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Mechanisms of Resilience to Megafire in Californian Wildlife Communities

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By

Kendall Calhoun

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Committee in charge:

Professor Justin Brashares, Chair
Professor Scott Stephens
Professor Arthur Middleton

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Abstract

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Anthropogenic pressures continue to shift the patterning and intensity of ecological disturbances globally. These changes in disturbance dynamics threaten conservation efforts of biodiversity in ecosystems around the world. One of the most conspicuous examples of this are novel, rapid changes in global fire regimes that have increased the frequency and severity of wildfires in fire-prone ecosystems. These megafires have the potential to quickly and dramatically change entire landscapes in ways that may impact the natural resilience of ecosystems and their wildlife communities. In this dissertation, I explore the potential mechanisms in which ecological resilience to severe fire may be facilitated and potentially enhanced in Californian wildlife communities, predominantly in oak woodland savannas.

This work addresses the interaction between principles of resilience and fire disturbance at multiple ecological scales. In Chapter 1, I present an overview of the ways wildfire in California spatially overlaps areas of conservation priority as well as broad categories of land cover types. In Chapters 2-4, I then zoom into a specific case study to address how a specific megafire, the 2018 Mendocino Complex Fire, impacts the resilience of wildlife communities (Chapter 2 and Chapter 4) and the adaptive capacity and behaviors of an ecologically dominant ungulate species (Chapter 3). Specifically, in Chapter 2, I examine the impacts of this fire on the recovery and response of mammal species using an array of trail cameras before, during, and after this fire event. In Chapter 3, I focus on the specific behavioral responses of a single species (*Odocoileus hemionus columbianus*) to this wildfire event and discuss how these behaviors may influence interspecies interactions at broader ecological scales. Finally, in Chapter 4 I examine the impacts of this wildfire event on broad patterns of species diversity and community assemblages across bird and bat communities using a set of acoustic monitors. Understanding how these qualities of resilience are realized, and potentially enhanced by human action, will become increasingly critical as fire regimes across the state, and globally, continue to change in response to anthropogenic pressures.

Table of Contents

Acknowledgements

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While the lab provided a strong home base, the support I received from the broader ESPM community proved invaluable to my perseverance in completing this dissertation as well. Collaboration is etched strongly into the culture of our department, and I've enjoyed each and every opportunity I've had to work with friends throughout the department. Each of these friendships and conversations have been so important in my own development and in defining the type of scientist I want to be. As will probably always be the case, I came to grad school with an unshakeable sense of imposter syndrome, but working and learning with these collaborators, friends, and labmates really helped me feel like I belong in this shared space too. In this same vein, I'm truly indebted to the work of the ESPM Graduate Diversity Council (ESPM GDC) for their work in creating space that fostered this sense of belonging for people of color and queer people who don't often see themselves in academic settings. In addition, I've been inspired by my time with the ESPM GDC to continue to advocate for diversity and equity in academia for marginalized groups wherever I choose to go next. Thank you ESPM community: Alexandra Kahn, Wenjing Xu, Ben Goldstein, Katherine Siegel, Kari Norman, Chelsea Andreozzi, Whitney Mgbara, Cesar Estien, Harshad Karandikar, Zachary Steel, Avery Shawler, Robin Lopez, Chippie Kislik, Sean Perez, Annie Taylor, Kenzo Esquivel, Ryann Madden, Sam Maher, Kristin Barker, Carmen Tubbesing, Ashton Wesner, Aidee Guzman and many, many more. Thank you for inspiring me to do what I do!

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Much of my dissertation involved a significant amount of work at the Hopland Research and Extension Center (HREC) in Mendocino County, California. Here, I'd like to acknowledge the history and injustices suffered by the indigenous communities on the unceded lands where the university (Berkeley) and HREC (Hopland) now stand. I recognize that UC Berkeley sits on the territory of xučyun (Huichin), the ancestral and unceded land of the Chochenyo speaking Ohlone people, the successors of the sovereign Verona Band of Alameda County. This land was and continues to be of great importance to the Muwekma Ohlone Tribe and other familial descendants of the Verona Band. In addition, I recognize that the land that HREC now sits on is the traditional land of the Sho-Ka-Wah of the Central Pomo people and continues to be of great cultural importance to their local communities.

I'd like to extend a big thank you to all the staff members of the Hopland Research and Extension Center who made all of the field work we performed for this dissertation possible. A significant portion of my dissertation work involved various field components, and all the work that we completed would not have been possible without the hands-on support of HREC staff. I'd like to give a huge thank you to Alison Smith, Troy McWilliams, and Greg Solberg for their work and expertise in keeping our field projects running. Alison Smith, specifically, was the heart of so much of this work and her dedication continues to inspire me. I'd also like to thank John Bailey, Jackie Mara Beck, and Hannah Bird for their continuous support and encouragement while completing my work at HREC that created an atmosphere of belonging for me.

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It's weird looking back at yourself at the end of this 6-year journey and noticing all the things that have changed within yourself. What at the time felt like a start of a half-baked idea has developed into this sprawling journey. It’s taken me to different continents, transformed me into a “data scientist”, deepened my love for the world around us, and pushed me to grapple with some of my biggest fears (i.e. public speaking). I still have plenty of half-baked ideas on my plate as I finish my PhD, but I feel like I have the confidence and tools now to know how to finish them. And for that I’m eternally grateful, and happy! But what’s even more important to me are all the things that haven’t changed, and in so many ways it’s been the relationships and support I’ve received from all of you. Thank you all, I couldn’t have done this without you!

Introduction

Rapid global change defines our age and drives our greatest conservation challenges. Biodiversity loss continues to escalate, with current estimates of species extinction rates outpacing the average background rates in geologic time (Barnosky et al. 2012). The causes of current defaunation loss are multi-faceted and involve a variety of human influences. Overharvesting, habitat loss, land conversion, invasive species, disease, pollution, and anthropogenic climate change all contribute to pronounced declines in global species diversity and have altered ecological communities around the globe (Dirzo et al. 2014; Young et al. 2016). One underappreciated result of these species declines is the loss of ecological interactions, which are integral for the persistence of many ecosystem functions and services. The loss of one species can have considerable direct and indirect impacts on the viability of its interacting partners (Brodie et al. 2014; Pérez-Méndez et al. 2016). Furthermore, these environmental stressors and species losses cause "rewiring" of food webs that can reverberate throughout communities. Food web rewiring can be topological, affecting the structure of food webs, or can involve shifts in interaction strengths, which alters the degree to which one species interacts with other species in its community (Bartley et al. 2019). Both forms of rewiring can have lasting impacts on how communities respond to future pressures and disturbances. Despite these challenges, humans still have the opportunity to adapt our actions and ecosystems to better conserve and coexist with the species around us.

Enhancing the resilience of ecosystems is often suggested as the best option to pre-emptively prepare ecological communities for the future stresses of global change. As a concept, resilience encapsulates some of the foremost goals embodied in recent conservation work which embodies a holistic model that takes into account entire ecosystems as well as the integration of human livelihoods and institutions (Heller and Zavaleta 2009; Dawson et al. 2011; Chornesky et al. 2015). The mechanisms to improve resiliency, however, are not well understood. "Resilience" as a term is nebulous in the scientific literature, but it is broadly defined as the capacity for ecological systems to absorb disturbances and recover to their initial state (Peterson et al. 1997). This definition has evolved over time to encompass how species, interactions, structures, and functions reorganize after disturbances (Desjardins et al. 2015). This inherent ability to reassemble after disturbances is essential for the sustainable functioning of ecosystems (Elmqvist et al. 2003), but extreme events have the potential to dramatically alter ecological communities (Scheffer et al. 2001), sometimes producing alternative ecological states that are highly resistant to recovery (Standish et al. 2014). Understanding how resilience is created and lost at multiple ecological scales and how it interacts with different types and intensities of disturbance will be an integral component of predicting, preventing, and combating the effects of global change on nature.

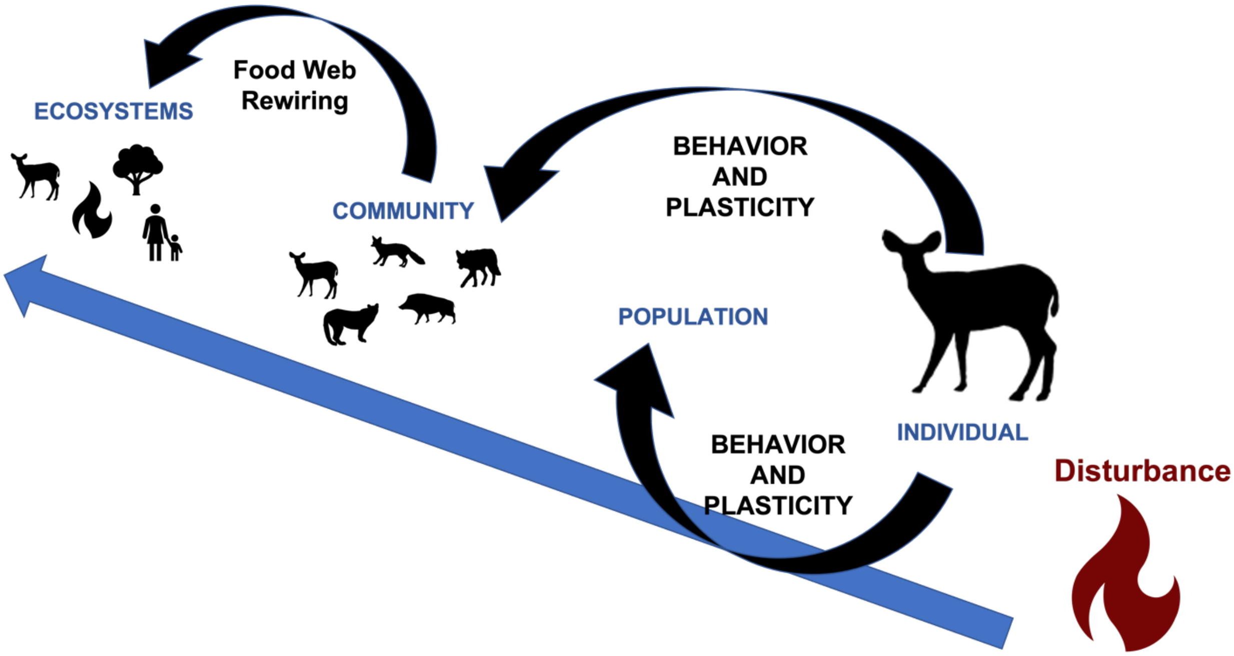


Figure 1. Conceptual diagram illustrating how response to disturbance at various ecological scales may scale up to affect broader communities and ecosystems. Resilience at various scales is potentially created and sustained by the drivers at lower levels. Top-down management decisions made my people at the human scale could also influence the ways wildlife are able to respond to disturbances at these varying scales.

Recent shifts in the frequency and intensity of wildfires observed across the planet present a frightening example of potential radical change to ecosystem structure, function, and services. Nowhere is this more apparent than in California where megafires (uncharacteristically large and severe fires with dramatic socio-ecological impacts) have become an annual occurrence. Shifting fire regimes in California present a natural experiment to investigate how forms of global change are impacting the structure of ecological communities and their resilience to change. California has a long history of fire being integrated into its ecosystems. For thousands of years, indigenous groups have utilized fire as an important management tool to facilitate the production of food and material resources (Anderson 2006; van Wagtendonk et al. 2018; Taylor et al. 2016). As a result, much of California's flora and fauna has coevolved with a broad range of fire regimes. Coastal chaparral historically burned relatively infrequently, but with high severity crown fires (M. A. Moritz et al. 2014). Oak woodlands burned more frequently, but at lower severity, burning the understory of trees with low flame lengths (J. Keeley 2011). Other parts of the state are composed of a combination of vegetation types and were characterized by mixed-severity fire regimes (Agee 2005). Anthropogenic influences, including suppression, urbanization, and climate change, have altered the historical patterning of fire in many of these systems (Lydersen et al. 2017; Syphard et al. 2007). A warming climate across the state has extended the fire season and decreases fuel moisture which changes fire behavior (Westerling and Bryant 2008). Historical suppression of fire has caused a build-up of fuels that create larger and more severe fires in some ecosystems (Collins and Stephens 2007). The expanse of the Wildland Urban Interface (WUI) increases ignitions and the frequency of fire in other ecosystems (Radeloff et al. 2018). Each of these pressures challenge the natural capacity of these systems (including their ecological interactions) to react and regenerate in response to altered fire regimes.

The 2018 Mendocino Complex fire is one of the latest examples in a trend of increasingly large and frequent megafires, fires larger than 100 km^2 (Linley et al. 2022), within California. This fire burned more than 1,800 km^2, becoming the largest wildfire in California recorded history at the time. The response of the wildlife community and species interactions to this type of extreme environmental shock is not well understood, but this fire created an important opportunity to examine how characteristics of fire may differentially affect species and mechanisms of reassembly. To take advantage of this opportunity, I monitored the ecological responses of wildlife to the Mendocino Complex fire at the Hopland Research and Extension Center (hereafter HREC) in Mendocino County, CA.

The River Fire, the southern half of the Mendocino Complex, entered HREC in late July and burned approximately 12.14 km^2 acres (over half of the center's total area). The center is composed of a diverse range of habitat types including grassland, oak woodland, and chaparral, all represented by plant species characteristic of a mixed-severity fire regime. HREC is situated at an intersection of wildlands and ranchlands; it provides habitat for a diverse range of wildlife and also serves as pastoral land for people and livestock. As is becoming increasingly common while human populations expand outward towards wilderness lands, HREC straddles landscapes for both wildlife and human settlement. These Urban-Wildland Interfaces have also received recent attention as being areas of high risk for future fires. As more of California begins to resemble Hopland and other WUIs, HREC presents itself as a unique and powerful opportunity to study the future implications of fire for the rest of the state and, perhaps, provide insights on how we can best build ecosystems resilient to this threat.

To better understand the mechanisms of recovery in post-fire wildlife communities, as well as the potential role human actions may play in influencing these mechanisms, I examined both broad- (state-wide) and local-scale (at HREC) impacts of wildfire on biodiversity:

1. In Chapter 1 I examine how wildfires in California spatially overlap with a) different dominant vegetation types and b) different areas of conservation emphasis. We then compare these findings with the historical coverage of wildfires in both media and research literature to facilitate a discussion of potential research gaps surrounding the impacts of wildfire in western US ecosystems. To do so, we compiled a dataset of Californian wildfires from 2000-2020 and compare these to broad land cover categories, CDFW defined Areas of Conservation Emphasis, and WUI-defined areas.

2. In Chapter 2 I examine the effects of the aforementioned megafire, the 2018 Mendocino Complex Fire, on a diverse woodland savanna mammal community. I used a grided network of trail cameras to compare the distributions of 8 medium to large-sized mammal species before, during, and after this megafire. From these observations, I discuss the resistance of certain mammal species to severe fire in these ecosystems, as well as community-wide impacts.

3. In Chapter 3 I zoom into a finer ecological scale to examine how movement and behavior influence the adaptative capacity of a single species, Black-tailed deer (*Odocoileus hemionus columbianus*), following the same megafire event (the 2018 Mendocino Complex Fire). To do so, I combine GPS-data across 28 individual female deer to explore how home range size, habitat selection, and the distribution of behavioral modes change

before and after this fire as well as in response to specific fire characteristics, such as severity.

4. Lastly, in Chapter 4 I zoom back out to explore how specific characteristics of the 2018 Mendocino Complex Fire influence patterns of species' distributions across bird and bat communities at the Hopland Research and Extension Center. To achieve this, I deployed acoustic monitors throughout the study site to record the presence of bird and bat species, and used an occupancy modeling framework to examine whether species presence was associated with burn severity and pyrodiversity.

Taken together, these questions and studies highlight the process in which ecological resilience to fire across wildlife communities may be facilitated at multiple scales (Figure 1). Understanding how these qualities of resilience are realized, and potentially enhanced by human action, will become increasingly critical as fire regimes across the state continue to change in response to anthropogenic pressures. I hope that the work of this dissertation can help advance ongoing conversations in conservation and wildlife management in California, as well as more broadly, in ways that pre-emptively prepare our shared ecosystems to rapid environmental change.

Chapter 1

Spatial overlap of wildfire and biodiversity in California highlights gap in non-conifer fire research and management

This chapter has been previously published (Calhoun et al., 2021) and is included here with permission from the dissertation chair.

Kendall L. Calhoun, Melissa Chapman, Carmen Tubbesing, Alex McInturff, Kaitlyn M. Gaynor, Amy Van Scoyoc, Christine E. Wilkinson, Phoebe Parker-Shames, David Kurz, Justin S. Brashares

Abstract

Global change has spurred the escalation of megafires in California over the last 20 years throughout a variety of ecosystems. Here, we examine the spatial distribution of California wildfires and megafires from the last two decades (2000–2020) in relation to ecosystem types and biodiversity metrics. We offer insights into the prevalence of fire across vegetation types and its potential implications for biodiversity, and for fire and land management. These results challenge the prevailing discourse that wildfire in California is chiefly an issue of forest management. We calculated burned area across vegetation types from 2000 to 2020 by integrating fire perimeter and land cover data and compared this to a content analysis of coverage of wildfires by media and scientific research across California. We then compared the distribution of fire perimeters across biodiversity metrics (richness and endemism) for five terrestrial taxonomic groups (birds, reptiles, plants, mammals and amphibians) and against the distribution of the wildland-urban interface (WUI). Total burned area from 2000 to 2020 was highest in shrubland ecosystems (38%), followed by conifer (36%), hardwood (17%) and grasslands (9%). In aggregate, ecosystems other than conifer make up the majority (64%) of the area burned in wildfires over the last 20 years. Fires most likely to impact endemic species, overlap areas of high species richness or burn within the WUI occurred predominantly in non-conifer ecosystems. Fires outside of forests have burned biodiverse areas critical to endemic species, but recent research and management in fire ecology continues to focus disproportionately on forests. Non-conifer forested areas in California represent an important gap in fire research and management. As fire regimes shift dramatically in the state, other ecosystem types must be part of the wider conversation on fire management and policies to better protect people and biodiversity.

Introduction

Global change has accelerated the frequency of large-scale ecological disturbances around the globe (Stott 2016). These large-scale disturbances, or environmental shocks, often dwarf the level of historical disturbance most ecosystems have experienced and potentially threaten the long-term resilience of affected ecological communities (Gaiser et al. 2020). Powerful examples of this trend are megafires, here defined as fires exceeding 100,000 acres in size, that greatly surpass the size and severity of historical fires and have disproportionate impacts on social and ecological systems (Stephens et al. 2014; Tedim et al. 2018). The immediate and secondary effects of megafires can dramatically alter ecosystem processes that sustain biodiversity (Adams 2013; van Wagtendonk et al. 2018). At a global scale, modified fire regimes are a threat to at least 15% of IUCN identified threatened and endangered species (Kelly et al. 2020). It is therefore important to develop appropriate management tools to reduce and mitigate the effects of megafires on biodiversity.

Fire science in California serves as an emblematic case study as recent megafires in the state have prompted intense debates over the best policy and strategies in response to the escalation of massive, destructive wildfires. Many of these discussions have entered the political sphere (e.g. in the 2020 U.S. presidential debates). California often serves as a bellwether of future environmental policy at the national scale and the outcomes of these public discussions could directly impact the future of biodiversity conservation in fire-prone ecosystems. While many contemporary U.S. fire management strategies stem from a long, intertwined history between fire, forestry and industry (e.g. wood products), strategies for managing fire in other, non-forest ecosystems are not widespread (Smith and United States. Forest Service, Colo. 2017; Minor and Boyce 2018). Furthermore, as many fire ecologists and land managers have recently noted, conifer forest management alone is not enough to address California's escalating wildfires (Schwartz et al. 2020). While recent work has defined the broad range of fire regime ecoregions across California (Syphard and Keeley 2020), we lack a comprehensive and detailed comparison of wildfire distribution across the state that includes the most severe fire seasons to date, like those of 2018 and 2020, and how these overlap with patterns of biodiversity within California.

To address this research gap, we must examine the role of changing fire regimes in California and its impact on biodiversity. Humans have and continue to play a significant role in shaping fire regimes across the state (Norgaard 2014; Taylor et al. 2016). Global pressures, including fire suppression, colonialism, land use change, invasive species and climate change, have altered many of the state's historic fire regimes (Westerling et al. 2006; Stephens et al. 2014; Abatzoglou, Williams, and Barbero 2019). For example, fire suppression since the 1930's has decreased the frequency of fire in California and caused a build-up in fire fuels in forested regions like the Sierra Nevada (van Wagtendonk et al. 2018; Syphard et al. 2007). Today, human activity and urban expansion into more wildland spaces also play significant roles in altering fire regimes in certain ecosystems (Radeloff et al. 2018). The wildland-urban interface (WUI), the transition zone between unoccupied land and human development, is associated with increased fire ignition and is quickly expanding across the United States (Hammer, Stewart, and Radeloff 2009).

Recent work has observed more frequent wildfires in hardwood and shrubland ecosystems, less frequent but more severe fires in conifer ecosystems and an overall increase in the size of wildfires across the state due to these synergistic pressures (Safford and Van De Water 2014; Parks et al. 2015; L. A. L. Hill et al. 2020; Li and Banerjee 2021). Severe departures from historic fire return intervals could indirectly impact the presence of endemic and native species by altering existing habitats over time. In certain regions, dramatic alterations to fire frequency may also impact the likelihood of megafires occurring (Parks et al. 2018). In chaparral (shrubland) ecosystems, where the pre-colonial fire regime was characterized by infrequent severe fire, biodiversity and ecosystem integrity are now potentially threatened by increased fire frequency near the WUI (Halsey and Syphard 2015). Additionally, much of the structural damage, costs to repair those damages and the potential loss of human life occurs within the WUI (Kramer et al. 2019). The influence of these global change pressures on fire ecology must be considered for wildfire management in fire-prone landscapes, particularly those of high biodiversity value.

California is recognized as a global biodiversity hotspot (Burge et al. 2016), and its diverse ecosystems offer an ideal context for studying the impact of changing fire regimes on biodiversity. California's biodiversity stems from a wide range of topographic, geographic and climatic variation across many ecosystem types (Davis and Richardson 1995, 109:199) and includes endemic species across many taxonomic groups (Harrison 2013). Fire plays an important role in maintaining a variety of ecological processes (Kelly, Brotons, and McCarthy 2017; Nimmo et al. 2019; He, Lamont, and Pausas 2019) and previous work has explored the specific mechanisms by which fire influences patterns of Californian biodiversity (Schuette et al. 2014; Tingley et al. 2016; Ponisio et al. 2016; Newman et al. 2018; Z. L. Steel et al. 2019). However, in modern fire regimes, fire may instead play an increasingly disruptive role in ecosystems across California.

Dramatic, anthropogenic-driven shifts in fire severity, size, frequency and seasonality may harm vulnerable species and interrupt important ecological processes (Stephens et al. 2014). Many species in fire-prone landscapes are fire-adapted, but even fire-adapted species could be threatened when fire regimes shift drastically from historical norms (Stillman et al. 2019). Ongoing research, however, reveals that these fire patterns are changing in different ways and magnitudes across ecosystem types (Parks et al. 2015; Williams et al. 2019). In a global analysis, (Kelly et al. 2020) found that species extinction risk from changes in fire regimes was greater in savannas, grasslands and shrublands than in forests. Thus, the omission of non-coniferous ecosystems from robust fire management strategies in California could have far-reaching consequences for biodiversity and ecosystem health (M. Moritz et al. 2004; Wilkin et al. 2017; Schriver et al. 2018; Newman et al. 2018). The combined impacts of shifting fire regimes and their management responses on biodiversity are likely ecosystem-specific, and discussions of impacts and their solutions need to be sufficiently nuanced to capture these dynamics.

As a region on the front lines of escalating wildfires in a diversity of ecosystem types within the most populous state in the United States, California is an important model for other fire-prone and biodiverse regions of the world in developing management strategies and policies that address the challenges presented by changing fire regimes and environmental shocks. Although the distribution of California's ecoregions is geographically distinct and land jurisdiction within the state includes an extent of federal land, we chose to focus our attention at the state-scale to match the scope of recent political discussions, the scale of data availability, and to inform state-level policy decisions that ultimately influence local levers for fire management. To provide improved context for these discussions on fire management and biodiversity conservation broadly, we conducted spatial analyses detailing the distribution of fires in California over the last two decades (2000–2020). We compared the land cover composition of megafires to all wildfires over the last 20 years to investigate whether megafires occur in distinctly different areas from milder wildfires. For our study, we limit our focus to wildfires occurring in the last

20 years to examine the recent intensification in fire size and destructiveness (L. A. L. Hill et al. 2020; Li and Banerjee 2021).

To understand the potential impacts of the distribution of wildfires and megafires on biodiversity, we compared the distribution of burned land cover classes and shifts in historical fire frequencies to the distribution of designated areas of conservation emphasis (Supplement S1: CDFW, 2019[a-b]) across the state for bird, plant, mammal, reptile, and amphibian native species diversity and endemism. To assess whether departures from historical fire frequencies affected observed patterns of species richness and endemism across California, we compared the same biodiversity metrics with spatial variation in recorded fire return intervals. We also compared burned land cover to the distribution of the WUI across the state to examine where fires overlap with areas of urban expansion. Finally, to assess our contention that forest science and management have dominated the discussion of wildfire, we performed a bounded media content analysis to categorize articles written about wildfires in California within the academic literature and news media. Together, these findings highlight (1) a potential mismatch in the prevalence of forest and non-forest fire in published literature, (2) the actual distribution of wildfires and (3) the potential effects of those distributions on biodiversity.

Methods

Study Area

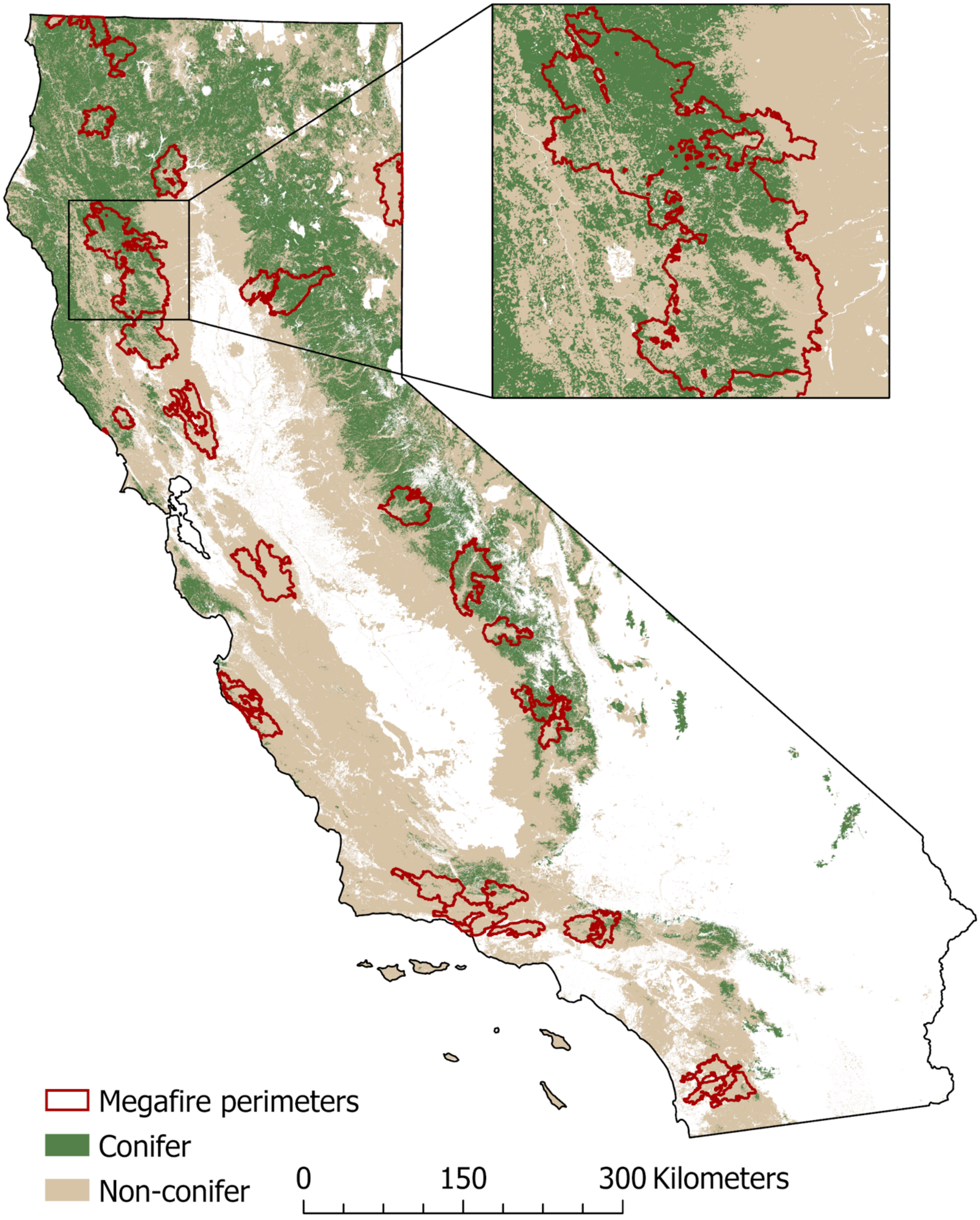
We examined wildfire from 2000 to 2020 across the state of California, USA. Like other Mediterranean climate regions of the world, California experiences dry summers and mild winters and has many fire-prone landscapes (Moreira et al. 2020). Peak fire season historically occurred during September and October, though climate change and other factors have increased the duration of this window (Westerling et al. 2003). Some of the ecosystem types found in the state include conifer forests, oak woodland savanna, freshwater wetlands and coastal shrublands, which provide habitat for a wide variety of threatened biodiversity.

Literature and media content analysis

To better understand the relative degree of scientific and media attention given to fires in forest versus non-forest habitats, we systematically searched library databases. We used the search terms “California AND forest* AND fire*” for fires in forest habitats and “California AND (shrub* OR brush OR grass* OR woodland) AND fire*” for fires in non-forest habitats. We chose these search terms after our initial exploration revealed that they best captured the range of studies about wildfires in California with references to specific habitat types. We searched for academic literature on the Web of Science Core Collection and identified the number of articles published in 2000–2020 for which the search terms were found in the title, abstract and/or keywords. We searched for news media on Access World News and identified the number of newspaper articles published in the United States in 2000–2020 for which the search terms were found anywhere in the text. We conducted all searches on 9 November 2020 using the University of California, Santa Barbara, and University of California, Berkeley library databases.

Fire perimeters and land cover data

To quantify burned area in each land cover type over the 20-year period from 2000 to 2020, we intersected fire perimeters with Cal Fire's vegetation land cover map (Supplement S1: CALFIRE–FRAP, 2015; Figure 1, Supplement S2: Figure S1). We derived our land cover classes by aggregating California Wildlife Habitat Relationship classes (https://wildlife.ca.gov/Data/CWHR/Wildlife-Habitats) from fveg. These categories included the following: Conifer, Desert, Grassland, Hardwood, Shrubland and Urban/Agriculture. A full list of land cover class aggregations can be found in Supplement S2: Table S2.1. For this study, we only consider fire-prone land cover classes and therefore exclude "Desert" and "Urban/Agriculture" classes from our analysis. We combined fire perimeter data from the years 2000 to 2019 (Supplement S1: CALFIRE–FRAP, 2020) with fire perimeters from 2020 (Supplement S1:National Interagency Fire Center, 2020). The CALFIRE-FRAP only contains burn perimeters for fires greater than 300 acres, so for the analysis, we only consider fires 300 acres or larger in both databases (n = 1,208 fires). We then intersected the compiled fire perimeter dataset with fveg land cover types and then calculated the area burned in each class in each year. Finally, to find the relative distribution of wildfire between land cover types, we divided the total area burned for each land cover type by the total area available of that land cover type. We performed the spatial intersection in ArcGIS Pro 2.6.0 and the data cleaning and summarizing in R (v.4.0.2) (R Core Team 2021). A list of these land cover and fire perimeter data sources can be found in "Supplement S1: Data Sources". To compare these results to the distribution of areas burned by megafires in the same time period, we performed the same analysis with a subset of data that only included megafires, or fires greater than 10,000 km^2 (n = 28 megafires).



Megafire perimeters
Conifer
Non-conifer
0
150
300 Kilometers

Figure 1. Map of California land cover composition with megafires in the last 20 years displayed on top. In this map, land cover is divided into "Conifer" and "Non-Conifer" fire-prone land cover categories. Non-Conifer land cover included the grouped "Grassland", "Hardwood" and "Shrubland" land cover categories. "Urban", "Agricultural" and "Desert" were not considered for analyses and left uncolored within the map. Megafire perimeters (in red) were defined as fires >10,000 km^2 (n = 28) and were obtained from the CALFIRE and NIFC databases (2000–2020). The inset map (top-right corner) shows a zoomed image of the burn perimeter of the August Complex fire, California's largest recorded wildfire to date. Though widely considered a "forest fire", the inset shows that the August Complex megafire did not burn purely within Conifer, but instead a mix of several different land cover types. Megafires in southern California burn primarily outside of Conifer, but pose some of the biggest threats to people and infrastructure.

Biodiversity metrics

To assess the potential impacts of current changes in fire dynamics on biodiversity, we examined the degree to which recent fires have overlapped with regions of "high conservation priority" using the California Department of Fish and Wildlife (CDFW) Areas of Conservation Emphasis (Supplement S1: CDFW 2019[a-b]). We define areas of "conservation priority" as regions with "high" or "very high" native species richness as defined in the CDFW ACE dataset and/or regions containing at least one endemic species. These datasets provide maps of the distribution of species richness and endemism via collected occurrence models and predicted species ranges.

We considered native species richness and species endemism across five terrestrial taxonomic groups: birds, reptiles, plants, mammals and amphibians. For native species richness, we used the "Terrestrial Native Species Richness Summary" dataset for each taxonomic group (Supplement S1: CDFW 2019). Using the "sf" package in R (Pebesma 2018), we filtered each taxonomic dataset to delineate regions we define here as "high species richness" which contained the upper two quantiles (or upper 40%) of observed or predicted native species occurrence. This delineation follows the categorizations of "high" and "very high" species richness provided by the CDFW ACE dataset. We applied this filtering approach to each taxonomic group independently to identify regions that were particularly biodiverse across taxonomic groups. We then overlaid these regions of "high species richness" with the previously created dataset of fire perimeters by land cover class. We summed the area of these intersections to assess which regions of high biodiversity burned across each land cover type for each taxonomic group. To determine the relative importance of these burned areas for biodiversity, we divided the area of burned land cover types identified as having high species richness by the total area burned of that land cover type. This provided a proportion of the total area burned that may be of high conservation priority.

To examine how species endemism overlaps with recently burned areas, we followed a similar workflow. For each taxonomic group, we downloaded the corresponding "Terrestrial Irreplaceability Summary" dataset which counts the number of endemic species in each spatial plot (Supplement S1: CDFW, 2019) and filtered it to identify areas of the state containing at least one endemic species. These areas of endemism were then intersected with the aforementioned shapefile of fire perimeters by land cover type. We then totaled the area of burned land cover types. To observe the relative importance of burned land cover class to endemism, we again divided the area of the calculated burned areas of endemism by the total area burned in each land cover class. A list of biodiversity data sources can be found in Supplement S1: Data Sources.

Spatial analyses for both biodiversity metrics (richness and endemism) were repeated with the subset dataset of megafires to allow comparison with the dataset containing all fires.

Wildland-urban interface data

To examine how urban expansion overlaps with wildfire in California, we explored the land cover composition of fires in the wildland-urban interface (WUI). To do this, we analyzed how the land cover composition of fires overlapped with the 2010 WUI Assessment layer for California (Supplement S1). This dataset is based on US Census housing data and the US Geological Survey's National Land Cover Database (Supplement S1; (Radeloff et al. 2018)). Using ArcMap 10.8 (Esri 2011), we combined both "interface," where houses and wildland vegetation meet, and "intermix," where houses and wildland vegetation intermingle, into a single WUI layer which we intersected with the burned land cover layer. We totaled the area of burned WUI by each land cover type. The data source for WUI layers can also be found in Supplement S1: Data Sources. Spatial analyses for the WUI were repeated with the subset dataset of megafires to allow comparison with the dataset containing all fires.

Fire return interval departure analysis

In order to observe how alterations in fire frequency may impact biodiversity, we performed an analysis to observe whether departures from historical fire frequencies affect observed patterns of species richness and endemism across California. For this analysis, we compared the above biodiversity metrics provided by the CDFW ACE dataset (Supplement S1: CDFW, 2019) with the Fire Return Interval Departure (FRID) dataset provided by USDA (Supplement S1: USDA, 2020) hypothesizing that greater departures from historical fire return intervals would be associated with less native species richness and decreased species endemism. We compared this relationship between biodiversity metrics and FRID across taxonomic groups as well as across coarse ecosystem types (conifer versus. non-conifer). A full description of the methods used in this analysis can be found in Supplement S3.

Results

Media and literature content analysis

Based on our review of the published scientific academic literature, studies on fires in forested habitats (1,605 articles) were more than twice as abundant as those based in non-forested habitats (705 articles). Forest fires also received more attention than fires in other land cover types in popular news coverage (164,568 articles compared to 126,546; Supplement S2: Figure S2).

Fire perimeters and land composition

We found that most of the area burned in California wildfires from 2000 to 2020 was outside of conifer ecosystems (Figure 2a; Supplement S2: Table S2). Furthermore, shrubland and hardwood burned a greater percentage of their total available area than conifer ecosystems (Figure 2b), highlighting the prevalence of fires within these unique ecosystems.

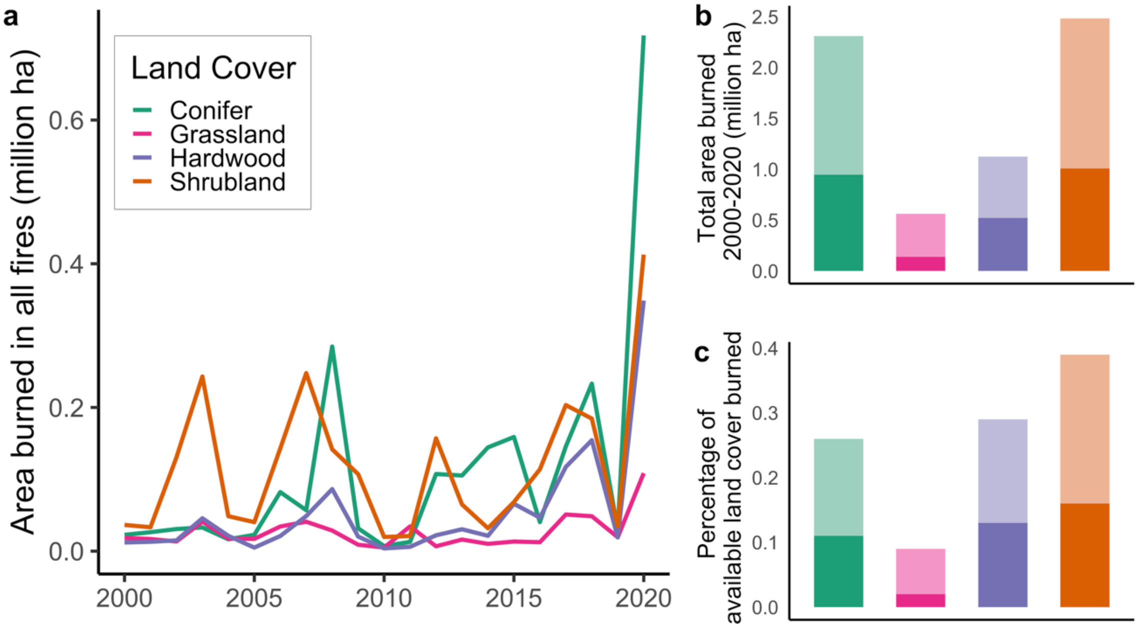


Figure 2. Breakdown of land cover types burned in California from 2000 to 2020. Panel "a" displays the total yearly area burned by all wildfires in million hectares across each land cover type from 2000 to 2020. Panel "b" displays the total summed burned area (2000–2020) for each land cover category. Light shading displays the total area burned by all wildfires, while dark shading displays the total area burned by megafires in each land cover category (bars are not additive). Panel "c" displays the percentage of each land cover category's total available area that burned during our study period (2000–2020). Light shading displays the percentage of all available land cover that was burned by all fires from 2000 to 2020; dark shading displays what percentage of all available land cover was burned by megafires from 2000–2020.

Non-conifer ecosystems make up 64% of the area burned in California during the last 20 years, totaling 4.17 million hectares burned (Supplement S2: Table S2). Among distinct habitat types, shrubland ecosystems had the greatest amount of area burned (2.48 million hectares) and made up 38% of the total burned area. Conifer forest burned the second greatest amount of area with 2.31 million hectares burned, making up 36% of the total burned area. Hardwood (which also included savanna habitats) and grassland regions comprise the remaining 26% of the total burned area (Figure 2a, Supplement S2: Table S2). Shrubland burned at the greatest percentage of total available area over our study period (39%; Figure 2b). This was followed by hardwood where 29% of its available land cover burned, and then conifer where 26% of its total available cover burned. Across all land cover types, burned area varied each year, but in 2020 there was a sharp increase in burned area across all land cover types and most notably in conifer (Figure 2c). The total area burned in 2020 was greater than the area burned in any other year from the 20-year study period.

Megafire and land cover composition

Prior to 2018, the majority of area burned by megafires was within shrubland habitat (Supplement S2: Figure S3). Megafires burned one million hectares of shrubland during the study period, 39% of the total area burned in shrublands overall (Supplement S2: Table S3). Megafires burned the second most area in conifer (947,000 ha), followed by hardwood

(522,000 ha) and finally grassland (139,000). A chi-square goodness-of-fit test found significant differences between the expected distribution of areas burned across ecosystem types based on the complete fire dataset and the observed area burned by megafires in each land cover type ($\chi^2 = 44{,}724.07$, $df = 3$, $p < .0001$). Megafires tended to burn more in conifer and hardwood and less in grassland areas than expected.

Fire perimeters and species richness

Areas of high species richness for different taxonomic groups burned within a range of land cover types. Areas within the top two quantiles of species richness for birds, reptiles and amphibians burned most predominantly outside of conifer ecosystems. For each of these three taxonomic groups, shrubland was the most common land cover type burned in areas of high species richness, with 1.30 million ha burned in critical areas for birds, 1.05 million ha burned for reptiles and 1.58 million ha burned for amphibians (Figure 3b,d,j). Burned areas of highest plant and mammal richness were most often in conifer forest ecosystems, with 2.08 million ha burned in areas of high plant richness and 2.05 million ha burned for mammals (Figure 3d,f).

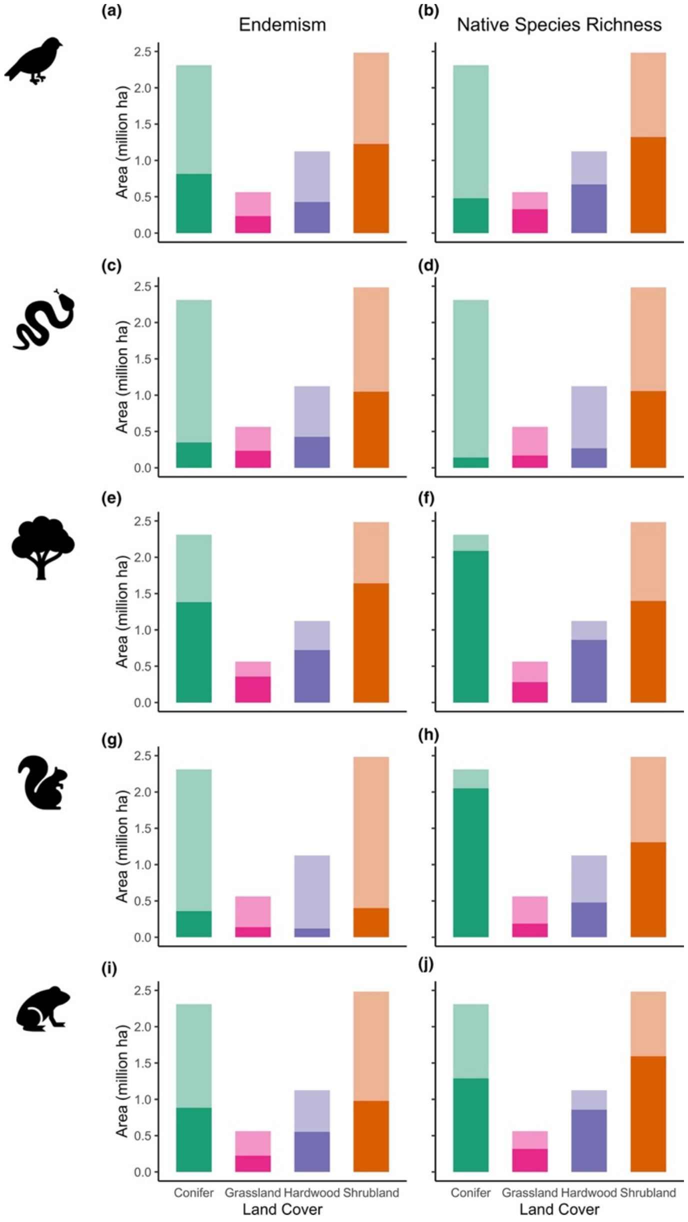


Figure 3. Total area burned by all wildfires (2000–2020) in areas of high biodiversity and endemism across land cover classes in California. Regions that contained the upper two quantiles (or upper 40%) of predicted native species occurrence were identified as being regions of "high species richness" for each taxonomic group. Regions that contained at least one endemic species were identified as regions with species endemism. In both richness and endemism plots, light shading displays the total area burned in each land cover type (2000–2020) while dark shading displays the total area burned in areas of high species richness and endemism. The burned area of these identified regions is displayed in Figure 3a,b for birds, Figure 3c,d for reptiles, Figure 3e,f for plants, Figure 3g,h for mammals and Figure 3i,j for amphibians.

Although the total area burned in hardwood was less than that in shrubland and conifer habitats, burned areas of hardwood were more likely to support high species richness for birds, plants and amphibians. For plants, 77% of the total burned hardwood area from 2000 to 2020 was categorized as areas of high plant species richness. For birds, 59% of burned hardwood areas were also areas of high species richness, and for amphibians, 76% of burned hardwood areas were also areas of high amphibian species richness. A full table of hectares burned in areas of "high species richness" can be found in Supplement S2: Table S4.

Fire perimeters and species endemism

Burned areas containing at least one endemic species were predominantly outside of conifer forests (Figure 3). From 2000 to 2020, shrubland was the dominant land cover type for burned areas with endemic species for each taxonomic group, with 1.22 million ha burned for birds (Figure 3a), 1.04 million ha for reptiles (Figure 3c), 1.64 million ha for plants (Figure 3e), 0.40 million ha for mammals (Figure 3g) and 0.97 million ha for amphibians (Figure 3i). The proportion of areas with endemic species that burned relative to the total area burned for each land cover type was relatively equal across land cover types. A full table of hectares burned in areas with endemic species can be found in Supplement S2: Table S6.

Megafire and biodiversity metrics

Megafires overlapped areas of high species richness most often in hardwoods for birds, in shrublands for amphibians and reptiles and in conifer for plants and mammals. In areas with endemic species, megafires overlapped shrubland most often across all taxonomic groups except mammals. A full table of hectares burned by megafires in areas of high species richness and with endemic species can be found in Supplement S2: Table S5 and Supplement S2: Table S7.

In regions of high species richness and endemism, chi-square goodness-of-fit tests revealed significant ($p < .05$) differences in the distribution of areas burned by ecosystem type between megafires and the complete fire dataset. Across most taxonomic groups (e.g. birds, reptiles, mammals and amphibians), a greater area of hardwood was burned by megafires in areas of high species richness than was evident in the complete fire dataset. Megafires were less likely to burn in grasslands with endemic species and/or high species richness. A full table of chi-square significance test results for each biodiversity metric and taxonomic group can be found in Supplement S2: Table S8.

Fire perimeters in the WUI

Hardwood was the most common ecosystem type that overlapped with the WUI followed by grassland, conifer and finally shrubland (Figure 4). However, shrubland was the predominant land cover type burned in the WUI, burning 104,000 hectares from 2000 to 2020 (Figure 4). Shrubland in the WUI burned nearly three times the area burned in conifer. Shrubland was followed closely by hardwood where 71,000 hectares burned. Burned conifer forest made up just 14% of the total burned WUI areas. A full list of hectares burned in WUI can be found in Supplement S2: Table S9.

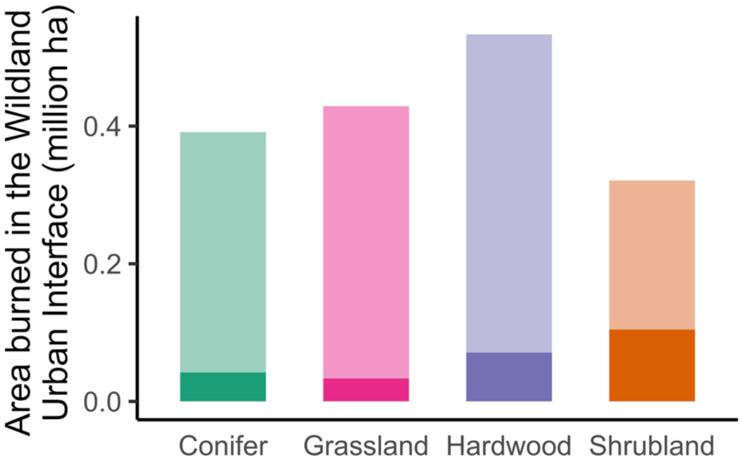


Figure 4. Area burned in million hectares from all wildfires across land cover categories in California's wildland-urban interface (WUI) summed from 2000 to 2020. Light shading displays the total area of the WUI available to burn in each ecosystem type while dark shading displays the total area of the WUI that burned during our study period (2000–2020).

Megafire and the WUI

The land cover composition of megafires within the WUI matches the overall distribution of wildfires in the WUI from the complete fire dataset. Shrubland megafires in the WUI account for the most area burned during our study period (30,000 ha), followed by hardwood (25,000 ha), then conifer (14,000) and finally grassland (9,000 ha). Using a chi-squared test, we found significant differences in the composition of WUI megafires, with a greater area of conifer and hardwood WUI areas being burned than would be expected when compared to the complete fire dataset within WUI ($\chi^2 = 915.3304$, $df = 3$, $p < .0001$). A full list of hectares burned by megafires in WUI can be found in Supplement S2: Table S10.

Fire return interval departure analysis results

We found the overall effect of the departure from historic fire return intervals varied by taxonomic group and across coarse habitat types. Trends in species richness varied greatly across taxonomic groups as FRID increases (Supplement S3: Figure S1, Figure S1). In contrast, endemic species were less likely to be observed as FRID increased in non-conifer ecosystems than in conifer ecosystems (Supplement S3: Figure S2, Figure S2). A full description of results and their discussion can be found in Supplement S3.

Discussion

California's megafires and wildfires burned across all of the state's ecosystems over the last 20 years, but media and scientific coverage of forest and non-forest wildfire within the state does not reflect this fact. We found that both wildfires and megafires overlapped with regions of high species richness and species endemism across different land cover types for several taxonomic groups. However, the relationship between ecosystem type and biodiversity was taxon-specific (e.g. of burned regions with high native bird richness, a greater area burned within shrubland ecosystems than any other burned ecosystem type). Finally, we found that fires burned predominantly in shrubland in the wildland-urban interface. Taken together, our results suggest an urgent need for increased research on megafires and wildfires outside of forests, and they support the call for land stewardship and adaptation strategies that support ecosystem-specific solutions.

Megafire and wildfire in California do not occur in one land cover type, but across a diverse range of ecosystems. Of the land cover classes we examined, no single ecosystem type made up the majority of burned areas in the past 20 years, though the largest single land cover category burned was in shrubland habitat. Similarly, burned non-conifer ecosystems have considerable biodiversity value and the potential loss of this biodiversity from megafire and/or changing fire regimes merits further attention. Though not all taxa are negatively affected by a single fire, changing fire regimes and growing megafires may threaten many ecologically and economically important species, particularly those outside of forests (Kelly et al. 2020). Fire-prone Mediterranean regions around the world all contain multiple ecosystem types and support a breadth of unique biodiversity (Cox and Underwood 2011). As evidenced in California, this diversity in ecosystems must be considered to effectively address the challenges presented by megafires and changing fire regimes. Furthermore, as previous research has addressed, the predominance of burned land cover classes is geographically distinct (Syphard and Keeley 2020). Northern California has predominantly burned conifer ecosystems and southern California has predominantly burned shrubland ecosystems. Despite this difference, both regions are still managed, in large, by the policies and guidelines created at the shared state level. The mechanisms underlying how ecosystem-specific fire regimes maintain patterns of biodiversity will be essential for designing applicable fire and land management practices that promote conservation.

Of all burned land cover types, shrubland in particular deserves increased consideration given (a) the high value of shrublands in California for biodiversity, and (b) our finding that shrubland burned more than any other land cover class when considering all wildfires, only megafires, and WUI fires. Most fire policies in the United States originated in historical forest management (Minor and Boyce 2018), but many of the tools that are successful for fire management in conifer forests often have unintended effects in shrublands. For example, more frequent prescribed fire and thinning restore natural landscape heterogeneity and ecological processes in some conifer forest ecosystems (Collins and Stephens 2007; Boisramé et al. 2017; Knapp et al. 2017), but these types of strategies can erode ecological integrity in many shrubland systems. Frequent burning and mastication can provide opportunities for invasion by non-native annual grass species that may further alter the shrubland's fire regime (Halsey and Syphard 2015; J. E. Keeley and Brennan 2012; Wilkin et al. 2017). Shifts in fire regimes and frequent megafire in shrubland regions could endanger valuable biodiversity, particularly endemic species across all studied taxonomic groups. Diverse management strategies are required to meet each of their unique fire management challenges. Alternative strategies such as powerline hardening, zoning or other forms of landscape modification that are more appropriate for shrublands are necessary to preserve the fire regimes and biodiversity in these unique ecosystems (Kolden and Henson 2019; McWethy et al. 2019).

Wildfire in the WUI plays an important role in how fire regimes are changing across the state and we found that this interface burns predominantly outside of conifer ecosystems. Human activity at the WUI has the potential to alter future fire regimes, and the impacts of these fires on biodiversity and the built environment may be exacerbated by urban expansion. Shrubland and hardwood ecosystems were the predominant land cover type burned within WUIs and their fire regimes may be affected more often by their proximity to urban areas than other ecosystems. Large wildfires in the WUI pose the greatest risk to people, cause considerable structural and economic damage and strain important ecosystem services that connect biodiversity to human livelihoods (Kramer et al. 2019). Hardwood ecosystems make up the greatest proportion of the total WUI within California and provide a plethora of ecosystem services (Huntsinger et al. 2010); thus, concerted efforts are needed to prepare communities living in these areas for future fires. This is particularly true for communities living in the WUI within shrubland ecosystems, an area that burns the most despite being less common that other habitat types within the WUI. In shrubland ecosystems, proximity to the WUI increases the frequency of fires in areas that historically burned infrequently (Haidinger and Keeley 1993). For areas outside of California, the ecosystem composition of the WUI must be taken into consideration to identify areas of prioritization and in designing appropriate management strategies.

From 2000 to 2020, megafires were recorded across each of the ecosystem types examined in this analysis. Management of megafires, specifically, warrants increased emphasis and priority due to their potential to quickly alter entire ecosystems and threaten biodiversity and people. Though megafires burned significantly more conifer and hardwood area than expected, the majority of area burned by megafires was in non-conifer ecosystems. The overall prevalence of megafires across ecosystem types closely resembles the distribution of all fires, reiterating the need for new management strategies that meet the unique challenges presented in each ecosystem to prevent or mitigate future megafires. Megafires around the world are likely to alter ecosystems in profound and enduring ways similar to outcomes observed with other environmental shocks such as flooding and extreme drought (Bartley et al. 2019; Bodmer et al. 2018; Prugh et al. 2018). Recent work has already explored some of the dramatic effects megafire has on local biodiversity by homogenizing entire landscapes in forested ecosystems (Z. L. Steel et al. 2019; Wintle, Legge, and Woinarski 2020; Jones et al. 2020; Pickrell and Pennisi 2020), but these results highlight the need for more research on effects of megafires on biodiversity in non-forest habitats. Additionally, the impacts of megafires in each of these ecosystem types may extend far past their initial, short-term effects and create reverberations that influence future habitat quality as well as the composition of ecological communities within the ecosystems they disturb (Gaiser et al. 2020).

Megafire is a pulse disturbance in that it occurs quickly and acutely, but some disturbances, like changes in fire frequency, present longer-term alterations to ecosystems. For example, urbanization, climate change and other global change pressures have altered ignition patterns in recent years across the state (J. E. Keeley and Syphard 2018). Recent anthropogenic shifts in the fire return interval in certain ecosystems can change the composition and structure of ecological communities (Brooks and Matchett 2006; Safford and Van De Water 2014; Horn and St. Clair 2017). In our analysis of changes in fire frequency, we examined whether altered fire return intervals impact broad patterns of native species richness and endemism, hypothesizing that greater changes in fire return interval would result in decreased species richness and endemism

(Supplement S3: Fire Return Interval Departure Analysis). Though we did not find strong evidence to support our hypothesis, we list several suggestions for future research that may expand our understanding of the relationship between altered fire return intervals and patterns of biodiversity. Furthermore, current observed patterns in species richness and endemism are likely more strongly informed by longer evolutionary history than recent shifts in fire return intervals. We anticipate, however, that continued departure from historic fire return intervals could influence future patterns of communities, species and endemism. Future work should take advantage of opportunities to explore the implications of press disturbances (long-term changes in fire regimes and ignition patterns) and pulse disturbances (megafire) for biodiversity and how these fire disturbance dynamics interact.

Despite evidence that wildfire has a broad distribution across ecosystems, policy, media and even scientific literature do not reflect the nuanced importance of ecosystem-specific strategies in their reporting on wildfire. Recent political and scientific attention on California wildfires has centered primarily on forest fire (Christopher 2020). As reflected in Supplement S2: Figure S2, academic papers examining California wildfires in forests made up the large majority of all research on wildfires in California over the last 20 years (70%). The distribution of scientific literature does not match the observed distribution of wildfire between conifer and non-conifer ecosystems. The analysis of news coverage of California wildfires revealed a similar result, although with a smaller majority of coverage of forest fires over other forms of fire (57%). Forest fire science and management has benefited from a history of synonymizing fire with forests in the psyche and policies of the United States (Minor and Boyce 2018). In addition, management of conifer forests is often supported by various incentives including the cap-and-trade market and timber industry (Daniels 2010; Smith and United States. Forest Service, Colo. 2017; Dass et al. 2018). Established management practices, including prescribed burning and thinning, often provide more examples of “win-wins” in conifer forests by improving ecological integrity, reducing fire severity and reducing risk to humans (Vaillant, Fites-Kaufman, and Stephens 2009; Boisramé et al. 2017; Lydersen et al. 2017). These “win-wins” are, thus far, rarer for non-conifer ecosystems, but we argue that continued research is needed in management, adaptation and policy that can address gaps in non-forested systems. Reducing fire risk through vegetation management may be difficult or ineffective in some of California's ecosystems, but strategies such as ignition-reduced zoning, urban planning, defensible space, home hardening, linear fuel breaks and other forms of fuel modification could bring us closer to adapting and coexisting with fire (J. E. Keeley 2002; Syphard, Brennan, and Keeley 2014; M. A. Moritz et al. 2014).

Conclusion

Conifer forest management has been the crux of fire policy, management and research throughout the United States for decades, yet our results emphasize that fire management for biodiversity and ecosystem health does not have a one-size-fits-all solution. Our results also reveal an important disconnect between how media and scientific research reports on fire and where fires are occurring. Given that most megafires in California do not occur in conifer ecosystems, fire management in conifer forests alone will not address the breadth of California's recent wildfire challenges. Regions of endemism and high native species richness are afflicted by megafire across all ecosystem types, highlighting a solutions gap for protecting California's biodiversity. To improve fire adaptation, management and policy decisions must reflect the specific needs of the diverse ecosystems in fire-prone regions of the world and must be informed by research that is specific to these systems. Nuanced, ecosystem-specific approaches will be essential for robust conservation and wildfire management.

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Supplement for Chapter 1

Supplement S1 – Data Sources

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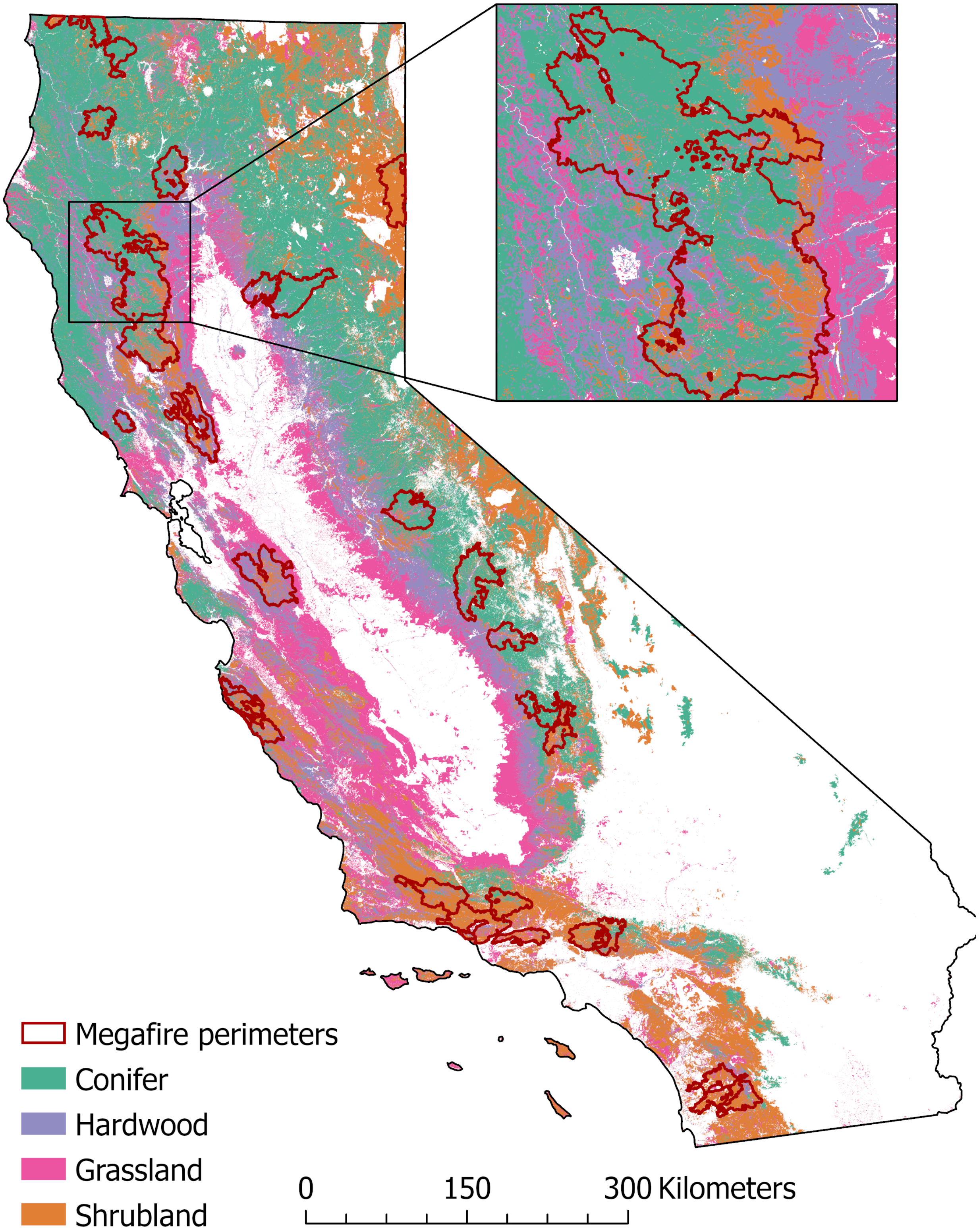
Supplement S2 – Additional Figures and Tables

Table S1. Aggregated list of land cover classes for California generated from the CALFIRE fveg land cover data source. Original land cover classes are on the left, aggregated classes used for analysis are on the right. Hardwood and conifer are given distinct categories for analyses. Hardwood ecosystems include the distinctly Californian rolling hills of oak woodland. Though these woodlands have trees, their ecology and fire histories are distinct from forests and they require very different approaches to fire mitigation.

CALFIRE fveg Land Cover Class Aggregation	
Original Classes	Aggregated Classes
Agriculture	Urban/Agriculture/Desert
Urban	Urban/Agriculture/Desert
Water	Urban/Agriculture/Desert
Wetland	Urban/Agriculture/Desert
Desert Shrub	Urban/Agriculture/Desert
Desert Woodland	Urban/Agriculture/Desert
Conifer Forest	Conifer
Conifer Woodland	Conifer
Herbaceous	Grassland
Barren/Other	Urban/Agriculture/Desert
Hardwood Forest	Hardwood
Hardwood Woodland	Hardwood
Shrub	Shrubland



Megafire perimeters
Conifer
Hardwood
Grassland
Shrubland
0
150
300 Kilometers

Figure S1. Map of California megafires in the last 20 years and land cover composition. In this map, land cover is divided into the four fire-prone classes used in the analysis: “Conifer”, “Hardwood”, “Grassland”, and “Shrubland”. “Urban”, “Agricultural”, and “Desert” land cover categories were not considered for analyses and left uncolored within the map. Megafire perimeters (in red) were defined as fires > 100,000 acres (n = 28) and were obtained from the CALFIRE and NIFC databases (2000-2020). The inset map (top-right corner) shows a zoomed image of the burn perimeter of the August Complex fire, California’s largest recorded wildfire to data. Though widely considered a “forest fire”, the inset shows that the August Complex megafire did not burn purely within Conifer, but instead a mix of several different land cover types. Megafires in southern California burn primarily outside of Conifer, but pose some of the biggest threats to people and infrastructure.

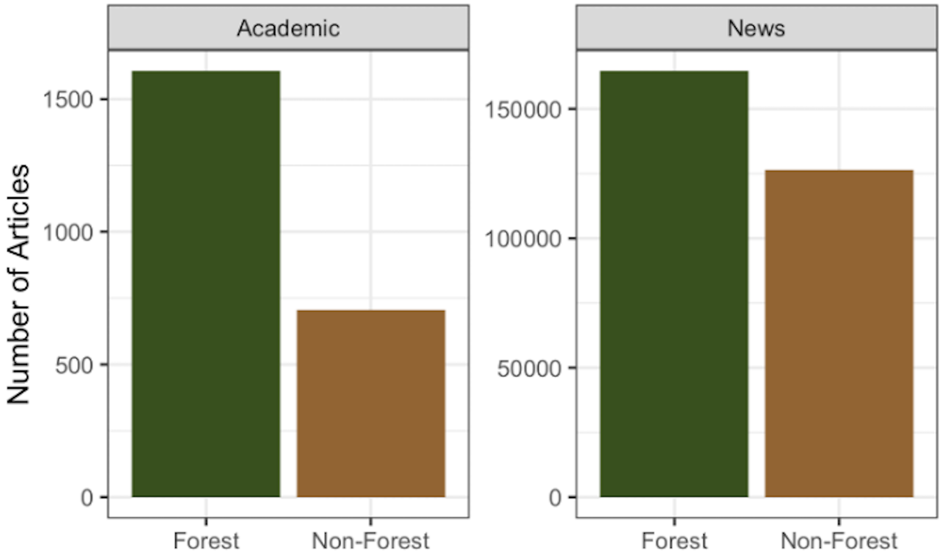


Figure S2. Comparison of articles written on forest and non-forest fires in California in academic literature (left) and news media (right) over the last twenty years (2000-2020). In the published scientific academic literature, there were 1,605 articles on fires in forest ecosystems and 705 articles on fires in non-forest ecosystems Forest fires also received more attention in the news media (164,568 articles, as compared to 126,546 articles on fires in non-forest ecosystems).

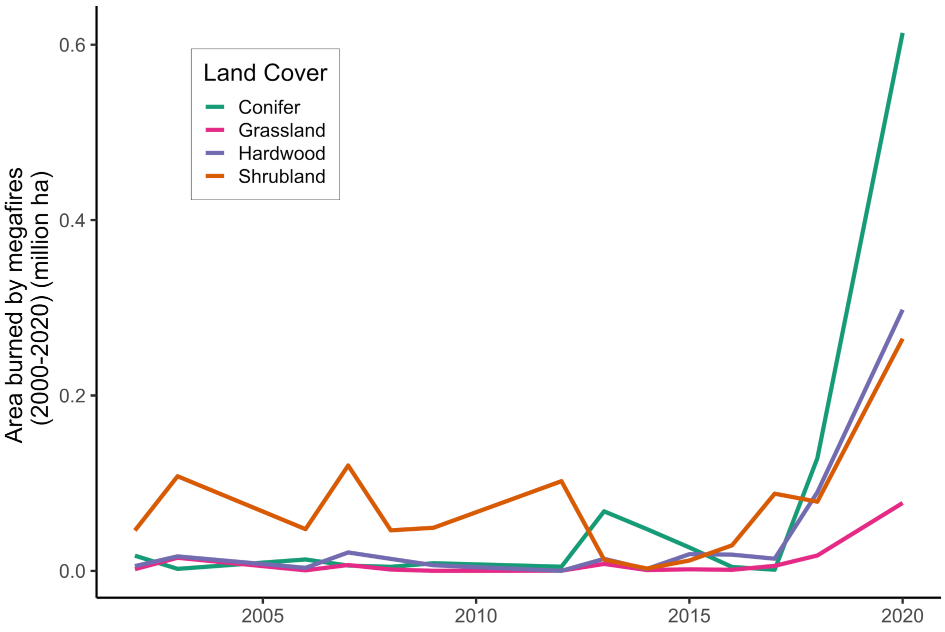


Figure S3. Yearly total area by land cover type in hectares burned over time by megafire. Prior to 2018, megafires burned predominantly in shrubland ecosystems.

Table S2. Total area burned by land cover class in California wildfires from 2000-2020. The top section of the table is divided into the six land cover categories. The "Total Area Available" column shows the total area of each land cover types within California. The "Percentage of Total Area Burned" column shows the burned areas in a given land cover class, divided by the total area burned across all land cover classes in the 20-year period. The "Percentage of Total Available Land Cover Burned" column shows the percentage each land cover class burned of the total available land cover to burn for that respective land cover. The bottom section splits the total burned area into conifer and non-conifer land cover aggregations.

TOTAL AREA BURNED BY LAND COVER CLASS (2000-2020)

LAND COVER	**Total Area Available (Hectares)**	**Area Burned (Hectares)**	**Percentage of Total Area Burned**	**Percentage of Total Available Land Cover Burned**
CONIFER	8,777,000	2,310,000	36 %	26 %
GRASSLAND	5,979,000	563,000	9 %	9 %
HARDWOOD	3,909,000	1,125,000	17 %	29 %
SHRUBLAND	6,300,000	2,484,000	38 %	39 %
CONIFER	8,777,000	2,310,000	36 %	26 %
NON-CONIFER	16,188,000	4,171,000	64 %	25 %

Table S3. - Total area burned by land cover class in California megafires from 2000-2020. The top section of the table is divided into the six land cover categories. The "Total Area Available" column shows the total area of each land cover types within California. The "Percentage of Total Area Burned" column shows the burned areas in a given land cover class, divided by the total area burned across all land cover classes in the 20 year period. The "Percentage of Total Available Land Cover Burned" column shows the percentage each land cover class burned during megafires of the total available land cover to burn for that respective land cover. The bottom section splits the total burned area into conifer and non-conifer land cover aggregations.

TOTAL AREA BURNED BY LAND COVER CLASS IN MEGAFIRES (2000-2020)

LAND COVER	**Total Area Available (Hectares)**	**Area Burned (Hectares)**	**Percentage of Total Area Burned**	**Percentage of Total Available Land Cover Burned**
CONIFER	8,777,000	947,000	36 %	11 %
GRASSLAND	5,979,000	139,000	5 %	2 %
HARDWOOD	3,909,000	522,000	20 %	13 %
SHRUBLAND	6,300,000	1,008,000	39 %	16 %
CONIFER	8,777,000	947,000	36%	11 %
NON-CONIFER	16,188,000	1,669,000	64 %	10 %

Table S4. – Area burned in areas of high species richness by land cover type and taxonomic group in California. Regions that contained the upper two quantiles (or upper 40%) of predicted native species occurrence were identified as being regions of "high species richness" for each taxonomic group. The "Percentage of Total Burned Land Cover" column shows what percent of the total burned land cover was burned in areas with high species richness.

Hectares Burned in Areas with High Species Richness (2000-2020)			
	Area Burned (Hectares)	**Percentage of Total Burned Land Cover**	**Taxa**
Conifer	480,000	21 %	Birds
Grassland	328,000	58 %	Birds
Hardwood	648,000	59 %	Birds
Shrubland	1,308,000	53 %	Birds
Conifer	142,000	6 %	Reptiles
Grassland	170,000	30 %	Reptiles
Hardwood	268,000	24 %	Reptiles
Shrubland	1,056,000	43 %	Reptiles
Conifer	2,087,000	90 %	Plants
Grassland	280,000	50 %	Plants
Hardwood	864,000	77 %	Plants
Shrubland	1,398,000	56 %	Plants
Conifer	2,050,000	89 %	Mammals
Grassland	187,000	33 %	Mammals
Hardwood	477,000	42 %	Mammals
Shrubland	1,307,000	53 %	Mammals
Conifer	1,288,000	56 %	Amphibians
Grassland	317,000	56 %	Amphibians
Hardwood	858,000	76 %	Amphibians
Shrubland	1,594,000	64 %	Amphibians

Table S5. Area burned from megafires in areas of high species richness by land cover type and taxonomic group in California. Regions that contained the upper two quantiles (or upper 40%) of predicted native species occurrence were identified as being regions of "high species richness" for each taxonomic group. The "Percentage of Total Burned Land Cover" column shows what percent of the total burned land cover was burned in areas of high species richness by megafires.

Hectares Burned by Megafires in Areas with High Species Richness (2000-2020)

	Area Burned (Hectares)	Percentage of Total Burned Land Cover	Taxa
Conifer	165,000	7 %	Birds
Grassland	83,000	15 %	Birds
Hardwood	283,000	25 %	Birds
Shrubland	513,000	21 %	Birds
Conifer	47,000	2 %	Reptiles
Grassland	45,000	8 %	Reptiles
Hardwood	141,000	13 %	Reptiles
Shrubland	416,000	17 %	Reptiles
Conifer	883,000	38 %	Plants
Grassland	103,000	18 %	Plants
Hardwood	433,000	39 %	Plants
Shrubland	637,000	26 %	Plants
Conifer	843,000	37 %	Mammals
Grassland	52,000	9 %	Mammals
Hardwood	239,000	21 %	Mammals
Shrubland	496,000	20 %	Mammals
Conifer	556,000	24 %	Amphibians
Grassland	120,000	21 %	Amphibians
Hardwood	408,000	36 %	Amphibians
Shrubland	762,000	31 %	Amphibians

Table S6. Area burned in areas containing endemic species by land cover class and taxonomic groups in California (2000-2020). The "Percentage of Total Burned Land Cover" column shows what percent of the total burned land cover was burned in areas with endemic species.

Hectares Burned in Areas with Species Endemism (2000-2020)

	Area Burned (Hectares)	Percentage of Total Burned Land Cover	Taxa
Conifer	814,000	35 %	Birds
Grassland	236,000	42 %	Birds
Hardwood	429,000	38 %	Birds
Shrubland	1,228,000	49 %	Birds
Conifer	350,000	15 %	Reptiles
Grassland	234,000	42 %	Reptiles
Hardwood	426,000	38 %	Reptiles
Shrubland	1,047,000	42 %	Reptiles
Conifer	1,382,000	60 %	Plants
Grassland	357,000	63 %	Plants
Hardwood	724,000	64 %	Plants
Shrubland	1,641,000	66 %	Plants
Conifer	360,000	16 %	Mammals
Grassland	138,000	25 %	Mammals
Hardwood	120,000	11 %	Mammals
Shrubland	402,000	16 %	Mammals
Conifer	883,000	38 %	Amphibians
Grassland	224,000	40 %	Amphibians
Hardwood	552,000	50 %	Amphibians
Shrubland	979,000	39 %	Amphibians

Table S7. Area burned by megafires in areas containing endemic species by land cover class and taxonomic groups in California (2000-2020). The "Percentage of Total Burned Land Cover" column shows what percent of the total burned land cover was burned in areas with endemic species.

Hectares Burned by Megafires in Areas with Species Endemism (2000-2020)			
	Area Burned (Hectares)	**Percentage of Total Burned Land Cover**	**Taxa**
Conifer	402,000	17 %	Birds
Grassland	57,000	10 %	Birds
Hardwood	219,000	20 %	Birds
Shrubland	579,000	23 %	Birds
Conifer	185,000	8 %	Reptiles
Grassland	57,000	10 %	Reptiles
Hardwood	209,000	19 %	Reptiles
Shrubland	426,000	17 %	Reptiles
Conifer	583,000	25 %	Plants
Grassland	85,000	15 %	Plants
Hardwood	336,000	30 %	Plants
Shrubland	668,000	27 %	Plants
Conifer	144,000	6 %	Mammals
Grassland	19,000	3 %	Mammals
Hardwood	52,000	5 %	Mammals
Shrubland	125,000	5 %	Mammals
Conifer	405,000	18 %	Amphibians
Grassland	68,000	12 %	Amphibians
Hardwood	264,000	24 %	Amphibians
Shrubland	416,000	17 %	Amphibians

Table S8. We used Chi Square Goodness of Fit Tests to observe whether the distribution of megafire across ecosystem types in areas of high species richness/endemism matched the distribution of all wildfires across ecosystem types in areas of high species richness/endemism. In each Goodness of Fit test, expected values were calculated using the percentage composition of each land cover type from the complete fire data set and compared to the observed total area burned by megafires across land cover types. All Goodness of Fit tests revealed significant differences between the composition of megafire and all wildfires across biodiversity metrics and taxonomic groups.

Chi Square Goodness of Fit Tests - Megafire and Biodiversity Metrics

	χ^2	**Degrees of Freedom**	**p-value**
Native Bird Richness	19,024.69	3	< 0.0001
Native Reptile Richness	20,167.86	3	< 0.0001
Native Plant Richness	12,754.57	3	< 0.0001
Native Mammal Richness	20,632.68	3	< 0.0001
Native Amphibian Richness	8,348.27	3	< 0.0001
Bird Endemism	30,149.36	3	< 0.0001
Reptile Endemism	32,116.51	3	< 0.0001
Plant Endemism	31,698.04	3	< 0.0001
Mammal Endemism	25,115.19	3	< 0.0001
Amphibian Endemism	12,339.68	3	< 0.0001

Table S9. Total area burned by land cover class in California wildfires from 2000-2020 within the Wildland Urban Interfaces (WUIs). The "Total Area Available" column shows the total area of overlap between each land cover type and the WUI. The "Percentage of Total Area Burned" shows the percentage each land cover in the WUI burned of the total area burned within the WUI. The "Percentage of Total Area Available" column shows the percentage each land cover burned within the WUI of the total available area in that respective land cover.

Hectares Burned within the WUI (2000-2020)

Land Cover	**Total Area Available (Hectares)**	**Area Burned (Hectares)**	**Percentage of Total Area Burned**	**Percentage Burned of Total Area Available**
Conifer	391,000	42,000	17 %	11 %
Grassland	429,000	33,000	13 %	8 %
Hardwood	533,000	71,000	28 %	13 %
Shrubland	321,000	104,000	42 %	32 %

Table S10. Total area burned by megafires across land cover types in California from 2000-2020 within the Wildland Urban Interfaces (WUIs). The "Total Area Available" column shows the total area of overlap between each land cover type and the WUI. The "Percentage of Total Area Burned" shows the percentage each land cover in the WUI burned of the total area burned within the WUI. The "Percentage of Total Area Available" column shows the percentage each land cover burned within the WUI of the total available area in that respective land cover.

Hectares Burned within the WUI (2000-2020) by Megafires

Land Cover	Total Area Available (Hectares)	Area Burned (Hectares)	Percentage of Total Area Burned	Percentage Burned of Total Area Available
Conifer	391,000	14,000	18 %	11 %
Grassland	429,000	9,000	12 %	8 %
Hardwood	533,000	25,000	32 %	13 %
Shrubland	321,000	30,000	38 %	32 %

Supplement S3 – Fire Return Interval Departure Analysis

Motivation

Long-term changes in fire frequency may have broad-scale impacts on the patterning of species richness and endemism as well as influencing the likelihood of megafire in certain habitat types. In this analysis, we examined whether departure from historic fire return intervals influences patterns of biodiversity, hypothesizing that increased departure from historic fire return intervals would result in lower levels of native species richness and endemism across taxonomic groups. The analysis did not produce conclusive results but invites the opportunity for future work to explore the potential relationship between changes in fire frequency and broad patterns of biodiversity.

Methods

To explore whether changes in fire frequency, a major component of fire regimes, affects broad patterns of species richness and endemism, we compared the Fire Return Interval Departure (FRID) dataset (USFS) to the ACE Biodiversity datasets ("Native Richness" and "Irreplaceability") using a linear regression and a logistic regression respectively (CDFW, 2019; CDFW, 2020; USDA, 2020). The FRID dataset contains polygon data across California logging the percentage difference between contemporary and historical fire return intervals. For this analysis, we took the absolute value of these percentage values within each polygon, ignoring directionality (whether fires are occurring more or less often) and instead focusing on the magnitude of change. These polygons were rasterized and the mean Percentage FRID was extracted for each ACE Biodiversity polygon cell. The most common fveg land cover type was also extracted to each ACE Biodiversity polygon cell. Land cover types were collapsed to a binary variable – "Conifer" or "Non-Conifer". Previous work has found significant differences in the change of fire return intervals between Conifer and Non-Conifer ecosystems (Safford and Van De Water 2014; Parks et al. 2015). Therefore, we create separate models for Conifer and

Non-Conifer ecosystems to account for these previously observed differences and increase interpretability.

A linear regression was run for each taxonomic group's "Native Richness" dataset using the absolute value of FRID as the explanatory variable.

Native Species Count ~ FRID

A logistic regression was run for each taxonomic group's "Irreplaceability" dataset using the absolute value of FRID as the explanatory variable. Endemic species counts from the CDFW "Irreplaceability" dataset were regrouped into two groups – "0" where no endemic species were present in a cell and "1" where 1 or more endemic species were present.

Endemic Species Presence ~ FRID

Results

FRID was a significant predictor in all of the fitted richness models. Species richness increases slightly with increased FRID within many of these models (especially in plants), which opposes our initial hypothesis. There is considerable variation in the distribution of data for each model. This along with low r-squared values across most models suggest that these models may not adequately explain the distribution of observed species data.

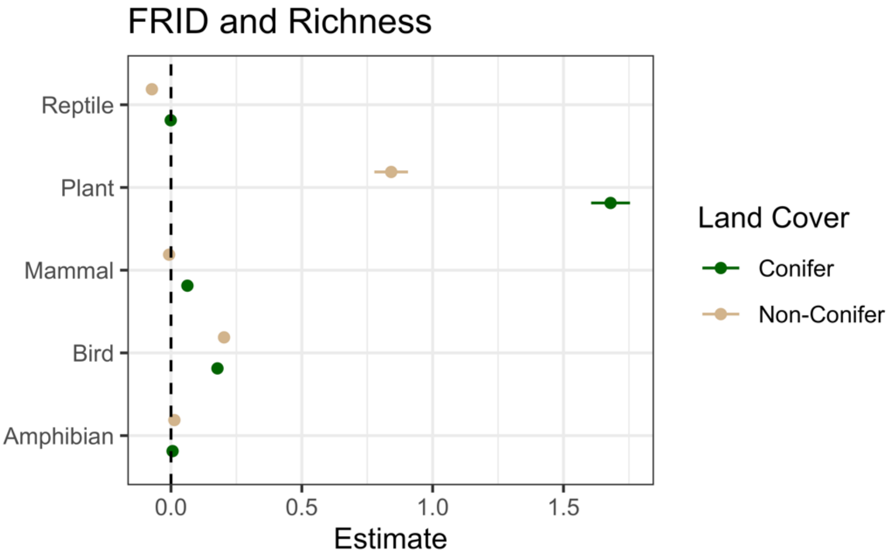


Figure S1. Plotted coefficient values and standard error bars of the "FRID and Richness" linear regression models for each taxonomic group (from top to bottom – birds, reptiles, plants, mammals, and amphibians) and across ecosystem types (Conifer and Non-Conifer).

Figure S1. Output summary for each FRID and Richness model across all five taxonomic groups and across grouped ecosystem types (Conifer and Non-Conifer). Coefficients and standard errors are displayed for each covariate in the table. Taxonomic groups from left to right – birds, reptiles, plants, mammals, and amphibians.

	(Intercept)		**FRID**		**N**	**R2**	
Bird Richness - Conifer	115.28 ***	(0.50)	0.14 ***	(0.01)	13866	0.03	
Bird Richness - Non Conifer	132.38 ***	(0.29)	0.02 **	(0.01)	12479	0.00	
Reptile Richness - Conifer	16.52 ***	(0.10)	-0.01 ***	(0.00)	13866	0.01	
Reptile Richness - Non Conifer	21.93 ***	(0.07)	-0.07 ***	(0.00)	12479	0.22	
Plant Richness - Conifer	1386.85 ***	(4.74)	1.75 ***	(0.07)	13866	0.05	
Plant Richness - Non Conifer	1241.01 ***	(2.12)	0.37 ***	(0.04)	12479	0.01	
Mammal Richness - Conifer	54.61 ***	(0.12)	0.06 ***	(0.00)	13866	0.07	
Mammal Richness - Non Conifer	51.82 ***	(0.08)	0.00 ***	(0.00)	12479	0.00	
Amphibian Richness - Conifer	6.04 ***	(0.09)	0.01 ***	(0.00)	13866	0.00	
Amphibian Richness - Non Conifer	5.89 ***	(0.03)	-0.01 ***	(0.00)	12479	0.01	***** p < 0.001; ** p < 0.01; * p < 0.05.**

FRID was a significant predictor of species endemism in each model except in the models for reptile and amphibian endemism in conifer ecosystems. The probability of endemic species being observed decreases as FRID increases across all taxonomic groups. As in the richness models, considerable variation and overdispersion within the data may suggest that these models do not adequately explain the distribution of the data.

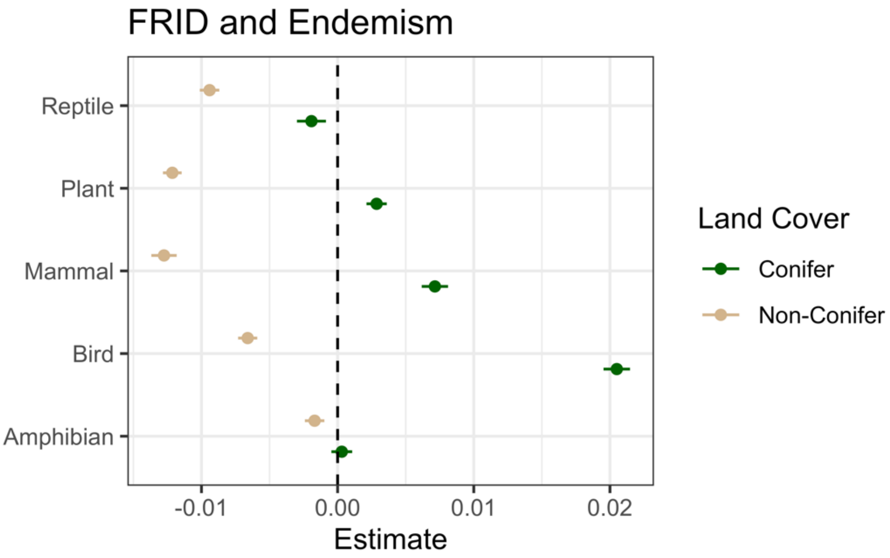


Figure S2. Plotted coefficient values and standard error bars of the "FRID and Endemism" logistic regression models for each taxonomic group (from top to bottom – birds, reptiles, plants, mammals, and amphibians) and across ecosystem types (Conifer and Non-Conifer).

Figure S2. Output summary for each FRID and Endemism model across all five taxonomic groups and across grouped ecosystem types (Conifer and Non-Conifer). Coefficients and standard errors are displayed for each covariate in the table. Taxonomic groups from left to right – birds, reptiles, plants, mammals, and amphibians.

Amphibian Endemism - Non	-0.75 ***	(0.04)	-0.00 *	(0.00)	12479	15348.44	15363.30	0.00	***** p < 0.001; ** p < 0.01; * p < 0.05.**
Amphibian Endemism - Conifer	-0.53 ***	(0.05)	0.00	(0.00)	13866	18357.70	18372.78	0.00	
Mammal Endemism - Non	-1.18 ***	(0.04)	-0.01 ***	(0.00)	12479	10445.56	10460.42	0.03	
Mammal Endemism - Conifer	-1.76 ***	(0.07)	0.01 ***	(0.00)	13866	14539.39	14554.46	0.01	
Plant Endemism - Non	0.92 ***	(0.04)	-0.01 ***	(0.00)	12479	16589.73	16604.60	0.03	
Plant Endemism - Conifer	0.11 *	(0.05)	0.00 ***	(0.00)	13866	18898.98	18914.05	0.00	
Reptile Endemism - Non	-0.40 ***	(0.04)	-0.01 ***	(0.00)	12479	15244.43	15259.29	0.02	
Reptile Endemism - Conifer	-1.75 ***	(0.08)	0.00	(0.00)	13866	10831.14	10846.21	0.00	
Bird Endemism - Non	-0.42 ***	(0.04)	-0.01 ***	(0.00)	12479	15710.13	15724.99	0.01	
Bird Endemism - Conifer	-2.13 ***	(0.07)	0.02 ***	(0.00)	13866	17090.63	17105.70	0.05	
	(Intercept)		**FRID**		**N**	**AIC**	**BIC**	**Pseudo R2**	

Discussion

This analysis takes an important first step in examining how long-term changes in fire frequency and fire regimes may influence broad patterns of species endemism and richness. Our results suggest that changes in fire return intervals in different ecosystem types may have differential impacts on biodiversity. This appears most significantly in the endemism models where greater changes in FRID appears to result in a decrease in probability of endemic species being observed. Though our models suggest that changes in fire return intervals may play some role in influencing patterns of richness and endemism, more comprehensive models that consider several additional covariates are necessary to properly explain the large variation within the data. Additionally, both the independent and dependent variables within these models are spatially autocorrelated to a great extent, potentially skewing the estimates we are able to make from these models. Finally, data availability in the FRID dataset is biased towards conifer and hardwood ecosystems where historical fire records are more readily available. Future work should take all of these into consideration when designing more comprehensive models.

Chapter 2

Mammalian resistance to megafire in in western U.S. woodland savannas

This chapter has been previously published (Calhoun et al., 2023) and is included here with permission from the dissertation chair.

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Abstract

Increasingly frequent megafires are dramatically altering landscapes and critical habitats around the world. Across the western U.S., megafires have become an almost annual occurrence, but the implication of these fires for the conservation of native wildlife remains relatively unknown. Woodland savannas are among the world's most biodiverse ecosystems and provide important food and structural resources to a variety of wildlife, but they are threatened by megafires. Despite this, the great majority of fire impact studies have only been conducted in coniferous forests. Understanding the resistance and resilience of wildlife assemblages following these extreme perturbations can help inform future management interventions that limit biodiversity loss due to megafire. We assessed the resistance of a woodland savanna mammal community to the short-term impacts of megafire by using camera trap data collected before, during, and after the fire. Specifically, we utilized a 5-year camera trap data set (2016-2020) from the Hopland Research and Extension Center to examine the impacts of the 2018 Mendocino Complex Fire, California's largest recorded wildfire at the time, on the distributions of 8 observed mammal species. We used a multi-species occupancy model to quantify the effects of megafire on species' space use, assess the impact on species size and diet groups, and to create robust estimates of fire's impacts on species diversity across space and time. Megafire had a negative effect on the detection of certain mammal species, but overall, most species showed high resistance to the disturbance and returned to detection and site use levels comparable to unburned sites by the end of the study period. Following megafire, species richness was higher in burned areas that retained higher canopy cover relative to unburned and burned sites with low canopy cover. Fire management that prevents large scale canopy loss is critical to providing refugia for vulnerable species immediately following fire in oak woodlands, and likely other mixed-forest landscapes.

Introduction

In an era of unprecedented global change, 21st century megafires present an intensifying threat to critical habitat and wildlife species in fire-prone ecosystems around the world (Nimmo et al. 2021). Megafires, defined as wildfires that are larger than 10,000 hectares (Linley et al. 2022), drive dramatic and lasting changes to entire ecosystems (Stephens et al. 2014). These far-reaching environmental shocks can quickly homogenize landscapes and present short- and long-term challenges for wild animal species (Adams 2013; Zachary L. Steel et al. 2021). As megafires continue to increase in frequency and scale, the gap in our understanding of how wildlife species respond and recover to megafire events becomes more glaring (Jolly et al. 2022). Such information is essential to the conservation of fire-prone landscapes and the formation of management strategies that bolster resilience to severe wildfire. Like other regions of the world (Bowman et al. 2020), California, and the western U.S. generally, have experienced its largest and most severe fires in the last 20 years (Li and Banerjee 2021). With a wide range of ecosystems (Burge et al. 2016; Harrison 2013), California presents an important opportunity to understand the impacts of megafire on diverse ecological communities and to observe how patterns of species vulnerability or resilience may interact with these perturbations.

To address the challenges presented by megafire and other disturbances, contemporary conservation often emphasizes building resistance and resilience to better protect ecosystems from future change (C. Miller et al. 2021; Heller and Zavaleta 2009). Resilience, the long-term ability of a community or population to recover to baseline conditions following disturbance (Holling 1973), and resistance, the degree to which a population or community, changes directly following a disturbance (Pimm 1984), are key elements that interact to maintain ecological integrity following disturbances. Immediate resistance to disturbance is often conceptualized as an important component of longer-term resilience (Walker et al. 2004). Though resistance and resilience are useful theoretical concepts, they are often difficult to evaluate due to the challenges of characterizing and quantifying them (Standish et al. 2014; Ingrisch and Bahn 2018). Application is made more difficult by the rarity and dynamic nature of baseline ecological information to compare against recent change (Soga and Gaston 2018; Cammen, Rasher, and Steneck 2019). A deeper understanding of context-specific resilience and resistance to disturbance is needed at multiple ecological scales (species, community, and ecosystem) to predict, prevent, and combat the effects of global change.

At the scale of species, resilience and resistance to wildfire will be governed, in large part, by species' traits, e.g., home range size, diet, trophic level (Pocknee et al. 2023; Jager et al. 2021). For example, body mass is a key trait that determines how species interact with their environment by dictating how they interact with other species (e.g., diet and competition) and how they navigate space. Across Mammalia, species with larger home range sizes and body masses are able to move more readily across space (Reiss 1988). Therefore, home range size and body mass may directly impact the ability of populations to cope with expansive disturbances like megafire. Species with larger home ranges or without specific habitat requirements (e.g., generalists and opportunists) may be better equipped to adapt to the sudden shifts caused by megafire (Nimmo et al. 2019). Additionally, species whose diets depend directly on plant material (herbivores) may be disproportionately impacted by megafires that deplete these resources, at least in the immediate aftermath before vegetation regrows and could encourage improved foraging (Cherry et al. 2018). Conversely, predators, such as carnivores, may be able to take advantage of exposed areas following wildfire to catch prey more effectively (Geary et al. 2020). Cursorial predators (like coyote) may be more successful at hunting postfire with less cover obstructing their vision of prey (Cherry, Warren, and Conner 2017), while ambush predators (like bobcat and mountain lion) may have less cover to utilize for ambushing potential prey (Abernathy et al. 2022). It is therefore critical to assess community-wide resilience to major disturbances such as megafire, as the responses of individual species may have cascading consequences across multiple species by reshaping species interactions, such as predation and herbivory.

Characteristics of a wildfire itself, such as severity, heterogeneity, burn patch size, and time since burning, may also interact with species traits to determine species-specific responses to wildfire. Fire severity, specifically the measure of change in above and below ground biomass as a result of fire, is thought to be an important characteristic of fire regimes that directly impacts wildlife (J. E. Keeley 2009). By altering available food resources, megafire may change the distribution of wildlife species in recently burned landscapes (Cherry et al. 2018; Allred et al. 2011). Changes to the structure of the physical landscape may also alter how species are able to navigate habitat (Kreling et al. 2021). These changes, in turn, may reshape species interactions, such as predation (Jennings et al. 2016). Both mechanisms – changes to resource availability and physical habitat – may influence the distribution of wildlife species following extreme fire events, but the context in which they do may be species and fire dependent (Geary et al. 2020). Additionally, the availability of resources on recently burned landscapes may be linked to the amount of time that has passed following fires to allow vegetation to regrow (Green et al. 2015).

Taking both species and wildfire characteristics into account is vital towards shoring up the resistance and resilience of fire-prone ecosystems across the Western US. California's fire-prone oak woodland rangelands provide an excellent model ecosystem to explore how these characteristics interact across a very biodiverse and sociocultural significant landscape. Oak woodlands are one California's most biodiverse ecosystems (Hilty and Merenlender 2003), but changes in California's historical fire regimes are creating new challenges for the resilience of oak woodland ecosystems and the wildlife species that reside within them. Historically, indigenous groups frequently burned oak woodlands with low severity, ground fires to create resources for food and other products (Anderson 2006). Today, fire suppression and climate change have increased the likelihood of severe fires burning within oak woodlands (Syphard and Keeley 2020). High severity fire in woodlands may burn the crown tops of trees, greatly transforming canopy cover in the burned areas. Mature oak trees and the acorns they produce are the primary food resource for several mammal species during the driest months of the year (William J. McShea 2000; Koenig et al. 2013), and their reduction due to high severity fire may impact population dynamics of herbivorous woodland species (Mcshea et al. 2007), as well as species at higher trophic levels (i.e. their predators) (Jorge et al. 2020).

In this study, we explored the influence of fire occurrence and canopy cover on the distribution of oak woodland mammal species over time by taking advantage of an opportunistic natural experiment. We assessed the impacts of the Mendocino Complex Fire, one of the largest fires in recorded California history, on the occupancy of 8 medium- and large-bodied mammal species at the University of California Hopland Research and Extension Center (hereafter HREC) in northern California. We apply the conceptual framings of resilience theory to assess ecological resistance at the species, species group (e.g. body-size and diet-groups), and community scales and theorize how these initial responses may translate to longer-term resilience to megafire. By using camera trap data collected before, during, and after the fire, along with an occupancy modeling framework (MacKenzie et al. 2002), we had the opportunity to assess how species distributions and patterns of diversity changed immediately following wildfire ("resistance"). As established in previous work (Moss et al. 2021), we deemed species "resistant" to fire if our occupancy model estimated no negative effect of fire effects on species distributions.

In terms of species-level responses, we predicted that the greatest decrease in species' distributions would occur directly following megafire due to the immediate loss of food and structural resources. Thus, by our own definition, most species would have low resistance to the immediate effects of megafire. We anticipated that species would slowly recover across the lag years following fire as vegetation recovered until eventually returning to pre-fire conditions. Due to resistance to disturbance being an important component of resilience, we predicted that species that were deemed "resistant" to megafire would likely be "resilient" to megafire following the study as well. In assessing group-level responses to megafire in this system, we predicted that larger species and carnivores would be more likely to be resistant to megafire due to their increased vagility and enhanced ability to locate prey in cover reduced habitats. We predicted that overall species richness would decrease in recently burned areas that had limited habitat resources and slowly return to pre-burned conditions over time in areas that maintained high canopy cover. Detailing the capacity of these species to recover is vital to inform better conservation decisions for woodland mammal communities by 1) identifying vulnerable species that may need to be prioritized in post-fire recovery management, and 2) identifying landscape features that may enhance the resilience and resistance of mammal communities to megafire.

Methods

Study Area and Fire History

We conducted our study at the 21.54 km^2 U.C. Hopland Research and Extension Center (HREC) in Mendocino County, northern California (39°00′ N, 123°04' W). The HREC ecosystem is composed of a diverse range of habitat types including grassland, oak woodland, and chaparral shrubland. HREC is situated at an intersection of wildlands and ranchlands; it provides habitat for a diverse group of wildlife and serves as pastoral land for people and livestock. HREC consists of a combination of rolling valleys and peaks throughout with its lowest elevation being 164 meters and its highest at 934 meters. The region is characterized by a Mediterranean climate, with mild seasons and rains in the winter.

On July 27, 2018, the 2018 River Fire, part of the much larger 2018 Mendocino Complex Fire, burned over 13.76 km^2 of the Hopland Research and Extension Center (Figure 1). At the time, the Mendocino Complex Fire was the largest fire in California's recorded history, burning 1,858 km^2. This fire was the first wildfire that burned a significant portion of the center in over 60 years. The scale and severity of this fire contrasted the historical fire regime in this region, which is characterized by frequent, cooler fires in woodlands (5-10 years) and infrequent, more severe burns in shrubland habitats (30-80+ years) (Syphard and Keeley 2020). To date, there have been minimal on-site post-fire management interventions, providing an opportunity to identify the baseline in how this ecosystem recovers.

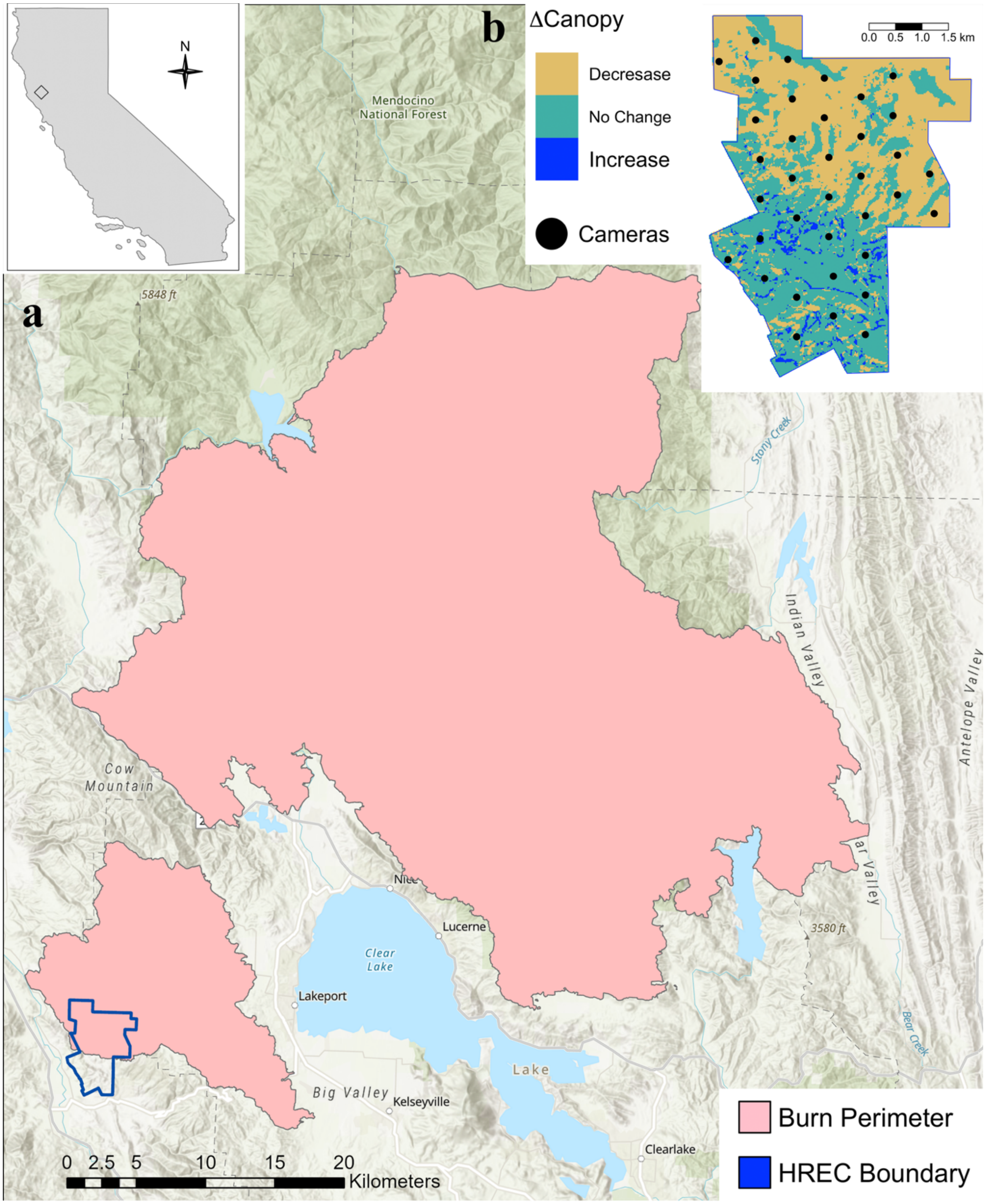

Figure 1. Maps of the 2018 Mendocino Complex Fire and the study site, the University of California Hopland Research and Extension Center (HREC) (39°00′ N, 123°04’ W). Map “a” displays the total burn perimeter of the Mendocino Complex Fire, composed of the northern Ranch fire and the southern River Fire. This fire burned into HREC on July 27, 2018. The River Fire burned half of the property. Map “b” displays the change in canopy cover caused by the fire in addition to the deployed camera grid. Decreases in canopy cover are denoted in brown, no change in canopy cover is denoted in green and increases in canopy cover are denoted in blue.

Camera Survey and Study Species

To survey mammal species diversity, we created a sampling grid across HREC composed of hexagonal grid cells measuring 750 meters across. We placed a motion-sensor camera trap at the most suitable location (e.g., pointed to look down and across game trails or other microsite attractants such as roads and water troughs) within 50 m of each grid cell's centroid to maximize detection probability of species. Seasonal grass growth in this region often results in tall grass growing in front of camera traps, which obscures the detection of wildlife. We therefore deployed all cameras 1 meter above the ground and angled them slightly downward to avoid misfires. In total, we deployed a grid of 36 motion-sensor camera traps (Reconyx Hyperfire HC600) beginning March 2016. Cameras were visited approximately every three months to download the recorded pictures, check and change camera batteries, and to trim grass in front of cameras to maximize detection of species. For the purposes of this study, we have extracted photos taken from March 2016 to December 2020. We programmed cameras to take 3 photos per trigger, with a 0 second delay period between triggers. Of the 36 total cameras, 25 were within the fire perimeter of the 2018 Mendocino Complex Fire. Thirteen of these cameras were not operational following the fire and were replaced when conditions were safe to do so in August 2018. For these reasons, and due to a natural increase in biodiversity detected in the fall months due to concurrent acorn masting, we restrict our sampling window for analyses to October 1st – November 30th for each year.

The species in all collected images were classified by two independent observers who were members of the Brashares Lab at the University of California, Berkeley. When two observers disagreed on species classification, they either met separately to discuss and decide on a classification of the image, or a more senior, third member of the group (often a graduate student) would decide on the classification. We created species record tables for each year from these cataloged images using the 'camtrapR' package in R (v.2.2.0) (Niedballa et al. 2016; R Core Team 2021). To create independent detections for analyses, we aggregated images of the same species and site that were recorded within 15 minutes of each other.

For this study, we modeled occupancy for all mammal species detected at 10 or more unique camera stations across the entire study period to ensure each species included in analyses had enough observations to be modeled appropriately. We also excluded black bear (*Ursus americanus*) which have home ranges much larger than the appropriate scope of our specific study. As a result, we included eight species in our final multi-species model: bobcat (*Lynx rufus*), coyote (*Canis latrans*), black-tailed deer (*Odocoileus hemionus columbianus*), gray fox (*Urocyon cinereoargenteus*), western gray squirrel (*Sciurus griseus*), black-tailed jackrabbit (*Lepus californicus*), raccoon *(Procyon lotor*), and striped skunk (*Mephitis mephitis*).

Covariate Development

We use an occupancy modeling framework to describe species distributions over time which predicts the probability of a species occurring at a given site ("occupancy") while controlling for the detectability of a species at that same site ("detection probability") (MacKenzie et al. 2002). Both occupancy and detection probability can be associated with environmental covariates, and we predicted fire effects would influence both across the 8 modeled species.

We predicted that canopy cover, time since burn, and elevation would be associated with the spatial distribution, or occupancy, of species throughout our study. Canopy cover is an important predictor of mammal habitat use (Allen et al. 2015; Bose et al. 2018) and canopy cover loss following fire serves as an important proxy for fire severity in the burned areas of our study site. We originally considered using quantified fire severity (the Normalized Burn-Difference Ratio) to assess the effect of fire on species occupancy and species richness at each site, but we found that these initial models fit the data poorly, likely due to our limited sample size of post-fire species occurrence data at burned sites. Finally, we included "time since burn" to account for certain species preferentially occupying or avoiding burned areas depending on how much time had passed since the area burned (González et al. 2022). To assess changes in local-scale site usage across species of varying body sizes, we extracted the mean value of all continuous covariates at a consistent 100-meter buffer around each camera station.

We obtained elevation for each site using the ASTER Global Digital Elevation Model (NASA and METI 2011). Average values were extracted from a 100m buffer around each camera site. We estimated canopy cover using 20-meter resolution imagery from Sentinel Hub (Sentinel Hub 2022) to create canopy rasters via object-based image analysis and supervised classification in ArcGIS Pro (Esri 2011) for each year (2016-2020). These rasters were visually verified using fine scale, 3-m resolution imagery via Planet Labs (Tilahun 2015; Planet Team 2017; Sunde et al. 2020). A full description of methods used to create and verify canopy rasters can be found within Supplement S1 (Supplement S1: Table S1; Supplement S1: Table S2). Canopy cover values were extracted from a 100m buffer around each camera site for each year to calculate percent canopy cover within the buffered radius.

We created a "time since burn" categorical variable that varied by site and year to describe whether a site was unburned, recently burned, or burned in the past. We considered 5 different categorical parameterizations (Table 1) and used a model selection approach to choose its final parameterization (see Occupancy Modeling Framework section).

We predicted that time since burning, the presence of microsite attractants (roads and water troughs), and changes in camera viewshed caused by fire would impact the detectability and intensity of use of species across sites and observation periods. Wildfire may directly affect the detection process by clearing vegetation that may otherwise obscure wildlife in the viewshed of the camera trap. To take this change into account, we created a viewshed variable that varied by camera station and year. We tested and recorded maximum detection distance of each camera station upon initial deployment, which we then used as an estimate of viewshed for each site pre-fire. To estimate how viewshed changed post-fire, two independent observers visually estimated viewshed using misfire photographs collected during the study period at each camera station and for each post-fire year. Pre-fire misfire photographs with known maximum detection distances were used to calibrate estimates. In cases where the two independent observers disagreed on estimated viewshed, the two observers met separately to discuss and eventually come to a mutual agreement on the estimate. We predicted that cameras with greater viewshed, including cameras immediately following fire, would have a greater probability of detecting species. We also originally considered camera height as a covariate that may influence probability of detection but found in our initial modeling that camera height was not a significant predictor of detection, thus, we chose not to include this covariate in our final model.

Simultaneously, by dramatically changing the structure of the physical landscape, wildfire may also alter established game trails and movement behaviors of wildlife species, thus impacting their continued detectability at camera stations, but not necessarily their occupancy of the surrounding area. We represent these landscape-wide changes caused by fire using the time since burn categories to assess changes in intensity of use of burned sites by species. We predicted that species would be less likely to be detected by cameras immediately following fire due to these broader changes in movement, but that as vegetation recovered over time, original game trails and paths may be reutilized.

Lastly, roads and artificial water catchments have been shown to strongly attract usage by various species (J. E. Hill, DeVault, and Belant 2021; Rich et al. 2019). These objects influence the way animals navigate across space as well as how often they visit certain areas within their given home range. To account for these features in our study, we created a site-specific "microsite attractant" binary categorical variable that indicated whether a camera was pointed towards the attractants present in our study, e.g. roads (n = 1 camera station) or water troughs (n = 2 camera stations).

All continuous covariates were standardized to have a mean of 0 and standard deviation of 1. We visually inspected for collinearity between each continuous covariate to ensure multi-collinearity would not confound analyses (Supplement S2: Figure S1, Supplement S2: Table S1).

Occupancy Modeling Framework

We fit a community occupancy model (Devarajan, Morelli, and Tenan 2020; MacKenzie et al. 2002; Royle and Dorazio 2008) to investigate the effects of megafire on species-specific distributions and patterns of species richness, while accounting for imperfect detection. Occupancy models consist of two linked submodels describing two processes: occupancy probability (Ψ), the probability that a given species occurs at a site, and detection probability (p), the probability that a given species is detected at a site, given that that site is occupied by the species. Several observed species in this study are wide-ranging, with home ranges that may contain more than one camera trap station and potentially violate the assumption of spatial closure between sites (Neilson et al. 2018). To avoid the possibility of modeling the distribution of a single individual animal, we removed species whose home ranges were likely larger than HREC (i.e. black bear). Coyote and bobcat have homeranges that encompass more than one camera station, but their density across the region makes it unlikely multiple stations are recording the same individual within each year's study window. We, therefore, interpret site-level occupancy probability, Ψ, as "site use" as described in Kays et al., 2020 (Kays et al. 2020). We make this distinction to indicate that Ψ does not represent true occupancy for all species in our modeling framework. We defined a binary latent true space use variable, $z_{i,j}$, where $z_{i,j} = 1$ indicates that at least one individual of species (i) used the area covered by a camera station (j) in that year and 0 indicates that no individual of species (i) used a camera station (j) in that year. We assumed site use ($z_{i,j}$) was drawn from a Bernoulli distribution with probability ($\Psi_{i,j}$):

$$z_{i,j} \sim \text{Bernoulli}(\psi_{i,j})$$

We treated each sampled week at a camera station as a sampling occasion (k), with each station containing 7-8 occasions. Previous work has shown that detection probability, p, can be correlated with local species abundances (Royle 2004; Royle and Nichols 2003) and/or changes in behavior to avoid perceived risk (Suraci et al. 2021). We therefore represent detection as a combination of species-specific detectability and species' intensity of use of occupied sites (hereafter referred to as intensity of use) to observe how wildfire may influence intensity of use at burned sites. We estimated the probability of observing a species, $y_{i,j,k}$, as being conditional on that species' detection probability at each site, $p_{i,j}$, and the latent site use state of that species, ($z_{i,j}$):

$$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j} * z_{i,j})$$

We incorporated site-specific environmental covariates that were predicted to influence species-specific site use ($\psi_{i,j}$) and site- and species-specific detection probability ($p_{i,j}$) via the following equations:

$$\text{logit}(\psi_{i,j}) = \alpha 0_i + \alpha 1_i * \text{Elevation}_\text{j} + \alpha 2_i * \text{Canopy}_j + \alpha 3_i * \text{TimeSinceBurn}_j + \alpha 4_i * \text{Canopy}_j * \text{TimeSinceBurn}_j + \text{Site Random Effect}_j$$

$$\text{logit}(p_{i,j}) = \beta 0_i + \beta 1_i * \text{Attractant}_j + \beta 2_j * \text{Viewshed}_j +$$

$$\beta 3_i * \text{TimeSinceBurn}_j + \text{Site Random Effect}_j$$

In addition to site-specific covariates influencing site use (elevation and canopy cover) and site-specific covariates influencing detection (presence of attractant and viewshed) we included the fixed effect of "time since burn" in both "site use" and "detection" sub-models. In the occupancy sub-model, we use an interaction term between canopy cover and "time since burn" ($\text{Canopy}_j * \text{BurnCategory}_j$) as a proxy for fire severity. We predicted that most species would increase their use of burned sites with high canopy cover which represent a less comprehensive burn event at that site. We ran five different MSOMs for each of the burn category parameterizations (Table 1).

We treated each camera in each year as a unit of closure, assuming a shared underlying site use and intensity of use state. To account for pseudo-replication we included species-specific site random effects within the site use and detection submodels to account for non-independence between surveys at sites. We chose to use this method instead of fitting a dynamic occupancy model due to data limitations and because our primary question focused on understanding the effects of megafire on species site use (ψ) and less so on colonization and extinction between sites. We considered including a random effect of "year" to account for annual differences between years, such as acorn masting and drought, but ultimately decided against including this as it could confound the temporal variation already represented by the "time since burn" covariate.

$$\text{Site Random Effect}_{i,j} \sim \text{Normal}(0, \sigma)$$

We modeled the effect of each variable on the occupancy and detection of each observed species as a random effect from a normally distributed community-level hyperparameter with a shared hyperparameter mean μ_α and standard deviation σ_α (Zipkin et al. 2010):

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha)$$

This approach enables robust inference on community-level variables (Iknayan et al. 2014). We use these community-level hyperparameter estimates to assess the relationship between modeled covariates and species richness across sites. To understand how richness predicted by our model varied with burn condition and canopy cover, we used posterior predictive sampling. We provided hypothetical site data representing a site at each of four unburned levels crossed with a gradient of canopy cover, providing all mean values for all other occupancy covariates. For visualization purposes, we also computed derived occupancy probabilities for each species at these hypothetical sites, then calculated predicted richness as the sum of occupancy probabilities across species, thereby obtaining Bayesian credible intervals for richness (Zipkin et al. 2010). We chose not to employ data augmentation in the estimation of richness due to the data limitations created by our limited number of sites, and due to the fact that average site use probability (ψ) across species was estimated to be low, which may lead to erroneous estimates of augmented species richness (Tingley, Nadeau, and Sandor 2020; Guillera-Arroita, Kéry, and Lahoz-Monfort 2019).

We fit two additional MSOMs with identical model parameterizations as the community MSOM, this time assigning hyperparameters to groups of species as defined by traits (i.e. body size and diet), rather than the entire community, to assess how species traits may dictate how certain groups respond to megafire. Species-level coefficients for each model (body size model and diet model) were drawn from group-level (*g)* hyperparameters from a group-mean of μ_g and standard deviation of σ_g following the community modeling construction given above.

First, to explore the influence of body size on species responses to fire, we grouped species into 3 categorical body mass groups from which each had its own group-level hyperparameter: “Small” (< 5kg), Medium (5-15 kg), and Large (>15kg) (Wilman et al. 2014) (Wilman et al, 2014). Second, to explore the influence of diet, we grouped species into 3 broad diet-group categories: “Herbivores” (diet does not contain animal material), “Omnivores” (diet contains < 60% animal material) and “Carnivores” (> 60% of diet contains animal material) (Wilman et al, 2014). Species groups classifications can be found in Supplement 1 (Supplement 2 – Table S1.2).

Across all models, we used weakly informative priors. We set priors for the means and standard deviations ("hyperparameters") of the community's coefficients for each covariate. Hyperparameter mean coefficients for each covariate were given normal priors with mean 0 and standard deviation 2.5, and all random effect and hyperparameter standard deviation priors were half-Cauchy with scale parameter 2.5 (Northrup and Gerber 2018). To conceptualize our results in terms of species resistance to megafire, we deemed a species or species-group as being resistant to megafire if we estimated that fire effects (“time since burn” and its interaction terms) had no statistically significant negative effects on either site usage or intensity of use. We deemed species as being moderately resistant if site use and/or intensity of use decreased during the first year of the fire (i.e. time since burn = “Recently Burned”), but “recovered” during the “BurnLag” period.

Model Selection and Model Fit

To select a most parsimonious model parameterization for the “time since burn” covariate, we fit the community multi species occupancy model using each of the burn category parameterizations and compared their Watanabe-Akaike information criterion (WAIC) values (Andrew Gelman, Hwang, and Vehtari 2014), using the WAIC function from the nimble package in R (v.0.11.1) (de Valpine et al. 2017). We considered five competing parameterizations of the time since burn variable for modeling: (1) no effect of fire, and therefore no parameters; (2) a single effect of "burn" associated with the burned sites following the fire; (3) two postfire levels: "recently burned" and "lag burn", associated with burned sites immediately following the fire and in subsequent years, respectively; (4) three burned levels: "recently burned", "burn lag 1" associated with the burned cameras the first year following fire, and "burn lag 2" associated with burned sites the second year following fire; and (5) the three aforementioned burn levels and an additional "Unburned Lag" category to describe the unburned cameras in the years following the fire (Table 1). These five parameterizations represented competing hypotheses about the effect of fire on site use during and after the fire. In all parameterizations, we assigned a reference level of "unburned" to all pre-burn sites as well as unburned sites following the fire (except in parameterization #5 where unburned sites following the fire received their own category). Example images of a single burned site across the entire study can be found in Supplement S3: Figure S2.

Table 1. Schematic of five parameterizations of the "time since burn" categorical effect, ordered by increasing complexity. After the fire in the summer of 2018, we group sites affected by the fire into 1 of 4 categories: (1) "Burned" for burned sites during the year of the fire, (2) "Burn Lag" for burned sites during any of the years following fire, (3) "Burn Lag 1" for burn sites 1-year post-fire, and (4) "Burn Lag 2" for burn sites 2 years post-fire. In parameterization #5, "Unburned Lag" represents unburned sites post-fire. We also consider a null parameterization, parameterization #1 (no fire effects). "Unburned" sites were used as the reference category in each parameterization. We selected between these five parameterizations with WAIC. ΔWAIC shows the difference in WAIC values between each parameterization and the selected model. * denotes selected parameterization based on WAIC.

Parameterization	***Pre-fire sites (2016-2017)***	***Burned sites (2018)***	***Burned sites (2019)***	***Burned sites (2020)***	***Unburned sites Post-fire (2018-2020)***	***WAIC Score***	***ΔWAIC***
(1)	None	None	None	None	None	6401.49	+46.43
(2)	Unburned	Burned	Burned	Burned	Unburned	6357.05	+1.99
(3)*	Unburned	Recently Burned	Burn Lag	Burn Lag	Unburned	6355.06	0
(4)	Unburned	Recently Burned	Burn Lag 1	Burn Lag 2	Unburned	6362.23	+7.17
(5)	Unburned	Recently Burned	Burn Lag 1	Burn Lag 2	Unburned Lag	6368.50	+6.27

We implemented all MSOMs and estimated them with Markov chain Monte Carlo (MCMC) using the R packages NIMBLE and nimbleEcology (v.0.4.0) (de Valpine et al. 2017; Goldstein et al. 2021). We ran all three multi-species occupancy models for 30,000 iterations, with a 2,000 iteration burn in across 5 chains and used NIMBLE custom samplers to increase the efficiency of MCMC mixing (Andrew Gelman, Hwang, and Vehtari 2014). All data and model code used to perform analyses are available within this project's Dryad repository (https://doi.org/10.6078/D1W70R).

We assessed model fit for the community MSOM using posterior predictive checks. We simulated a new dataset using the parameters in each MCMC sampling iteration. We calculated the deviance of each of these datasets, yielding a posterior distribution of deviances produced from data simulated under the true model. We compared observed model deviances to this posterior to check for evidence that the data do not correspond to the fit model (Andrew Gelman, Meng, and Stern 1996; MacKenzie et al. 2017). We assessed a covariate as being a "significant" predictor of occupancy or intensity of use if the 90% credible interval for that variable did not overlap zero. We use this threshold to describe significance under Bayesian inference in the following cases.

Results

Camera Trap Survey Results

We collected > 500,000 photographs over the windows of interest (October-November) across the five years of the study period (2016-2020). We observed 12,270 independent detections across 13 mammal species over a total of 10,427 trap nights. Black-tailed deer were the most detected species (n = 9,479), while brush rabbits (*Sylvilagus bachmani*) were photographed least often (n = 1) (Supplement S2: Table S3). Species detected but ultimately not included in analyses due to too few independent detections included: California ground squirrel (*Otospermophilus beecheyi*), brush rabbit, wild boar (*Sus scrofa*), and mountain lion (*Puma concolor*). Example photographs of each detected species can be found in Supplement S3 (Supplement S3: Figure S1). Summarized detection rates of modeled species can be found in Figure 2.

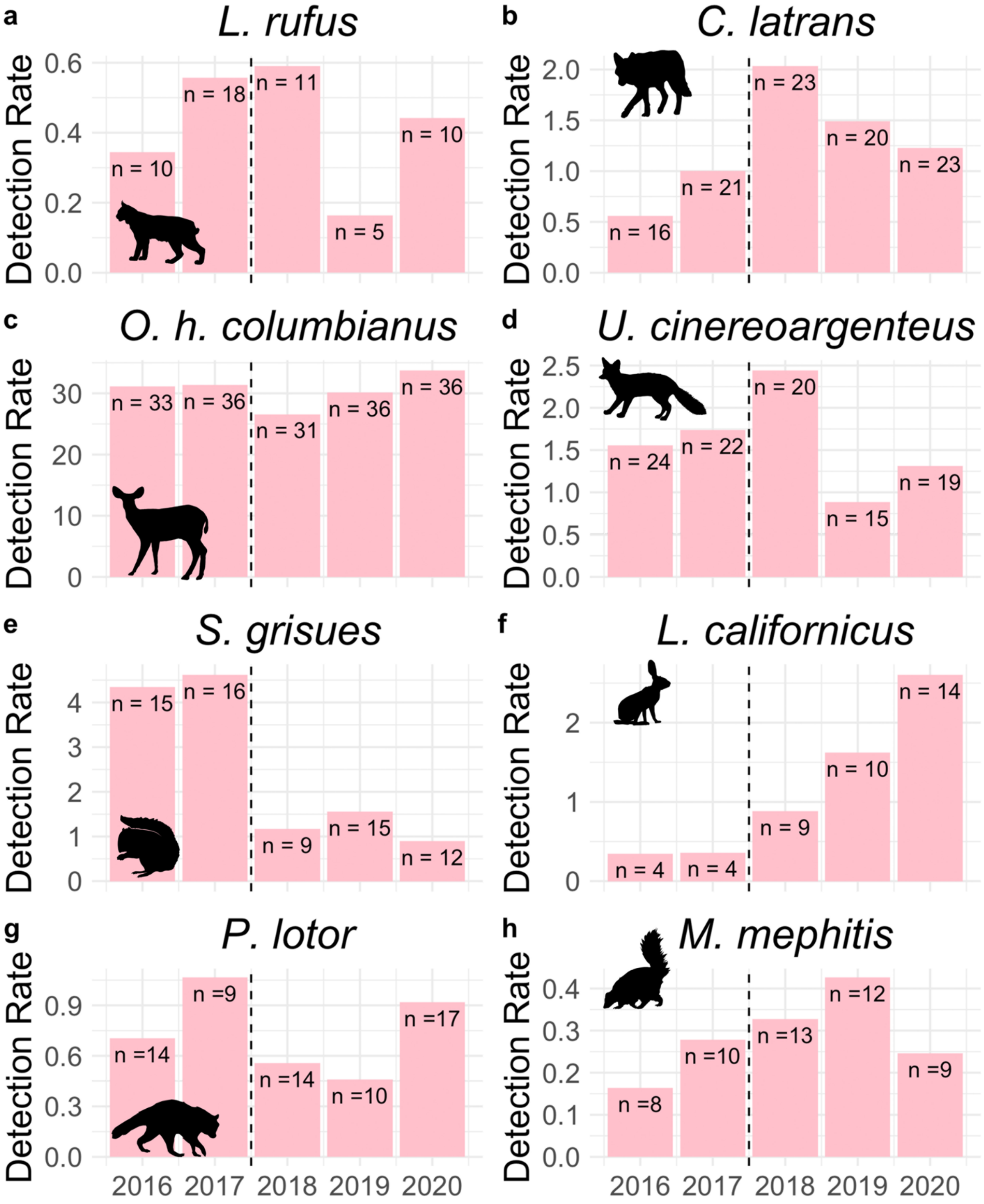

Figure 2. Detection rate of modeled mammal species sampled at camera stations during the sampling period (Oct-Nov) each year at the Hopland Research and Extension Center, CA, USA. The y-axis shows the detection rate (number of detections divided by the number of nights of operation). Each column corresponds to a year during the study period (2016 – 2020). The dashed line between 2017 and 2018 is representative of the date of the Mendocino

Complex Fire. The number of unique camera sites each species was detected at within each year is noted within each bar plot. *Note - scale of y-axis is different between species.

Model Selection and Goodness of Fit Results

Five multi-species occupancy model parameterizations of the effect of fire were compared by the Watanabe-Akaike information criterion (WAIC). The parameterized model with the lowest WAIC score was model (3), which included effects for "recently burned" and one combined "Burn Lag" effect. The next best fitting model was model (2) which included effects only for "burned" and "unburned" (ΔWAIC = 1.99). Models (4) and (5) were the next best fitting models, both of which included effects of "Burn Lag" that varied over time ("Burn Lag 1" and "Burn Lag 2") (ΔWAIC = 7.17 and 6.27, respectively). The worst fitting model parameterization was model (1), the null model (ΔWAIC = 46.43) (Table 1). Models (2) and (3) were within 2 WAIC points of each other, but we decided to proceed with analyzing model (3) in order to examine how fire effects may impact species' site use and intensity of use over time.

Posterior predictive checks indicated goodness of fit within acceptable bounds. The observed deviance in the top model did not differ from the posterior distribution of simulated deviances (Supplement S2: Figure S2).

Species-level and Community-level Summaries

We assessed the effects of megafire on community-level and species-specific resistance using the community MSOM (without group-structure). We found that 6 of 8 modeled species were resistant to the immediate effects of fire, showing no significant decrease in site use or intensity of use during the "recently burned" or "burn lag" time periods relative to unburned sites (Figures 3 and 4). Western gray squirrel and black-tailed deer showed immediate vulnerability to megafire.

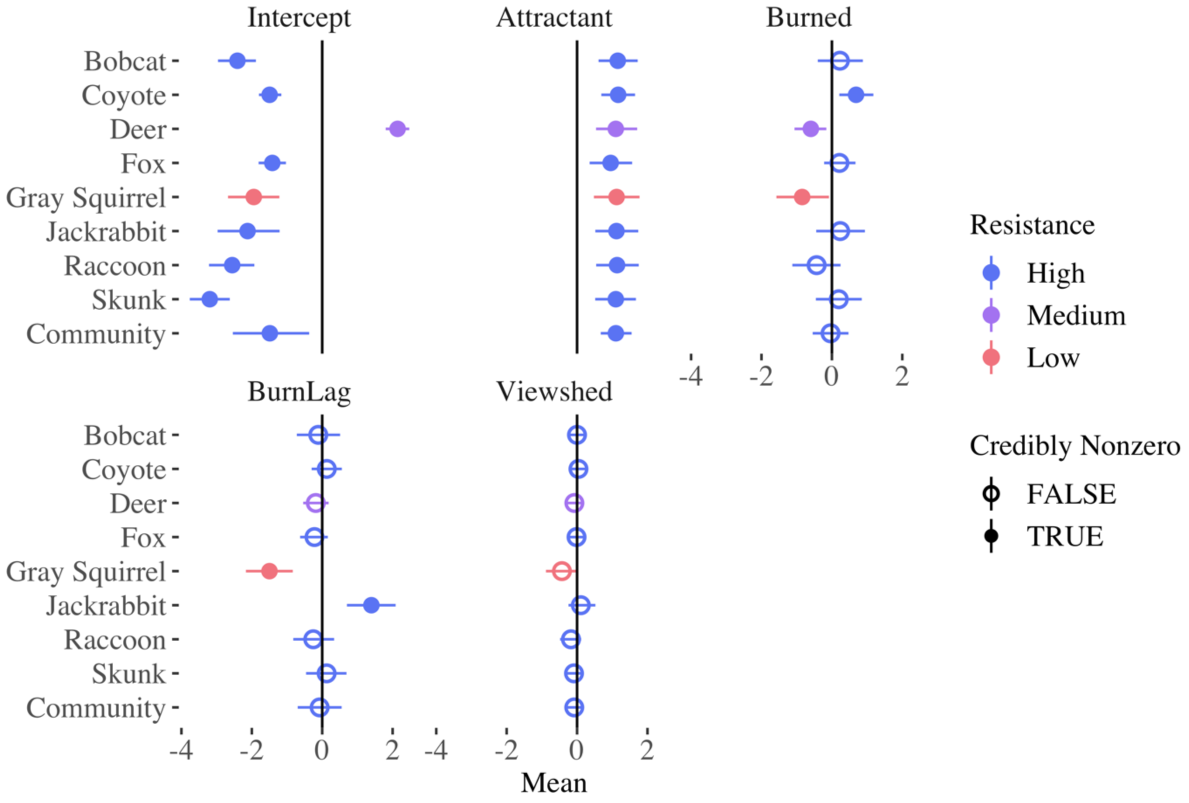

Figure 3. Estimated coefficients of all site-specific covariates on probability of site use (*Ψ*) from the community multi-species occupancy model (MSOM) fit from camera trap data collected from the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Species-specific estimates are displayed along the y-axis. “Community” at the bottom of each column represents the community-level hyperparameter used in the MSOM. We deemed species resistant to megafire if the species-specific estimates from the multi-species occupancy model showed no effect of time since burn on intensity of use or site use relative to unburned sites, or if we estimated an increase in intensity of use or site use associated with fixed fire effects. Resistance to megafire was color-coded with species with high resistance colored in blue, species with moderate resistance in purple (non-resistant in recently burned sites but resistant during the BurnLag), and species with low resistance in red (non-resistant at both Recently Burned and BurnLag sites). All species except deer and gray squirrel showed strong resistance to the initial effects of megafire.

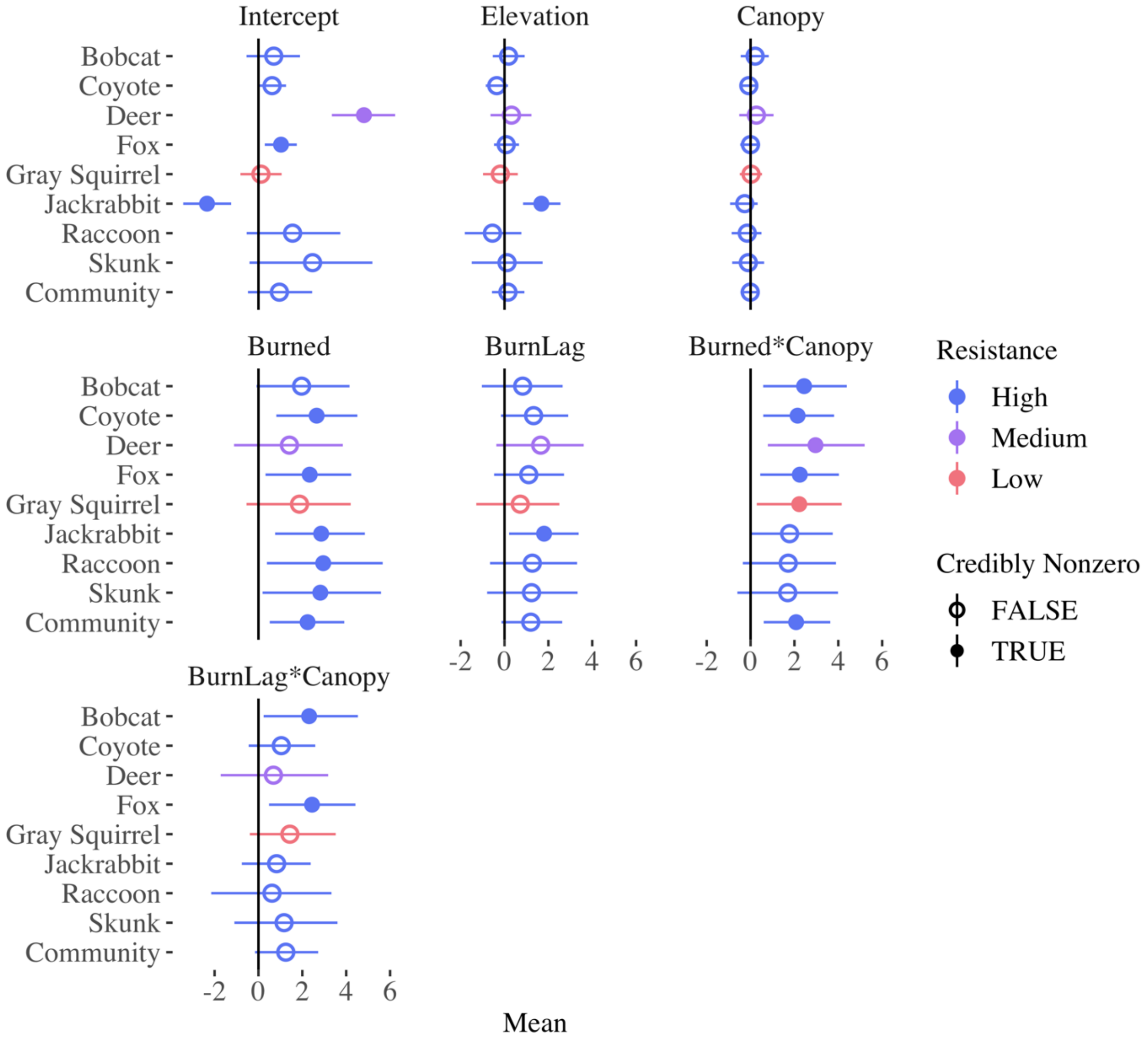

Figure 4. Estimated coefficients of all site-specific covariates on intensity of use (*p*) from the community multi-species occupancy model (MSOM) fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Species names are displayed on the y-axis. "Community" at the bottom of each column corresponds to the community-level hyperparameter used in the MSOM. We deemed species resistant to megafire if the species-specific estimates from the multi-species occupancy model showed no effect of time since burn on intensity of use or site use relative to unburned sites, or if we estimated an increase in intensity of use or site use associated with fixed fire effects. Resistance to megafire was color-coded with species with high resistance colored in blue, species with moderate resistance in purple (non-resistant in recently burned sites but resistant during the BurnLag), and species with low resistance in red (non-resistant at both Recently Burned and BurnLag sites).

Site use varied considerably across modeled species, with probability of site use highest for black-tailed deer with a mean ψ across all sites of 0.98 (SD ± 0.03) and was lowest for black-tailed jackrabbit (mean = 0.28, 90% SD ± 0.30) (Supplement S2: Table S4). Recently burned sites (i.e. time since burn = "Burned") were associated with increased site use for 5 of the 8 modeled species: coyote (Mean = 2.65, 90% CI [0.82, 4.51]), black-tailed jackrabbit (Mean = 2.86 [0.76, 4.85]), gray fox (Mean = 2.34 [0.32, 4.23]), raccoon (Mean = 2.95 [0.39, 5.67]), and striped skunk (Mean = 2.82 [0.19, 5.59]. Canopy cover at recently burned sites (i.e. Canopy * Burned) was positively related to site use for several species (5 of 8 – all species except jackrabbit, raccoon, and striped skunk). The positive effect of this interaction continued during the year following fire (i.e. Canopy * Burn Lag) for gray fox (Mean = 2.24 [0.44, 4.03]) and bobcat (Mean = 2.44 [0.58, 4.39]) specifically.

Time since burning had a significant effect on the detection probability (including intensity of use) of 4 species: black-tailed jackrabbit, coyote, western gray squirrel, and black-tailed deer (90% CI did not overlap zero) (Figure 4, Supplement S2: Table S5). During the year of the fire (i.e. time since burning = "Burned"), detection probability increased for coyotes at burned sites (Mean = 0.69 [0.21, 1.18]), but decreased for black-tailed deer (Mean = -0.60 [-1.06, -0.16]) and western gray squirrel (Mean = -0.84 [-1.58, -0.08]). Detection at burned sites of gray squirrels continued to be lower relative to unburned sites in the years following fire as well (i.e. time since burning = "Burn Lag") (Mean = -1.50 [-2.17, -0.84]). Black-tailed jackrabbit detection probability at burned sites significantly increased during the lag years following megafire (Mean = 1.40 [0.70, 2.09]).

Species richness ranged from 3.76 to 7.71 across camera stations, with a mean of 5.26 species across all sites (SD ± 0.70). Mean probability of site use (ψ) of the community was 0.66 (SD ± 0.27). We found that probability of site-use at the community-level was higher in recently burned sites (i.e. "Burned") relative to unburned sites (Mean = 2.24 [0.52, 3.91]). Recently burned sites that maintained high canopy cover (i.e. Burned * Canopy) were also associated with higher community-level site use (mean = 2.08 [0.60, 3.63]). We visualized this relationship using derived richness values predicted across sites in Figure 5. Community-level intensity of use was positively associated with microsite attractants (Mean = 1.10 [0.67, 1.55]) (Figure 4, Supplement S2: Table S5).

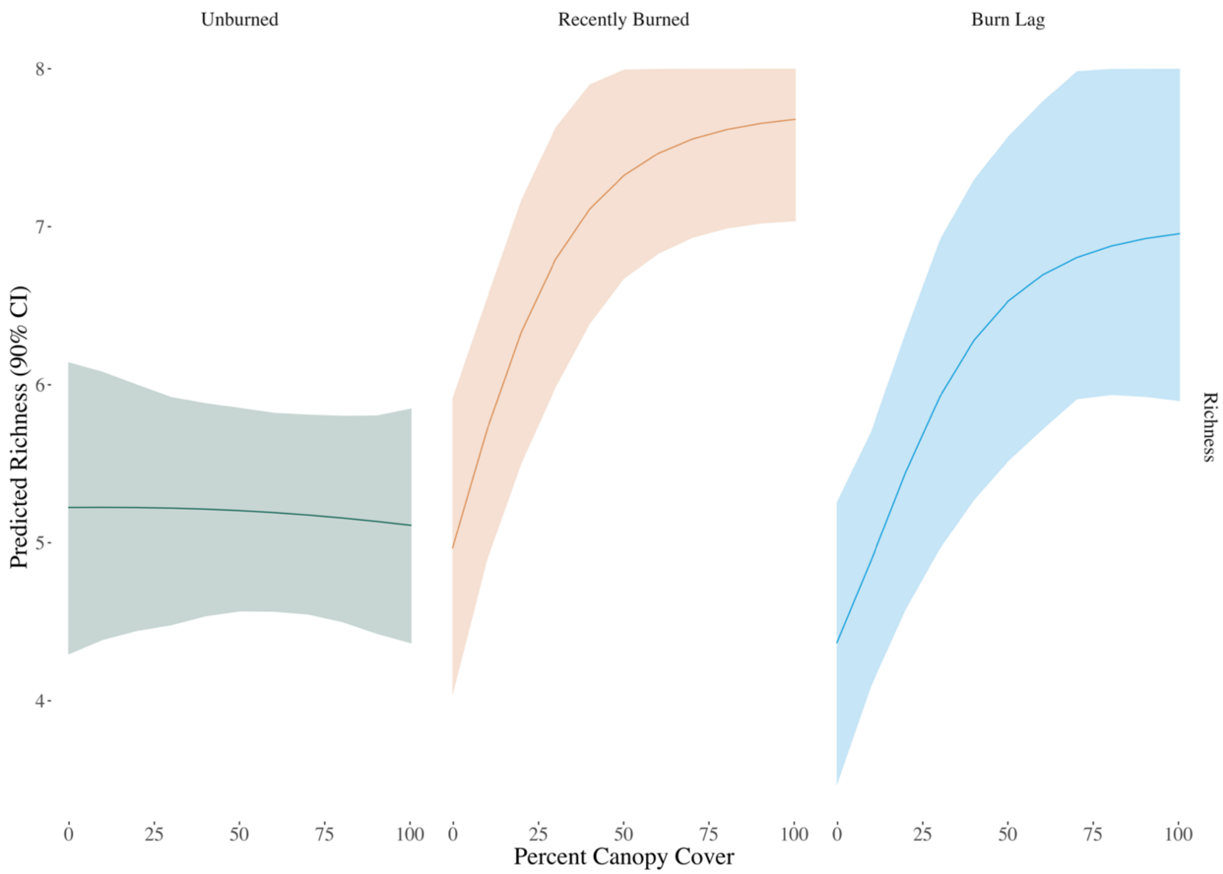

Figure 5. Predicted species richness estimates from the multi-species occupancy model (MSOM) across "time since burned" categories and canopy cover fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. All other occupancy covariates were set to their mean values. Panel "a" represents all sites that were unburned by the fire. Panel "b" represents sites that were burned during the year of the fire (2018). Panel "c" represents burned sites in the years following fire.

Group-level Summaries

At the species group level, site use of small and medium-sized species was associated with burned sites immediately following the fire, though not significantly (90% CI overlaps zero) (Mean = 1.69 [-0.45, 3.96] and Mean = 1.78 [-0.71, 4.37], respectively) (Supplement S2: Figure S3; Supplement S1: Table S6). Intensity of use was not significantly associated with any burn effects (Supplement S2: Figure S4; Supplement S2: Table S7).

We found no significant effects of burn effects on site use associated with diet-groups (Supplement S2: Figure S5; Supplement S2: Table S8). We did find, however, that Carnivores had a positive association, albeit non-significant, with burned sites that maintained higher canopy cover (i.e. Burned * Canopy) (Mean = 1.70 [-0.70, 4.17]. We also found no significant associations between fire effects and intensity of use across diet groups (Supplement S2: Figure S6; Supplement S2: Table S9).

Discussion

Despite the widespread change to habitat caused by the 2018 Mendocino Complex Fire, we found compelling evidence of species resistance following this extreme wildfire event. We did find that patterns of wildlife site use, intensity of use, and species richness changed subtly following megafire in this northern California oak woodland, but to a much small degree than we initially hypothesized. Most species were resistant (6 of 8) to the immediate effects of megafire within the scope of this study. At the species group-level, we did not find any relationship between body size or diet with the likelihood of a species being resistant to megafire, contrary to our initial hypotheses. Site use of individual mesopredator species increased in recently burned areas relative to unburned areas, with these species potentially taking advantage of burned areas that may have a decreased presence of larger predators and increased exposure of prey species. Detection decreased for a few species; two species immediately following megafire (black-tailed deer and western gray squirrel) and one species during the "Burn Lag" period (western gray squirrel). Despite observed decreases in detection (potentially attributable to differences in intensity of use), site use across species did not decrease following megafire indicating that the overall distributions of most species remained resistant to the impacts of megafire. We found that community-level site use increased at sites that maintained high canopy cover during the year of the fire. These sites of higher canopy cover may act as temporary refugia for several species amidst a severely burned landscape.

We observed that most species examined in this study were resistant (6 of 8) to the impacts of megafire. This corroborates findings of mammal resistance to wildfire in other ecosystems types (Lewis et al. 2022) and across mammal species globally (Pocknee et al. 2023). We also found evidence to suggest that the degree of species resistance likely exists along a continuum and is not just a dichotomous distinction. For example, species like black-tailed deer were vulnerable to the effects fire immediately following the megafire, but resistant to the effects of fire in the years following ("Burn Lag"). This may indicate that among the two vulnerable species, deer are more resistant than western-gray squirrels, and likely more resilient to the longer-term effects (resistance translation to resilience). For these vulnerable species that were non-resistant to megafire (deer and western gray squirrel), megafire only impacted the intensity of use of burned sites, but not site use. Megafire at this scale may, therefore, specifically alter mechanisms that influence species' intensity of use, such as demography and movement patterns, as opposed to presence at burned sites.

For larger, more mobile species like black-tailed deer, changes in intensity of use may represent shifts in activity centers, alterations in movement paths, or avoidance of burned areas altogether following wildfire (Jager et al. 2021). As severe fire modifies the structure of vegetation, animals may adjust their navigation of landscapes to minimize risk (Kreling et al. 2021; Ganz et al. 2022) and maximize access to remaining resources (Nimmo et al. 2019). This behavioral response may grant these larger-bodied species some level of improved resistance and longer-term resilience to quickly leave areas that are recently burned and return when conditions are more favorable. The limited spatial scale of our study design, however, may make these patterns more difficult to decipher for more wide-ranging species in the study (such as coyote and bobcat) underlining the need for more post-fire studies performed at broader spatial scales. In our study, we assumed that each species' use of each site was independent from nearby that of nearby sites, conditional on modeled variables and site-level random effects. In practice the movement of a few species with larger home ranges between nearby sites could lead to spatial autocorrelation in site use which might be misattributed to spatially correlated environmental variables such as burn history. However, due to our limited sampling window (2 months) of the study and density of these species at our study site, we think the rate of this occurring would be relatively rare.

For smaller species that are less mobile (i.e. western gray squirrel) significant changes in detection may instead suggest local-scale changes in abundance and demography (Griffiths and Brook 2014). Our findings further corroborate other recent studies at our site that have found significant decreases in the detection rate of small-bodied mammals following this megafire, including gray squirrel and gray fox (Pascoe et al. 2023). This also mirrors general trends found in Pockene et al. 2023 which observed overall resilience across mammal species to fire in a global meta-analysis, but highlighted that species with relatively high reproductive rates (such as small-bodied mammals like squirrels) were more likely to be vulnerable to the effects of fire (Pocknee et al. 2023). In this study, we use species presence/absence to draw an understanding of species responses to megafire over time and are limited in our ability to tease out how long-term movement and demography patterns of vulnerable species are affected by fire. Future work examining the exact mechanisms that lead to these observed responses in non-resistant species could help better define the response capacities of these species and guide potential conservation interventions if deemed necessary.

Despite these species-specific findings, we did not find evidence to support our hypotheses that certain species-groups would be more resistant to megafire than other groups. We predicted that carnivores would be more likely to use sites that burned recently relative to other diet groups, but found all diet groups were resistant to fire effects. Furthermore, all body-size groups were deemed resistant to fire effects in our study as well, contrary to our hypothesis that small-bodied species may be more vulnerable. However, we did observe that species-level site use of mesopredators, such as coyote, gray fox, striped skunk, and racoon, increased in recently burned areas. These results mirror the response of mesopredators to wildfire observed in similar studies across California (Schuette et al. 2014; Jennings et al. 2016; Furnas, Goldstein, and Figura 2021). The realized responses of these species are likely a combination of different species-level characteristics (or functional traits) such as diet, body size, hunting mode, and trophic level. Building a more mechanistic understanding of how these traits interact to produce the observed responses could help guide the prioritization of post-fire conservation objectives.

Given our relatively small sample sizes, we were unable to explicitly investigate the effects of megafire on species interactions. The limited spatial scale of our study also prevented us from explicitly examining how megafire impacted the distributions of larger predators whose individual home ranges encompass the entire research property. However, camera and anecdotal evidence that large predators (i.e. black bears and mountain lions) became much rarer in the study area following megafire may suggest that site use of mesopredator species, such as coyote, may also be an indirect response to the temporary removal or decreased presence of these larger predators, as observed in other studies (Estes et al. 2011). Previous work shows that a variety of global change pressures can trigger this “rewiring” of species composition and trophic webs (Bartley et al. 2019; Suraci et al. 2021). Megafire could, at least temporarily, intensify this effect, and exacerbate existing stressors on large carnivores, especially as the frequency, size, and severity of megafires continues to increase. More research is necessary to examine the impacts of megafire on these larger predators over a broader spatial and temporal context to explicitly examine how and for how long these effects may alter species interactions, such as predation (Doherty et al. 2022) and interspecies competition (Gigliotti et al. 2022).

The presence of fire and its effect over time played a significant role in shaping wildlife distributions. Model parameterizations that included fire and fire lag effects performed much better than the null model. At the community-scale, the overall wildlife community was resistant to the effects of megafire as well. Previous work has established that fire in several California ecosystems can enhance habitat for a variety of native wildlife species by increasing productivity and by creating a diversity of habitat types (Jones and Tingley 2021; Connor et al. 2022). Some of these established benefits, at the community-level, may have been reproduced within our own study, especially given that the study site has not been burned by wildfire in over 60 years. Translating these potential benefits into management guidelines, however, requires more specific knowledge of what burn severities and burn patch sizes create the desired benefits for wildlife at the community-scale without harming species resistance and resilience (Donaldson et al. 2019). These recommendations are plentiful for conifer ecosystems in California, but rarer in other fire-prone ecosystems such as oak woodland landscapes (Calhoun et al. 2021). Future work that specifically examines how fire severity and size across a breadth of oak woodland wildfires impact wildlife will help steer guidelines for prescribed burning that best enhance wildlife habitat in these landscapes.

Areas that recently burned but maintained high canopy cover had a significant increase in estimated species richness relative to unburned sites and sites post-fire (2019 and 2020), suggesting that these sites may provide refugia for additional species directly following fire. These canopied “islands” may provide important resources (forage and cover) that are lacking in other parts of the recently burned landscape. This positive effect was true for the two species deemed vulnerable to megafire (deer and gray squirrel), highlighting its potential importance in supporting these vulnerable species immediately following megafire. Simultaneously, however, this may intensify inter-species interactions, such as competition and predation, as inter- and intra-species spatial overlap increases in these limited, intact patches of habitat. Using pre-emptive prescribed burning and land modification tools that prevent large contiguous megafire burns could help ensure multiple patches of refugia remain following fire. This may be one of the best strategies to enhance the long-term resilience of these ecological communities from global change disturbances like megafire (McWethy et al. 2019; C. Miller et al. 2021). This attractant effect towards canopied areas post-megafire is apparent the year of the fire and decreases in the years following. Therefore, refugia following megafire may be most critical in the immediate months following wildfire to ensure species have access to resources before vegetation is able to recover naturally.

Changes in historic fire regimes may pose a greater threat to woodland savanna ecosystems and their wildlife communities relative to other ecosystem types worldwide (Kelly et al. 2020; Calhoun et al. 2021). Due to the key services and habitat they provide around the world (Veldman et al. 2015; Eastburn et al. 2017), it is essential that we prioritize developing effective fire management tools for woodland savannas to protect their long-term ecological integrity against shifting fire regimes. Our study highlights the vulnerability and resistance of certain woodland savanna wildlife species to megafire in the short-term, but more work is needed to understand how these initial responses translate over longer time periods (“resilience”) and across different land cover types. Additionally, the short and long-term effects of fire on habitat and wildlife are likely related to the composition of microhabitats within oak woodland savannas (i.e. woodlands, grasslands, and shrublands) due the different speeds at which they recover. For example, grassland ecosystems typically recover faster following fire relative to shrubland and woodland systems (Halofsky et al. 2011), which may lead species to preferentially choose to use these areas in the time following megafire. Though we were unable to account for these differences within our study, our analysis does incorporate an important proxy for resource availability as estimated through canopy cover. Most grassland savannas are far less productive during the late dry months in regions with Mediterranean climates, limiting viable food options for most wildlife species. During these months, shrubs and especially acorns from oak trees, are the primary means of acquiring food resources for most wildlife (Mazur, Klimley, and Folger 2013; W. J. McShea and Healy 2002). Therefore, our study design effectively examines how these critical resources shape species distributions following megafire during arguably the most resource-depleted time of the year. Broader scale studies that include multiple microhabitat types in their scope could help confirm how different post-fire vegetation types influence the distribution of wildlife species during similar dry seasons.

Conclusion

Frequent megafires have the potential to alter wildlife communities in fire-prone ecosystems around the world. We found evidence of resistance to megafire in a woodland savanna mammal community, potentially made possible by the availability of refugia following megafire. These findings further corroborate the importance of spatial burn patchiness in mixed-severity fire regimes, specifically from the perspective of wildlife. In woodland ecosystems, management that can 1) prevent megafire or 2) facilitate the creation of more heterogeneous landscapes following megafire may be the best strategies to enhance the resistance and resilience of mammal communities to future megafires.

Acknowledgements

We recognize that UC Berkeley sits on the territory of xučyun (Huichin), the ancestral and unceded land of the Chochenyo speaking Ohlone people, the successors of the sovereign Verona Band of Alameda County. This land was and continues to be of great importance to the Muwekma Ohlone Tribe and other familial descendants of the Verona Band. In addition, we recognize that the land this research was conducted on is the traditional land of the Sho-Ka-Wah of the Central Pomo people.

We would like to thank Janelle Dorcy for her support throughout this project in data collection and organization. We thank the dedicated staff of the Hopland Research and Extension Center (Alison Smith, Troy McWilliams, Gregory Solberg, and John Bailey) who assisted with data collection and project logistics. We would also like to enthusiastically thank all the Berkeley undergraduate students (> 20 students and volunteers) who have been involved in processing camera trap data across several years as part of the Berkeley Undergraduate Research Apprenticeship Program. Finally, we'd like to thank Asia Murphy and Lindsey Rich for their statistics and modeling advice early in the project.

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Supplement for Chapter 2

Supplement S1 – Canopy Cover Estimation

Data Description

Sentiel-2 satellite imagery was downloaded from USGS EarthExplorer (https://earthexplorer.usgs.gov/). The Hopland Research and Extension Center Shapefile Boundary was uploaded to define the spatial area of interest. Cloud Cover Range was set to "0% - 10%". "Sentinel-2" was selected under datasets and dates were restricted to October 1st – October 31st for each year for which imagery was acquired (2016-2020). Planet Labs satellite imagery was downloaded from Planet Labs (https://www.planet.com/explorer/). The Hopland Research and Extension Center Shapefile Boundary was uploaded to define the spatial area of interest. The "PlanetScope Scene" data product was selected from Imagery type. Cloud cover was changed to "0 – 10%". Dates were restricted to October 1st – October 31st for each year for which imagery was acquired (2016 - 2020).

Table S1. Canopy Cover Imagery Description Table

Data	**Source**	**Projected Coordinate System**	**Description**
Planet Imagery	Planet Labs	WGS 1984 UTM Zone 10N	3m resolution, 4 bands, collected from the month of October from years 2016-2020
Sentinel Imagery	Sentinel Hub	WGS 1984 UTM Zone 10N	20m resolution, 3 bands, collected from the month of October from years 2016-2020
HREC Boundary	Hopland Research and Extension Center	WGS 1984 UTM Zone 10N	Shapefile, used to clip imagery before classification

Methodology

We estimated canopy cover using 20-meter resolution imagery from Sentinel hub (Sentinel Hub, 2021) to create canopy rasters via object-based and supervised classification in ArcGIS Pro (ESRI, 2011) for each year (2016-2020) (Tilahun 2015; Sunde et al. 2020). For this analysis, we categorized imagery d as either 'Covered', which included trees, shrubbery, and other similar vegetation, or 'Uncovered', which included grass, bare ground/soil, and burnt vegetation. We collected satellite imagery from the month of October from each respective year before the start of annual rainfall so grass and bare ground would not look similar to other vegetation. We verified the classified layers using higher resolution imagery obtained from Planet Labs (3m resolution) (Planet Team, 2017) from which we could visually confirm canopy status. For each raster, fifty accuracy assessment points were created and were visually compared to the higher resolution Planet Labs Imagery. Confusion matrices were computed based on the accuracy assessment points to produce overall accuracies for each raster. This supervised classification process was repeated until each raster had an overall accuracy of 80% or higher. Canopy cover values were extracted from a 100m buffer around each camera site for each year to calculate percent canopy cover within the buffered radius.

Table S2. Canopy cover classification accuracy table. We used object-based image analysis (OBIA) to classify Sentinel Hub Imagery (20m resolution) from Hopland into Canopy or No Canopy raster layers. Imagery was collected for each year of the study (2016-2020) during the month of October. We created a confusion matrix of 50 randomly generated points across the annual canopy cover rasters and compared canopy classification with the finer scale resolution Planet Labs imagery (3m resolution). We used the finer scale Planet Labs imagery to visually assess the accuracy of each raster layer. Raster layers that had 80% or higher accuracy were accepted and used to calculate % canopy cover covariate for analyses.

Year	**Accuracy**
2016	86%
2017	88%
2018	84%
2019	80%
2020	82%

Supplement S2 – Additional Figures and Tables

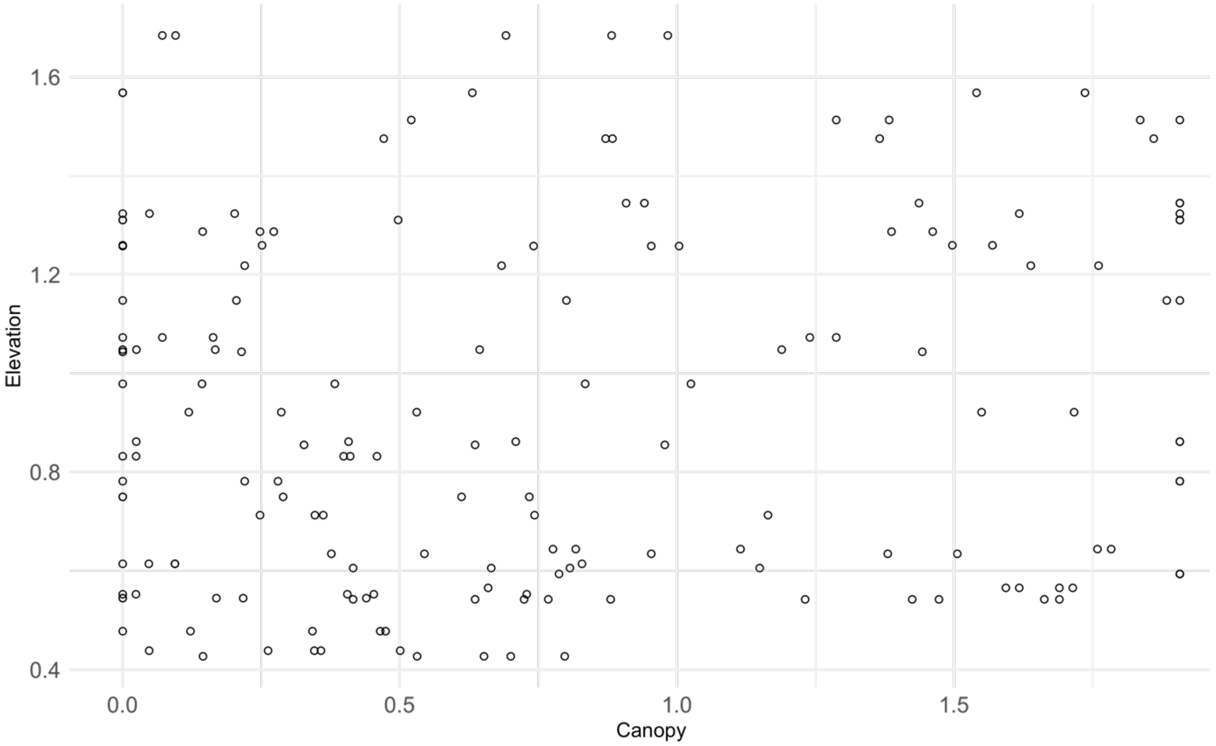

Figure S1. Covariate correlation plot matrix of continuous covariates extracted from sampled camera stations at the Hopland Research and Extension Center, CA, USA. Correlation plot compares values of all continuous covariates included in the site use (Ψ) sub-model of the multi-species occupancy model (elevation and canopy cover). We found no significant trends in covariance between remaining covariates.

Table S1. Range, mean, and original resolution of continuous covariates used in the site use (*Ψ*) and intensity of use (*p*) multi-species occupancy sub-models run from camera trap data collected at the Hopland Research and Extension Center, CA, USA.

Covariate	Range	Mean	Original Resolution
Canopy (%)	0 – 100	39	20 m
Elevation (m)	226 – 897	495	.003 m
Viewshed (m)	8 – 20	14	At Site

Table S2. Species grouping categories used in the group-level multi-species occupancy models for camera trap data collected at the Hopland Research and Extension Center, CA, USA. Species were grouped by (1) body size and (2) diet to investigate whether certain species groups were more or less resistant and resilient to megafire. We grouped species into 3 categorical body mass groups from which each had its own group-level hyperparameter: Small (< 5kg), Medium (5-15 kg), and Large (>15kg) (Wilman et al, 2014). We then grouped species into 3 broad diet-group categories: Herbivores (diet does not contain animal material), Omnivores (diet contains < 60% animal material) and Carnivores (> 60% of diet contains animal material) (Wilman et al, 2014).

Scientific Name	Common Name	Size Group	Diet Group
L. rufus	Bobcat	Medium	Carnivore
C. latrans	Coyote	Medium	Carnivore
O. hemionus columbianus	Black-tailed Deer	Large	Herbivore
U. cinereoaregenteus	Gray Fox	Small	Omnivore
S. griseus	Western Gray Squirrel	Small	Herbivore
L. californicus	Black-tailed Jackrabbit	Small	Herbivore
P. lotor	Raccoon	Medium	Omnivore
M. mephitis	Striped Skunk	Small	Omnivore

Table S3. Camera trap survey results from the duration of the study (Oct-Nov, 2016-2020) at the Hopland Research and Extension Center, CA, USA. Naïve psi (Ψ) was calculated by summing the number of sites each species was detected at and dividing by the total number of sites sampled (175 sites). Model estimates of mean psi (Ψ) and its standard deviation that correct for imperfect detection were calculated from the community multi-species occupancy model (MSOM). Total number of detections sums the number of independent detections (15-minute independence between detections) across the entire study. The number of unique sites each species was detected at (max = 36) is also displayed.

Scientific Name	**Common Name**	**Naïve *Ψ***	**Mean Psi (*Ψ*)**	**St. Dev. Psi (*Ψ*)**	**Detection #**	**# Cams**
L. rufus	Bobcat	0.31	0.57	± **0.17**	130	29
C. latrans	Coyote	0.59	0.68	± **0.11**	387	36
O. hemionus columbianus	Black-tailed Deer	0.98	0.98	± **0.03**	9479	36
U. cinereoaregenteus	Gray Fox	0.57	0.67	± **.19**	496	32
S. griseus	Western Gray Squirrel	0.38	0.51	± **.28**	787	21
L. californicus	Black-tailed Jackrabbit	0.23	0.28	± **0.30**	364	16
P. lotor	Raccoon	0.37	0.74	± **0.16**	231	26
M. mephitis	Striped Skunk	0.30	0.82	± 0.07	88	28
U. americanus	Black Bear	0.14	NA	**NA**	NA	NA
S. bachmani	Brush Rabbit	.01	NA	NA	1	1
O. beecheyi	California Ground Squirrel	0.03	NA	NA	34	3
S. scrofa	Wild Boar	0.05	NA	NA	39	6
P. concolor	Mountain Lion	0.06	NA	NA	16	7

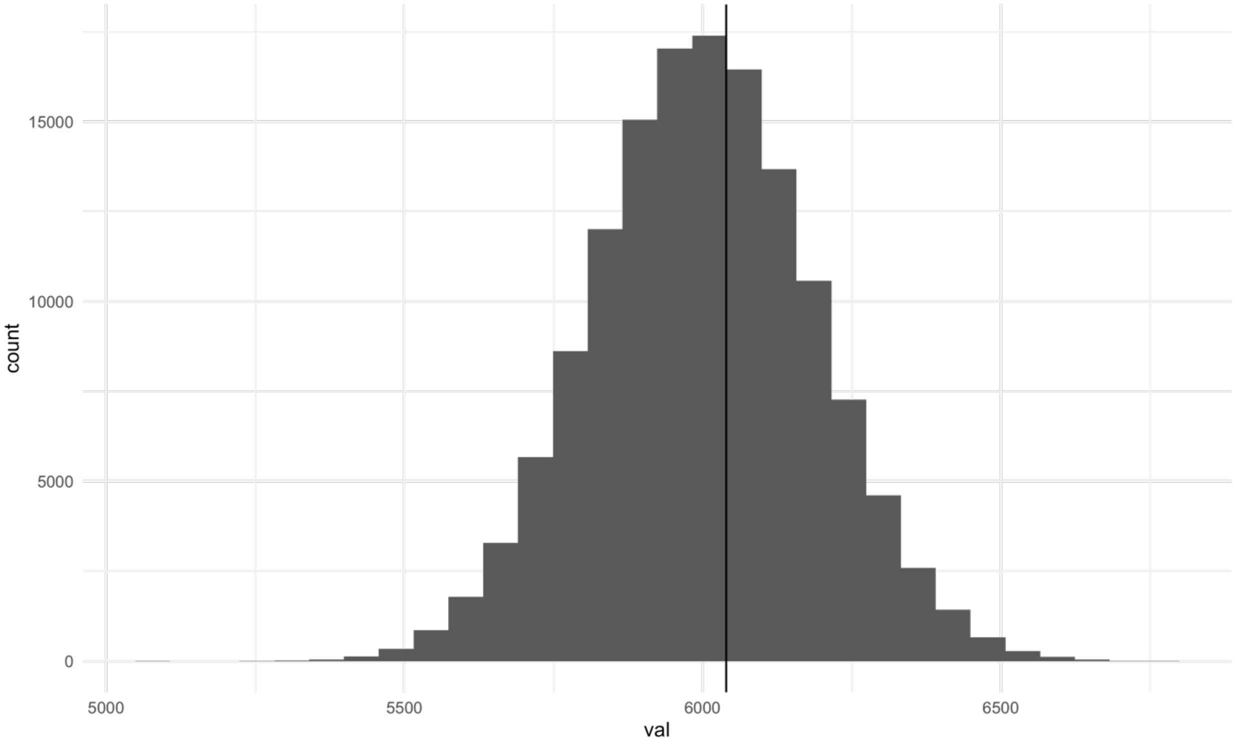

Figure S2. Observed deviances of fit from the community multi-species occupancy model (MSOM) fit on camera trap data collected at the Hopland Research and Extension Center, CA, USA. The MSOM did not visibly differ from the posterior distributions of deviances generated from simulated datasets, meaning that we found no evidence of poor model fit.

Table S4. Covariate coefficients for the site use sub-model of the community multi-species occupancy model fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Mean estimates and 90% confidence intervals are given for each estimate.

Species	**Parameter**	**Estimate**
Bobcat	Intercept	0.7 (-0.54, 1.89)
Bobcat	Elevation	0.18 (-0.53, 0.92)
Bobcat	Canopy	0.21 (-0.45, 0.83)
Bobcat	Burned	1.97 (-0.09, 4.15)
Bobcat	facBurnLag	0.83 (-1.03, 2.65)
Bobcat	Burned*Canopy	2.44 (0.58, 4.39)
Bobcat	facBurnLag*Canopy	2.31 (0.24, 4.53)
Coyote	Intercept	0.62 (-0.03, 1.26)
Coyote	Elevation	-0.35 (-0.86, 0.16)
Coyote	Canopy	-0.08 (-0.51, 0.35)
Coyote	Burned	2.65 (0.82, 4.51)
Coyote	facBurnLag	1.33 (-0.16, 2.9)
Coyote	Burned*Canopy	2.14 (0.58, 3.81)
Coyote	facBurnLag*Canopy	1.04 (-0.45, 2.59)
Black-tailed Deer	Intercept	4.81 (3.35, 6.23)
Black-tailed Deer	Elevation	0.32 (-0.64, 1.23)

Black-tailed Deer	Canopy	0.26 (-0.52, 1.05)
Black-tailed Deer	Burned	1.41 (-1.11, 3.85)
Black-tailed Deer	facBurnLag	1.65 (-0.37, 3.61)
Black-tailed Deer	Burned*Canopy	2.96 (0.79, 5.2)
Black-tailed Deer	facBurnLag*Canopy	0.68 (-1.72, 3.18)
Gray Fox	Intercept	1.03 (0.29, 1.75)
Gray Fox	Elevation	0.08 (-0.48, 0.66)
Gray Fox	Canopy	0 (-0.47, 0.44)
Gray Fox	Burned	2.34 (0.32, 4.23)
Gray Fox	facBurnLag	1.1 (-0.47, 2.71)
Gray Fox	Burned*Canopy	2.24 (0.44, 4.03)
Gray Fox	facBurnLag*Canopy	2.44 (0.48, 4.42)
Gray Squirrel	Intercept	0.11 (-0.82, 1.06)
Gray Squirrel	Elevation	-0.19 (-0.98, 0.6)
Gray Squirrel	Canopy	0.02 (-0.49, 0.52)
Gray Squirrel	Burned	1.87 (-0.54, 4.21)
Gray Squirrel	facBurnLag	0.72 (-1.29, 2.5)
Gray Squirrel	Burned*Canopy	2.22 (0.28, 4.15)
Gray Squirrel	facBurnLag*Canopy	1.43 (-0.39, 3.52)
Black-tailed Jackrabbit	Intercept	-2.35 (-3.43, -1.24)
Black-tailed Jackrabbit	Elevation	1.68 (0.85, 2.55)
Black-tailed Jackrabbit	Canopy	-0.26 (-0.93, 0.32)
Black-tailed Jackrabbit	Burned	2.86 (0.76, 4.85)
Black-tailed Jackrabbit	facBurnLag	1.8 (0.21, 3.38)
Black-tailed Jackrabbit	Burned*Canopy	1.78 (-0.04, 3.75)
Black-tailed Jackrabbit	facBurnLag*Canopy	0.83 (-0.76, 2.38)
Raccoon	Intercept	1.56 (-0.54, 3.73)
Raccoon	Elevation	-0.55 (-1.81, 0.77)
Raccoon	Canopy	-0.15 (-0.86, 0.5)
Raccoon	Burned	2.95 (0.39, 5.67)
Raccoon	facBurnLag	1.27 (-0.66, 3.31)
Raccoon	Burned*Canopy	1.72 (-0.35, 3.89)
Raccoon	facBurnLag*Canopy	0.62 (-2.15, 3.33)
Striped Skunk	Intercept	2.47 (-0.41, 5.2)
Striped Skunk	Elevation	0.12 (-1.49, 1.74)
Striped Skunk	Canopy	-0.1 (-0.84, 0.62)
Striped Skunk	Burned	2.82 (0.19, 5.59)
Striped Skunk	facBurnLag	1.23 (-0.79, 3.33)
Striped Skunk	Burned*Canopy	1.69 (-0.6, 3.99)
Striped Skunk	facBurnLag*Canopy	1.17 (-1.1, 3.6)
Community	Intercept	0.96 (-0.48, 2.45)
Community	Elevation	0.16 (-0.57, 0.91)
Community	Canopy	-0.01 (-0.46, 0.41)
Community	Burned	2.24 (0.52, 3.91)
Community	facBurnLag	1.2 (-0.14, 2.63)
Community	Burned*Canopy	2.08 (0.6, 3.63)

Community	facBurnLag*Canopy	1.25 (-0.16, 2.72)

Table S5. Covariate coefficients for the intensity of use sub-model of the community multi-species occupancy model fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Mean estimates and 90% confidence intervals are given for each estimate.

Species	Parameter	Estimate
Bobcat	Intercept	-2.41 (-2.96, -1.88)
Bobcat	Attractant	1.16 (0.61, 1.72)
Bobcat	Burned	0.23 (-0.4, 0.88)
Bobcat	facBurnLag	-0.11 (-0.72, 0.51)
Bobcat	Viewshed	0 (-0.24, 0.25)
Coyote	Intercept	-1.49 (-1.8, -1.16)
Coyote	Attractant	1.17 (0.69, 1.65)
Coyote	Burned	0.69 (0.21, 1.18)
Coyote	facBurnLag	0.13 (-0.3, 0.56)
Coyote	Viewshed	0.04 (-0.15, 0.24)
Black-tailed Deer	Intercept	2.14 (1.8, 2.47)
Black-tailed Deer	Attractant	1.1 (0.54, 1.71)
Black-tailed Deer	Burned	-0.6 (-1.06, -0.16)
Black-tailed Deer	facBurnLag	-0.18 (-0.54, 0.18)
Black-tailed Deer	Viewshed	-0.08 (-0.29, 0.13)
Gray Fox	Intercept	-1.42 (-1.81, -1.03)
Gray Fox	Attractant	0.95 (0.36, 1.56)
Gray Fox	Burned	0.21 (-0.22, 0.67)
Gray Fox	facBurnLag	-0.22 (-0.63, 0.16)
Gray Fox	Viewshed	-0.02 (-0.24, 0.24)
Gray Squirrel	Intercept	-1.94 (-2.68, -1.22)
Gray Squirrel	Attractant	1.12 (0.48, 1.77)
Gray Squirrel	Burned	-0.84 (-1.58, -0.08)
Gray Squirrel	facBurnLag	-1.5 (-2.17, -0.84)
Gray Squirrel	Viewshed	-0.43 (-0.88, 0.03)
Black-tailed Jackrabbit	Intercept	-2.12 (-2.97, -1.21)
Black-tailed Jackrabbit	Attractant	1.12 (0.52, 1.74)
Black-tailed Jackrabbit	Burned	0.23 (-0.45, 0.94)
Black-tailed Jackrabbit	facBurnLag	1.4 (0.7, 2.09)
Black-tailed Jackrabbit	Viewshed	0.11 (-0.24, 0.52)
Raccoon	Intercept	-2.56 (-3.22, -1.93)
Raccoon	Attractant	1.14 (0.54, 1.75)
Raccoon	Burned	-0.43 (-1.12, 0.25)
Raccoon	facBurnLag	-0.25 (-0.82, 0.34)
Raccoon	Viewshed	-0.17 (-0.48, 0.12)
Striped Skunk	Intercept	-3.19 (-3.76, -2.63)
Striped Skunk	Attractant	1.1 (0.52, 1.67)
Striped Skunk	Burned	0.19 (-0.46, 0.85)
Striped Skunk	facBurnLag	0.13 (-0.46, 0.69)

Striped Skunk	Viewshed	-0.09 (-0.34, 0.18)
Community	Intercept	-1.49 (-2.54, -0.37)
Community	Attractant	1.1 (0.67, 1.55)
Community	Burned	-0.04 (-0.55, 0.47)
Community	facBurnLag	-0.07 (-0.7, 0.55)
Community	Viewshed	-0.08 (-0.29, 0.14)

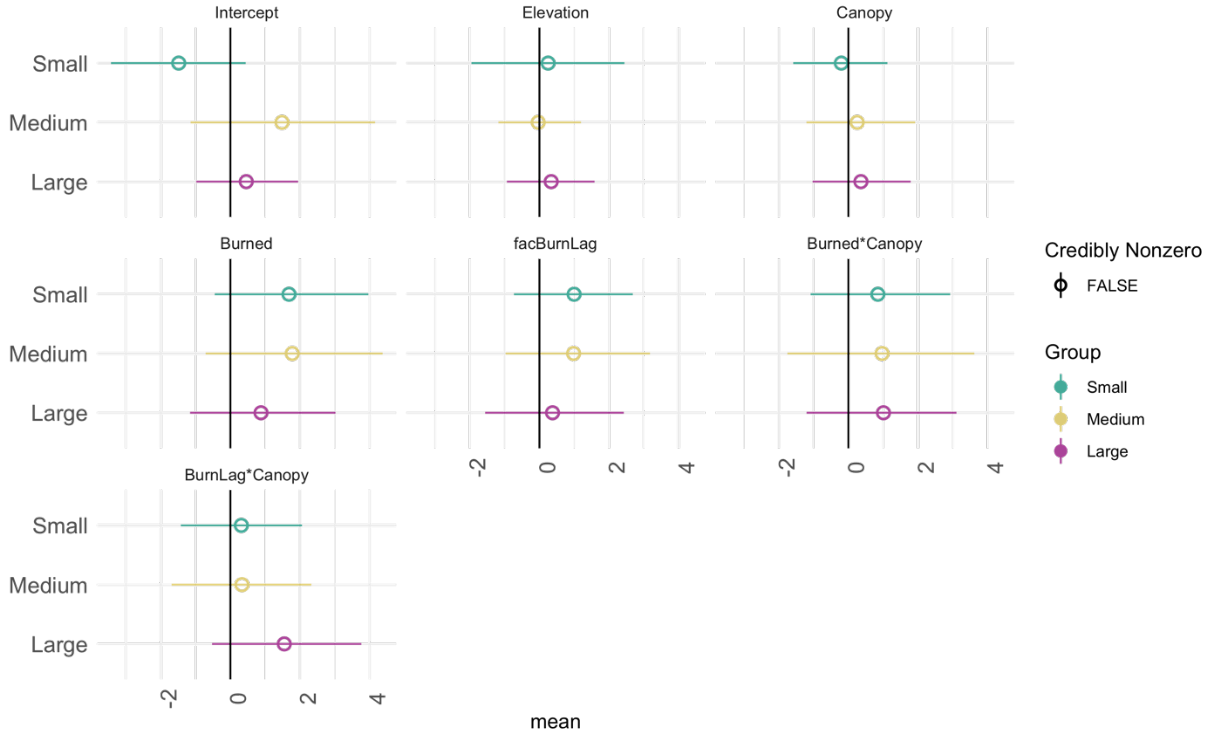

Figure S3. Estimated coefficients for site-specific covariates on probability of site use (Ψ) from the size group multi-species occupancy model (MSOM) fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Group-level estimates are displayed along the y-axis. Coefficient estimates that had 90% confidence intervals that did not overlap zero (Credibly Nonzero) are represented with filled circles.

Table S6. Covariate coefficients for the site use (Ψ) sub-model of the group-size multi-species occupancy model fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Mean estimates and 90% confidence intervals are given for each estimate.

Group	Parameter	Estimate
Large	Intercept	0.46 (-0.98, 1.95)
Large	Elevation	0.34 (-0.93, 1.59)
Large	Canopy	0.36 (-1.03, 1.79)
Large	Burned	0.88 (-1.16, 3.02)
Large	facBurnLag	0.38 (-1.56, 2.42)
Large	Burned*Canopy	1.01 (-1.2, 3.1)
Large	BurnLag*Canopy	1.55 (-0.53, 3.76)
Medium	Intercept	1.48 (-1.14, 4.16)
Medium	Elevation	-0.03 (-1.18, 1.19)
Medium	Canopy	0.25 (-1.2, 1.92)
Medium	Burned	1.78 (-0.71, 4.37)
Medium	facBurnLag	0.98 (-0.97, 3.18)
Medium	Burned*Canopy	0.97 (-1.75, 3.62)
Medium	BurnLag*Canopy	0.33 (-1.69, 2.33)
Small	Intercept	-1.48 (-3.43, 0.44)
Small	Elevation	0.25 (-1.95, 2.44)
Small	Canopy	-0.2 (-1.59, 1.12)
Small	Burned	1.69 (-0.45, 3.96)
Small	facBurnLag	1 (-0.73, 2.68)
Small	Burned*Canopy	0.85 (-1.09, 2.92)
Small	BurnLag*Canopy	0.32 (-1.42, 2.06)

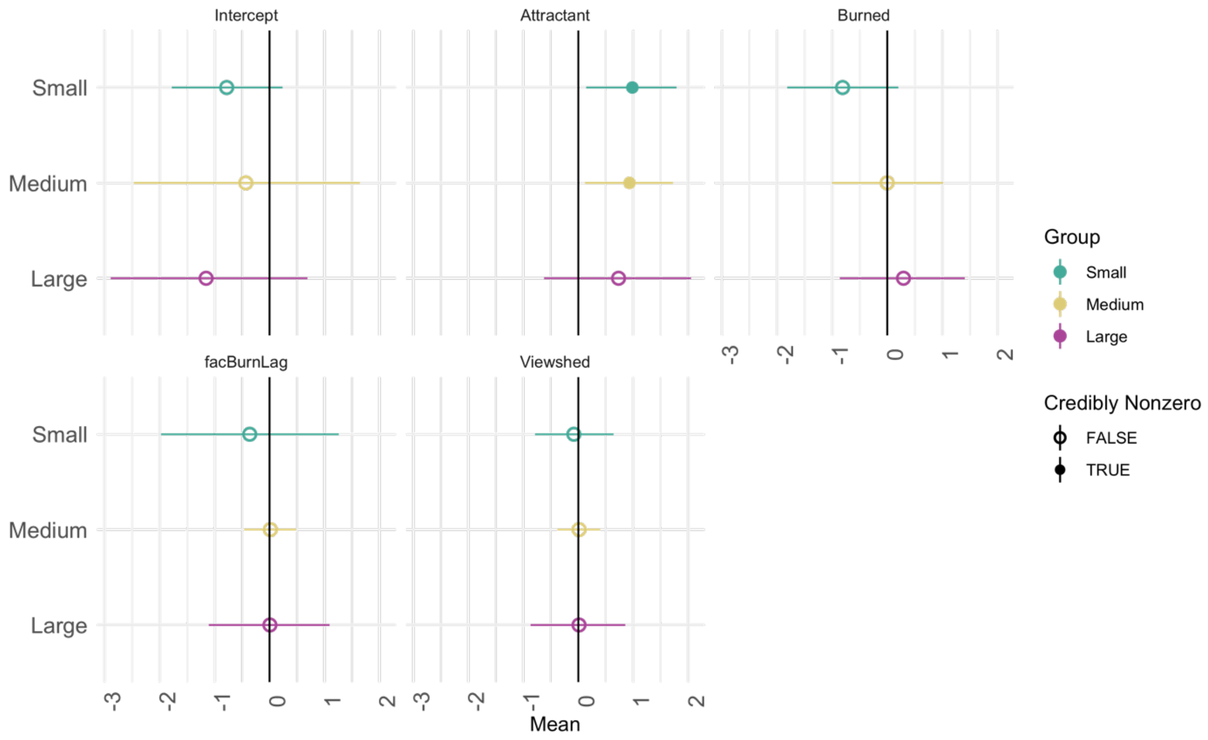

Figure S4. Estimated coefficients of site-specific covariates on intensity of use (*p*) from the size group multi-species occupancy model (MSOM) fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Group-level estimates are displayed along the y-axis. Coefficient estimates that had 90% confidence intervals that did not overlap zero (Credibly Nonzero) are represented with filled circles.

Table S7. Covariate coefficients for the intensity of use (*p*) sub-model of the group-size multi-species occupancy model fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Mean estimates and 90% confidence intervals are given for each estimate.

Group	Parameter	Estimate
Large	Intercept	-1.15 (-2.89, 0.69)
Large	Attractant	0.73 (-0.62, 2.05)
Large	Burned	0.3 (-0.86, 1.41)
Large	facBurnLag	0.01 (-1.1, 1.09)
Large	Viewshed	0.01 (-0.87, 0.85)
Medium	Intercept	-0.43 (-2.47, 1.64)
Medium	Attractant	0.93 (0.12, 1.72)
Medium	Burned	0 (-1, 1.01)
Medium	facBurnLag	0.02 (-0.46, 0.49)
Medium	Viewshed	0.01 (-0.38, 0.4)
Small	Intercept	-0.78 (-1.78, 0.24)
Small	Attractant	0.98 (0.14, 1.79)
Small	Burned	-0.81 (-1.82, 0.2)
Small	facBurnLag	-0.36 (-1.97, 1.26)
Small	Viewshed	-0.08 (-0.79, 0.64)

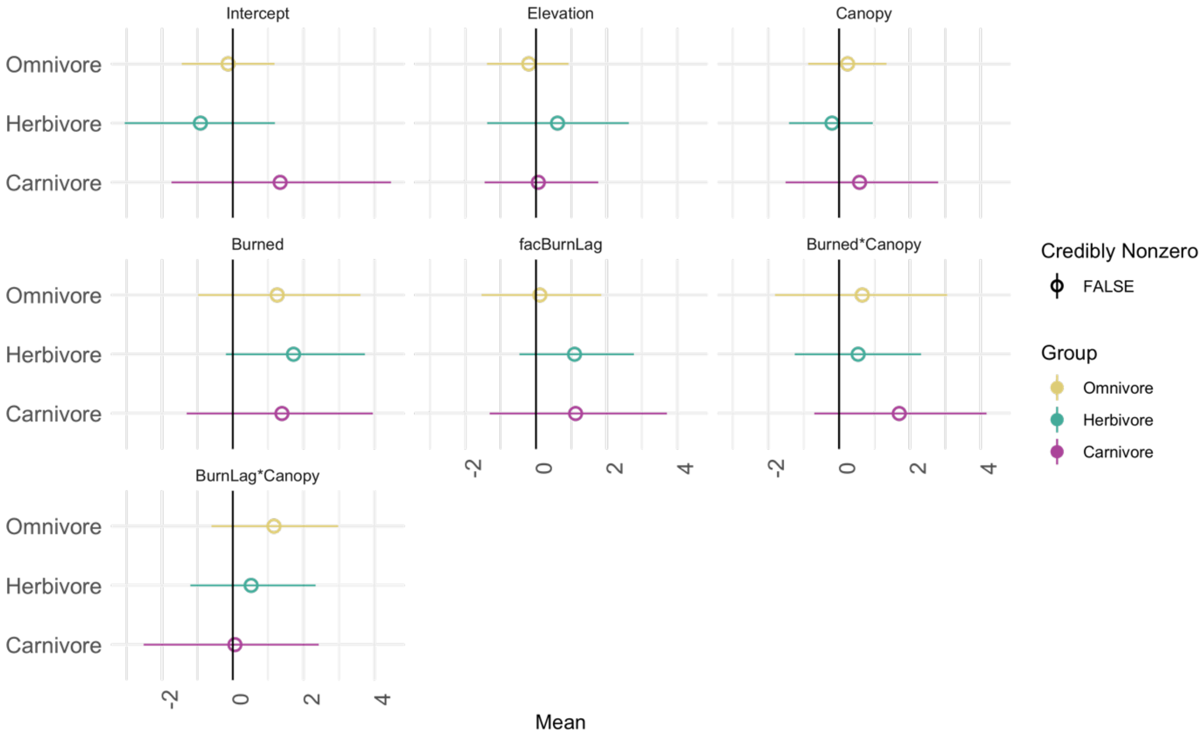

Figure S5. Estimated coefficients of site-specific covariates on probability of site use (Ψ) from the diet group multi-species occupancy model (MSOM) fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Group-level estimates are displayed along the y-axis. Coefficient estimates that had 90% confidence intervals that did not overlap zero (Credibly Nonzero) are represented with filled circles.

Table S8. Covariate coefficients for the site use (Ψ) sub-model of the diet-group multi-species occupancy model fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Mean estimates and 90% confidence intervals are given for each estimate.

Group	Parameter	Estimate
Carnivore	Intercept	1.34 (-1.73, 4.47)
Carnivore	Elevation	0.07 (-1.45, 1.76)
Carnivore	Canopy	0.58 (-1.51, 2.8)
Carnivore	Burned	1.39 (-1.3, 3.96)
Carnivore	facBurnLag	1.12 (-1.31, 3.7)
Carnivore	Burned*Canopy	1.7 (-0.7, 4.17)
Carnivore	BurnLag*Canopy	0.06 (-2.52, 2.43)
Herbivore	Intercept	-0.92 (-3.06, 1.19)
Herbivore	Elevation	0.61 (-1.38, 2.62)
Herbivore	Canopy	-0.2 (-1.41, 0.95)
Herbivore	Burned	1.72 (-0.2, 3.73)
Herbivore	facBurnLag	1.09 (-0.47, 2.77)
Herbivore	Burned*Canopy	0.54 (-1.25, 2.32)
Herbivore	BurnLag*Canopy	0.52 (-1.2, 2.34)
Omnivore	Intercept	-0.13 (-1.44, 1.18)
Omnivore	Elevation	-0.2 (-1.38, 0.92)
Omnivore	Canopy	0.24 (-0.87, 1.34)
Omnivore	Burned	1.25 (-0.98, 3.61)
Omnivore	facBurnLag	0.11 (-1.54, 1.84)
Omnivore	Burned*Canopy	0.66 (-1.81, 3.05)
Omnivore	BurnLag*Canopy	1.16 (-0.6, 2.98)

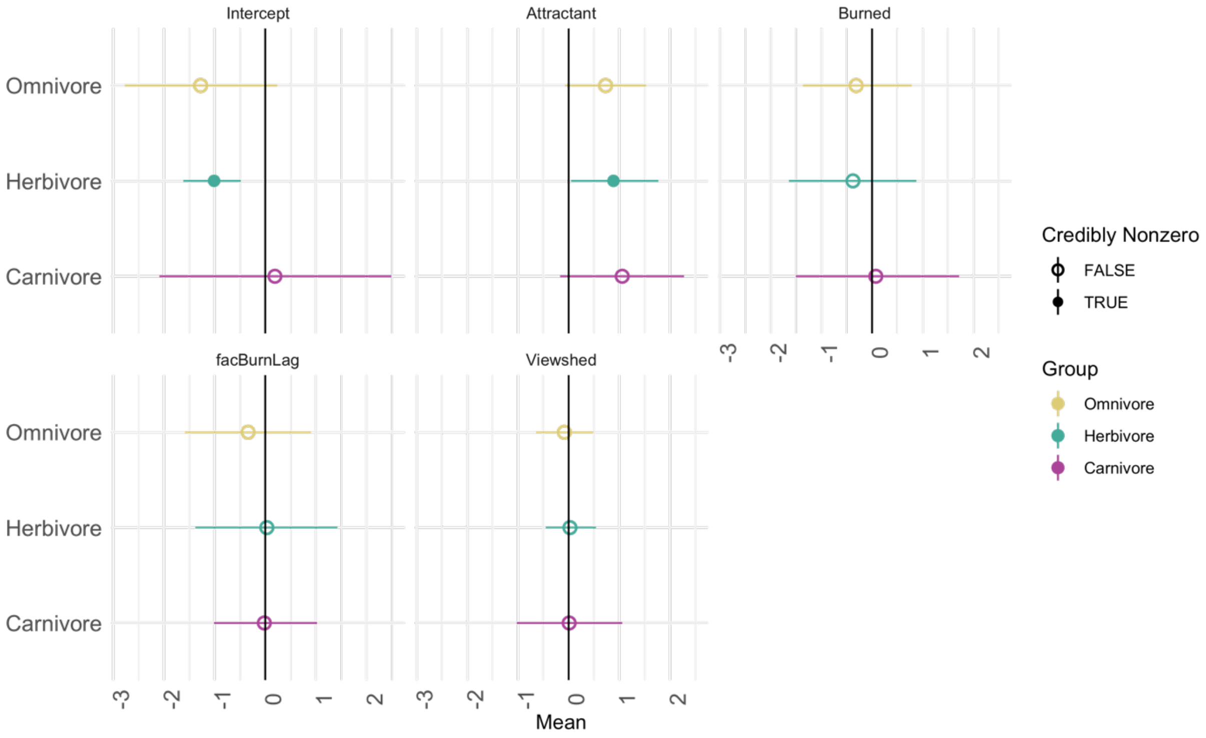

Figure S6. Estimated coefficients of site-specific covariates on intensity of use (*p*) from the diet group multi-species occupancy model (MSOM) fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Group-level estimates are displayed along the y-axis. Coefficient estimates that had 90% confidence intervals that did not overlap zero (Credibly Nonzero) are represented with filled circles.

Table S9. Covariate coefficients for the intensity of use (*p*) sub-model of the diet-group multi-species occupancy model fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Mean estimates and 90% confidence intervals are given for each estimate.

Group	Parameter	Estimate
Carnivore	Intercept	0.19 (-2.09, 2.49)
Carnivore	Attractant	1.06 (-0.17, 2.28)
Carnivore	Burned	0.07 (-1.5, 1.72)
Carnivore	facBurnLag	-0.02 (-1.01, 1.02)
Carnivore	Viewshed	0.01 (-1.02, 1.06)
Herbivore	Intercept	-1.01 (-1.62, -0.48)
Herbivore	Attractant	0.88 (0.05, 1.77)
Herbivore	Burned	-0.38 (-1.64, 0.87)
Herbivore	facBurnLag	0.03 (-1.38, 1.42)
Herbivore	Viewshed	0.03 (-0.45, 0.54)
Omnivore	Intercept	-1.28 (-2.77, 0.24)
Omnivore	Attractant	0.73 (-0.07, 1.53)
Omnivore	Burned	-0.31 (-1.37, 0.78)
Omnivore	facBurnLag	-0.34 (-1.59, 0.9)
Omnivore	Viewshed	-0.09 (-0.64, 0.49)

Supplement 3 – Example Images

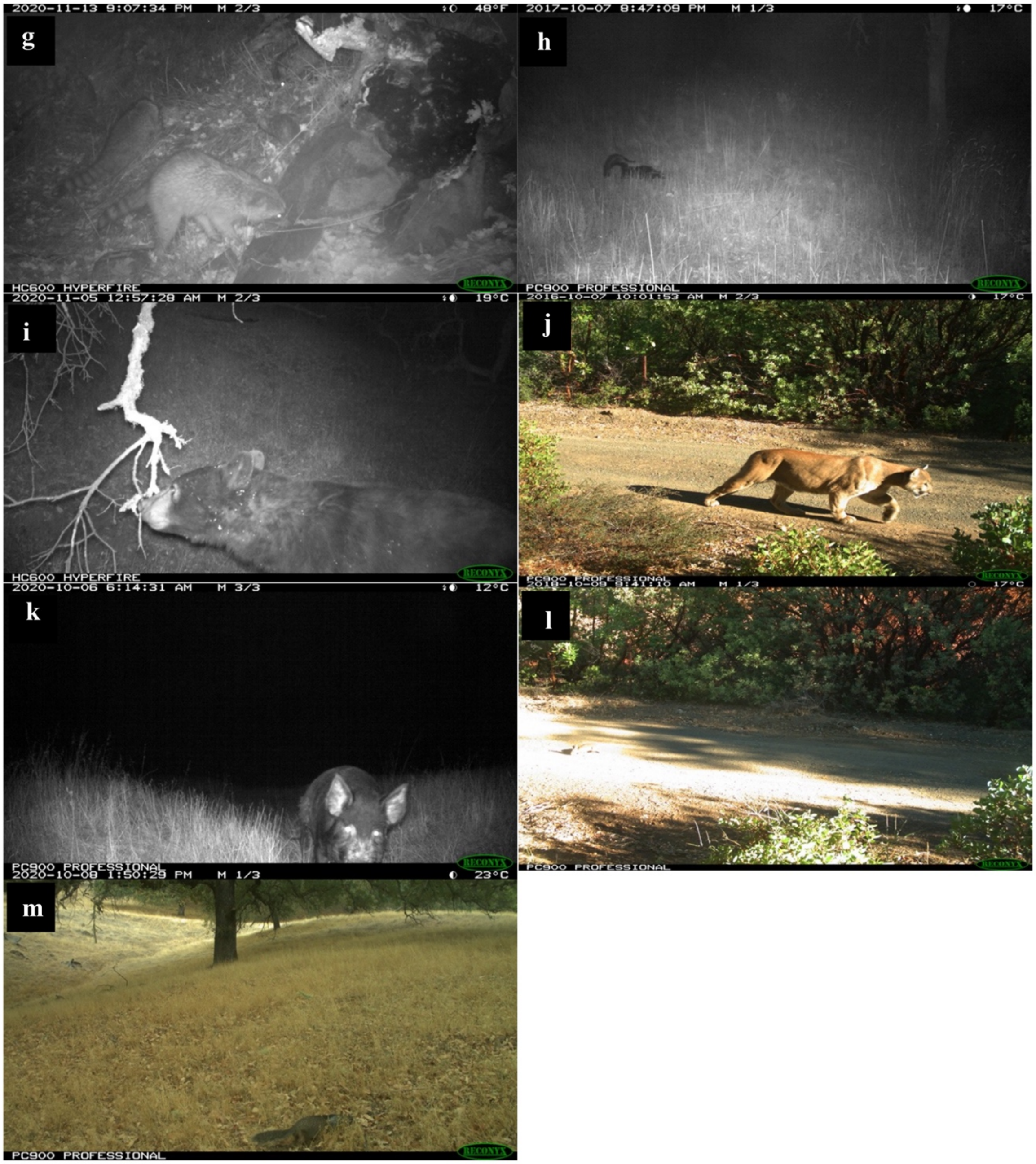

Figure S1. Camera trap images of each detected species at the Hopland Research and Extension Center, CA, USA both before and after the 2018 Mendocino Complex Fire. Detected species included: (a) Bobcat (*Lynx rufus*), (b) Coyote (*Canis latrans*), (c) Black-tailed deer (*Odocoilues hemionus columbianus*), (d) Gray fox (*Urocyon cinereoargenteus*), (e) Western gray squirrel (*Sciurus griseus*), (f) Black-tailed jackrabbit (*Lepus californicus*), (g) Raccoon (*Procyon lotor*), (h) Striped skunk (*Mephitis mephitis*), (i) Black bear (*Ursus americanus*), (j) Mountain lion (*Puma concolor*), (k) Wild boar (*Sus scrofa*), (l) Brush rabbit (*Sylvilagus bachmani*), (m) California Ground Squirrel (*Otospermophilus beecheyi*).

Figure S2. Camera Trap images of a single site (D06) at before, during and after the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center, CA, USA. Photo (a) represents the site before the fire ("Unburned") and (b) illustrates the severity of the fire during the actual event. Post-fire images are representative of the fire parameterizations used within occupancy models: photo (c) shows the recently burned site ("Burned"), (d) shows one year post-fire ("Burn Lag1"), and (e) shows two years post-fire ("Burn Lag 2").

Chapter 3

Movement behavior in a dominant ungulate underlies successful adjustment to a rapidly changing landscape following megafire

Kendall L. Calhoun, Thomas Connor, Kaitlyn M. Gaynor, Amy Van Scoyoc, Alex McInturff, Samantha Kreling, Justin S. Brashares

Abstract

Movement plays a key role in allowing animal species to adapt to sudden environmental shifts. Anthropogenic climate and land use change have accelerated the frequency of some of these extreme disturbances, including megafire. These megafires dramatically alter ecosystems and challenge the capacity of several species to adjust to a rapidly changing landscape. Ungulates and their movement behaviors play a central role in the ecosystem functions of fire-prone ecosystems around the world. Previous work has shown behavioral plasticity is an important mechanism underlying whether large ungulates are able to adjust to recent changes in their environments effectively. Ungulates may respond to the immediate effects of megafire by adjusting their movement and behavior, but how these responses persist or change over time following disturbance is poorly understood. We examined how an ecologically dominant ungulate with strong site fidelity, Columbian black-tailed deer (*Odocoileus hemionus columbianus*), adjusted its movement and behavior in response to an altered landscape following a megafire. To do so, we collected GPS data from 21 individual female deer over the course of a year and used resource selection functions (RSFs) and hidden Markov movement models (HMMs) to assess changes in behavior and habitat selection. We found compelling evidence of adaptive capacity across individual deer in response to megafire. Deer avoided exposed and severely burned areas that lack forage and could be riskier for predation immediately following megafire, but they later altered these behaviors to select for areas that burned at higher severities, potentially to take advantage of enhanced forage. These results suggest that despite their high site fidelity, deer can navigate altered landscapes to track rapid shifts in predation risk and resource availability. This successful adjustment of movement and behavior following extreme disturbance could help facilitate resilience at broader ecological scales.

Introduction

Movement is a key trait that allows animal species to adjust to dynamic landscapes (Abrahms et al. 2021). This ability has become increasingly critical in an age of constant anthropogenic global change and extreme environmental disturbances, such as increasingly frequent and severe megafires (Stott 2016). In fire-prone ecosystems, megafires, defined as wildfires larger than 100 km^2 that surpass the size and severity of historical fires, have become increasingly prevalent (Linley et al. 2022). Fire has served an important ecological and evolutionary role in many of these ecosystems (McLauchlan et al. 2020), but historical policy, climate change, and land use change are responsible for the increasing number of unprecedented megafires. Megafires can dramatically alter ecosystems by suddenly removing resources and triggering rapid conversions in habitat (Linley et al. 2022). Though many wild animal species in these fire-prone ecosystems have adaptations to coexist with their historic fire regimes (Jones et al. 2020; Pausas and Parr

2018), novel megafire regimes may challenge, and even overwhelm, the behaviors and adaptive capacity of individual animals.

By quickly altering landscapes, megafire may impact how some animals are able to navigate and use habitat. Burn severity is a characteristic of fire that defines the loss of below and/or above ground organic matter (J. E. Keeley 2009). High severity fires can remove important structural resources from landscapes (Zachary L. Steel et al. 2021) and even cause direct mortality to animals (Jolly et al. 2022). Changes in structural cover in these systems may alter interspecies interactions, such as predator-prey dynamics, by altering the success of predator hunting strategies and prey predator-avoidance strategies (Doherty et al. 2022). High severity fires may also remove important vegetation food resources (i.e., forbs, grasses, seeds, etc.) and, in turn, populations of herbivorous species (Rickbeil et al. 2017), which may impact populations of species at higher trophic levels. Finally, the short and long-term effects of fire on habitat may be directly related to the dominant vegetation type of that habitat. For example, grassland ecosystems typically recover faster following fire relative to shrubland and woodland systems (Halofsky et al. 2011), which may lead animals to preferentially choose these areas in the time following megafire.

Movement plays a critical role in defining an animal's capacity to adapt and adjust to novel disturbance regimes. Recent work has documented the role movement and behavioral plasticity play in governing the adaptive capacity of species to other forms of global change (Hammond, Palme, and Lacey 2018; Riddell et al. 2018; Schell et al. 2018). For large-bodied animals, plasticity in movement and behavior allows individuals to adjust to changes in their local environments (Suraci et al. 2021; Gaynor et al. 2018). For fire specifically, larger-bodied animals may partition their space-use across recently burned landscapes to take advantage of new resources or avoid risky areas (Nimmo et al. 2019).

Ungulates serve key ecological roles in many fire-prone ecosystems around the world through their herbivory and by serving as a link between different trophic levels. Changes in their movement and behaviors following fire may have important implications for ecosystem-level processes. Fire may influence patterns of ungulate herbivory across landscapes over space and time (Roerick, Cain, and Gedir 2019; Cherry et al. 2018). Past work has specifically documented a "magnet effect" across several ungulate species, where individuals select moderately burned areas that have improved forage post-fire (Allred et al. 2011; Archibald et al. 2005). Following more severe fire events, recent work suggests that ungulate behavioral plasticity may buffer the short-term impacts of megafire as ungulates select for covered, woodland habitat and expand their home ranges to compensate for a decrease in foraging resources (Kreling et al. 2021). Kreling et al. (2021) also ask whether these adjustments could become maladaptive to these populations as megafires become more frequent. The seasonality of fire events may also modulate short- and long-term responses of ungulates, with fires potentially increasing scarcity of rare vegetation resources during the dry seasons or limiting required resources during energetically costly periods of the year (i.e. spring breeding season) (Proffitt et al. 2019).

Adaptive capacity mediated by movement may play an important role in influencing the resilience of ungulate populations to major wildfire events and changes to local fire regimes. Variation in behavior across space permits animals to respond accordingly to dynamic landscapes (Peters et al. 2022; Chimienti et al. 2021). Unlike other large ungulates, behavioral plasticity of mule deer migratory movement specifically has been found to be non-plastic (Sawyer et al. 2018). Alternatively, previous work has also established that mule deer are capable of efficiently navigating burned landscapes to simultaneously minimize predation risk from a variety of predators whilst simultaneously identifying and using areas with forage (Ganz et al. 2022). Therefore, understanding the conditions and thresholds under which behavioral plasticity is adopted as an adaptive strategy may be key in tailoring management for this species following major environmental disturbances. Megafires may overwhelm this capacity and it may take much longer for species to recover to pre-fire conditions due to the dramatic changes imposed on the landscape. In addition, understanding how ungulates spatially compartmentalize specific behaviors across severely burned landscapes, as well as how the distribution of these behaviors changes across time, is essential in defining whether these species can remain resilient to future changes in global fire regimes and how management may best enhance this capacity.

In this study, we examine the long-term consequences of megafire on an ecologically and economically important Californian ungulate, the black-tailed mule deer (*Odocoileus hemionus columbianus*). As a direct follow-up study to the Kreling et al., 2021 study, we investigate how the examined short-term movement responses of deer to megafire vary over the year following fire. We predicted that deer would preferentially use habitat that burned at low severity immediately following the fire to avoid exposure to predators and select for areas more likely to have forage remaining. In line with the magnet effect, we predicted black-tailed deer would select for areas that burned at moderate severities the following growing season due to the increased nutritional value of forage in these areas. We also take a deeper look at the spatial distribution of movement behavioral modes across the burned landscape to determine how behavioral decisions also contribute to adaptive capacity of deer following megafire. Due to the assumed long-lasting impacts of the megafire's size and severity on habitat, we predicted that changes in habitat selection would persist throughout the year following fire. In terms of behavioral modes, we anticipated that black-tailed deer would be more likely to travel through severely burned areas to avoid exposure, and to rest in low severity burned areas where perceived risk may be lower. We predicted that these behavioral adjustments would be apparent throughout the study period.

Methods

Study Site and Fire History

We conducted this study at the Hopland Research and Extension Center (HREC hereafter) in Mendocino County in northern California (39°00′ N, 123°04' W) (Figure 1). HREC is composed of a diverse set of vegetation types including chaparral shrublands, oak woodland savannah, and open grassland. HREC is characterized by a Mediterranean climate with cool, wet winters and warm, dry summers. HREC also operates as a working rangeland landscape, containing a sheep farming facility and several agricultural plots throughout the property.

On July 27, 2018, the River Fire (southern half of the Mendocino Complex Fire), swept through the northern half of HREC, burning approximately 13.76 km^2 (65%) of the property. The 2018 Mendocino complex fire burned 1,858 km^2 total and is currently the third largest wildfire in California's recorded history (CALFIRE-FRAP, 2022). Fires in this region typically burn frequently at relatively low severities in the more open woodland and grassland habitats and more infrequently, but more severely in the dense shrubland chaparral habitats (Syphard and Keeley 2020; van Wagtendonk et al. 2018). The River Fire burned a much larger contiguous area and much more severely than recent fires within HREC. Atypical of fires in woodland fire regimes, several oak trees (*Q. kelloggii*, *Q. douglassi*, and *Q. lobata*), whose acorn masting normally provides a key food resource for local deer populations, were top-killed in certain high severity patches of the this fire.

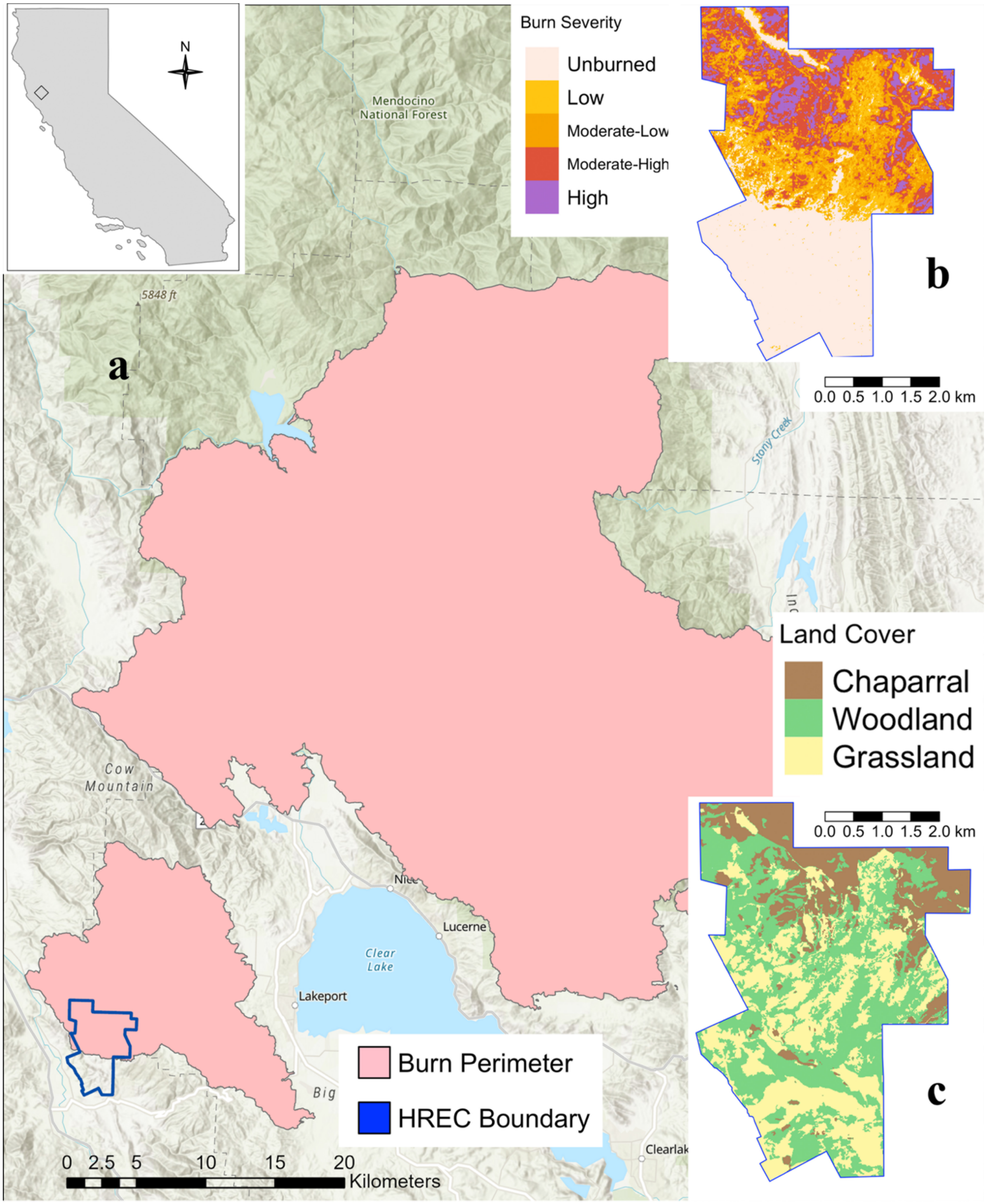

Figure 1. Maps of the 2018 Mendocino Complex Fire and the study site, the U.C. Hopland Research and Extension Center (HREC) (39°00′ N, 123°04’ W). Map “a” displays the total burn perimeter of the Mendocino Complex Fire. This fire burned into HREC on July 27, 2018. Map “b” displays the severity of the fire across the HREC property boundary. Sentinel-2 satellite imagery was acquired via Google Earth Engine to calculate fire severity. Fire severity was quantified as the Differenced Normalized Burn Ratio (dNBR). For visualization purposes, dNBR values were binned into categorical values based on those established by USGS as follows (Unburned = 0-99,

Low = 99-269, Moderate-Low = 269-439, Moderate-High = 439-659, High = 659+). Map "c" displays the compositional makeup of dominant vegetation types across HREC. In this map, yellow denotes grassland, green denotes woodland, and brown denotes chaparral shrubland.

Monitoring Black-tailed Deer Movement and Home Range Estimation

We deployed GPS-collars (Vertex Plus and Lotek Iridum Track M) across 28 female deer between July 2017 and July 2019. These data provided the basis for a natural experiment to observe the effects of megafire on deer movement and behavior. We programmed all collars to record GPS locations once per hour. Deer were captured using Clover traps and were manually restrained to place collars on, without the use of chemical immobilizers in accordance to our permit (permit #P1680002). We monitored deer remotely post-capture for multiple days to ensure that each deer remained healthy following capture and collaring.

To observe how deer movement and behavior changed over time following megafire, we subset the collected GPS data to only include deer that had GPS points that overlapped the fire perimeter of the Mendocino Complex Fire, excluding 4 individual deer. We then subset the collected GPS points temporally into three two-month-long time periods: just after the fire (August 1st – October 1st 2018), the first spring green up following the fire (March 1st – May 1st 2019), and one year post-fire (August 1st – October 1st 2019) (Supplement S1 - Table S1). We included two additional pre-fire time periods to compare deer home range size before and after the fire and to examine any seasonal differences in home range size that may impact our results. These additional pre-fire time periods included: two separate spring seasons before the fire (March 1st – May 1st 2017 and March 1st – May 1st 2018) and just before the fire (May 25th – July 25th 2018). Within each time period, we only included individual deer that had at least 500 recorded GPS locations, excluding 4 individual deer and using the remaining 21 for analyses. We removed 10 erroneous, outlier GPS locations that were greater than 2km from their consecutive points for these deer between hour fixes.

For each deer and within each study period, we used the two months of collected GPS data to estimate individual home range sizes. We used the local convex hull (LoCoH) method to obtain more conservative estimates of home range size (Getz et al. 2007). We calculated 95% isopleths for each individual within each study period using the "adehabitatHR" (v.0.4.19) and "tlocoh" (v.1.40.7) packages in R to create these home ranges (Calenge 2006; Lyons 2018; R Core Team 2021). We used a *k*-nearest neighbor approach with $k = 15$ and did not consider temporal effects ($s = 0$) based on previously determined acceptable k-values for deer in this study area (Kreling et al. 2021; Dougherty, Seidel, and Getz 2018). Of the 21 unique individuals collared across these five time periods, 13 individuals maintained their collars across two or more study periods, resulting in 38 study period-specific home ranges (Supplement S1 – Table S1). To assess whether deer home range sizes continue to change following megafire, we used paired Welch's unequal variance t-test to compare deer home range sizes 1) just after fire ("Recently Burned"), 2) the first spring following fire ("First Spring"), 3) one full year post-fire ("1 Year Post-Fire"), 4) the spring season before fire ("Pre-spring"), and 5) just before the fire burned ("Pre-fire").

Environmental Covariates

We compiled fire and other environmental covariates alongside deer movement data to evaluate black-tailed deer movement responses to megafire over time. We expected that fire severity, predation risk, vegetation type, and time since burning would be strong predictors of both deer habitat selection and deer movement during each post-fire time period. Originally, we planned to include NDVI as a measure of forage availability across the landscape, but measures of NDVI were highly correlated with measures of fire severity, our primary covariate of interest. Therefore, we included fire severity and excluded NDVI. To quantify fire severity on the landscape (Eidenshink et al. 2007), we calculated the differenced Normalized Burn Ratio (NBR) collected via Sentinel-2 (Sentinel Hub 2022) satellite imagery (10m resolution) and processed in Google Earth Engine (Gorelick et al. 2017) from both before (July 25th, 2018) and after (August 25th, 2018) the fire. NBR was calculated using the following equations (J. E. Keeley 2009):

$$\Delta NBR = NBR_{prefire} - NBR_{postfire}$$

$$NBR = \text{Near-infrared (NIR)} - \text{shortwave infrared (SWIR)} / \text{Near-infrared (NIR)} + \text{shortwave infrared (SWIR)}$$

We also included a quadratic term for fire severity to examine whether deer may preferentially select for moderately burned areas that, according to the magnet effect, may eventually have more nutritious forage after vegetation regrowth.

To account for predation risk across the landscape for this study, we included a high-resolution mountain lion habitat suitability map produced for the entire State by Dellinger et al. 2020 in our analyses (Dellinger et al. 2020). This habitat suitability modeling effort used a suite of biotic and abiotic variables, including terrain ruggedness, canopy cover, and a rough categorical estimate of deer density. Mountain lions are the primary predator of black-tailed deer in this system, and we used this habitat suitability map to serve as a proxy of landscape of fear effects (Gaynor et al. 2019) for deer across our study site.

We classified the study site into three broad land cover categories: woodland, shrubland (chaparral), and grassland. To do this, we hand digitized vegetation layers using high-resolution (<1 meter) aerial imagery from the National Agriculture Imagery Program (2014-2015). In 2015, we ground-truthed these digitizations by checking 50 randomly generated points across the study site to validate classifications (results were 98% accurate).

We checked the VIF score of covariates to ensure there was no underlying collinearity between modeled covariates (VIF < 3) and qualitatively inspected plotted covariates as well (Supplement S1: Figure S1Supplement S1: Figure S2).

Resource Selection Functions

We used Resource Selection Functions (RSFs) to assess black-tailed deer habitat selection across each post-fire time period. For the RSFs specifically, we used 95% Kernel Utilization Densities (KUD) in the "adehabitatHR" package in R to home ranges for each deer (Calenge 2006; R Core Team 2021; Barker, Mitchell, and Proffitt 2019). We use KUDs to define homeranges for the RSF to provide better estimates of available space to use for individual animals for probabilistic analyses (Lichti and Swihart 2011). We modeled habitat selection for all time periods combined to improve interpretability of model results. We also included an interaction term between time period and severity (Severity*BurnLag). We included a random effect of "Deer ID" within our

RSF to account for individual differences in behavior and resource availability for each deer (individual deer retained their same “Deer ID” across time periods). For each deer’s time period-specific estimated home range, we randomly generated four-times as many “non-use” points from within each deer’s estimated KUD home range (Kreling et al. 2021). Non-use points were stratified by time period so that the number of non-use points had the same ratio across time periods as the true use points. We compared the environmental characteristics of “used” and “available” GPS points using a logistic regression via the “lme4” (v.1.1.27.1) package in R (R Core Team 2021; Bates et al. 2014).

We used an *a priori* hypothesis-driven approach to select a model to describe deer habitat selection, that included fire severity and its quadratic term (to account for nonlinear effects), predation risk, vegetation type (chaparral, woodland, or grassland), and time since burn as covariate predictors. We used woodland as the reference vegetation category within these RSFs. We randomly sampled “time since burn” for each non-use point as a randomly selected date from within its respective time period. Prior to modeling, we standardized each of the included covariates (mean = 0, standard deviation = 1).

To assess goodness of fit of the RSF model, we used the “performance” (v.0.7.3) package in R (Lüdecke et al., 2021) to calculate marginal and conditional R^2 values for the model and visually inspect overall model fitting.

Hidden Markov Movement Models

While examining habitat selection provides an important opportunity to uncover *where* animals tend to spend time across landscapes, it is equally important to understand *how* animals use the time they spend in the areas they are selecting for and/or against as mediated by behavior.

By defining certain movement parameters (*i.e.* turning angle and step-length), hidden Markov models (HMMs herafter) allow us to predict behavioral states of animals at individual GPS-fixes and compare how the distribution of these states may change in response to environmental covariates across a landscape, such as fire (McClintock et al. 2020). These behavioral states represent types of responses to an animal’s environment such as “foraging”, “traveling”, or “resting” (Clontz et al. 2021).

To assess how deer behavioral decisions were impacted by megafire, we fit a hidden Markov model (HMM) across the combined, three post-burn time periods within our study using the “moveHMM” (v.1.8) package within R (Michelot, Langrock, and Patterson 2016). To understand how deer navigate severely burned landscapes, we modeled an HMM with two behavioral states (state 1 = resting, state 2 = traveling) to increase interpretability and to specifically observe whether deer traveling behavior changes across landscape variables to potentially avoid perceived risks (exposure, predation risk, etc.). We used step length (via von Mises distributions) and turning angle (via gamma distribution) to characterize the two behavioral states. We randomly generated 25 different pairs of starting values from a determined range of plausible starting values for each movement parameter (turning angles and step lengths) (Supplement S1: Table S2). We ran each randomly generated pair on the null-HMM (without covariates) and compared the negative-log likelihood of each. We checked that each model had similar/the same maximum log-likelihood values and we selected the best fitting pair of movement parameters based on maximum likelihood (Michelot et al. 2017).

Using these starting values, we fit a single hidden Markov model with a set of *a priori* selected covariates (*Severity* + *Predation Risk* + *Distance to Water* + *Time Since Burn* + *Vegetation Cover* + *Severity*Time Since Burn*) to estimate how the probability of being in a certain behavioral state (*i.e*. resting vs. traveling) changed as a function of these environmental factors. We then used the "stationary" function of the "moveHMM" package to estimate the probability of each GPS point being in a given behavioral state and used these to create activity budgets by summing the estimated probabilities for being in each state at each recorded GPS point (Langrock et al. 2012). We used a Chi-squared test to assess whether the proportions of the two behavioral states were significantly different across time periods.

We assessed goodness of fit for the HMM using pseudo-residuals drawn from the fit model. Pseudo-residuals of the step length parameter should be normally distributed given good model fit (Farhadinia et al. 2020; Patterson et al. 2009). Therefore, we visually inspected step length pseudo residuals and used a Shapiro-Wilk normality test using a random subset of pseudo residual values (n = 1000).

Results

Home Range Comparison Across Seasons

The average deer home range size across all time periods was 0.33 km^2 (sd ± 0.18). Deer home range sizes were largest in the two time periods directly following the fire ("Recently Burned" and "First Spring") and were smallest in the two pre-fire time periods ("Prespring" and "Prefire") as well as "1 Year Post Fire). The average home range size was 0.40 km^2 (sd ± 0.15) during the "Recently Burned" period and 0.49 km^2 (sd ± 0.15) during the "First Spring" period. During the "1 Year Post Fire" time period the average home range size was 0.19 km^2 (sd ± 0.07). Finally, during the pre-fire time periods, the average deer home range size was 0.24 km^2 (sd ± 0.10) for the "Prespring" time period and 0.18 km^2 (sd ± 0.06) during the "Prefire" time period. (Supplement S1: Table S1; Figure 2). We found no significant difference between deer home range sizes during the "Recently Burned" and "First Spring Periods (t = -1.43, df = 16.87, p-value = 0.17). We did find a significant difference in deer home range size between the "Recently Burned" and "1 Year Post Fire" periods (t = 3.523, df = 11.69, p-value < 0.01), as well as between the "First Spring" and "1 Year Post Fire" periods (t = 5.80, df = 14.79, p-value < 0.01). We found no significant differences between the home range sizes of the two pre-fire time periods, "Prespring" and "Prefire" (t = 1.26, df = 6.11, p-value = 0.25). We also found no significant difference in home range size between the "1 Year Post Fire" and "Prespring" periods (t = -0.92, df = 6.95, p-value = 0.39), as well as between the "1 Year Post Fire" and "Prefire" periods (t = 0.41, df = 10.11, p-value = 0.69) (Table S3).

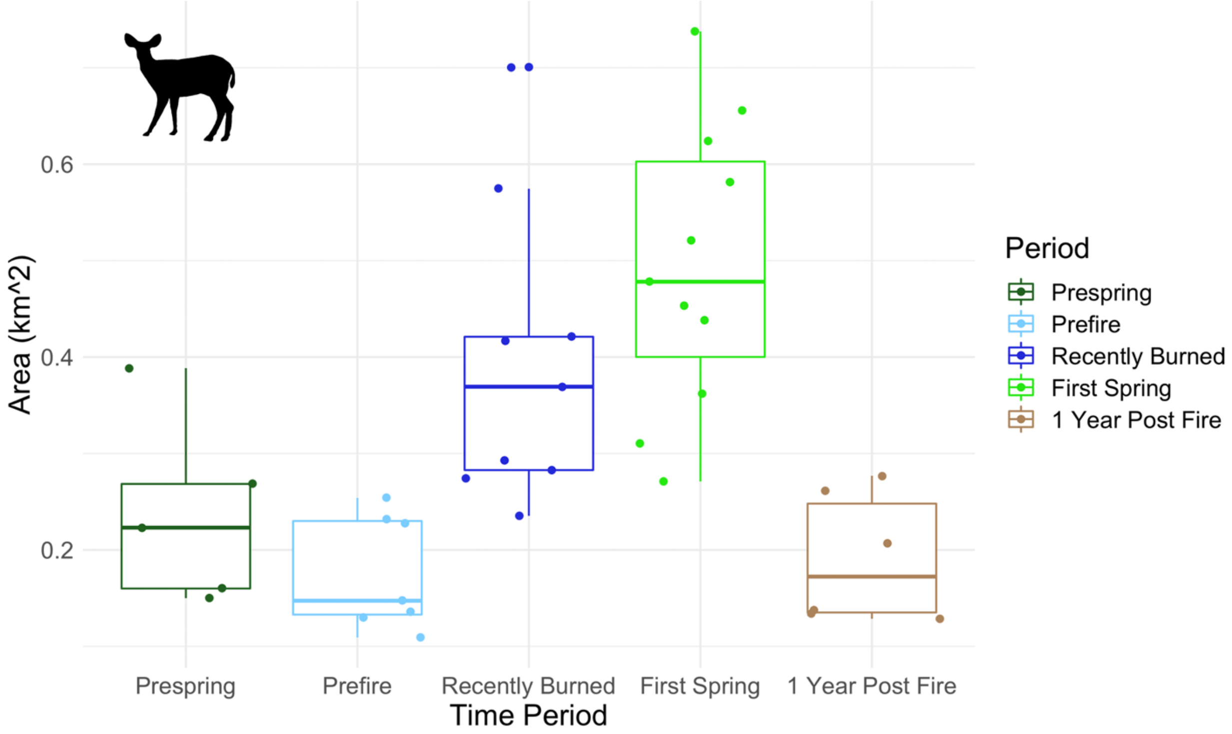

Figure 2. Home range size of black-tailed deer (*O. hemionus columbianus*) across five time periods both before and after the 2018 Mendocino Complex Fire in Hopland, California, USA. The Mendocino Complex Fire burned July 27th, 2018. These study periods include: 2017 Spring and 2018 Spring before the fire ("Prespring"), the summer season just before the fire burned ("Prefire"), directly following the fire ("Recently Burned"), the first spring following the fire ("First Spring"), and 1 full year post fire ("1 Year Post Fire") (*from left to right*).

Resource Selection Functions

Overall, deer avoided areas that burned at high severity, but their selection against burn severity was nonlinear and probability of use was actually highest at intermediate severities (Table 1). However, deer habitat selection of fire burned areas changed over time as an interaction with time since burn. During the "Recently Burned" time period, deer were more likely to avoid high severity areas (Supplement S1: Figure S3). Conversely, fire severity had little effect on deer habitat selection during the "First Spring" time period, and deer selected for higher severity burned areas during the final "1 Year Post Fire" period (Figure 3).

Table 1. Listed output estimates for each covariate of the Resource Selection Function for black-tailed deer (*O. hemionus columbianus*) following the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center in Mendocino County, CA, USA. Beta-coefficients, standard errors, and p-values are listed for each covariate included in the model. For categorical vegetation types, "woodland" was used as the categorical variable. * Indicates statistically significant predicter of habitat selection within the model.

Covariate	**β-Coefficient**	**95% CI**	**p-value**
Intercept	-1.21	[-1.15, -1.26]	<0.001*
Severity	-0.02	[-0.02, -0.03]	0.001*
Severity Squared	-0.04	[-0.03, -0.04]	<0.001*
Predation Risk	-0.09	[-0.08, -0.10]	<0.001*
Chaparral	-0.41	[-0.39, -0.42]	<0.001*
Grassland	-0.16	[-0.15, -0.18]	<0.001*
Time Since Burn	0.02	[0.03, 0.01]	0.01*
Distance to Water	0.01	[0.01, - 0.01]	0.90
Severity * Time Since Burn	0.16	[0.17, 0.15]	<0.001*
Observations	170708		
Conditional R^2	0.030		
Marginal R^2	0.018		

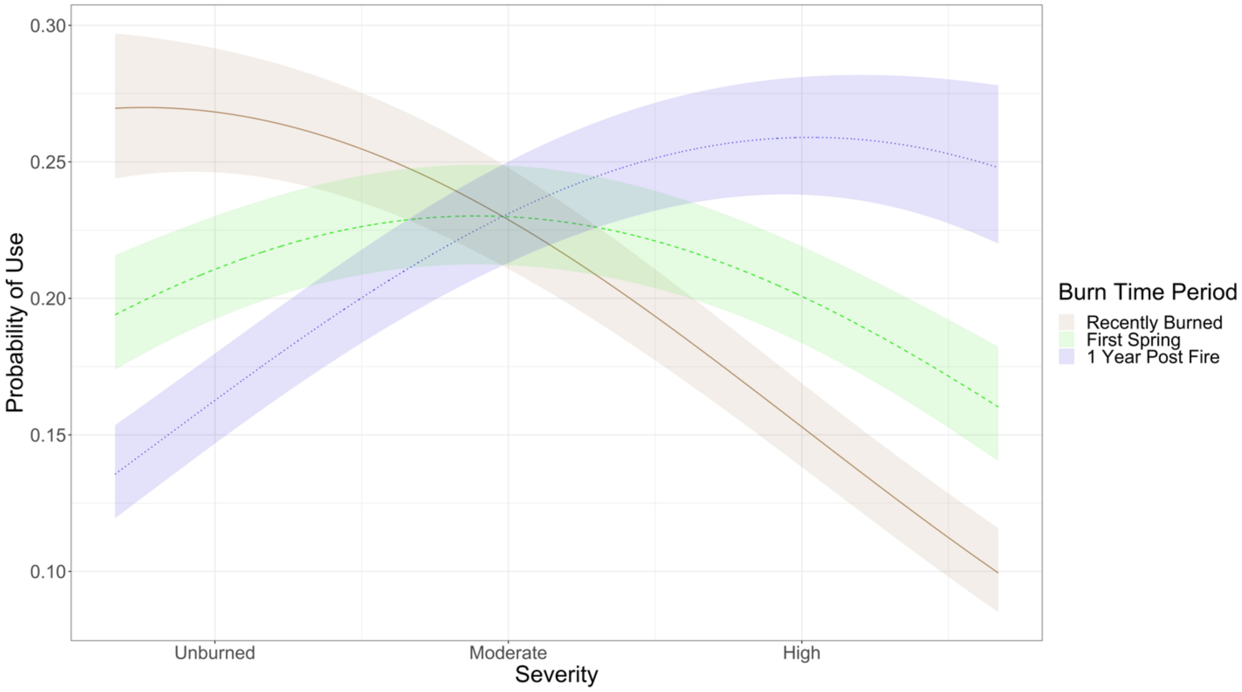

Figure 3. Plotted response curves of deer (*O. Hemionus columbianus*) habitat selection in response to fire severity and time since fire, as predicted from a resource selection function following the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center, CA, USA. To visualize the interaction, we used the midpoint date of each time period to represent a categorical "Time Since Burn" variable in the plot.

Deer preferred woodland habitat over grassland and chaparral following the fire. These vegetation cover preferences persisted across burn severities (Supplement S1: Figure S4) and over time.

Hidden Markov Movement Model Results

We found that the 25 iterations of our null model converged on very similar scores of maximum likelihoods (mean = 266750.40; sd = 956.38). Our best fit hidden Markov model estimated two deer behavioral states: a "resting" state with shorter step-lengths and wider turn angles and a "traveling" behavioral state with longer step-lengths and near 0 turning angles (Supplement S1: Figure S5; Supplement S1: Figure S6). We found a significant difference in the composition of behavioral states between all time periods, with deer spending a greater proportion of time traveling than resting immediately following fire and during the first spring ($\chi^2 = 232.97$, df = 2, p-value < 0.001) (Figure 4; Supplement S1: Table S4) compared to the proportion of time spent in each state during the "1 Year Post Fire" time period.

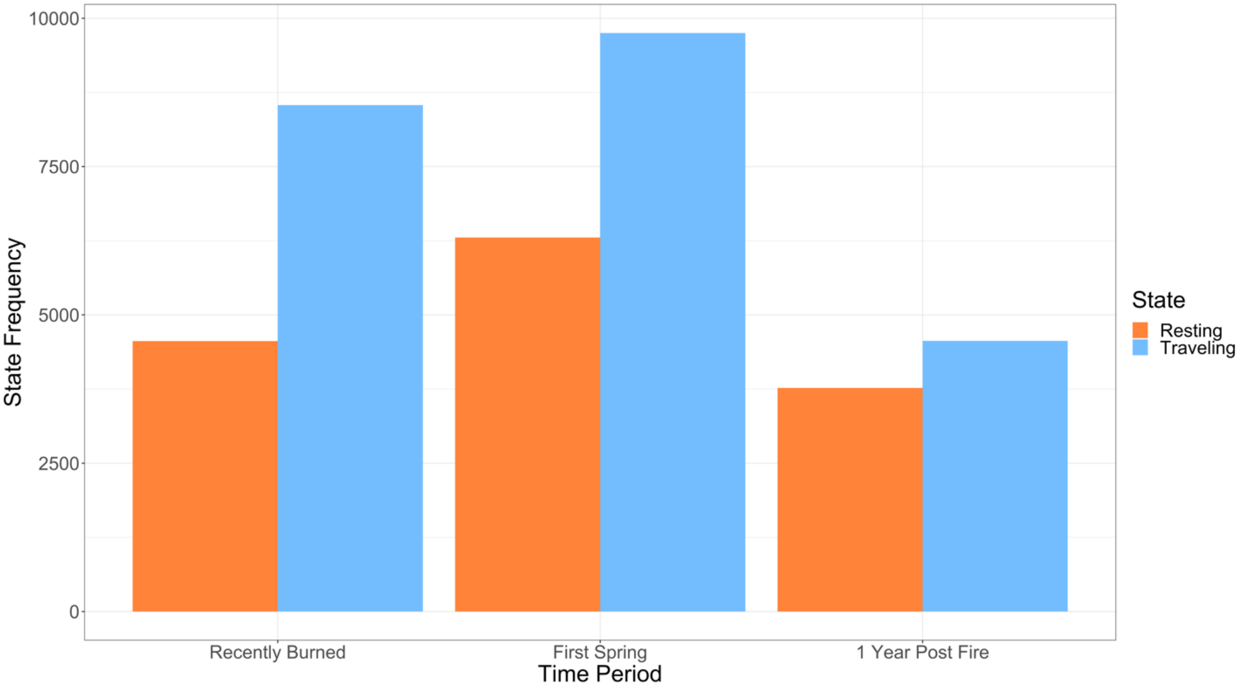

Figure 4. Behavioral state proportions for black-tailed deer (*O, hemionus columbianus*) at the Hopland Research and Extension Center in Mendocino County, California. Behavioral states for deer tracks were estimated for each post-fire time period by the hidden Markov model. State frequencies represented the summed probabilities of each GPS point being in a specific behavioral state.

Deer behavioral states changed as a function of fire severity. Deer were most likely to be in the "resting" behavioral state in unburned and moderately burned areas across all time periods (Figure 5a). At high severities, deer were more likely to be in the "traveling" behavioral state. The probability of deer being in the "traveling" behavioral state at high severities was significantly higher during the "Recently Burned" time period than the other two time periods (Figure 5b). The effect of fire severity on deer behavioral states remained constant across vegetation types as well (Supplement S1: Figure S7).

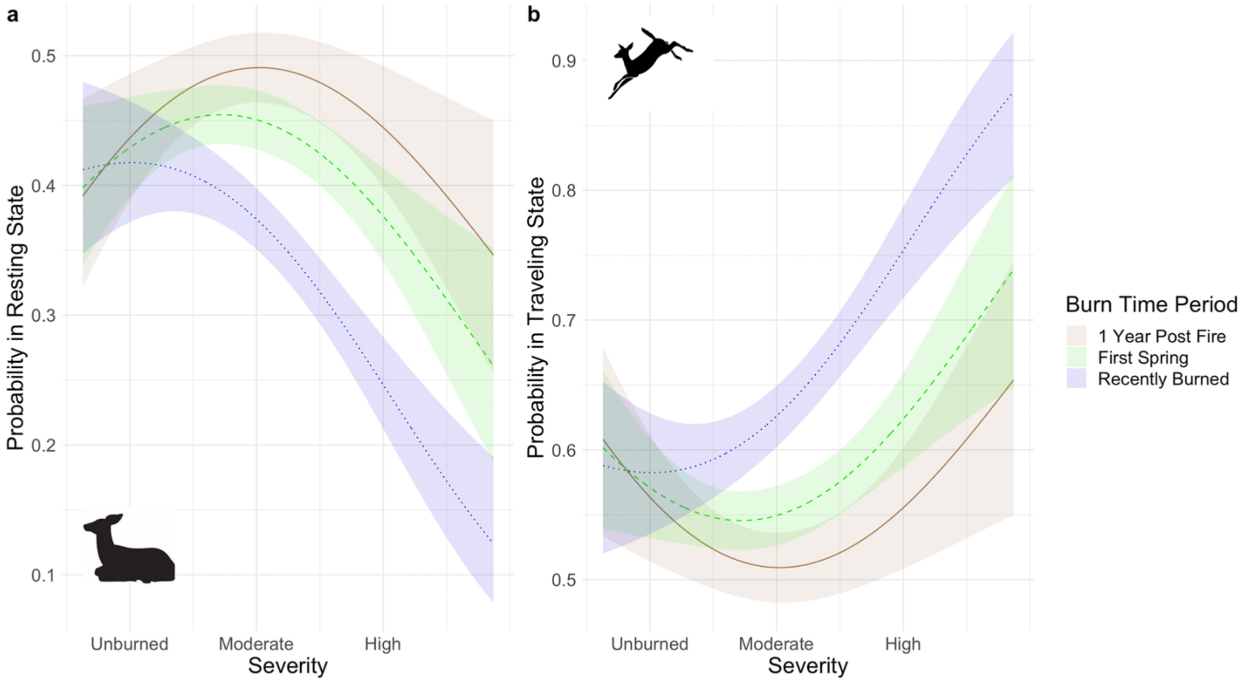

Figure 5. Behavioral state probabilities of black-tailed deer (*O. hemionus columbianus*) as a function of fire severity and time periods following the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center in Mendocino County, California. Plot a) displays the probability of deer being in the "resting" behavioral state as a function of fire severity across the three time periods ("Recently Burned", "First Spring" and "1 Year Post Fire"). Plot b) displays the probability of deer being in the traveling as a function of across the three same time periods. *Note that y-axis scaling of plots a and b are different.

Pseudo residuals drawn from the HMM suggested good model fit for the deer track data. Overall, plotted pseudo-residuals of deer step-lengths appeared normally distributed (Supplement S1: Figure S8). We failed to reject the null hypothesis of the Shapiro-Wilks significance test (W = 0.99, p-value = 0.61), suggesting pseudo-residuals were drawn from a normal distribution.

Discussion

We found evidence to suggest that deer are resilient to the impacts of megafire across a one-year time scale. By adapting their fine-scale behavioral movements, black-tailed deer were able to effectively adjust to a shifting landscape following megafire. We found that black-tailed deer habitat selection and the composition of movement-inferred behavioral states changed as a function of fire severity and time. As Kreling et al., 2021 outlined, ungulate home ranges were larger directly following megafire, but we found that this effect does not persist over time. Deer home range size was significantly higher during the first two time periods following megafire ("Recently Burned" and "First Spring") compared to the pre-fire time periods ("Prespring" and "Prefire") and "1 Year Post-Fire". The scale of the change in home range size observed in this study exceeds what has previously been observed in other studies caused by normal inter-season variation (Ganz et al. 2022; Forrester, Casady, and Wittmer 2015), suggesting megafire had a significant effect on deer home range size and space usage. Directly following megafire, deer strongly avoided areas that burned at high severity, but this effect waned in the initial spring months following fire and inverted by the “1-Year Post-Fire” time period, with deer instead selecting for habitat that burned at higher severities. Similarly, deer were more likely to move than to rest in high severity areas immediately following megafire, but this effect diminished over the course of the year. Though Kreling et al., 2021 previously theorized that megafire could negatively impact the short-term fitness of deer by decreasing the body condition of individuals in this region, our results suggest that the behavioral adjustments made by individuals are effective coping mechanisms for the potential consequences of megafire. This observed behavioral plasticity may also allow deer to eventually take advantage of the resulting resources that become available over time.

Fire severity was a significant predictor of deer habitat selection, but we found that the direction of selection (against high severity areas vs towards high severity areas) changed as an interaction with the amount of time that had passed since the fire burned. As observed in previous studies (Kreling et al. 2021), black-tailed deer avoided high severity burned areas in the immediate aftermath following the fire, potentially to avoid exposure to predators in cover-less areas or to select for areas with higher forage availability. During the first spring green-up following megafire, however, we found that deer began to select for areas that burned at moderate severities. Finally, and contrary to our initial hypotheses, we found that deer actually selected for high severity burned areas during the final time period of the study (“1-Year Post-Fire”). We expected that the high severity burned areas would be depleted of resources for the duration of our study, but these results suggest that once the vegetation in these severely burned areas is able to recover, these areas may attract herbivorous species (Funk, Koenig, and Knops 2016). This is at least partially supported by a brief, qualitative look at the relationship between forage quality, as represented by EVI, and fire severity in the latter time periods of the study (Supplement S1: Figure S9) in which forage quality is higher at moderate severities during “First Spring” and increases at high severities during “1 Year Post Fire”. Both findings during the “First Spring” and “1 Year Post-Fire” time periods support the observed “magnet effect” seen in several other studies in which ungulate species preferentially chose to use recently burned areas that have enhanced forage (Raynor, Joern, and Briggs 2015; Gureja and Owen-Smith 2002), highlighting the important role fire continues to play in these ecosystems for ungulate species despite broader changing trends in fire regimes and climate change.

The proportion of estimated deer behavioral states changed over the course of the study and the probability of being in certain behavioral states (traveling vs resting) varied significantly with fire severity. However, contrary to our initial hypotheses, we found the probability of deer being in a certain behavioral state as function of severity was not constant across time periods, but instead changed across time. Initially following megafire, we found that deer were more likely to travel through severely burned areas and spent more time resting in low severity areas. This strategy may allow deer to avoid spending too much time in riskier, exposed areas, and to spend more time in the limited areas that contain food and shelter (Nimmo et al. 2019). Immediately following megafire, deer moved across larger areas with a higher frequency of larger step-lengths. This, as both a result of and in combination with an overall decrease in resource availability, may potentially result in the decreased body condition of ungulates following megafire observed in the study area (Kreling et al. 2021). However, the probability of deer being in the traveling state in severely burned areas decreased over time. Our results suggest that black-tailed deer in this study area have great capacity for short-term behavioral plasticity to allow quick adjustments of their behavior patterns in response to disturbance and vegetation recovery.

This mirrors similar findings in nearby deer populations that were found to adjust to seasonal changes in food availability by adjusting their habitat selection in the summer and winter months (Bose et al. 2018) and may suggest a broader evolutionary adaptation to these types of extreme fire regimes (Romme et al. 2011). The initial drawbacks of high site fidelity following megafire may be offset by the eventual regrowth of increased vegetation resources in burned areas that deer can take advantage of as time passes, facilitating their choice to remain in these areas following fire (Morrison et al. 2021). While previous work has shown that species traits and fire characteristics play an important part in creating mammalian resilience to fire disturbances (Pocknee et al. 2023), this study highlights the key role of behavior underlying these observed effects.

Changes in deer habitat selection and behavior over time may depend on how and when vegetation cover recovers. We found that deer strongly selected for woodland habitat and, as expected, strongly selected against chaparral habitat, which burns naturally at high severities and is very exposed following wildfire. Deer likely avoided these open areas to avoid conspicuous encounters with predators (Pierce, Bowyer, and Bleich 2004). We did not find a relaxation in the avoidance of high predation risk areas over time following wildfire as anticipated, but predator avoidance may instead be represented by the selection against fire severity and/or certain vegetation type parameters within the model. Future work that utilizes concurrent movement data from both ungulates and their predators could help fill this gap by explicitly examining how predator-prey interactions change following megafire and elucidate whether and for how long these events amplify or diminish the intensity of these interactions (Doherty et al. 2022).

During this study, we observed a preference for burned areas by black-tailed deer in the latter time periods, potentially highlighting some of the benefits of returning wildfire to fire adapted ecosystems. Whereas megafire is a more extreme example of fire disturbance, more moderate disturbances such as prescribed fire and/or managed wildfire are known to perform important ecological work in maintaining key ecosystem functioning for local communities (Sangha et al. 2021) and generating improved habitat and resources for wildlife (Connor et al. 2022), without the more deleterious impacts created initially by megafire. These managed wildfire approaches also serve an important function in reducing the incidence of megafires by promoting landscape heterogeneity and reducing continuous fuel loads (Coppoletta, Merriam, and Collins 2016; Stephens et al. 2014). Thus, utilizing fire management may simultaneously accomplish important wildlife conservation goals (habitat creation and maintenance) and wildfire management goals (megafire prevention) in similar fire-prone ecosystems.

We found evidence to suggest that deer are resilient to the impacts of megafire on a 1-year time scale, but more work is necessary to understand whether these initial responses translate into longer term resilience. The lagged effects of megafire may present more challenges to species by altering longer cycles in resource availability (Abella and Fornwalt 2015) as well as interspecies interactions (Nimmo et al. 2021). For example, in oak woodland savannas where acorn masting is a primary food resource for many herbivorous species (Schnurr, Ostfeld, and Canham 2002; W. J. McShea and Schwede 1993), megafires that top-kill mature oak trees could dramatically alter the availability of these resources until oaks are able to regenerate and begin masting again. These indirect impacts could have powerful effects on future population dynamics through responses like individual fitness and reproduction across the previously burned landscape. Future work that examines how megafire influences the density and demographic trends of mule deer across longer time periods could help assess the resilience of the species across broader temporal scales and help define the potential consequences of megafire on longer-term interspecies interactions such as herbivory and predation.

Conclusion

Despite having naturally high site fidelity in the region of our study, we found that this black-tailed deer population had a great deal of adaptive capacity to change their movement and behavior to respond to the impacts and eventual resources following megafire. Climate change and climatic disturbances (such as megafire) may have a more severe impact on species that are unable to adjust their behavior to accommodate sudden changes in their environments. Resilience of dominant herbivores could help facilitate ecological resilience at broader trophic levels following disturbance. We can help facilitate and boost the natural resilience we observed of mule deer and other ungulates through land and fire management that promote the benefits of fire while simultaneously avoiding the immediate drawbacks of megafire. Identifying the mechanism by which these layers of resilience are produced would not be possible without uncovering the nuances of animal behavior that underly these observed responses.

Acknowledgements

We recognize that UC Berkeley sits on the territory of xučyun (Huichin), the ancestral and unceded land of the Chochenyo speaking Ohlone people, the successors of the sovereign Verona Band of Alameda County. This land was and continues to be of great importance to the Muwekma Ohlone Tribe and other familial descendants of the Verona Band. In addition, we recognize that the land this research was conducted on is the traditional land of the Sho-Ka-Wah of the Central Pomo people.

We would like to thank Janelle Dorcy, Alison Smith, Troy McWilliams, and the rest of the Hopland Research and Extension Center staff for their support in making the fieldwork component of this study possible. The California Department of Fish and Wildlife and the University of California—Berkeley Animal Care and Use Committee approved all capture procedures. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Supplement for Chapter 3

Supplement S1 – Additional Figures and Tables

Table S1. Sample size and average home range size of deer (*Odocoileus hemionus* columbianus) collared at the Hopland Research and Extension Center, CA, USA before and after the Mendocino Complex Fire in 2018. The Mendocino Complex Fire burned on July 27th, 2018.

Time Period	***Dates***	***n (Number of Collared Deer)***	***Average Home Range Size (km^2)***	***Home Range Size SD***
Prespring	March 1, 2017 – May 1, 2018 March 1, 2018 – May 1, 2018	n = 5	0.24	±0.10
Prefire	May 25, 2018 – July 25, 2018	n = 7	0.18	±0.06
Recently Burned	August 1, 2018 – October 1, 2019	n = 9	0.40	±0.15
First Spring	March 1, 2018 – May 1, 2018	n = 11	0.49	±0.15
1 Year Post Fire	August 1, 2019 – October 1, 2019	n = 6	0.19	±0.07

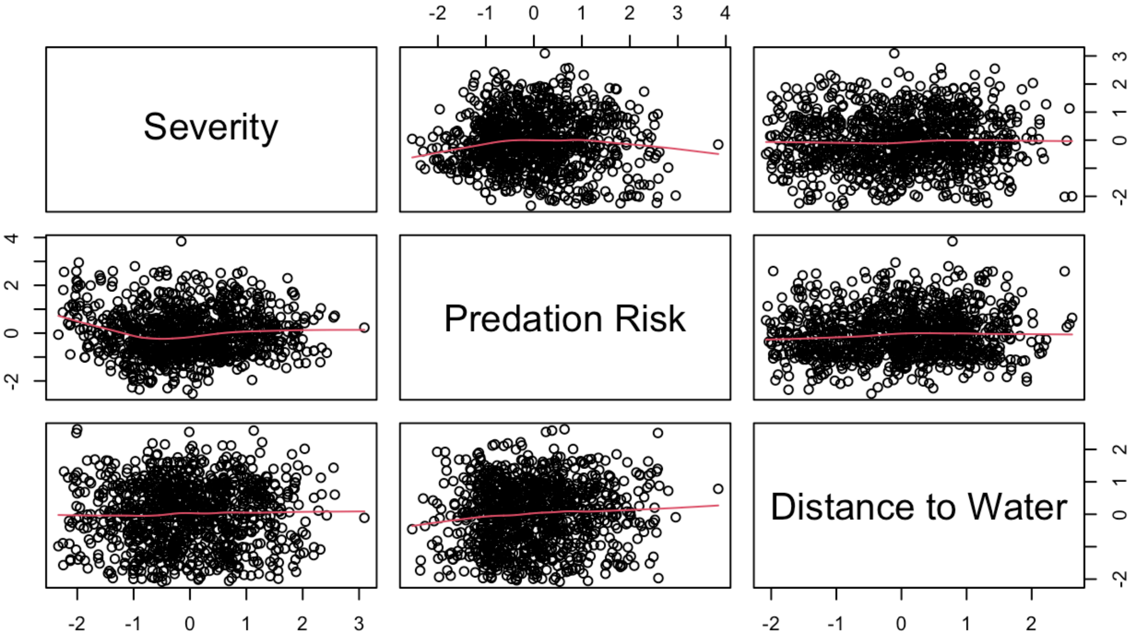

Figure S1. Pairwise plots of continuous covariates extracted at the Hopland Research and Extension Center CA, USA used for deer resource selection function models and hidden Markov models. Plots were visually inspected to ensure there was no underlying covariance within models.

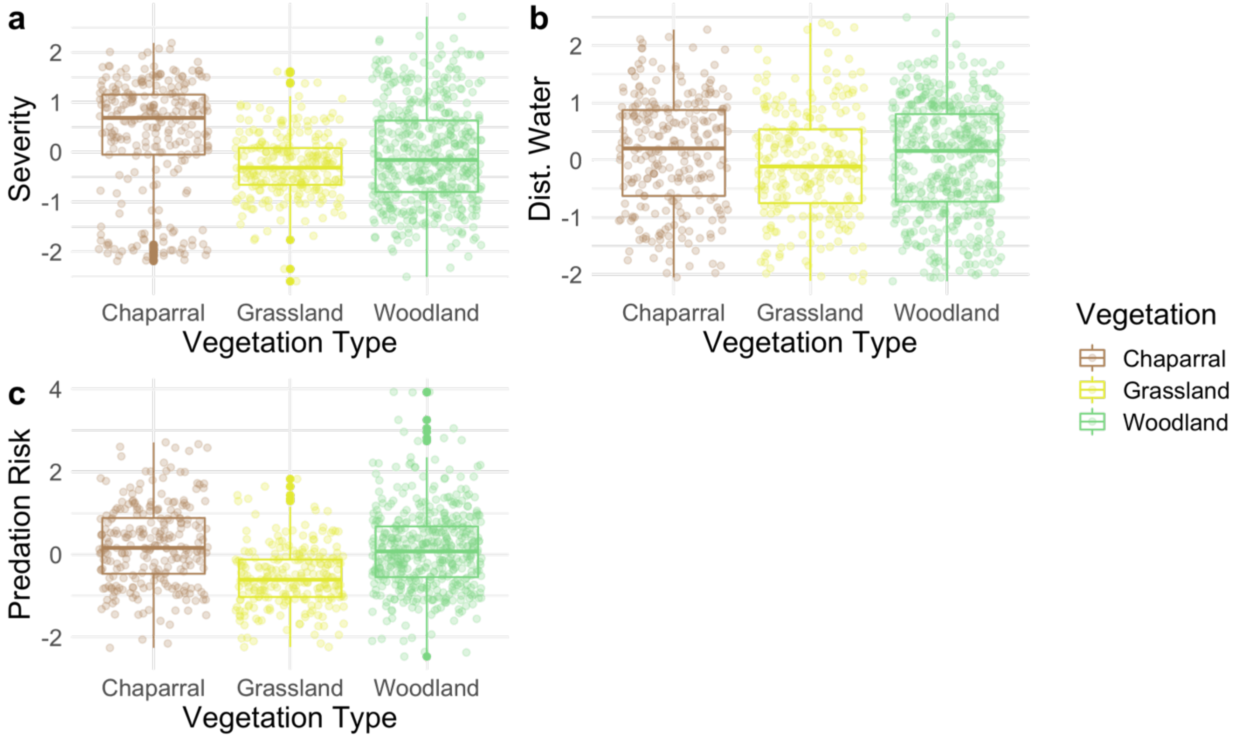

Figure S2. Pairwise plots of continuous covariates extracted at the Hopland Research and Extension Center, CA, USA against categorical dominant vegetation types. These covariates were used for deer resource selection function models and hidden Markov models. Plots were visually inspected to ensure there was no underlying covariance within models.

Table S2. Starting parameter value ranges for deer behavioral state estimation at the Hopland Research and Extension Center, CA, USA via the two-state hidden-Markov model (HMM). We estimated two behavioral states using the HMM: 1) Resting and 2) Traveling. We randomly selected values from within these ranges for each state in 25 model iterations. We compared the Maximum Likelihood across models to ensure they converged similarly and selected the starting parameters from the model that had the best fit in terms of maximum likelihood.

Parameter		***Resting***	***Traveling***
Step Length mean	min	0	400
	max	100	500
Step Length standard deviation	min	50	100
	max	75	200
Turning Angle mean		π	0
Turning Angle concentration	min	0.1	0.5
	max	0.5	3
Zero mass parameter		0.001040555	0.001040555

Table S3. Welch's t-test results of home range size comparisons across different time periods before and after the 2018 Mendocino Complex Fire. The 2018 Mendocino Complex Fire burned through the Hopland Research Extension Center July 27, 2019. "Recently Burned" corresponds to deer home ranges estimated between August 1st, 2018 – October 1st, 2018. "First Spring" corresponds to home ranges estimated between March 1st, 2019 – May 1st, 2019. "1 Year Post Fire" corresponds to home ranges estimated between August 1st, 2019 – October 1st, 2019. "Prespring" corresponds to two combined springs seasons that occurred before the date of the fire: March 1st, 2017 – May 1st, 2017 and March 1st, 2018 – May 1st, 208. "Prefire" corresponds to deer home ranges estimated between May 25th, 2018 – July 25th, 2018. * denotes significant difference in home range estimates.

Test	**t**	**df**	**p-value**
Recently Burned x First Spring	-1.434	16.868	0.170
Recently Burned x 1 Year Post Fire	3.523	11.689	0.004*

Recently Burned x Prespring	2.355	11.645	0.037*
Recently Burned x Prefire	3.921	10.786	0.002*
First Spring x 1 Year Post Fire	5.802	14.786	0.001*
First Spring x Prespring	4.122	11.652	0.002*
First Spring x Prefire	6.385	14.184	0.001*
1 Year Post Fire x Prespring	- 0.915	6.9523	0.391
1 Year Post Fire x Prefire	0.408	10.113	0.692
Prespring x Prefire	1.258	6.112	0.254

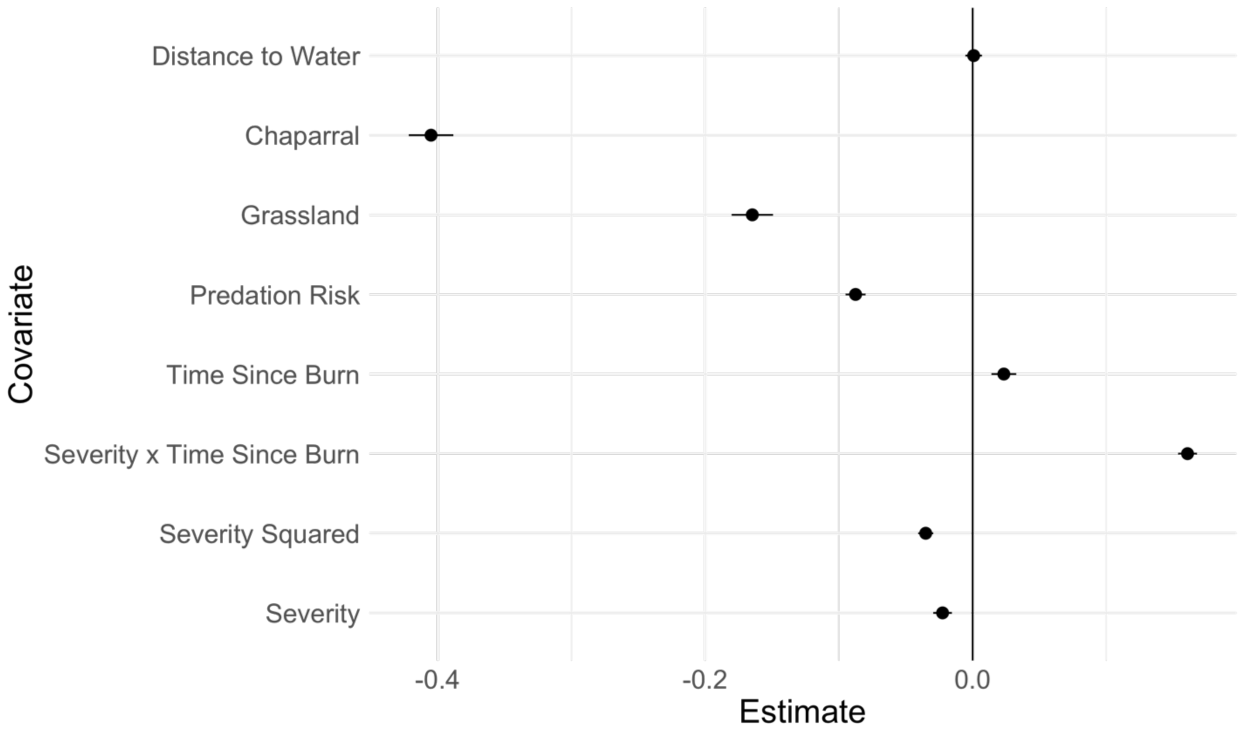

Figure S3. Plotted beta coefficients of the Resource Selection Function model for black-tailed deer (*O. hemionus columbianus*) following the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center, CA, USA. Associated standard error bars for each covariate are also plotted. All covariates to the left of the origin (0.0) are negatively associated with deer habitat selection all covariates to the right of the origin are associated with positive habitat selection. Covariates whose standard error ranges that do not overlap 0 were found to be statistically significant relationships.

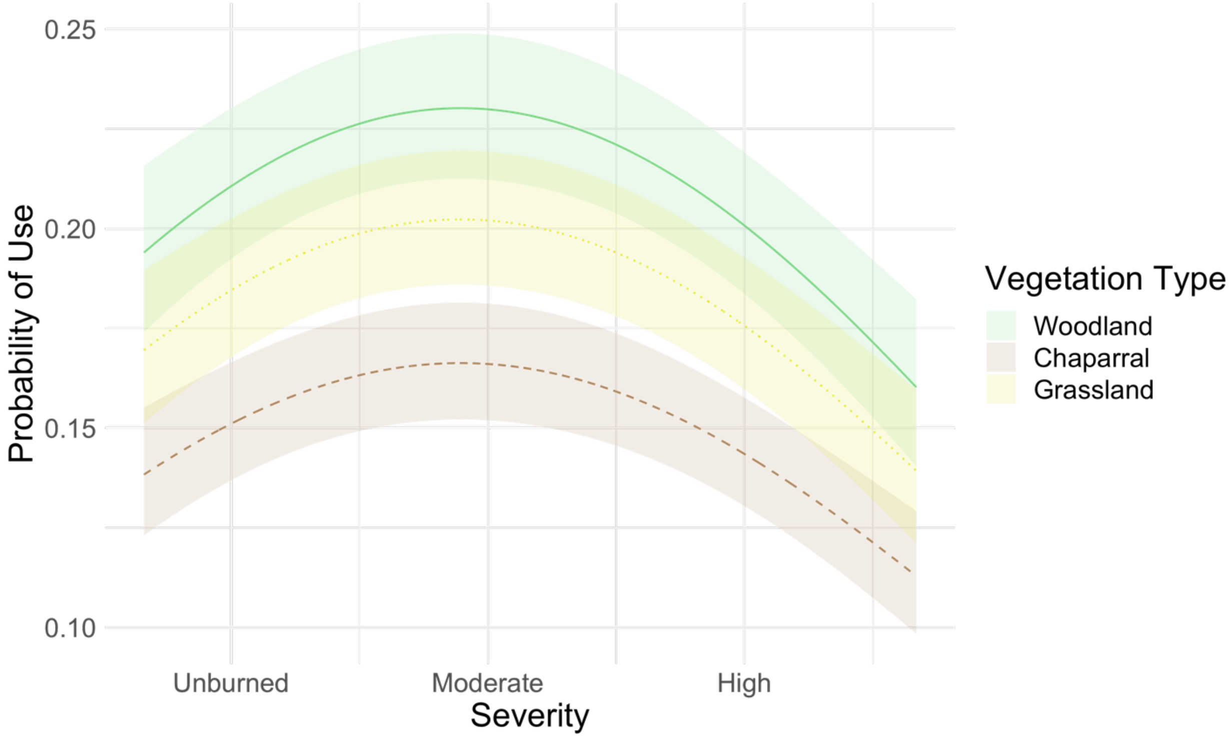

Figure S4. Plotted effects of fire severity and vegetation type on black-tailed deer (*O. hemionus columbianus*) habitat selection, as predicted from a Resource Selection Function following the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center, CA, USA. To visualize the interaction, we used the midpoint date of each time period to represent a categorical "Time Since Burn" variable in the plot.

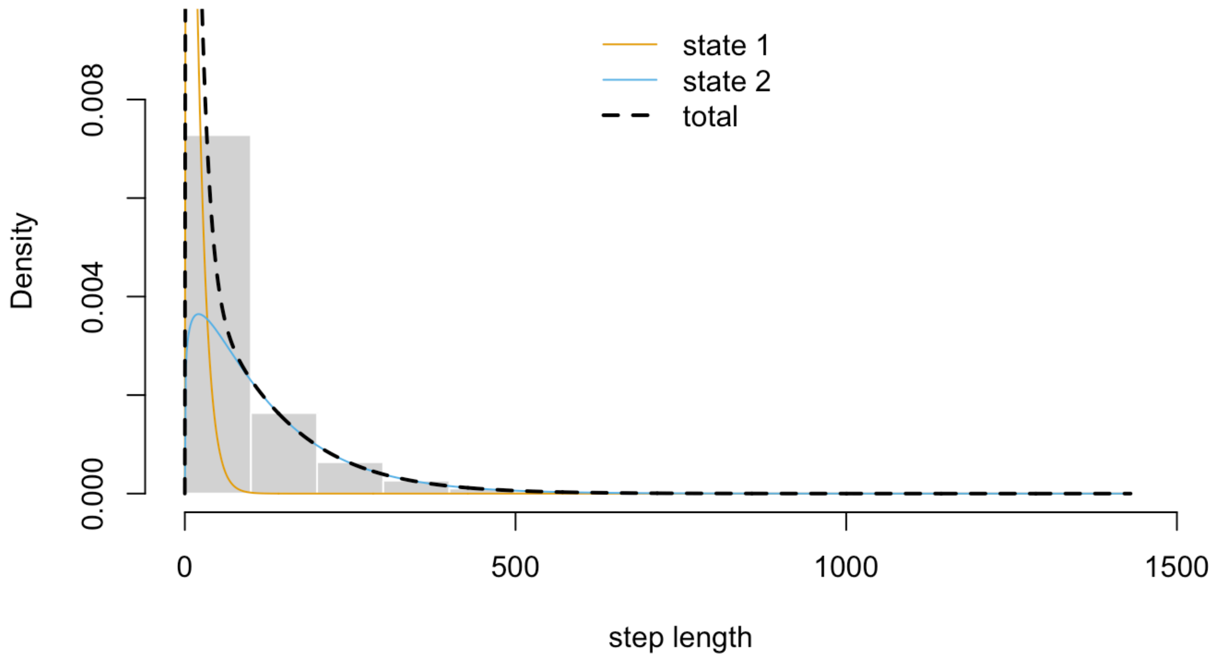

Figure S5. Histogram of step lengths and density of each predicted state from the best fitting hidden Markov model for deer behavior at the Hopland Research and Extension Center, CA, USA. State 1 corresponds to “resting” and State 2 corresponds to “traveling”.

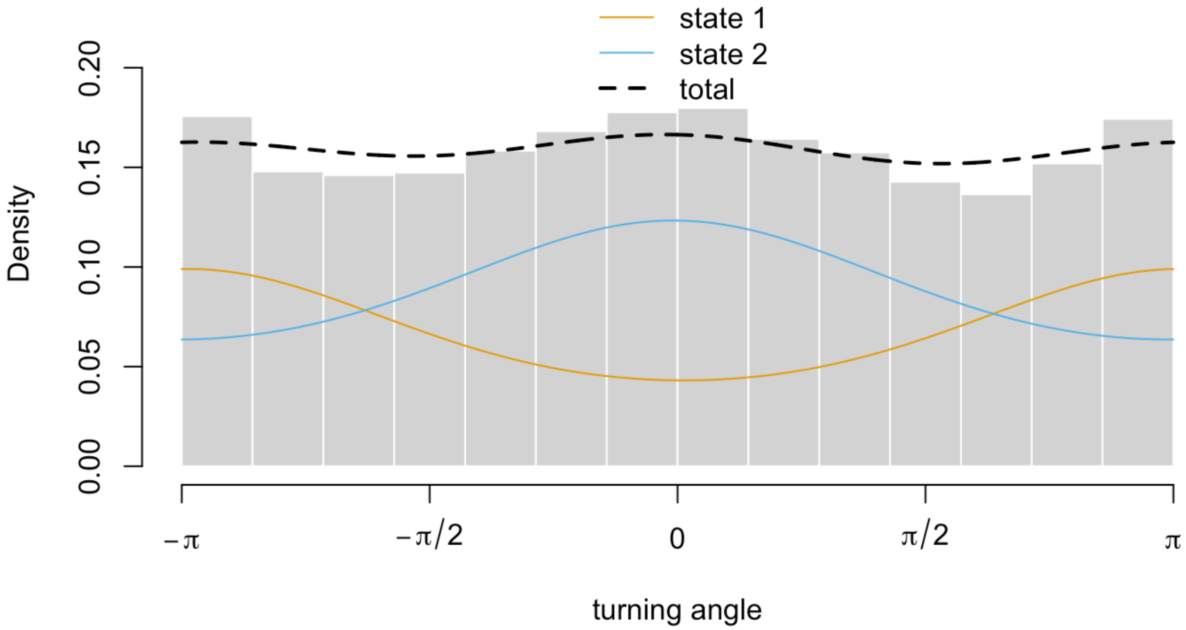

Figure S6. Histogram of turning angles and density plots of each predicted state from the best fitting hidden Markov model for deer behavior at the Hopland Research and Extension Center, CA, USA. State 1 corresponds to "resting" and State 2 corresponds to "traveling".

Table S4. Contingency table of deer behavioral states as estimated from the hidden Markov model for deer behavior at the Hopland Research and Extension Center. Behavioral states for each GPS-point were estimated using the "stationary" function of the "moveHMM" (v.1.8) package in R where State 1 = resting and State 2 = traveling. State probabilities for each GPS-point were then summed across within each Time Period (*Recently Burned, First Spring, or 1 Year Post Fire*).

State	*Recently Burned*	*First Spring*	*1 Year Post Fire*
1 (Resting)	4558.304	6304.815	3767.693
2 (Traveling)	8553.696	9750.185	4562.307

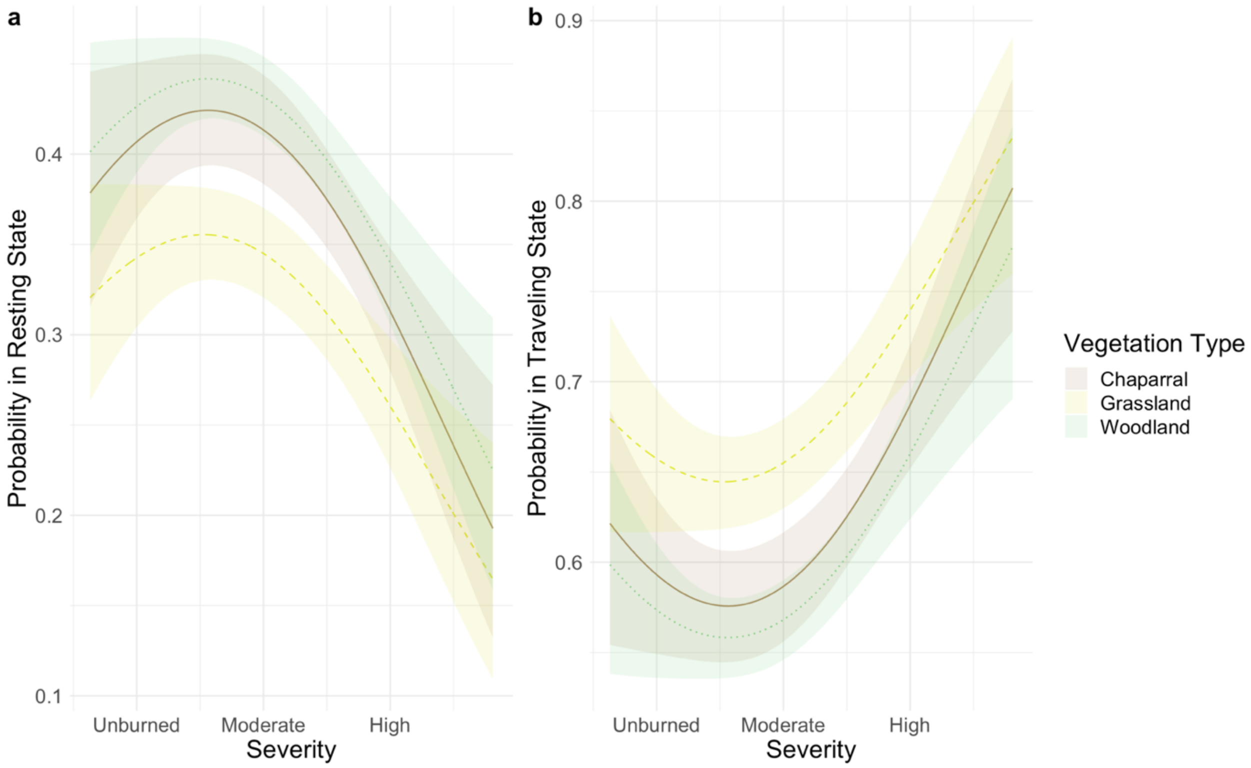

Figure S7. Behavioral state probabilities of black-tailed deer (*O. hemionus columbianus*) as a function of fire severity and dominant vegetation type. Plot a) displays the probability of deer being in the "resting" behavioral state as a function of severity across the three dominant vegetation types ("Chaparral", "Grassland", and "Woodland"). Plot b) displays the probability of deer being in the traveling state as a function of severity and across the three dominant vegetation types. *Note that y-axis scaling of plots a and b are different.

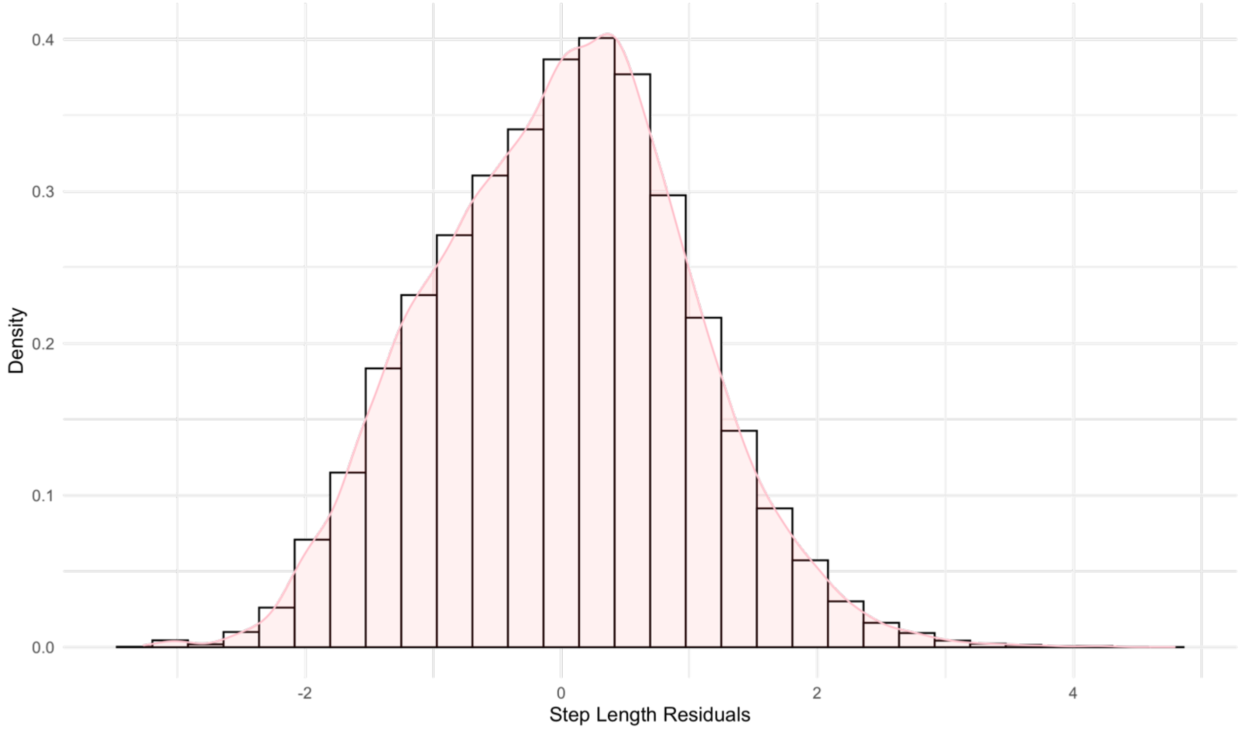

Figure S8. Plotted histogram of step-length pseudo residuals from the fit hidden Markov model. The hidden Markov model was fit on deer GPS data following the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center, CA, USA. We drew a random sample of pseudo-residuals from the fitted HMM to check goodness of fit of the model (n = 1000).

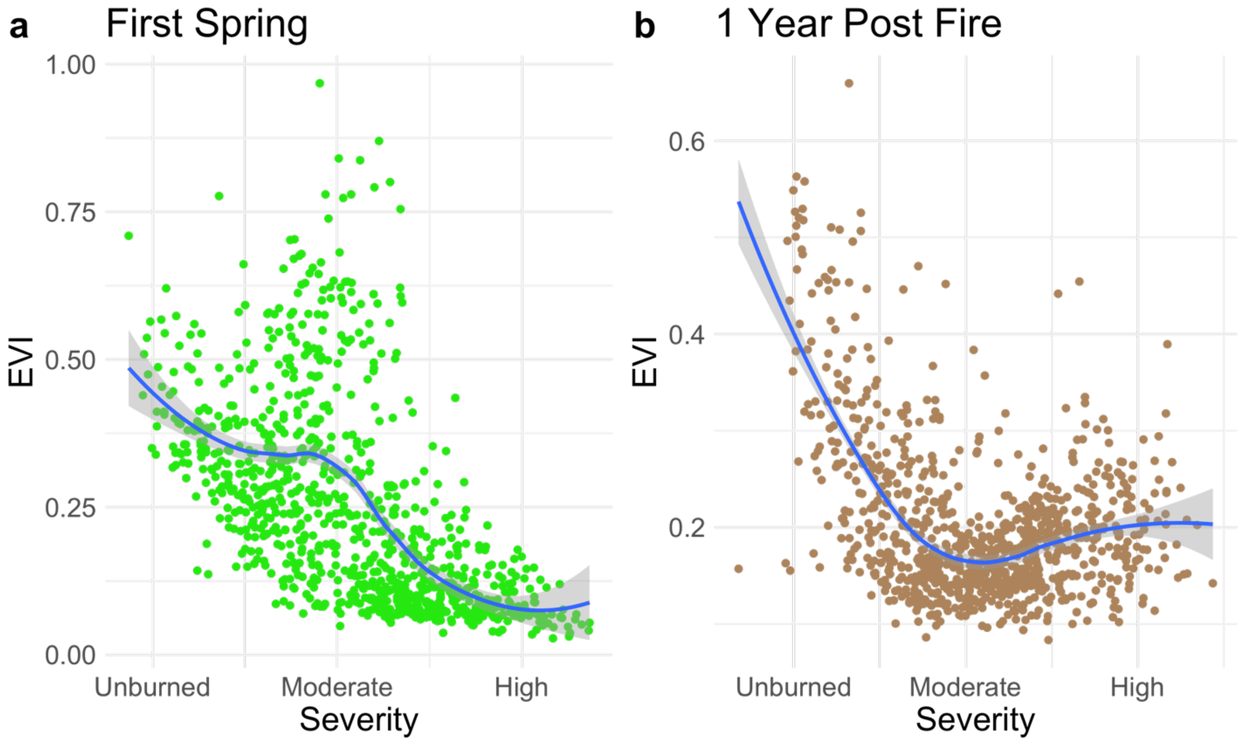

Figure S9. Plotted relationship of forage quality, as represented by EVI, and fire severity in the last two time periods of the study following the 2018 Mendocino Complex Fire at the Hopland Research and Extension Center, CA, USA. 1000 points were sampled across the study area and EVI and severity values were extracted at each point.

Chapter 4

Severity and pyrodiversity shape avian and bat species distributions following an oak woodland megafire

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Abstract

Anthropogenic pressures have altered fire regimes across the western US. These altered fire regimes, and the megafires they often produce, threaten ecologically and economically critical ecosystems and biodiversity across this region. Oak woodland savannas, in particular, may be sensitive to altered fire regimes, but there remains a significant gap in our understanding of how different characteristics of wildfire impact these ecosystems and the wildlife species that reside within them. In this study, we use an occupancy modeling framework to investigate how fire severity and pyrodiversity of a major wildfire in northern California impact the distributions of bird and bat species assemblages. We use acoustic monitors deployed across the Hopland Research and Extension Center following the 2018 Mendocino Complex Fire to examine how patterns of fire severity and pyrodiversity influence habitat preferences across a diverse community of woodland bird and bat species. We find that both taxonomic groups were resilient to the impacts of this megafire over time. While local scale pyrodiversity had negligible effects on species distributions, we found that moderate severity fire increased occupancy of bats, insectivorous birds, and tree nesting birds, but high severity fire decreased occupancy of ground nesting birds and granivorous birds. Due to the variable effects of severity across different species groups, fire and land management that can produce a variety of fire severity patches (broader scale pyrodiversity) can help preserve landscape heterogeneity in woodland savannas and improve regional wildlife biodiversity.

Introduction

Fire plays a major role in shaping patterns of species distributions and diversity in many ecosystems across the world (McLauchlan et al. 2020; Viljur et al. 2022). The historical and contemporary anthropogenic use of fire in particular is an important tool for managing ecosystems in ways that benefit wildlife use and ecosystem services (Christianson et al. 2022). However, researchers continue to debate the exact mechanisms by which fire produces some of these observed effects (Jones and Tingley 2021). Simultaneously, land-use change and climate change have greatly increased the frequency of fires that exceed 100 km^2, also known as megafires, that greatly exceed the severity and size of historical wildfires (Linley et al. 2022). These megafires threaten large landscapes, potentially altering resource availability for wildlife across both space and time.

Fire severity and pyrodiversity are key mechanisms that shape biodiversity in many fire-prone landscapes. Fire severity, or the measured change in living vegetation in response to fire, may play a significant role in driving the distributions of wildlife species following fire. For example, high severity fires potentially remove food, nesting, and other habitat resources for certain species (J. E. Keeley 2009), while low and moderate severity fires may serve as intermediate disturbances that enhance habitat as well (Novoa et al. 2021). The dynamics of fire severity also vary across time and space, which is measured by pyrodiversity, or the variation in fire regime characteristics across landscapes (Zachary L. Steel et al. 2021). Variation in fire severity across space ("spatial pyrodiversity") and variation in the timing of burns ("temporal pyrodiversity") across landscapes may encourage the production of a diverse mosaic of vegetation types and interact with fire severity to create more complex dynamics. For example, some species, such as the black-backed woodpecker, may depend on habitat types or resources, such as woodboring beetle, generated by fire (Tingley et al. 2023). Overall, however, greater habitat heterogeneity created by pyrodiversity is expected to support greater species diversity at a broad community-scale (Beale et al. 2018; Ponisio et al. 2016) and may even enhance community resistance to future disturbances (Ponisio 2020). Theoretically, wildlife communities are adapted to the historic regimes of an area, and deviations from these historic patterns (e.g. uncharacteristically frequent or severe fire or reduced pyrodiversity) may have negative effects on wildlife communities (Jones and Tingley 2021). Understanding how severity and pyrodiversity shape wildlife communities in burned landscapes will be key to informing conservation actions that support wildlife species in our current era of global change. These insights are especially critical in non-forested fire-prone ecosystems, like woodland savannas and shrublands, where we have relatively limited research on the impacts of fire on ecological communities (Calhoun et al. 2021).

A better understanding of the role fire regimes play in non-forested ecosystems can help guide the implementation of prescribed burning in landscape and wildlife management in oak woodland landscapes. Amidst ongoing global change pressures, fire continues to play a key role in several ecosystem (McLauchlan et al. 2020), including ecologically diverse oak woodland savannas in the Western US. Oak woodlands often serve as important working landscapes by providing critical ecosystem services, such as agricultural production and pest control, to the human communities around them while simultaneously supporting key wildlife communities (Kremen and Merenlender 2018; Huntsinger and Oviedo 2014). Historically, Indigenous communities used fire in woodland-scrublands to burn the understory in order to facilitate hunting and resource acquisition (Anderson 2006). Shifting fire regimes caused by more recent fire suppression and other anthropogenic pressures such as climate change may cause significant damage to the short- and long-term composition and functioning of these landscapes by increasing tree mortality of mature oaks that are top-killed by excessively severe fires. Furthermore, changes in fire regimes are predicted to have greater consequences for biodiversity in savanna-type ecosystems, such as oak woodlands, than other fire prone-ecosystems (Kelly et al. 2020).

Bird and bat communities provide key ecological functions that support broader ecosystem services in these oak woodland communities such as agricultural pest removal (López-Hoffman et al. 2010) and oak regeneration (Martínez-Baroja et al. 2021), but the potential positive and negative effects of wildfire on these species' distributions in these ecosystems remains poorly understood. Previous work in conifer forest ecosystems suggests that high severity fire may negatively influence the presence of tree and primary cavity nesting birds (Steel et al. 2021) and certain insectivorous and granivorous birds (Latif et al. 2016). In contrast, increased pyrodiversity in these same systems has been shown to increase diversity in bird and bat communities (Tingley et al. 2016; Steel et al. 2019; Jorge et al. 2022). To date, these dynamics of pyrodiversity and severity have yet to be investigated in oak woodland ecosystems, which are both ecologically and economically critical in the Western US. This omission in our understanding leaves a profound gap in our collective approach to manage both wildlife and wildfire in these oak woodland systems as fire regimes continue to change, especially in the Wildland-Urban Interfaces where most of these woodland fires take place (Calhoun et al. 2021).

In this study, we disentangled the roles fire severity and pyrodiversity play in shaping patterns of diversity in bird and bat communities following a major oak woodland megafire in Northern California. We use automatic recording units (ARUs) to survey the presence of bird and bat species across a large oak woodland-shrubland savanna in Mendocino County, USA following the historic 2018 Mendocino Complex Fire. We predicted that high severity would decrease the presence of certain nesting (tree) and diet groups (granivores) of birds. However, we also predicted that increased pyrodiversity, or variation in severity across space, would increase diversity in bird and bat communities. In teasing apart how each of these characteristics of fire (severity and pyrodiversity) influence bird and bat communities in this system, we help inform future management objectives in using fire to benefit wildlife and mitigate the impacts of future megafires.

Methods

Study Site

We conducted our study at the 21.54 km^2 U.C. Hopland Research and Extension Center (HREC) in Mendocino County, northern California (39°00′ N, 123°04’ W). HREC is composed of a diverse range of habitat types including open grassland, oak woodland, and chaparral shrubland, providing habitat to a diversity of bird and bat species. As is swiftly becoming more common across California, HREC is situated at an important intersection of wildlands and ranchlands; it provides habitat for a diverse group of wildlife and serves as pastoral land for people and livestock. HREC consists of a combination of rolling valleys and peaks with its lowest elevation being 164 meters and its highest at 934 meters. The region is characterized by a Mediterranean climate, with mild seasons and rains in the winter.

On July 27, 2018, the 2018 River Fire, part of the much larger 2018 Mendocino Complex Fire, burned over 13.76 km^2, or roughly half, of the Hopland Research and Extension Center (Figure 1). At the time, the Mendocino Complex Fire was the largest fire in California’s recorded history, burning 1,858 km^2. This megafire was the first wildfire that burned a significant portion of HREC in over 60 years. The scale and severity of this fire contrasted the historical fire regime in this region, which is characterized by frequent, cooler fires in woodlands (5-10 years) and infrequent, more severe burns in shrubland habitats (30-80+ years) (Syphard and Keeley 2020).

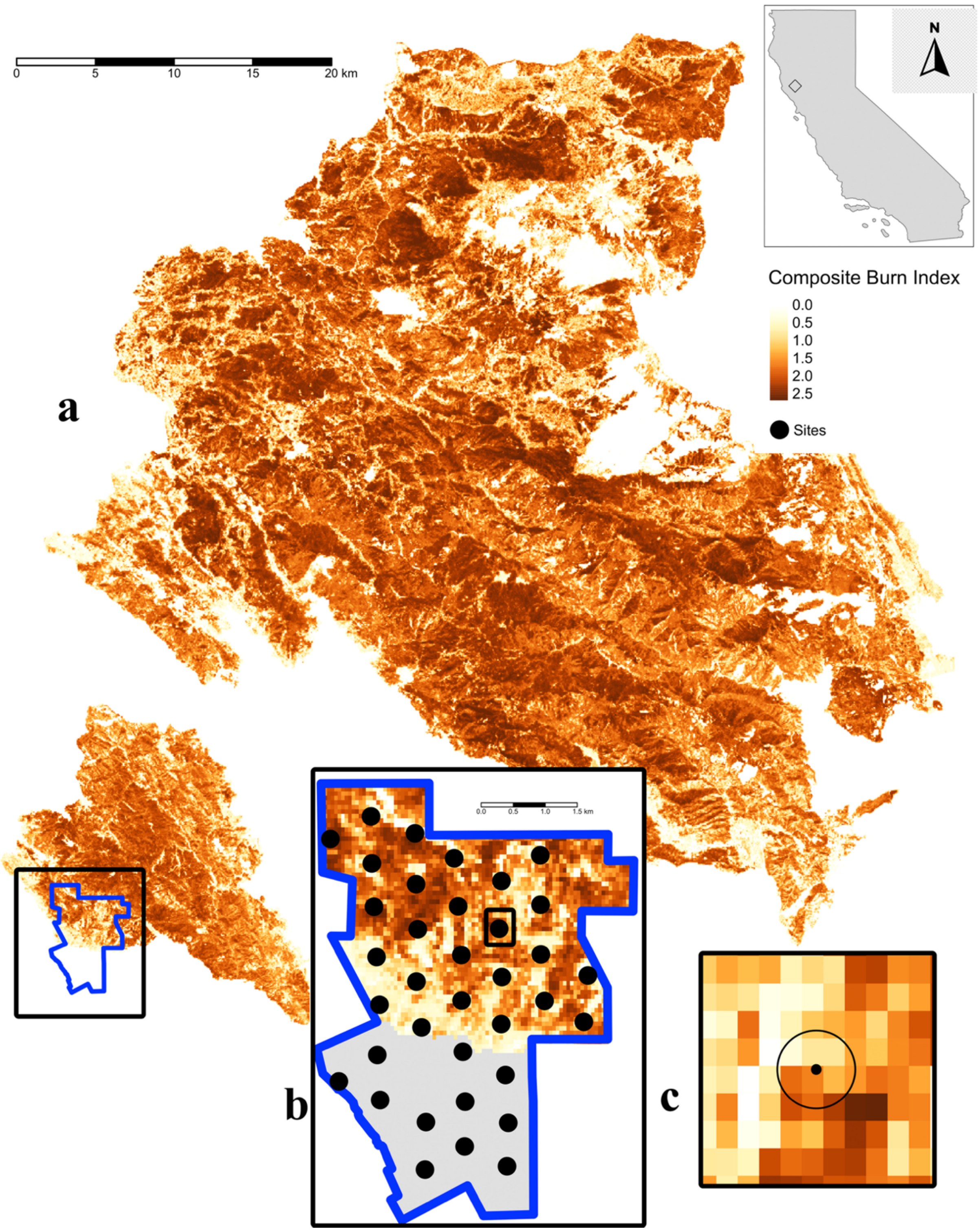

Figure 1. Map of study region and study site, the Hopland Research and Extension Center (HREC). Map 1a) displays the total coverage and severity of the Mendocino Complex Fire and where it overlapped with b) the Hopland Research and Extension Center HREC (outlined in blue). Grayed areas at the southern half of the map are

unburned areas of HREC. Map 1c) depicts the variation in burn severities surrounding a single site at the 100-meter buffer scale used to examine pyrodiversity in this study.

Acoustic Monitoring and Data Management

To sample bird diversity following the 2018 Mendocino Complex Fire, we developed a sampling grid across HREC composed of hexagonal grid cells measuring 750 m across. Starting two years after the Mendocino Complex Fire, we deployed and rotated a set of acoustic ARU's (Audiomoths model v1.1.0) across 36 sites near the centroid of each hexagonal grid in 2020-2022. We conducted acoustic monitoring surveys during the spring-early summer (March 15th-July 6th) each year, which corresponded with the critical nesting season. ARUs were placed in a plastic Ziploc bag with a small desiccant pack and fastened to a tree or fence post at least 2-meters off of the ground. To sample the dawn chorus when songbirds are most dependably active, we programmed ARUs to record three 5-minute recording clips: one 30-minutes before sunrise, one at sunrise, and one 30-minutes after sunrise (15-minutes per day total, sampling frequency = 32 khz) (Furnas and Callas 2015). We sampled each site for a minimum of 4 days (range = 4 – 62 days, median = 8 days).

To classify species recorded at each sampling site, we used BirdNet (Kahl et al. 2021) to auto-classify each detected bird vocalization within our recorded acoustic data. BirdNet detects and auto-classifies birdsong in 3-second segments to species-level identifications which can then be used as presence/absence data for modeling. To guide BirdNet auto-classification, we created a custom species list generated from eBird sightings of birds at HREC (Supplement S1: Table S1). Consistent point counts of birds are performed at HREC annually by researchers and community science activities that support these up-to-date species lists (Pascoe et al. 2023; Newman et al. 2018). For initial classification purposes only, we set the confidence threshold for auto-classifications at 0.01 to include as many detections as possible and left all other BirdNet settings as default.

For analyses, we followed the established guidance of Toenies and Rich (2021) and Cole et al. (2022) to process the collected acoustic data using a set of validation and tiered filtering methods to remove probable false positive detections (Toenies and Rich 2021; Cole et al. 2022). Whereas in bat ultrasonic call validation (see Ultrasonic Monitoring and Data Management) we were able to conservatively validate the presence of species for each sampling night per site, we were unable to vet the presence of every detected bird species for each site and each occasion due to the much larger number of bird species and sampling occasions. Firstly, we removed all detections with confidence scores less than 0.50 across all detected bird species. We randomly selected 50 of the remaining 3-second calls annotated by BirdNet from each detected bird species and validated whether the detection was a true or false positive. At least two team members validated a subset of the 50 total detection calls for each species. For species with less than 50 calls, all calls detected by BirdNet were validated (n = 25 species). We created a species-specific confidence threshold by selecting the false positive detection with the highest confidence score (as generated by BirdNet) and adding a buffer of 0.05, filtering out all detection calls with confidence scores lower than this threshold (Cole et al. 2022). For species with no false positives in their 50 validated calls, we set the threshold to be 0.05 greater than the lowest true positive score for that species. After validation-based filtering, we only included bird species detected at

5 or more sites for modeling to ensure each modeled species had enough detections to obtain accurate estimates from our models (n = 40 species). Once complete, we produced a record table of these bird detections for analyses in R (R Core Team 2021) using "camtrapR" (Niedballa et al. 2016) (v.2.2.0).

Ultrasonic Monitoring and Data Management

To sample bat diversity across HREC following the Mendocino Complex Fire, we used a similar sampling method as the bird acoustic study design. We deployed ultrasonic ARU's (Wildlife Acoustics Minibats, model #SMU01050) across the same sampling sites as the Audiomoths from 2020-2022. Minibats were deployed from late May through early July each year, corresponding to the critical maternal season. Minibats were programmed to record triggered recordings of passing bat calls each night, as opposed to continuous recording. Each bat ARU was deployed at a site for a minimum of 3 consecutive nights (range = 3 – 10 nights, median = 4 nights). Minibats were fastened onto trees or fences 2-meters or more above the ground and positioned to face gaps in tree clutter to facilitate clearer recordings of ultrasonic calls.

We used Sonobat West (v.19.9.27.0) and western regional library with reference calls for all 12 detected bat species to classify, visualize, and vet recorded bat calls by species (www.sonobat.com). First, we used the "Sonobat Batch Scrubber" feature to filter out non-bat ultrasonic calls from the recorded data. Next, we used the "SonoBatch" classifier feature to classify detected calls as recorded bat species. We set the classifier region setting to "Western US" to guide these classifications. We set the acceptable quality threshold for bat calls to 0.80, sequence decision threshold to 0.90, and allowed a maximum of 8 calls to be considered per file. Sonobat automated classification is purposefully conservative to reduce the likelihood of false positive detections across species. Once classified by Sonobat, we vetted species classifications at each site, conservatively ensuring that at least one detected call for each species was a true positive for each monitoring night at each site. False positive species detections during specific monitoring nights were removed. Once complete, we produced a record table of all bat species detections across all sites and years.

Fire Covariates

We use an occupancy modeling framework to describe species distributions over time which predicts the probability of a species occurring at site ("occupancy") given how detectable it is at a site ("detection probability") (MacKenzie et al. 2002). Both occupancy and detection probability can be associated with environmental covariates, and we predicted fire effects and other environmental covariates would influence the detection and occupancy of bird and bat species during our study.

To quantify fire severity on the landscape, we used the Composite Burn Index (CBI) layer of the 2018 Mendocino Complex Fire generated using pre- and post- fire LandSat imagery following Parks et al. (2019) (Parks et al. 2019). CBI is a characterization of burn severity based on the impact of fire on above ground vegetation (litter, herbs, shrubs, and trees) and thus provides an ecologically relevant quantification of fire's effects on wildlife habitat. From this raster, we extracted the average severity value from within a 100m and 500m buffer surrounding each acoustic sampling site predicting that local scale fire severity would drive species occupancy. We predicted that species' responses to fire severity may be non-linear, with some species potentially attracted to moderately burned sites, and therefore included a quadratic term for CBI in the occupancy sub-model. To quantify pyrodiversity, or the variation in fire severity surrounding sites, we extracted the standard deviation of fire severity from a 100m and 500m buffer surrounding each acoustic sampling site. As a derivation of severity, pyrodiversity is often highly correlated with fire severity. We therefore follow the guidance of Steel et al. (2019) to calculate variation while correcting for mean severity and derive pyrodiversity$_i$ as the residual values from the equation Severity_StandardDeviation$_i$ = Severity_mean$_i$ + Severity$^2{}_i$ (Steel et al. 2019). To account for how the amount of time since burning may impact occupancy, we assigned the number of years that had passed since the fire occurred for each sampled site-year (3-5 years).

Environmental Covariates

In addition to fire severity and pyrodiversity, we also expected that pre-fire canopy cover, elevation, and time since burning would influence bird and bat species presence. Canopy cover and elevation has been found to influence bird and bat communities at broad regional scales by providing food, nesting, roosting, and microhabitats for species (Herrando and Brotons 2002; Fuentes-Montemayor et al. 2013; Mendelsohn et al. 2008). Furthermore, we expected that pre-fire canopy cover was indicative of site-specific habitat types (open grassland vs. woodland or shrublands) and therefore predicted that pre-fire canopy cover would influence species presence following fire.

We estimated canopy cover using 20-meter resolution imagery from Sentinel Hub (Sentinel Hub 2022) to create canopy rasters via object-based image analysis and supervised classification in ArcGIS Pro (Esri 2011) for the years 2017 and 2020 to obtain pre- and post-fire canopy cover estimates (Calhoun et al. 2023). These rasters were visually verified using fine scale, 3-m resolution imagery via Planet Labs (Tilahun 2015; Planet Team 2017; Sunde et al. 2020). We used pre-fire canopy cover as a predictor in the occupancy submodel and post-fire canopy cover as a predictor in the detection submodel (below). We extracted 2017 canopy cover values (1 = canopy, 0 = no canopy) from a 100m buffer around each sampling location and calculated percent canopy cover in the buffered radius to represent canopy cover for each site. We obtained elevation for each site using the ASTER Global Digital Elevation Model (NASA and METI 2011). Average values were extracted from a 100m buffer around each camera site.

We predicted calendar date, wind speed, temperature and canopy cover would affect the detectability of bird and bat species at recording stations. To account for certain birds and bats being more or less active during the beginning, middle, or end of the spring season (Furnas and McGrann 2018), we incorporated Julian day, and its quadratic term, for each detection in our occupancy models. Similarly, daily temperatures may impact the activity and call rate of both birds (Puswal, Jinjun, and Liu 2021) and bats (Jorge et al. 2021), so we extracted daily temperature data across HREC to account for this. Detections of bird song and bat calls may be further influenced by ambient noise caused by wind or the density of vegetation in the surrounding area ("canopy cover"). HREC contains six weather stations located across the property that record wind speed and temperature once per hour. We downloaded both logs to calculate average daily temperatures (°F) and wind speeds (mph) across the property for each sampling day of our study. Finally, we used post-fire canopy cover estimates (year = 2020) described above to examine how canopy cover and openness influence detectability. All continuous covariates were checked for non-collinearity and standardized to have a mean of 0 and standard deviation of 1. See Table 1 for mean, range, and resolution of all covariates.

Table 1. Mean, range, and resolution of covariates included in detection and occupancy sub-models of the multi-species occupancy model for acoustic data collected at the Hopland Research and Extension Center following the 2018 Mendocino Complex Fire.

Covariate	***Mean***	***Range***	***Resolution***
Detection Covariates			
Julian Date	-	74 – 187 (March 15th – July 6th)	-
Wind Speed	2.98 mph	1.2 – 6.5 mph	Daily average across HREC
Temperature	59.81 F°	39.7 – 84.3 F°	Daily average across HREC
Post-Fire Canopy Cover (%)	77.23 %	0 – 100 %	100 m buffer
Sampling Effort	11.13 days (Birds) 4.84 days (Bats)	4 – 62 days (Birds) 3 – 10 days (Bats)	-
Occupancy Covariates			
Elevation	489.54 m	213.07 – 898.45 m	100 m buffer
Pre-Fire Canopy Cover (%)	68.41 %	3.80 – 100 %	100 m buffer
Composite Burn Index (CBI)	0.89	0 – 2.46	100 m buffer
Pyrodiversity (Variation in CBI)	0.10	0 – 0.42	100 m buffer
TimeSinceBurn	4 years	3-5 years	-

Occupancy Modeling Framework

We fit two multi-species community occupancy models (Devarajan, Morelli, and Tenan 2020; MacKenzie et al. 2002; Royle and Dorazio 2008), one for each taxonomic group, to investigate the effects of fire severity and pyrodiversity on patterns of species' distributions and community richness. Occupancy models consist of two, linked estimated parameters from two sub-models: occupancy probability (Ψ), the probability that a given species occurs at a site, and detection probability (p), the probability that a given species is detected at a site, given that that site is occupied by the species. Multi-species occupancy models contain an additional layer which links each individual species together under a common community-level hyperparameter. Our acoustic sampling methodology was designed to sample across a diversity of bird and bat species to inform our assessment of community composition and richness, but there may be some limitations in interpreting species-specific results for each species. For example, our modeling framework relies on the assumption of non-independence between sites to obtain estimates of occupancy (Ψ), but one bird species, common raven (*C. corax*), may violate this assumption due to it having a home range size that may encompass more than one acoustic sampling location. Due to this potential for non-independence, we do not interpret occupancy estimates (Ψ) for this species as true-occupancy and instead use it as a measure of relative use between sites (Kays et al. 2020). Specifically, model estimates in this regard may be overly confident for ravens if a single individual is detected across multiple sites (pseudo-replication). We believe, however, that this occurrence would be relatively rare given our relatively short sampling windows and the relationship between site use and the examined covariates should be robust to these rare model violations (O'Connell et al. 2006). We defined a binary latent true occupancy variable, $\mathrm{z}_{\mathrm{i,j}}$, where $z_{i,j} = 1$ indicates that at least one individual of species (i) used the area covered by the acoustic sampling station in year (j) and $\mathrm{z}_{i,j} = 0$ indicates that no individual of species (i) used the area covered by the acoustic sampling station in year (j). We assumed that occupancy was drawn from a Bernoulli distribution with probability ($\Psi_{\mathrm{I,j}}$):

$$Z_{i,j} \sim \text{Bernoulli}(\Psi_{I,j})$$

We treated each survey morning or night (depending on taxa) as a sampling occasion (k) within our occupancy model. We estimated the probability of detecting a species, $y_{i,j,k}$, as being conditional on the species' detection probability at each site, $p_{i,j}$, and the latent occupancy state of that species, ($z_{i,j}$):

$$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j} * z_{i,j})$$

We incorporated site-specific fire and other environmental covariates that were predicted to influence species-specific occupancy ($\Psi_{i,j}$) and site- and species-specific detection probability ($p_{i,j}$) via the following equations:

$$\text{Logit}(\Psi_{I,j}) = \alpha 0_i + \alpha 1_i * \text{Elevation}_j + \alpha 2_i * \text{PreFireCanopy}_j + \alpha 3_i * \text{Severity}_j + \alpha 4_i * \text{Severity}^2_j + \alpha 5_i * \text{Pyrodiversity}_j + \alpha 6_i * \text{TimeSinceBurn}_j + \text{Site Random Effect}_j$$

$$\text{Logit}(\mathrm{p}_{i,j}) = \beta 0_i + \beta 1_i * \text{Date}_{j,k} + \beta 2_i * \mathit{Date}^2_{j,k} + \beta 3_i * \text{WindSpeed}_{j,k} + \beta 4_i * \text{Temperature} + \beta 5_i * \text{PostFireCanopy}_j + \text{Site Random Effect}_j$$

We considered including an interaction between "pyrodiversity" and "Time Since Burning" to represent how the effects of pyrodiversity may be strengthened over time, but decided the temporal scale of our study was too short to capture this aspect (3-5 post-fire).

We treated each site-year as a unique site, which, unaccounted for, would assume a shared underlying occupancy and detection state between years of sampling. To account for pseudo-replication, we included species-specific site random effects within the occupancy and detection sub-models to account for non-independence between surveys at sites. Due to data limitations, we chose not to represent data collected across years as a dynamic occupancy model.

$$\text{Site Random Effect}_{i,j} \sim \text{Normal}(0, \sigma)$$

To gain community-level inferences on our data, we modeled the effects of each variable on the occupancy and detection of each observed species as a random effect from a normally distributed community-level hyperparameter with a shared mean of μ_α and a standard deviation of σ_α (Zipkin et al. 2010):

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha)$$

This multi-species modeling approach enables robust inference on community-level variables while simultaneously examining the effects of covariates on species-level occupancy and detection (Iknayan et al. 2014). We use the community-level hyperparameters to assess the relationship between modeled covariates and species richness across sites.

We fit two additional multi-species occupancy models using the bird occurrence data and with identical model parameterizations as the community-level MSOM, this time assigning hyperparameters to groups of species as defined by nesting (tree, primary cavity, secondary cavity, ground, shrub) and diet (granivore, insectivore, omnivore, nectarivore) guilds, rather than the entire community. These guilds were assigned to modeled species according to their known life histories (Wilman et al. 2014). Birds whose diets were of greater than 60% of plant material were grouped as "granivores" and birds whose diets were composed of greater than 60% of invertebrates were grouped as "insectivores". Bird species whose diets were composed of less than 60% of either plant-material or invertebrates were grouped as "omnivores". Species-level coefficients for each model (nesting guild model and diet guild model) were drawn from group-level (g) hyperparameters from a group-mean of μ_g and standard deviation of σ_g following the community model framework given above. See Supplement S1: Table S1 for groupings of individual species into nesting and diet groups.

Across all multi-species models we used weakly regularizing priors to avoid overfitting. We set priors for the means and standard deviation hyperparameters of the community's coefficients for each covariate. Hyperparameter mean coefficients for each covariate were given normal priors with a mean of 0 and standard deviation of 2.5. All random effects and hyperparameter priors were half-Cauchy with scale parameter 2.5 (Northrup and Gerber 2018).

Model Implementation and Fit

We implemented and estimated all multi-species occupancy models with Markov chain Monte Carlo (MCMC) using the R packages nimble (v.0.11.1) and nimbleEcology (v.0.4.0) (de Valpine et al. 2017; Goldstein et al. 2021). We also used a model selection approach to decide what spatial scale of severity and pyrodiversity (100m or 500m) best fit each of the taxonomic multi-species occupancy models. We fit a model for each fire covariate at each spatial scale, independently of the other fire covariate (severity or pyrodiversity were included) to compare 4 pairs of competing models (Table 1). We compared the Watanabe-Akaike information criterion (WAIC) values (Andrew Gelman, Hwang, and Vehtari 2014) of each parameterization using the WAIC function of the nimble package in R (v.0.11.1). We ran all 3 bird multi-species models for

30,000 iterations with a 2,000 iteration burn in across 3 chains and used nimble custom samplers to increase the efficiency of MCMC mixing (A Gelman et al. 2004). We found that the bat multi-species model had not converged when using these settings. Therefore, we ran the bat model for 30,000 iterations with a 2,000 iteration burn in across 4 chains and used nimble custom samplers to aid in MCMC mixing to allow it to converge. Parameter chains for all models were assessed visually for convergence (Supplement S2 – Figures S1-S4).

We assessed model fit for both the bat and bird the community multi-species occupancy models using posterior predictive checks. We simulated a new dataset using the parameters in each MCMC sampling iteration. We calculated the deviance of each of these datasets to obtain a posterior distribution of deviances produced from data simulated under the true model. We compared observed model deviances to these posterior checks for evidence that the data do not correspond to the fit models (Andrew Gelman, Meng, and Stern 1996; MacKenzie et al. 2017). We assessed a covariate as being a “significant” predictor of occupancy or detection if the 90% credible interval for that variable did not overlap zero and use this definition to describe significance under Bayesian inference.

Results

Bird Acoustic Survey Results

We collected 17,190 hours of avian acoustic recordings over the course of 1,146 sampled mornings and across 103 site-years at 36 locations (2020-2022). From these recordings, BirdNet annotated over 800,000 individual detections of bird song. We validated the presence of 67 detected species (listed in Supplement S1: Table S1). Ultimately, 40 species had enough validated detections, post confidence-threshold filtering (see Acoustic Monitoring and Data Management section), to be included in the multi-species occupancy model. Across modeled species, Acorn Woodpecker (*Melanerpes formicivorus*) was the most detected species (n = 8,422) and Brown-headed Cowbird (*Molothrus ater*) was the least commonly detected species (n = 10) (Supplement S1: Table S2).

Bat Ultrasonic Survey Results

We collected over 190,000 ultrasonic bat detections over 1,146 sampled nights and across 99 site-years (2020-2022) at 36 individual sites/locations. Of these detections, we subset a total of 14,916 bat detections that were vetted to the species-level which included 13 different bat species (Supplement S1: Table S3). Mexican free-tailed bat (*Tadarida brasiliensis*) were the most detected species (n = 5,645) and Townsend’s big-eared bat (*Corynorhinus townsendii*) were the least detected species (n = 3) (Supplement S1: Table S3). We ultimately did not include Townsend’s big-eared bat in multi-species occupancy models due to few detections but incorporated the remaining 12 species into the bat multi-species community model.

Model Selection and Goodness-of-Fit Results

We compared eight parameterizations (four for each taxonomic group) of the community multi-species models and compared their WAIC values (Table 2). We found that WAIC was not significantly different between the 100m and 500m spatial scales of the fire covariates across most models. The bat severity models were the only exception to this, with the 100m buffer severity model performing better (i.e. lower WAIC score) than the 500m buffer severity model (ΔWAIC = +7.39). For this reason, and to facilitate easier comparison of results across all community and group-level models, we chose to implement the 100m buffer for both severity and pyrodiversity in all multi-species occupancy models and interpret those results below (i.e. bird community model, best nesting group model, bird diet group model, and bat community model).

Posterior predictive checks of the bird multi-species community model (Supplement S1: Figure S1) and bat multi-species occupancy model (Supplement S1: Figure S2) demonstrate goodness of fit within acceptable bounds. The observed deviance in the top model did not differ from the posterior distribution of simulated deviances.

Table 2. Comparison of WAIC scores of competing multi-species occupancy models with different spatial buffers of fire covariates (100m or 500m). Only the community-level models for the bird and bat taxonomic groups were used for model selection (no group-level models). All paired models performed similarly except for the bat severity model where the 100m buffer performed significantly better. For this reason, we chose to implement the 100m buffer of fire covariates for all occupancy models.

Covariate	Taxonomic Group	Resolution	WAIC	ΔWAIC
Severity	Bird	100m	14782.58	0
	Bird	500m	14782.75	+ 0.17
	Bat	100m	4877.54	0
	Bat	500m	4884.92	+ 7.38
Pyrodiversity	Bird	100m	14780.65	0
	Bird	500m	14780.78	+ 0.13
	Bat	100m	4885.36	+ 0.33
	Bat	500m	4885.03	0

Bird Multi-Species Occupancy Community- and Group-level Model Results

We used the community-level multi-species bird occupancy model to examine the species-specific effects of fire covariates on occupancy. Fire severity and pyrodiversity did not significantly influence species-specific occupancy (Ψ) of any modeled bird species across sites (90% CI overlapped zero) (Supplement S1: Table S4; Supplement S1: Table S5). Lag year, however, significantly influenced the occupancy of one species, lazuli bunting (*Passerina amoena*). Lazuli buntings were more likely to occupy sites in the years closer to the year of the fire (Mean = -1.08 [-1.85, -0.31]). Fire effects were not a significant predictor of community-level occupancy (Figure 2), but “LagYear” was positively associated with community-level (hyperparameter) occupancy (Mean = 0.19 [-0.08, 0.45]).

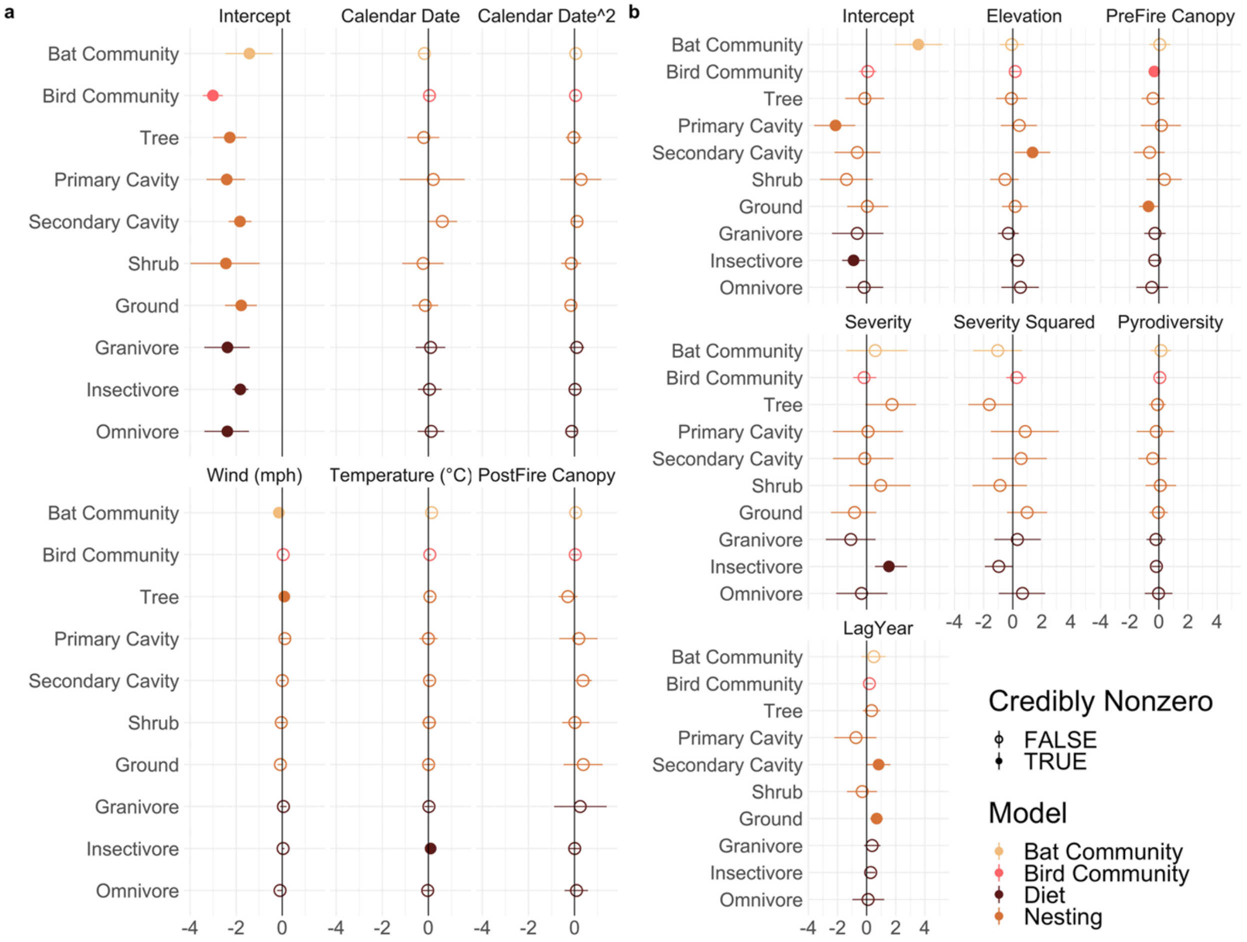

Figure 2. Model coefficients from the bird community, diet-group, and nesting-group multi-species occupancy models. Acoustic and ultrasonic data used in models was collected across the Hopland Research and Extension Center following the 2018 Mendocino Complex Fire. Detection covariate coefficients are on the left (a) and occupancy coefficients are on the right (b).

We found that fire severity and pyrodiversity did not significantly impact group-level occupancy (Ψ) for any of the bird nesting groups (90% CI overlaps zero) (Figure 2). However, fire severity had a strong, non-linear correlation with the occupancy of tree nesters and shrub nesters, with both groups being more likely to occupy sites that burned at moderate severities (Figure 3). Fire severity was negatively correlated (non-significantly) with the occupancy of ground nesters (Mean = -0.83[-2.45, 0.66]) (Supplement S1: Table S6, Supplement S1: Table S7). Occupancy was positively associated with lag time following fire for secondary cavity nesters (Mean = 0.82 [0.04, 1.63]) and ground nesters (Mean = 0.69 [0.23, 1.12]).

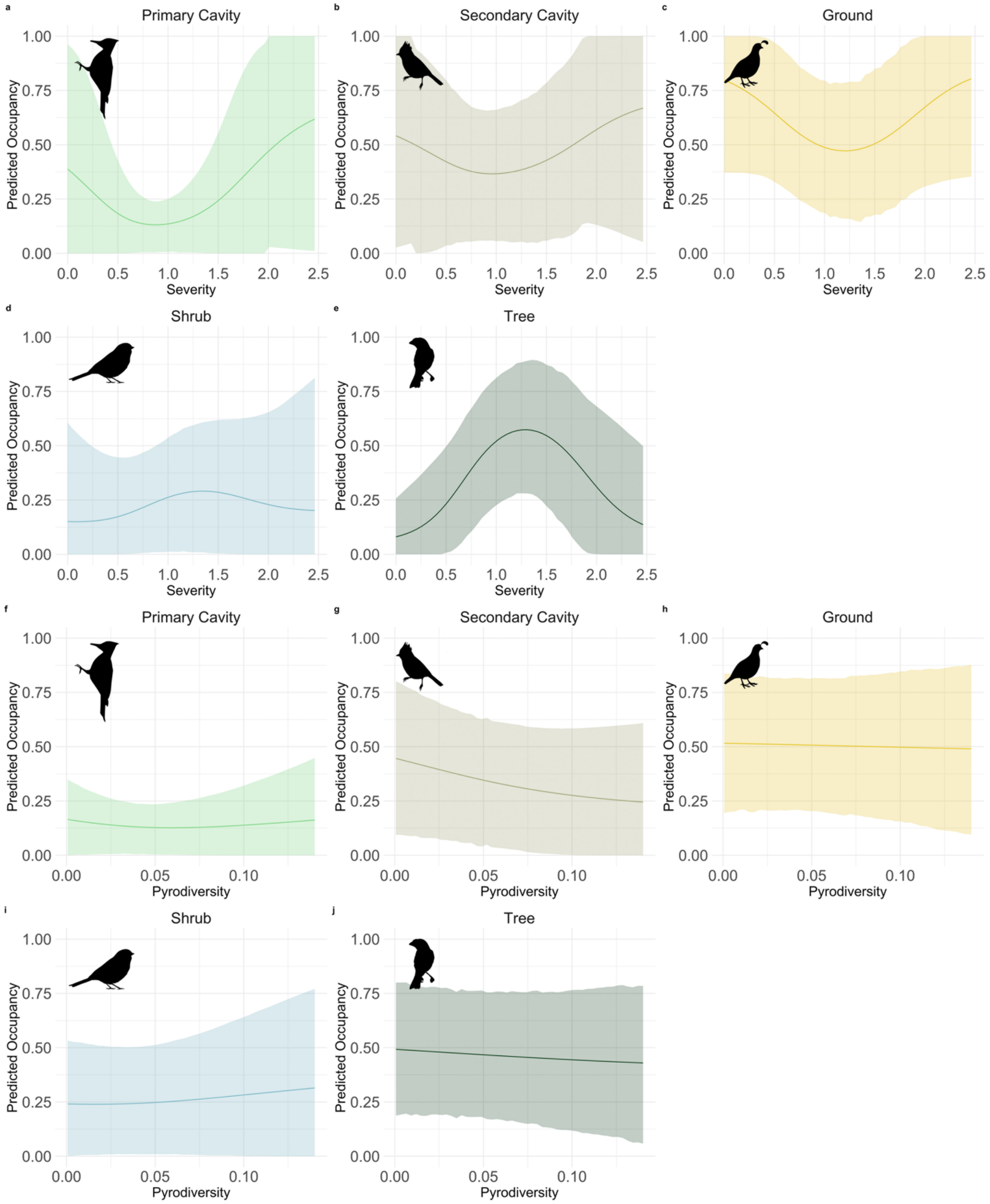

Figure 3. Severity (a-e) and Pyrodiversity (f-j) response curves of occupancy across bird nesting guilds from the nest-group multi-species model.

In the bird diet-group occupancy model, we found a significant, non-linear relationship between insectivore occupancy (Ψ) and fire severity, with insectivorous birds also more likely to occupy sites that burned at moderate severities (Figure 4). Granivorous birds were more likely to use sites that were unburned or burned at lower severities (Mean = -1.09 [-2.81, 0.62]) (Supplement S1: Table S8, Supplement S1: Table S9). Lag time since burning was positively associated (non-significantly) with granivorous birds (Mean = 0.38 [-0.17, 0.95]) and insectivorous birds (Mean = 0.28 [-0.04, 0.06]).

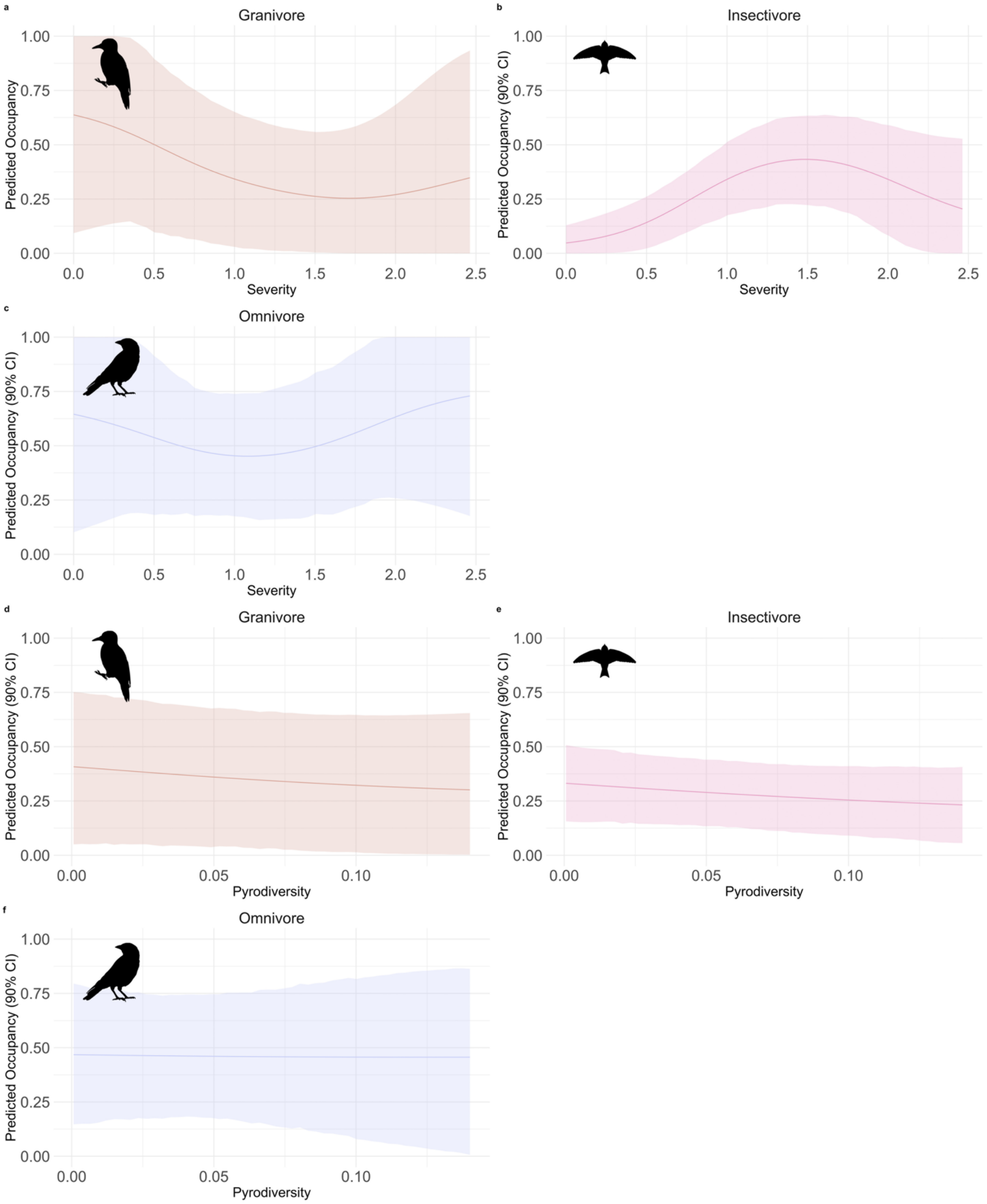

Figure 4. Severity (a-c) and pyrodiversity (d-f) response curves of occupancy across bird diet groups from the diet-group multi-species model. Nectarivores were removed due to the group only having one representative species in the group-level model (*C. anna*).

Bat Multi-Species Occupancy Community Model Results

We used the bat multi-species occupancy model to examine species-specific effects of fire severity, pyrodiversity, and "LagYear" on bat occupancy. We found that fire severity and pyrodiversity were not significant predictors of bat species' occurrence across sites. However, bat occupancy across most species (11 of 12) had a non-linear relationship with fire severity, with these species more likely to occur at sites that burned at moderate severities (Supplement S1: Table S10, Supplement S1: Table S11). "LagYear" was a significant, positive predictor of species-specific occupancy for pallid red bat (*Antrozous pallidus*) (Mean = 1.70 [0.06, 3.43]) and silver-haired bat (*Lasionycteris noctivagans*) (Mean = 0.78 [0.07, 1.48]). Fire covariates were not a significant predictor of community-level (hyperparameter) occupancy, but the community hyperparameter showed a strong, non-linear correlation with fire severity (Figure 2).

Discussion

Though severe, widespread fire has the potential to cause profound harm to afflicted wildlife communities, we found that both bird and bat communities in our study displayed relatively high resistance to its effects. At the community-levels, high severity fire did not have detrimental impacts to community occupancy (community-level hyperparameters) for either taxonomic group. At finer species-specific and group-specific scales, we found that severity did influence habitat preferences both positively (insectivorous birds, tree-nesters, and several bat species) and negatively (granivorous birds and ground nesting birds). Surprisingly, we found that pyrodiversity had a relatively weak influence on occupancy at the community, group, and species-specific scales. This may be influenced by the overall recentness of this study relative to the fire event, with the effects of pyrodiversity potentially becoming more pronounced as time goes on. Correspondingly, time since burning ("LagYear") was an important predictor of community-, group-, and species-level occupancy. Our results underline how wildlife communities in oak woodlands remain resistant, and can even benefit, from wildfire and prescribed burning with characteristics that replicate the regimes of historical fire patterns.

Fire severity was a strong, non-linear predictor of occupancy for several species. As found across a variety of other studies examining the impact of fire severity on wildlife habitat usage (Steel et al. 2019; Furnas, Goldstein, and Figura 2021; Albanesi, Dardanelli, and Bellis 2014), we found species across both taxonomic groups (bats and birds) were most likely to occupy sites that burned at moderate severities. In this way, moderately burned areas may emulate the intermediate disturbance hypothesis (Shea, Roxburgh, and Rauschert 2004) and create new habitat and environmental niches for species within both taxonomic communities. Though we did not find severity to be a key driver of community-level patterns of occupancy, severity was an important predictor of occupancy across several individual species and species-groups. Most bat species (11 of 12) in our study showed a very strong (albeit statistically non-significant) negative relationship with the quadratic-term of severity, signifying occupancy across these species was positively correlated with sites that burned at moderate severities. Steel et al. (2019) found similar findings in their own study examining the effects of fire severity on similar bat communities in conifer ecosystems in the Sierra Nevada suggesting this dynamic may be shared across bat communities within the broader region (Steel et al. 2019). Too few sampling sites within our own study limit our ability disentangle whether the effects of severity on bat populations are just relatively weaker in oak woodlands than these conifer systems or if we simply lack the statistical power to estimate this relationship precisely. Future work that expands the scale of this work to consider additional burned oak woodland sites at a more regional scale could lend the needed statistical power to estimate this relationship more precisely.

Fire severity had varied effects on bird occupancy dependent on species trait groupings. Both insectivorous bird and tree-nesting bird groupings were more likely to occupy sites that burned at moderate severities. As shown in previous work (Steel et al. 2019; Saab et al. 2022), moderate severity fires may benefit both insectivorous bats (all bat species in this study) and insectivorous birds that are able to take advantage of insects attracted to these areas following the initial burn. Moderate severity burning that does not top-kill oak trees may also open new nesting opportunities over time for tree-nesting birds. Conversely, and in support of our original hypothesis, granivorous birds were less likely to occupy severely burned areas, likely due to an immediate decrease in plant-based food following high severity burning. In addition, and opposite to what's been observed in conifer systems (Steel et al. 2021), ground-nesting birds were most likely to occupy sites on either extreme of fire severity (unburned and high severity). This seemingly paradoxical relationship may be due to confounding elements unrepresented in our current model such as vegetation type. Characterized by very heterogenous landscapes and habitat patches (Eastburn et al. 2017) oak woodland fire regimes are often described as having mixed-severity fire regimes (Agee 2005), burning at a variety of severities across different sub-habitat types. Ground-nesting birds may prefer sites in both grassland and shrubland dominated areas, which burn naturally at opposite ends of the severity spectrum (low and high respectively). In previous iterations of our model we've included percent land cover as a predictor covariate of occupancy, but found similar patterns in the relationship between occupancy and severity across trait groups. Instead, future work that can increase the number of sites sampled across the three dominant sub-habitat types (grassland, woodland, and chaparral) could help disentangle the impacts of severity from habitat preferences for species and species groups.

Time since burning (represented by "LagYear") was also a significant predictor of occupancy for several species and species-groups. At the community-scale, both bird and bat community hyperparameters were positively associated with "LagYear", suggesting that community richness and composition likely changed overtime following the initial fire event. Similar to the findings of Pascoe et al. (2023), we found species and species-groups were more likely to occupy recently burned areas at different stages of the regeneration process (Pascoe et al. 2023). Some species, like lazuli bunting (*P. amoena*), are most likely to occupy sites in the years closer to the fire event, while other species (e.g. pallid bat and silver-haired bat) and species-groups (e.g. secondary cavity nesting birds and ground nesting birds) are more likely to occupy sites in the years further from the fire date, likely waiting for nesting and food resources to recover before returning. Similar to more forested systems (Latif et al. 2016; Latif, Saab, and Dudley 2021), fires in oak woodlands may hollow tress and provide new nesting opportunities that secondary cavity nesters are able to take advantage of once conditions regenerate to a certain threshold. Importantly, species that may be sensitive to high severity patches of fire (e.g. granivorous birds and ground-nesting birds) appear to be able to recolonize previously burned sites in the later lag years of the study. Similarly, these ground-nesting and granivorous birds likely wait to return to recently burned sites until vegetation recovers enough to supply food and/or cover (Ensbey et al. 2023).

Contrary to our original hypotheses, pyrodiversity was not a strong predictor of occupancy in any of the multi-species occupancy models. Within the given timescale of our study and given the metric for pyrodiversity we used, severity appears to play a bigger role in influencing species distributions relative to pyrodiversity. However, the observed impacts of pyrodiversity may be dependent on the temporal scale and derivation of the term (Steel et al. 2021; Jones and Tingley 2021). As observed in other work (Tingley et al. 2016; Stillman et al. 2023) the effects of pyrodiversity may become more pronounced as an interaction with time. The limited timescale of our own study (3-5 years post-fire) may prevent us from observing the realized effects pyrodiversity may have in shaping species distributions over time. Furthermore, we only consider a single dimension of pyrodiversity within our study ("spatial pyrodiversity") when a combination of both "spatial" and "temporal" (variance in fire age classes across landscapes) pyrodiversity likely influence species diversity and distributions over time (Kelly, Brotons, and McCarthy 2017). HREC's recent history of minimal fire activity and limited prescribed burning somewhat limit the diversity of fire age-classes found throughout the study site, but a broader, regional-based study could better represent the multi-dimensional aspects of pyrodiversity and how they influence oak woodland wildlife communities.

Our findings in comparing the effects of severity and pyrodiversity in this study are also likely influenced by the tools we have available to define both terms. Most quantifications of fire severity, such as the Composite Burn Index, used in ecological modeling are based on metrics calibrated in forested ecosystems. The realized ecological effects of these metrics have been thoroughly studied in systems such as California's mixed-conifer forests (Miller and Thode 2007; Miller et al. 2009), but a large gap remains in our understanding of how these metrics translate to non-forested systems such as woodland savannas and shrublands. Though recent work has begun to interrogate what these differences may be (Stambaugh, Hammer, and Godfrey 2015; Huang et al. 2020), the same severity metrics (low, medium, or high severity burning) may have variable realized effects across different ecosystem types. For example, green-up in many oak woodland systems occurs much more rapidly following fire than in many forested systems, even in high severity patches (Huerta et al. 2022). Developing improved tools to quantify both severity and pyrodiversity may help future studies better discern the effects of both fire characteristics on patterns of biodiversity in oak woodland savannas.

Within the timeframe of our study, we found both bird and bat community assemblages to be very resistant to the short-term impacts of megafire. Our findings further demonstrate the natural resistance and resilience of a variety of bat (Loeb and Blakey 2021; Ancillotto et al. 2021) and bird (Lindenmayer et al. 2022) species to severe fire effects that has been established in past work. Species that were potentially vulnerable to the initial fire effects of severe fire (e.g. granivorous and ground-nesting birds) had returned to previously burned areas as time passed, showcasing some resilience. Because a variety of species seem to prefer different severities of burning, fire management that takes this into account to produce a diversity of burned effects would be critical for maximizing species diversity and a broader landscape scale (Prowse et al. 2017). In this way, considering regional pyrodiversity (not just the spatial diversity of severities surrounding a site) would be key in producing these intended effects with prescribed burning in oak woodland systems.

Conclusion

Oak woodlands are renowned for their natural resilience following wildfire. Likewise, our study shows that, overall, oak woodland bird and bat communities showed considerable resistance and resilience to the impacts of megafire in oak woodland systems. Species-specific and group-specific distributions varied by fire severity and time since burning. Therefore, fire and land management that can produce pyrodiversity at broader scales via variation in fire severity and fire age-classes across landscapes could improve habitat for a variety of species. We believe there is significant opportunity to employ these findings in existing structures of fire and land management in California rangelands and woodland savannas. In this way, goals to improve wildlife management in these spaces can become better integrated into current objectives of fire management to reduce the risk of extreme fire on ecosystems, human safety and livelihoods.

Acknowledgements

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Supplement for Chapter 4

Supplement S1 – Additional Figures and Tables

Table S1. List of bird species previously recorded at the Hopland Research and Extension Center in Mendocino County, CA, USA. This list of species was fed to BirdNet as a custom species list to guide autoclassification of recorded birdsong. Species that were included in modeling (detected at 5 or more site-years after tiered validation filtering) were given nesting group and diet group categories based on known life history traits.

Species	Scientific Name	Nesting	Diet	Included in Model?
Acorn Woodpecker	*Melanerpes formicivorus*	Cavity_Primary	Insectivore	Y
American Crow	*Corvus brachyrhynchos*			N
American Goldfinch	*Spinus tristis*			N
American Robin	*Turdus migratorius*	Tree	Insectivore	Y
Anna's Hummingbird	*Calypte anna*	Shrub	Nectar	Y
Ash-throated Flycatcher	*Myiarchus cinerascens*	Cavity_Secondary	Insectivore	Y
Band-tailed Pigeon	*Patagioenas fasciata*			N
Bell's Sparrow	*Artemisiospiza belli*			N
Bewick's Wren	*Thryomanes bewickii*	Cavity_Secondary	Insectivore	Y
Black Phoebe	*Sayornis nigricans*	Cavity_Secondary	Insectivore	Y
Black-headed Grosbeak	*Pheucticus meSilver-haired Batcephalus*	Tree	Insectivore	Y
Black-throated Gray Warbler	*Setophaga nigrescens*	Tree	Insectivore	Y
Blue-gray Gnatcatcher	*Polioptila caerulea*	Shrub	Insectivore	Y
Brewer's Blackbird	*Euphagus cyanocephalus*			N
Brown-headed Cowbird	*Molothrus ater*	Tree	Granivore	Y
Bullock's Oriole	*Icterus bullockii*	Tree	Insectivore	Y
Bushtit	*Psaltriparus minimus*	Shrub	Insectivore	Y
California Quail	*Callipepla californica*	Ground	Granivore	Y
California Scrub-Jay	*Aphelocoma californica*	Shrub	Omnivore	Y
California Thrasher	*Toxostoma redivivum*			N
California Towhee	*Melozone crissalis*	Shrub	Granivore	Y
Common Raven	*Corvus corax*	Tree	Omnivore	Y
Dark-eyed Junco	*Junco hyemalis*	Ground	Granivore	Y
European Starling	*Sturnus vulgaris*			N
Fox Sparrow	*Passerella iliaca*			N
Golden-crowned Sparrow	*Zonotrichia atricapilla*	Ground	Granivore	Y
Hermit Thrush	*Catharus guttatus*			N
House Finch	*Haemorhous mexicanus*	Tree	Granivore	Y
Hutton's Vireo	*Vireo huttoni*			N
Lark Sparrow	*Chondestes grammacus*			N
Lazuli Bunting	*Passerina amoena*	Shrub	Omnivore	Y
Lesser Goldfinch	*Spinus psaltria*	Tree	Granivore	Y
Lewis's Woodpecker	*Melanerpes lewis*			N
Lincoln's Sparrow	*Melospiza lincolnii*			N
Mountain Quail	*Oreortyx pictus*	Ground	Granivore	Y
Mourning Dove	*Zenaida macroura*	Tree	Granivore	Y
Northern Flicker	*Colaptes auratus*	Cavity_Primary	Insectivore	Y
Northern Mockingbird	*Mimus polyglottos*			N
Nuttall's Woodpecker	*Picoides nuttallii*	Cavity_Primary	Insectivore	Y
Oak Titmouse	*Baeolophus inornatus*	Cavity_Secondary	Insectivore	Y

Olive-sided Flycatcher	*Contopus cooperi*			N
Orange-crowned Warbler	*Leiothlypis celata*	Ground	Insectivore	Y
Pacific-slope Flycatcher	*Empidonax difficilis*	Tree	Insectivore	Y
Pileated Woodpecker	*Dryocopus pileatus*	Cavity_Primary	Insectivore	Y
Pine Siskin	*Spinus pinus*			N
Purple Finch	*Haemorhous purpureus*			N
Red-winged Blackbird	*Agelaius phoeniceus*			N
Rock Wren	*Salpinctes obsoletus*			N
Ruby-crowned Kinglet	*Corthylio calendula*			N
Rufous-crowned Sparrow	*Aimophila ruficeps*	Ground	Omnivore	Y
Savannah Sparrow	*Passerculus sandwichensis*			N
Say's Phoebe	*Sayornis saya*			N
Song Sparrow	*Melospiza melodia*			N
Spotted Towhee	*Pipilo maculatus*	Ground	Omnivore	Y
Steller's Jay	*Cyanocitta stelleri*	Tree	Omnivore	Y
Tree Swallow	*Tachycineta bicolor*			N
Vaux's Swift	*Chaetura vauxi*			N
Violet-green Swallow	*Tachycineta thalassina*	Cavity_Secondary	Insectivore	Y
Warbling Vireo	*Vireo gilvus*	Tree	Insectivore	Y
Western Bluebird	*Sialia mexicana*	Cavity_Secondary	Insectivore	Y
Western Kingbird	*Tyrannus verticalis*	Tree	Insectivore	Y
Western Meadowlark	*Sturnella neglecta*	Ground	Omnivore	Y
Western Wood-Pewee	*Contopus sordidulus*	Tree	Insectivore	Y
White-breasted Nuthatch	*Sitta carolinensis*	Cavity_Secondary	Omnivore	Y
White-crowned Sparrow	*Zonotrichia leucophrys*			N
Wrentit	*Chamaea fasciata*	Shrub	Omnivore	Y
Yellow Warbler	*Setophaga petechia*			N

Table S2. Bird detections summary table collected at the Hopland Research and Extension Center in Mendocino, California, USA following the 2018 Mendocino Complex Fire.

Common Name	**Scientific Name**	**Detections**	**nSites**
Acorn Woodpecker	*Melanerpes formicivorus*	8422	82
American Robin	*Turdus migratorius*	652	40
Anna's Hummingbird	*Calypte anna*	35	6
Ash-throated Flycatcher	*Myiarchus cinerascens*	443	33
Bewick's Wren	*Thryomanes bewickii*	420	21
Black Phoebe	*Sayornis nigricans*	639	12
Black-headed Grosbeak	*Pheucticus meSilver-haired Batcephalus*	175	10
Black-throated Gray Warbler	*Setophaga nigrescens*	35	5
Blue-gray Gnatcatcher	*Polioptila caerulea*	529	20
Brown-headed Cowbird	*Molothrus ater*	10	7
Bullock's Oriole	*Icterus bullockii*	57	12
Bushtit	*Psaltriparus minimus*	283	17
California Quail	*Callipepla californica*	1208	59
California Scrub-Jay	*Aphelocoma californica*	853	53
California Towhee	*Melozone crissalis*	5702	74
Common Raven	*Corvus corax*	160	25
Dark-eyed Junco	*Junco hyemalis*	581	37

Golden-crowned Sparrow	*Zonotrichia atricapilla*	22	7
House Finch	*Haemorhous mexicanus*	66	16
Lazuli Bunting	*Passerina amoena*	1438	30
Lesser Goldfinch	*Spinus psaltria*	332	25
Mountain Quail	*Oreortyx pictus*	1741	27
Mourning Dove	*Zenaida macroura*	1193	56
Northern Flicker	*Colaptes auratus*	361	46
Nuttall's Woodpecker	*Picoides nuttallii*	164	31
Oak Titmouse	*Baeolophus inornatus*	3273	81
Orange-crowned Warbler	*Leiothlypis celata*	1261	46
Pacific-slope Flycatcher	*Empidonax difficilis*	1169	22
Pileated Woodpecker	*Dryocopus pileatus*	36	9
Rufous-crowned Sparrow	*Aimophila ruficeps*	373	25
Spotted Towhee	*Pipilo maculatus*	420	26
Steller's Jay	*Cyanocitta stelleri*	344	41
Violet-green Swallow	*Tachycineta thalassina*	1460	60
Warbling Vireo	*Vireo gilvus*	150	12
Western Bluebird	*Sialia mexicana*	505	41
Western Kingbird	*Tyrannus verticalis*	115	7
Western Meadowlark	*Sturnella neglecta*	462	10
Western Wood-Pewee	*Contopus sordidulus*	78	6
White-breasted Nuthatch	*Sitta carolinensis*	561	49
Wrentit	*Chamaea fasciata*	186	18

Table S3. Bat detections summary table collected at the Hopland Research and Extension Center in Mendocino, California, USA following the 2018 Mendocino Complex Fire.

Common Name	**Scientific Name**	**Detections**	**nSites**
Big Brown Bat	*Eptesicus fuscus*	1543	72
California Myotis	*Myotis californicus*	4057	89
Canyon Bat	*Parastrellus hesperus*	315	56
Fringed Myotis	*Myotis thysanodes*	9	6
Hoary Bat	*Lasiurus cinereus*	1135	73
Little Brown Bat	*Myotis lucifugus*	10	9
Long-eared Myotis	*Myotis evotis*	126	48
Mexican Free-tailed Bat	*Tadarida brasiliensis*	5645	95
Pallid Bat	*Antrozous pallidus*	86	28
Silver-haired Bat	*Lasionycteris noctivagans*	810	67
Western Red Bat	*Lasiurus blossevillii*	402	61
Yuma Myotis	*Myotis yumanensis*	775	86
Townsend's Big-eared Bat	*Corynorhinus townsendii*	3	2

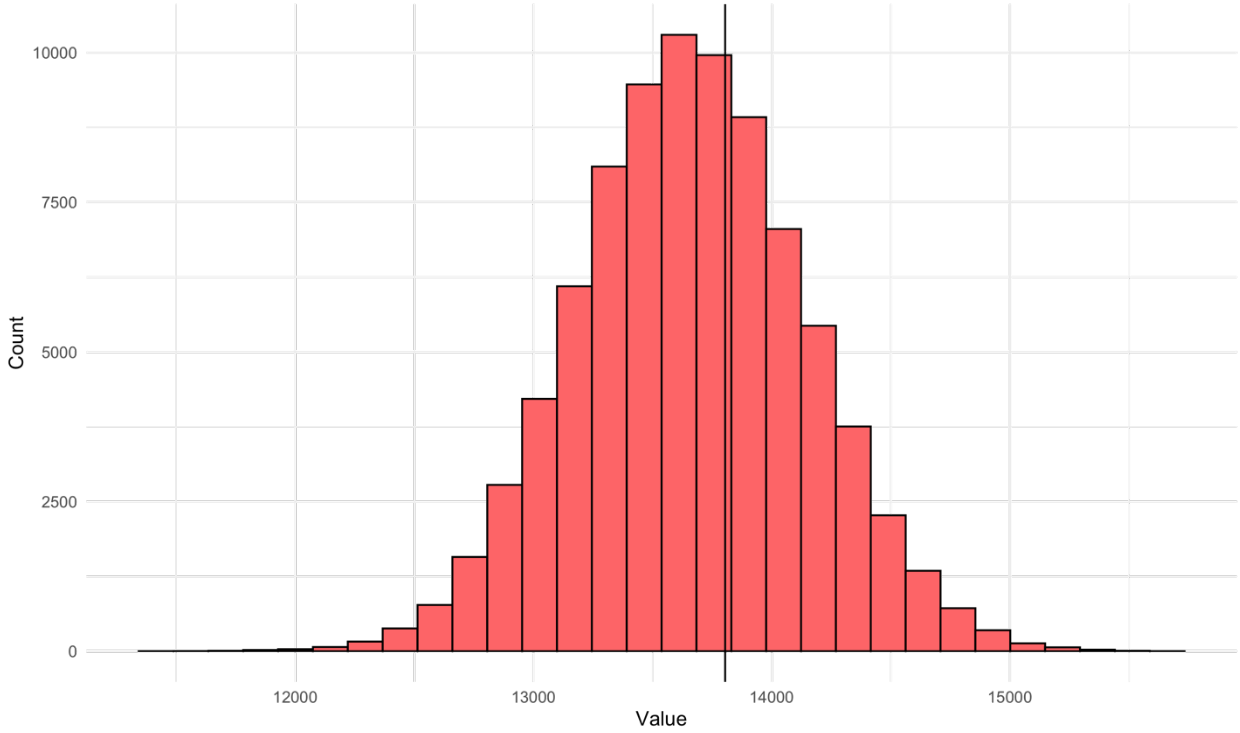

Figure S1. Goodness-of-fit plot for bird community multi-species occupancy model. Posterior predictive checks demonstrate acceptable fit of multi-species occupancy mode to the collected bat data.

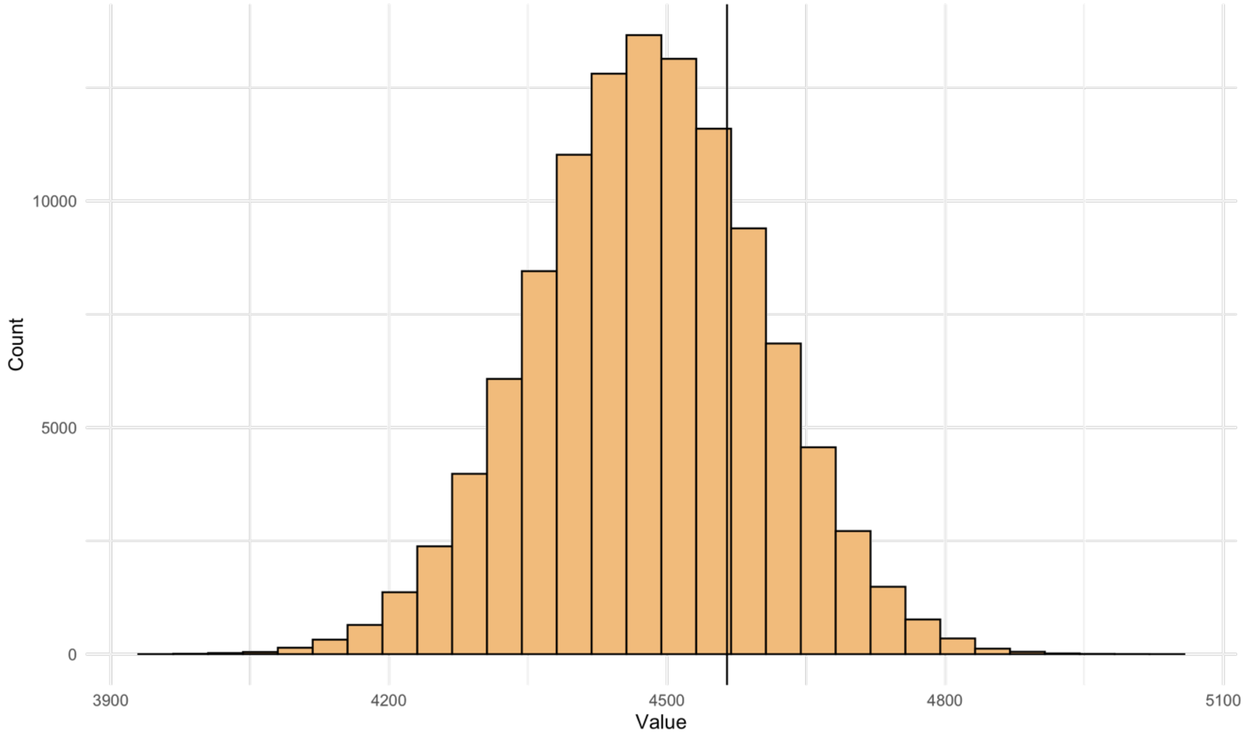

Figure S2. Goodness-of-fit plot for bat community multi-species occupancy model. Posterior predictive checks demonstrate acceptable fit of multi-species occupancy mode to the collected bat data.

Table S4. Species-specific covariate coefficients from the detection submodel for the bird community-level multi-species occupancy model.

Species	**Parameter**	**Estimate**
Acorn Woodpecker	Intercept	-0.19 (-0.65, 0.27)
Acorn Woodpecker	Julian Day	0.92 (0.51, 1.31)
Acorn Woodpecker	Julian Day^2	0.51 (0.27, 0.73)
Acorn Woodpecker	Wind (mph)	0.06 (-0.01, 0.15)
Acorn Woodpecker	Temperature (°C)	0.03 (-0.1, 0.14)
Acorn Woodpecker	PostFire Canopy	0.18 (-0.22, 0.6)
American Robin	Intercept	-3.53 (-4.2, -2.83)
American Robin	Julian Day	-0.31 (-0.92, 0.25)
American Robin	Julian Day^2	0.17 (-0.09, 0.45)
American Robin	Wind (mph)	0.05 (-0.03, 0.14)
American Robin	Temperature (°C)	0.03 (-0.11, 0.18)
American Robin	PostFire Canopy	-0.02 (-0.39, 0.34)
Anna's Hummingbird	Intercept	-3.88 (-6.04, -1.59)
Anna's Hummingbird	Julian Day	-0.34 (-1.28, 0.58)
Anna's Hummingbird	Julian Day^2	0.16 (-0.24, 0.54)
Anna's Hummingbird	Wind (mph)	0.04 (-0.05, 0.14)
Anna's Hummingbird	Temperature (°C)	0.07 (-0.1, 0.23)
Anna's Hummingbird	PostFire Canopy	0.04 (-0.79, 0.89)
Ash-throated Flycatcher	Intercept	-2.59 (-3.37, -1.75)
Ash-throated Flycatcher	Julian Day	0.83 (0.36, 1.34)
Ash-throated Flycatcher	Julian Day^2	-0.08 (-0.37, 0.22)

Ash-throated Flycatcher	Wind (mph)	0.05 (-0.04, 0.14)
Ash-throated Flycatcher	Temperature (°C)	0.04 (-0.12, 0.18)
Ash-throated Flycatcher	PostFire Canopy	0.33 (-0.24, 0.9)
Bewick's Wren	Intercept	-3.4 (-4.49, -2.21)
Bewick's Wren	Julian Day	0.54 (-0.03, 1.08)
Bewick's Wren	Julian Day^2	0.24 (-0.09, 0.55)
Bewick's Wren	Wind (mph)	0.05 (-0.04, 0.15)
Bewick's Wren	Temperature (°C)	0.06 (-0.08, 0.22)
Bewick's Wren	PostFire Canopy	-0.02 (-0.74, 0.69)
Black Phoebe	Intercept	-4.84 (-6.26, -3.41)
Black Phoebe	Julian Day	0.01 (-0.73, 0.7)
Black Phoebe	Julian Day^2	0.04 (-0.3, 0.39)
Black Phoebe	Wind (mph)	0.04 (-0.05, 0.14)
Black Phoebe	Temperature (°C)	0.08 (-0.07, 0.24)
Black Phoebe	PostFire Canopy	0.16 (-0.54, 0.91)
Black-headed Grosbeak	Intercept	-4.17 (-5.72, -2.64)
Black-headed Grosbeak	Julian Day	-0.59 (-1.42, 0.21)
Black-headed Grosbeak	Julian Day^2	0.09 (-0.28, 0.44)
Black-headed Grosbeak	Wind (mph)	0.05 (-0.04, 0.15)
Black-headed Grosbeak	Temperature (°C)	0.07 (-0.08, 0.22)
Black-headed Grosbeak	PostFire Canopy	0.42 (-0.24, 1.07)
Black-throated Gray Warbler	Intercept	-4.84 (-6.46, -3.19)
Black-throated Gray Warbler	Julian Day	0.01 (-0.81, 0.92)
Black-throated Gray Warbler	Julian Day^2	0.04 (-0.34, 0.41)
Black-throated Gray Warbler	Wind (mph)	0.04 (-0.05, 0.14)
Black-throated Gray Warbler	Temperature (°C)	0.07 (-0.09, 0.24)
Black-throated Gray Warbler	PostFire Canopy	-0.25 (-0.89, 0.38)
Blue-gray Gnatcatcher	Intercept	-2.55 (-3.43, -1.69)
Blue-gray Gnatcatcher	Julian Day	-0.38 (-1.2, 0.39)
Blue-gray Gnatcatcher	Julian Day^2	0.11 (-0.3, 0.52)
Blue-gray Gnatcatcher	Wind (mph)	0.04 (-0.05, 0.13)
Blue-gray Gnatcatcher	Temperature (°C)	0.05 (-0.1, 0.2)
Blue-gray Gnatcatcher	PostFire Canopy	-0.14 (-0.7, 0.44)
Brown-headed Cowbird	Intercept	-4.43 (-5.72, -3.15)
Brown-headed Cowbird	Julian Day	0.04 (-0.69, 0.8)
Brown-headed Cowbird	Julian Day^2	0.03 (-0.34, 0.38)
Brown-headed Cowbird	Wind (mph)	0.04 (-0.05, 0.14)
Brown-headed Cowbird	Temperature (°C)	0.05 (-0.11, 0.2)
Brown-headed Cowbird	PostFire Canopy	-0.02 (-0.6, 0.59)
Bullock's Oriole	Intercept	-1.76 (-3.25, -0.29)
Bullock's Oriole	Julian Day	0.58 (-0.35, 1.51)
Bullock's Oriole	Julian Day^2	-0.12 (-0.5, 0.25)
Bullock's Oriole	Wind (mph)	0.04 (-0.06, 0.13)
Bullock's Oriole	Temperature (°C)	0.09 (-0.06, 0.25)
Bullock's Oriole	PostFire Canopy	0.58 (-0.29, 1.43)
Bushtit	Intercept	-3.46 (-4.49, -2.41)
Bushtit	Julian Day	-0.24 (-0.96, 0.43)
Bushtit	Julian Day^2	0.14 (-0.21, 0.49)
Bushtit	Wind (mph)	0.05 (-0.04, 0.15)
Bushtit	Temperature (°C)	0.05 (-0.11, 0.2)
Bushtit	PostFire Canopy	-0.13 (-0.75, 0.47)
California Quail	Intercept	-1.49 (-1.99, -1)
California Quail	Julian Day	-0.21 (-0.63, 0.23)

California Quail	Julian Day^2	-0.16 (-0.39, 0.09)
California Quail	Wind (mph)	0.03 (-0.04, 0.11)
California Quail	Temperature (°C)	0.02 (-0.11, 0.15)
California Quail	PostFire Canopy	0.4 (-0.02, 0.85)
California Scrub-Jay	Intercept	-2.13 (-2.65, -1.6)
California Scrub-Jay	Julian Day	0.29 (-0.18, 0.75)
California Scrub-Jay	Julian Day^2	0.08 (-0.17, 0.34)
California Scrub-Jay	Wind (mph)	0.04 (-0.04, 0.13)
California Scrub-Jay	Temperature (°C)	0.06 (-0.07, 0.2)
California Scrub-Jay	PostFire Canopy	-0.24 (-0.66, 0.19)
California Towhee	Intercept	-0.68 (-1.07, -0.28)
California Towhee	Julian Day	0.74 (0.34, 1.13)
California Towhee	Julian Day^2	0.14 (-0.07, 0.36)
California Towhee	Wind (mph)	0.06 (-0.02, 0.14)
California Towhee	Temperature (°C)	0.12 (-0.01, 0.26)
California Towhee	PostFire Canopy	0.45 (0.05, 0.83)
Common Raven	Intercept	-3.92 (-4.76, -3.07)
Common Raven	Julian Day	-0.31 (-0.96, 0.33)
Common Raven	Julian Day^2	0.17 (-0.11, 0.45)
Common Raven	Wind (mph)	0.05 (-0.04, 0.14)
Common Raven	Temperature (°C)	0.07 (-0.06, 0.23)
Common Raven	PostFire Canopy	-0.38 (-0.73, -0.02)
Dark-eyed Junco	Intercept	-2.68 (-3.24, -2.14)
Dark-eyed Junco	Julian Day	-0.17 (-0.74, 0.38)
Dark-eyed Junco	Julian Day^2	-0.1 (-0.38, 0.18)
Dark-eyed Junco	Wind (mph)	0.04 (-0.05, 0.12)
Dark-eyed Junco	Temperature (°C)	0.03 (-0.12, 0.17)
Dark-eyed Junco	PostFire Canopy	-0.66 (-0.94, -0.36)
Golden-crowned Sparrow	Intercept	-5.15 (-7, -3.32)
Golden-crowned Sparrow	Julian Day	0 (-0.87, 0.84)
Golden-crowned Sparrow	Julian Day^2	0.07 (-0.29, 0.46)
Golden-crowned Sparrow	Wind (mph)	0.04 (-0.06, 0.14)
Golden-crowned Sparrow	Temperature (°C)	0.05 (-0.11, 0.21)
Golden-crowned Sparrow	PostFire Canopy	0.09 (-0.65, 0.83)
House Finch	Intercept	-2.61 (-3.67, -1.5)
House Finch	Julian Day	0.74 (0.09, 1.37)
House Finch	Julian Day^2	0.22 (-0.11, 0.55)
House Finch	Wind (mph)	0.04 (-0.06, 0.13)
House Finch	Temperature (°C)	0.03 (-0.14, 0.18)
House Finch	PostFire Canopy	0.46 (-0.21, 1.13)
Lazuli Bunting	Intercept	-2.53 (-3.48, -1.49)
Lazuli Bunting	Julian Day	-0.59 (-1.37, 0.28)
Lazuli Bunting	Julian Day^2	-0.11 (-0.45, 0.26)
Lazuli Bunting	Wind (mph)	0.04 (-0.05, 0.13)
Lazuli Bunting	Temperature (°C)	0.04 (-0.1, 0.18)
Lazuli Bunting	PostFire Canopy	0.35 (-0.17, 0.84)
Lesser Goldfinch	Intercept	-3.9 (-4.8, -3)
Lesser Goldfinch	Julian Day	0.07 (-0.5, 0.64)
Lesser Goldfinch	Julian Day^2	0.17 (-0.16, 0.47)
Lesser Goldfinch	Wind (mph)	0.02 (-0.07, 0.12)
Lesser Goldfinch	Temperature (°C)	0.04 (-0.11, 0.19)
Lesser Goldfinch	PostFire Canopy	0.47 (-0.09, 1.04)
Mountain Quail	Intercept	-2.56 (-3.38, -1.75)

Mountain Quail	Julian Day	-1.13 (-1.84, -0.42)
Mountain Quail	Julian Day^2	0.23 (-0.08, 0.56)
Mountain Quail	Wind (mph)	0.04 (-0.04, 0.13)
Mountain Quail	Temperature (°C)	0.05 (-0.11, 0.19)
Mountain Quail	PostFire Canopy	-0.37 (-0.72, -0.01)
Mourning Dove	Intercept	-2.53 (-3.07, -1.96)
Mourning Dove	Julian Day	-0.16 (-0.65, 0.29)
Mourning Dove	Julian Day^2	0.01 (-0.23, 0.23)
Mourning Dove	Wind (mph)	0.05 (-0.03, 0.13)
Mourning Dove	Temperature (°C)	0.07 (-0.06, 0.19)
Mourning Dove	PostFire Canopy	0.27 (-0.2, 0.7)
Northern Flicker	Intercept	-3.27 (-3.81, -2.7)
Northern Flicker	Julian Day	-0.26 (-0.79, 0.29)
Northern Flicker	Julian Day^2	0.15 (-0.12, 0.41)
Northern Flicker	Wind (mph)	0.05 (-0.04, 0.13)
Northern Flicker	Temperature (°C)	0.06 (-0.08, 0.2)
Northern Flicker	PostFire Canopy	0.28 (-0.13, 0.69)
Nuttall's Woodpecker	Intercept	-3.02 (-3.92, -2.11)
Nuttall's Woodpecker	Julian Day	0.36 (-0.17, 0.86)
Nuttall's Woodpecker	Julian Day^2	0.01 (-0.3, 0.29)
Nuttall's Woodpecker	Wind (mph)	0.04 (-0.05, 0.13)
Nuttall's Woodpecker	Temperature (°C)	0.05 (-0.1, 0.2)
Nuttall's Woodpecker	PostFire Canopy	0.41 (-0.13, 0.94)
Oak Titmouse	Intercept	-1.08 (-1.45, -0.71)
Oak Titmouse	Julian Day	0.07 (-0.31, 0.48)
Oak Titmouse	Julian Day^2	-0.02 (-0.21, 0.17)
Oak Titmouse	Wind (mph)	0.04 (-0.04, 0.11)
Oak Titmouse	Temperature (°C)	0.1 (-0.01, 0.23)
Oak Titmouse	PostFire Canopy	0.11 (-0.21, 0.42)
Orange-crowned Warbler	Intercept	-2.53 (-3.08, -1.96)
Orange-crowned Warbler	Julian Day	-0.57 (-1.11, -0.01)
Orange-crowned Warbler	Julian Day^2	0.08 (-0.16, 0.32)
Orange-crowned Warbler	Wind (mph)	0.04 (-0.05, 0.12)
Orange-crowned Warbler	Temperature (°C)	0.15 (-0.01, 0.31)
Orange-crowned Warbler	PostFire Canopy	-0.21 (-0.55, 0.14)
Pacific-slope Flycatcher	Intercept	-3.1 (-4.2, -2.04)
Pacific-slope Flycatcher	Julian Day	0.2 (-0.44, 0.78)
Pacific-slope Flycatcher	Julian Day^2	-0.09 (-0.38, 0.21)
Pacific-slope Flycatcher	Wind (mph)	0.01 (-0.08, 0.1)
Pacific-slope Flycatcher	Temperature (°C)	0.05 (-0.09, 0.2)
Pacific-slope Flycatcher	PostFire Canopy	-0.44 (-1, 0.12)
Pileated Woodpecker	Intercept	-4.79 (-5.71, -3.82)
Pileated Woodpecker	Julian Day	-0.04 (-0.74, 0.68)
Pileated Woodpecker	Julian Day^2	0 (-0.34, 0.33)
Pileated Woodpecker	Wind (mph)	0.05 (-0.04, 0.14)
Pileated Woodpecker	Temperature (°C)	0.03 (-0.13, 0.19)
Pileated Woodpecker	PostFire Canopy	-0.86 (-1.27, -0.4)
Rufous-crowned Sparrow	Intercept	-4.06 (-5, -3.03)
Rufous-crowned Sparrow	Julian Day	-0.17 (-0.74, 0.36)
Rufous-crowned Sparrow	Julian Day^2	-0.02 (-0.34, 0.29)
Rufous-crowned Sparrow	Wind (mph)	0.05 (-0.04, 0.15)
Rufous-crowned Sparrow	Temperature (°C)	0.06 (-0.07, 0.22)
Rufous-crowned Sparrow	PostFire Canopy	0.35 (-0.29, 0.94)

Spotted Towhee	Intercept	-1.75 (-2.51, -1)
Spotted Towhee	Julian Day	0.95 (0.39, 1.54)
Spotted Towhee	Julian Day^2	0.15 (-0.16, 0.46)
Spotted Towhee	Wind (mph)	0.06 (-0.03, 0.16)
Spotted Towhee	Temperature (°C)	0.1 (-0.04, 0.27)
Spotted Towhee	PostFire Canopy	0.01 (-0.4, 0.4)
Steller's Jay	Intercept	-2.45 (-2.97, -1.89)
Steller's Jay	Julian Day	0.04 (-0.49, 0.56)
Steller's Jay	Julian Day^2	-0.05 (-0.32, 0.22)
Steller's Jay	Wind (mph)	0.06 (-0.03, 0.15)
Steller's Jay	Temperature (°C)	0.03 (-0.12, 0.16)
Steller's Jay	PostFire Canopy	0.04 (-0.3, 0.39)
Violet-green Swallow	Intercept	-1.04 (-1.45, -0.61)
Violet-green Swallow	Julian Day	-0.24 (-0.75, 0.26)
Violet-green Swallow	Julian Day^2	-0.22 (-0.46, 0.01)
Violet-green Swallow	Wind (mph)	-0.01 (-0.11, 0.08)
Violet-green Swallow	Temperature (°C)	0.08 (-0.04, 0.2)
Violet-green Swallow	PostFire Canopy	-0.56 (-0.81, -0.29)
Warbling Vireo	Intercept	-4.37 (-5.49, -3.22)
Warbling Vireo	Julian Day	-0.37 (-1.08, 0.37)
Warbling Vireo	Julian Day^2	-0.09 (-0.44, 0.25)
Warbling Vireo	Wind (mph)	0.05 (-0.04, 0.15)
Warbling Vireo	Temperature (°C)	0.05 (-0.1, 0.21)
Warbling Vireo	PostFire Canopy	-0.64 (-1.14, -0.14)
Western Bluebird	Intercept	-3.25 (-4.04, -2.41)
Western Bluebird	Julian Day	-0.11 (-0.66, 0.39)
Western Bluebird	Julian Day^2	0.05 (-0.24, 0.34)
Western Bluebird	Wind (mph)	0.04 (-0.05, 0.13)
Western Bluebird	Temperature (°C)	0.1 (-0.04, 0.26)
Western Bluebird	PostFire Canopy	0.53 (0.04, 1.04)
Western Kingbird	Intercept	-2.97 (-4.79, -1.15)
Western Kingbird	Julian Day	1.32 (0.4, 2.19)
Western Kingbird	Julian Day^2	-0.06 (-0.44, 0.34)
Western Kingbird	Wind (mph)	0.04 (-0.06, 0.14)
Western Kingbird	Temperature (°C)	0.07 (-0.08, 0.24)
Western Kingbird	PostFire Canopy	0.49 (-0.24, 1.2)
Western Meadowlark	Intercept	-4.41 (-5.97, -2.63)
Western Meadowlark	Julian Day	-0.19 (-0.93, 0.57)
Western Meadowlark	Julian Day^2	-0.08 (-0.41, 0.23)
Western Meadowlark	Wind (mph)	0.02 (-0.07, 0.11)
Western Meadowlark	Temperature (°C)	0.03 (-0.14, 0.17)
Western Meadowlark	PostFire Canopy	-0.15 (-0.95, 0.65)
Western Wood-Pewee	Intercept	-3.8 (-5.62, -2.01)
Western Wood-Pewee	Julian Day	-0.03 (-0.94, 0.87)
Western Wood-Pewee	Julian Day^2	-0.04 (-0.41, 0.36)
Western Wood-Pewee	Wind (mph)	0.05 (-0.04, 0.15)
Western Wood-Pewee	Temperature (°C)	0.08 (-0.08, 0.23)
Western Wood-Pewee	PostFire Canopy	0.31 (-0.57, 1.17)
White-breasted Nuthatch	Intercept	-2.15 (-2.74, -1.54)
White-breasted Nuthatch	Julian Day	-0.18 (-0.73, 0.36)
White-breasted Nuthatch	Julian Day^2	-0.15 (-0.41, 0.12)
White-breasted Nuthatch	Wind (mph)	0.05 (-0.03, 0.13)
White-breasted Nuthatch	Temperature (°C)	0.07 (-0.06, 0.21)

White-breasted Nuthatch	PostFire Canopy	-0.04 (-0.44, 0.35)
Wrentit	Intercept	-3.69 (-5.04, -2.43)
Wrentit	Julian Day	0.81 (0.23, 1.41)
Wrentit	Julian Day^2	0.19 (-0.16, 0.54)
Wrentit	Wind (mph)	0.04 (-0.06, 0.13)
Wrentit	Temperature (°C)	0.11 (-0.04, 0.28)
Wrentit	PostFire Canopy	-0.32 (-0.96, 0.31)
Community Mean	Intercept	-3.01 (-3.44, -2.58)
Community Mean	Julian Day	0.05 (-0.21, 0.3)
Community Mean	Julian Day^2	0.05 (-0.07, 0.16)
Community Mean	Wind (mph)	0.04 (0, 0.09)
Community Mean	Temperature (°C)	0.06 (0, 0.13)
Community Mean	PostFire Canopy	0.03 (-0.15, 0.22)

Table S5. Species-specific covariate coefficients from the occupancy submodel for the bird community-level multi-species occupancy model.

Species	**Parameter**	**Estimate**
Acorn Woodpecker	Intercept	2.37 (1.44, 3.29)
Acorn Woodpecker	Elevation	-0.36 (-1.34, 0.56)
Acorn Woodpecker	PreFire Canopy	-0.42 (-1.08, 0.22)
Acorn Woodpecker	Severity	-0.46 (-1.61, 0.71)
Acorn Woodpecker	Severity Squared	-0.33 (-1.37, 0.67)
Acorn Woodpecker	Pyrodiversity	0.23 (-0.35, 0.84)
Acorn Woodpecker	LagYear	0.29 (-0.26, 0.82)
American Robin	Intercept	1.56 (0.02, 3.23)
American Robin	Elevation	-0.19 (-1.3, 0.96)
American Robin	PreFire Canopy	-0.1 (-0.77, 0.69)
American Robin	Severity	-0.32 (-1.46, 0.77)
American Robin	Severity Squared	0.24 (-0.84, 1.21)
American Robin	Pyrodiversity	-0.07 (-0.7, 0.51)
American Robin	LagYear	-0.04 (-0.87, 0.88)
Anna's Hummingbird	Intercept	-3.33 (-5.26, -1.66)
Anna's Hummingbird	Elevation	0.16 (-0.84, 1.18)
Anna's Hummingbird	PreFire Canopy	-0.19 (-0.92, 0.59)
Anna's Hummingbird	Severity	0.06 (-1.02, 1.19)
Anna's Hummingbird	Severity Squared	0.63 (-0.47, 1.68)
Anna's Hummingbird	Pyrodiversity	0.01 (-0.61, 0.61)
Anna's Hummingbird	LagYear	0.12 (-0.75, 0.94)
Ash-throated Flycatcher	Intercept	0.9 (-0.86, 2.75)
Ash-throated Flycatcher	Elevation	0.11 (-0.98, 1.21)
Ash-throated Flycatcher	PreFire Canopy	-0.36 (-1.14, 0.36)
Ash-throated Flycatcher	Severity	-0.09 (-1.16, 1.03)
Ash-throated Flycatcher	Severity Squared	0.47 (-0.62, 1.58)
Ash-throated Flycatcher	Pyrodiversity	-0.11 (-0.82, 0.6)
Ash-throated Flycatcher	LagYear	0.7 (-0.11, 1.53)
Bewick's Wren	Intercept	-0.37 (-2.01, 1.37)
Bewick's Wren	Elevation	0.47 (-0.58, 1.62)
Bewick's Wren	PreFire Canopy	-0.38 (-1.18, 0.38)
Bewick's Wren	Severity	0.15 (-1.02, 1.35)
Bewick's Wren	Severity Squared	0.75 (-0.48, 1.93)
Bewick's Wren	Pyrodiversity	0.02 (-0.63, 0.65)
Bewick's Wren	LagYear	0.48 (-0.37, 1.32)

Black Phoebe	Intercept	-0.45 (-2.68, 2.01)
Black Phoebe	Elevation	-0.06 (-1.22, 1.13)
Black Phoebe	PreFire Canopy	-0.45 (-1.3, 0.3)
Black Phoebe	Severity	-0.41 (-1.62, 0.85)
Black Phoebe	Severity Squared	0 (-1.28, 1.24)
Black Phoebe	Pyrodiversity	0.02 (-0.64, 0.66)
Black Phoebe	LagYear	0.43 (-0.52, 1.39)
Black-headed Grosbeak	Intercept	-1.42 (-2.82, -0.1)
Black-headed Grosbeak	Elevation	0.31 (-0.65, 1.29)
Black-headed Grosbeak	PreFire Canopy	-0.18 (-0.89, 0.56)
Black-headed Grosbeak	Severity	-0.17 (-1.21, 0.95)
Black-headed Grosbeak	Severity Squared	0.14 (-0.87, 1.12)
Black-headed Grosbeak	Pyrodiversity	0.07 (-0.51, 0.66)
Black-headed Grosbeak	LagYear	-0.1 (-0.88, 0.65)
Black-throated Gray Warbler	Intercept	-0.75 (-3.33, 1.87)
Black-throated Gray Warbler	Elevation	0.68 (-0.46, 1.88)
Black-throated Gray Warbler	PreFire Canopy	-0.16 (-0.94, 0.71)
Black-throated Gray Warbler	Severity	0 (-1.15, 1.24)
Black-throated Gray Warbler	Severity Squared	0.37 (-0.85, 1.59)
Black-throated Gray Warbler	Pyrodiversity	0.26 (-0.35, 0.92)
Black-throated Gray Warbler	LagYear	-0.1 (-1.11, 0.85)
Blue-gray Gnatcatcher	Intercept	-1.54 (-2.32, -0.77)
Blue-gray Gnatcatcher	Elevation	0.53 (-0.15, 1.25)
Blue-gray Gnatcatcher	PreFire Canopy	-0.24 (-0.81, 0.37)
Blue-gray Gnatcatcher	Severity	0.13 (-0.93, 1.21)
Blue-gray Gnatcatcher	Severity Squared	0.63 (-0.41, 1.67)
Blue-gray Gnatcatcher	Pyrodiversity	0.14 (-0.34, 0.64)
Blue-gray Gnatcatcher	LagYear	-0.37 (-0.98, 0.3)
Brown-headed Cowbird	Intercept	0.05 (-2.33, 2.45)
Brown-headed Cowbird	Elevation	0.29 (-0.85, 1.44)
Brown-headed Cowbird	PreFire Canopy	-0.08 (-0.88, 0.8)
Brown-headed Cowbird	Severity	0.07 (-1.02, 1.3)
Brown-headed Cowbird	Severity Squared	0.53 (-0.55, 1.74)
Brown-headed Cowbird	Pyrodiversity	0.09 (-0.54, 0.74)
Brown-headed Cowbird	LagYear	0.22 (-0.71, 1.13)
Bullock's Oriole	Intercept	-1.69 (-2.68, -0.73)
Bullock's Oriole	Elevation	0.03 (-0.69, 0.76)
Bullock's Oriole	PreFire Canopy	-0.6 (-1.27, 0.06)
Bullock's Oriole	Severity	-0.12 (-1.08, 1.02)
Bullock's Oriole	Severity Squared	0.13 (-0.86, 1.07)
Bullock's Oriole	Pyrodiversity	0.23 (-0.3, 0.8)
Bullock's Oriole	LagYear	-0.5 (-1.1, 0.15)
Bushtit	Intercept	-1.2 (-2.29, -0.14)
Bushtit	Elevation	0.46 (-0.43, 1.32)
Bushtit	PreFire Canopy	-0.11 (-0.76, 0.61)
Bushtit	Severity	-0.27 (-1.3, 0.8)
Bushtit	Severity Squared	0.23 (-0.76, 1.19)
Bushtit	Pyrodiversity	-0.06 (-0.73, 0.51)
Bushtit	LagYear	-0.26 (-0.89, 0.38)
California Quail	Intercept	1.04 (0.23, 1.81)
California Quail	Elevation	0.7 (-0.08, 1.45)
California Quail	PreFire Canopy	-0.5 (-1.16, 0.13)
California Quail	Severity	-0.27 (-1.32, 0.81)

California Quail	Severity Squared	0.15 (-0.79, 1.05)
California Quail	Pyrodiversity	0.13 (-0.36, 0.6)
California Quail	LagYear	0.44 (-0.1, 0.99)
California Scrub-Jay	Intercept	1.61 (0.26, 2.96)
California Scrub-Jay	Elevation	0.29 (-0.69, 1.28)
California Scrub-Jay	PreFire Canopy	-0.45 (-1.23, 0.31)
California Scrub-Jay	Severity	-0.18 (-1.21, 0.91)
California Scrub-Jay	Severity Squared	0.33 (-0.75, 1.33)
California Scrub-Jay	Pyrodiversity	-0.07 (-0.74, 0.5)
California Scrub-Jay	LagYear	0.5 (-0.23, 1.25)
California Towhee	Intercept	1.44 (0.62, 2.23)
California Towhee	Elevation	0.57 (-0.18, 1.33)
California Towhee	PreFire Canopy	-0.35 (-0.86, 0.19)
California Towhee	Severity	0 (-0.96, 0.99)
California Towhee	Severity Squared	0.4 (-0.63, 1.3)
California Towhee	Pyrodiversity	0.08 (-0.42, 0.59)
California Towhee	LagYear	0.18 (-0.32, 0.66)
Common Raven	Intercept	0.75 (-0.98, 2.43)
Common Raven	Elevation	-0.3 (-1.38, 0.85)
Common Raven	PreFire Canopy	-0.28 (-1.02, 0.47)
Common Raven	Severity	-0.53 (-1.69, 0.75)
Common Raven	Severity Squared	-0.19 (-1.45, 0.98)
Common Raven	Pyrodiversity	0.11 (-0.42, 0.71)
Common Raven	LagYear	0.48 (-0.34, 1.27)
Dark-eyed Junco	Intercept	0.42 (-0.6, 1.4)
Dark-eyed Junco	Elevation	0.21 (-0.7, 1.13)
Dark-eyed Junco	PreFire Canopy	-0.12 (-0.73, 0.53)
Dark-eyed Junco	Severity	0.14 (-0.93, 1.23)
Dark-eyed Junco	Severity Squared	0.79 (-0.3, 1.94)
Dark-eyed Junco	Pyrodiversity	0.04 (-0.52, 0.6)
Dark-eyed Junco	LagYear	0.75 (-0.04, 1.55)
Golden-crowned Sparrow	Intercept	-0.87 (-3.58, 2.04)
Golden-crowned Sparrow	Elevation	0.05 (-1.14, 1.23)
Golden-crowned Sparrow	PreFire Canopy	-0.34 (-1.16, 0.48)
Golden-crowned Sparrow	Severity	-0.12 (-1.26, 1.12)
Golden-crowned Sparrow	Severity Squared	0.22 (-1, 1.4)
Golden-crowned Sparrow	Pyrodiversity	0.21 (-0.44, 0.89)
Golden-crowned Sparrow	LagYear	0.3 (-0.69, 1.26)
House Finch	Intercept	-1.37 (-2.68, -0.26)
House Finch	Elevation	-0.06 (-0.88, 0.8)
House Finch	PreFire Canopy	-0.64 (-1.45, 0.07)
House Finch	Severity	-0.7 (-1.97, 0.6)
House Finch	Severity Squared	-0.27 (-1.58, 0.86)
House Finch	Pyrodiversity	0.06 (-0.53, 0.61)
House Finch	LagYear	0.26 (-0.45, 0.93)
Lazuli Bunting	Intercept	-0.53 (-1.32, 0.29)
Lazuli Bunting	Elevation	0.44 (-0.37, 1.2)
Lazuli Bunting	PreFire Canopy	-0.15 (-0.79, 0.53)
Lazuli Bunting	Severity	-0.01 (-1, 1.05)
Lazuli Bunting	Severity Squared	0.27 (-0.65, 1.17)
Lazuli Bunting	Pyrodiversity	0.22 (-0.33, 0.81)
Lazuli Bunting	LagYear	-1.08 (-1.85, -0.31)
Lesser Goldfinch	Intercept	1.03 (-0.83, 2.95)

Lesser Goldfinch	Elevation	-0.08 (-1.13, 0.92)
Lesser Goldfinch	PreFire Canopy	-0.28 (-1.07, 0.52)
Lesser Goldfinch	Severity	-0.01 (-1.11, 1.16)
Lesser Goldfinch	Severity Squared	0.55 (-0.53, 1.67)
Lesser Goldfinch	Pyrodiversity	0.04 (-0.63, 0.66)
Lesser Goldfinch	LagYear	0.41 (-0.72, 1.55)
Mountain Quail	Intercept	-1.61 (-2.48, -0.79)
Mountain Quail	Elevation	1.69 (0.75, 2.58)
Mountain Quail	PreFire Canopy	0.03 (-0.65, 0.78)
Mountain Quail	Severity	0.22 (-0.89, 1.31)
Mountain Quail	Severity Squared	0.67 (-0.34, 1.69)
Mountain Quail	Pyrodiversity	0.33 (-0.22, 0.85)
Mountain Quail	LagYear	-0.23 (-0.91, 0.44)
Mourning Dove	Intercept	2.21 (0.74, 3.7)
Mourning Dove	Elevation	0.23 (-0.77, 1.26)
Mourning Dove	PreFire Canopy	-0.29 (-1.06, 0.5)
Mourning Dove	Severity	-0.04 (-1.11, 1.12)
Mourning Dove	Severity Squared	0.29 (-0.84, 1.36)
Mourning Dove	Pyrodiversity	0.17 (-0.45, 0.8)
Mourning Dove	LagYear	0.21 (-0.63, 1.06)
Northern Flicker	Intercept	1.7 (0.14, 3.23)
Northern Flicker	Elevation	0.35 (-0.59, 1.28)
Northern Flicker	PreFire Canopy	-0.39 (-1.23, 0.47)
Northern Flicker	Severity	-0.16 (-1.24, 0.93)
Northern Flicker	Severity Squared	0.32 (-0.71, 1.3)
Northern Flicker	Pyrodiversity	0.01 (-0.66, 0.61)
Northern Flicker	LagYear	0.49 (-0.34, 1.35)
Nuttall's Woodpecker	Intercept	0.82 (-0.8, 2.43)
Nuttall's Woodpecker	Elevation	-0.11 (-1.2, 1)
Nuttall's Woodpecker	PreFire Canopy	-0.36 (-1.08, 0.35)
Nuttall's Woodpecker	Severity	-0.14 (-1.18, 1.01)
Nuttall's Woodpecker	Severity Squared	0.36 (-0.67, 1.36)
Nuttall's Woodpecker	Pyrodiversity	-0.04 (-0.71, 0.57)
Nuttall's Woodpecker	LagYear	-0.09 (-0.9, 0.71)
Oak Titmouse	Intercept	2.3 (1.14, 3.45)
Oak Titmouse	Elevation	-0.18 (-1.19, 0.86)
Oak Titmouse	PreFire Canopy	-0.33 (-0.95, 0.27)
Oak Titmouse	Severity	0.1 (-0.94, 1.19)
Oak Titmouse	Severity Squared	0.55 (-0.54, 1.55)
Oak Titmouse	Pyrodiversity	0.15 (-0.42, 0.76)
Oak Titmouse	LagYear	0.28 (-0.38, 0.98)
Orange-crowned Warbler	Intercept	1.03 (0.05, 2.02)
Orange-crowned Warbler	Elevation	-0.18 (-0.99, 0.66)
Orange-crowned Warbler	PreFire Canopy	-0.43 (-1.12, 0.29)
Orange-crowned Warbler	Severity	-0.19 (-1.17, 0.86)
Orange-crowned Warbler	Severity Squared	0.41 (-0.54, 1.33)
Orange-crowned Warbler	Pyrodiversity	0.12 (-0.41, 0.65)
Orange-crowned Warbler	LagYear	0.35 (-0.39, 1.1)
Pacific-slope Flycatcher	Intercept	-0.36 (-2.01, 1.2)
Pacific-slope Flycatcher	Elevation	-0.14 (-1.1, 0.84)
Pacific-slope Flycatcher	PreFire Canopy	-0.28 (-1.04, 0.48)
Pacific-slope Flycatcher	Severity	-0.37 (-1.45, 0.76)
Pacific-slope Flycatcher	Severity Squared	0.35 (-0.69, 1.28)

Pacific-slope Flycatcher	Pyrodiversity	-0.21 (-0.93, 0.47)
Pacific-slope Flycatcher	LagYear	-0.48 (-1.27, 0.3)
Pileated Woodpecker	Intercept	1.67 (-0.51, 3.78)
Pileated Woodpecker	Elevation	0.15 (-1.01, 1.33)
Pileated Woodpecker	PreFire Canopy	-0.21 (-0.99, 0.63)
Pileated Woodpecker	Severity	-0.31 (-1.51, 0.94)
Pileated Woodpecker	Severity Squared	0.12 (-1.1, 1.4)
Pileated Woodpecker	Pyrodiversity	0.16 (-0.44, 0.76)
Pileated Woodpecker	LagYear	0.33 (-0.67, 1.33)
Rufous-crowned Sparrow	Intercept	1.03 (-0.97, 3)
Rufous-crowned Sparrow	Elevation	0.35 (-0.75, 1.52)
Rufous-crowned Sparrow	PreFire Canopy	-0.3 (-1.14, 0.56)
Rufous-crowned Sparrow	Severity	-0.17 (-1.25, 1.07)
Rufous-crowned Sparrow	Severity Squared	0.24 (-0.97, 1.43)
Rufous-crowned Sparrow	Pyrodiversity	0.03 (-0.62, 0.7)
Rufous-crowned Sparrow	LagYear	0.3 (-0.67, 1.26)
Spotted Towhee	Intercept	-1.05 (-1.96, -0.15)
Spotted Towhee	Elevation	0.32 (-0.56, 1.21)
Spotted Towhee	PreFire Canopy	0.05 (-0.62, 0.74)
Spotted Towhee	Severity	0.26 (-0.86, 1.38)
Spotted Towhee	Severity Squared	0.8 (-0.33, 1.88)
Spotted Towhee	Pyrodiversity	0.11 (-0.41, 0.62)
Spotted Towhee	LagYear	0.49 (-0.08, 1.06)
Steller's Jay	Intercept	1.45 (-0.05, 2.95)
Steller's Jay	Elevation	0.03 (-0.96, 0.94)
Steller's Jay	PreFire Canopy	0.01 (-0.75, 0.86)
Steller's Jay	Severity	-0.18 (-1.18, 0.97)
Steller's Jay	Severity Squared	0.38 (-0.64, 1.37)
Steller's Jay	Pyrodiversity	-0.02 (-0.65, 0.5)
Steller's Jay	LagYear	0.59 (-0.32, 1.48)
Violet-green Swallow	Intercept	1.02 (0.32, 1.7)
Violet-green Swallow	Elevation	-0.67 (-1.28, -0.06)
Violet-green Swallow	PreFire Canopy	-0.58 (-1.19, 0.03)
Violet-green Swallow	Severity	-0.38 (-1.33, 0.67)
Violet-green Swallow	Severity Squared	0.24 (-0.63, 1.09)
Violet-green Swallow	Pyrodiversity	-0.31 (-0.83, 0.23)
Violet-green Swallow	LagYear	0.21 (-0.31, 0.76)
Warbling Vireo	Intercept	0.19 (-1.74, 2.04)
Warbling Vireo	Elevation	-0.4 (-1.57, 0.82)
Warbling Vireo	PreFire Canopy	-0.42 (-1.25, 0.37)
Warbling Vireo	Severity	-0.47 (-1.68, 0.81)
Warbling Vireo	Severity Squared	-0.05 (-1.29, 1.14)
Warbling Vireo	Pyrodiversity	-0.06 (-0.74, 0.55)
Warbling Vireo	LagYear	0.19 (-0.73, 1.13)
Western Bluebird	Intercept	1.01 (-0.65, 2.66)
Western Bluebird	Elevation	0.61 (-0.41, 1.73)
Western Bluebird	PreFire Canopy	-0.49 (-1.23, 0.25)
Western Bluebird	Severity	-0.09 (-1.09, 1.1)
Western Bluebird	Severity Squared	0.28 (-0.82, 1.36)
Western Bluebird	Pyrodiversity	0.17 (-0.44, 0.79)
Western Bluebird	LagYear	0.37 (-0.31, 1.1)
Western Kingbird	Intercept	-1.94 (-3.83, -0.07)
Western Kingbird	Elevation	0.03 (-0.95, 1)

Western Kingbird	PreFire Canopy	-0.4 (-1.15, 0.33)
Western Kingbird	Severity	-0.44 (-1.63, 0.81)
Western Kingbird	Severity Squared	-0.09 (-1.27, 1.11)
Western Kingbird	Pyrodiversity	0.01 (-0.62, 0.65)
Western Kingbird	LagYear	0.01 (-0.82, 0.84)
Western Meadowlark	Intercept	-1.18 (-3.26, 1.08)
Western Meadowlark	Elevation	0.12 (-1.04, 1.25)
Western Meadowlark	PreFire Canopy	-0.55 (-1.47, 0.3)
Western Meadowlark	Severity	-0.25 (-1.37, 0.97)
Western Meadowlark	Severity Squared	0.12 (-1.11, 1.34)
Western Meadowlark	Pyrodiversity	0.1 (-0.56, 0.74)
Western Meadowlark	LagYear	0.39 (-0.6, 1.4)
Western Wood-Pewee	Intercept	-3.22 (-5.14, -1.5)
Western Wood-Pewee	Elevation	0.1 (-0.89, 1.11)
Western Wood-Pewee	PreFire Canopy	-0.51 (-1.31, 0.24)
Western Wood-Pewee	Severity	-0.33 (-1.46, 0.79)
Western Wood-Pewee	Severity Squared	0.16 (-0.89, 1.16)
Western Wood-Pewee	Pyrodiversity	-0.03 (-0.65, 0.62)
Western Wood-Pewee	LagYear	0.36 (-0.45, 1.17)
White-breasted Nuthatch	Intercept	1.05 (-0.15, 2.24)
White-breasted Nuthatch	Elevation	-0.4 (-1.34, 0.57)
White-breasted Nuthatch	PreFire Canopy	-0.36 (-1.06, 0.39)
White-breasted Nuthatch	Severity	-0.58 (-1.84, 0.68)
White-breasted Nuthatch	Severity Squared	-0.32 (-1.6, 0.76)
White-breasted Nuthatch	Pyrodiversity	0.02 (-0.57, 0.61)
White-breasted Nuthatch	LagYear	0.19 (-0.49, 0.84)
Wrentit	Intercept	-0.71 (-2.61, 1.16)
Wrentit	Elevation	0.48 (-0.65, 1.56)
Wrentit	PreFire Canopy	-0.39 (-1.21, 0.43)
Wrentit	Severity	-0.33 (-1.5, 0.95)
Wrentit	Severity Squared	-0.01 (-1.24, 1.17)
Wrentit	Pyrodiversity	0.19 (-0.4, 0.81)
Wrentit	LagYear	0.53 (-0.29, 1.37)
Community Mean	Intercept	0.07 (-0.53, 0.67)
Community Mean	Elevation	0.17 (-0.21, 0.54)
Community Mean	PreFire Canopy	-0.31 (-0.63, -0.01)
Community Mean	Severity	-0.17 (-0.93, 0.66)
Community Mean	Severity Squared	0.27 (-0.45, 0.93)
Community Mean	Pyrodiversity	0.06 (-0.21, 0.34)
Community Mean	LagYear	0.19 (-0.08, 0.45)

Table S6. Group-specific covariate coefficients from the detection submodel for the bird nesting-group multi-species occupancy model.

Group	Parameter	Estimate
Ground	Intercept	-1.78 (-2.48, -1.1)
Ground	Julian Day	-0.14 (-0.71, 0.43)
Ground	Julian Day^2	-0.16 (-0.37, 0.04)
Ground	Wind (mph)	-0.08 (-0.2, 0.03)
Ground	Temperature (°C)	0.01 (-0.2, 0.22)
Ground	PostFire Canopy	0.38 (-0.47, 1.22)
Primary Cavity	Intercept	-2.41 (-3.29, -1.61)
Primary Cavity	Julian Day	0.21 (-1.24, 1.58)

Primary Cavity	Julian Day^2	0.29 (-0.61, 1.16)
Primary Cavity	Wind (mph)	0.11 (-0.15, 0.38)
Primary Cavity	Temperature (°C)	0 (-0.39, 0.4)
Primary Cavity	PostFire Canopy	0.19 (-0.66, 1)
Secondary Cavity	Intercept	-1.84 (-2.33, -1.34)
Secondary Cavity	Julian Day	0.61 (-0.03, 1.25)
Secondary Cavity	Julian Day^2	0.11 (-0.12, 0.36)
Secondary Cavity	Wind (mph)	0 (-0.13, 0.13)
Secondary Cavity	Temperature (°C)	0.05 (-0.12, 0.22)
Secondary Cavity	PostFire Canopy	0.37 (-0.02, 0.76)
Shrub	Intercept	-2.45 (-3.98, -0.98)
Shrub	Julian Day	-0.23 (-1.13, 0.67)
Shrub	Julian Day^2	-0.14 (-0.58, 0.29)
Shrub	Wind (mph)	-0.04 (-0.24, 0.16)
Shrub	Temperature (°C)	0.04 (-0.28, 0.34)
Shrub	PostFire Canopy	0.02 (-0.53, 0.65)
Tree	Intercept	-2.28 (-3.01, -1.55)
Tree	Julian Day	-0.2 (-0.91, 0.48)
Tree	Julian Day^2	-0.03 (-0.38, 0.32)
Tree	Wind (mph)	0.09 (0.02, 0.16)
Tree	Temperature (°C)	0.07 (-0.05, 0.2)
Tree	PostFire Canopy	-0.29 (-0.7, 0.13)

Table S7. Species-specific covariate coefficients from the occupancy submodel for the bird group-level multi-species occupancy model.

Group	**Parameter**	**Estimate**
Ground	Intercept	0.04 (-1.34, 1.48)
Ground	Elevation	0.17 (-0.74, 1.06)
Ground	PreFire Canopy	-0.71 (-1.36, -0.05)
Ground	Severity	-0.83 (-2.45, 0.66)
Ground	Severity Squared	0.99 (-0.39, 2.36)
Ground	Pyrodiversity	-0.04 (-0.66, 0.62)
Ground	LagYear	0.69 (0.23, 1.12)
Primary Cavity	Intercept	-2.14 (-3.6, -0.78)
Primary Cavity	Elevation	0.45 (-0.82, 1.66)
Primary Cavity	PreFire Canopy	0.17 (-1.24, 1.51)
Primary Cavity	Severity	0.1 (-2.32, 2.5)
Primary Cavity	Severity Squared	0.86 (-1.5, 3.17)
Primary Cavity	Pyrodiversity	-0.18 (-1.52, 1.04)
Primary Cavity	LagYear	-0.73 (-2.22, 0.67)
Secondary Cavity	Intercept	-0.64 (-2.2, 0.95)
Secondary Cavity	Elevation	1.36 (0.13, 2.58)
Secondary Cavity	PreFire Canopy	-0.63 (-1.72, 0.39)
Secondary Cavity	Severity	-0.12 (-2.31, 1.84)
Secondary Cavity	Severity Squared	0.58 (-1.41, 2.34)
Secondary Cavity	Pyrodiversity	-0.42 (-1.41, 0.54)
Secondary Cavity	LagYear	0.82 (0.04, 1.63)
Shrub	Intercept	-1.38 (-3.19, 0.42)
Shrub	Elevation	-0.53 (-1.55, 0.4)
Shrub	PreFire Canopy	0.38 (-0.86, 1.57)
Shrub	Severity	0.97 (-1.2, 3.02)
Shrub	Severity Squared	-0.88 (-2.77, 0.97)

Shrub	Pyrodiversity	0.1 (-0.92, 1.18)
Shrub	LagYear	-0.3 (-1.35, 0.71)
Tree	Intercept	-0.12 (-1.46, 1.2)
Tree	Elevation	-0.09 (-1.14, 1)
Tree	PreFire Canopy	-0.41 (-1.19, 0.38)
Tree	Severity	1.74 (-0.09, 3.4)
Tree	Severity Squared	-1.61 (-3.06, 0.01)
Tree	Pyrodiversity	-0.1 (-0.68, 0.47)
Tree	LagYear	0.34 (-0.26, 0.95)

Table S8. Species-specific covariate coefficients from the detection submodel for the bird diet-group multi-species occupancy model.

Group	**Parameter**	**Estimate**
Granivore	Intercept	-2.38 (-3.38, -1.41)
Granivore	Julian Day	0.1 (-0.55, 0.73)
Granivore	Julian Day^2	0.1 (-0.24, 0.42)
Granivore	Wind (mph)	0.05 (-0.09, 0.19)
Granivore	Temperature (°C)	0.02 (-0.17, 0.22)
Granivore	PostFire Canopy	0.25 (-0.88, 1.4)
Insectivore	Intercept	-1.82 (-2.16, -1.47)
Insectivore	Julian Day	0.05 (-0.45, 0.58)
Insectivore	Julian Day^2	0.02 (-0.22, 0.26)
Insectivore	Wind (mph)	0.04 (-0.02, 0.09)
Insectivore	Temperature (°C)	0.1 (0.01, 0.19)
Insectivore	PostFire Canopy	0.01 (-0.26, 0.28)
Nectar	Intercept	-1.73 (-4.18, 1.23)
Nectar	Julian Day	-0.07 (-2.34, 2.22)
Nectar	Julian Day^2	0.14 (-2.12, 2.3)
Nectar	Wind (mph)	0.03 (-2.2, 2.15)
Nectar	Temperature (°C)	-0.1 (-2.25, 2.16)
Nectar	PostFire Canopy	0.04 (-2.17, 2.24)
Omnivore	Intercept	-2.38 (-3.38, -1.44)
Omnivore	Julian Day	0.12 (-0.47, 0.69)
Omnivore	Julian Day^2	-0.12 (-0.34, 0.1)
Omnivore	Wind (mph)	-0.1 (-0.22, 0.02)
Omnivore	Temperature (°C)	-0.03 (-0.25, 0.19)
Omnivore	PostFire Canopy	0.09 (-0.43, 0.58)

Table S9. Species-specific covariate coefficients from the occupancy submodel for the bird diet-group multi-species occupancy model.

Group	Parameter	Estimate
Granivore	Intercept	-0.65 (-2.38, 1.16)
Granivore	Elevation	-0.3 (-1.02, 0.41)
Granivore	PreFire Canopy	-0.27 (-1.01, 0.46)
Granivore	Severity	-1.09 (-2.81, 0.62)
Granivore	Severity Squared	0.32 (-1.26, 1.93)
Granivore	Pyrodiversity	-0.2 (-0.85, 0.45)
Granivore	LagYear	0.38 (-0.17, 0.95)
Insectivore	Intercept	-0.9 (-1.68, -0.11)
Insectivore	Elevation	0.32 (-0.18, 0.82)
Insectivore	PreFire Canopy	-0.28 (-0.67, 0.12)

Insectivore	Severity	1.53 (0.57, 2.78)
Insectivore	Severity Squared	-0.96 (-1.92, 0.03)
Insectivore	Pyrodiversity	-0.17 (-0.5, 0.16)
Insectivore	LagYear	0.28 (-0.04, 0.6)
Nectar	Intercept	1.17 (-2.26, 4.69)
Nectar	Elevation	-1.01 (-4.44, 2.49)
Nectar	PreFire Canopy	0.6 (-2.7, 3.89)
Nectar	Severity	-0.11 (-3.62, 3.27)
Nectar	Severity Squared	0.21 (-3.06, 3.6)
Nectar	Pyrodiversity	-0.05 (-3.18, 3.2)
Nectar	LagYear	-0.56 (-4.17, 3.12)
Omnivore	Intercept	-0.17 (-1.42, 1.14)
Omnivore	Elevation	0.53 (-0.78, 1.79)
Omnivore	PreFire Canopy	-0.49 (-1.55, 0.63)
Omnivore	Severity	-0.35 (-2.09, 1.43)
Omnivore	Severity Squared	0.67 (-0.97, 2.23)
Omnivore	Pyrodiversity	-0.03 (-0.97, 0.93)
Omnivore	LagYear	0.1 (-0.98, 1.21)

Table S10. Species-specific covariate coefficients from the detection submodel for bat multi-species occupancy model.

Species	**Parameter**	**Estimate**
Pallid Bat	Intercept	-2.59 (-3.28, -1.88)
Pallid Bat	Calendar Date	-0.03 (-0.32, 0.25)
Pallid Bat	Calendar Date^2	0.06 (-0.05, 0.17)
Pallid Bat	Wind (mph)	-0.26 (-0.52, -0.02)
Pallid Bat	Temperature (°C)	0.38 (0.07, 0.7)
Pallid Bat	PostFire Canopy	0.04 (-0.14, 0.22)
Big Brown Bat	Intercept	-1.01 (-1.29, -0.74)
Big Brown Bat	Calendar Date	-0.2 (-0.38, 0)
Big Brown Bat	Calendar Date^2	0.04 (-0.07, 0.13)
Big Brown Bat	Wind (mph)	-0.21 (-0.39, -0.04)
Big Brown Bat	Temperature (°C)	0.28 (0.07, 0.48)
Big Brown Bat	PostFire Canopy	0.09 (-0.06, 0.23)
Western Red Bat	Intercept	-1.46 (-1.95, -0.98)
Western Red Bat	Calendar Date	-0.09 (-0.3, 0.12)
Western Red Bat	Calendar Date^2	0.04 (-0.06, 0.14)
Western Red Bat	Wind (mph)	-0.14 (-0.32, 0.03)
Western Red Bat	Temperature (°C)	-0.46 (-0.71, -0.19)
Western Red Bat	PostFire Canopy	0.05 (-0.12, 0.22)
Hoary Bat	Intercept	-0.86 (-1.19, -0.52)
Hoary Bat	Calendar Date	-0.89 (-1.12, -0.66)
Hoary Bat	Calendar Date^2	0.06 (-0.04, 0.16)
Hoary Bat	Wind (mph)	-0.03 (-0.21, 0.16)
Hoary Bat	Temperature (°C)	0.16 (-0.05, 0.37)
Hoary Bat	PostFire Canopy	0.02 (-0.15, 0.18)
Silver-haired Bat	Intercept	-0.64 (-1, -0.3)
Silver-haired Bat	Calendar Date	-0.37 (-0.57, -0.17)
Silver-haired Bat	Calendar Date^2	0.07 (-0.04, 0.16)
Silver-haired Bat	Wind (mph)	-0.23 (-0.41, -0.04)
Silver-haired Bat	Temperature (°C)	0.53 (0.3, 0.77)
Silver-haired Bat	PostFire Canopy	0.03 (-0.13, 0.2)

California Myotis	Intercept	1.26 (0.79, 1.73)
California Myotis	Calendar Date	-0.11 (-0.32, 0.12)
California Myotis	Calendar Date^2	0.08 (-0.03, 0.19)
California Myotis	Wind (mph)	-0.21 (-0.4, -0.03)
California Myotis	Temperature (°C)	0.52 (0.26, 0.77)
California Myotis	PostFire Canopy	0.08 (-0.11, 0.27)
Long-eared Myotis	Intercept	-2 (-2.53, -1.48)
Long-eared Myotis	Calendar Date	0.08 (-0.18, 0.32)
Long-eared Myotis	Calendar Date^2	0.04 (-0.07, 0.14)
Long-eared Myotis	Wind (mph)	-0.04 (-0.24, 0.16)
Long-eared Myotis	Temperature (°C)	0.19 (-0.06, 0.43)
Long-eared Myotis	PostFire Canopy	0.08 (-0.1, 0.26)
Little Brown Bat	Intercept	-4.87 (-6.26, -3.66)
Little Brown Bat	Calendar Date	-0.01 (-0.49, 0.45)
Little Brown Bat	Calendar Date^2	0.07 (-0.06, 0.19)
Little Brown Bat	Wind (mph)	-0.18 (-0.45, 0.08)
Little Brown Bat	Temperature (°C)	0.09 (-0.37, 0.6)
Little Brown Bat	PostFire Canopy	0.04 (-0.16, 0.24)
Fringed Myotis	Intercept	-5.06 (-7.23, -3.13)
Fringed Myotis	Calendar Date	-0.32 (-0.83, 0.22)
Fringed Myotis	Calendar Date^2	0.05 (-0.08, 0.16)
Fringed Myotis	Wind (mph)	-0.12 (-0.38, 0.16)
Fringed Myotis	Temperature (°C)	-0.03 (-0.52, 0.49)
Fringed Myotis	PostFire Canopy	0.04 (-0.16, 0.24)
Yuma Myotis	Intercept	-0.51 (-0.78, -0.24)
Yuma Myotis	Calendar Date	0.01 (-0.17, 0.18)
Yuma Myotis	Calendar Date^2	0.04 (-0.05, 0.13)
Yuma Myotis	Wind (mph)	-0.12 (-0.27, 0.04)
Yuma Myotis	Temperature (°C)	-0.03 (-0.21, 0.16)
Yuma Myotis	PostFire Canopy	0.07 (-0.08, 0.22)
Canyon Bat	Intercept	-1.93 (-2.42, -1.44)
Canyon Bat	Calendar Date	0.24 (0, 0.47)
Canyon Bat	Calendar Date^2	0.05 (-0.06, 0.15)
Canyon Bat	Wind (mph)	-0.15 (-0.33, 0.05)
Canyon Bat	Temperature (°C)	0.1 (-0.15, 0.35)
Canyon Bat	PostFire Canopy	0.05 (-0.13, 0.23)
Mexican Free-tailed Bat	Intercept	1.17 (0.87, 1.47)
Mexican Free-tailed Bat	Calendar Date	-0.37 (-0.57, -0.18)
Mexican Free-tailed Bat	Calendar Date^2	0.06 (-0.04, 0.16)
Mexican Free-tailed Bat	Wind (mph)	-0.07 (-0.25, 0.11)
Mexican Free-tailed Bat	Temperature (°C)	-0.05 (-0.25, 0.17)
Mexican Free-tailed Bat	PostFire Canopy	0.01 (-0.15, 0.17)
Community Mean	Intercept	-1.43 (-2.47, -0.42)
Community Mean	Calendar Date	-0.17 (-0.38, 0.04)
Community Mean	Calendar Date^2	0.05 (-0.02, 0.13)
Community Mean	Wind (mph)	-0.15 (-0.26, -0.03)
Community Mean	Temperature (°C)	0.14 (-0.06, 0.35)
Community Mean	PostFire Canopy	0.05 (-0.07, 0.17)

Table S11. Species-specific covariate coefficients from the occupancy submodel for the bat multi-species occupancy model.

Species	**Parameter**	**Estimate**

Pallid Bat	Intercept	1.86 (-0.51, 4.4)
Pallid Bat	Elevation	-0.11 (-1.15, 1)
Pallid Bat	PreFire Canopy	-0.32 (-1.71, 0.97)
Pallid Bat	Severity	-0.17 (-2.76, 3.1)
Pallid Bat	Severity Squared	-2.03 (-4.52, 0.55)
Pallid Bat	Pyrodiversity	0.08 (-0.92, 1.12)
Pallid Bat	LagYear	1.7 (0.06, 3.43)
Big Brown Bat	Intercept	4.28 (1.35, 6.99)
Big Brown Bat	Elevation	-0.06 (-1.19, 1.12)
Big Brown Bat	PreFire Canopy	0.23 (-0.67, 1.25)
Big Brown Bat	Severity	0.9 (-1.51, 3.27)
Big Brown Bat	Severity Squared	-0.64 (-2.73, 1.33)
Big Brown Bat	Pyrodiversity	0.3 (-0.69, 1.31)
Big Brown Bat	LagYear	-0.11 (-1.59, 1.26)
Western Red Bat	Intercept	4.02 (0.84, 6.98)
Western Red Bat	Elevation	-0.02 (-1.07, 1.14)
Western Red Bat	PreFire Canopy	0.29 (-0.75, 1.47)
Western Red Bat	Severity	0.59 (-1.93, 3.22)
Western Red Bat	Severity Squared	-0.75 (-2.89, 1.19)
Western Red Bat	Pyrodiversity	0.09 (-0.89, 1.05)
Western Red Bat	LagYear	-0.35 (-1.98, 1.27)
Hoary Bat	Intercept	4.64 (2.16, 6.98)
Hoary Bat	Elevation	0.07 (-1.06, 1.24)
Hoary Bat	PreFire Canopy	-0.05 (-1.31, 1.07)
Hoary Bat	Severity	0.47 (-1.91, 3.22)
Hoary Bat	Severity Squared	-1.56 (-3.73, 0.61)
Hoary Bat	Pyrodiversity	0.13 (-0.75, 1.02)
Hoary Bat	LagYear	0.53 (-0.63, 1.7)
Silver-haired Bat	Intercept	2.59 (1.23, 4.04)
Silver-haired Bat	Elevation	0 (-0.87, 0.88)
Silver-haired Bat	PreFire Canopy	0.24 (-0.41, 0.88)
Silver-haired Bat	Severity	1.32 (-1.07, 3.5)
Silver-haired Bat	Severity Squared	0.12 (-2.44, 2.47)
Silver-haired Bat	Pyrodiversity	0.21 (-0.58, 0.99)
Silver-haired Bat	LagYear	0.78 (0.07, 1.48)
California Myotis	Intercept	4.57 (2.7, 6.24)
California Myotis	Elevation	-0.21 (-1.19, 0.76)
California Myotis	PreFire Canopy	0.38 (-0.6, 1.47)
California Myotis	Severity	0.88 (-1.36, 3.15)
California Myotis	Severity Squared	-0.75 (-2.71, 1.24)
California Myotis	Pyrodiversity	0.09 (-0.82, 0.92)
California Myotis	LagYear	0.63 (-0.5, 1.69)
Long-eared Myotis	Intercept	4.93 (1.68, 7.95)
Long-eared Myotis	Elevation	-0.29 (-1.61, 1.23)
Long-eared Myotis	PreFire Canopy	0.08 (-1.13, 1.29)
Long-eared Myotis	Severity	0.6 (-1.77, 3.16)
Long-eared Myotis	Severity Squared	-0.74 (-2.97, 1.44)
Long-eared Myotis	Pyrodiversity	0.18 (-0.8, 1.16)
Long-eared Myotis	LagYear	0.12 (-1.6, 1.72)
Little Brown Bat	Intercept	3.41 (-0.78, 7.5)
Little Brown Bat	Elevation	-0.06 (-1.25, 1.26)
Little Brown Bat	PreFire Canopy	0.07 (-1.37, 1.43)
Little Brown Bat	Severity	0.45 (-2.25, 3.27)

Little Brown Bat	Severity Squared	-1.28 (-4.11, 1.3)
Little Brown Bat	Pyrodiversity	0.11 (-1.03, 1.19)
Little Brown Bat	LagYear	0.5 (-1.31, 2.28)
Fringed Myotis	Intercept	2.44 (-3.51, 6.33)
Fringed Myotis	Elevation	0 (-1.25, 1.31)
Fringed Myotis	PreFire Canopy	0.07 (-1.35, 1.4)
Fringed Myotis	Severity	0.67 (-2.22, 3.5)
Fringed Myotis	Severity Squared	-1.03 (-4, 1.68)
Fringed Myotis	Pyrodiversity	0.14 (-0.94, 1.28)
Fringed Myotis	LagYear	0.67 (-1.29, 2.74)
Yuma Myotis	Intercept	4.84 (2.27, 7.45)
Yuma Myotis	Elevation	-0.21 (-1.4, 1)
Yuma Myotis	PreFire Canopy	-0.24 (-1.6, 0.87)
Yuma Myotis	Severity	0.76 (-1.59, 3.23)
Yuma Myotis	Severity Squared	-0.81 (-2.99, 1.17)
Yuma Myotis	Pyrodiversity	0.1 (-0.92, 1.03)
Yuma Myotis	LagYear	0.3 (-1.07, 1.58)
Canyon Bat	Intercept	4.14 (1.36, 6.72)
Canyon Bat	Elevation	0.08 (-1.09, 1.26)
Canyon Bat	PreFire Canopy	0.05 (-1.3, 1.4)
Canyon Bat	Severity	0.3 (-2.39, 3.16)
Canyon Bat	Severity Squared	-1.95 (-4.51, 0.65)
Canyon Bat	Pyrodiversity	0.19 (-0.89, 1.26)
Canyon Bat	LagYear	0.61 (-0.69, 2.03)
Mexican Free-tailed Bat	Intercept	5.2 (3.1, 7.29)
Mexican Free-tailed Bat	Elevation	-0.07 (-1.1, 0.97)
Mexican Free-tailed Bat	PreFire Canopy	-0.1 (-1.23, 0.96)
Mexican Free-tailed Bat	Severity	0.35 (-1.97, 2.84)
Mexican Free-tailed Bat	Severity Squared	-1.33 (-3.12, 0.56)
Mexican Free-tailed Bat	Pyrodiversity	0.08 (-0.77, 0.89)
Mexican Free-tailed Bat	LagYear	0.67 (-0.4, 1.75)
Community Mean	Intercept	3.55 (1.91, 5.2)
Community Mean	Elevation	-0.07 (-0.89, 0.77)
Community Mean	PreFire Canopy	0.06 (-0.66, 0.78)
Community Mean	Severity	0.59 (-1.4, 2.81)
Community Mean	Severity Squared	-1.04 (-2.71, 0.63)
Community Mean	Pyrodiversity	0.14 (-0.58, 0.83)
Community Mean	LagYear	0.49 (-0.34, 1.3)

Conclusion

As anthropogenic change continues to rapidly alter our planet, the need to restore and adapt degraded ecological communities has become increasingly clear. Many of the social, economic, and cultural systems that we’ve come to depend on are intimately tied to the biodiversity that supports them. Without these integral pieces, many of the services we’ve come to enjoy and take for granted may cease to exist. The escalation of various climate-related disturbances, such as extreme wildfire, threatens the sustainability of many of these species, processes, and ecosystems. In light of all of this, tapping into the natural ability of these systems to recover and adapt to these challenges has become a primary objective of conservation work worldwide. In many instances, we find that ecosystems have a natural propensity to regenerate if given the space, time, and resources to respond to disturbances.

The need to find, create, and nurture ecological resilience for changing climate and fire dynamics, specifically, has become increasingly apparent as well. Fire has played a deep, integral role in shaping terrestrial ecosystems around the world. This history is intricately tied with deliberate land stewardship practices by indigenous communities around the globe. But in cruel twist of fate, this tool has increasingly become a devastatingly destructive force in the very landscapes it helped shape. However, just as humans used fire to mold these landscapes before, our decisions today continue to play a profound role in influencing how fire affects the landscapes around us. We need more deliberate action that can recreate and sustain the historical dynamics of fire regimes and find ways to adapt these for a new age of global change. Underpinning all of this is a need to develop a deeper understanding of the natural mechanisms of resistance and resilience existing in fire-prone ecosystems and how they may be enhanced.

This dissertation highlights some of the potential mechanisms by which resistance and resilience to changes in fire dynamics may be produced in wildlife communities in oak woodland savannas. In Chapters 2 and 4, we show that a major megafire had no or limited impacts on the distributions of mammal and bird species assemblages. Species-specific effects of megafire did vary, with certain species showing some vulnerability to its initial effects. We found, however, that these vulnerabilities can be buffered by certain landscape features such as unburned refugia patches. Furthermore, Chapter 3 highlights that species-specific behaviors can interact with these landscape features to produce the examined effects of resilience, such as when black-tailed deer adjusted their movement behaviors to best take advantage of these existing patches of refugia. Chapters 2, 3, and 4 echo the key role fire clearly continues to play in these woodland ecosystems where a variety of species preferentially choose to use areas that have burned both recently or over time. Utilizing fire management to encourage positive feedbacks in creating landscape heterogeneity (especially in oak woodland savannas) is therefore critical in providing improved habitat for a variety of different species sustainably. Finally, and as opined in Chapter 1, developing a deeper understanding of how fire and resilience play out across different contexts necessitates much more work in non-forested ecosystems before climate change and fire cause them irreparable harm.

Building upon the findings of this dissertation, and in recognition of the gaps that continue to exist, I plan to expand on these topics within my future work by:

1. **Continuing to develop our understanding of how novel disturbance regimes may rewire existing wildlife communities.** Severe disturbance may elicit responses from certain species that may have reverberating effects throughout their community. These changes in community structure and composition could have crippling impacts on the functioning of ecological communities and the services they provide to people.

2. **Expanding and modernizing our sensors of biodiversity.** Key to understanding how these ecological communities are being affected by disturbance is developing a strong set of tools to monitor wildlife biodiversity. Developing a standardized set of tools and procedures that can be used to facilitate broader scale studies on the impacts of these large scale disturbances will be critical towards informing successful wildlife management.

3. **Evaluating the impacts of megafire and climate change on human wildlife interactions.** Findings from the dissertation highlight that movement away from fire is a key response for many large mammals. Many wide-ranging species in this work (such as mountain lion and black bear) were found to temporarily leave areas that recently burned to, theoretically, use unburned, intact habitat within their vast home ranges. While effective for avoiding the direct impacts of fire, these adjustments in movement may push these species into more human-dominated areas more often. Even more broadly, as fire and climate change continues to constrain available habitat for wildlife, humans and wildlife species may come to depend on increasingly shrinking pools of resources, potentially exacerbating human-wildlife conflict (Abrahms 2021).

4. **Highlighting and advocating indigenous management practices and knowledge in managing oak woodland landscapes with fire.** Oak woodlands have been critical landscapes for indigenous groups across California. The vast biodiversity of California oak woodlands is due in large part to the practices used by these groups for thousands of years to maintain these landscapes. Continuing to incorporate these ways of knowing into oak woodland management today is integral in protecting them from the effects of climate change and altered fire regimes.

5. **Expanding our understanding of fire's impacts on wildlife in other non-forested ecosystems.** We know we have limited work exploring how fire outside of forests impacts wildlife communities. This dissertation and research like it are the first in a major step to help fill these existing gaps. Future work should continue to fill these gaps across the major understudied ecosystem types outlined in Chapter 1 (hardwood, shrubland, and grassland).

Addressing the threats presented by altered fire dynamics in California to biodiversity follows a similar story as other complex environmental issues around the world. Just as the issues we face here are multi-faceted, our solutions must be equally nuanced and adaptable. For global conservation, we must continue to push towards a new paradigm that recognizes both fire and wildlife as integrated, necessary pieces within a much larger system that includes people too. In the case of climate disturbances like megafire, drought, and flood (harbingers of escalating climate change) we must also consider the impacts on vulnerable communities, necessitating the incorporation of new topics such as environmental justice. Both wildfire and several wildlife species (particularly large predators) have long been vilified and labeled as enemies of the “greater good”. We urgently need a new framework that understands the intrinsic values of each of these elements and uses this understanding to rebuild a stronger world and environment for our future.

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