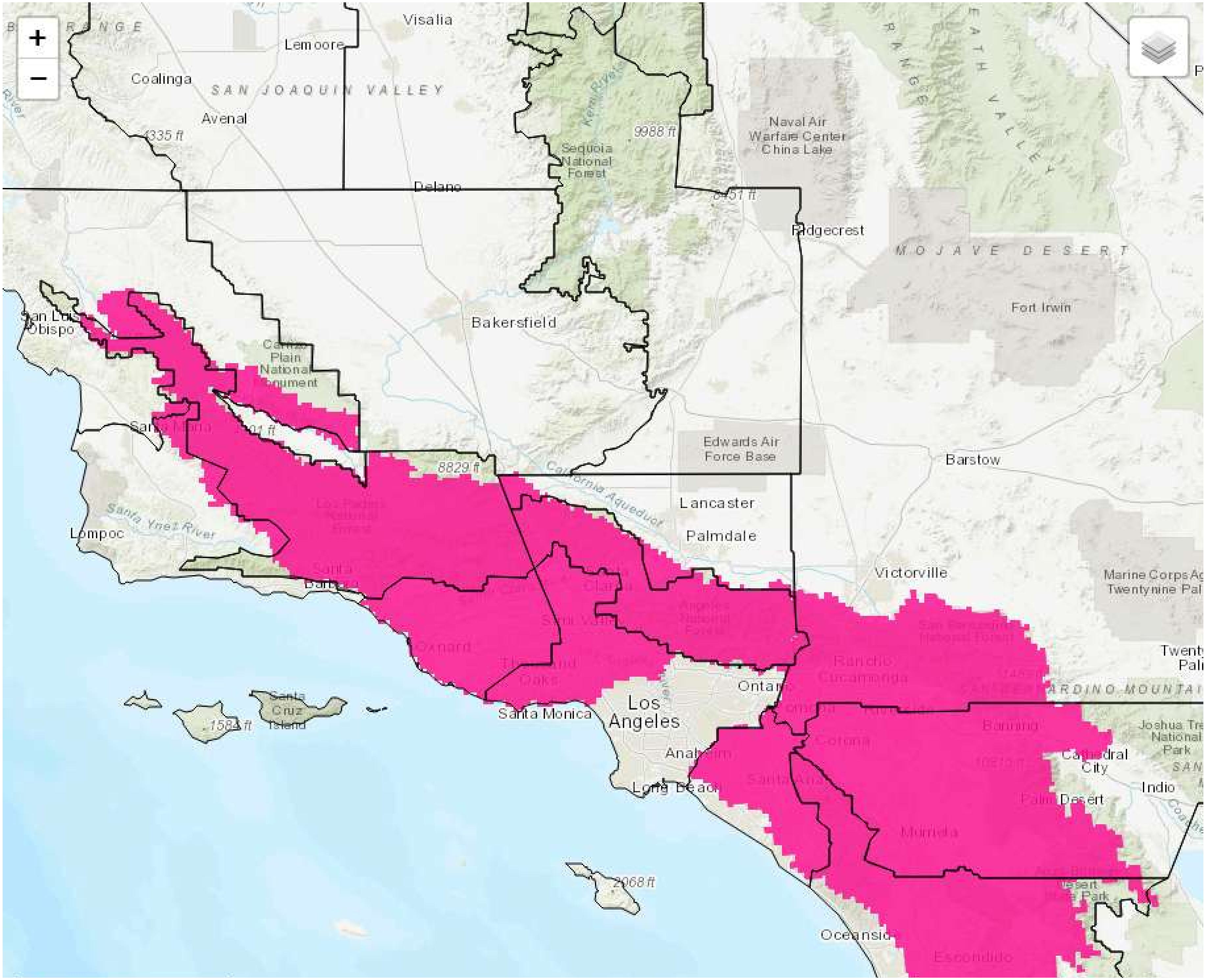
Readings from Jan. 8 show an extreme deficit across much of inland Southern California. Such conditions can draw much of the moisture from living plants, so fires become almost unstoppable once they start.

“When it’s that dry, wind has ultimate power,” said UC Merced climatology professor John Abatzoglou.

In Malibu Canyon, local gauges recorded 53 degrees Fahrenheit and relative humidity of 36% on Jan. 4. Three days later, on the day that the Palisades and Eaton fires began, the air temperature was 64 degrees while the relative humidity had dropped to 13%, more than doubling the vapor pressure deficit.

These levels are “literally off the charts,” Battles said.

This combination of conditions crossed a dangerous threshold, priming the landscape throughout much of Southern California for high risk of wind-whipped fires. Across seven counties, drought has sapped the air, soil and vegetation of moisture.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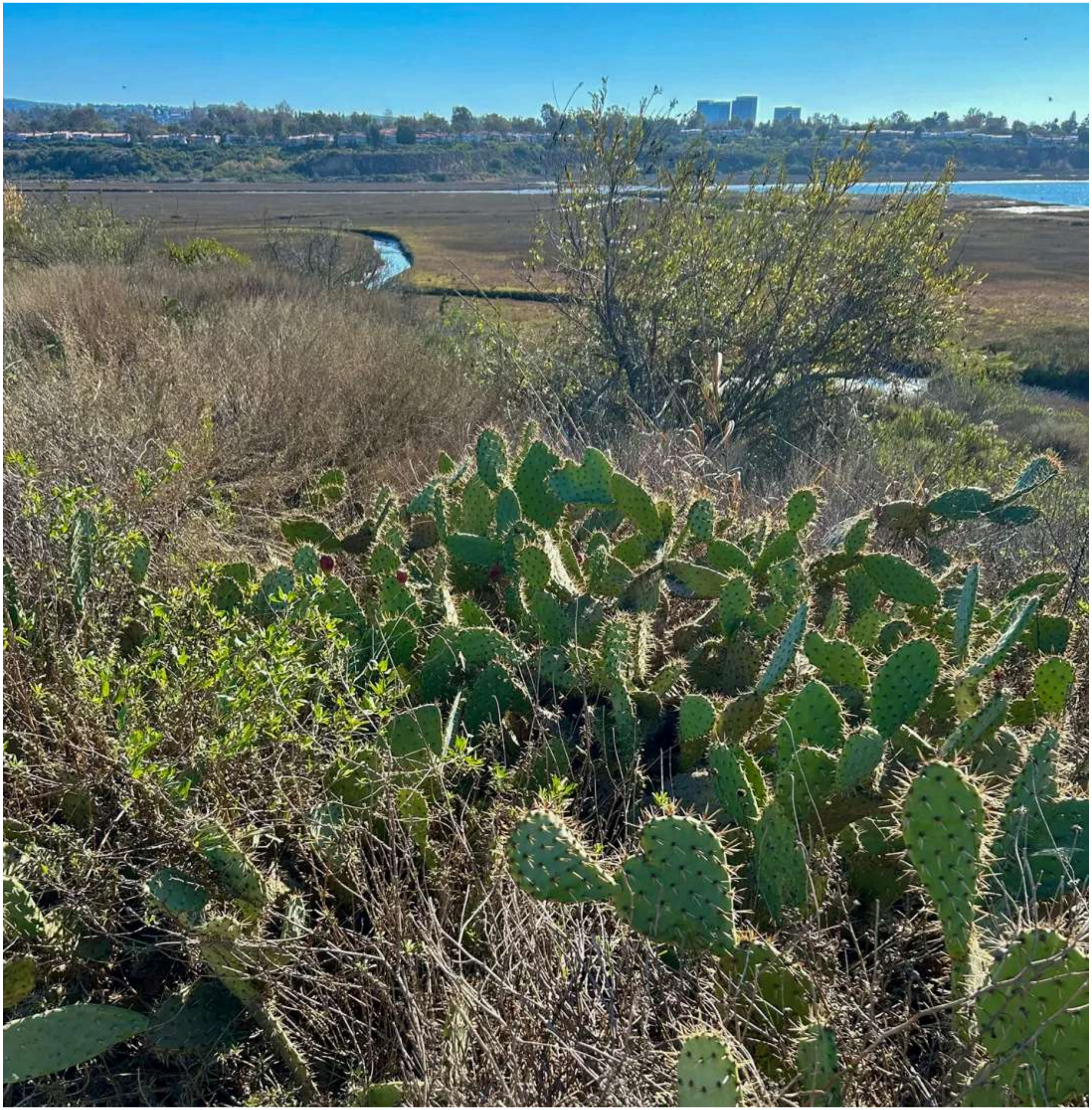
Victorville
Oxnard
Rancho Cucamonga
Ontario
Los Angeles
Santa Monica
Santa Cruz Island
Corona
Banning
Anaheim
Long Beach
Santa Ana
Cathedral City
Indio
Palm Desert
Murrieta
2068 ft
Escondido

The National Weather Service has declared red flag conditions for nearly all of Southern California. The warnings are triggered when relative humidity is 15% or less and gusts are 25mph or stronger. Both conditions must occur simultaneously for at least 3 hours in a 12-hour period. Fire weather watches are dry areas flagged as high to extreme danger with critical weather conditions within the next 48 hours.

The National Weather Service issued a **warning** Tuesday of critical fire weather or red flag warnings from the Mexican border to San Luis Obispo County. The alert predicted gusts up to 50 mph, humidity of a lip-splitting 10%, and virtually no chance that rain would relieve the conditions anytime soon. This comes on the heels of the **third hottest summer** in coastal Southern California since at least 1895.

The threat goes far beyond Los Angeles, affecting much of Southern California. Across Orange County "current live and dead fuel moistures remain at or below established critically low thresholds," said Sean Doran, a public information officer with the Orange County Fire Authority. He called Tuesday's fire danger level in Orange County "extreme." The county has dried-out canyons, near residential areas, full of ultra-flammable chaparral and sage scrub.



Chaparral and sage scrub in Orange County's Upper Newport Bay is bone-dry after months with no rain. Jan. 11, 2025. Fire officials called the danger "extreme" in the county. Photo by Marla Cone, CalMatters

Officials and researchers routinely weigh samples of vegetation, dehydrate them and weigh them again. This allows them to calculate the "live fuel moisture" percentage, which tells them how flammable the landscape is.

These measurements and related data are critical to firefighters, who monitor them regularly so they can gauge the risk of a fire erupting and determine which tools, vehicles and equipment are needed to fight the blazes, explained Scott McLean, a Cal Fire public information officer.

Last May, the **live fuel moisture** content of Santa Monica Mountains chamise — a prominent chaparral plant — was a wet and heavy 143%. That means that the weight of the water in the plants was almost 1.5 times the weight of its woody material. (A reading of 100% means equal parts water and plant mass.)

By November, live fuel moisture in the same region had dipped to just over 60%.

Even more recently, on Jan. 7, measurements from Santa Barbara vegetation showed levels of 61% — substantially below the 77% average for this time of year. That means their water weight was less than two-thirds of their plant material.

"Once the live fuel moisture hits around 60%, that is the critical danger zone," said UC Merced's Abatzoglou, explaining that below this level, vegetation loses much of its resistance to fire.

To put it another way, he said, at and below about 60%, "the live fuels behave and burn more like dead fuels."

> **"Once the live fuel moisture hits around 60%, that is the critical danger zone…The live fuels behave and burn more like dead fuels."**
>
> — UC MERCED CLIMATOLOGY PROFESSOR JOHN ABATZOGLOU.

Abatzoglou cited research from 2009 suggesting that a critical threshold between vegetation that can and cannot support a large fire lies around 79% — which would put current conditions much deeper into the danger zone.

Dead vegetation, baked by the sun for months or years, is also perilously dry. "By January 7th of 2025, dead-fuel moisture was 6th lowest on record for that date," the UCLA team wrote in Monday's report.

Brush clearing wouldn't help much, experts say

While President-elect Donald Trump has claimed on social media that incompetent state leadership led to the wildfires and hindered efforts to tame the flames, experts say there is little that could have prevented the disaster.

The extremely dry conditions have been aggravated by winds gusting up to 100 miles per hour — what UCLA climate researcher Daniel Swain recently likened to using an atmospheric blow dryer on bone-dry terrain.

Alexandra Syphard, a senior research ecologist at the Conservation Biology Institute and an adjunct professor at San Diego State University, said the extreme conditions have rendered humans powerless, at least in the nearterm, to subdue wildfire threats.

“I do not believe there is anything that wildland management could have done to qualitatively or substantially alter the outcome of these fires,” she said.

> **“I do not believe there is anything that wildland management could have done to qualitatively or substantially alter the outcome of these fires.”**
>
> — ALEXANDRA SYPHARD, CONSERVATION BIOLOGY INSTITUTE RESEARCH ECOLOGIST

While thinning trees or conducting controlled burns can reduce fire dangers in some forests, the same approach does not work in the areas of Southern California dominated by chaparral, Syphard said. These areas are too vast to clear brush, encompassing thousands of square miles.

She said such clearing tends to increase fire danger in chaparral landscapes by killing off both mature plants and the natural seed bank in the soil, triggering a long-lasting conversion to grasslands, which she says create an “explosively flammable” duff layer each summer and fall.

The best preventative strategies for reducing fire danger in a chaparral landscape, Syphard said, are to “create very strategically placed fuel breaks that enable safe firefighter access” as well as to “rethink where homes are constructed and how to make houses more resilient.”

Reducing greenhouse gas emissions, though it's not likely to provide any immediate relief of the dangers facing millions of Californians living in or near flammable landscapes, is another difficult but necessary solution, experts say. Global warming is conditioning the already arid Southwest to burn.

As much as 88% of the increasing average vapor pressure deficit in the western United States is linked to human-caused warming, according to a 2021 UCLA **paper**. Compared to the 1980s and 1990s, the number of days with an extreme vapor pressure deficit nearly doubled in the first two decades of this century, the researchers found.

> **"These are global conditions playing out … There's very little California can do to reshape these weather patterns."**
>
> — JOHN BATTLES, UC BERKELEY FOREST ECOLOGY PROFESSOR

And with rates of global emissions increasing in spite of international pledges to reduce them, this increasing aridity is only going to get worse.

"This change in risk requires urgent and effective societal adaptation and mitigation responses," the UCLA scientists wrote.

The new UCLA report noted that linking weather anomalies to climate change "requires deep analysis." But the authors were confident about one potential connection: "The clearest way in which climate change may have intensified the January 2025 wildfires is the anomalously warm summer and fall of 2024," they wrote.

With or without a climate change link, the extremes seen in Southern California over the past two years have been exceptional, including a hurricane-driven cloudburst in August 2023, an extraordinarily wet February last year that delivered an average of almost half an inch of rain daily, and a dry streak that is quickly catching up with 1962-1963 as the **longest** in the region's history.

Battles, at UC Berkeley, said the likely role of climate change in the weather extremes that are clobbering California makes direct human intervention almost negligible, and better planning key to safety.

“These are global conditions playing out … There’s very little California can do to reshape these weather patterns,” he said.

“With the climate making things drier, we need to think about how we transition into a new state, and how we deal with wildfire and development and public safety. These are not hard science questions, but they’re super hard policy questions.”

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Health and Social Care in the community
Health and Social Care in the Community (2017) **25**(3), 799–812 doi: 10.1111/hsc.12311

Review

Social isolation, loneliness and health in old age: a scoping review

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What is known about this topic

- Social isolation and loneliness are risk factors for poor mental and physical health.
- They are particularly problematic in old age due to reduced social networks, decreasing economic resources and changes in family structures.

What this paper adds

- Loneliness is more frequently researched than isolation; depression and cardiovascular health are the most researched health outcomes.
- Still little is known about interventions that would affect loneliness and health, about causal mechanisms or service use of isolated or lonely older people.
- Future research should link the evidence on risk factors for loneliness and social isolation and the evidence on their impact on different health domains, with longitudinal designs needed to understand associations.

Abstract

The health and well-being consequences of social isolation and loneliness in old age are increasingly being recognised. The purpose of this scoping review was to take stock of the available evidence and to highlight gaps and areas for future research. We searched nine databases for empirical papers investigating the impact of social isolation and/or loneliness on a range of health outcomes in old age. Our search, conducted between July and September 2013 yielded 11,736 articles, of which 128 items from 15 countries were included in the scoping review. Papers were reviewed, with a focus on the definitions and measurements of the two concepts, associations and causal mechanisms, differences across population groups and interventions. The evidence is largely US-focused, and loneliness is more researched than social isolation. A recent trend is the investigation of the comparative effects of social isolation and loneliness. Depression and cardiovascular health are the most often researched outcomes, followed by well-being. Almost all (but two) studies found a detrimental effect of isolation or loneliness on health. However, causal links and mechanisms are difficult to demonstrate, and further investigation is warranted. We found a paucity of research focusing on at-risk sub-groups and in the area of interventions. Future research should aim to better link the evidence on the risk factors for loneliness and social isolation and the evidence on their impact on health.

Keywords: health, loneliness, mental health, older people, scoping review, social isolation

Introduction

An increasing number of older people are living alone and are at risk of being socially isolated (Victor *et al.* 2002, Savikko *et al.* 2005, Sundström *et al.* 2009). Social isolation has been identified as a risk factor for poor health, reduced well-being, mortality (e.g. Patterson and Veenstra 2010, Steptoe *et al.* 2013), depression (Heikkinen and Kauppinen 2004) and cognitive decline (Wilson *et al.* 2007). It has been argued that health risks associated with isolation and loneliness are equivalent to the well-established detrimental effects of smoking and obesity (Holt-Lunstad *et al.* 2010). Social isolation and loneliness are particularly problematic in old age due to decreasing economic and social resources, functional limitations, the death of relatives and spouses, and changes in family structures and mobility.

New research in the area is accumulating. We therefore sought to review the evidence on social isolation and loneliness, and their impacts on health, well-being and service use.

Our review addresses two research questions: (i) What evidence exists on the relationships between isolation, loneliness and health? (ii) What are the limitations and gaps in the evidence base? We address these two questions by scoping the literature. We focus on recent findings about the associations between social isolation and poorer health and well-being outcomes, differential effects across population groups, as well as the methodological challenges associated with the design and evaluation of interventions aimed at reducing or addressing the consequences of isolation.

Methods

We followed the five-stage methodological framework for scoping studies suggested by Arksey and O'Malley (2005): (i) identify the research question; (ii) identify relevant studies; (iii) select studies; (iv) chart the data; and (v) collate, summarise and report the results. The stages of the review are detailed below, with steps 4 and 5 conflated together.

Identifying the research question

As stated above, this review is guided by two research questions: (i) What evidence exists on the relationships between isolation, loneliness and health? (ii) What are the limitations and gaps in the evidence base? Definitions of both social isolation and loneliness have been debated (Nummela *et al.* 2011, Giuli *et al.* 2012). For example, social isolation is often defined as the lack of integration of individuals in their social environment. However, recent research has distinguished specific components of isolation in old age (e.g. quality of relationships), with implications for measurement of social isolation (Cornwell and Waite 2009). We did not predefine social isolation or loneliness as we wanted to compare the definitions and associated measurements in the literature as part of our review. Given our purpose, a broad range of health outcomes was also included.

Identifying relevant studies

The scoping review identified, retrieved and evaluated information from empirical peer-reviewed articles that examined the impacts of isolation and/or loneliness on physical and mental health. We focused on studies published between 2000 and 2013. This timeframe was selected as it closely parallels that of recently published reviews of interventions aimed at reducing loneliness and isolation in old age (e.g. Hagan *et al.* 2014). Our study differs from previous reviews in that we focus on the impact of isolation and loneliness on health in old age in particular.

We searched nine databases between July and September 2013 (PubMed, SCOPUS, PsycINFO, Medline, International Bibliography of Social Sciences, Public Affairs Information Service, EconLit, and from the Thomson Reuters Web of Knowledge platform, Web of Science and Current contents connect).

We used a combination of search terms related to our population group of interest, social isolation and loneliness, and a broad range of physical and mental health outcomes (Table 1).

Selecting studies

Only empirical papers with an English language abstract were included. Because the aim of the scoping was to describe the breadth of relevant research, we did not exclude studies based on the same sample of respondents. We considered all types of research design.

We applied the following exclusion criteria at two stages of study selection (screening by title and abstract, and full text):

- Studies focusing on countries other than Western Europe and USA;
- Studies focusing on issues other than social isolation and loneliness;
- Studies not assessing physical or mental health outcome(s);
- Editorials, letters, book reviews;
- Studies covering population groups other than older people (defined here as people aged 50 and over).

Figure 1 summarises the selection process. The search yielded 11,736 articles (11,392 through the nine databases and 344 through a selection of websites). When duplicates were removed there were 5342 references, of which 94% were excluded based on screening of the title and abstract. Full texts of the remaining 288 papers were accessed. Of these papers, 156 articles (54%) were excluded. One hundred and twenty-eight articles were included in the scoping review.

Table 1 Keywords and search terms employed in the database searches

Population or target group	Issue	Health outcome
Aged	Loneliness	Health
Ageing	Isolation	Physical health
Ageing	Social isolation	Mental health
Senior	Solitude	Mental health problems
Elderly		Mental disorder
Elder people		Well-being
Old age		Well-being
Older people		Depression
Old people		

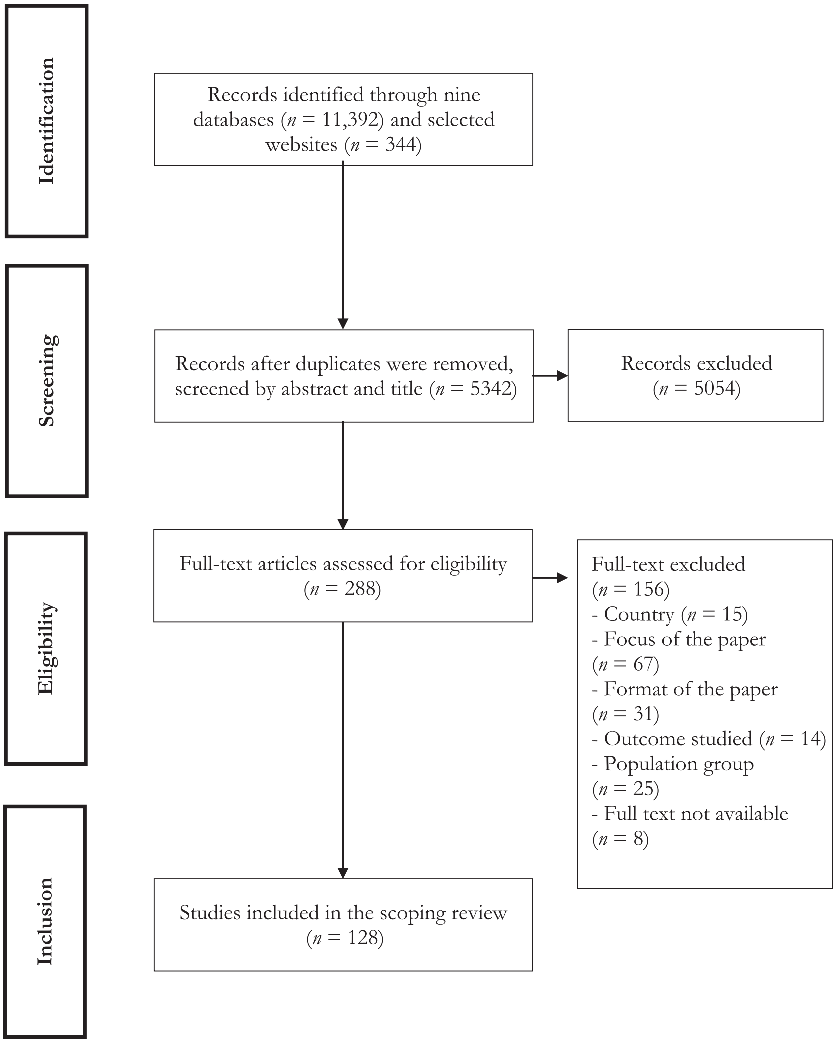

Figure 1 Flow chart of the search strategy and results.

Charting the data, summarising and reporting the findings

We used the 'narrative review' approach to collect similar information on all studies (Pawson 2002). We recorded information on first author, year of publication, study objectives, type of data and research design, study setting, sample size, issue studied, measurement of isolation or loneliness, health outcome, population group and main findings.

Results

Study context

Research on the impact of social isolation and loneliness on health constitutes a large and growing body of literature, with 54% of the included articles published between 2010 and 2013 (Figure 2).

Table 2 presents the main characteristics of the 128 studies. The papers spanned 15 countries. Half focused on the USA, followed by the UK and the Netherlands. Loneliness and social isolation attract multidisciplinary attention. First authors' disciplines included medicine, psychology, epidemiology, public health and nursing.

Study design

Half the studies collected primary data. The vast majority used a quantitative approach, with only 5% being qualitative and 3% using mixed methods. Over half of the studies used samples representative of the population.

Definitions and measurements

Just over half of the 128 studies included a formal definition of isolation or loneliness, mostly the latter.

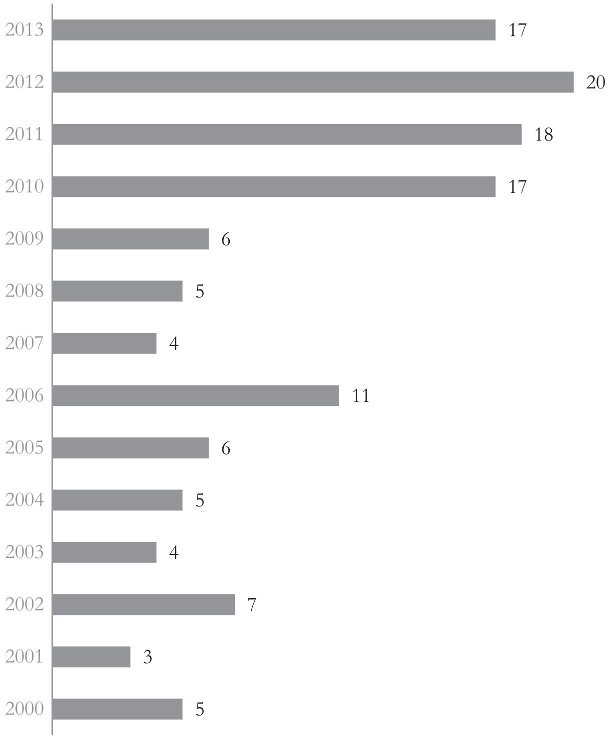

Figure 2 Number of studies included in the scoping review, by year of publication.

First, the concept of loneliness was usually defined as an undesirable subjective experience, related to 'unfulfilled intimate and social needs' (Peplau and Perlman 1982). The notion was often considered as unidimensional as only 23% of studies on loneliness contrasted different dimensions, such as sense of belonging or the nature of discrepancies between experienced and expected relationships (e.g. Martina and Stevens 2006); or between social and emotional loneliness (e.g. Dong *et al.* 2012, Drageset *et al.* 2013a, b). We found a variety of measures (Table 3). Seventeen studies used a single-item question on loneliness. More complex measures have also been introduced. Most studies (47%) used the UCLA Loneliness scale (Russell 1996) or its shorter revised version. Although most studies using this scale focused on the USA, it was also used by the studies based on the English Longitudinal Survey of Ageing (e.g. Shankar *et al.* 2011). Seven studies used the de Jong Gierveld scale (1987) – specifically designed to measure loneliness in old age.

Second, in the area of social isolation, most papers defined the notion as a unidimensional concept, i.e. an objective measure of the number of contacts with family and friends. Only a few studies considered isolation as a multidimensional concept, adding the

Table 2 Overview of the studies characteristics

Variable	Number of studies	Percentage of studies
Study context		
Country of the first author*		
USA	65	51
UK	10	8
Netherlands	9	7
Discipline of the first author†		
Medicine	24	18
Psychology	19	15
Public health	15	12
Epidemiology	15	12
Nursing	13	10
Study setting		
Community-based	114	90
Facility-based	14	10
Sample size		
Minimum	6	
Median	430	
Maximum	44,573	
Type of data		
Primary data	65	51
Secondary data	63	49
Study design		
Case–control	1	1
Controlled before and after	2	2
Cross-sectional	68	52
Longitudinal	42	33
Mixed methods	4	3
Other	1	1
Qualitative	6	5
Randomised control trial	4	3

*Only the first three countries with the highest number of publications are reported here.
†Only the first five disciplines with the highest number of publications are reported.

notion of quality of relationships (e.g. Cornwell and Waite 2009, Ha and Ingersoll-Dayton 2011). Measurement of social isolation was heterogeneous. Most studies used an *ad hoc* index composed of measures of marital status, household composition and number of friends and relatives (e.g. Coyle and Dugan 2012, Stafford *et al.* 2013), and counts of meetings with relatives (e.g. Tilvis *et al.* 2012). A few studies included a previously developed scale such as the Berkman–Syme Social Network Index (Michael *et al.* 2001, Eng *et al.* 2002, Rodriguez *et al.* 2011) or the Duke Social Support Index (Hastings *et al.* 2008, Parsons *et al.* 2013).

Focus of the studies

Half the studies included in the scoping review aimed at describing the association between isolation or loneliness and a health outcome. A quarter investi-

Table 3 Most commonly used measures of loneliness

Measure	Authors	Description	Examples of studies using this measure
UCLA Loneliness scale or its revised version	Russell (1996)	Twenty-item scale, with each item rated from 1 (never) to 4 (often). A number of studies use a shorter revised version (R-UCLA)	Beeson (2003); Cacioppo *et al.* (2002) Cacioppo *et al.* (2006, 2010); Grov *et al.* (2010); Hackett *et al.* (2012); Hawkley *et al.* (2006, 2010a,b); Kahlbaugh *et al.* (2011); Krause-Parello (2008, 2012); Luo *et al.* (2012); Nezlek *et al.* (2002); Ong *et al.* (2012); Perissinotto *et al.* (2012); Poulin *et al.* (2012); Routasalo *et al.* (2009); Shankar *et al.* (2011, 2013); Sorkin *et al.* (2002); Steptoe *et al.* (2004, 2013); Theeke *et al.* (2012); Theeke and Mallow (2013); VanderWeele *et al.* (2011, 2012); Zebhauser *et al.* (2013); Fessman and Lester (2000); Adams *et al.* (2004); Norman *et al.* (2013)
De Jong Gierveld scale	de Jong Gierveld (1987)	Eleven-item scale, combining emotional and social loneliness	Alma *et al.* (2011); Jongenelis *et al.* (2004); La Grow *et al.* (2012); Martina and Stevens (2006); Newall *et al.* (2013); Wilson *et al.* (2007); Han and Richardson (2010)
Single item		Item from the CES-D scale of depressive symptoms	Ayalon and Shiovitz-Ezra (2011); Beeson *et al.* (2000); O'Luanaigh *et al.* (2011, 2012); Tiikkainen and Heikkinen (2005); Kvaal *et al.* (2013); Theeke (2010b).
		Item on the frequency of feelings of loneliness	Conroy *et al.* (2010); Holmen and Furukawa (2002); Losada *et al.* (2012); Nummela *et al.* (2011); Park *et al.* (2013); Patterson and Veenstra (2010); Paul *et al.* (2006); Stephens *et al.* (2010, 2011); Tilvis *et al.* (2011); Holwerda *et al.* (2012)

Adapted from O'Luanaigh and Lawlor (2008).

gated at-risk population groups and 15% looked at the mediating effects of isolation or loneliness between stress and health (Lefrançois *et al.* 2000, Paul *et al.* 2006, Aanes *et al.* 2010), between depression and health (Bisschop *et al.* 2004, Wang *et al.* 2006), or between alcohol consumption and all-cause mortality (Greenfield *et al.* 2002). Describing or evaluating an intervention was the aim of 7% of studies. The level of health service use of isolated older people was investigated in 2% of papers. A similar proportion of papers described the health of isolated older people. In terms of the issue studied, 53% of the 128 papers focused on loneliness and 21% on social isolation.

Associations with health outcomes

A wide range of health outcomes was examined (Table 4). Overall, we found a balance between mental health and physical health. Across the 128 studies, only two did not find a negative association between social isolation or loneliness and health (Wattanakit *et al.* 2005, Wilby 2011). It should be noted that a number of studies looked at the impact of isolation and loneliness on biomarkers such as cortisol levels or C-reactive protein (a marker of systemic infection) (10 studies in total; 80% published between 2010 and 2013).

The most commonly studied outcome was depression, followed by cardiovascular health. We report here findings for these two outcomes only (Table 5). We chose this focus because depression and cardiovascular are major contributors to the burden of disease in old age (Marengoni *et al.* 2008).

In our sample, 75% of studies on depression looked at loneliness, whereas 72% of studies on cardiovascular health investigated social isolation. Important variations were also found in terms of study design. Only 25% of papers investigating depression used longitudinal data, compared to almost half of the studies focused on cardiovascular health. Further details of these studies are provided in Appendix S1.

Out of the 32 papers on depression, 25 looked at its association with loneliness. A difficulty is that the two concepts are overlapping, and loneliness may be a symptom of depression. However, recent literature has found depression and loneliness to be separate entities (Stek *et al.* 2005). The evidence reviewed clearly shows that loneliness is an independent risk factor for depression in old age (Alpass and Neville 2003, Adams *et al.* 2004, Paul *et al.* 2006, Theeke *et al.* 2012). Longitudinal research has confirmed these findings: loneliness is an independent risk factor for depression, controlling for a number of covariates such as demographic characteristics, marital status, social isolation and psychosocial risk factors (Cacioppo *et al.* 2010). Gender differences were also consistently reported. For instance, the detrimental effect of living alone on depression was more often due to loneliness for men than for women (Park *et al.* 2013).

Table 4 Health outcomes studied*

Outcome	Number of studies	Percentage of studies
Depression	32	25
Cardiovascular health	15	13
Quality of life and well-being	15	13
General health and physical function	11	9
Biological measures	10	8
Health and mental health	9	7
Mortality	6	4
Cognitive function	5	4
Mental health	4	3
Dementia	3	3
Disability	2	2
Stress-related reactions	2	2
Substance abuse	2	2
Anxiety	1	1
Passive death wishes	1	1
Physiological processes	1	1
Diabetes	1	1
Unspecified	1	1
Total	121	100

*Seven studies on service use and at-risk groups are excluded from this table.

Only three studies investigated the impact of social isolation on depression. Sjoberg *et al.* (2013) found interesting differences between two Swedish cohorts of older people: frequency and perception of social contacts were related to depressive symptoms in the first cohort but not in the second. A mixed-method study of chronic depression in older British Pakistani women found that the persistence of depression was partly explained by social isolation (Gask *et al.* 2011). Interestingly, one of the two studies which did not find an association between isolation and health focused on depression: Wilby (2011) found that depressed older people were not socially isolated but were on the contrary more likely to report contacts than non-depressed respondents. To explain these findings, the authors emphasised the need to better understand the quality and meaning of different types of social relations in old age.

Cardiovascular health was the focus of 13% of the studies included in the review. Social isolation has been consistently found to be associated with coronary artery disease (Brummett *et al.* 2001), chronic heart failure (Friedmann *et al.* 2006), congestive heart failure (Murberg 2004) and hospitalisation due to heart failure (Cene *et al.* 2012). In addition, two studies researched the impact of loneliness on cardiovascular health. Both reported that loneliness was associated with cardiovascular risk factors (Sorkin *et al.* 2002, Kamiya *et al.* 2010). Differences across population groups have not been well-researched to date, but Wang *et al.* (2005, 2006) did find an association between social isolation and the progression of coronary artery disease, specifically among women.

Table 5 Overview of the characteristics of the studies focused on depression and cardiovascular health

	Number of studies	Percentage of studies
Depression		
Study setting		
Community-based	27	84
Facility-based	5	16
Study design		
Cross-sectional	18	57
Longitudinal	8	25
Mixed methods	2	6
Other	2	6
Qualitative	1	3
Randomised control trial	1	3
Focus		
Loneliness	26	75
Social isolation	3	16
Other	2	9
Outcome measure		
CES-D scale or its revised version	20	62
Geriatric depression scale	8	26
Other scales*	2	6
DSM-IV medical diagnosis	2	6
Cardiovascular health		
Study setting		
Community-based	14	94
Facility-based	1	6
Study design		
Cross-sectional	7	47
Longitudinal	7	47
Mixed methods	1	6
Focus		
Loneliness	2	14
Social isolation	11	72
Other	2	14
Outcome measure		
Cardiovascular and urinary measures†	9	60
Medical diagnosis	4	27
Medical records‡	2	13

*Other depression scales found in the reviewed literature include for instance the Hamilton Rating Scale for Depression, the Psychiatric Symptom Index or the Zung Depression Scale.
†Including the measurement of hypertension and cardiovascular activity, heart failure survival score, cardiac index, arteriography and angiography.
‡Including reason for hospitalisation and cause of death.

Mechanisms and causal links

Potential mechanisms between isolation, loneliness and health were the focus of 15% of the studies. These depend on the outcome being studied, but a number of studies have suggested that health behaviours (Cacioppo *et al.* 2002, Eng *et al.* 2002), poorer sleep quality (Cacioppo *et al.* 2002) and vital exhaustion (Eng *et al.* 2002) were potential mediators between loneliness and a range of physical health outcomes. Other studies have investigated the role of social mechanisms such as perceived togetherness (Tiikkainen and Heikkinen 2005).

A third of the studies investigated causal links between isolation, loneliness and health. The use of longitudinal data enabled the issue of reverse causality between loneliness, isolation and health to be (partially) addressed. The evidence is mixed. Green *et al.* (2008) found a cross-sectional association between social networks and cognition and functional status in old age, but not a longitudinal association. Out of 42 studies which used panel data, 23 provided a basis for inference about causal links by using, for instance, a cross-lagged panel analysis (e.g. Cacioppo *et al.* 2010, Hawkley *et al.* 2010b, Luo *et al.* 2012) or by adjusting for health status at baseline (e.g. Michael *et al.* 2001, Eng *et al.* 2002, Bisschop *et al.* 2003, Patterson and Veenstra 2010, Perissinotto, Stijacic Cenzer and Covinsky 2010, Ayalon and Shiovitz-Ezra 2011, Nummela *et al.* 2011, Holwerda *et al.* 2012, Udell *et al.* 2012, Shankar *et al.* 2013).

The issue of reverse causality was particularly salient in the case of depression. Out of the 32 studies which looked at depression, eight used longitudinal data and implemented appropriate analytical strategies to infer causal links. Again, the findings were mixed. Luo *et al.* (2012) found that loneliness both affected and was affected by depression and functional limitations over time. Cacioppo *et al.* (2006) also demonstrated that loneliness and depressive symptoms in old age have strong reciprocal impact. A similar effect has been found between loneliness and subjective well-being in old age (VanderWeele *et al.* 2012). In contrast, cross-lagged panel analysis showed that loneliness predicted subsequent changes in depression but not vice versa (Cacioppo *et al.* 2010).

Life course approaches also provided interesting evidence: the detrimental impacts of early trauma on pulse pressure were partially dependent on the level of perceived social isolation in old age, as older adults with low isolation levels did not display a significant association between early trauma and the health outcome (Norman *et al.* 2013).

Differential impact of isolation and loneliness

Eleven studies focused on the differential impact of isolation and loneliness, with 75% published since 2010. Among these studies, 54% used longitudinal data. Although no clear pattern could be discerned due to the small number of studies, mortality and biological processes appeared to be the most commonly studied health outcomes in this area.

To date, results have been mixed. Tilvis *et al.* (2011, 2012) found that groups of older people who are isolated or lonely only partially overlap and that only loneliness (and not social isolation) was an independent mortality risk factor in old age. Similar findings were reported in the Netherlands: feelings of loneliness rather than social isolation were found to be a major risk factor for increased mortality in older men (Holwerda *et al.* 2012). Steptoe *et al.* (2013) reached the opposite conclusion using UK data, as the effects of loneliness in their study on mortality were not independent of the demographic characteristics and health status of the respondents, contrary to the effects of social isolation. Other studies have found that both isolation and loneliness were independent risk factors for a range of health outcomes (Shankar *et al.* 2011, 2013, Coyle and Dugan 2012).

Interventions

Associations between social isolation, loneliness and health have received relatively little attention in the intervention literature, and the results of studies were quite modest. There have been studies looking at other outcomes, including a reduction in loneliness itself. We found only nine studies (7%) that evaluated interventions.

The first type of intervention covered was befriending initiatives. One of these programmes – focused on older women – reported success in attracting lonely older people but not in improving the well-being of participants (Martina and Stevens 2006). Different results were found for a club targeting men in a care home, as participants reported a significant reduction in their depression and anxiety levels (Gleibs *et al.* 2011). A randomised control trial looking at the effects of psychosocial group rehabilitation on social functioning, loneliness and well-being of older people also had mixed results. Routasalo *et al.* (2009) reported that a large proportion of participants had found new friends via the programme and that their well-being levels increased significantly. However, their loneliness scores were not affected by taking part in the programme, suggesting that there are other mechanisms at play. Similar results were found for group activities. A randomised control trial of a model of restorative home care on physical health and social support showed significant improvements in physical function but no changes in perceived levels of social support (Parsons *et al.* 2013). Kahlbaugh *et al.* (2011) measured the effects of playing console games on physical activities, loneliness and mood: older people who engaged in games reported lower levels of loneliness, but no difference was found with the control group in terms of life satisfaction or physical activity.

Another type of intervention was professionally-led support for isolated carers. Telephone-based support for female carers of people with dementia was found to be associated with lower isolation and depression after 6 months for older carers (Winter and Gitlin 2006).

Finally, a number of promising trials were underway at the time we conducted this review. The Senior Connection programme fosters peer companionship for older adults, with the aim of reducing suicide risk in later life: preliminary results from a randomised control trial suggest that socially disconnected older adults were at considerably higher risk of suicide (Van Orden *et al.* 2013).

Service use

We found only three studies that focused on the level of health service use of isolated or lonely older people, only one using longitudinal data. Social isolation was found by Mistry *et al.* (2001) to predict re-hospitalisation among isolated older American veterans. Burr and Lee (2013) examined the association between social relationships and dental care service use among older adults: older people who exhibit loneliness and are under financial strain were less likely to visit a dentist. Finally, gender differences were reported. Lower levels of isolation and a supportive environment were predictive of receiving preventive home visits for older Danish women but not for their male counterparts (Avlund *et al.* 2008).

At-risk groups

One third of the studies included in the scoping review explicitly explored differences across population groups. As reported previously, considerable gender differences are found in terms of the association between isolation, loneliness and health. Two-thirds of the papers which looked at differences across population groups focused on gender. The findings were mixed. For example, Zebhauser *et al.* (2013) found that, although levels of loneliness were equally distributed among men and women in their study, loneliness had a detrimental impact only on the mental health of men. In contrast, another study found that women were more sensitive to the impact of loneliness on biological responses (Hackett *et al.* 2012). A potential explanation is that men and women experience different types of loneliness, with different impacts on their physical and mental health (Nummela *et al.* 2011).

Differential effects across age groups were the focus of 16% of the studies. For instance, Ayalon and Shiovitz-Ezra (2011) found that loneliness is a major risk factor for passive death wishes for people aged 50 and over, but that the effect was not noticeable for respondents aged over 75.

In recent years, differences by socioeconomic or ethnic backgrounds have also started to be investigated. For example, a US study found that Hispanic respondents who were socially isolated had a greater risk of increased left ventricular mass compared to isolated older people from other ethnic backgrounds (Rodriguez *et al.* 2011). Poulin *et al.* (2012) also showed that the association between perceived support and depression was stronger for elderly American people than for elderly Chinese people.

Finally, a number of studies focused on groups at higher risk of isolation and loneliness and of associated negative health outcomes, including older people who are cancer survivors (Jaremka *et al.* 2013), unpaid carers (Jaremka *et al.* 2013), and substance users (Smith and Rosen 2009) who are HIV-positive (Grov *et al.* 2010) or who have a history of institutionalisation (Smith and Hirdes 2009).

Discussion

We set out to describe the available literature on the relationships between social isolation, loneliness and health outcomes. The research evidence on these associations has significantly expanded since 2000. We found that the majority of the available evidence comes from the USA and has focused on loneliness. It should be noted that a growing number of studies are concerned with the differential impacts of loneliness and isolation on health. The most researched outcomes are depression and cardiovascular health. Almost all studies included in our review found that social isolation and loneliness have detrimental effects on physical and mental health in old age. Although limited in number, longitudinal designs have allowed researchers to investigate potential mechanisms and causal pathways.

Our review highlights a number of gaps in the evidence base. First, a lack of consistency in the definition and measurement of isolation and loneliness considerably limits the comparisons that can be made between studies, and hence the broader conclusions that can be drawn. Isolation and loneliness are multidisciplinary concepts and to date there is no agreement across disciplines as to the best way to define or measure them. Loneliness and social isolation are also linked to other concepts such as the availability of social support or lack thereof (e.g. social capital or social network). As noted by Valtorta and Hanratty (2010), this has contributed to the richness of the research findings but potentially limits their usefulness to policy makers and practitioners. Differences in measurements are also problematic. Measures of loneliness, for instance, range from single-item questions to 20-item scales designed to measure different dimensions. Although previous studies have shown that a single-item measure correlates strongly with more sophisticated scales (Victor *et al.* 2005), recent research has emphasised the importance of contrasting different dimensions of loneliness (Coyle and Dugan 2012). The UCLA and de Jong Gierveld scales are the most commonly used measures of loneliness. A recent assessment of both scales has shown the relative superiority of the de Jong Gierveld scale for the study of middle-aged and older adults (Penning *et al.* 2013).

There are similar debates in relation to social isolation (Cornwell and Waite 2009). Fiori *et al.* (2006) stress the importance of combining structural (e.g. number of contacts) and functional (e.g. type and quality of support received) aspects of social isolation. There is at least one interesting way forward. As noted by O'Luanaigh and Lawlor (2008), integrating research on the drivers of loneliness and isolation with research on their impacts on health would allow researchers to understand better which dimensions are crucial to include in their studies. Indeed, very broad and general measures that fail to distinguish between isolation, feelings of loneliness and their different dimensions may not be able fully to detect the impacts on physical and mental health of older adults (Coyle and Dugan 2012), and therefore could ultimately hold back development of effective interventions.

Second, only a third of the studies included in the review used a longitudinal design. The fact that most studies are cross-sectional means that still relatively little is known about mechanisms and causal links. More longitudinal studies are needed to disentangle the independent or interacting effects of loneliness and isolation on health. A better understanding of these mechanisms is crucial for designing appropriate interventions. Indeed, results from longitudinal studies have shown that the experiences of loneliness and isolation are not uniform across the life course. On the contrary, older people may become lonelier or more isolated, be chronically isolated or become so because of trigger events such as retirement or bereavement (Ha and Ingersoll-Dayton 2011, Bekhet and Zauszniewski 2012). Studies adopting a life course approach are also needed as they can provide very useful insights on potential triggers of loneliness (Savikko *et al.* 2005), which have to be considered for the design of interventions.

Health and social care service use by isolated older people is also under-researched. Available studies focusing on other population groups provide helpful insights for future research. A Dutch study found that general (medical) practitioners acknowledged the importance of patients' feelings of loneliness in their daily practice but that they had difficulty responding to these feelings and faced a lack of therapeutic options. The authors suggest that a distinction between chronic and transitory loneliness is helpful for general practitioners (van der Zwet *et al.* 2009). Another study suggests that more isolated people in the USA have lower access to adequate health information (Askeslon *et al.* 2011), while a Canadian study argued that front-line health professionals such as nurses have a role to play (Wilson *et al.* 2011).

Our review also identified a paucity of research on population sub-groups, despite evidence of ethnic and socioeconomic differences in the impact of loneliness and isolation on health. It should also be noted that the available evidence focuses almost exclusively on individual-level analyses. We suggest that to understand the scope and magnitude of the impact of loneliness and isolation on health, future research should further take into account ecological factors such as the characteristics of communities and neighbourhoods where older individuals live. 'Ageing-in-place' policies have become a key component of European strategies for older people, on the grounds of both concerns about public expenditure as the population ages and the desire of older people to remain autonomous (Means 2007, Wiles *et al.* 2012). In that context, thinking about isolation and loneliness together with access to transport, health, community and local social services is crucial.

Finally, we identified little published work on interventions which have been evaluated for their impacts on health outcomes, clearly indicating a gap for evidence-based practice. Since 1984, nine reviews of the loneliness intervention literature have been published (Rook 1984, McWhirter 1990, Cattan & White 1998, Findlay 2003, Cattan *et al.* 2005, Perese and Wolf 2005, Hawkley and Cacioppo 2010, Theeke 2010a, Hagan *et al.* 2014). Most of these reviews consider possible ways to reduce loneliness and isolation, and only one focuses explicitly on the impact on health outcomes (Cattan *et al.* 2005). It is not easy to draw out consistent messages on the most successful methods from these reviews. According to Cattan *et al.* (2005), only interventions with an educational element succeeded in reducing loneliness among older people, whereas one-to-one interventions were less successful. In contrast, Findlay (2003) found a positive effect only for one-to-one interventions. More recently, Hagan *et al.* (2014) have identified 17 studies relating to loneliness interventions. Out of these, four studies (three on new technologies such as web-based communications, one on group interventions) identified significant reductions in loneliness.

It was equally difficult to draw a consistent message from the evaluations considered in the present review. This is likely to be due to the difficulty of adequately measuring concepts as complex as social isolation and loneliness in old age. As noted above, the lack of exploration of the societal and policy contexts within which these interventions are operating also renders it difficult to draw firm conclusions about these interventions.

As the findings of further longitudinal research are becoming available, potential causal mechanisms have to be considered in the design of these interventions. A clear conceptual model of loneliness or isolation is also needed as different target populations will potentially respond differently to interventions aimed at reducing social or emotional loneliness. As noted by Hawkley and Cacioppo (2010), a crucial question is whether modifying the feeling of loneliness can have an impact on health. To date, the available evidence is insufficient to provide an answer, and this should be a priority for future research.

Our scoping review has both strengths and weaknesses. It covered a broad range of health outcomes and included both loneliness and isolation as risk factors for poor health in old age. However, it has two main limitations, with implications for the scope of the evidence covered. First, we only included studies with English language abstracts and we limited our search to western countries. A number of relevant articles focused on South Asian countries, for example, have been excluded from this review as the limited research available points to important cultural differences in the meaning and experience of loneliness and isolation (Rokach *et al.* 2001). Also, we did not include 'grey literature' or doctoral theses. Second, we conducted a scoping review and not a systematic literature review. In that sense, we did not assess or exclude papers based on their quality.

Conclusion

Social isolation and loneliness are common among older people and can be both negatively associated with mental and physical health, although still relatively little is known about causal links. Our scoping review has shown that a sizeable body of literature, coming from a variety of disciplines and making use of a range of methods, is focused on assessing the associations between isolation, loneliness and health. An important limitation to the development of the evidence base for both researchers and policy makers is the diversity of definitions and measurements. One way forward would be to pool the evidence from the literature on the drivers of isolation and loneliness in old age and the research on their impact on health, so that important domains and dimensions are measured. There is also a challenge in relation to interventions, as data are still very limited. To date, the evidence is not sufficient to determine whether modifying social isolation levels or feelings of loneliness will have an impact on subsequent health. Better understanding of the causal pathways through which loneliness and isolation affect health is needed to inform the development of appropriate interventions.

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An asterisk (*) indicates that the reference has been included in the scoping review.

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Could this Irvine neighborhood be the blueprint for a more fire-resistant L.A.?

An aerial view of Orchard Hills in Irvine, where homes were planned and built to be fire-resistant. The master-planned community, which straddles the wildland-urban interface, was in the path of the 2020 Silverado fire but escaped damage.

By Jack Flemming
Staff Writer
Photography by **Allen J. Schaben**

Feb. 19, 2025 3 AM PT

Four years before the Palisades and Eaton fires ravaged L.A., Irvine braced for a blaze of its own.

A bone-dry summer left the landscape parched and primed to ignite as Santa Ana winds roared through the region at 80 mph. On the morning of Oct. 26, 2020, the Silverado fire erupted.

Firefighters deployed. The city initiated its emergency plan. Residents of Orchard Hills — a master-planned community straddling the wildland-urban interface and sitting in the path of the quickly growing fire — fled, not knowing whether they'd ever see their homes again.

Orange County Fire Authority firefighters work to protect homes in the Orchard Hills neighborhood of Irvine during the Silverado fire in October 2020.

All of them would. The flames licked at the neighborhood's outskirts, toasting a few leaves at the perimeter, but didn't damage a single residence in the community.

The firefight was an unequivocal victory — a product of the meticulous planning of the neighborhood, the design of its homes and the painstaking plan set in place by the city.

As L.A. looks to fortify itself against future fires, Orchard Hills could serve as the road map to get there.

Of course, the comparison isn't exact. Irvine is a newer city with modern homes built using lessons learned from dozens of deadly fires over the years. Altadena and Pacific Palisades are communities with tree canopies and century-old houses navigated by narrow, sometimes winding roads chock-full of vegetation.

But as climate change sees Southern California burn time and time again, experts say that success stories should be extracted and mined for all they're worth.

You could argue that Orchard Hills' fire resistance began a century ago, when Irvine Valencia Growers planted an avocado orchard in the hills above the community. The orchard grew into one of the nation's largest avocado producers in the decades since, with roughly 100,000 trees across 800 acres.

It offers the neighborhood a lot more than guacamole.

"The orchards have a built-in irrigation system, so when a fire starts, the landscape is already watered," said Sean Doran, a fire captain with the Orange County Fire Authority.

Doran, who fought the Silverado fire, said his team had a leg up thanks to a decade-long partnership between Orchard Hills and the fire authority stretching back to when the developer, Irvine Co., broke ground in 2014.

In Irvine, building plans must go through the fire authority as a condition of a developer's conditional use permit.

"It's inherent in the process," Doran said. "If you're a developer, at some point you're going to be walking through our door."

The partnership between the developer and the fire authority brings strict rules for what can and can't be built, and many homebuyers are grateful for the regulations.

Ron Nestor, an Orchard Hills resident and senior principal at William Hezmalhalch Architects, noticed a small coil of smoke while walking his dog on the morning of the Silverado fire. An hour later, he evacuated his home.

Ron Nestor and his dog, Enzo, enjoy his backyard in Orchard Hills in Irvine this month.

He was gone for three days. When he returned, there was no damage whatsoever.

“It’s a testament to the way this place was planned,” he said.

When Nestor moved into Orchard Hills five months before, the neighborhood’s fire plan, which Irvine Co. touts on its website, was a factor for moving in. The parameters were created by the developer, the fire authority and a third-party fire behavior analyst who examined wind patterns, topography and fire history.

Orchard Hills is designed with numerous levels of defense for an oncoming fire: in the open land surrounding the neighborhood, in the yards and in the homes themselves.

It starts with the fuel modification zone — open space around the community that can be modified to reduce fire risk by replacing combustible vegetation with fire-resistant shrubs. Orchard Hills' zone is filled with prickly pear cacti, Japanese honeysuckle and Formosa firethorn.

Orange County's fire guidelines call for three different tiers of fuel modification zones, with different construction requirements and shrub removal rates typically extending up to 200 feet outside the perimeter. If a developer wants to tighten that zone down to 100 feet, they have to make up for it in other ways, such as building an exterior wall around the neighborhood, or adding extra fortification on homes at the edge of the neighborhood, so they don't ignite and bring the fire inward.

Open space around Orchard Hills is filled with prickly pear cacti, Japanese honeysuckle and Formosa firethorn.

“Not everything is concrete, so we can give some leeway in one area and tighten up another,” Doran said. “We’re here to support a fire-hardened community. Whatever makes that happen is a success for both parties.”

In the case of Orchard Hills, the fire authority worked with farmers to tweak the spacing of avocado trees to have fewer trees per acre and cleared the brush and sage in the orchards to limit flammable objects in the 170-foot fuel modification zone.

The next level of defense comes where the open space meets the outer rim of homes.

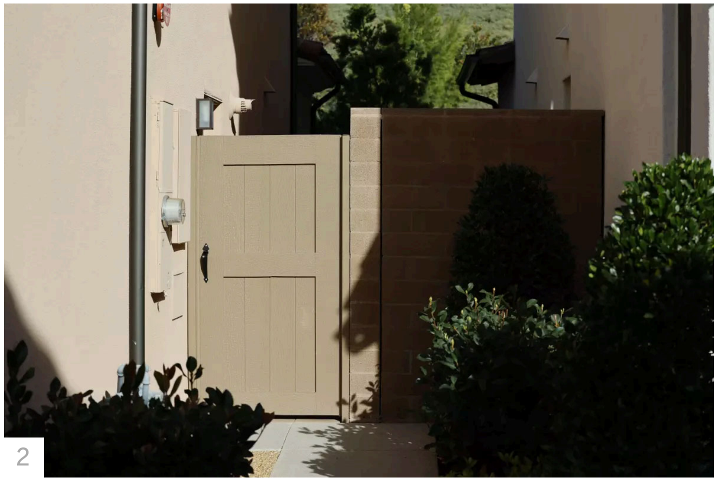
Irvine Co. erected a 6-foot wall around an enclave on the north part of the neighborhood — where a Santa Ana wind-driven fire would most likely hit first — to protect the most vulnerable properties from radiant heat and keep low-flying embers out of the development.

It beefed up the homes along that rim beyond the fire-hardening standards required in the rest of the neighborhood. These sections call for fire-rated exterior doors and stringent guidelines on outdoor features such as decks and trellises.

The last line of defense comes inside the neighborhood.

You won’t find wood-shingled Craftsmans in Orchard Hills. In fact, there’s not much exposed wood at all, and if there is, it’s treated to be fire-retardant. Masonry walls and vinyl fences separate properties, and the few wooden gates are isolated by metal posts so they can’t spread fire to the house, Nestor said.


1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1. A view of asphalt shingle vents that are placed on roof tiles on homes. **2.** Masonry walls and vinyl fences separate properties, and the few wooden gates are isolated by metal posts so they can't spread fire to the house. **3.** Ron Nestor's home, which was built to be fire-resistant.

Orchard Hills homes are constructed with two factors in mind: radiant heat and ember intrusion. Radiant heat is the heat projected by fire; if a home's exterior is made of flammable materials, the house can heat up to the point of igniting. So houses are mostly Mediterranean, wrapped with stucco or fiber cement — noncombustible materials — with a few splashes of stone and brick thrown in.

The other factor, ember intrusion, is when embers enter a home through an opening and ignite it from within. Orchard Hills homes are outfitted with tempered glass, which is stronger than single-pane windows that tend to break in fires. Roof vents have mesh filters that block embers. And roofs are laid with either concrete or clay tile. The concrete tile lies flat, stopping embers from entering. With the barrel clay tiles, the opening on the bottom of each row is plugged with a bird stop, which keeps out birds — and embers.

The HOA guidelines are rigorous and firm, dictating acceptable plant types and where trees are allowed to be planted. Nestor said he appreciates the precautionary measures.

"People are confident that their homes will survive because when the neighborhood was put to the test, it held up," Nestor said. "Everything went exactly according to plan."

Doran said the fuel modification zone, combined with the wall, helped stop the Silverado fire in its tracks.

“I watched the fire burn up to the edge of the wall and then die down,” he said.

Fire after fire has shown that one of the most crucial aspects of the emergency are the roads. In the Camp fire in 2018, eight of the 84 people who died were stuck in a traffic jam when the flames roared over them.

Most of Irvine is navigated by smooth, wide roads, making it much easier for people to evacuate and firetrucks to get to the fire. In Orchard Hills, 7-foot-wide paths run behind the properties, so fire crews and vehicles can better access the back sides of homes.

Bobby Simmons, Irvine’s emergency services manager, helps coordinate the city’s strategy.

In 2019, in the wake of the Camp and Woolsey fires and a year before the Silverado fire, Simmons helped form a 25-person initiative to create an all-inclusive wildfire plan so if one ever broke out in Irvine, every city department would know its role exactly.

Firefighters defend homes in Orchard Hills in 2020. The Silverado fire licked at the Irvine neighborhood’s outskirts but didn’t damage any houses in the community.

The police department dispatches patrols to specific intersections to aid evacuations. The traffic management center remotely controls signals, avoiding traffic jams by turning all the lights green for street lanes going away from the fire. Simmons said the Office of Emergency Management mobilizes an emergency operations center and activates an emergency landing page on its website leading to a real-time evacuation map — with bandwidth for more than 3 million visitors over three days without crashing.

“We developed the plan, challenged it and tested it so much that when rubber met the road on Oct. 26, we provided a structured process for a chaotic event,” Simmons said. “All things considered, it went smoothly.”

During the Silverado fire, the city evacuated 90,000 people in four hours from northern Irvine communities such as Orchard Hills and Portola Springs.

The Silverado fire turns the sky orange as it burns close to a home in Orchard Hills in 2020.

Ultimately, the Silverado fire still took a toll. Although there was no damage in Orchard Hills, five structures were destroyed elsewhere, 11 were damaged, and two firefighters were critically injured. And although traffic quickly flowed out of the neighborhoods, cars were backed up for more than a mile because the lights getting onto the 5 Freeway were controlled by Caltrans, not Irvine, and couldn't be programmed to accept the droves of cars coming from the northeast.

There’s always more to learn.

“Now, we identify the lessons we learned to get ready for the next one,” Simmons said.

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Dry Vegetation Fuels L.A. Fires as Wind Speeds Drop

The largest of the blazes expanded east on Friday, even as wind speeds, which fueled the initial blaze, fell to normal levels.

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By Amy Graff, Yan Zhuang and Shawn Hubler
Amy Graff reported from Los Angeles

Jan. 11, 2025

The focus this week has been on how extreme winds have fueled the most destructive fires in Los Angeles's history. But that's not the only concern.

On Friday, even as slowing wind speeds increased hopes that firefighters would contain the blazes, dry vegetation and steep terrain pushed the Palisades fire, the biggest, east, putting a new swath of Los Angeles under mandatory evacuation orders.

The blaze was burning along the tops of the ridges of Mandeville Canyon, said Kenichi Haskett, a division chief with the Los Angeles County Fire Department, on Friday night. The fire tore through a steep area full of dry vegetation and threatened the neighborhood of Encino in the north.

The spread was being driven by the landscape rather than wind, Mr. Haskett said. “We’re not getting strong winds the way we got on Tuesday and Wednesday.” The Palisades fire has now burned more than 21,000 acres in five days.

The rains that usually fall in autumn and early winter did not come, leaving most of Southern California bone dry and leaving vegetation primed to burn. Most locations south of Ventura County have recorded about a quarter-inch of rain or less in the past eight months, while the Los Angeles area has received only sprinklings of rain since April.

That means the Santa Ana winds, the strong, dry gusts that have driven the wildfires, have had a particularly dramatic effect. Even as they have subsided, the parched vegetation has continued to fuel the Palisades fire, experts said. Stronger winds are expected to return to Los Angeles and Ventura counties Saturday afternoon, reaching the highest speeds overnight into Sunday morning and heightening the risk of rapid wildfire spread.

Wind speeds over the fire were light — under 15 miles per hour — on Friday night, said Dave Gomberg, a meteorologist with the National Weather Service. In comparison, Wednesday saw wind gusts of over 90 m.p.h. “I think a big component is the fuels are exceptionally dry,” Mr. Gomberg said of Friday’s expansion.

The Palisades fire was “following the terrain and the fuels,” said Craig Clements, director of the Wildfire Interdisciplinary Research Center at San Jose State University. Fires thrive in hilly terrain and move faster uphill than downhill, he said, adding, “The steeper the terrain, the faster the fire can go.”

The fire chewing its way through Mandeville Canyon is a “plume-dominated fire,” that is being fueled by its own wind, said Redondo Beach Fire Chief Patrick Butler, a former assistant chief for the Los Angeles Fire Department who has led the response to many Southern California fires. Such blazes often shoot upward and then collapse, scattering embers for miles in concentric patterns, he said.

On Friday evening, ash was falling in the Brentwood neighborhood to the south of the canyon.

Wildfires are notoriously hard to fight in Mandeville Canyon, which has poor radio communication and an extremely narrow road, Mr. Butler said: “There’s basically one way in and one way out.”

Yan Zhuang is a Times reporter in Seoul who covers breaking news.

Shawn Hubler is based in Sacramento and covers California news, policy trends and personalities. She has been a journalist for more than four decades.

Multi-population puma connectivity could restore genomic diversity to at-risk coastal populations in California

Running title: Population genomics of California pumas

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AUTHOR CONTRIBUTIONS

KDG, MRB, JAD, and HBE designed the study. KDG, RBG, JLR, and MEFL performed laboratory research. MRB, TWB, SPDR, JAS, and JAD performed field research. KDG, RBG, MRB, MEFL, and HBE analyzed the data. KDG, RBG, MRB, TWV, SPDR, JAS, JLR, JAD, MEFL, and HBE wrote the paper.

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ABSTRACT

Urbanization is decreasing wildlife habitat and connectivity worldwide, including for apex predators, such as the puma (*Puma concolor*). Puma populations along California's central and southern coastal habitats have experienced rapid fragmentation from development, leading to calls for demographic and genetic management. To address urgent conservation genomic concerns, we used double-digest restriction-site associated DNA (ddRAD) sequencing to analyze 16,285 genome-wide single-nucleotide polymorphisms (SNPs) from 401 pumas sampled broadly across the state. Our analyses indicated support for 4–10 geographically nested, broad- to fine-scale genetic clusters. At the broadest scale, the 4 genetic clusters had high genetic diversity and exhibited low linkage disequilibrium, indicating pumas have retained genomic diversity statewide. However, multiple lines of evidence indicated substructure, including 10 finer-scale genetic clusters, some of which exhibited fixed alleles and linkage disequilibrium. Fragmented populations along the Southern Coast and Central Coast had particularly low genetic diversity and strong linkage disequilibrium, indicating genetic drift and close inbreeding. Our results demonstrate that genetically at-risk populations are typically nested within a broader-scale group of interconnected populations that collectively retains high genetic diversity and heterogeneous fixations. Thus, extant variation at the broader scale has potential to restore diversity to local populations if management actions can enhance vital gene flow and recombine locally sequestered genetic diversity. These state- and genome-wide results are critically important for science-based conservation and management practices. Our nested population genomic analysis

highlights the information that can be gained from population genomic studies aiming to provide guidance for the conservation of fragmented populations.

Key words: conservation genetics, mountain lion, nested population structure, population genetics, *Puma concolor,* SNP

INTRODUCTION

Human development is reducing habitat on a global scale, undermining efforts to conserve ecosystem structure and function (Newbold et al., 2016). Reports of fragmented wildlife populations and the increasing need for human housing and associated agriculture and energy have emphasized the necessity for development to avoid impacting the long-term sustainability of wildlife populations (Jordan et al., 2007; Kiesecker et al., 2011; Saha & Paterson, 2008). One of the most developed states in the United States is California, which contains the largest census size with over 39 million people (US Census, 2019). Although the development of California has led to historical extirpations of other apex predators, such as the grizzly bear (*Ursus arctos*; Herrero, 1970) and gray wolf (*Canis lupus*; Schmidt, 1991), the puma (*Puma concolor;* also known as mountain lion and cougar) has maintained a widespread distribution throughout the state (Dellinger et al., 2020a).

The puma is a large-bodied felid that originated in South America, migrated and expanded throughout North America, and experienced a human-induced range restriction to the western United States, with an extant remnant population in Florida (Culver, Johnson, Pecon-Slattery, & O'Brien, 2000). Currently, approximately half of all apparent puma habitat in California is conserved and the remainder could be subject to further development (Dellinger et al., 2020a). Much of the inland areas of California have continous stretches of protected habitat (Dellinger et al., 2020a) supporting puma populations with high genetic diversity and large effective populations sizes (Gustafson et al., 2019). However, movement corridors among coastal mountain ranges are increasingly being degraded by human development (Burdett et al., 2010; Suraci, Nickel, & Wilmers, 2020; Zeller et al., 2017). Despite the natural long-range dispersal abilities of pumas (Gonzalez-Borrajo, López- Bao, & Palomares, 2017), interstate highways limit dispersal via avoidance and direct mortality in some urban areas (Riley et al., 2014; Vickers et al., 2015). Although human-caused mortality from vehicle collisions and lethal removal after wildlife–livestock conflicts are concerns (Guerisoli, Luengos Vidal, Caruso, Giordano, & Lucherini, 2020; Torres, Mansfield, Foley, Lupo, & Brinkhaus, 1996), a larger concern for long-term population viability is the genetic isolation of pumas within small or shrinking patches of habitat, which has led to high levels of intraspecific competition and mortality (Benson, Sikich, & Riley, 2020) and low genetic diversity in some areas (Ernest et al., 2014; Gustafson et al., 2019; Riley et al., 2014).

Previous studies have reported that two isolated puma populations in southern California, including the Santa Ana Mountains and the Santa Monica Mountains (**Fig. 1**), had the lowest genetic diversity estimates measured throughout the range of *P. concolor* (Ernest et al., 2014; Riley et al., 2014), apart from the endangered Florida panther (*P. c. coryi*). In both the Santa Ana and Santa Monica Mountains, phenotypic evidence of inbreeding depression has been observed, similar to Florida panthers (Ernest et al., 2014; Huffmeyer, Sikich, Vickers, Riley, & Wayne, In Press; Roelke, Martenson, & O'Brien, 1993). For both populations, freeway traffic is isolating pumas (Ernest et al., 2014; Riley et al., 2014; Vickers et al., 2015) and contemporary gene flow has been severely limited. Detailed pedigree analyses following the immigration of one male into each region showed evidence of natural genetic rescue (Ernest et al., 2014; Gustafson, Vickers, Boyce, & Ernest, 2017; Riley et al., 2014). Although migrant effects were positive, projection models predict the extirpation of these populations in 50 years without enhanced demographic dispersal and gene flow (Benson et al., 2016; 2019).

Recently published genome-resequencing data that included 4 pumas from California, 2 from the Santa Monica Mountains and 2 from the Central Coast North region in the Santa Cruz Mountains, indicated these individuals had ~20–40% of their genomes represented as long runs of homozygosity, resulting from recent inbreeding (Saremi et al., 2019). However, these runs of homozygosity were not shared among individuals, and different populations exhibited different homozygous haplotypes, suggesting genetic restoration (Hedrick, 2005; Tallmon, Luikart, & Waples, 2004) is possible because genetic variation still exists.

The complex distribution of pumas throughout California along a continuum of high genetic diversity populations occupying abundant habitat, to strongly isolated populations displaying evidence of inbreeding depression, requires a thorough characterization of statewide genomic diversity to achieve proper conservation. In this study, our objective was to characterize patterns of genomic diversity at varying geographic scales. Such an approach has the potential to aid conservation strategies because it can identify at-risk, low-diversity local populations that would benefit from restored gene flow within a broader geographic region. We identified 16,285 single-nucleotide polymorphisms (SNPs) from 401 individuals using a double-digest, restriction-site associated DNA sequencing method (ddRAD; Peterson, Weber, Kay, Fisher, & Hoekstra, 2012). Specifically, our aims were to determine population genomic structure, genetic diversity, evidence for selection, and linkage disequilibrium.

METHODS

Sample collection and DNA extraction

We obtained 354 tissue samples collected by the California Department of Fish and Wildlife between 2011–2017 from pumas either hit-by-car (~6%), found dead (~2%), poached (<1%), or through depredation permits (>90%) which had never been used in any previous genetic survey. Samples were well-distributed throughout the state, except for smaller populations in smaller mountain ranges. To bolster our sample size in the Los Angeles region of southern California, we added the only remaining DNA extracts (N = 144) from pumas collected between 2002–2015 (Riley et al. 2014; Vickers et al., 2015). After genomic and bioinformatic filtering (described below), we retained 401 out of 498 samples in the final dataset, which spanned the majority of puma habitat in California, excluding desert regions (**Fig. 1**). For samples that lacked a precise GPS location, we used the nearest address or town where they were collected as their GPS point. Samples were stored at -80˚C until DNA was extracted using Omega Bio-tek Mag-Bind Blood & Tissue DNA HDQ Kits (Omega Bio-tek, #M6399-01) with a manufacturer-designed protocol for the Kingfisher Duo Prime (ThermoFisher Scientific, #5400110) automated DNA purification system. We measured the concentration of DNA from each sample using a Qubit 3.0 fluorometer (Invitrogen, #Q33216) with Qubit dsDNA high-sensitivity kits (Invitrogen, #Q32854).

Double digest restriction site associated DNA library preparation and sequencing

We reduced the genome size of our samples and identified single-nucleotide polymorphisms (SNPs) using modifications to the double digest restriction-site associated DNA sequencing (ddRAD) protocols developed by Peterson et al. (2012). We used a library construction scheme which pooled 48 samples per library based on barcode availability, cost effective multiplexing, and sufficient coverage per individual. For each pooled library, we first normalized DNA concentrations to the sample with the lowest concentration within a library, with the goal to be above 200 ng DNA starting material in 25 µL elution buffer (>8 ng/µL). The library with the lowest normalized starting concentration for each sample had 17.8 ng/µL DNA, whereas the library with the highest starting material had 51.6 ng/µL DNA. We used digestion enzymes and protocols established with previous puma work (Trumbo et al., 2019). After DNA was normalized, we double-digested the DNA from each individual using NlaIII (New England BioLabs, #R0125S) and EcoRI (New England BioLabs, #R3101S) restriction enzymes (37 °C for 3 hours, then held at 4 °C) at manufacturer-recommended enzyme concentrations and used AMPure XP beads (Beckman Coulter, #A63881) at a 1.5X ratio to retain only DNA from the digestion. We omitted the Peterson et al. (2012) DynaBeads cleanup step and again used the Qubit to measure DNA concentrations and to guide another round of normalization. After normalization, the library with the lowest per-sample concentration had 2.1 ng/µL (in 29 µL) and the library with the highest per-sample concentration had 8.1 ng/µL.

We then ligated 48 uniquely barcoded P1 adaptors (e.g., P1.1 through P1.48) and two common P2 adapter pairs (i.e., P2.1 and P2.2) to each sample's double-digested fragments using the protocols of Peterson et al. (2012) to identify individual puma samples. Following ligation with individual barcodes, we pooled all 48 samples into a single tube and used AMPure XP beads to clean the library. We used TE buffer (rather than molecular-grade water) as the final step in this cleanup, which is recommended by the manufacturer for running size selection in the Pippin Prep (Sage Science, Beverly, Massachusetts). We selected fragments ranging from 375–475 bp (including 75 bp of adapters) using 2% dye-free gels run on a Pippin Prep. To minimize random polymerase chain reaction (PCR) duplicate errors, we split the library and ran 5 high-fidelity Phusion (New England BioLabs, #M0530) PCRs for 12 cycles on a SimpliAmp thermal cycler (ThermoFisher Scientific, #A24811). We then recombined the 5 PCR products and used an AMPure XP bead clean up on the amplified library. Sample concentrations after size selection averaged 2.0 ng/µL DNA (range 0.82–3.7) and, after the PCR, averaged 8.2 ng/µL (range 3.6–15.0). We shipped the unfrozen DNA with freezer packs to the University of Oregon's Genomics and Cell Characterization Core Facility (https://gc3f.uoregon.edu/) for 150 bp single-end sequencing on an Illumina HiSeq 4000 (Illumina, San Diego, CA).

Bioinformatic SNP filtering

We ran standard quality control analyses using program *FastQC* v0.11.5 (Andrews, 2010). We used the *process_radtags* program in the *Stacks* v2.55 (Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013) package to de-multiplex the reads based on unique barcodes, to assign each sequence to an individual puma sample, to remove sequences with a Phred quality score below 20 (99% accuracy), and to remove Illumina adapter sequences from the data. We then aligned reads for each individual to PumCon1.0—the *Puma concolor* draft reference genome —using program *bwa* (Li & Durbin, 2009). We identified and filtered SNPs with *Samtools* (Li et al., 2009). We discarded loci with a mapping quality score below 20, minimum base quality less than 20, with more than two alleles at a site, and with a maximum depth greater than 100. We skipped indels and used only a random SNP per read to reduce linkage disequilibrium.

Using *vcftools*, we tested the effects of multiple filtering parameters on our dataset, specifically looking at which parameters produced unreliable and inconsistent heterozygosity estimates, inbreeding coefficients, and relatedness values. We retained loci with a minor allele frequency ≥ 0.05 as lower frequency SNPs could be sequencing error. The relationship between minimum depth of reads per individual and heterozygosity was asymptotic and plateaued at about 3–4 reads. To be conservative, we selected a minimum depth of 4 reads per individual to reliably acquire genotypes based on both alleles. We also retained SNPs that had genotypes for at least 50% of the individuals. We iteratively removed samples with more than 50% missing data to maximize the number of SNPs retained in the dataset. Being more conservative with the percent of missing data decreased the number of SNPs in the final dataset but did not affect heterozygosity estimates, inbreeding coefficients, and relatedness values. We scanned for duplicate samples using relatedness values in *vcftools*, but, as expected, found none because all DNA samples were removed from dead pumas. We also removed two potentially contaminated samples based on negative F statistics in *vcftools*.

In each library of 48 samples, we strategically included puma samples from across a large geographic area so libraries would have no correlation with spatial location. For example, there was no significant difference between mean sample latitudes ($F_{7;309} = 1.108$, $p = 0.358$) or longitudes ($F_{7;309} = 1.533$, $p = 0.155$) among libraries. However, because the southern California libraries constructed from pre-existing extracts were from a small geographic region, there ended up being some latitudinal ($F_{10;395} = 33.76$, $p < 0.001$) and longitudinal ($F_{10;395} = 33.89$, $p < 0.001$) mean differences between those libraries and the libraries constructed from the new samples. However, as indicated below, there were no detectable biases of including the southern California libraries in any analyses.

To test for library-effect biases (i.e., differences among sequencing lanes), we used *BayeScan* to identify outlier SNPs while treating sequencing lanes as "populations" and using a false discovery rate of 0.05 (Foll & Gaggiotti, 2008). There were no outlier loci among any of the libraries, including the southern California libraries. We also assessed bias with various genetic structure analyses. Genotypes resulting from the pre-existing DNA extracts consistently clustered with those genotypes resulting from the new samples collected from southern California. With no apparent library-effect biases, we retained 16,285 bi-allelic variants (mean ± SD = 12,245 ± 2749) with a mean depth at each locus of 11.7 ± 5.1 and a mean depth per locus per individual of 11.7 ± 7.1.

Population structure and outlier loci

We used multiple approaches to identify genetic clusters of individuals, including a linear principal components analysis (PCA) and a spatially-explicit population structure analysis in program R (R Core Team, 2020). We ran the PCA using *adegenet* 2.1.1 (Jombart, 2008) and the structure analysis in *tess3r* 1.1.0 (Caye, Deist, Martins, Michel, & François 2016). We used *adegenet::colorplot* to present linear structure identified by the first 3 principal component axes. In *tess3r*, we ran 20 replicates for each K (1–20) at 100,000 iterations each. We kept the most highly supported model (i.e., "best" based on cross-entropy scores) within each of the 20 replicates. To test for evidence of loci under selection, we identified outlier loci among populations (Narum & Hess, 2011) using *BayeScan* and *tess3r* with the Benjamini–Hochberg statistical correction and the recommended α-value of 0.0001.

Genetic diversity, effective population size, genetic differentiation, and linkage decay

For each genetic cluster identified in *tess3r*, we calculated observed heterozygosity (H_O), gene diversity (H_S), and allelic richness (A_r) using *hierfstat::basic.stats* (Goudet, 2005; Nei, 1987). To test for Wahlund effects within broad-scale clusters, we used t-tests to test for differences between H_O and H_S. We calculated private alleles (A_p) using *poppr::private*_alleles

(Kamvar, Tabima, & Grünwald, 2014). We used *NeEstimator* 2.1 (Do et al., 2014) to estimate effective population size (N_e), using the linkage disequilibrium model, random mating, allele frequencies >0.05, and with a correction factor of 19 haploid chromosomes (Hsu, Rearden, & Luquette, 1963) as recommended by (Waples, Larson, & Waples, 2016). We used *hierfstat::pairwise.neifst* and *hierfstat::pairwise.WCfst* to estimate pairwise genetic differentiation based on F_{ST} according to Nei (1987) or Weir and Cockerham (1984).

We used *Plink* 2.0 (Purcell et al., 2007) to estimate linkage disequilibrium among loci (--ld-window-r2 0 --ld-window 999999 --ld-window-kb 8000). To determine the level of non-random segregation of alleles across the genome, we assessed linkage decay in each genetic cluster by plotting the correlation of loci (R^2) based on genomic distance between SNPs. We correlated loci using binned intervals of 100,000bp from 0 to the maximum scaffold size of PumCon1.0. Meiosis should break up linkage, resulting in low R^2 values. However, populations experiencing strong selection, low mutation, inbreeding, low migration, or strong genetic drift will have higher R^2 values. In short, SNPs that are close together on chromosomes are expected to be correlated (i.e., inherited as chromosomal/haplotype segments), but SNPs far away are expected to assort randomly during recombination. However, if sequences are too similar, which they may be in small and inbred populations, we are not be able to detect events of crossing over despite their occurrence, resulting in higher estimates of linkage disequilibrium, which is still an important indicator of genetic diversity and N_e.

RESULTS

Population structure and outlier loci

We recovered 16,285 SNPs that were randomly distributed among 125 draft-genome scaffolds. The first three axes of the PCA accounted for 14.6% of the variance and indicated there were 4 broad-scale genetic clusters distributed across California (**Fig. 2**). When each puma was plotted on a map of California (**Fig. 2A**), the 4 clusters were geographically concordant with the Sierra Nevada (SN), North Coast (NC), Central Coast (CC), and Southern Coast (SC). The first eigenvector separated the negative-valued CC and SC groups from the positive-valued SN and NC (**Figs. 2B & 2C**). The second eigenvector separated negative-valued CC from positive-valued SC (**Fig. 2B**). Finally, the third eigenvector separated negative-valued NC from all other groups (**Fig. 2C**).

A spatially-explicit population structure analysis indicated that there was broad- to fine-scale nested genetic structure with support for 4–10 genetic clusters (**Fig. 3**). Root mean square error (inset plot in K = 2 panel of **Fig. 3**) and cross-entropy scores (inset plot in K = 3 panel of **Fig. 3**) provide statistical evidence for nested genetic structure; values begin to curve at K = 4 and there is a major increase in variance at K = 5, but there is a steady increase in statistical support at higher K values. However, single pumas formed individual clusters at K > 10 at which point K lost biological meaning. When K was set to 4, the genetic clusters corresponded to the broad-scale genetic groups identified by the PCA (**Figs. 2 & 3**). Briefly, at K = 5, pumas in the Central Coast North (CC-N) emerged; at K = 6, the Eastern Sierra Nevada (ESN) cluster separated from the Western Sierra Nevada (WSN); at K = 7, the Santa Ana (SA) cluster separated from the Eastern Peninsular Range (EP); at K = 8, the San Gabriel–San Bernardino (SGSB) cluster emerged; at K = 9, the Klamath–Cascades (KC) cluster emerged; and at K = 10, the Central Coast South (CC-S) cluster separated from Central Coast Central (CC-C; **Fig. 3**). We observed no significant evidence for outlier loci using the Benjamini–Hochberg statistical correction in *tess3r* nor *BayeScan* for either K = 4 or K = 10.

Genetic diversity, effective population size, genetic differentiation, and linkage decay

For K = 4, calculations of observed heterozygosity (H_O), gene diversity (H_S), polymorphic loci (*Poly*), allelic richness (A_r), and the private alleles (A_p) indicate that the Sierra Nevada cluster had higher genetic diversity than the Southern Coast, Central Coast, and North Coast (**Table 1**). Although significant, the North Coast was the only broad-scale genetic cluster that did not exhibit a strong Wahlund effect (i.e., significantly lower H_O compared to H_S; SN: t=-50.6, p<0.001; SC: t=-48.2, p<0.001; CC: t=-58.5, p<0.001; NC: t=-10.6, p<0.001) or finer-scale substructure. Effective population sizes were not reported for broad-scale clusters because substructure introduced major biases (i.e., near-zero values) into N_e estimates.

Broad-scale genetic clusters were moderately differentiated based on F_{ST} estimates which ranged from ~0.1–0.2 (**Table 2**). The Sierra Nevada cluster was least differentiated from the others and the lowest F_{ST} estimates were between the Sierra Nevada and the North Coast clusters. In contrast, the Southern Coast cluster was the most differentiated from the others and the highest F_{ST} estimates were between the Southern Coast and the North Coast, followed by the

Southern Coast and the Central Coast. At the broad scale, the linkage decay plot indicated that linkage disequilibrium (LD) was lowest in the Sierra Nevada and slightly increased in the Central Coast, Southern Coast, and North Coast clusters (**Fig. 4A**). When ignoring population assignments, California pumas (N = 401) had a LD R^2 of ~0.3 which decreased rapidly to less than 0.1 at a distance of 0.3 Mbp, then approached 0 at farther distances. Nearly the same result was observed in the Sierra Nevada. The Central Coast also had a major reduction in LD with distance but did not fall under 0.1 until ~3 Mbp in distance. In contrast, the Southern Coast and North Coast started with an LD R^2 of ~0.4 which remained above 0.1 even at distance of 8 million bp (**Fig. 4A**).

The nested genetic clusters within the Sierra Nevada — including KC, WSN, and ESN — had the highest genetic diversity estimates, as well as the highest estimates of N_e. Only the WSN had an N_e above 50, a threshold commonly considered to be sustainable over the long-term (**Table 1**; Franklin, 1980). Pairwise F_{ST} estimates among nested genetic clusters within the Sierra Nevada suggested weak substructure, with little genetic differentiation (i.e., pairwise $F_{ST} < 0.05$), indicating substantial gene flow throughout this region (**Table 2**). Within the Sierra Nevada, the ESN showed slightly higher LD than KC or WSN, and all three retained a high proportion of polymorphic loci (i.e., 87–91%).

The nested genetic clusters within the Southern Coast — including EP, SGSB, and the SA — exhibited lower genetic diversity estimates when compared to the Sierra Nevada, as well as large differences when compared to each other (**Table 1**). Estimates were generally lowest in SA, whereas EP and SGSB had similar overall estimates. However, both SA and SGSB had extremely low estimates of N_e. Unlike the Sierra Nevada, nested genetic clusters within the Southern Coast had moderate to strong genetic differentiation from one another (pairwise F_{ST} values ~0.1–0.2; **Table 2**). Except for the moderate differentiation with EP (i.e., pairwise F_{ST} of ~0.1), SA was the most differentiated among the 10 finer-scale genetic clusters (pairwise F_{ST} values range: ~0.2–0.3). The SGSB cluster had relatively lower pairwise F_{ST} estimates with the Sierra Nevada and EP clusters, moderate F_{ST} estimates with CC-C and CC-S, and was more strongly differentiated from the CC-N and NC. The EP cluster showed similar patterns of differentiation but was least differentiated from the geographically adjacent SA and SGSB clusters. Although EP exhibited LD estimates similar to the Southern Coast as a whole, SGSB and SA started with a high LD R^2 of ~0.5 which decreased to just above 0.3 at a distance of 0.3 Mbp, then remained high (above 0.25) at farther distances (**Fig. 4**).

The nested genetic clusters within the Central Coast exhibited the most variation in estimates of genetic diversity (**Table 1**). The CC-C cluster had the highest diversity within the region, including the largest estimate of N_e. The CC-S cluster had intermediate levels of diversity but exhibited the lowest N_e in the region. The CC-N cluster had as low, or lower, genetic diversity estimates than most of the 10 fine-scale genetic clusters examined overall, but had one of the higher N_e estimates outside of the Sierra Nevada. Differentiation within the Central Coast was moderate overall (pairwise F_{ST} ~0.06–0.15) and appeared to correlate with distance (i.e., CC-N more differentiated from CC-S than CC-C; **Table 2**). Within the Central Coast, CC-C had the lowest LD R^2 values (**Fig. 4**). The CC-N cluster had higher LD values, especially at lower distances between SNPs, and CC-S had among the highest LD R^2 values, comparable to those of SGSB and SA in the Southern Coast.

Finally, the NC had genetic diversity estimates that were lower than the Sierra Nevada and comparable to the Southern Coast and Central Coast, with an N_e estimate of 14.1 (**Table 1**). Overall, the NC showed strong differentiation from the other fine-scale genetic clusters with the exception of KC and WSN for which differentiation was moderate (**Table 2**). The linkage decay plot indicates the NC had similar LD R^2 values to that of ESN and EP (**Fig. 4**).

DISCUSSION

Our analyses of genetic diversity and linkage disequilibrium based on 16,285 SNPs from 401 pumas throughout California demonstrated that the complex geography and land use patterns in California result in equally complex patterns of gene flow and population structure. The high-density SNP data provided resolution to detect both four broad-scale genetic clusters with high genetic diversity, as well as substructure at a finer scale that we designate as 10 genetic populations with highly variable genetic diversity. Our data further support the notion that puma populations in California form a "horseshoe" network around the Central Valley with San Francisco Bay acting as a barrier to gene flow along the coast (Gustafson et al., 2019). For the Sierra Nevada cluster, the nested finer-scale populations had consistently high genetic variation. However, within the coastal groups, genetic variation within certain fine-scale genetic populations was concerningly low, while others appeared to have retained sufficient variation as to be capable of serving as sources of genetic rescue under various management scenarios to restore connectivity. In fact, our linkage decay analysis indicated that populations with low genetic diversity and high linkage disequilibrium may not necessarily share the same fixed loci, consistent with what was suggested by Saremi et al. (2019). Specifically, when individuals from nested populations were combined within the 4 broader-scale groups, linkage decay values were much lower, indicating variation still exists among populations. Therefore, maintaining and enhancing connectivity within and among broad-scale groups could increase genetic diversity to entire regions and could decrease the apparent effects of genetic drift and inbreeding to some at-risk coastal populations (Ernest et al., 2003; 2014; Gustafson et al., 2017; Riley et al., 2014).

The support for four broad-scale genetic groups from SNPs is different than previous studies using microsatellites (Ernest et al., 2003; Gustafson et al., 2019) indicating the importance of using genomic methods in the study of broader-scale wildlife conservation genetics. Our data further support the claim that the Sierra Nevada region is a major refugium of puma genetic diversity in California (Gustafson et al., 2019). Therefore, it is important to protect the Sierra Nevada group from habitat degradation and foster conservation actions that can enhance gene flow with the North Coast, Central Coast, and Southern Coast clusters as well as with the Great Basin to the east (Gustafson et al., 2019). The broad-scale Southern Coast group is least connected to the other genetic clusters in the state but had higher genetic diversity and more private alleles than the Central Coast or North Coast. This indicates that the Southern Coast group retains unique genomic variation that must be conserved in order to maximize genetic diversity among pumas in California. Further, our finding of greater genetic diversity at lower latitudes is consistent with a previous study of gene flow among puma populations across southwestern North America, which found both higher microsatellite allelic diversity and a greater number of private alleles among pumas in southern Arizona and New Mexico (McRae, Beier, Dewald, Huynh, & Keim, 2005). Those authors suggested the pattern was consistent with recolonization of North America following a late-Pleistocene extinction (Culver et al., 2000); range expansion from the south was accompanied by decreasing diversity in more northern populations because of serial founder events. Our finding of high genetic diversity in the Southern Coast group suggests the genetic legacy of recolonization is generally consistent across the contemporary range of pumas in North America.

Although the four major genetic clusters are highly consistent among our structure analysis and PCA, there was also statistical support for substructure (i.e., *tess3r* results and moderate to high pairwise F_{ST} values within and among the broad-scale groups) indicating 10 genetic populations at a finer scale. Generally, the 10 genetic populations identified with SNPs correspond strongly to those identified in previous studies using microsatellite markers and different samples (Ernest et al., 2003, Gustafson et al., 2019). However, the northern-most Klamath–Cascade population was not observed previously with microsatellites (Gustafson et al., 2019). This is likely because there were very few pumas available for analysis in the Klamath or Cascade Mountains during the 2019 microsatellite study. It is also possible that 42 microsatellites may not have been sufficient to detect the low genetic differentiation (F_{ST} = 0.022) observed between the Klamath–Cascade and Western Sierra Nevada populations. The 10 populations varied considerably in genetic diversity estimates (H_O range 0.22–0.32; H_S range 0.24–0.33; *Poly* range: 0.63–0.91; A_r range: 1.24–1.33), effective population sizes (N_e range 2.3–54.4), and genetic differentiation (F_{ST} range: 0.22–0.32), as discussed below.

A major difference between this and previous studies is the observation that pumas in the Central Coast North population have genetic diversity estimates as low as those in the Santa Ana and Central Coast South populations, which are highly isolated by urbanization and transportation infrastructure and exhibit evidence of inbreeding depression (Benson et al., 2020; Ernest et al., 2014; Gustafson et al. 2017; Riley et al., 2014; Vickers et al., 2015). Our results are consistent with those of Saremi et al. (2019), which indicated that inbreeding metrics between pumas from the Santa Monica Mountains (in Central Coast South) and pumas from the Santa Cruz Mountains (in Central Coast North) were similar. Interestingly, N_e for the Central Coast North was much higher than both the Santa Ana and Central Coast South populations. These observations are consistent with a large breeding population experiencing genetic drift due to dispersal barriers to the north (i.e., San Francisco Bay) and gene flow occurring only with the Central Coast Central population to the south. This pattern could also be driven by carrying capacity processes associated with habitat limitations (Dellinger, Gustafson, Gammons, Ernest, & Torres, 2020b). If dispersal is limited by continued development southeast of the Central Coast North population, rapid genetic drift and inbreeding may ensue (Mills & Allendorf, 1996; Wang, 2004) and local extinctions may occur as predicted in the Central Coast South and Santa Ana populations (Benson et al., 2016; 2019). Thus, puma population viability will be facilitated when land management agencies and land developers in the region work proactively to preserve or enhance wildlife corridors.

Notably, the San Gabriel–San Bernardino population had the lowest N_e, but had intermediate levels of genetic diversity. Occasional migrants could alter N_e estimates and temporarily inflate estimates of heterozygosity (Gustafson et al., 2017). We suggest this could also be the result of metapopulation dynamics—i.e., a small local population with frequent turnover located at the intersection of dispersal corridors for the Sierra Nevada, Central Coast, and Southern Coast groups. Although the genetics of this population are complex and somewhat uncertain, this region is of critical importance for maintaining statewide puma gene flow. Enhancing connectivity through the Transverse Ranges (including the Tehachapi Mountains, Sierra Pelona, San Gabriel Mountains, and San Bernardino Mountains; **Fig. 1B**) is a critical conservation priority in order to maintain gene flow between the Southern Coast populations and the Sierra Nevada or Central Coast groups.

The three populations with the lowest N_e, including the San Gabriel–San Bernardino, Santa Ana, and Central Coast South populations, have the smallest available amount of habitat (Dellinger et al., 2020b), and had the highest linkage disequilibrium throughout their genomes. As we observed, there was great variation among populations in the decay curves, with the Central Coast North population having the next highest linkage disequilibrium after these three populations. Given the genetic diversity, N_e, and linkage data, the San Gabriel–San Bernardino and Central Coast North populations may be approaching levels of genetic drift and inbreeding similar to the well-monitored and genetically depauperate Santa Ana and Central Coast South populations (Ernest et al., 2014; Gustafson et al., 2017; Riley et al. 2014).

Populations with intermediate genetic diversity include the North Coast, Central Coast Central, and Eastern Peninsular Range. Measures of genetic diversity were lower than expected for the North Coast population given there are no obvious anthropogenic barriers to gene flow with the Klamath–Cascade, Western Sierra Nevada, or pumas from Oregon (Gustafson et al., 2019). However, the majority of our samples from this genetic cluster came from just north of the San Francisco Bay, an area of substantial human density and restricted gene flow on three sides. Thus our results may not be truly representative of this region as a whole and may represent the most isolated pumas on a “peninsula” of habitat. Future studies would benefit from increased sampling throughout this genetic cluster, north to (and including) Oregon. Nonetheless, pumas and other animals would benefit if decisions for future development between the North Coast and Sierra Nevada consider the future connectivity of private timber land holdings along the coast with the inland National Forests.

The Central Coast Central population has ample habitat for maintaining a breeding population (Dellinger et al., 2020b). Given the apparent absence of gene flow across the Central Valley, this population may be the only consistent source of migrants for the Central Coast North and Central Coast South, which have concerningly low levels of genetic diversity and evidence of inbreeding. Thus, we consider the Central Coast Central population to be essential for the long-term viability of both adjacent populations and urge that habitat in this region is not fragmented further.

Despite having less than half of the overall habitat of the Central Coast Central population (Dellinger et al., 2020b), the Eastern Peninsular Range population has roughly similar genetic diversity estimates, but a much lower N_e. Dispersal in and out of the Eastern Peninsular Range is extremely limited and the degree to which pumas disperse across the border between USA and Mexico remains unknown (Gustafson et al., 2019). Given that the Eastern Peninsular Range is the only population known to exchange individuals with the Santa Ana population, management actions which enhance gene flow between these areas remain critical to the recovery of pumas in the Santa Ana Mountains.

Our linkage decay analysis suggests that in the Central Coast South, San Gabriel–San Bernardino, Santa Ana, and perhaps the Central Coast North populations, pumas may have long runs of homozygosity that are identical-by-descent. This is consistent with the genome resequencing results of Saremi et al. (2019) in the Santa Cruz (i.e., Central Coast North) and Santa Monica Mountains (i.e., Central Coast South), which suggested close and recent inbreeding led to runs of homozygosity. Although Saremi et al. (2019) sequenced individuals only from California populations known to have low genetic diversity, our linkage decay results from populations throughout the state indicate that the genome-level problems of inbreeding are not universal throughout California. Instead, the Klamath–Cascades, Western Sierra Nevada, Eastern Sierra Nevada, Central Coast Central, and the Eastern Peninsular Range populations all have low linkage disequilibrium throughout the genome. Additionally, when the inbred populations are analyzed with their broad-scale group, linkage decay curves demonstrated the potential for gene flow with adjacent populations to reduce linkage to negligible levels. We observed up to 30–37% of the SNPs as fixed in the Central Coast–South, Santa Ana, and Central Coast North populations. Our linkage decay curves and the resequencing results of Saremi et al. (2019) demonstrate that fixed regions of the genome often differ among populations. Thus, genetic restoration is possible even among genetically depauperate populations. When considering that genetic diversity is much higher in several California puma populations than in those heavily studied along urban coasts, there is high potential for the long-term persistence of pumas throughout the majority of the state.

Genetic restoration or rescue has been successfully demonstrated for isolated, large-felid populations, such as the African lion (*Panthera leo*; Miller et al., 2020) and Florida panther (*P. concolor*; Ralls et al., 2018). There has also been calls for genetic rescue of other large-felids such as isolated populations of tigers (*Panthera tigris*; Armstrong et al., 2021) and leopards (*Panthera pardus*; Perez, Geffen, & Mokady, 2006). Thus, it is becoming increasingly evident that large-bodied cats and other apex predators will need habitat and connectivity for long-term evolutionary survival. Natural events of genetic restoration among fragmented populations of pumas in California (Ernest et al., 2014; Gustafson et al. 2017; Riley et al., 2014) combined with our linkage decay analysis indicates pumas and other apex predators may need to be managed in a metapopulation framework that incorporates genomic data (Farquharson et al., 2021).

We tested for outlier loci using multiple methods (Narum & Hess, 2011) but found no evidence of local adaptation when K = 4 or K = 10. Detection of outlier loci with RADseq is limited by the reduced representation of the genome, yet it has often been shown to be an effective approach (Catchen et al., 2017). Pumas are long-distance dispersers (Hawley et al., 2016; Sweanor, Logan, & Hornocker, 2000) and inhabit all major mountain ranges in California (Dellinger et al., 2020b), suggesting local adaptation may be unlikely. Our results provide preliminary evidence that outbreeding depression resulting from potential active genetic management may be of minimal concern (Frankham et al., 2011). Recent modelling (Kyriazis, Wayne, & Lohmueller, 2021) does suggest, however, that attempts to maximize genetic diversity in a population can introduce hidden deleterious recessive mutations, enhancing extinction risk. The modelling of Kyriazis et al. (2021) has faced criticisms (Garcia-Dorado & Caballero, 2021), however, and Ralls, Sunnucks, Lacy, and Frankham (2020) argue that the benefits of increasing genetic diversity outweigh the risks. Thus, managers could consider actions (e.g., wildlife overpasses/underpasses, translocation of individuals between populations, etc.) to improve viability of some coastal populations, as was empirically demonstrated to have shifted the trajectory of Florida panther population from extinction (Ralls et al., 2018). However, we suggest whole genome resequencing methods better suited for detecting selection (Fuentes-Pardo & Ruzzante, 2017) be implemented before such efforts, especially over long distances. Managers would also need to consider other risks as well, such as the movement of pathogens or the ethical implications of moving large carnivores (Bevins et al., 2012). Wildlife managers will have to weigh these concerns against their obligation to minimize the risks of extirpation such as those predicted for the Santa Ana and Central Coast South populations (Benson et al., 2019), and shown here to be a concern in the Central Coast North population as well. Should connectivity be re-established, then these factors, as well as possible local adaptation, should be weighed carefully. It is our opinion that current efforts to construct or improve wildlife crossing structures that can facilitate natural movement among coastal populations should be considered the primary management strategy for conserving viable puma populations in that region.

CONCLUSION

Our population genomic analyses provide decision makers a contemporary and thorough evaluation of the genetic diversity, effective population sizes, and connectivity of puma populations throughout California. These state- and genome-wide results are critically important for conservation and management practices in California, especially considering the increasing demand for development and the current political climate surrounding the petition to list pumas in Southern and Central California as Threatened under the California Endangered Species Act (Yap & Rose, 2019). In brief, puma populations are widespread throughout the mountains of California. Populations range from major genetic sources to populations with issues of low genetic diversity and inbreeding. Multiple lines of evidence suggest inbred populations do not share the same runs of homozygosity and therefore genetic diversity could be restored through enhanced gene flow. Current challenges to puma populations are highly regional and should be addressed by focusing on how natural geography and human development impacts puma habitat and movements locally. Attention is understandably given to those populations that are highly imperiled, but it is important to note that California has several thriving populations throughout the state which represent an important resource for any genetic management strategy. Protecting tracts of contiguous habitat to preserve large populations will provide greater protection for the species as a whole. Specifically, further fragmentation of habitat in the Sierra Nevada group could be catastrophic to population viability of pumas in the state because it serves as a genetic refugium. Protecting, enhancing, and creating movement corridors to allow statewide "stepping-stone" connectivity at broad and fine scales will allow for the migrants needed to counteract the local extirpations faced by some coastal populations.

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DATA ACCESSIBILITY

Individual genotype data and associated location data are provided on Open Science Framework (doi: XXXXXX to be made public upon acceptance for publication; temporary anonymous link for peer review: https://osf.io/huf4k/?view_only=c723d0623c5c441a98513af06ed3357d).

Table 1. Heat map of genetic diversity statistics for K = 4 broad-scale and K = 10 nested fine-scale genetic clusters, including sample size (N), observed heterozygosity (H_O); gene diversity (H_s), proportion of polymorphic loci out of 16,285 (*Poly*), allelic richness corrected for sample size (A_r), private alleles (A_p), and effective population size (N_e). Values for N_e are not presented for the K = 4 Sierra Nevada (SN), Southern Coast (SC), Central Coast (CC), or North Coast (NC) because of model assumption violations. There were no private alleles at K = 10, including Klamath–Cascades (KC), Western Sierra Nevada (WSN), Eastern Sierra Nevada (ESN), Eastern Peninsular (EP), San Gabriel–San Bernardino (SGSB), Santa Ana (SA), Central Coast Central (CC-C), Central Coast South (CC-S), Central Coast North (CC-N), and North Coast (NC). Heat map colors bound the minimum (white) and maximum (darkest grey) values within rows.

Genetic diversity	Genetic Cluster									
K = 4	SN			SC			CC			NC
N	193			96			79			33
H_O	0.31			0.26			0.24			0.26
H_s	0.34			0.29			0.28			0.27
Poly	0.93			0.79			0.77			0.78
A_r	1.79			1.69			1.67			1.67
A_p	37			34			17			0
K = 10	KC	WSN	ESN	EP	SGSB	SA	CC-C	CC-S	CC-N	NC
N	53	110	27	66	13	25	27	17	35	28
H_O	0.32	0.31	0.31	0.27	0.29	0.23	0.27	0.24	0.22	0.25
H_s	0.33	0.33	0.33	0.29	0.30	0.24	0.29	0.27	0.24	0.26
Poly	0.91	0.90	0.87	0.78	0.78	0.64	0.77	0.70	0.63	0.74
A_r	1.33	1.33	1.33	1.29	1.30	1.24	1.29	1.27	1.24	1.26
N_e	28.9	54.4	42.2	14.8	2.3	3.5	26.9	4.1	19.0	14.1

Table 2. Heat map of mean pairwise genetic distance values for the broad-scale K = 4 and fine-scale K = 10 genetic clusters. Weir and Cockerham F_{ST} is presented below the diagonal and Nei's F_{ST} is presented above the diagonal (WC\Nei). All pairwise F_{ST} estimates were significant (p < 0.001) based on a bootstrapping analysis using *hierfstat::boot.ppfst.* Sierra Nevada (SN), Southern Coast (SC), Central Coast (CC), North Coast (NC), Klamath–Cascades (KC), Western Sierra Nevada (WSN), Eastern Sierra Nevada (ESN), Eastern Peninsular (EP), San Gabriel–San Bernardino (SGSB), Santa Ana (SA), Central Coast Central (CC-C), Central Coast South (CC-S), Central Coast North (CC-N). Heat map colors bound the minimum (white) and maximum (darkest grey) values either below or above the diagonals.

WC\Nei F_{ST}	Genetic Cluster									
K=4	SN			SC			CC			NC
SN	-			0.133			0.124			0.100
SC	0.129			-			0.173			0.198
CC	0.120			0.173			-			0.156
NC	0.094			0.196			0.156			-
K=10	KC	WSN	ESN	EP	SGSB	SA	CC-C	CC-S	CC-N	NC
KC	-	0.022	0.041	0.141	0.109	0.215	0.117	0.146	0.183	0.093
WSN	0.022	-	0.045	0.149	0.111	0.222	0.121	0.147	0.188	0.126
ESN	0.041	0.045	-	0.163	0.116	0.226	0.168	0.189	0.233	0.183
EP	0.141	0.146	0.166	-	0.130	0.100	0.164	0.196	0.231	0.214
SGSB	0.105	0.106	0.113	0.132	-	0.212	0.140	0.163	0.210	0.205
SA	0.202	0.203	0.221	0.095	0.217	-	0.254	0.287	0.319	0.301
CC-C	0.114	0.116	0.168	0.163	0.141	0.251	-	0.060	0.098	0.164
CC-S	0.137	0.136	0.183	0.192	0.164	0.289	0.059	-	0.148	0.202
CC-N	0.178	0.176	0.237	0.227	0.221	0.320	0.100	0.152	-	0.229
NC	0.090	0.118	0.183	0.211	0.210	0.300	0.164	0.203	0.230	-

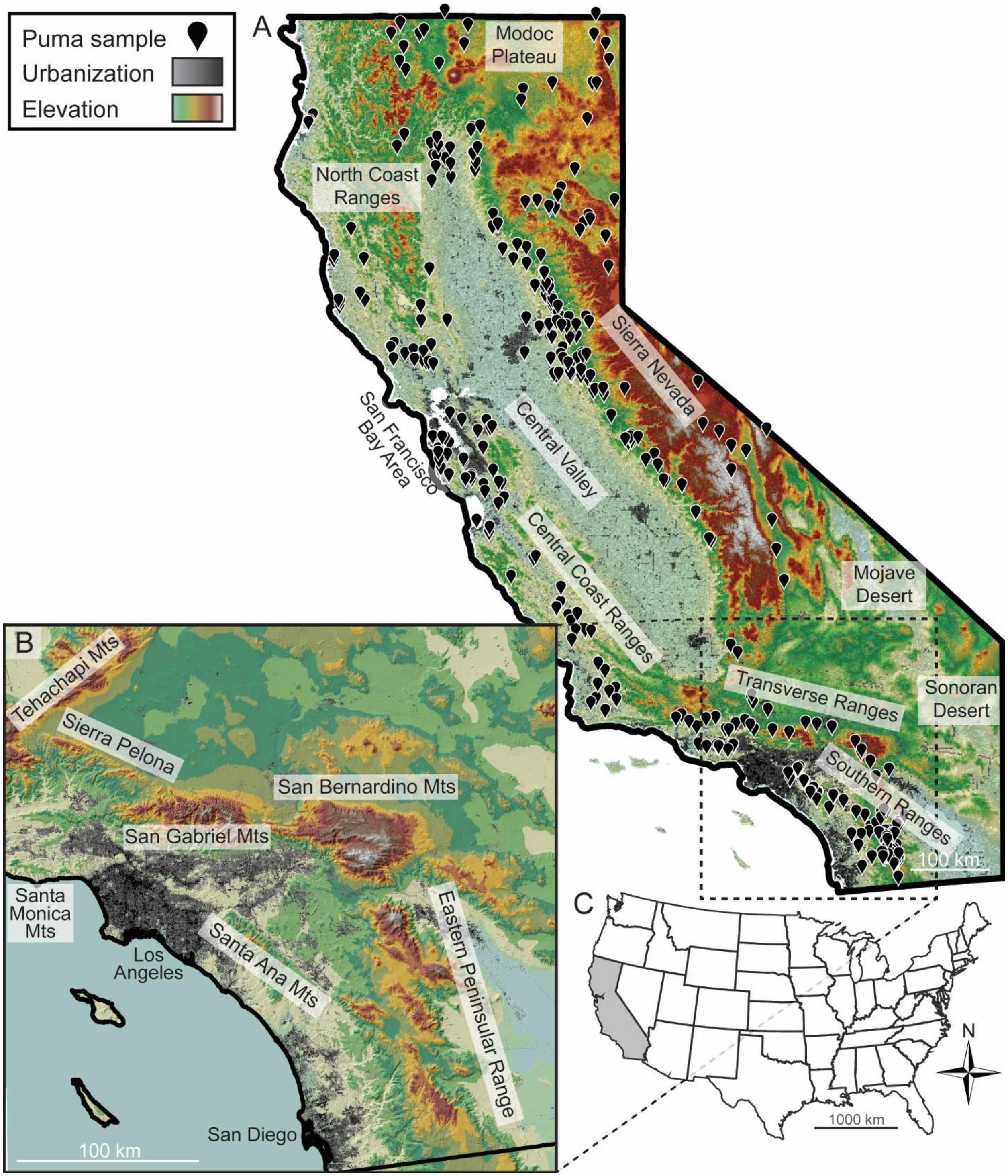

Figure 1. Location of 401 sampled pumas used in analyses, including (**A**) sample distribution across California, (**B**) geography of the mountain ranges surrounding the Los Angeles and San

Diego regions, and (**C**) inset map showing the location of California in the United States of America.

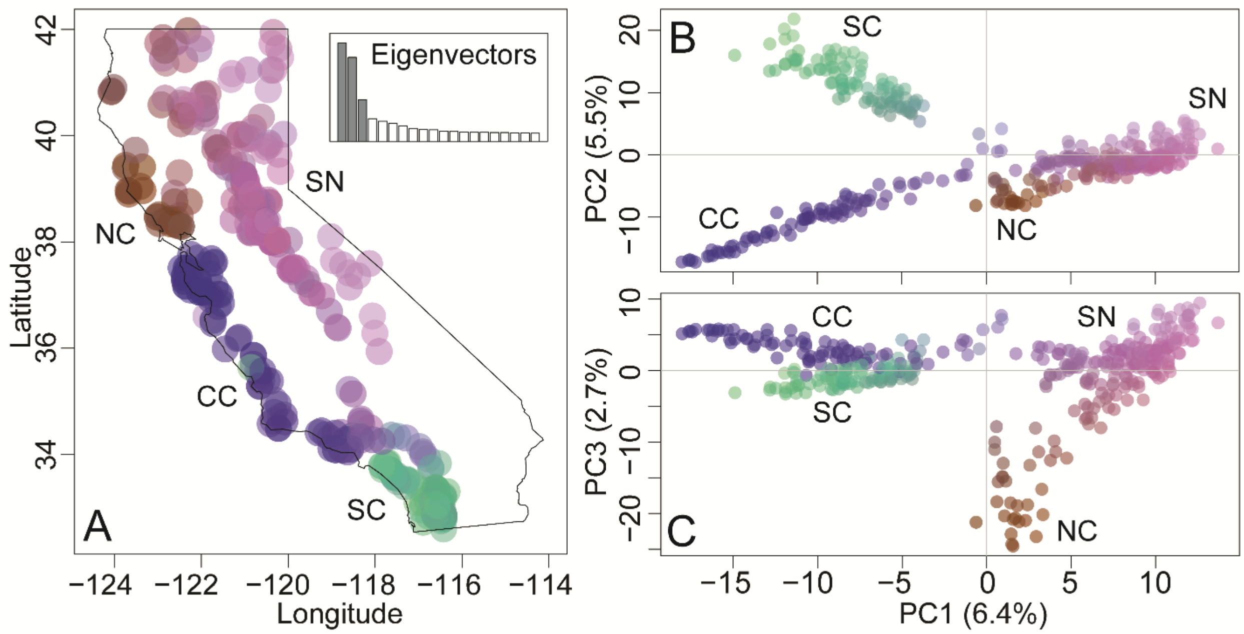

Figure 2. Principal component analysis (PCA) of 401 pumas at 16,285 SNPs reveals four genetic clusters. **(A)** The colorplot (R package *adegenet*) of the PCA represents colors corresponding to a combination of the first 3 eigenvectors. The inset plot shows the proportion of the variance explained by shaded PC eigenvectors 1–3 compared to other eigenvectors. The color values are plotted at sample locations to demonstrate geographic structure. Colorplots of **(B)** PC1 and PC2 and **(C)** PC1 and PC3 resolved the 4 broad-scale genetic clusters.

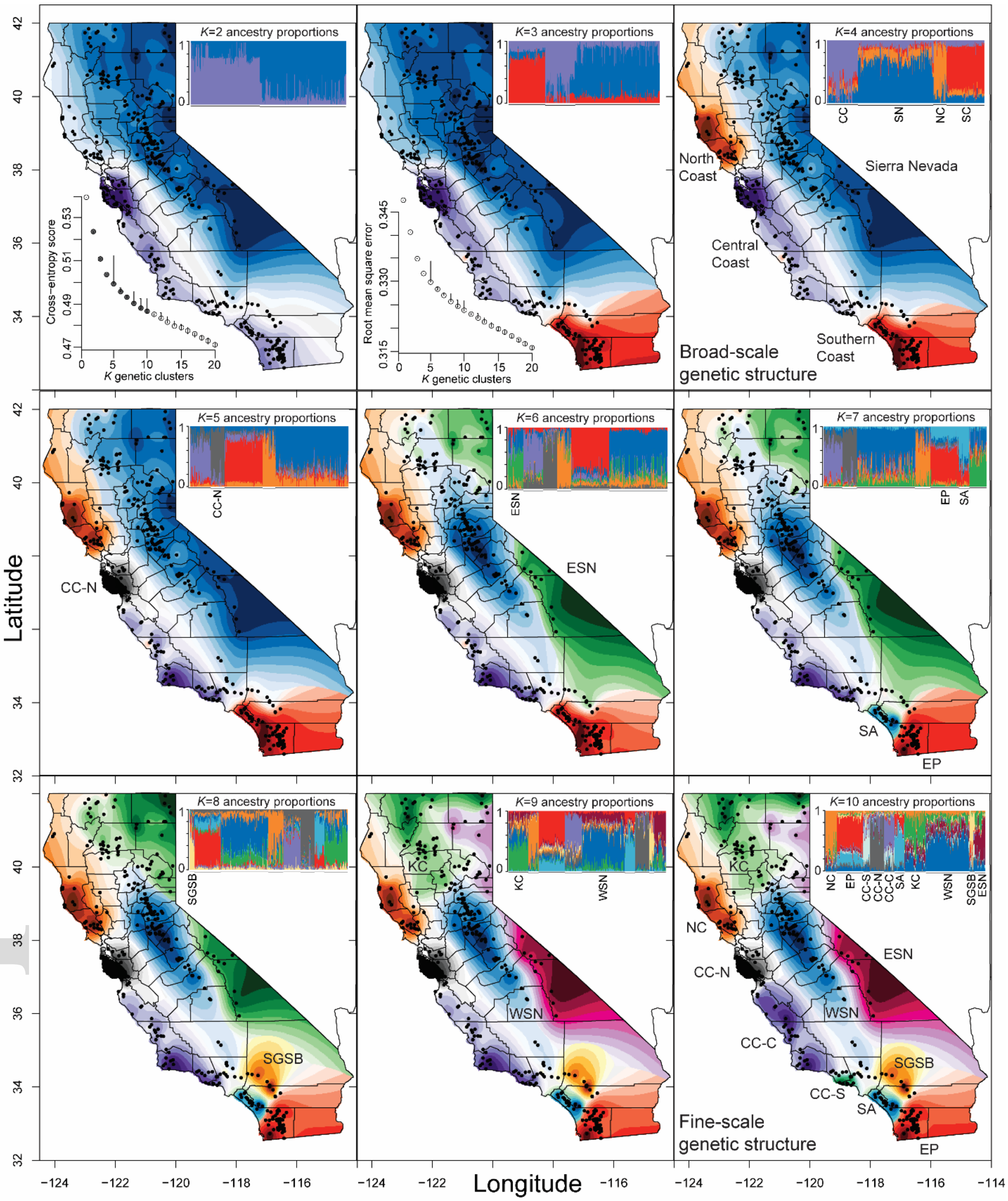

Figure 3. Interpolated ancestry proportions from *tess3r*, demonstrating the geographic distribution of biologically meaningful genetic clusters (*K*) ranging from 2–10. The "best" iterations of each *K*, based on cross-entropy score, is presented (shaded circles of inset plot in *K*=2 panel). Root mean square error is also presented (inset plot in *K*=3 panel). Both *tess3r* and

the PCA (Fig. 2) support *K*=4 and therefore the genetic clusters are labeled. At *K*=10, nested genetic clusters are labeled consistent with previous microsatellite data (Gustafson et al. 2019). For visualization, at each *K*, the genetic cluster that emerges is labeled. In alphabetical order, acronyms include Central Coast Central (CC-C), Central Coast North (CC-N), Central Coast South (CC-S), Eastern Peninsular Range (EP), Eastern Sierra Nevada (ESN), Klamath–Cascades (KC), North Coast (NC), Santa Ana (SA), San Gabriel–San Bernardino (SGSB), and Western Sierra Nevada (WSN).

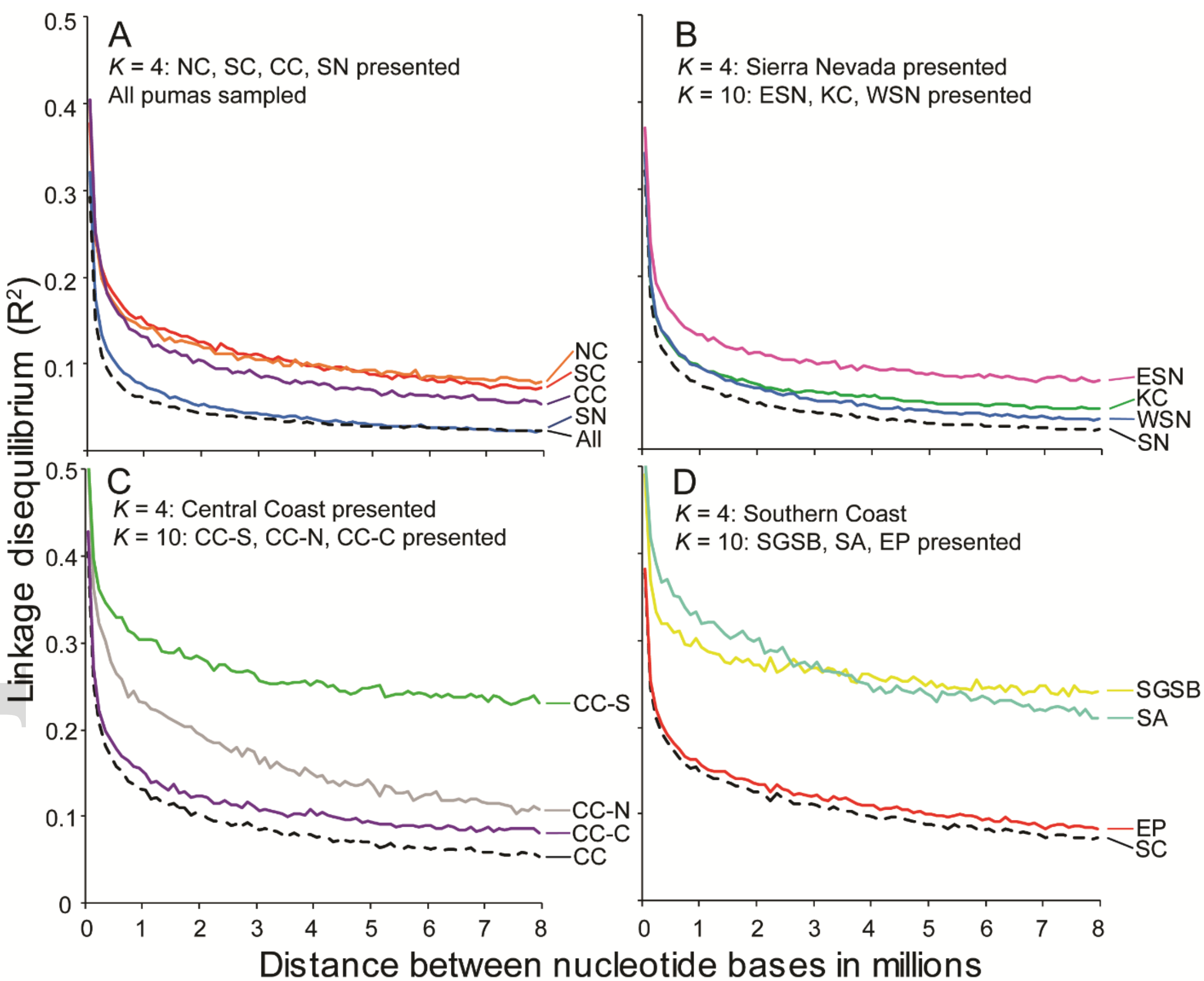

Figure 4. Correlation of SNPs with genomic distance, ranging from hundreds to 8 million nucleotides in distance. Based on pairwise estimates from 16,285 SNPs, linkage decay is presented for all 401 pumas sampled in California (All), from the *K* = 4 broad-scale genetic clusters (**A**: North Coast, NC; Southern Coast, SC; Central Coast, CC; Sierra Nevada, SN), and

from the K = 10 fine-scale genetic clusters (**B**–**D**). The nested and finer-scale clusters are presented within their corresponding broad-scale group. The NC is presented only in the first panel because it did not exhibit substructure. (**B**) Eastern Sierra Nevada (ESN), Klamath–Cascades (KC) and Western Sierra Nevada (WSN) are nested within SN. (**C**) Central Coast South (CC-S), Central Coast North (CC-N), and Central Coast Central (CC-C) are nested within CC. (**D**) San Gabriel–San Bernardino (SGSB), Santa Ana (SA), and Eastern Peninsular Range (EP) are nested within SC. In each figure, the dashed line represents the broadest-scale designation within the group.

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.

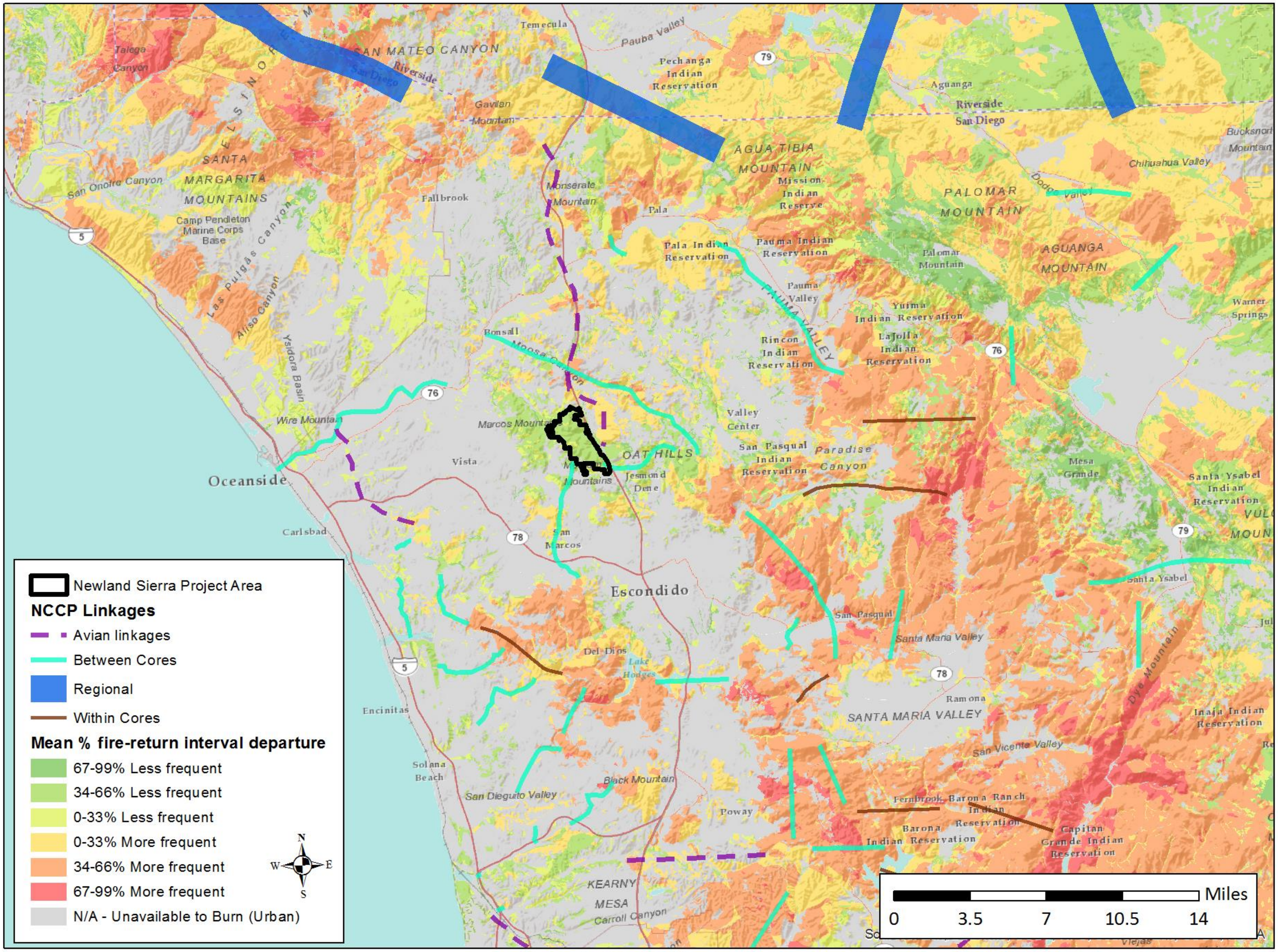

Figure 1. Map of fire-return interval departure (Safford and Van de Water 2014) for northern San Diego County and linkages identified in the Management Strategic Plan Connectivity documents for San Diego's NCCP areas.

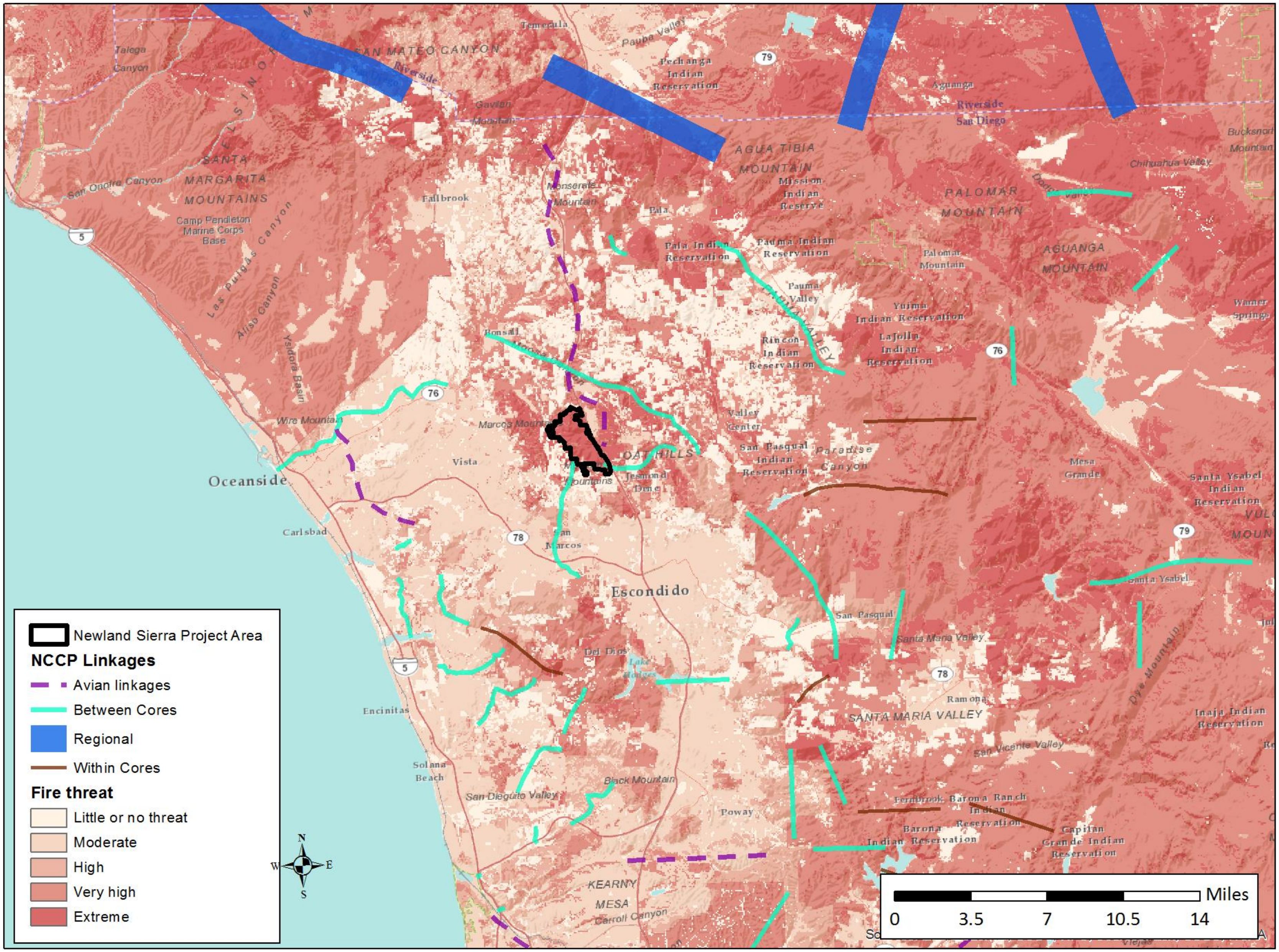

Figure 2. Map of fire threat for northern San Diego County as classified by [California's Fire and Resource Assessment Program]() and linkages identified in the [Management Strategic Plan Connectivity documents]() for San Diego's NCCP areas.

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Fire as a Threat to Biodiversity in Fire-Type Shrublands[1]

Jon E. Keeley[2]

Abstract

Chaparral and coastal sage scrub communities have a disproportionately high number of rare and endangered plants and thus are of particular conservation concern. Unnaturally high fire frequency has been a leading cause of degradation of chaparral and coastal sage scrub ecosystems. Although these shrublands are fire-adapted, below a certain threshold of fire frequency, resilience is inversely related to the fire return interval: this threshold is 3-5 years in coastal sage scrub and 10-20 years in chaparral, with the higher values more typical of interior sites. High fire frequency depletes the native flora and increases the proportion of non-native herbaceous species. Resilience to different fire regimes varies across growth forms, and thus it is of particular significance that the growth form distribution of rare species is significantly different from the proportions of growth forms in these communities.

Key words: chaparral, endangered species, high fire frequency, resilience, sage scrub

Introduction

The California landscape has been altered in many ways, with the potential for profound impacts on biodiversity and ecosystem functioning (Keeley and Swift 1995). Other than direct development, one of the more important changes in shrubland ecosystems has been the anthropogenic alteration of the natural fire regime. Despite a long-standing policy of fire suppression, the primary impact has been a dramatic acceleration of fire occurrence (Keeley and Fotheringham 2002, Keeley and others 1999, Moritz 1997). Although species in these shrublands are "fire adapted," they are not adapted to all fire regimes, and one can distinguish species differences and broad growth form differences in resilience to increased fire occurrence. This is of particular concern because both chaparral and coastal sage scrub communities have a disproportionately high number of rare and endangered plants.

Shrubland Biodiversity

The California Native Plant Society (CNPS) list of rare and endangered plant species (Skinner and Pavlick 1994) places chaparral first in number of taxa that are of concern (*table 1*). Although coastal sage scrub ranks fifth, both shrub communities have a much higher number of rare taxa than expected based on their area occupied. If all the rare and endangered taxa in the top five habitats were distributed randomly,

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[1] An abbreviated version of this paper was presented at Planning for Biodiversity: Bringing Research and Management Together, a Symposium for the California South Coast Ecoregion, February 29-March 2, 2000, California State Polytechnic University, Pomona, CA.

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Table 1—*Top-ranking habitats of California's rare plants according to all CNPS lists (data from Skinner and Pavlik 1994). These observed values are contrasted with the values expected based upon the amount of land area occupied by each habitat (data from Jones and Stokes 1987).*

Rank	Habitat	Taxa	
		Observed	Expected
1	Chaparral	516	432
2	Lower coniferous forests	359	294
3	Cismontane woodland	311	362
4	Valley/foothill grassland	247	431
5	Coastal scrub	211	132

($p < 0.001$; $\Pi^2 = 164.2 >>> \Pi^2_{0.999[3]} = 16.3$)

one would expect chaparral to top the list based just on areal extent of this vegetation, but chaparral contains 18 percent more species than expected. Coastal sage scrub contains nearly 40 percent more taxa than predicted by its areal extent.

In both chaparral and coastal sage scrub, herbaceous perennials, typically geophytes, top the list of growth forms that are rare or endangered (Skinner and Pavlick 1994). If we contrast these numbers just for southern California chaparral and coastal sage vegetation with those expected, based on extensive surveys of postfire peak of diversity (Keeley 1998a), we see that rarity is not randomly distributed across growth forms (*table 2*). Annuals are very under-represented. If rarity were randomly distributed with respect to growth form we would expect three times as many annuals as observed in the lists. On the other hand, there are three times as many herbaceous perennials as expected and double the number of shrub species.

Resilience to different fire regimes varies across growth forms (Keeley 2000), and thus it is of interest to consider rarity in terms of fire specialization. Fire is a frequent ecological factor and has played an obvious evolutionary role in these communities. Most non-woody plant species reach their greatest population sizes, and thus greatest potential for spread, in the postfire environment. However, not all species or even all growth forms are equally specialized towards fire. Annuals comprise a rich diversity of species that range from extreme specialization—strictly fire-stimulated germination (Keeley and Fotheringham 1998)—to generalized opportunistic species that occupy many types of disturbance. Cursory examination of the rare annuals listed in Skinner and Pavlick (1994) indicates they are not highly restricted to burned sites. Herbaceous perennials, particularly geophytes, in these shrublands lack obvious specialization to fire, and their life cycle is not substantively different from that of geophytes in other less fire-prone habitats (Rundel 1996). At the time of fire most geophytes are dormant and nearly all have transient seed banks that do not require specialized fire cues (Keeley1991). Thus, most rare herbaceous species do not appear to be highly specialized for postfire recruitment.

This pattern is not evident in the rare shrubs, where a large proportion are species of *Ceanothus* and *Arctostaphylos* that have seedling recruitment strictly tied to postfire conditions (Keeley 1998b). Thus, it is to be expected that the direct effects of alterations in fire regime would affect some components of the rare plant flora more than others.

Table 2—*Growth form distribution of CNPS rare and endangered taxa in southern California chaparral and coastal sage scrub (data from Skinner and Pavlik 1994). Expected values based on distribution of growth forms following fire in 90 0.1 ha sites in southern California (Keeley 1998a)*

	Annual	Herbaceous perennial	Suffrutescent	Subshrub/ shrub/tree
Observed	43	79	17	63
Expected	131	27	16	28

($p < 0.001$; $\Pi^2 = 202.5 >>> \Pi^2_{0.999[2]} = 13.8$)

This is well illustrated by the extreme event of back-to-back wildfires studied by Zedler and others (1983). At four *Adenostoma fasciculatum* dominated sites, postfire frequency of this shrub increased following a fire in mature vegetation but decreased dramatically following the second fire. The impact was most profound on the non-resprouting shrub *Ceanothus oliganthus*, which was present from seed in three-fourths of the plots after the first fire but nearly absent after the second fire. In contrast, these repeat fires had little impact on the herbaceous perennials *Calochortus weedii* and *Dichelostemma pulchella*.

Fire suppression has been frequently cited as a major threat to fire type rare species, for example, the rare locoweed *Astragalus brauntonii* that is restricted to sites around the Los Angeles Basin (Skinner and Pavlick 1994). This idea is a logical extension of the well-documented threat of fire suppression in many western coniferous forests (SNEP 1996). However, fire records show that in southern California fire suppression has not effectively excluded fire (Conard and Weise 1998, Keeley and others 1999). Indeed, urban mountain ranges such as the Santa Monica Mountains in Los Angeles and Ventura Counties have a fire rotation interval of less than 15 years, and this is likely many times shorter than the natural regime (Keeley 2002a). Lack of fire is not likely a threat to the persistence of these shrublands or rare species within them. A far greater threat in many areas, particularly the Los Angeles Basin, is habitat degradation due to increased fire frequency.

Fire-Induced Habitat Degradation

Unnaturally high wildfire frequency has long been a leading cause of degradation of chaparral and coastal sage scrub ecosystems, second only to land development. While these shrublands are fire-adapted, below a certain threshold of fire frequency resilience is inversely related to the fire return interval. This threshold is probably about 3 years in coastal sage scrub (but longer for interior sage scrub sites) and 10-20 years in chaparral (Keeley 2000). Generally speaking, as fire frequency increases, herbaceous vegetation is favored over woody growth forms (Sauer 1975, Wells 1962). Numerous studies have shown that unnaturally high fire frequency depletes the native flora and increases the proportion of non-native herbaceous species (Haidinger and Keeley 1993, Zedler and others 1983). In California it is quite likely that, except on fine-textured argillaceous soils, grasslands are degraded shrubland sites (Cooper 1922, Keeley 1990, 1993; Wells 1962), and even grasslands on certain argillaceous soils may have been dominated by the shallow rooted summer-deciduous coastal sage scrub (Kirkpatrick and Hutchinson 1980, Wells 1962).

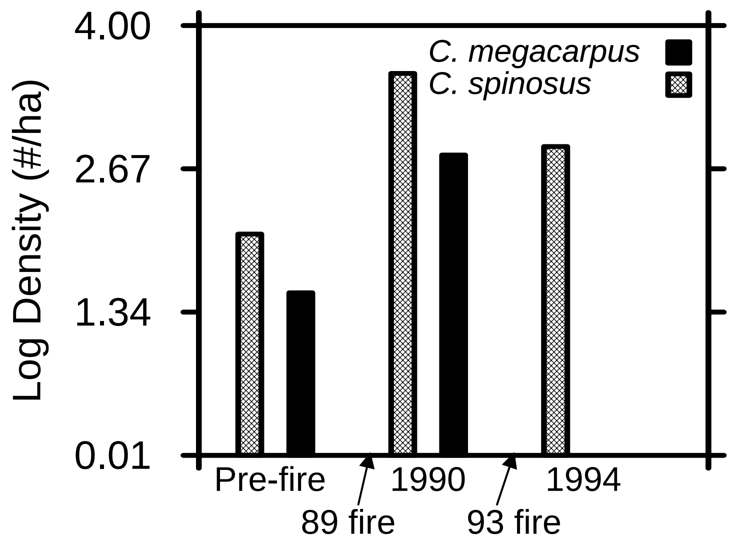

Figure 1—Effect of repeat fires on the populations of an obligate-seeding shrub, *Ceanothus megacarpus*, and a facultatively-seeding shrub*, C. spinosus*, in the Santa Monica Mountains. The first fire occurred in mature chaparral in 1989, the second in 1993 (from Keeley 2000).

The impact of frequent fires on the native shrub populations is well illustrated by the back-to-back wildfires that Zedler and others (1983) discussed, above. This extreme event resulted in the near extirpation of one obligate-seeding shrub population, and this can occur with even longer intervals between fires. *Figure 1* shows the extirpation of a non-sprouting shrub with fires four years apart, whereas a resprouting congener survived this high fire frequency, albeit at a lower density.

As native shrub cover is reduced due to high fire frequency, there is typically a type conversion to an herbaceous community dominated by non-native species. This is illustrated in the study by Haidinger and Keeley (1993) showing vegetation changes on adjacent sites experiencing different fire regimes. For example, two fires in six years reduced shrub populations of *Adenostoma fasciculatum* and *Salvia mellifera* but favored the suffrutescent *Lotus scoparius* (*fig. 2*). Three fires in six years were detrimental to most natives but conducive to the spread of non-native invasives such as *Brassica nigra* and species of *Bromus*. The results of this chronosequence study are corroborated by similar observations on a single site over time (*fig. 3*). In this study a mature coastal sage scrub site burned in 1993, and over the following three growing seasons the exotic cover declined as the native shrubs recovered. Following a second fire in 1996 the exotics exploded; within two years they dominated the site.

Such type conversions of shrublands to grasslands are not always the result of wildfires but have long been a goal of prescription burning programs (CDF 1978, Sampson 1944). Sometimes these are done for “range improvement,” to increase deer and livestock range, but other times for reducing fire hazard. These herbaceous (grassland) associations generate far less intense fires than shrub associations, and these grassland fires are more safely suppressed than chaparral fires (Keeley 2002a).

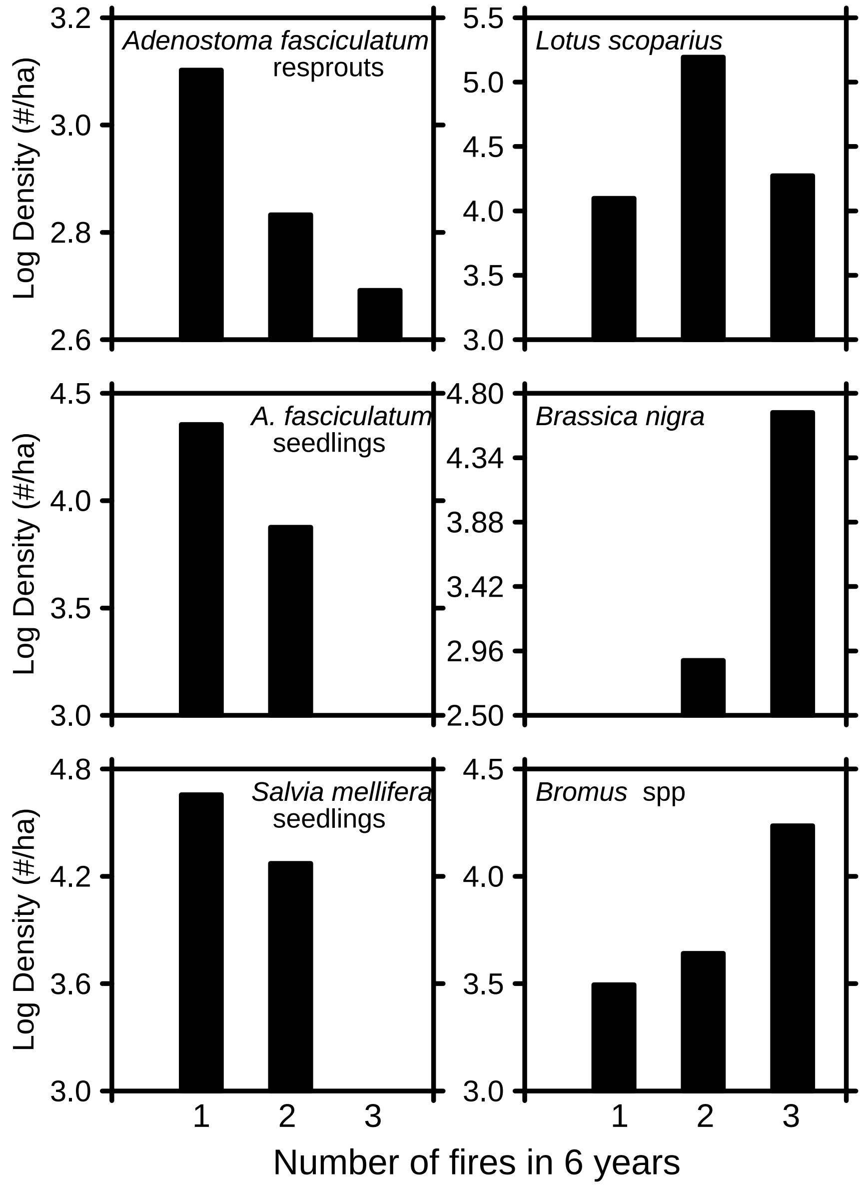

Figure 2—First growing season shrub and herb density in adjacent stands of mixed chaparral and coastal sage scrub burned once, twice, and three times in 6 years (redrawn from Haidinger and Keeley 1993).

Type conversion not only alters fire intensity, but also it often leads to increased fire frequency (Keeley 2002a). This results from several factors. These herbaceous species dry rapidly during the late spring and thus greatly expand the seasonal window of opportunity for fire. In addition, they constitute fine fuels that ignite readily and spread fire both horizontally through the stand and vertically into the shrubs with little wind. As the extent of herbaceous cover increases, it sets the stage for repeat fires in a self feed-back process where more fires thin the shrub overstory and increase the presence of a persistent herbaceous layer. Over time, repeating this process will type-convert shrublands to annual grasslands dominated by non-native species, which in turn alters the fire regime by increasing further expansion of the seasonal window for fire because non-native species dry earlier in the spring than most native herbaceous species (Keeley and Fotheringham 2003).

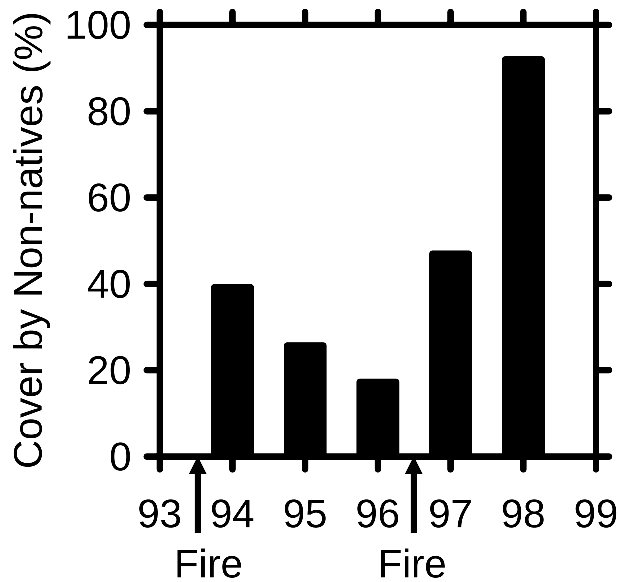

Figure 3—Percentage ground surface covered by non-native species on a coastal sage scrub site in the Santa Monica Mountains burned at 21 years of age in 1993 and reburned three years later in 1996 (data from Keeley and Fotheringham, unpublished data).

Sites differ greatly in their propensity for repeat fires. In general, interior sites are far more vulnerable to frequent fires than coastal sites due to the slower rate of shrub recovery (*fig. 4*). In another study of 90 sites burned during the same week in 1993, total herbaceous cover was positively correlated with parameters such distance from the coast, soil phosphorous, organic matter, and sand content (*table 3*). Postfire herbaceous cover was negatively correlated with stand age prior to the fire and estimated annual insolation. In short, herbaceous cover sufficient to carry a repeat fire is most likely when fires occur in young stands on fertile sites in the interior.

History of Type Conversion

Cooper (1922) believed there was abundant evidence, based upon his observations in the Coast Ranges, to say that burning by Indians accounted for a shift from woody vegetation to grasslands. He contended that this process of type conversion continued with the colonization by Europeans. Bauer (1930) believed the same applied to the grasslands of the Tehachapi Mountains farther south and cited examples of relictual patches of shrubland as evidence.

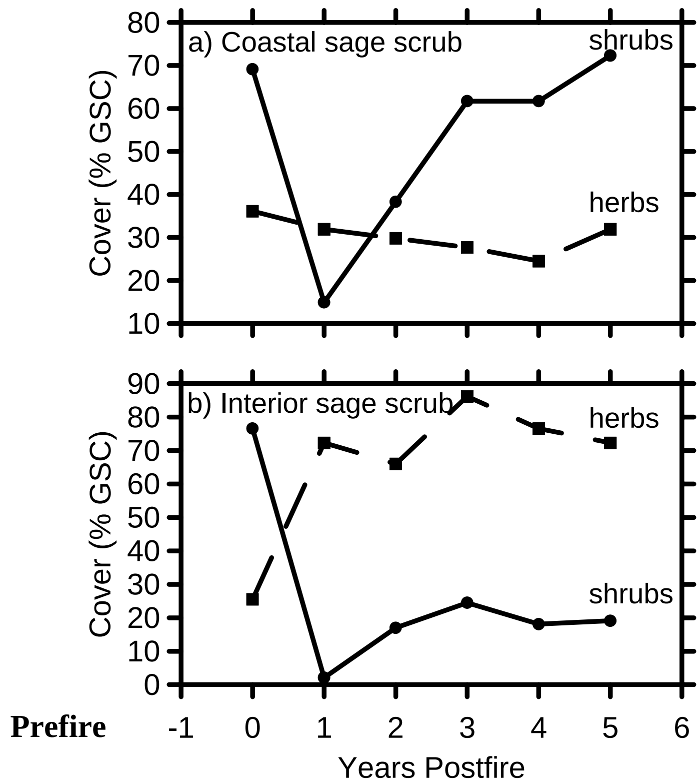

Figure 4—Foliar cover before and after fire at coastal and interior sage scrub sites (redrawn from O'Leary and Westman 1988).

Today the coastal ranges south of San Francisco have 25 percent of their landscape dominated by alien grasses, and there is reason to believe this derives from shrubland type conversion beginning with Native Americans (Keeley 2002b). Brown and Show (1944) recounted the history of rural land use in California, which included the use of fire to convert "useless" brush to "more productive" grasslands. This type conversion process accelerated in the latter part of the 19th century with increasing competition for suitable grazing land. During the latter part of the last century such type conversion was officially sanctioned by the issuing of brush burning permits for "range improvement" by the California Division of Forestry (CDF 1978). Throughout the 20th century, type conversion of shrublands occurred from other types of disturbance as well (Stylinksi and Allen 1999).

Presently, we have relatively limited information on the extent of such type conversions. However, there are reasons to believe this was done on a massive scale. One is the extensive distribution of non-native grasslands in the Coast Ranges of central California and the lack of any obvious correlation with environmental parameters such as soil type or slope exposure (Wells 1962). Another is the widespread distribution of grasslands in the foothills east of San Francisco and the demonstration of their rapid conversion to woody vegetation upon cessation of grazing (McBride and Heady 1968). Finally, quantitative measures of type conversion in southern California coastal sage scrub indicate that over the past 60 years more than half of the vegetation has been partially or completely type converted to grassland (Minnich and Dezzani 1998).

Table 3—*Stepwise multiple regression of postfire herbaceous cover vs. environmental variables at 90 sites of coastal sage scrub and chaparral (from Keeley and Fotheringham unpublished data).*

$r^2 = 0.42$ $P < 0.001$	
	2-tail *P*
Positively correlated:	
Distance from coast	0.000
Percentage sand	0.002
Soil phosphorus level	0.003
Soil organic matter	0.009
Negatively correlated:	
Prefire stand age	0.002
Annual solar insolation	0.033

Conclusions

Besides human development, the greatest threat to biodiversity in Mediterranean-climate shrublands of California is changes in the natural fire regime. Fire suppression alters the fire regime by increasing the fire return interval and potentially threatens the persistence of species with fire-dependent recruitment. However, this impact is offset by the abnormally high number of fire occurrences due to human-caused ignitions. Consequently, the fire return intervals in southern California shrublands are higher than was historically the case, and the greatest threat to the persistence of these vegetation types is type conversion to herbaceous species more resilient to and more conducive to frequent fires. In general, non-native grasses and forbs are most favored by the current fire regime of frequent fires.

In general the majority of rare herbaceous species show no specialized response to fire. However, areas heavily affected by human-induced acceleration of fire return intervals may not be suitable sites for these natives because of the intense competition from non-native invasives that are favored by high fire frequency.

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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

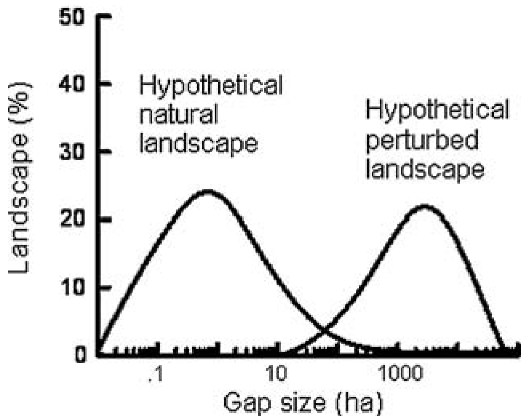

Figure 1. Hypothetical distribution of fire-generated gaps expected for natural fire regimes and future fire regimes in Sierra Nevada mixed conifer forests perturbed by a century of fire exclusion (from Keeley & Stephenson 2000).

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 seedbank 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).

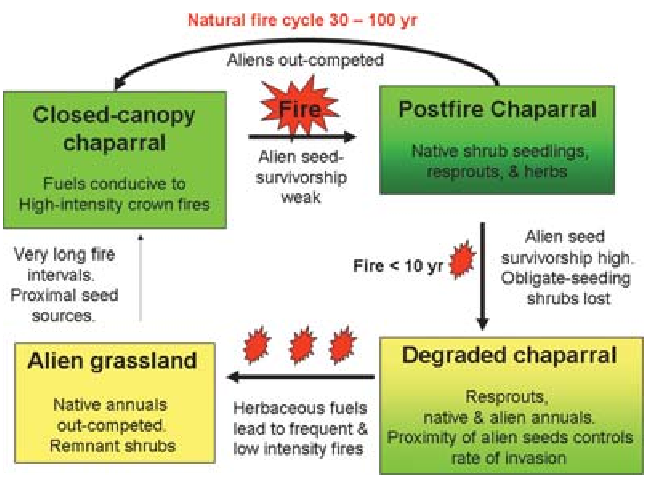

Figure 3. Model of fire and alien species interactions in California chaparral.

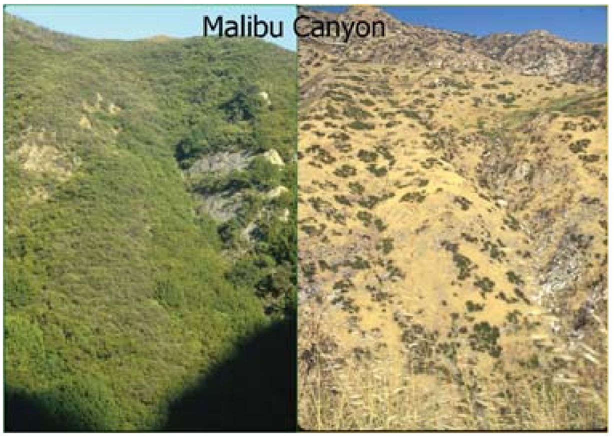

Figure 4. Type conversion recorded for Malibu Canyon, Santa Monica Mountains, California: left, natural chaparral landscape representative of chaparral in Malibu Canyon (photo by Anna Jacobsen); right, landscape dominated by alien annual grass after three fires in 12 years (based on Jacobson et al. 2004; photo by Steve Davis).

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).

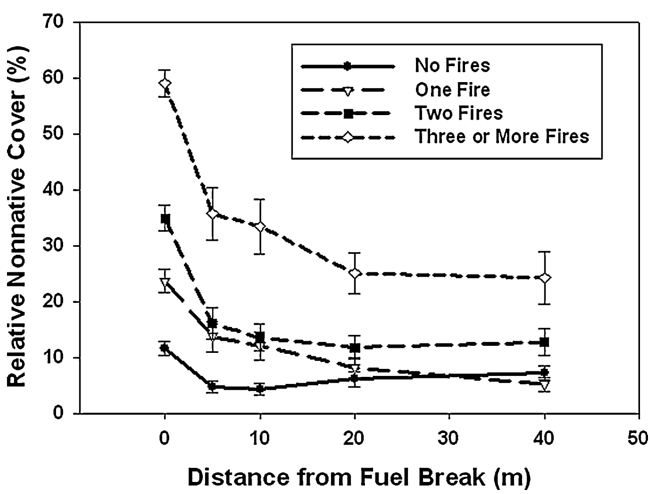

Figure 5. Interaction between number of fires and distance from the fuel break. Error bars represent + 1 SE (from Merriam et al. 2006).

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.

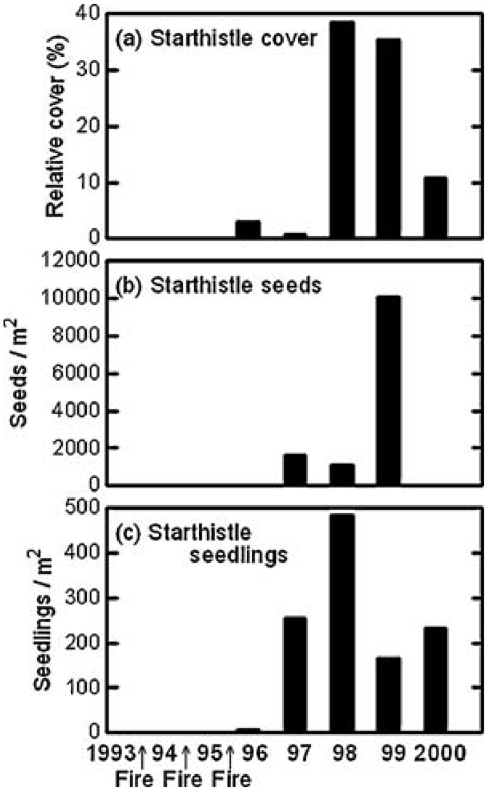

Figure 6. Yellow starthistle (a) cover, (b) seed, and (c) seedling production following three consecutive annual burns applied to extremely dense populations of this noxious alien weed. Immediate postfire results were promising (DiTomaso et al. 1999), but follow-up studies indicate that burning destabilized 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.

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Rural and non-rural digital divide persists in older adults: Internet access, usage, and attitudes toward technology

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Abstract

Background: The digital age divide remains persistent despite the recent increase in internet use among older adults. Additionally, older rural residents are at greater risk of being digitally disconnected.
Objective: Guided by the social determinants of health framework, our study aims to examine how one's residential area relates to (1) internet use, (2) subtypes of usage patterns, and (3) attitudes toward technology use in later life.
Method: Cross-sectional data were drawn from the 2012 Health and Retirement Study. The analytic sample consisted of 1,566 older adults aged 50 and above. Chi-square tests and logistic regression analyses were performed.
Results: Internet access rates were significantly lower in rural residents (54%) compared to the urban (66%) or the suburban group (61%). Compared to urban residents, those residing in suburban areas were less likely to use health technology while those living in rural areas had lower odds of communication, financial, and media technology use. Furthermore, the association between urban-rural residence and attitudes toward technology was compared among non-users (N = 633). Older adults in rural areas showed more unfavorable perceptions of technology than urban residents. They were less likely to conceive technology as "easily available," but more likely to perceive it as "too complicated" and "too hard to learn." No significant differences were found between rural and suburban residents.
Conclusion: Our findings suggest that older adults in rural areas, notably lag in using and adopting digital technology. Comprehensive intervention efforts are needed to narrow the digital divide for rural communities.

Keywords: technology, digital divide, rural, urban, attitude, older adults

Introduction

With the pervasive spread of technology and digital technologies used in every aspect of life, research has noted the development of a digital divide (Ball et al., 2019; van Dijk, 2006). As elaborated through these studies, a digital divide refers to a division in access to digital technologies for certain populations. More specifically, van Dijk and Hacker (2003) proposed four access-related gaps that might lead to a digital divide. The first was a mental gap, which refers to emotional or psychological gaps that emerge from people's lack of experience with digital technologies. Next was the material access gap, referring to the more traditional lack of access, such as lack of access to technologies. Third, they referred to a lack of skills, referring to how experience with technologies would increase an individual's technology skills. Lastly, they mention the usage gap, referring to differences in usage that lead to various usage patterns (such as simpler communication tasks only vs. more complex, social capital building tasks, for instance). Despite these multiple aspects of digital technology use, most previous studies on the digital divide have been primarily focused on accessibility (whether the participants can use the technology or not), leaving usage patterns and personal attitudes underexplored.

The digital divide literature has conceptualized three levels of the digital divide: (1) the first-level divide focusing on disparities in Internet access; (2) the second-level divide referring to unequal Internet skills and usage; (3) the third-level divide related to the outcomes of Internet use (van Dijk, 2020). While more recent research attention shifts towards the second-and third-level divide as mobile broadband becomes nearly ubiquitous, the first-level digital divide still calls for further investigation in the context of socioeconomic disparities (Gonzales, 2016). On the other hand, theoretical frameworks have suggested two distinct reasons for the non-use of the Internet. First, a lack of material resources may push individuals involuntarily away from Internet use (Livingstone & Helsper, 2007). Second, psychological factors such as motivation, attitudes, and interest may drive individuals' voluntary decisions not to use digital technologies (van Dijk, 2005). Studies found that inequalities in Internet access are likely to be attributable to involuntary exclusion, while disparities in Internet skills and usage are also shaped by personal motivations and attitudes (Eynon & Helsper, 2011; Yu et al., 2016). The current study aims to investigate the role of one's residential area in relation to the first- and second-level digital divides using a representative sample of older Americans. We consider internet access and specific types of technology usage as outcome variables. In addition, we focus on non-users of communication technologies to examine what contributes to their attitudes toward technology.

It is important to note that the digital divide is nuanced and shows different patterns of change depending on which aspects are considered: some digital gaps are narrowing down over the last few decades while others remain. For example, the rate of Americans who don't use the internet has decreased rapidly from 48% in 2000 to 7% in 2021 (Perrin & Atske, 2021). Similarly, recent studies found that the vast majority of people have a smartphone or technological divide (Barrantes & Vargas, 2017). While the general access to the internet or technology has been improved, individuals with low-income, rural residents, and minorities have a limited number of digital devices for online access and rely primarily on smartphones (Vogels, 2021a). They are also less likely to have broadband internet at home, creating other disparities such as educational and health inequalities (Ong, 2020; Vogels, 2021b).

The digital divide leads to the exclusion of populations based on different factors. Age has been a major leading factor in the digital divide, placing older adults into one of the largest affected populations (Tsai et al., 2015). As of 2019, 27% of Americans aged 65 and older and 12% of adults aged 50 to 64 were not using the internet, which is a sharp contrast to the nearly ubiquitous internet usage among young adults; 100% of 18–29-year-olds and 97% of 30–49-year-olds reported using the internet (Pew Research Center, 2019). Although one of the largest populations affected by the digital divide is older adults (Tsai et al., 2015), digital technologies may be most beneficial to this population. Older adults' technology use spans various avenues of life. Using information and communication technologies (ICTs) has shown to have increased feelings of mattering among older adults (Francis et al., 2019), connecting them with loved ones (Heo et al., 2015; Quan-Haase et al., 2017; Sum et al., 2008), and assisting with managing their health through medical and health-related technologies (Levine et al., 2016; van Deursen, 2020). With increasing medical treatment improvements, older adults account for large percentages of both the U.S. and global populations. By 2030, 20% of the U.S. population will be older adults – the largest population of older adults in U.S. history (Centers for Disease Control and Prevention., 2013). Given the beneficial effects of technology use and demographic changes, more research efforts are needed to close the older population's digital divide.

In addition to the generally low technology adoption rates among older adults, it is vital to understand the within-group heterogeneity. Those with lower socioeconomic status and poor health have been reported to be at greater risk of being excluded from technology use (Gell et al., 2015; Silver, 2014). Amongst various predictors of older adults' technology use, a recent growing body of literature has shown that rural living is significantly associated with limited access to the internet and electronic devices (Berner et al., 2015; Calvert et al., 2009). Moreover, in qualitative studies, older adults living in suburban or rural areas reported negative perceptions of using technologies, such that lack of knowledge about how technologies function or difficulty in learning how to use them greatly limited their use (Marston et al., 2019; O'Brien et al., 2014). Prior studies suggested low rural residents' socioeconomic status levels partly contributing to the urban-rural differences in technology use (Hale et al., 2010). However, underdeveloped infrastructure and broadband services in rural communities, which are related to high-speed internet access, can also result in their residents' limited technology use (Anderson, 2018; Greenberg et al., 2018; Korupp, 2005). Indeed, having access to technology, particularly high-speed internet, is a critical facilitator of older adults' technology use (Hanson, 2010; Marston et al., 2019).

The observed digital divide by age and residential area is well encapsulated in the social determinants of health framework (World Health Organization [WHO], 2010), which posits that the source of health inequities originates from "the conditions in which people are born, grow, work, live, and age, and the wider set of forces and systems shaping the conditions of daily life." (WHO, 2020, p.1). According to the framework, the digital divide could occur due to broader systemic and socioeconomic contexts and individual-level sociodemographic factors (i.e., age and gender). Thus, we argue that a geographic residence where older adults live would be an important social determinant of digital technology use by offering different opportunities and challenges embedded in regional infrastructure and community support.

The present study

Although prior studies suggested some valuable insights into the urban-rural digital divide for the older population, most relied on small convenient samples or measured a single aspect of technology use (i.e., internet access). In addition, there were few studies focused on different usage patterns or psychological factors. The current study aims to investigate whether one's residential area relates to (1) their internet use, (2) the subtypes of their technology usage patterns, and (3) their attitudes toward technology use. We conducted a series of regression analyses on data of a nationally representative sample of U.S. adults aged 50 or older. Building on the previous literature and the social determinants of health framework, we hypothesized the following:

Hypothesis 1: Older adults living in suburban and rural areas will use the internet less than their urban counterparts.

Hypothesis 2: Older adults living in suburban and rural areas will be less likely to use different technologies (communication, financial, health, and media) than urban residents.

Hypothesis 3: Older adults living in suburban and rural areas will have more unfavorable attitudes toward technologies than those residing in urban communities.

Methods

Data and sample

The Health and Retirement Study (HRS) is a nationally representative panel survey of approximately 20,000 Americans aged 50 or older. The HRS has been repeated biannually since 1992. Participants are asked a wide range of questions on aging (e.g., health, jobs, retirement, and social relationships) through face-to-face or telephone interviews. The HRS's sampling design, survey procedures, and questionnaires are described in detail at the HRS website (http://hrsonline.isr.umich.edu). We retrieved the respondent's socioeconomic and health information from the RAND HRS data file, which is cleaned and processed by the RAND Center for the Study of Aging (Santa Monica, California). The RAND HRS data set provides imputed values for income and health status that were generated using all information available with a consistent imputation method.

In 2012, a randomly selected subsample of participants was administered to an experimental module that included questions about technology use and perceptions of the barriers and benefits. A total of 1,620 community-living adults aged 50 or older completed the module. We excluded 54 respondents (3.33%) who had missing data on covariates, internet access, and internet usage variables, which resulted in an analytic sample of 1,566 individuals. Among the respondents, those who did not use any communication technologies such as email and social network sites (N = 633) were further asked about their attitudes toward technology. We use this subsample of respondents for the analyses of non-users ' attitudes toward technology. Ethical approval for the HRS was obtained from the University of Michigan Institutional Review Board and the National Institute on Aging. All respondents have given their written informed consent before the data collection.

Measures

Internet access

Participants' internet access was assessed with a single item: "Do you regularly use the Internet (or the World Wide Web) for sending and receiving email or for any other purpose, such as making purchases, searching for information, or making travel reservations?'' Responses were coded as 1 = yes or 0 = no.

Technology usage

Technology usage was measured by a checklist of various kinds of electronic technologies. The list included fifteen items (1 = yes for each), which can be grouped into four broad types of technology: (1) communication technology (i.e., email, social networks, online calls, online chatting, and smartphone); (2) financial technology (i.e., online bill payment and online banking); (3) health technology (i.e., online wellness program, online health information seeking, devise use of health monitoring, and Wii fit use); and (4) media technology (i.e., e-readers/tablets, MP3 players, live-streaming radio, T.V., or movies, and video games). Responses were dichotomized for each technology category, where 0 = non-user and 1 = users who checked one or more technology items in a given category.

Attitudes toward technology

Participants who reported no use of any communication technologies, or non-users, were further asked about their attitudes toward technology. They answered yes or no to eight questions: (1) if they would be interested in trying any communication technologies, (2) whether technology is too expensive, (3) easily available, (4) too complicated, (5) too hard to learn, (6) takes too much time to learn, (7) if they are opposed to learning new technologies, and (8) whether it is difficult to keep up with changes in technology.

Urban-rural residence

The residency was categorized as urban, suburban, and rural using the 2013 Beale Rural-Urban

Table 1. Sample characteristics by rural-urban residence (N = 1,566)

Variables	Urban (*n* = 850)		Sub-urban (*n* = 338)		Rural (*n* = 378)	
	Mean (S.E.)	%	Mean (S.E.)	%	Mean (S.E.)	%
Residence		51.9		22.6		25.5
Age in years (range: 50-98)	64.9 (0.39)		65.78 (0.63)		65.92 (0.57)	
Gender						
Female		50.6		53.2		56.5
Race/ethnicity						
Racial/ethnic minority		18.3		15.9		11.7 **
Marital status						
Married/partnered		65.3		61.7		65.0
Education in years (range: 0-17)	13.6 (0.13)		13.0 (0.25) *		12.87 (0.16) ***	
Annual household income (thousands)	87.2 (5.50)		91.3 (13.1)		62.2 (4.81) ***	
Chronic diseases (range: 0-8)	1.84 (0.06)		2.07 (0.09) *		2.24 (0.09) ***	
Functional limitation						
Yes (≥ 1 in activities of daily living)		11.0		14.0		16.2 *
Self-rated health (range: 1-5)	3.36 (0.05)		3.30 (0.07)		3.14 (0.07) **	
Depressive symptoms (range: 0-8)	1.29 (0.09)		1.37 (0.14)		1.44 (0.12)	

*$p < .05$; ** $p < .01$; *** $p < .001$.

Note. Estimates were weighted and column numbers were unweighted. Adjusted Wald tests were conducted by comparing each region with the urban group. Racial/ethnic minority = non-Hispanic black, Hispanic, American Indian, Alaskan Native, Asian, and Pacific Islander.

Continuum (RUC) codes. Developed by the S.U.S. Department of Agriculture's Economic Research Service, the RUC codes represent the degree of urbanization by population size and adjacency to metropolitan areas. Urban refers to metropolitan counties with a population size of 1 million or more (RUC code 1). Suburban indicates metropolitan counties of 250,000 to 1 million population (RUC code 2). Finally, rural areas include counties with fewer than 250,000 population, both adjacent or not adjacent to a metropolitan area (RUC code 3–9).

Covariates

Age (in years), gender (0 = male; 1 = female), race/ethnicity (0 = non-Hispanic White; 1 = racial/ethnic minority [non-Hispanic black, Hispanic, American Indian, Alaskan Native, Asian, or Pacific Islander]), and marital status (0 = separated, divorced, widowed, or never married; 1 = married or partnered) were included as demographic variables. Educational attainment (in years) and annual household income served as indicators of socioeconomic status. Education was assessed by the number of years of formal schooling completed (range: 0-17), and annual household income included income from all sources such as earnings, pensions, and social security. Because the distribution of annual household income was highly skewed, log-transformed values were used for multivariate analyses. As for indicators of health conditions, chronic diseases, functional limitations, self-rated health, and depressive symptoms were considered. Participants were asked to report whether or not they had any of the following chronic diseases diagnosed by a physician: high blood pressure, diabetes, cancer, lung disease, coronary heart disease, psychiatric problems, arthritis or rheumatism, and stroke. The number of chronic diseases was calculated by summing up all specific diseases (range 0-8). Functional limitation was assessed by asking participants' difficulties in performing activities of daily living (ADLs) such as bathing, dressing, walking across a room, and getting in and out of bed. The composite scores were dichotomized into 0 = no functional limitation and 1 = one or more functional limitations. Self-rated health status was measured with a single item, "Would you say your health is excellent, very good, good, fair, or poor?" Responses were coded as 1 = poor and 5 = excellent so that higher scores indicated better subjective health status. Depressive symptoms were measured with the 8-item version of the Center for Epidemiological Studies Depression (CES-D) scale (Andresen et al., 1994; Radloff, 1977). Participants were asked to report whether they have experienced eight depressive symptoms (e.g., lonely, feeling depressed, and sad) in the past week. Response options were 0 = no or 1 = yes. After reversing two positive mood items, total scores were computed by adding responses for each item. The CES-D scale's internal consistency was high in our sample, with the Kuder-Richardson 20 (KR-20) coefficient of .82.

Analytical strategy

Descriptive statistics were conducted to review the sample's demographic, socioeconomic, and health characteristics by urban-rural residence. Comparisons were made using adjusted Wald or chi-square statistics. Next, group differences in internet access and usage were compared across urban, suburban, and rural residents through chi-square tests. Separate multivariate logistic regression analyses were performed for each technology used to examine their association with rural-urban residence (N = 1,566). Similarly, we used multivariate logistic regression models to investigate the association between rural-urban residence and attitudes toward technology among non-users (N = 633). For the analysis of non-users' attitudes toward technology, the pairwise deletion was applied to make optimal utilization of available data (Ns = 556–629). We used sample weights to adjust for differential

Table 2. Internet access and usage by rural-urban residence (N=1,566)

Variables	% Urban (*n* = 850)	% Sub-urban (*n* = 338)	% Rural (*n* = 378)
Internet access	66.0	61.0	53.6 ***
Communication technology (yes, any)	70.5	66.4	59.8 **
E-mail	68.6	63.1	55.1 ***
Social network sites	32.0	31.3	29.0
Online calls	24.8	20.7	19.2
Online chatting	23.0	16.8	16.6 *
Smartphone	32.4	23.8 *	16.1 ***
Financial technology (yes, any)	51.8	43.0 *	38.2 ***
Online bill payment	44.1	34.4 *	31.7 **
Online banking	47.1	39.3	34.5 **
Health technology (yes, any)	68.1	57.5 **	61.7
Online wellness program	9.6	9.0	5.7
Online health information seeking	57.0	43.1 ***	44.0 ***
Device use for health monitoring	30.6	27.1	27.0
Wii fit use	9.0	6.0	8.2
Media technology (yes, any)	52.5	45.4	37.2 ***
E-readers or tablets	26.2	22.9	17.3 **
MP3 players	25.7	16.3 **	11.1 ***
Live-streaming radio, TV, or movies	33.9	23.2 **	20.0 ***
Video games	10.7	6.0	6.3 *

*$p < .05$; ** $p < .01$; *** $p < .001$
Note. Estimates were weighted and column numbers were unweighted. χ^2 tests were conducted by comparing each region with the urban group.

sampling probabilities and survey non-response. All analyses were performed using Stata version 14.2. (StataCorp. College Station, TX).

Results

Sample characteristics

Table 1 summarizes the sample characteristics by rural-urban residence. The sample was comprised of 52% urban, 23% sub-urban, and 25% rural residents. Compared to urban residents, the rural group included a lower proportion of racial/ethnic minorities and those with functional limitations. In addition, rural residents had lower annual household income levels and poorer self-rated health than their urban counterparts. Both suburban and rural residents had fewer years of education and reported more chronic diseases compared to the urban group. No significant group differences were found for age, gender, marital status, and depressive symptoms.

Urban-rural group differences in internet access and technology usage

Table 2 presents a cross-tabulation of internet access and different types of technology usage by urban-rural residents. About 66% and 61% of urban and suburban residents were regular internet users, whereas only 54% of rural residents regularly used the internet. In terms of communication technology use, significantly fewer individuals in the rural group (60%) reported use of at least one communication technology than their urban counterparts (71%). For specific technology, significance was found in email use (55% in rural vs. 69% in urban), online chatting (17% in rural vs. 23% in urban), and smartphone use (16% in rural and 24% in sur-urban vs. 32% in urban). Compared to urban residents, suburban and rural residents had fewer individuals who used one or more financial technologies (38% in rural and 43% in suburban vs. 52% in urban). About a third of suburban and rural residents used online bill payment, while more than 40% of urban residents did so. Rates of online banking users were also significantly lower among the rural group than their urban counterparts. Similarly, there were fewer individuals from the suburban group who used at least one health technology than the urban group. More urban residents sought online health information than the other two groups (57% in urban vs. 43% in sub-urban and 44% in rural). Finally, the rural group had significantly fewer media technology users (37%) compared to the urban group (53%). Specifically, significant differences between urban and rural residents were found in all sub-categories, whereas the differences between urban and suburban were only found in the use of MP3 players and live-streaming radio, T.V., or movies.

Logistic regression models of technology usage

We further examined the observed group differences in technology usage with multivariate logistic regression analyses. *Table 3* shows the association between rural-urban residence and four different technology use types after controlling for demographic, socioeconomic, and health covariates. Compared to urban residents, rural residents had lower odds of using all technology types except health technology. On the other hand, the suburban group showed decreased odds of using health technologies than the urban group. No significant associations were found in the use of communication, financial, and media technologies.

Logistic regression models of non-users' attitudes toward technology

Table 4 presents the models predicting attitudes toward technology among non-users of communication technology. We found that three particular attitudes toward technology were significantly associated with the rural-urban residency. Compared to urban residents, rural residents were less likely to report that technology is easily available and more likely to think that technology is too complicated and too hard to learn. It was noteworthy that no significant differences were found between suburban and urban residents in their attitudes. The associations of the rural-urban residence with other five types of attitudes

Table 3. Logistic regression models of technology usage (N=1,566)

Variables	Odds ratio (95% Confidence interval)			
	Communication technology	Financial technology	Health technology	Media technology
Rural-urban residence (Ref: urban)				
Sub-urban	1.07 (0.71–1.63)	0.77 (0.53–1.12)	0.65 (0.45–0.95) *	0.83 (0.57–1.21)
Rural	0.69 (0.47–0.99) *	0.64 (0.45–0.9)*	0.76 (0.55–1.05)	0.57 (0.40–0.80) **
Demographic characteristics				
Age (in years)	0.91 (0.90–0.93) ***	0.92 (0.91–0.94) ***	0.94 (0.93–0.96) ***	0.92 (0.91–0.94) ***
Female	1.89 (1.36–2.63) ***	1.30 (0.96–1.75)	1.54 (1.15–2.06) **	1.13 (0.84–1.51)
Racial/ethnic minority	0.42 (0.28–0.62) ***	0.54 (0.38–0.78) **	0.68 (0.48–0.96) *	0.62 (0.43–0.9) *
Married/partnered	1.43 (1.00–2.06)	1.19 (0.84–1.69)	1.38 (1–1.89) *	1.46 (1.04–2.04) *
Socio-economic status				
Educational attainment (in years)	1.47 (1.36–1.60) ***	1.22 (1.14–1.31) ***	1.15 (1.09–1.21) ***	1.15 (1.08–1.23) ***
Annual household income	1.17 (1.01–1.35) *	1.12 (0.97–1.29)	1.01 (0.91–1.12)	1.09 (0.95–1.24)
Health conditions				
Chronic diseases (numbers)	0.99 (0.87–1.12)	1.04 (0.92–1.18)	1.31 (1.17–1.47) ***	1.09 (0.97–1.22)
Functional limitation	0.61 (0.37–0.98) *	0.79 (0.49–1.26)	0.93 (0.6–1.43)	0.89 (0.56–1.41)
Self-rated health	1.28 (1.05–1.55) *	1.19 (1.00–1.42)	1.14 (0.95–1.36)	1.28 (1.07–1.51) **
Depressive symptoms	0.95 (0.86–1.04)	0.95 (0.86–1.03)	0.94 (0.87–1.02)	1.00 (0.91–1.09)

*$p < .05$; ** $p < .01$; *** $p < .001$.
Note. Estiamtes were weighted. Racial/ethnic minority = non-Hispanic black, Hispanic, American Indian, Alaskan Native, Asian, and Pacific Islander.

toward technology (i.e., have interest in trying technology, technology is too expensive, takes too much time to learn, too difficult to keep up with changes, and if they are opposed to learning new technologies) were not significant and thus not shown in the table for simplicity.

Discussion

Informed by the social determinants of health framework, we analyzed the HRS data to explore whether one's residence (urban, suburban, or rural) is associated with less use of the internet, limited usage patterns of different technologies, and more negative attitudes toward technology in later life. Our bivariate results indicate that individuals in rural communities use the internet at a lower rate (54%) as compared to urban populations (66%). Furthermore, rural living older adults used technology at lower rates for different technology usage sub-types, including communication, financial, and media technologies. Compared to urban residents, older adults living in suburban areas also reported lower usage rates of certain types of technology use, such as smartphones, online bill payments, and online health information seeking.

Our multivariate models of technology usage further showed that rural residency (vs. urban) was significantly associated with decreased odds of using communication, financial, and media technology, while suburban residency (vs. urban) was related to lower odds of health technology use. Overall, these findings add to the body of past research, pointing out a digital exclusion of rural populations in general (Greenberg et al., 2018; Perrin & Duggan, 2015) and in the older populations (Berner et al., 2015; Calvert et al., 2009). Importantly, our analyses on various usage patterns of ICTs extend the scope of the existing literature where a single aspect of technology use (i.e., internet use) was often focused.

Our findings documented that older rural residents particularly do not engage in online communication and media. Such exclusion could lead to many disadvantages, including connection with loved ones and personal mattering. This mattering and connectedness often occur through the usage of ICTs, which allow for the maintenance of social connectedness and receiving social support from their networks (Francis et al., 2019). Mattering has been explained as occurring due to social interactions among people, which helps reinforce their value to others (Fazio, 2009), but in situations where in-person interactions may not be possible, especially social interactions that reinforce ones' value to others (Fazio, 2009). Therefore, in lieu of and in addition to face-to-face interactions, using ICTs may be one way to enhance a sense of mattering among older adults and potentially improve their general well-being. This is even more relevant in times like the current COVID-19 pandemic, where people are required to socially distance and avoid social interaction, especially for older adults who are more susceptible to the illness. We also found lower usage of technology for financial reasons among rural residents. Today, most financial institutions allow consumers to perform tasks such as banking and bill payments online, making transactions easier, quicker, and even safer. Therefore, those residing in rural areas are more likely to lose all these advantages of being digitally connected.

Additionally, technology is being used in the health sector in every way today. Following our findings, older adults in both suburban and rural areas use ICTs at a lower level for health purposes (e.g., online health information seeking) than their urban counterparts. This is unfortunate, considering that the benefits of health technologies may be particularly pronounced for non-urban communities. For example, telehealth can provide healthcare services with no traveling and maximizing efficiency (Heinz et al., 2013). Furthermore, Ramsetty and Adams (2020) describe how social determinants of health play a role in the development of the digital divide

Table 4. Logistic regression models of attitudes toward technology among non-users (N=633)

Variables	Odds ratio (95% Confidence interval)		
	Easily available (*n* = 599)	**Too complicated (*n* = 611)**	**Too hard to learn (*n* = 599)**
Rural-urban residence (Ref: urban)			
Sub-urban	0.91 (0.46–1.80)	1.07 (0.62–1.86)	1.34 (0.77–2.35)
Rural	0.47 (0.26–0.85) *	1.81 (1.02–3.21) *	1.93 (1.13–3.30) *
Demographic characteristics			
Age (in years)	0.99 (0.97–1.01)	1.03 (1.01–1.06) **	1.05 (1.02–1.07) ***
Female	0.64 (0.37–1.11)	1.23 (0.77–1.97)	0.89 (0.56–1.41)
Racial/ethnic minority	0.48 (0.28–0.84) **	1.10 (0.62–1.96)	0.77 (0.45–1.33)
Married/partnered	1.83 (1.10–3.07) *	1.13 (0.66–1.93)	1.09 (0.67–1.78)
Socio-economic status			
Educational attainment (in years)	1.09 (1.01–1.17) *	0.83 (0.75–0.93) ***	0.83 (0.76–0.91) ***
Annual household income	1.06 (0.91–1.24)	0.81 (0.58–1.14)	0.88 (0.70–1.11)
Health conditions			
Chronic diseases (numbers)	0.95 (0.78–1.15)	1.13 (0.94–1.35)	1.05 (0.88–1.15)
Functional limitation	0.75 (0.39–1.45)	2.00 (1.00–4.01)	1.83 (0.95–3.52)
Self-rated health	1.07 (0.79–1.44)	1.02 (0.77–1.34)	0.96 (0.73–1.24)
Depressive symptoms	1.07 (0.94–1.21)	1.06 (0.92–1.23)	1.22 (1.07–1.39) **

* $p < .05$; ** $p < .01$; *** $p < .001$.
Note. Estimates were weighted. Racial/ethnic minority = non-Hispanic black, Hispanic, American Indian, Alaskan Native, Asian, and Pacific Islander.

(especially in the context of COVID-19) and can reinforce inequity based on social factors, including health and healthcare access (along with education and economic stability). The pandemic has further increased how technology is being used for healthcare, and older adults can now get some of the care they need inside their homes – exclusion through the digital divide is likely to increase adverse health outcomes.

Our analyses of non-users' attitudes toward technology deserve particular attention. We showed that older adults in rural areas were more likely to perceive that technology is less easily available, too complicated, and too hard to learn as compared to the urban group. These findings are in line with previous qualitative work where older suburban or rural residents reported that their use of technologies was limited due to lack of knowledge about technologies or difficulties in learning (Marston et al., 2019; O'Brien et al., 2014). However, there has been a dearth of quantitative studies, particularly with a nationally representative sample, that examined perceptions or attitudes toward technology use among older adults living in non-urban communities.

Overall, the present study findings support that older adults living in suburban and rural areas not only have lower access to the Internet (Hypothesis 1), but they also use fewer Internet-based technologies (Hypothesis 2) compared to those from the urban. Thus, our work demonstrates the presence of the digital divide's first level (inequal access to the Internet) and second level (different technology skills and usage) in the context of geographic location. Furthermore, we showed that non-users of communication technologies from suburban and rural areas have more unfavorable attitudes toward technologies than those in urban communities, supporting Hypothesis 3. Importantly, our results pertain to the conceptual discussion on the digital divide (Gonzales, 2016; van Dijk, 2005, 2020). According to van Dijk and Hacker (2003), the digital divide is not only related to the simple lack of access but also understood as usage patterns or psychological gaps, as shown in our study. In particular, rural non-users' more negative attitudes towards technology may serve as critical determinants of their voluntary decision not to use technology. Therefore, more research efforts should be paid to explore multiple aspects of the urban-rural digital divide.

Limitations

Despite our best efforts, we acknowledge certain limitations of our research. First, the HRS dataset is from 2012, so it is possible that this information could be a little outdated as compared to current technology usage patterns for older adults. For similar reasons, the dataset does not include more latest technologies such as wearable trackers, for instance. Critically, our study utilized cross-sectional data, which does not allow for making causal inferences. Future studies should use a longitudinal research design to provide a complete understanding of the relationship between one's residence and technology use in later life. In addition, although we included a wide range of information on specific types of technology use, data on frequency or duration of use was not obtained. Based on our findings, a next step forward may include those variables to examine whether the urban-rural residence relates to how long or frequently one uses digital technologies.

Conclusions

Despite these limitations, however, we believe that the results of our study provide valuable insights into the existing digital divide that excludes older adults, often based on their geographic location. Our results identify an urgent need for interventions to introduce digital technologies to older adults in rural areas. This is especially imperative in unprecedented isolating times, such as those created by the COVID-19 global pandemic. Digital technologies have helped people stay in touch with their loved ones and provide medical assistance. Such technologies in this situation are more important for older adults, who are more susceptible to the novel coronavirus and would benefit from integrating digitization into their daily lives. Future work could include interventions into marginalized communities to better understand the causes of this divide in greater detail, the community's needs, and what can be provided to them to prevent further exclusion. In addition, our work calls for further research attention to the role of geographic location. Although we focused on three categories from the Beale Rural-Urban continuum for this study, future work can examine different typologies of spatial locations (e.g., urban networks) and their implications on the digital divide.

Conflict of interest
The authors declare that there is no conflict of interest.

Author statement
Hee Yun Lee: Funding acquisition, Conceptualization, investigation, methodology, writing – review & editing. Shaheen Kanthawala: Conceptualization, investigation, writing – original draft. Eun Young Choi: Data curation, formal analysis, methodology, writing – original draft. Young Sun Kim: Supervision, Funding acquisition, resources, writing – review & editing.

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CALIFORNIA

California wildfires are burning deeper into urban areas like Altadena and finding new victims

A pedestrian walks past a makeshift memorial to the victims of the Eaton fire at the corner of North Lake Avenue and East Villa Street in Pasadena in January. (Genaro Molina / Los Angeles Times)

By Summer Lin and Terry Castleman

Feb. 25, 2025 3 AM PT

As California struggles to defend itself against increasingly destructive urban wildfires, recent fire deaths in Altadena highlight what researchers say is a growing trend in victim demographics.

Up until about the last decade, California wildfires traditionally have affected higher-income white households, with deaths skewing toward seniors and men. More recently, however, wildfires are increasingly touching more diverse communities as fires grow in intensity and extend into densely populated areas, according to researchers.

Of the 17 people killed by the Eaton fire, more than 70% were Black and 64% were women. More typically, however, those killed by the fire had a median age of 77 and at least a third of them suffered impairments that could affect their mobility, according to a Los Angeles Times analysis.

A 2023 study of California wildfires conducted by U.S. Forest Service researchers found that "new fire regimes are increasingly affecting more urban census tracts statewide, meaning greater numbers and more diverse groups of people are being and possibly will be affected by wildfires." These changes, authors wrote, meant that more Latino, Asian and Black Californians were being impacted by wildfire than ever before.

The trend, they say, could become even more pronounced in the future and potentially have serious consequences for wildfire readiness.

All 17 Eaton fire deaths occurred west of North Lake avenue

Terry Castleman LOS ANGELES TIMES

“The increasing occurrence of wildfires in urban areas suggests a need for increased outreach to residents of more urbanized neighborhoods and communities that have never experienced wildfires,” the study’s authors wrote.

“Even in those that have historically been sporadically affected by wildfire, their residents are likely to have lower perceptions of risk, believing that wildfires will not occur in their neighborhoods. Similarly, they are likely to be less prepared for wildfires, such as having a ‘go bag’ or completing home mitigation measures.”

In the case of the Eaton fire, emergency management officials have been harshly criticized for significant delays in the issuing of electronic evacuation orders — delays that some say cost residents their lives.

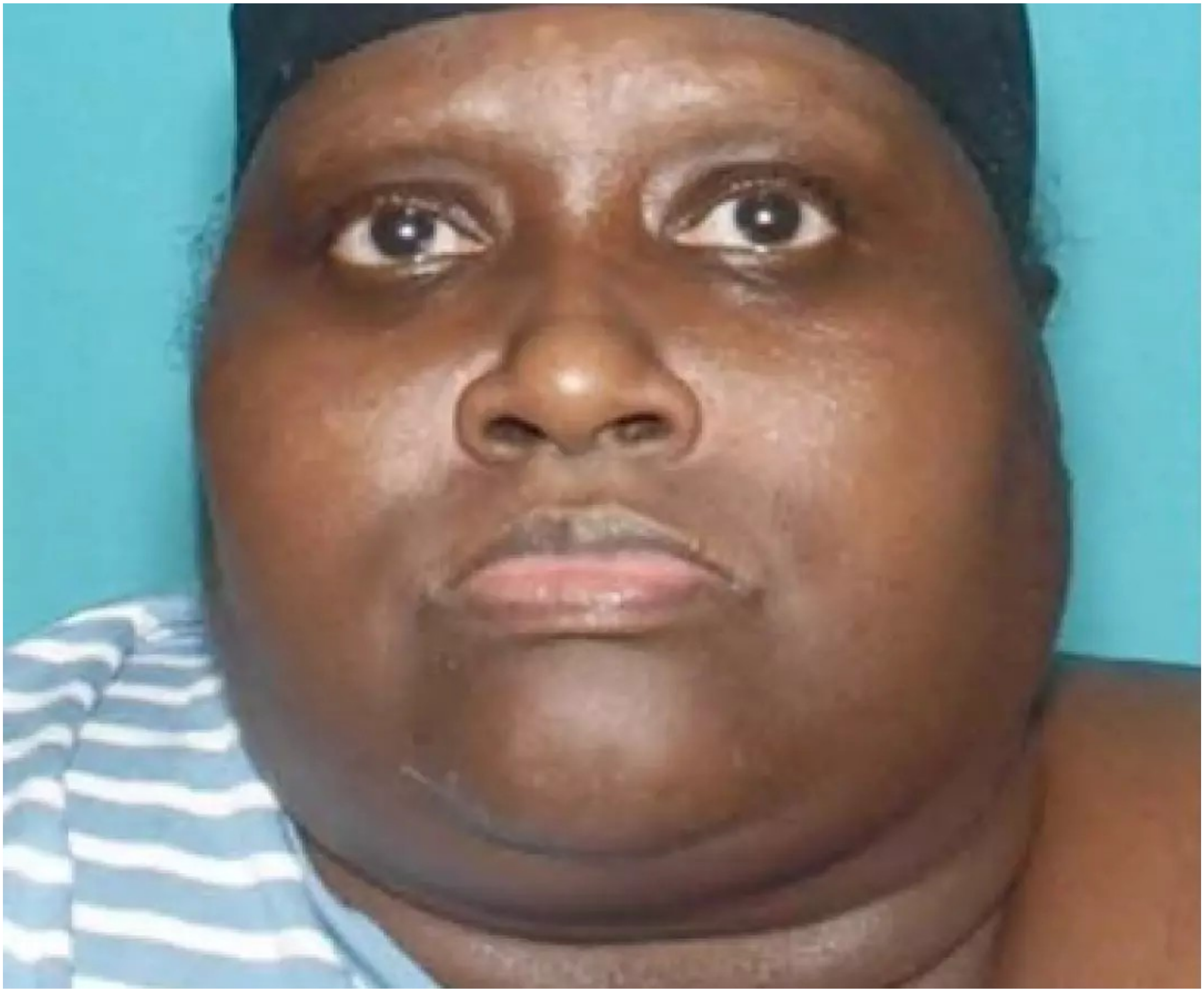
Eastern Altadena received a warning text and evacuation orders within about the first hour after the fire began on the evening of Jan. 7. The western boundary for the alerts, North Lake Avenue, would come to be a fateful dividing line: Altadena homes east of North Lake received evacuation orders at least eight hours before homes on the west side.

All 17 Eaton fire deaths happened west of North Lake, in areas that never received evacuation warnings or received evacuation orders hours after homes had already been reported to be on fire, a Times investigation found.

Many residents of western Altadena — which was shaped by discriminatory lending practices in the 1960s and '70s and has become known for its strong Black community — told The Times they felt forgotten. North Lake was the boundary line for these redlining efforts, and racial gaps have persisted: Altadena's east side is whiter and incomes are higher than those of the west side, according to census data.

Nearly a third of those killed in the Eaton fire suffered some form of disability. Among them was 56-year-old Carolyn Burns.

Burns, who used a wheelchair and walker to get around, lived with her 76-year-old mother.



Carolyn Burns, 56, died in the Eaton fire. (Los Angeles County Sheriff's D)

Burns' mother, who also is named Carolyn, told The Times that another of her daughters called the Los Angeles County Fire Department around 10 or 11 on the night of the fire to ask about conditions in their neighborhood. They were reportedly told that the street was safe at the moment and if they needed to be evacuated, someone would knock on the door.

At around 3:30 a.m. the mother woke to the sound of a neighbor banging on a window and yelling that the house was on fire. She jumped out of bed and saw flames in her kitchen. She managed to escape, but her daughter did not.

"I don't think they did their jobs because they didn't get over there in time or knock on our doors," the mother told The Times. "I think it was too late. Even if they needed to get her out of there, they didn't have enough time. We're very angry inside and we'll never be the same."

The county Fire Department declined to comment on the evacuation orders or Burns' death. In a statement, the agency said the L.A. County Board of Supervisors has opened an investigation into the evacuations and emergency notifications. Reports will be due back to the board every 90 days and shared with the public.

The Fire Department "acknowledges the immense loss and challenges faced by our communities during the wildfires and remain deeply committed to supporting those affected," according to the statement.

Eaton and Palisades fires

The devastating fires killed at least 28 people, destroying and damaging more than 18,000 buildings valued at more than $275 billion and leaving a burn zone 2½ times the size of Manhattan.

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Mark Ghilarducci, who served as the director of the California Governor's Office of Emergency Services for more than a decade, said it doesn't "sound normal" if disabled residents were left to evacuate on their own.

"There's generally an understanding of individuals who have access and functional needs where they can be supported," he said. "Sometimes the 911 centers know that they exist. A lot of the time, it's law enforcement going door to door to ensure that people are getting out and and being notified."

Senior citizens tend to be the ones who die in wildfires, he said, because they aren't as attuned with social media, could be more limited in their mobility or rely on others to drive them around.

"We need to figure out exactly what happened, why were decisions made the way they were, and if it was a failure in technology, we need to identify that as well and figure out, how do we address that?" Ghilarducci said. "It isn't normal. We want people to get out of harm's way."

Fires with large death tolls are relatively rare in California but have been growing in frequency over the last 10 years, said Michele Steinberg, a spokesperson for the wildfire division of the National Fire Protection Assn.

In all major incidents — including the Eaton and Palisades fires — seniors are the most vulnerable.

Steinberg said older residents may have difficulty evacuating, due to potential mobility issues, or they may simply refuse to leave.

In some previous cases Steinberg has reviewed, fatalities among those who were younger — in their 50s or 60s — died while trying to help others.

"You're trying to save pets, save people, take care of people," Steinberg said. "You yourself might be able and willing and ready, but you have someone else to look after."

Ultimately, life or death can come down to how quickly a person can react to a fast-moving and unexpected situation, she said. "People aren't just independently jumping in their car wide awake — it's chaos."

In Altadena, where the fire spread in the "middle of the night," residents probably had even less warning, Steinberg said, with the speed of the fire and possible issues with alerts making the situation more deadly.

Among the seniors killed in the Eaton fire were Dalyce "DeDe" Curry, 95, and Erliene Kelley, 83.

Dalyce Kelley with her 95-year-old grandmother, Dalyce Curry, who died in her home in Altadena during the Eaton fire. (Dalyce Kelley)

Curry was home alone on the night of the fire, while her granddaughter, Dalyce Kelley, was caring for a sick relative and checking in on her grandmother via text.

Kelley had fallen asleep at her home. At 6:38 a.m., she woke up and wrote to an Altadena neighborhood group chat: "My grandmother is still there. We got home around midnight. Have evacuation orders been implemented? … if they evacuate you all, I'll come immediately, just please grab her."

"Every one was evacuated at 3:30," a neighbor responded.

"Omg," Kelley replied. "Getting dressed now. Her phone is going straight to voicemail."

She rushed to her car and raced to her grandmother's house but was stopped at a police barricade. Kelley gave a police officer her grandmother's address and asked whether he could check on her. The officer called Kelley later, telling her that Curry's home had burned down.

The Los Angeles Medical Examiner pronounced Curry dead Jan. 11 and notified her family that her remains had been found on her property, according to Kelley.

One of Curry's neighbors, Ana Morales, 34, faults officials for failing to warn residents earlier. She said she and her husband decided not to wait for an official evacuation order and fled their home around 9 p.m.

"I don't think there was enough notice for everybody," Morales told The Times. "We were going off of our intuition and fear. They should've evacuated everybody when we left, told us to pack up everything we need and to leave. But nothing."

Briana Navarro, who lost her grandmother Erliene Kelley in the fire, agreed. She said her grandmother and others could have been saved with earlier notice from officials.

"A lot of the lives that were lost were either elderly or disabled, which is unfortunate because they're one of the vulnerable groups that need the most assistance from family or their support system," she said. "I think with a notice it would have given enough time for some of us to go help our family members."

Times staff writer Ruben Vives contributed to this report.

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Feb. 16, 2025

Summer Lin

Summer Lin is a reporter on the Fast Break Desk, the Los Angeles Times' breaking news team. Before coming to The Times, she covered breaking news for the Mercury News and national politics and California courts for McClatchy's publications, including the Miami Herald. An East Coast native, Lin moved to California after graduating from Boston College and Columbia University's Graduate School of Journalism. Lin was among The Times' staff members who covered the Monterey Park mass shooting in 2023, which was recognized by the Pulitzer Board as a finalist in breaking news.

Terry Castleman

Terry Castleman is a data reporter on the Fast Break Desk covering breaking news. In 2020, he was named alongside his colleagues as a Pulitzer Prize finalist in explanatory reporting. Previously, he worked at the New York Times and volunteered as a first responder for refugees arriving on the shores of Lesvos.

Weather, Wind And Flammable Flora Fuel California Fires

Deadly wildfires on the edge of Los Angeles are the result of two years of wet conditions, a year of drought and hurricane-force Santa Ana winds, University of Virginia experts said.

Several fires have combined to burn nearly 40,000 acres, destroying thousands of structures and killing at least two dozen people.

The National Weather Service issued red flag warnings and high wind warnings across Southern California on Monday and Tuesday with “particularly dangerous situation” warnings for most of the fire-affected area.

“Dryness is the major factor, and this fire was exacerbated by the winds that are occurring right now,” said Venkataraman Lakshmi, John L. Newcomb Professor of Engineering in UVA’s Department of Civil and Environmental Engineering. “The dry conditions have reduced the vegetation water content and as a result, the vegetation is very susceptible to burning.”

“The two previous years were very wet, with almost double the average annual rainfall. In these water-limited ecosystems, that leads to greater growth, more leaf growth and leaf litter, which desiccates under the hot, dry winds," Larry Band, UVA's Ernest Ern Professor of Environmental Science, said.

The Palisades fire, the largest of the four active blazes, began west of Los Angeles and north of Santa Monica. It burned toward Malibu and to the Pacific Ocean, while the Eaton fire burned parts of Pasadena and Altadena. Smaller fires, now mostly contained, also burn in the area.

Little to no rain has fallen in the area since last summer, with late autumn and winter being the usual wet seasons for the region. The National Drought Mitigation Center's data shows the area around Los Angeles morphed from normal conditions in October to severe drought by Jan. 7. The same source shows this year's soil moisture content in the region being the dryest since 2015.

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Venkataraman Lakshmi, the John L. Newcomb Professor of Engineering in UVA's Department of Civil and Environmental Engineering, left, and Larry Band, UVA's Ernest Ern Professor of Environmental Science. (Contributed photos)

The area's natural vegetation adds to the danger, UVA experts say.

"The native vegetation is chaparral, a family of species that are fire-adapted, burn periodically and resprout. They dominate local ecosystems, as the fires keep out competitors," Band said. "The chaparral survives the dry, hot Mediterranean climate summers by secreting a resin that coats their leaves, reducing water loss. The resin is very volatile and burns hot."

Airborne firefighters in a helicopter drop water on the Palisades fire. At least two dozen people have died in wildfires in the Los Angeles metropolitan area. (Photo by Cal Fire)

Band said Santa Ana winds are common in the fall and into early winter, but there is usually some rain during the winter wet season.

“The winds themselves can drop the relative humidity to a few percent, further drying out and making more fire-prone the chaparral and the leaf litter that accumulates on the ground,” Band said.

The combined dry climate and flammable flora have created fires and firestorms before. In October 1978, the Agoura-Malibu and Mulholland Canyon fires burned more than 500 homes and killed three people. The Agoura-Malibu fire grew into a firestorm, a fire so intense it creates its own wind system.

“Steep mountainous terrain tends to funnel fires upslope, but with the intense Santa Ana winds, the fire is swept downslope toward the ocean,” Band said. “That’s why there was so much devastation at lower elevations, like downtown Pacific Palisades.”

Band, who did graduate work at the University of California, Los Angeles, and spent time in the Santa Monica and San Gabriel mountains, said once the fires have been extinguished, new dangers could await the burned areas in a few months.

“The lack of vegetation and disintegration of root systems tends to lead to significant landslides,” he said. “If there are strong rains later this winter, we could see destructive landsliding and flooding in these areas."

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Review

Wildfires and Older Adults: A Scoping Review of Impacts, Risks, and Interventions

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Abstract: Climate change is leading to worsening disasters that disproportionately impact older adults. While research has begun to measure disparities, there is a gap in examining wildfire-specific disasters. To address this gap, this scoping review analyzed literature to explore the nexus of wildfires and older adults. We searched peer-reviewed literature using the following inclusion criteria: (1) published in a peer-reviewed journal; (2) available in English; (3) examines at least one topic related to wildfires; and (4) examines how criterion three relates to older adults in at least one way. Authors screened 261 titles and abstracts and 138 were reviewed in full, with 75 articles meeting inclusion criteria. Findings heavily focused on health impacts of wildfires on older adults, particularly of smoke exposure and air quality. While many articles mentioned a need for community-engaged responses that incorporate the needs of older adults, few addressed firsthand experiences of older adults. Other common topics included problems with evacuation, general health impacts, and Indigenous elders' fire knowledge. Further research is needed at the nexus of wildfires and older adults to highlight both vulnerabilities and needs as well as the unique experience and knowledge of older adults to inform wildfire response strategies and tactics.

Keywords: wildfires; climate change; disaster recovery; evacuation; adaptation; mitigation; older adults; elders

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1. Introduction

The growing threat of climate change has been well-documented in recent years. Since 2011, concentrations of greenhouse gases in the atmosphere have soared, pushing global surface temperatures to an estimated 1.3 degrees Celsius above pre-industrial levels [1]. Human-induced climate change has accelerated impacts of ecological degradation, biodiversity loss, and extreme weather events. These include, but are not limited to, increases in areas burned in wildfires, cyclone intensity attributed to sea-level rise, severe and prolonged droughts, heavier precipitation, and substantial—and in some cases irreversible—damages to biodiversity and ecosystems [1]. These impacts are not felt evenly, with already vulnerable populations suffering the brunt of the crisis. Those living in poverty, women, children, older adults, outdoor workers, people with disabilities, Indigenous populations, and people of color are facing adverse health events. These include increased morbidity and mortality from disease connected to heat stress, exposure to air pollution and smoke, and vector-borne illnesses, in addition to ongoing human rights violations during this era of climate crisis [2].

The social and ecological consequences of wildfires are areas of growing concern, with recent wildfire seasons breaking precedents for frequency and intensity [3]. In the U.S. alone, wildfire events are increasing, with an average of 6.9 million acres burned annually, more than double the annual acreage burned in the 1990s, with the top five worst wildfire seasons in the U.S. all occurring since 2006 [3]. Record-breaking wildfire seasons from Australia to the Arctic and in North and South America are an ominous sign of the ever-growing duration, frequency, and intensity of wildfire seasons to come [4]. Even in the best-case scenarios for curbing emissions, the risk of global wildfire occurrence will still increase by 31–57% by the end of the century [4]. Environmental change related to wildfires is also unique in that wildfires are exacerbated by climate change and are also a contributing factor in the worsening of climate change through the release of greenhouse gasses (GHG) and destruction of carbon stored in trees.

Beyond the environmental impacts, increasing wildfires are also a grave threat to human health. Smoke from wildfires worsens air quality and increases exposure to and inhalation of smoke and small particulates from ash, referred to as particulate matter smaller than 2.5 microns ($PM_{2.5}$) [5,6]. Wildfires lead to increased $PM_{2.5}$ and decreased air quality—increasing the odds of respiratory and health concerns such as burning eyes, runny nose, scratchy throat, headaches, respiratory illness, and exacerbation of pre-existing conditions such as asthma and COPD [6,7]. Breathing wildfire smoke is associated with increased outpatient visits, emergency visits, hospitalization, and death from a myriad of respiratory issues, which is only complicated by the current COVID-19 pandemic, as breathing $PM_{2.5}$ (the primary health concern related to wildfire smoke) is associated with increased morbidity and mortality of the novel coronavirus [7,8].

When a wildfire encroaches upon or destroys communities, emergency preparedness and response and mitigation strategies have also been investigated in conjunction with human health vulnerabilities during times of wildfire disaster. Studies concerning evacuation and emergency service systems in protecting human life and health have been carried out around the world [9]. Many studies indicate significant numbers of people delay evacuation during a wildfire event, often leading to increased evacuation danger [9]. In the immediate aftermath of a wildfire disaster, access to prescription medication, healthcare providers, and mental health services can be lacking [10]. Once these aftershocks have subsided, psychological distress following landscape and ecosystem loss—as well as personal loss or trauma—can be prevalent among the general populations [11].

The very same populations experiencing the most adverse health consequences from climate change are also vulnerable to impacts from other natural disasters, including wildfires, with older adults principal among them. Research has demonstrated that in addition to the usual concerns associated with natural disasters such as injuries and infectious disease outbreaks, older adults face added challenges due to functional or mobility limitations, decreased social supports, difficulty maintaining necessary health regimens, and limited access to information about disaster preparedness and recovery practices [12]. Due to the higher prevalence of chronic conditions among older adults, they often require specialized diets, medicine, and other medical treatments which can be more difficult to maintain or access following the trauma and disruptions caused by natural disasters [13]. Additionally, as people age, their social networks may shrink for a number of reasons, including spouses and close friends passing away or having their children move away, making it more difficult to reach out to others for help [14].

As a result of these age-related risks, older adults are disproportionately negatively impacted by natural disasters when compared to other age groups [15]. For example, while older adults made up only 15% of the New Orleans population, 71% of the people who died from Hurricane Katrina were over the age of 65 [15]. Studies have shown that older adults are often more likely to encounter life-threatening challenges while trying to evacuate during a natural disaster, are less likely to receive disaster warnings, and often experience greater financial losses following the destruction of natural disasters [16]. These disparate outcomes faced by older adults occur with all types of natural disasters, indicating that the needs of this population during these times of crisis need to be addressed [17].

While the disparate impact of natural disasters on older adults is well-documented in scholarly literature, most of this research has focused on hurricanes and flooding [18]. There is a gap in the literature examining the impact of wildfires on older adults [18]. While some findings from other natural disasters (e.g., evacuation, emergency communication, etc.) are relevant across disasters, wildfires have unique health impacts related to smoke and heat exposure that may pose multiple burdens and harms for older adults. This study seeks to examine this gap in the literature through a systematic scoping review of scholarly literature to understand the existing knowledge base on the impact of wildfires on older adults, as well as identify other gaps in data and priorities and directions for interventions and future research.

2. Materials and Methods

Due to the lack of literature on wildfires and older adults, the scoping review methodology was chosen due to its usefulness to "determine the scope or coverage of a body of literature on a given topic and give clear indication of the volume of literature and studies available as well as an overview (broad or detailed) of its focus" [19] (p. 2). The scoping review methodological framework followed guidelines from Arksey and O'Malley [20], as well as recommendations by Levac et al. [21] and Cloquhoun et al. [22]. The PRISMA-ScR checklist was followed for documenting and reporting findings [23].

2.1. Inclusion Criteria

To answer the research question "What is the extent and scope of literature on wildfires and older adults?" the following inclusion criteria were used:

1. Published in a peer-reviewed journal;
2. Available in English language;
3. Examines at least one topic related to wildfires;
4. Examines how criterion (3) relates to older adults in at least one way.

For criterion (1), peer-reviewed journal publications were chosen to explore academic literature relating to older adults and wildfires to gain an understanding of relevant evidence, themes, needs, and gaps in the literature. For criterion (2), references were limited to the English language due to the research team's inability to translate articles from other languages. For criterion (3), wildfires were specifically chosen as the disaster of focus due to gaps in the literature exploring the impacts of wildfires (versus other types of disasters such as hurricanes, flooding, etc.) on vulnerable populations, especially older adults. For criterion (4), we defined older adults as those who are 60 years and older, or who were referred to in the references as "older adults", "elderly", "elders", etc. (see search terms below). This age was chosen based on literature indicating that 60 is a common parameter for identifying this age group [24]. Further, criterion (4) means that included articles must specifically connect wildfires to older adults in some way, excluding those that discussed older adults and wildfires separately.

2.2. Literature Search and Screening

Search terms and protocols were established in consultation with a university librarian. Based on these discussions, the following databases were searched: PubMed, Web of Science, ProQuest (Agriculture and Environmental Sciences Collection, Sociological Abstracts, and Social Service Abstracts), and EBSCO Host (Academic Search Complete, Environment Complete, GreenFILE, PsycInfo, and SocINDEX).

In consultation with the librarian, the following search strings were created and run in each database:

1. "older adult*" OR senior* OR elder* OR "older person*" OR "older people" OR geriatric* OR gerontolog* OR "old age" OR "long term care" OR "nursing home*" OR "assisted living" OR "independent living" OR "skilled nursing facilit*" OR "memory care" OR "residential care" OR "retirement communit*";

   AND

2. wildfire* OR "wild fire*" OR bushfire* OR "bush fire*" OR bushfire* OR "forest fire*" OR "brush fire*" OR brushfire* OR "wildland fire*" OR "uncontrolled fire*" OR "fire season*".

Both search strings were searched "anywhere but full text (NOFT)" within the ProQuest database, and with the default search settings for other databases, which was the recommendation and guidance of the university librarian. The search, conducted in March of 2021, yielded 585 articles. After removing duplicate records, 261 remained.

The research team used Covidence systematic review software [25] to complete the screening process. Two authors independently reviewed the titles and abstracts of the 261 non-duplicate records. After title and abstract screening, 138 remained. Two authors then independently read the full text of these 138 remaining articles. Of these, 75 met the inclusion criteria (Figure 1) [18,26–99]. Throughout the screening and review process, any disagreements on inclusion/exclusion were discussed and reconciled as a team before making a final decision.

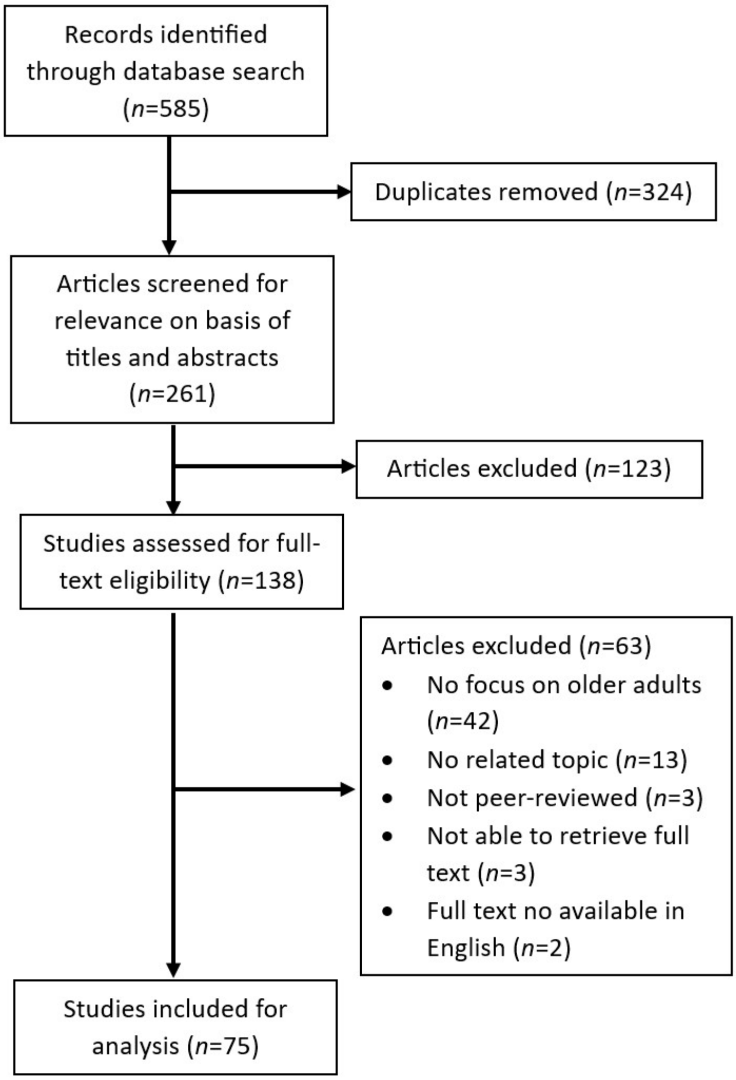

Figure 1. Flowchart of search, screen, and review process.

2.3. Data Extraction and Analysis

Data collected on each article included: (1) article characteristics and type; (2) information related to environmental issues including the disaster recovery cycle, specific hazards, etc.; (3) information on how older adults were included and relevant findings; and (4) whether articles addressed problems, used responses or interventions, or suggested solutions, recommendations, or areas of future research. We created, pilot tested, and refined our data collection tool using Google Forms. Once the final form was created, two members of the research team independently recorded data from each article. Any questions or disagreements were discussed and resolved as a team. During analysis, we also identified thematic topics arising from the literature.

First, basic characteristics included the year of publication, article title, author(s), journal title, country or geographic focus, study type, sample, and methods used. Second, information related to environmental issues included the hazards addressed (wildfires, air quality, heat, haze, or other types of hazards); specific disasters addressed; explicitly mentioning climate change or recommendations for climate adaptation and/or mitigation; focus on any part of the disaster recovery cycle (response, recovery, mitigation, preparedness); explicitly mentioning environmental justice or alluding to it; and the inclusion of Indigenous or Aboriginal traditional ecological knowledge (TEK). Third, questions related to older adults included whether the primary focus of the article was older adults and/or how older adults were included; focus on older adults in the community or in residential facilities; and relevant findings or recommendations related to older adults. Fourth, questions related to study focus included focus on problem description, measuring exacerbation of specific health problems, inclusion of responses or interventions, inclusion of Indigenous or Aboriginal knowledge of fire management, solutions or recommendations, areas of future research, and thematic topics arising in the literature. All criterion, except for thematic topics, were established during the creation and pilot testing of the data collection tool. Thematic topics arose during data collection as patterns emerged in the literature.

3. Results

3.1. Basic Characteristics of the Literature

A total of 75 peer-reviewed journal articles met study inclusion criteria. There was no limit on year of publication in our initial search; the earliest article was published in 2001, with the frequency of publications increasing over time (Figure 2). Only 3 of the 75 articles (4%) were published between 2001 and 2006, 10 (13.3%) were published between 2007 and 2011, 23 (30.7%) were published between 2012 and 2016, and 39 (52%) were published between 2017 and 2021 (Figure 2).

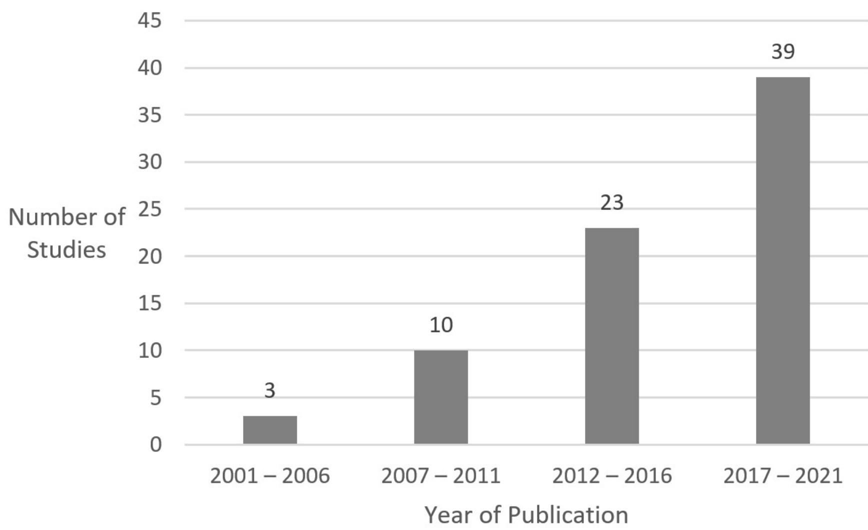

Figure 2. Year of publication.

Geographic regions discussed were diverse, but the majority were based in North America (44%) and Oceania and Australia (26.7%), and many were about wildfires or fire management on First Nations or Tribal land (18.7%) (Figure 3). The United States (U.S.) was the most represented country, representing 26 of the 33 total mentions of North America. Most of these focused on the western U.S. (n = 12), specifically California (n = 8). Of the eight articles focused on Canada, six were about wildfires on First Nations land. The 20 articles focusing on Oceania and Australia were almost exclusively focused on Australia, with 1 mentioning New Zealand and 6 of the 20 focusing on Aboriginal land. Seven articles focused on Northern and Western Europe (Spain, Portugal, Greece, and two from Finland), and five articles focused on South America, all of which were in Brazil's Amazon region. Five articles were based in Southeastern Asia (two in Malaysia, two in Indonesia, and one covering Singapore, Malaysia, Indonesia, Brunei, and Thailand). Finally, those that covered more than three countries were labeled as "global", though these predominantly focused on countries above including the U.S., Australia, Malaysia, and Indonesia. Notably, no articles covered geographic regions of Africa, Central America, or North and Central Asia, though one global article mentioned "Asia, Latin America, and Africa" [42] (p. 99).

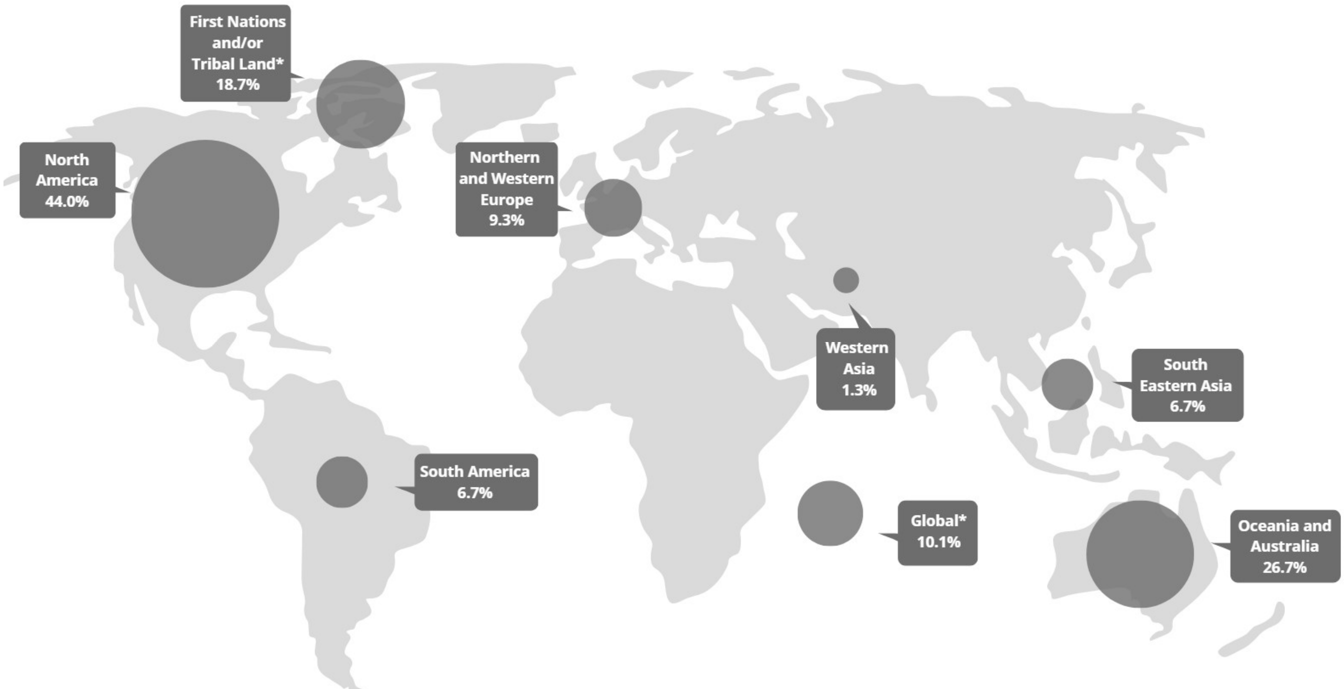

Figure 3. Geographic focus of articles. Note: Percentage exceeds 100% as some articles covered multiple regions. * Articles focusing on First Nations and/or Tribal lands were based in North America (Canada, n = 7; United States, n = 3) and Oceania and Australia (Australia, n = 6).

Of the 75 articles, 63 (84%) were empirical research articles or evaluations (Table 1). Most of these were quantitative (44%) or qualitative (26.7%), with a few being mixed methods (4%) or systematic reviews (9.3%). The 12 non-empirical articles (16%) were conceptual, descriptive, or commentaries. Methods used in empirical articles varied, with secondary data (37.3%) being the most prevalent. A large majority of articles focused on measuring morbidity and mortality related to wildfire smoke, with 22 articles (29.3%) using emergency room and hospital admissions or mortality rates as secondary data. The second most common method was remote-sensed environmental measures (29.3%), measuring air quality and pollution, particularly of $PM_{2.5}$ levels and other particulate matter. Interviewing was the third most prevalent method (21.3%). Other methods included systematic reviews (9.3%), surveys (9.3%), focus groups (8%), case studies (6.7%), field research (5.3%), biological data (5.3%), and other methods (8%; e.g., participatory action research, future modeling, ethnography, and Q methodology) (Table 1).

Table 1. Basic characteristics of the literature (*n* = 75).

Characteristic	*n* (%)
Paper Type	
Quantitative	33 (44)
Qualitative	20 (26.7)
Mixed Methods	3 (4)
Systematic/Scoping Review	7 (9.3)
Conceptual Papers	9 (12)
Other (e.g., commentary, interview transcript)	3 (4)
Method	
Secondary Data	28 (37.3)
Remote-Sensed Environmental Measures (Air Quality)	22 (29.3)
Interviews	16 (21.3)
Systematic Review	7 (9.3)
Survey	7 (9.3)
Focus Group	6 (8)
Case Study	5 (6.7)
Field Research	4 (5.3)
Biological Data	4 (5.3)
Other Methods	6 (8)
Not Applicable (e.g., conceptual papers or other paper type)	12 (16)

Note: Methods percentage exceeds 100% as some articles used multiple methods and/or data collection strategies.

3.2. Environmental: Hazards, Climate Change, and Disaster Recovery Cycle

We reviewed articles for specific information related to environmental issues including specific wildfires, other hazards, and language or information about climate change, environmental justice, or the disaster recovery cycle (Table 2). All articles discussed wildfires, bushfires, or forest fires in some way. Some articles also discussed other types of disasters such as flooding and hurricanes, but due to the proliferation of literature on these topics, we only collected data on hazards related to wildfires. Of these related hazards, 41 articles discussed air quality (54.7%), 12 covered heat (16%), and five discussed haze (6.7%). Almost half of articles were either about a specific wildfire (17.3%) or a specified wildfire season or time period where wildfires occurred (25.3%). Wildfire events or seasons that were covered in more than one article included: wildfires and associated “haze disaster” in Indonesia in 1997 [49,53]; wildfires in San Diego, California in 2007 [31,33]; a 2011 wildfire impacting Sandy Lake First Nation in Canada [27,28]; California’s 2017–2018 wildfire season [43,47,97]; and the catastrophic 2019–2020 wildfire season in southeastern Australia [40,50,89].

Table 2. Environmental hazards, climate change, and disaster recovery cycle (*N* = 75).

Environmental Categories	*n* (%)	Examples
Hazards		
Fire	75 (100)	• See articles with asterisks in reference list [18,26–99]
Air Quality	41 (54.7)	• Impacts of air quality and/or particulate matter [26,29,32,34,37,41,42,44–49,51,54,56–62,65,66,71,72,74,78,88–90]
Heat	12 (16)	• Impacts of heat [18,29,36,39,40,43,57,66,72,80,87,88]
Haze	5 (6.7)	• Haze disasters and/or impacts of haze [48,53,54,82,85]
Specific Wildfire(s)		
Specific Wildfire	13 (17.3)	• 1997 wildfire and “haze disaster” in Indonesia [49,53] • 2007 wildfire in San Diego, CA [31,33] • 2011 wildfire in Canada impacting Sandy Lake First Nation [27,28]
Wildfire Season/ Time Period	19 (25.3)	• California’s 2017–2018 wildfire season [43,47,97] • Australia’s 2019–2020 wildfire season [40,50,89]

Table 2. *Cont.*

Environmental Categories	*n* (%)	Examples
Climate Change (CC)		
Mentions	41 (54.7)	
Adaptation	41 (54.7)	• Individual-focused adaptations (e.g., adapting to heat, addressing disease burden, air filtration systems, individual survival plans) [18,29,34,39,41,42,61,66,80,84,85,88,91,96] • Facility or community-level emergency protocols (planning, preparation, evacuation, communication, etc.) [18,26,27,29,33,47,52,63,79,81,87,97] • Land-use management (including traditional ecological knowledge and burning practices) [29,36,38,50,55,67–70,75,83,94,98]
Mitigation	18 (24)	• Traditional ecological knowledge and burning practices [38,55,64,67–70,73,74,83,94,98] • Mentions or addresses need to reduce greenhouse gas emissions [29,58,71,80,88,93]
Article Focuses on CC	7 (9.3)	• Health impacts of climate change [29,72,80,88] • Disproportionate impact on older adults [18,66,71]
Disaster Recovery Cycle		
Mentions	42 (56)	
Recovery	9 (12)	• Needs of older adults in recovery period following wildfires (e.g., disruption in continuity of care, physical recovery, economic recovery, and trauma/mental health) [29,32,79,81,97] • Community recovery [50] • Debriefing sessions with facility staff following wildfire [31,86]
Response	24 (32)	• Needs of older adults during acute wildfire disaster (e.g., life-support equipment such as oxygen during power outages, immediate interventions for air quality, etc.) [9,17,18,34,79] • Evacuation (individuals, facilities, communities) [27,28,30,31,40,47,52,76,86,87,91,96] • Early warning systems, communication, and local response protocols [18,29,33,34,63,96] • Social support needs (families, caregivers, etc.) [18,27–29,79,81] • Response of health care providers and/or facilities [32,42,52,66,86,92,97]
Mitigation	25 (33.3)	• Building codes and updates, and facility emergency protocols [18,29,71] • Mitigating smoke exposure [34,41,88] • Public outreach, local contingency planning, community risk-reduction etc. [47,63,77,81,87] • Reintroducing "ecologically beneficial fire" [35] (p. 677) and Indigenous burning practices [35,38,55,64,67–70,73,83,94,98]
Preparation	22 (29.3)	• Barriers or facilitators to preparedness for older adults (e.g., socioeconomic factors, mobility and health issues, etc.) [39,77,79] • Incorporating needs of older adults into planning measures (recommendations, community-engagement, etc.) [29,32,63,66,79,87] • Recommendations for evacuation preparedness and/or facility emergency protocols [27,28,33,52,86,98] • Individual preparation (survival plans, preparing personal property, evacuating, etc.) [40,76,91,97]

Table 2. *Cont.*

Environmental Categories	*n* (%)	Examples
Environmental Justice (EJ)		
Explicit mention of EJ	2 (3)	• Intersectional analysis of subgroups of older adults most impacted by wildfire smoke using an environmental justice lens (e.g., race, gender, education) [40] • Mention of environmental justice as factor of vulnerability for respiratory disease [26]
Alludes to EJ	40 (53)	• Intersectional view of impacted older adults (more impacted based on race, socioeconomic status, gender, housing status, chronic disease, urban vs. rural, and/or) [18,29,32,34,36,39,64–66,77] • Calls for more focus on vulnerable populations in future research [18,34,57,65,71,82] • Connection of Indigenous sovereignty and knowledge, colonization, historical oppression, and resistance [38,55,64,69,70,75,83,94]
No Mention of EJ	33 (44)	
Indigenous or Aboriginal Peoples		
Traditional Fire Knowledge	12 (16)	• Co-management strategies and tensions between Indigenous elders and peoples and state, national, or other fire management groups [38,64,67–70,83] • Western science's need for Indigenous knowledge and tension between the two [38,64,75,94] • Description of Indigenous fire knowledge, experiences, and/or history [28,38,55,73,75,94,98]
Focus on Indigenous or Aboriginal Lands	14 (18.7)	• In addition to the above 12 articles, 2 focused on community experiences and needs during evacuation for Sand Lake First Nation [27,28]

Data have consistently shown that climate change is increasing the intensity and impact of wildfires [1,18,60]. However, not all disaster research makes the connection between climate change-related causes and impacts. We found that 41 articles (54.7%) mentioned climate change or global warming explicitly, but only 7 (9.3%) focused on climate change as a main topic. We also collected data on interventions, recommendations, or responses that may be climate mitigation or adaptation strategies, even if they were not named as such. We found that 41 articles (54.7%) addressed some form of adaptation strategies and 18 (24%) addressed mitigation strategies (Table 2).

In addition to climate change, data were collected on mentions of the disaster recovery cycle and specific phases including recovery, response, mitigation, and preparation (Table 2). A majority of articles mentioned the disaster recovery cycle or at least one phase (56%). Mitigation measures were the most prevalent phase discussed (33.3%), closely followed by response (32%) and preparation (29.3%). Recovery was the least discussed phase, addressed by eight articles (10.7%).

Because of the particular vulnerability of older adults to disasters, including wildfires, we noted whether articles specifically mentioned environmental justice. However, during analysis, we found that many articles alluded to environmental justice by discussing "disadvantaged and vulnerable populations" [65] or "vulnerable populations, including the elderly, socioeconomically disadvantaged groups, and those with underlying chronic disease . . . [who are] most affected [29]. While only two (3%) articles explicitly named environmental justice [46,60,64], more than half (53%) alluded to environmental justice by discussing disproportionate impacts or particularly vulnerable populations in some way (Table 2).

3.3. Older Adult Findings

When reviewing how articles discussed older adults (Table 3), 39 articles defined older adults based on either an age cutoff (e.g., 65 or older) or by naming this population (e.g., elders, older adults, seniors, etc.). A large portion of articles (41.3%) included older adults as a population they were specifically interested in looking at in addition to others, while 29.3% focused solely on older adults, and the remaining 29.3% made mention of this age group but did not have them as their primary focus. The majority of articles (69.3%) based their findings on older adults using information that was collected about them, rather than from them firsthand (24%), with some (6.7%) doing both. Most articles did not explicitly state the living conditions of the older adults that were included; however, out of the 24 articles that did make this specification, 20 focused on older adults living in the community while only 4 focused on older adults living in long-term care communities.

Table 3. Older adult findings (*N* = 75).

Categories Related to Older Adults	*n* (%)	Examples
Focus Demographic		
Older Adults Sole Focus	22 (29.3)	• Focus on Indigenous elders [28,68–70] • Focus on health impacts of older adults in disasters [18,32,54,60]
Focus on Older Adults in Addition to Others	31 (41.3)	• Focus on Indigenous elders in addition to others (other Indigenous people, non-Indigenous land management decision makers, etc.) [27,29,38] • Participants were stratified by age or age groups and included both older adults and younger participants [34,65,71,88,90,99]
Mentioned Older Adults, but not Focus	22 (29.3)	• Mentioned older adults as another group that could be affected but was not specifically studied in the article [35,47,63,76]
Data Sources		
From Older Adults	18 (24)	• Older adults participated in the study (e.g., completed survey, participated in interview, etc.) [70,75,83,91,94]
About Older Adults	52 (69.3)	• Medical records about older adults were obtained and analyzed [26,32,48,72,74] • Other individuals contributed information about older adults (e.g., caregivers, health professionals, first responders, etc.) [52,63]
Both	5 (6.7)	• A combination of information shared by older adults and obtained about older adults was used concurrently in the study [27,28,35,40,78]
Living Environment		
Community	20 (26.7)	• Articles focus on older adults living in community, not in long-term care [27,40,41,55,97]
Long-Term Care	4 (5.3)	• Articles focus on older adults living in long-term care communities [31,33,66,86]
Not Specified	51 (68)	• Articles do not specify the living setting of the older adult[s] in the study [26,44,56,62,78,95]

With respect to the findings and recommendations made for older adults in the context of wildfires, articles discussed the various ways that older adults are impacted by and respond to wildfires. A majority of articles (60%) discussed the health impacts that wildfires had on older adults, describing increased hospitalization and death rates for cardiovascular and respiratory issues during or following wildfires for this population [26,53,66,82,90]. These negative outcomes were increasingly worse for older women and older adults of color [60]. While a meta-analysis of these impact estimates was beyond the scope of this study, some examples of specific findings include a 7.2% increase in respiratory hospital admissions among Medicare enrollees in the Western U.S. during intense smoke days [59] and impairments to lung function, especially among the elderly, of 33.9% of participants at two-years post-exposure to smoke from a Montana wildfire in the U.S. [78].

Additionally, when it came to responding to a wildfire, most notably with evacuations, older adults faced a disproportionate amount of barriers and challenges including difficulty maintaining the level of care they needed, accessing medications, and staying connected with caregivers, demonstrating how the needs of older adults may not be fully considered and addressed during wildfire disasters [27,28]. Finally, findings illustrated the role that older adults play during wildfires in supporting their local community, family members, and friends. During evacuations, older adults offered additional support to one another by making meals for one another, helping with laundry, and providing emotional support [27,28].

3.4. Thematic Topics, Problem-Focus, Interventions, Recommendations, and Future Research

While reviewing included articles, authors made note of recurring themes of interest that provided additional insight on the impacts and experiences felt by older adults due to wildfires (Table 4). With respect to the experiences of older adults, 17.3% (n = 13) of articles discussed animals/pets, 12% (n = 9) included caregivers, 34.7% (n = 26) touched on evacuation efforts and experiences, 14.7% (n = 11), focused on intergenerational relationships during wildfires, and 37.3% (n = 28) mentioned the effect of social support/social capital for this population during these disasters. Additionally, some articles discussed more specific impacts on older adults during wildfires, including 25.3% (n = 19) that looked at mental health associations, and 48% (n = 36) focused on morbidity and/or mortality of wildfires and associated hazards (air pollution, particulate matter, heat, etc.) from an epidemiological focus on population health. Finally, it should be noted that the onset of the COVID-19 pandemic brought about additional issues, especially as they relate to an older adult's health and well-being, and 2.7% (n = 2) of articles discussed the added complexity to the impact of wildfires.

Table 4. Specific topics and themes (N = 75).

Thematic Topic	n (%)	Examples
Animals/Pets	13 (17.3)	• Traditional ecological knowledge including importance of animals in landscape, ecosystem, or relationality between humans and the more-than-human world [55,67–70,75,83,94,98] • "Animal guardians" or "animal ownership" and its impact on evacuation, preparedness, and/or emergency response [76,91,96]
Caregivers	9 (12)	• Importance of having caregivers of older adults involved in and/or educated on preparedness protocol for disasters [18,27,81] • How the presence of a caregiver can impact how well older adults do during wildfires [28,76]
COVID-19	2 (2.7)	• Wildfires and older adults within the context of COVID-19 [40,47]
Evacuation	26 (34.7)	• Individual/community evacuation preparedness and/or experiences (e.g., survival plans, etc.) [27,28,30,40,76,87,96] • Medical facilities' evacuation preparedness and/or experiences [31,33,52,86,97] • Needs of/impacts on older adults during evacuations (care disruption, communication, social support, etc.) [18,43,60,79,81,88] • Not focused on evacuation, but mention implications, needs, or considerations for evacuation [66,81,84,88]

Table 4. *Cont.*

Thematic Topic	*n* (%)	Examples
Health Issues	45 (60)	• Wildfire impacts on respiratory and/or cardiovascular health [26,34,54,62,84] • Heat-related hospitalizations, illnesses and/or deaths [36,66,80] • Effects of wildfires on cancer [81,82] • Complications for older adults with dementia [39,43]
Intergenerational	11 (14.7)	• How relationships between generations were impacted by wildfires or how these intergenerational relationships could be used as a protective factor against the negative impacts of these natural disasters [30,40] • Intergenerational transmission of Indigenous knowledge [55,64,67–69,83,94]
Mental Health	19 (25.3)	• General discussion of traumatic impact of disasters/wildfires, evacuation, etc. [27,30,40,86,96] • Disproportionate impact of disasters/wildfires on older adults' mental health [18,32,79,81] • Vulnerability of individuals with mental health issues during disasters and/or heat [29,32,36,39] • Gap in research on mental health impact of disasters/wildfires [81,82]
Morbidity/Mortality	36 (48)	• Secondary data of mortality rates related to wildfire smoke-related exposures ($PM_{2.5}$, PM_{10}, heat, etc.) [26,36,43,51,56,74,85] • Secondary data of hospital records measuring morbidity of diseases (respiratory, pulmonary, cardiovascular, cancer, etc.) [37,44,46,48,54,59–62,81,84,89,90,93,95] • Systematic reviews of morbidity and/or mortality from wildfire smoke and related exposures [32,34,57,82,99] • Primary data of health impacts related to wildfire smoke and related exposures [45,49,53,78] • Future projections of hospital admissions under climate forecasting scenarios [58] • General review of climate change impacts on morbidity and mortality [66,72,88]
Social Support or Social Capital	28 (37.3)	• Importance of shared social support networks on older adults' well-being, especially in disasters [19,28,43] • Social isolation as a risk factor for older adults during wildfires [18,39,79] • Use of social networks on a community level to prepare for and respond to wildfires [47,77,81]

Of the 75 articles, 56 (74.4%) were problem-focused, describing negative impacts of wildfires in some way (e.g., need for evacuation, impacts of air quality, needs of communities, etc.) (Table 5). Of the 56 that focused on problem description, 36 (48%) described problems of morbidity or mortality related to wildfires and/or wildfire smoke. Most of these used secondary, epidemiologic data such as hospital admissions and death rates to describe the health impacts of wildfire smoke and/or $PM_{2.5}$ (particulate matter smaller than 2.5 microns). Aside from morbidity and mortality, other articles described problems with evacuation, displacement, and/or issues with disaster response [27,28,40,47,86,87,91,96,97]; inequalities and vulnerabilities of certain populations to wildfires [29,77,79]; and general descriptions of health impacts without epidemiologic data [35,42,80].

Table 5. Responses or interventions, solutions and recommendations, and future research (N = 75).

Categories	*n* (%)	Examples
Problem Description	56 (74.7)	• Health impacts of wildfires and related exposures (smoke, heat, etc.) [26,32,41–46,51,53,54,56–62,72,74,78,80–82,84,85,88–90,93,95,99] • Problems/lessons from evacuation and/or disaster response (individuals, communities, and/or facilities) [27,28,40,47,86,87,91,96,97] • Disproportionate impact of wildfires and disasters on older adults [18,29,32,39,60,65,66,71,79]
Responses or Interventions	31 (41.3)	• Evacuation at individual, organizational, facility, or community levels [27,28,30,31,33,52,86,87] • Community-level disaster response (communication, first responders, coordination of services, increasing community-engagement and relationships, etc.) [31,33,47,63,87] • Individual level response/interventions (e.g., air filters, masking, survival plans, etc.) [34,41,53,76,84,91,96] • Indigenous response/interventions including traditional burning, integrating TEK into conservation/land "management", employing Indigenous peoples in land "management", etc. [38,55,64,67–70,73,75,94,98] • Community care, social capital, caring for one another during disasters [27,28,40,50] • Interventions by healthcare providers and/or facilities [42,52,86,92,97]
Solutions and Recommendations	61 (81.3)	• Need for community-level disaster response workers and coordinators to increase community engagement towards better response and preparedness (community-inclusiveness, responsiveness, education, trust building, outreach, etc. [36,39,43,47,63,77,79,81] • Needs for elders leading up to, during, and following evacuation [27,28,43,63,79] • Recommendations for healthcare providers and/or facilities regarding clinical or organizational response to wildfires [31,33,66,88,90] • Recommendations for public policy [34,60–62,71,78,81] • Recommendations for utilizing TEK into wildfire management agencies and tactics (in culturally sensitive, ethical ways) [38,67–70,75,83] • Greater need for community care, increased social support, etc. [18,27,28,40,43,47,50,79] • Recommendations for climate mitigation and/or drawdown strategies [29,64,71,88,93]
Future Research Directions	61 (81.3)	• Future research should work to better understand the impacts of wildfires on the health of older adults [26,31,48,57,65,81] • More research is needed on how to develop and evaluate community preparedness and response strategies and the effects of these strategies [27,28,47,84,87,97] • Additional research should look at and evaluate effective mitigation strategies [55,63,88] • More research should work to find ways to address specific needs of older adults and reduce risks faced by this population before, during, and following wildfires [18,66,77]

Many articles moved beyond problem description with 32 of the 75 (41.3%) articles describing responses or interventions during, after, or in preparation for wildfires. Interventions and responses included individual, organizational, and community-level efforts. Individual efforts included masking to avoid smoke exposure [53,84], installing in-home air filters [34,41,84], and creating survival plans [76,91,96]. Organizational interventions predominantly focused on organizations (e.g., long-term care facilities, rehabs, and hospitals) evacuation and/or disaster management plans [27,28,30,31,33,52,86,97], but also included treatment recommendations for providers [42,92]. Community-level responses included descriptions of families and neighbors caring for one another during acute disaster phases [27,28,30,40,50], and disaster management and coordinating systems at the community level [28,30,63,87]. Finally, many articles described traditional ecological knowledge (TEK) or Indigenous and Aboriginal elders as an important intervention for "hazard abatement" [55], as well as the opportunity for fire management institutions to listen to, learn from, and rematriate (e.g., return power to Indigenous peoples to reclaim ancestral traditions) [100] fire "management" as well as the ethics of fire management agencies "using" this knowledge [26,38,64,67–70,73,75,94,98].

In addition to interventions and solutions, 61 (81.3%) articles provided recommendations targeted at multiple levels and points of intervention including individuals, organizations, communities, policy, scholarly literature, and disaster and fire management agencies. Many recommendations intersected with other findings, such as recommended adaptation strategies [29,58,61,66,71,88] and the importance of individual survival plans, community evacuation plans, and organizational disaster management protocols and plans, especially in relation to communicating with older adults [28,39,52,54,76,77,79,81,97]. Community-centered disaster management planning and strategies were prolific across recommendations, with 26 of the 31 (83%) discussing community needs, community engagement, or community inclusion in disaster management planning in some way (Table 5).

Finally, most articles (81.3%) outlined areas for future research, describing the importance of utilizing more rigorous and longitudinal research methods to examine the long-term health effects on older adults due to wildfires, especially those from more minoritized communities (Table 5). Additionally, findings suggest community and local government officials need to consider the needs of older adults during wildfires and research should serve as a tool to evaluate the short- and long-term impacts of responses and interventions through all phases of the disaster recovery cycle [2,7].

3.5. Study Strengths and Limitations

One strength of this review is its systematic and rigorous approach to identifying relevant peer-reviewed literature, by using expansive search terms and searching more than 10 databases. This allowed a breadth of literature to be explored across geographic regions, fields of study, and disciplines. However, one limitation is the exclusion of gray literature (e.g., books, non-peer-reviewed articles, etc.) that may have had additional information related to the impact of wildfires on older adults and relevant recommendations or interventions. Further, our search was limited to publications available in English, which excluded two potential studies from full review, as well as other non-English publications that may have been excluded from our initial database search.

4. Discussion

4.1. Wildfires and Older Adults: Increased Engagement and Trends

While there is prolific literature on the impact of extreme heat and hurricanes on older adults, there is a gap in the literature "on the vulnerability of older adults to other health-related climate impacts, such as ... wildfire [and] changes in air quality" [18] (p. 21). This review systematically synthesized scholarly literature focusing on older adults and wildfires to help identify priorities and directions for addressing gaps in the literature on the impact of wildfires on older adults, and recommendations for interventions and future research. In a global search with no restriction on publication date, only 75 articles were found and most (52%) were published within the past 5 years (2017–2021). This may indicate the impact of wildfires on older adults is a newer area of research that requires additional exploration and evaluation.

Wildfires may have unique health impacts that spread beyond a specific boundary where the disaster occurred, as smoke and air quality transcend boundaries, with smoke from large fires sometimes traveling thousands of miles, across countries and even continents [54,101,102]. This was seen in multiple articles, with some specifically addressing "long-range transboundary air pollution" [54,85] and others examining health-related impacts of air quality even when the source of the fire was in a different geographic location [53,82,85].

Findings from this review show the particular vulnerabilities of older adults to wildfires, particularly due to poor air quality and exposure to smoke and particulate matter (i.e., $PM_{2.5}$). Many articles within the review explained that older adults are more susceptible to adverse health impacts of $PM_{2.5}$ [29,34,37,42], as are those with pre-existing respiratory or cardiovascular diseases and those with lower socioeconomic status (SES) [29,34,72]. While older adults are named as specifically susceptible, they also often have pre-existing conditions or may have lower incomes, exhibiting a double—or triple—burden related to poor air quality. While there is substantial research on health impacts related to particulate matter, some studies have found that $PM_{2.5}$ exposure from wildfires may be more toxic than equal doses of ambient $PM_{2.5}$ [59,103], highlighting the importance of examining wildfire-related air quality and health impacts, especially for older adults.

Impacts of air quality are compounded by heat exposure—another hazard related to wildfires. Many articles spoke to the health impacts of heat on older adults particularly, highlighting "the double burden that heat and socioeconomics play for low-income older adults who are unable to afford air conditioning or caregiver support during extreme heat" [66] (p. 7). Heat-related deaths are the most deadly "natural disaster", and accompany wildfires—along with poor air quality—illustrating the impact of wildfires on older adults even if they are not directly exposed to the epicenter of a wildfire event [36].

Aside from indirect—albeit very real—impacts of wildfires through air quality and smoke, many articles discussed acute phases of the disaster recovery cycle when a wildfire occurs, namely the response phase (32%) and evacuation (34.7%). The findings showed that older adults are particularly vulnerable during evacuation phases, noting the importance of considering elders when planning for community-level communications for evacuation [47,79,81] and physical difficulties elders may have with evacuation, especially without social support [18,27,28,79]. Even if older adults are not evacuated, being in the geographic region of a wildfire event with power outages may affect life-sustaining equipment such as oxygen, ventilators, CPAP machines, refrigeration for medications, power wheelchairs, elevators, and heating and cooling systems for body regulation [18,79]. Wildfires may also pose a threat to the continuity of care for older adults who need ongoing medical treatment such as dialysis, cancer treatment, obtaining medications, or other medical needs [18,79,97].

4.2. Dominant Narratives: Secondary Data and Epidemiological Studies

The most prolific finding in this review was the use of secondary data to measure morbidity and mortality from wildfires or associated hazards (e.g., heat, air quality, etc.). This aligns with findings from an included article stating, "in relation to extreme weather conditions, literature has highlighted the vulnerability of older adults as a cohort, though there is limited attention on how to prevent the cohort from experiencing increased risk" [39] (p. 974). The majority of articles (74.7%) focused on problem description, with 48% of all articles describing the problem of morbidity and mortality impacts—either focusing on older adults or whose findings skewed towards older adults. This illustrates the dominant narrative of wildfires and older adults, telling a story of risk and vulnerability. While many articles also discussed responses or interventions, these were still predominantly focused on describing problems within the intervention or response itself, such as lessons learned from evacuation or community responses or preparation. Epidemiologic findings are imperative to provide statistics to build a base of scientific knowledge about this issue, but they only tell a fraction of the story about older adults, leaving out vital information from older adults on their lived experiences and needs before, during, and after wildfires.

4.3. Older Adults: Lived Experiences and Primary Data Sources

The results demonstrate how most of the information on the intersection of wildfires and older adults is primarily data collected about older adults from other sources rather than from this population firsthand. Medical and hospital records were one of the main sources of information that articles drew from, focusing on the negative physical health effects of wildfires on this population, but articles rarely focused on learning from what older adults went through or how they felt about wildfires and their role in relation to these disasters. To adequately address the disproportionately negative issues faced by older adults in the face of wildfires, it is essential to better understand their perspectives and what they find to be their greatest challenges and needs during these disasters. Articles also demonstrated how older adults can be a vital source of knowledge in knowing how to reduce or respond to wildfires, as evidenced by the numerous articles on the role Indigenous elders have previously had in mitigation efforts (see also Section 4.4) [38,55,64,67–70,73,74,83,94,98]. It is important to understand that older adults are not simply victims of wildfires but can, in fact, play a major role in addressing these growing disasters.

4.4. Social Support and Community Focus

Articles demonstrated the importance of social support for older adults at both a community and individual level. Older adults who lacked social support were more likely to die during a wildfire as they did not receive adequate warning of the danger or were unable to evacuate on their own [43,79]. Caregivers were noted as a vital source of support for older adults but were still in need of the appropriate resources and financial assistance to prepare for and respond to wildfires [97]. Caregivers should be considered a valuable point of contact for older adults in providing needed public health and disaster response messaging to this population [81]. When formal institutional responses were not adequate in meeting the needs of older adults, articles stressed the importance and power of informal neighborhood and community responses to make up for this lack of support [43,50]. In fact, one study found the number of fatalities due to wildfires was reduced when communities supported their older adults [43]. A good social support network was also found to provide critical psychological and emotional support for older adults during wildfire evacuations, which older adults cited as the most prevalent and valuable support they received during this crisis [27,28].

Building on the importance of social support and community care, many articles discussed the need for community-engaged tactics within disaster management systems including first responders and emergency management agencies. Articles discussed the need for community-responsive practices, with one article asserting "community engagement to determine most appropriate strategies from the local level should become a focus of adaptation. For example, bushfire preparedness and management should incorporate knowledge of community, government, and industry groups to identify impacts on community safety" [29] (p. 754). Other articles reiterated this, highlighting the need to build partnerships between local, state, and federal emergency management and public health systems, and that these should be in conversation and relationship with community members and responsive to their needs [32,35]. Other findings highlighted the need for communication strategies to be developed in conjunction with communities [34,35] and a need for more education and "community activism … to promote outreach that assists vulnerable persons [e.g., older adults] during emerging hazardous weather situations" [43] (p. 383).

4.5. Elders and Traditional Ecological Knowledge (TEK)

An important finding of this review was the inclusion of Indigenous, First Nations, and/or Aboriginal elders' experiences and knowledge of fire. Almost 20% (n = 14) of articles focused explicitly on Indigenous, First Nations, or Aboriginal elders, with 12 focusing on fire knowledge and TEK and 2 focusing on the impacts of evacuation during a fire event [27,28]. While it is beyond the scope of this paper to fully explore the relevance of TEK to wildfires, this emergent finding became salient during data collection and analysis due to the volume of related articles. These articles highlighted the importance of community in a different way, illustrating the deeply held community and cultural ties of Indigenous peoples to each other and the land. In contrast with other articles focusing on evacuation, those focused on the evacuation of Indigenous peoples highlighted a deeper sense of social cohesion and therefore social disruption when evacuations occurred. A participant from one article discussed the way evacuation broke up "communityness" stating, "the evacuation breaks up families, it breaks up that 'communityness', how you feel home. It breaks that up and you're being sent to a strange land" [27] (p. 372). These findings illustrate not only recommendations for Indigenous elders during evacuations, but also aspects of building "communityness" and social cohesion that other communities may learn from as a form of disaster preparation and response.

The majority of articles focused on Indigenous elders' fire knowledge and how this contrasts with dominant "fire management" agencies, policies, and protocols. Fire knowledge included cultural and traditional burning practices that have been utilized by Indigenous peoples for generations, and how fire knowledge is a part of sacred and cultural practices of being in relationship with the land. Almost all of these articles discussed implications of fire knowledge for fire management agencies, and many included cross-cultural dialogues or comparisons between Indigenous elders and other fire management agencies [38,55,64,67–69,75,83]. Many of these articles discussed the difference between Indigenous peoples' ontological views of fire and those of fire management institutions, most of which are run by White settler nations (e.g., Australia, Canada, and the United States). One article explained the difference between TEK and scientific ecological knowledge (SEK) [64], explaining that TEK takes a relational view of nature whereas SEK views nature through lenses of control, domination, and subjugation. Other articles affirmed this, explaining the incongruity of "fire management" or "fire-fighting" with TEK's view of fire and land as something to be in balance and relationship with rather than managed or fought [38,64,68,75].

Findings provided examples for collaborative co-management between Indigenous elders and fire management agencies, highlighting the importance and potential of TEK in fire "management" practices, while also naming the tension and ethics of non-Indigenous peoples "using" TEK for fire mitigation and/or adaptation measures [64,70]. One article explained that Indigenous elders have difficulty trusting fire management agencies run by the government due to generational trauma of genocide, relocation, and colonialism, with an Indigenous elder stating "science means not us" [83] (p. 26). Other articles provided recommendations for adaptive co-management strategies to build relationships between fire management agencies and Indigenous peoples to create "cross-cultural partnerships directed towards fostering resilience" [68–70]. These findings illustrate a nuanced and complex picture of the role of TEK in fire "management". Indigenous people have been caretakers of the land for generations and TEK must be incorporated into any understanding of ecological care, including wildfire management. While ethics and use of TEK are beyond the scope of this paper, there is a breadth of literature that looks at the intersection of TEK and fire "management", building on the articles related to TEK in this review. For the purpose of this paper, these findings illustrate not only the impact that wildfires have on older adults, but also the positive impact older adults can have on adaptation, mitigation, or responses to wildfires.

4.6. Increased Focus on (Un)Natural Disasters: Climate Change and Environmental Justice

While a primary focus of this paper was the impact of wildfires on older adults, this impact cannot be understood without analyzing the causes of wildfires. While wildfires are not new, the frequency and intensity of wildfires have dramatically increased due to climate change, creating (un)natural disasters [1]. While only 7 (9.3%) articles had a primary focus on climate change, 41 (51.7%) mentioned climate change as a reason for increasing disasters, reaffirming the relationship between worsening wildfires and climate change. Of the seven articles focused on climate change, three highlighted the disproportionate impact of climate change on older adults [18,66,71] while others had findings that skewed towards older adults [29,72,80,88]. However, the low number of articles focusing on the intersection of climate change and older adults illustrates a need for further research in this area, particularly the relationship between climate change, wildfires, and older adults. This intersection will only become more pertinent, as 8 of the 10 worst global wildfire seasons have happened in the past decade. Coupling the increased intensity and frequency of wildfires with the ongoing COVID-19 pandemic, further research is needed to examine these intersectional crises and their impacts on older adults.

The findings from this review continually reiterated that the impact of disasters is not distributed equally. The disproportionate impact of environmental hazards on some groups of people more than others is known as environmental injustice. While only 2 (3%) articles named environmental justice specifically, 40 (53%) of articles alluded to environmental justice in some way. Most of these references were related to older adults as being particularly "vulnerable" to wildfires and associated hazards (e.g., heat, air quality), while others provided a more nuanced understanding of environmental justice with other intersecting identities such as race, class, ethnicity, gender, geographic location (i.e., urban versus rural), and socioeconomic status [18,29,64–66,77]. While environmental justice is well-documented within scholarly literature, these findings point to the importance of incorporating an environmental justice perspective into research on wildfires and older adults. Some articles that used the "dominant narrative" named above (i.e., epidemiological studies of morbidity and mortality) used variables to understand the impacts of intersectional identities, providing a framework to incorporate environmental justice, though others named the gap in understanding environmental justice through public health-related data [65]. Some articles explicitly named this as a limitation or need for future research [34,47,49,57,65]. Future studies of all kinds should incorporate environmental justice into their data collection, methods, or analysis to understand the nuanced and disproportionate burden or wildfires on vulnerable populations and ways to address these harms and uneven impacts. Studies may also build upon this literature base by incorporating climate justice into environmental justice, especially in the case of increasing and worsening wildfires [104].

5. Conclusions

Findings from this scoping review demonstrate how older adults can be an important source of knowledge for wildfire mitigation, response, recovery, and adaptation strategies and should be included in local community planning efforts. Additional efforts should be made to incorporate environmental justice and intersectionality to better understand the root causes in health disparities among older adults during and following wildfires. Overall, the literature on the different ways older adults respond to or are impacted by wildfires is still relatively new and needs further development and exploration to better learn from and support this population in the face of worsening wildfire disasters.

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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 35×10^6 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

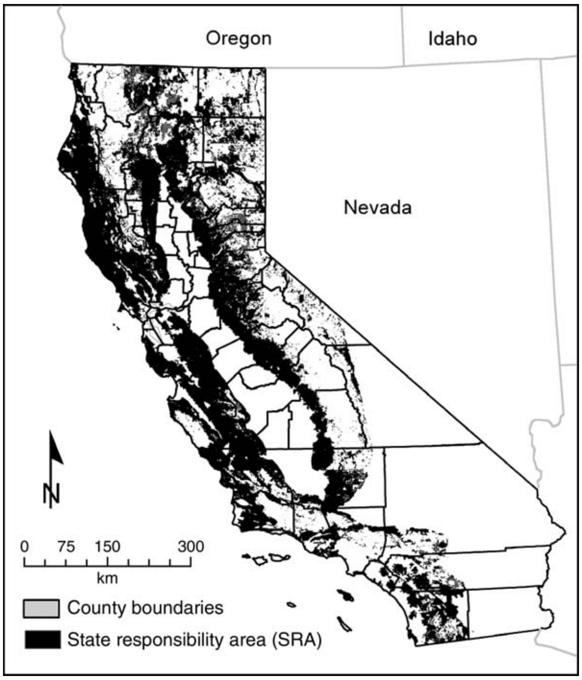

FIG. 1. Map of California Department of Forestry and Fire Protection (CDF) state responsibility areas (SRAs) within county boundaries of California, USA.

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).

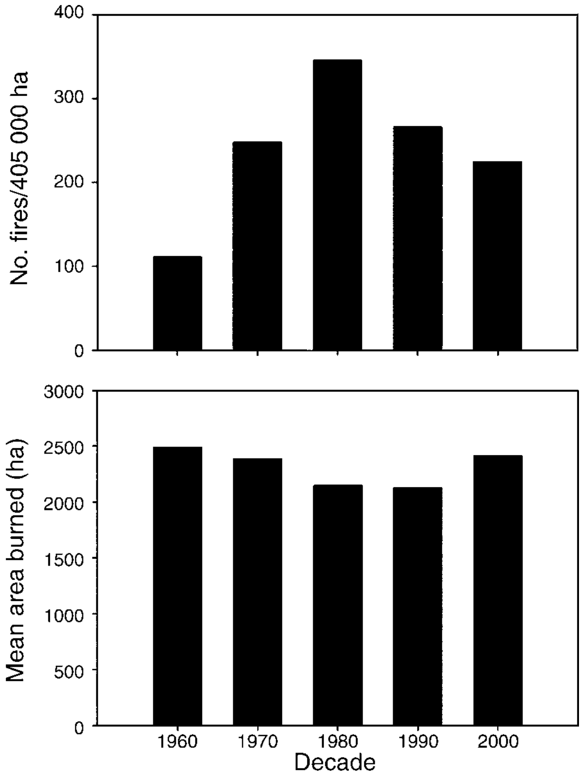

FIG. 2. Trends in number of fires and area burned for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

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).

[7] ⟨http://frap.cdf.ca.gov/data/frapgisdata/select.asp⟩

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

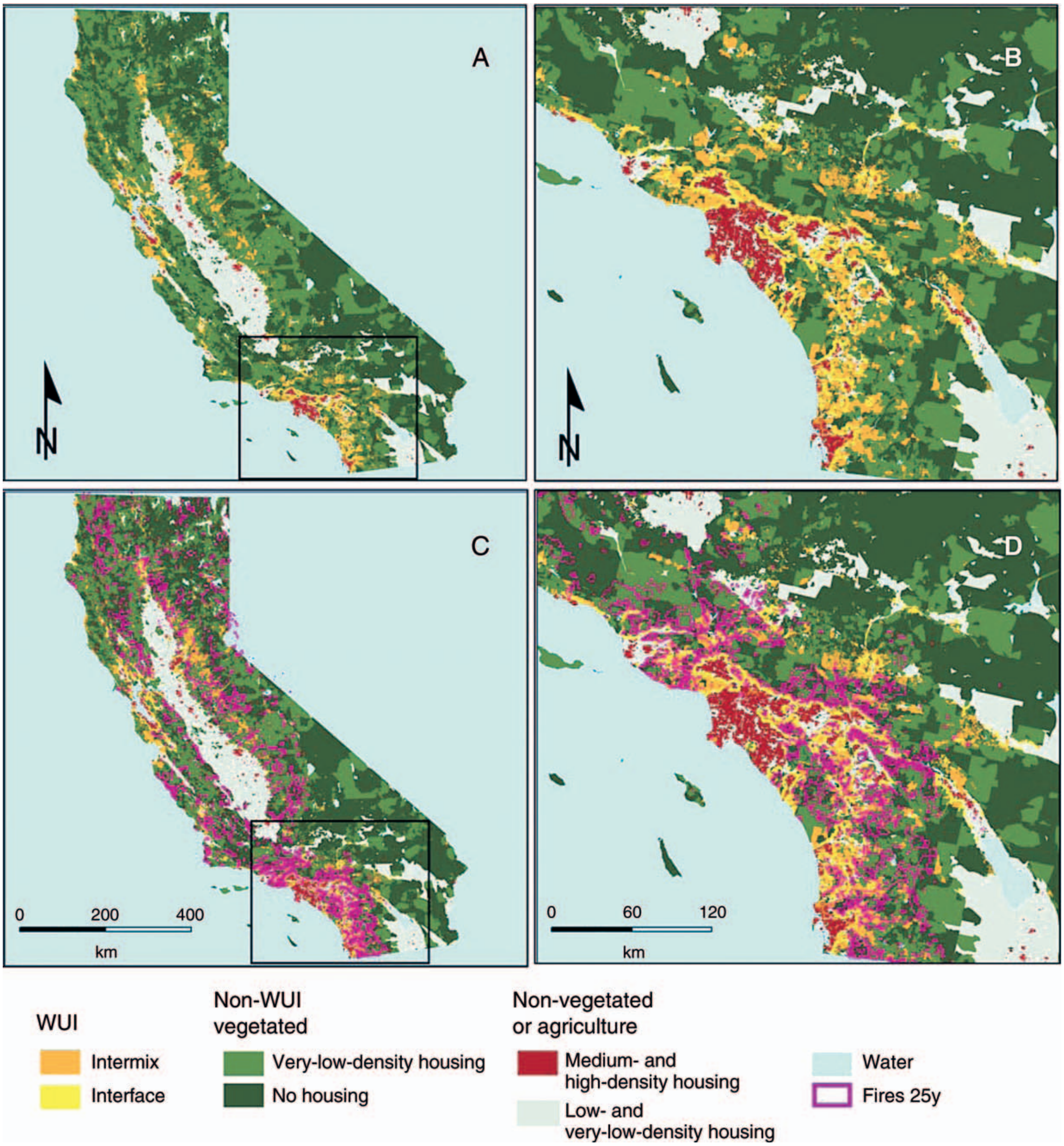

FIG. 3. The wildland–urban interface (WUI) in 2000 with and without fire perimeter overlays (from 1979 to 2004) in (A, C) California and (B, D) southern California. Housing density is defined as follows: very low, >0–6.17 housing units/km^2; low, 6.17–49.42 housing units/km^2; medium, 49.42–741.31 housing 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.

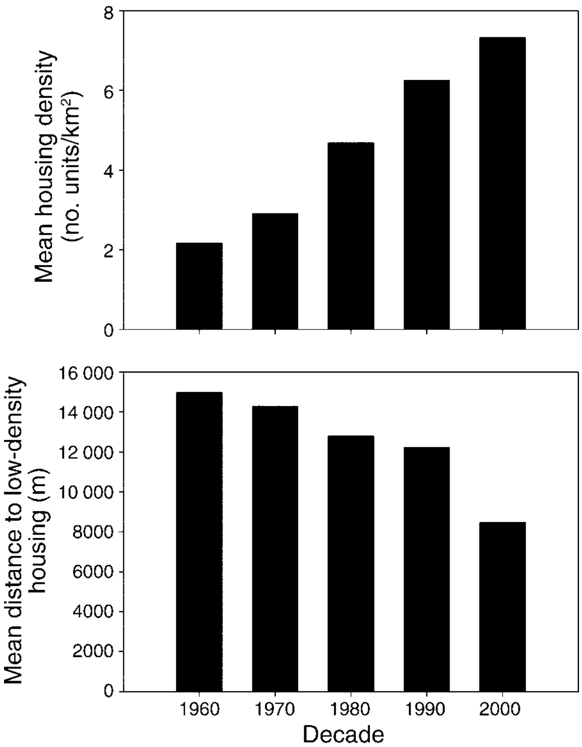

FIG. 4. Trends in housing density and distance to low-density housing (6.17–49.42 housing units/km^2) for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

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 ≤ 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.

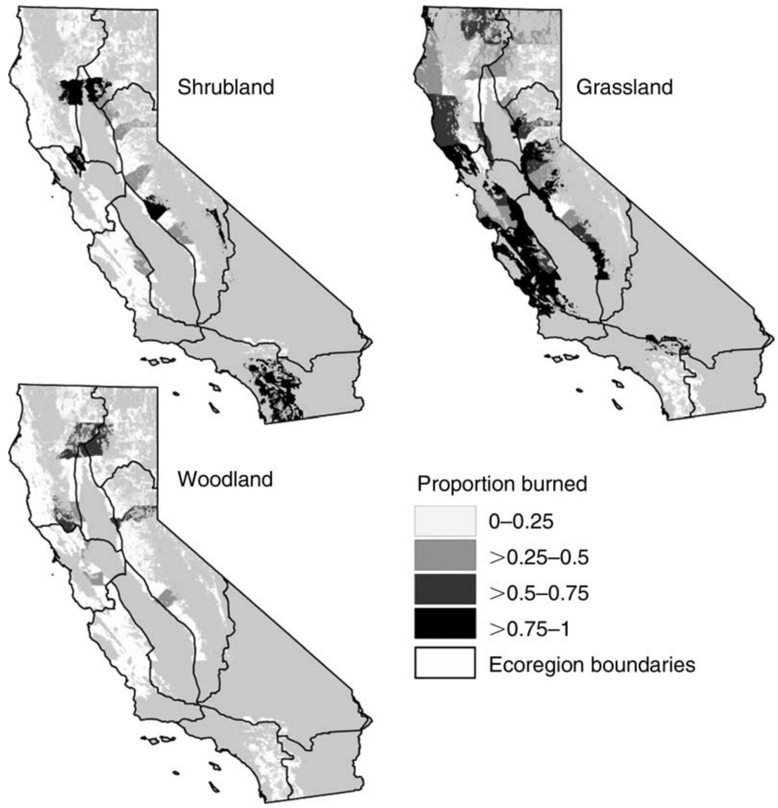

FIG. 5. Maps showing ecoregion boundaries and the proportion of area burned in shrubland, grassland, and woodland in 2000.

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

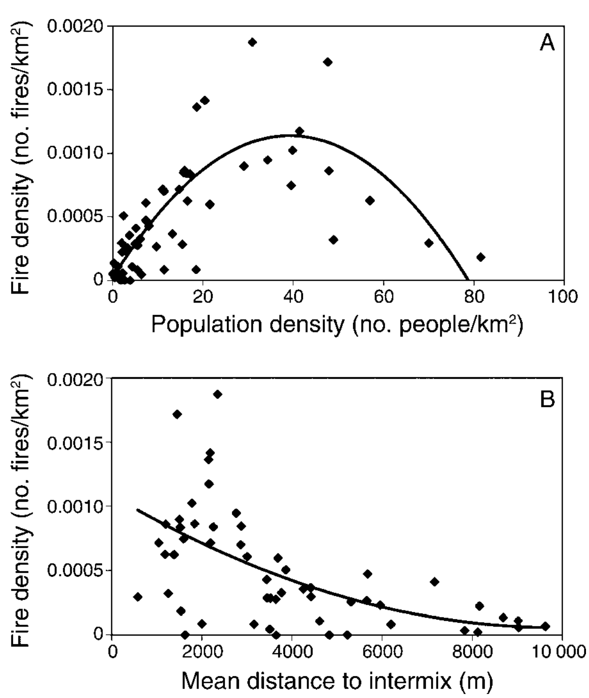

FIG. 6. The relationships between (A) the proportion of the number of fires and population density and (B) the proportion of the number of fires and mean distance to intermix wildland–urban interface (WUI).

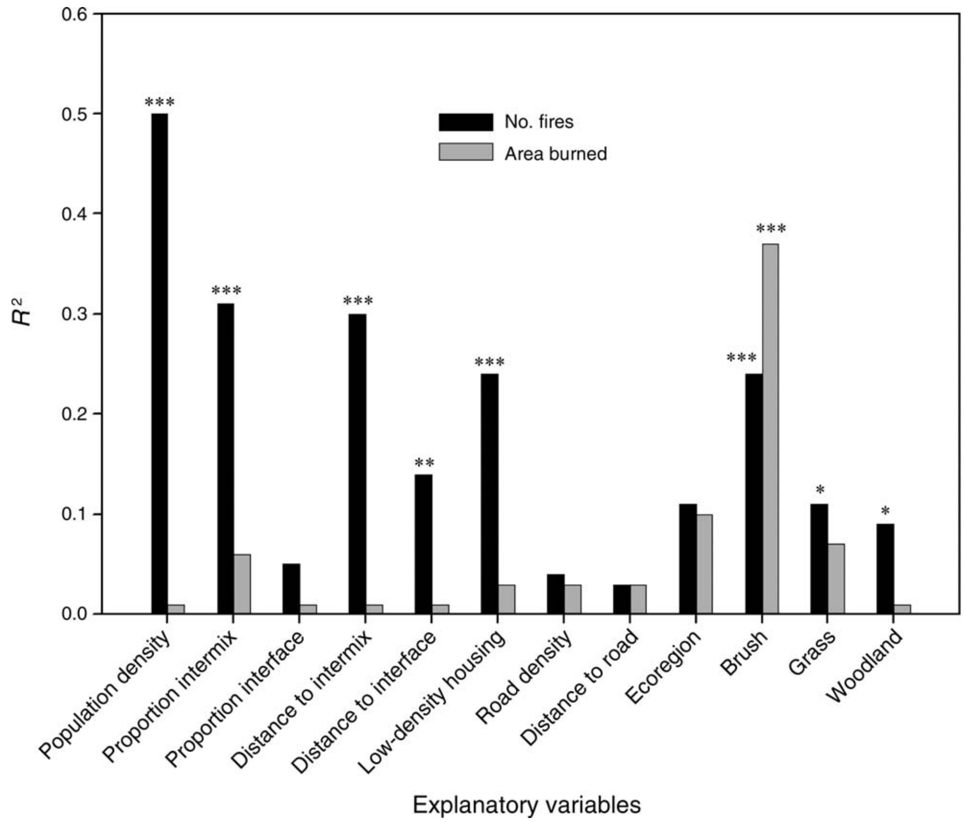

FIG. 7. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned in 2000.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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	-2×10^{-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

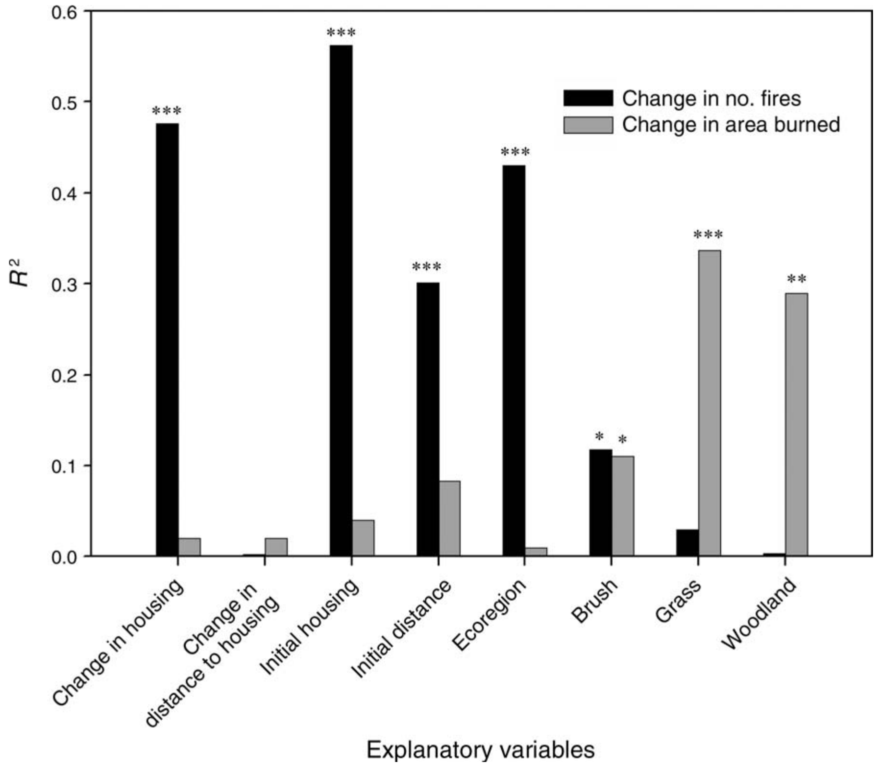

FIG. 8. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1960 to 1980.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

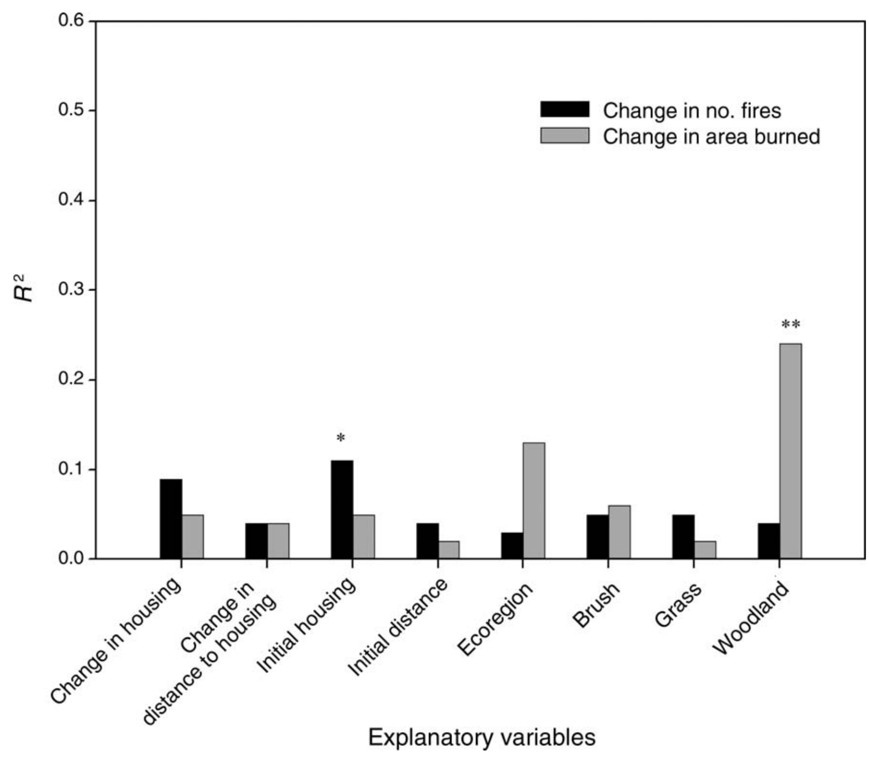

FIG. 9. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1980 to 2000.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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 90×10^6 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).*

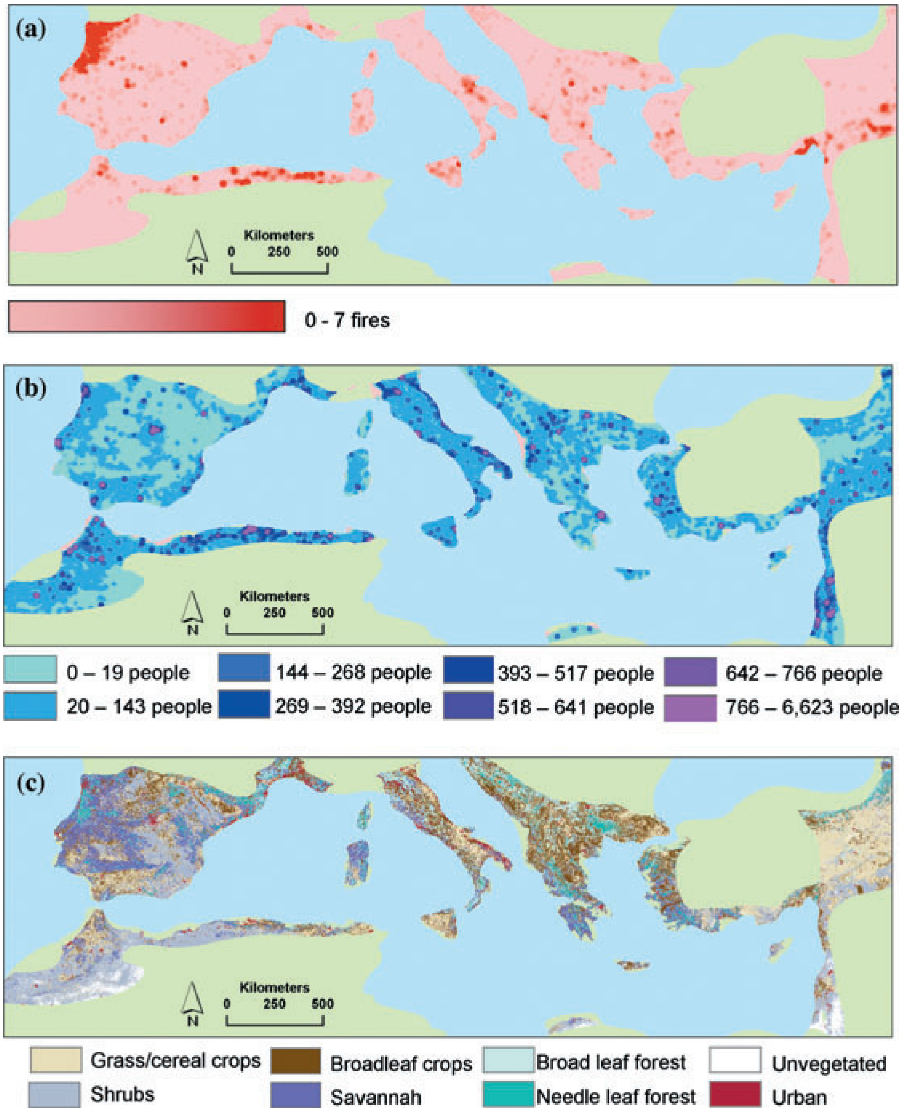


Figure 1. For the Mediterranean Basin, (a) MODIS active-fire detections in 2005, (b) LandScan population density in 2005, and (c) MODIS land-cover data. Fire and population density values are averaged across 225-km^2 pixels.

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.

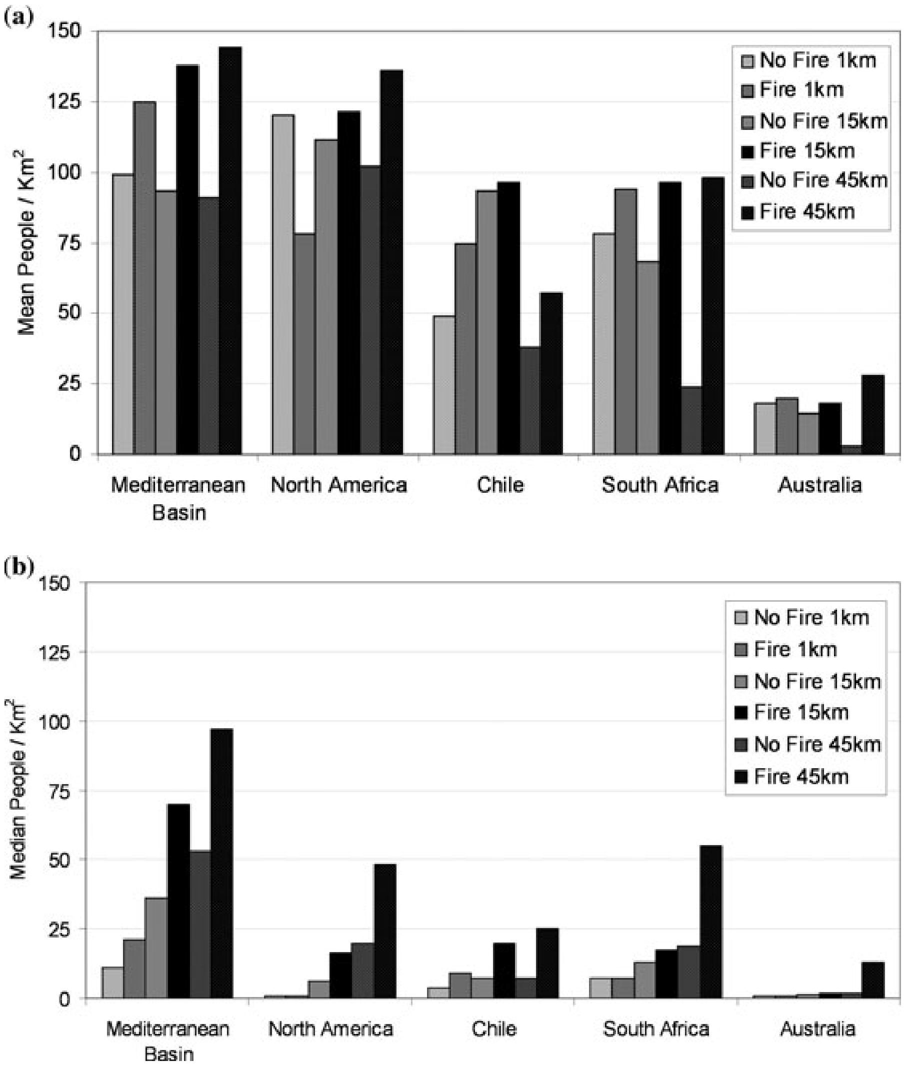


Figure 2. (a) Mean and (b) median population densities in areas with and without fires for 1-, 15-, and 45-km resolution windows. The y-axis scales differ.

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. Broadleaf 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.

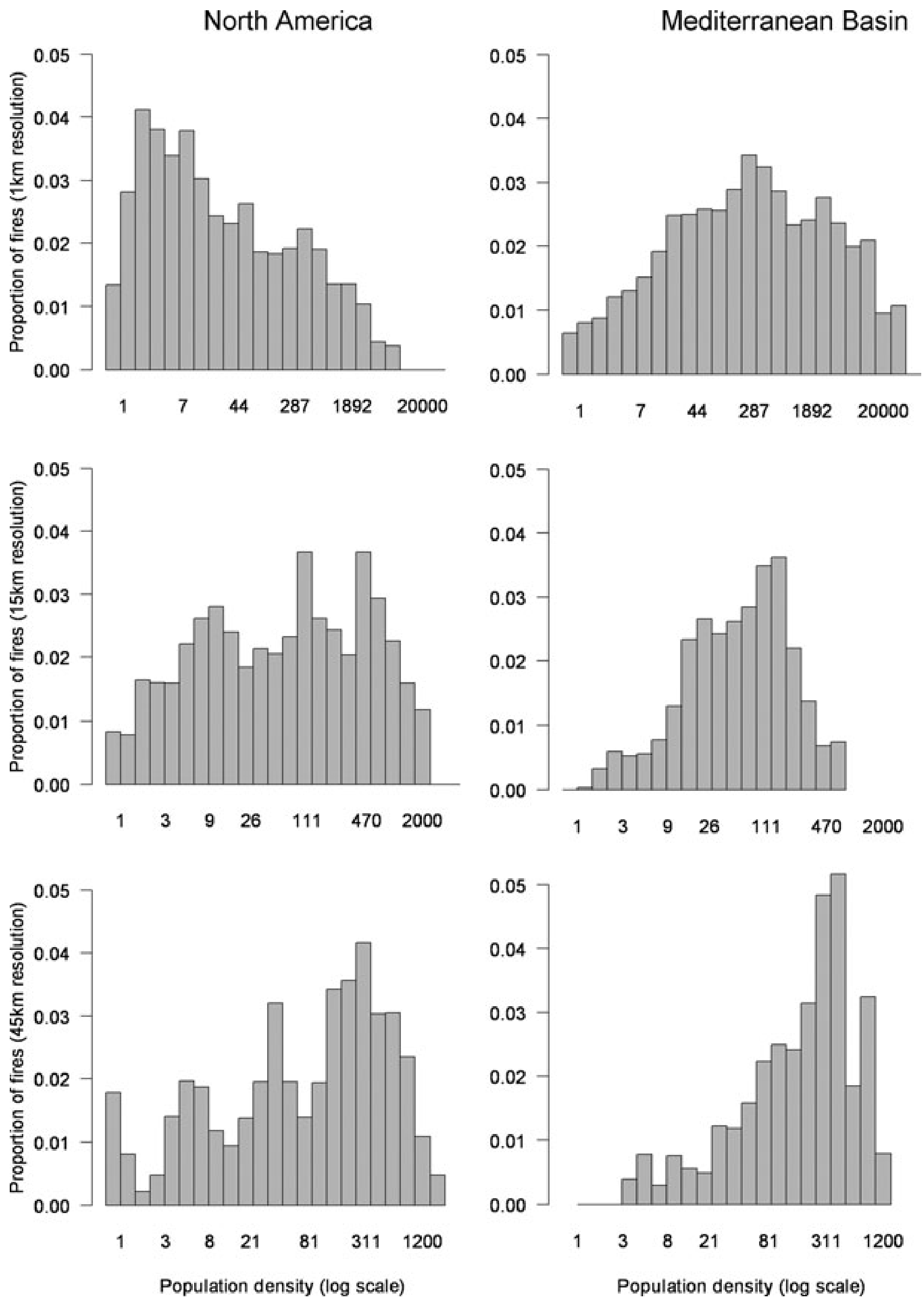


Figure 3. Proportion of fires within population density classes for 1-, 15-, and 45-km resolution windows.

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

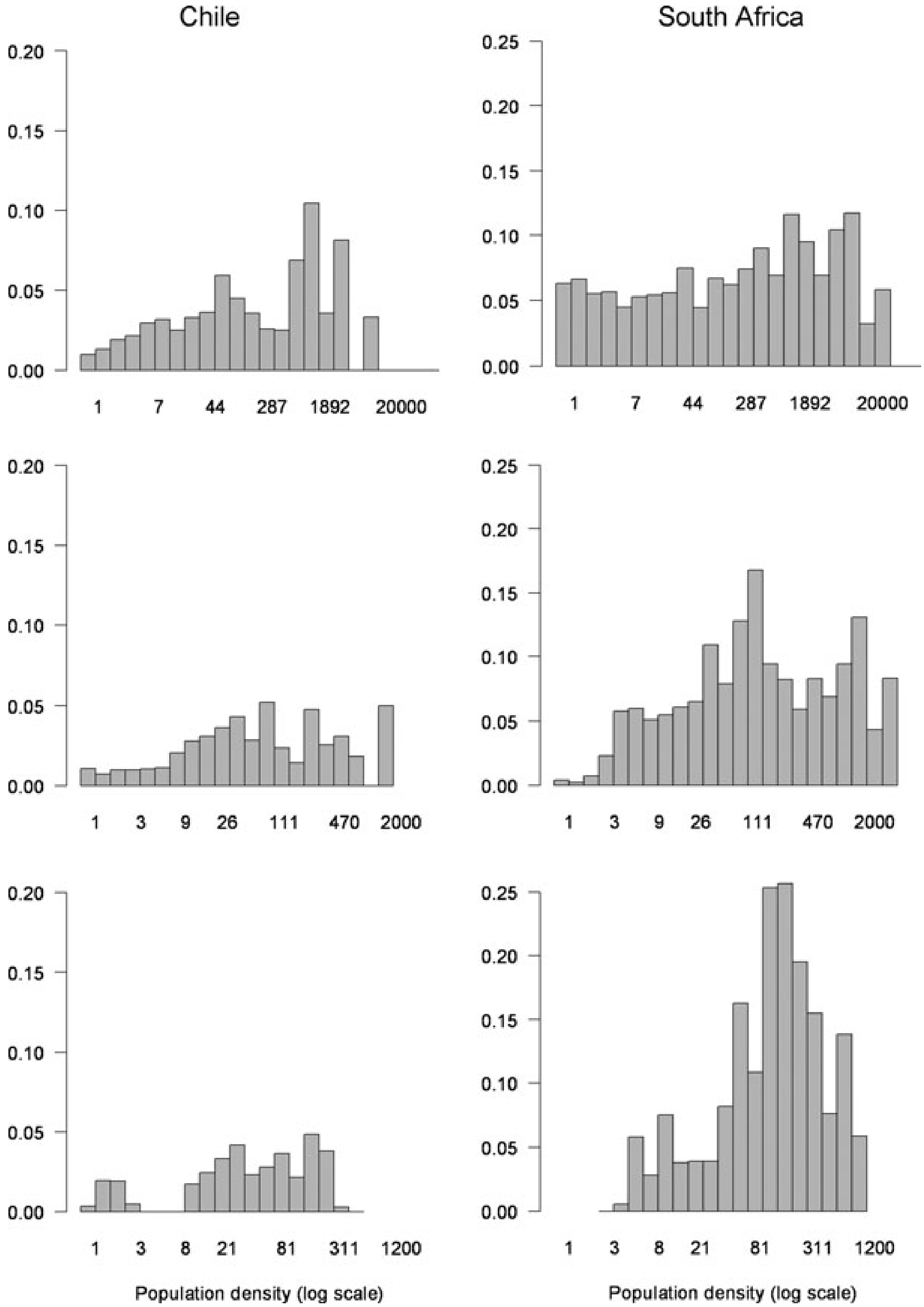
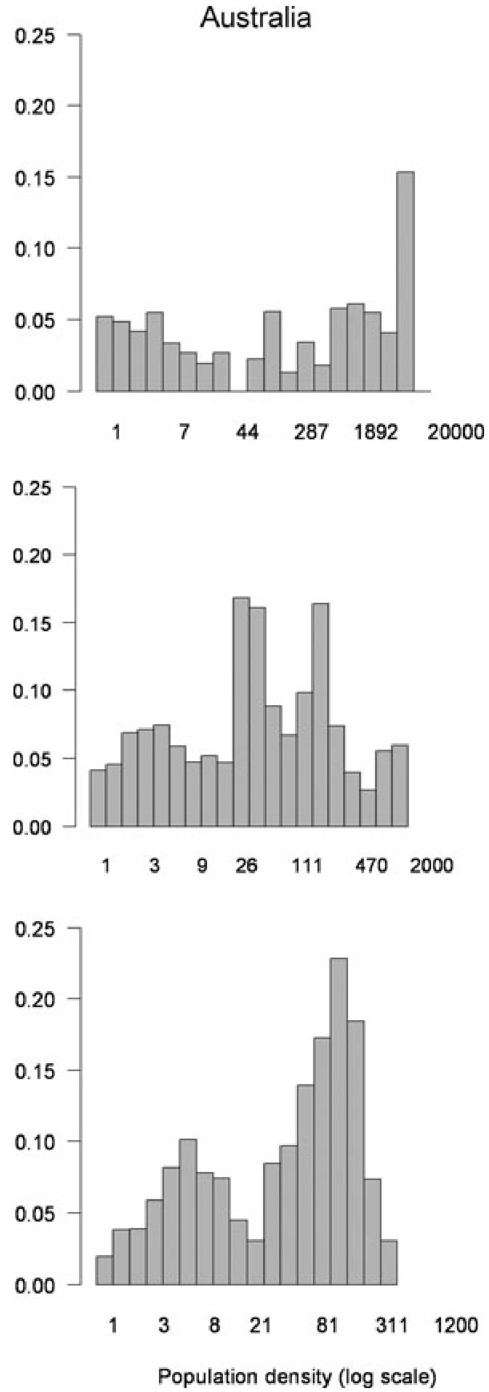


Figure 3. (continued)

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



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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.

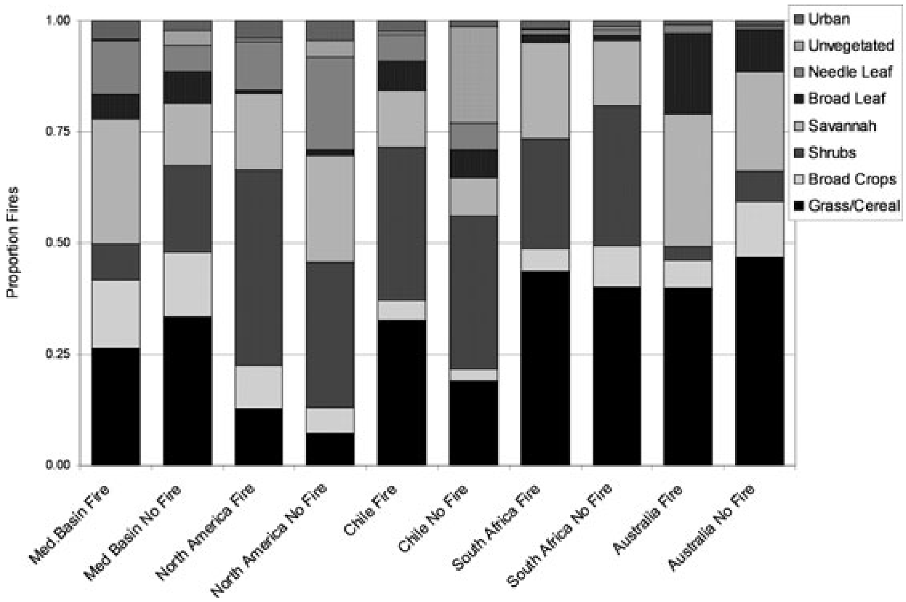

Figure 4. Aerial proportion of land-cover classes in the ecoregions and within pixels with an active fire in 2005.

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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Top 20 Most Destructive California Wildfires

	FIRE NAME *(CAUSE)*	DATE	COUNTY	ACRES	*STRUCTURES*	DEATHS
1	**CAMP** *(Powerlines)*	November 2018	Butte	153,336	**18,804**	85
2	**EATON** *(Under Investigation)**	January 2025	Los Angeles	14,021	**9,413**	17
3	**PALISADES** *(Under Investigation)**	January 2025	Los Angeles	23,707	**6,833**	12
4	**TUBBS** *(Electrical)*	October 2017	Napa & Sonoma	36,807	**5,636**	22
5	**TUNNEL - Oakland Hills** *(Rekindle)*	October 1991	Alameda	1,600	**2,900**	25
6	**CEDAR** *(Human Related)*	October 2003	San Diego	273,246	**2,820**	15
7	**NORTH COMPLEX** *(Lightning)*	August, 2020	Butte, Plumas, & Yuba	318,935	**2,352**	15
8	**VALLEY** *(Electrical)*	September 2015	Lake, Napa & Sonoma	76,067	**1,955**	4
9	**WITCH** *(Powerlines)*	October 2007	San Diego	197,990	**1,650**	2
10	**WOOLSEY** *(Electrical)*	November 2018	Ventura	96,949	**1,643**	3
11	**CARR** *(Human Related)*	July 2018	Shasta County, Trinity	229,651	**1,614**	8
12	**GLASS** *(Undetermined)*	September 2020	Napa & Sonoma	67,484	**1,520**	0
13	**LNU LIGHTNING COMPLEX** *(Lightning/Arson)*	August 2020	Napa, Solano, Sonoma, Yolo, Lake, & Colusa	363,220	**1,491**	6
14	**CZU LIGHTNING COMPLEX** *(Lightning)*	August 2020	Santa Cruz, San Mateo	86,509	**1,490**	1
15	**NUNS** *(Powerline)*	October 2017	Sonoma	54,382	**1,355**	3
16	**DIXIE** *(Powerline)*	July 2021	Butte, Plumas, Lassen, & Tehama	963,309	**1,311**	1
17	**THOMAS** *(Powerline)*	December 2017	Ventura & Santa Barbara	281,893	**1,063**	2
18	**CALDOR** *(Under Investigation)*	September 2021	Alpine, Amador, & El Dorado	221,774	**1,003**	1
19	**OLD** *(Human Related)*	October 2003	San Bernardino	91,281	**1,003**	6
20	**JONES** *(Undetermined)*	October 1999	Shasta	26,200	**954**	1

"Structures" include homes, outbuildings (barns, garages, sheds, etc) and commercial properties destroyed.
This list does not include fire jurisdiction. These are the Top 20 regardless of whether they were state, federal, local or tribal responsibility.
*Numbers not final *DINS Disclaimer: These numbers are preliminary based on aerial assessments dedicating heat sources which can include chicken coops, outbuildings, sheds, water containers, etc. *Validated inspections are currently being ground-verified by Damage Assessment Teams.

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USA TODAY

3 reasons California's wildfires got so dangerous so fast

Karissa Waddick
USA TODAY

Updated Jan. 8, 2025, 3:58 p.m. ET

Multiple wildfires ripped through Southern California Wednesday as a mix of powerful Santa Anna winds and dry vegetation created the perfect conditions for blazes to rage, destroying homes and causing thousands to evacuate.

West of downtown Los Angeles, near the coast in Pacific Palisades, a fire has scorched nearly 3,000 acres. Inland 28 miles, above Altadena, another broke out in Eaton Canyon, in the San Gabriel Mountains. And in the suburb of Sylmar in the San Fernando Valley, a smaller blaze tore through roughly 500 acres.

The causes of all three fires are currently under investigation, according to Cal Fire. The National Weather Service issued its highest alert for extreme fire conditions in the region before the fires ignited.

All three areas impacted by the fires have one thing in common: they sit at the edges of mountain regions which climate experts suggest may be more prone to fires than other parts of Los Angeles County.

Santa Ana Winds

The powerful Santa Ana winds that push dry air from inland areas toward the coast are among the most critical forces fueling the wildfires. As high-pressure systems move east to west over the Santa Ana Mountain range, wind is forced down where it's compressed and warms up.

Janice Coen, a project scientist at the National Center for Atmospheric Research in Boulder, Colorado, said these winds dry out vegetation on the mountain ridges as they pass and can carry embers over long distances – allowing fires to spread rapidly.

The Santa Monica Mountains, which include the Pacific Palisades, and San Gabriel Mountains, flanking the Eaton Canyon and Sylmar fires, are covered in dense vegetation that's especially flammable during dry seasons like the one Southern California is experiencing now. This ground cover makes the conditions ripe for fast-burning blazes.

Mountains, canyons and valleys

The steep slopes, canyons and valleys along the Santa Monica and San Gabriel Mountains add to the dangerous fire conditions.

Heat rises. When a fire ignites on the mountain slopes, it can pre-heat vegetation higher up, helping accelerate the spread of flames uphill, Jennifer Marlon a senior research scientist at Yale University explained**.** Canyons and valleys may also act as funnels for the Santa Ana winds, further accelerating the spread of wildfires in these more mountainous areas.

In contrast, areas closer to the coast, including some parts of Santa Monica, may have more moisture that can reduce the fire risk, Coen suggested. Some valleys and ridges across the Los Angeles area may serve as natural barriers that slow, or stop, the spread of the fire, she suggested.

Urban encroachment

Some of the most sought-after neighborhoods in the Greater Los Angeles area dot the coves on the edges of these mountain ranges. Pacific Palisades is often described by real estate brokers as understated and elegant. The average home in Altadena costs $1.3 million as of November, according to Realtor.com.

But development in these areas has also increased the risk of wildfires, Coen said.

She and other experts describe these communities as wildland-urban interfaces, or places where human populations meet natural habitats. An estimated quarter of the people in California live in these hazardous zones.

“Homes and infrastructure can ignite, creating embers, and a feedback loop that exacerbates fire heat release and ember spread,” Coen said.

More urban parts of Los Angeles County with less vegetation and fire-resistant building materials are likely better protected from fires than some neighborhoods that border nature.

Contributing: Phaedra Trethan and Doyle Rice, USA TODAY