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RESEARCH ARTICLE

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

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Abstract

Aim: 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.

Location: California, United States of America.

Methods: 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).

Results: 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.

Main Conclusions: 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.

KEYWORDS

biodiversity, California, endemism, richness, wildfire, wildland-urban interface

1 | 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; Collins 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 (USDA Forest Service, 2017; Minor & 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 & 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 et al., 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 (Collins et al., 2019; 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 et al., 2009; Radeloff et al., 2018).

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 Water, 2014; Parks et al., 2015; Hill et al., 2020; Li & 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 & 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 (Keeley & Swift, 1995) and includes endemic species across many taxonomic groups (Harrison, 2013). Fire plays an important role in maintaining a variety of ecological processes (Kelly & Brotons, 2017; Nimmo et al., 2019; He et al., 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; 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 (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 (Hill et al., 2020; Li & 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 (Appendix 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.

2 | METHODS

2.1 | 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.

2.2 | 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.

2.3 | 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 (Appendix S1–CALFIRE–FRAP, 2015; Figure 1, Appendix S2–Figure S2.1). 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 Appendix 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 (Appendix S1–CALFIRE–FRAP, 2020) with fire perimeters from 2020 (Appendix 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 4.0.2 (Team, R. C, 2020). A list of these land cover and fire perimeter data sources can be found in "Appendix S1 – Data Sources". To compare

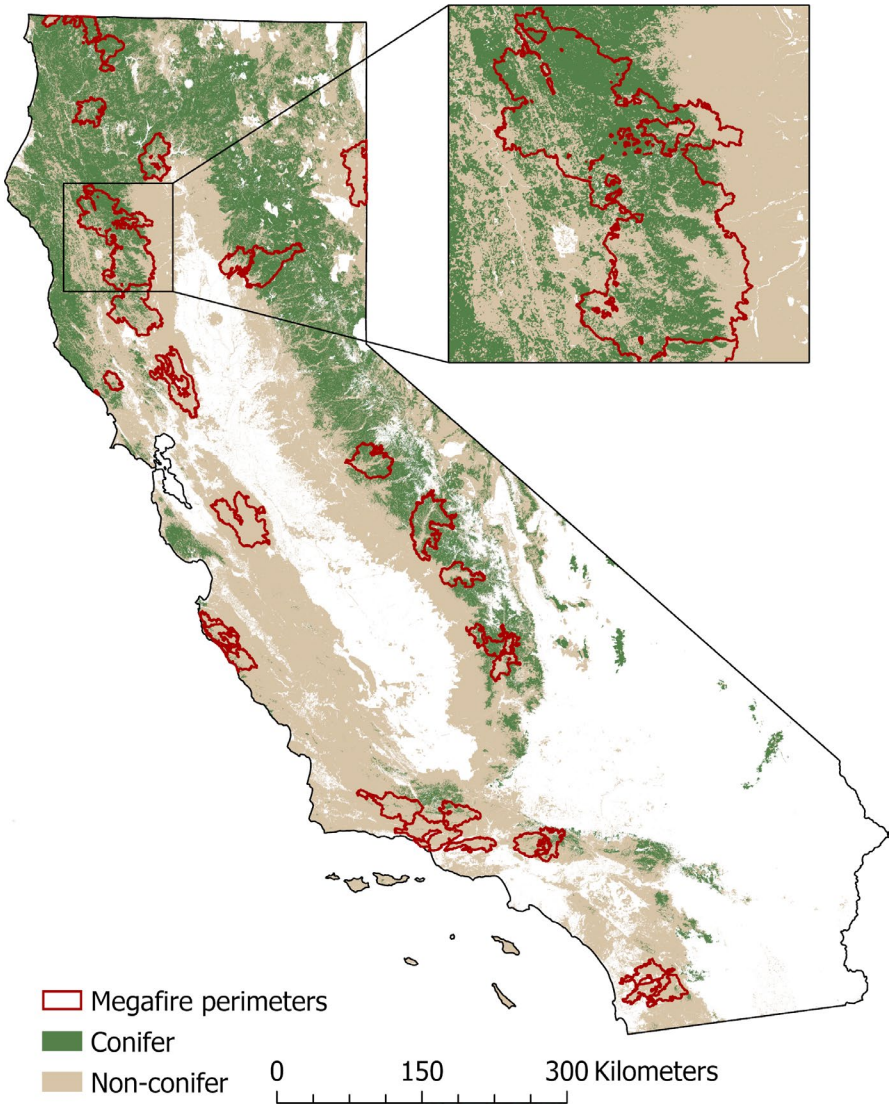

FIGURE 1 Map of California land cover composition with megafires in the last 20 years displayed on top. In this map, land cover is divided into "Conifer" and "Non-Conifer" fire-prone land cover categories. Non-Conifer land cover included the grouped "Grassland", "Hardwood" and "Shrubland" land cover categories. "Urban", "Agricultural" and "Desert" were not considered for analyses and left uncolored within the map. Megafire perimeters (in red) were defined as fires >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 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

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 100,000 acres (40,000 ha; $n = 28$ megafires).

2.4 | 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 (Appendix 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 (Appendix S1–CDFW 2019). Using the "sf" package in R (Pebesma, 2018; Team, R. C, 2020), 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 (Appendix 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 totalled 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 Appendix 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.

2.5 | 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 analysed how the land cover composition of fires overlapped with the 2010 WUI Assessment layer for California (Appendix S1–Mockrin & Radeloff, 2017). This dataset is based on US Census housing data and the US Geological Survey's National Land Cover Database (Appendix S1–Mockrin & Radeloff, 2017). 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 totalled the area of burned WUI by each land cover type. The data source for WUI layers can also be found in Appendix 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.

2.6 | 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 (Appendix S1–CDFW, 2019) with the Fire Return Interval Departure (FRID) dataset provided by USDA (Appendix 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 Appendix S3.

3 | RESULTS

3.1 | 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; Appendix S2–Figure S2.2).

3.2 | Fire perimeters and land cover composition

We found that most of the area burned in California wildfires from 2000 to 2020 was outside of conifer ecosystems (Figure 2a; Appendix S2—Table S2.2). 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.

Non-conifer ecosystems make up 64% of the area burned in California during the last 20 years, totaling 4.17 million hectares burned (Appendix S2—Table S2.2). 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, Appendix S2 – Table S2.2). 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.

3.3 | Megafire and land cover composition

Prior to 2018, the majority of area burned by megafires was within shrubland habitat (Appendix S2—Figure S2.3). Megafires burned one million hectares of shrubland during the study period, 39% of the total area burned in shrublands overall (Appendix S2—Table S2.3). 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.

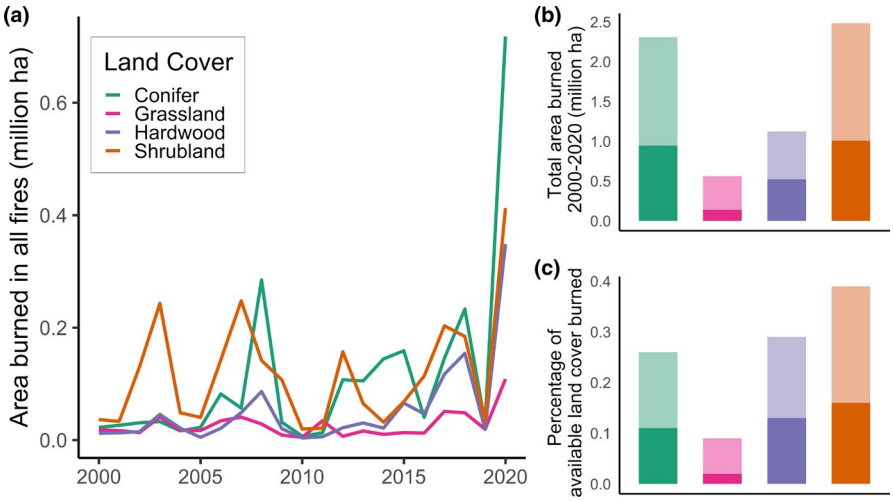

FIGURE 2 Breakdown of land cover types burned in California from 2000 to 2020. Panel "a" displays the total yearly area burned by all wildfires in million hectares across each land cover type from 2000 to 2020. Panel "b" displays the total summed burned area (2000–2020) for each land cover category. 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

3.4 | 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).

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 Appendix S2—Table S2.4.

3.5 | 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 Appendix S2—Table S2.6.

3.6 | 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 Appendix S2—Table S2.5 and Appendix S2—Table S2.7.

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 Appendix S2—Table S2.8

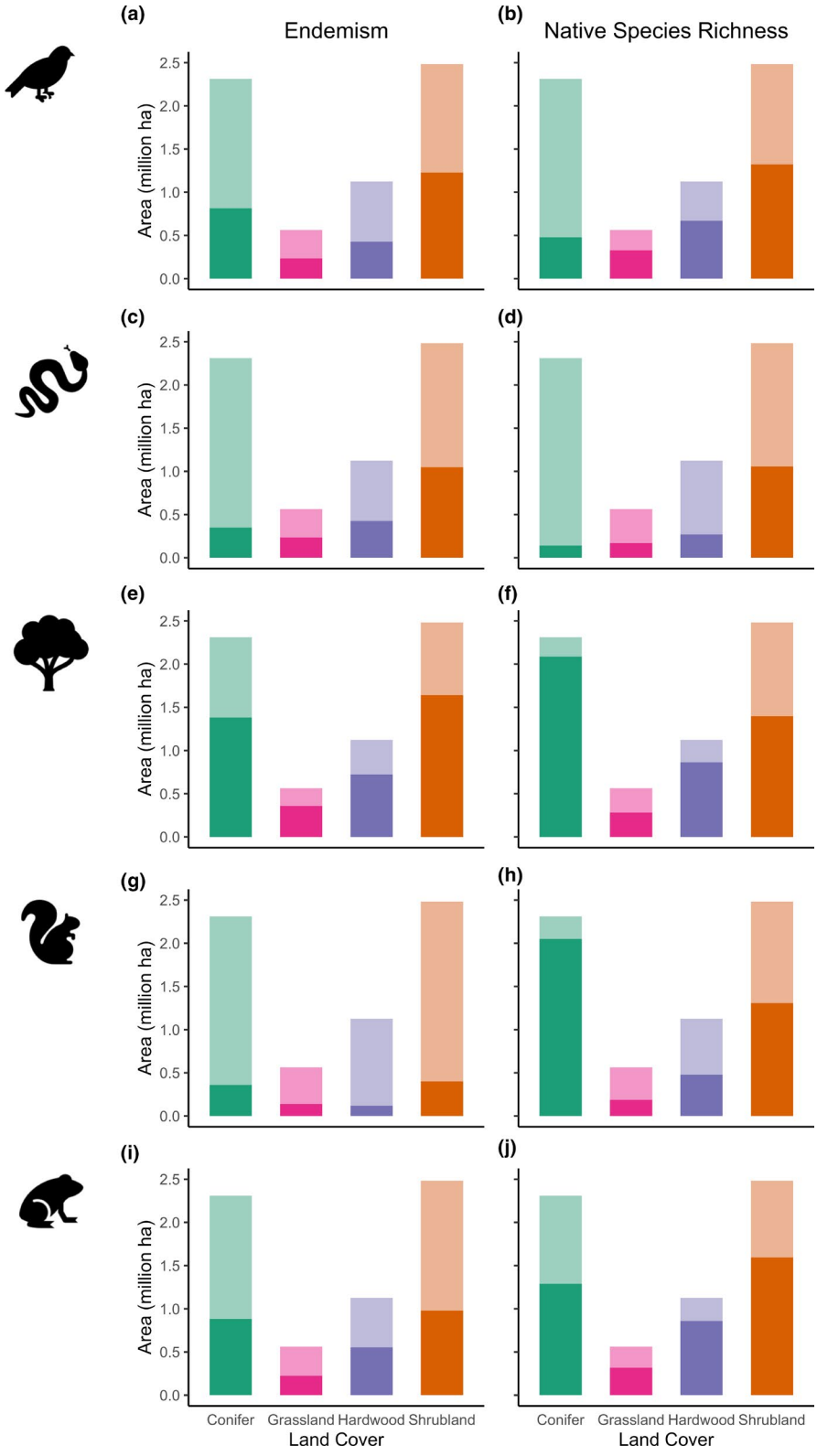

FIGURE 3 Total area burned by all wildfires (2000–2020) in areas of high biodiversity and endemism across land cover classes in California. Regions that contained the upper two quantiles (or upper 40%) of predicted native species occurrence were identified as being regions of "high species richness" 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

3.7 | 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 Appendix S2—Table S2.9.

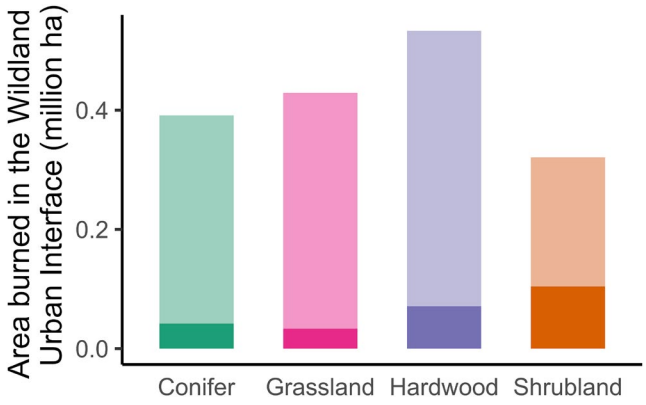

FIGURE 4 Area burned in million hectares from all wildfires across land cover categories in California's wildland-urban interface (WUI) summed from 2000 to 2020. Light shading displays the total area of the WUI available to burn in each ecosystem type while dark shading displays the total area of the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

3.8 | 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 Appendix S2—Table S2.10.

3.9 | 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 (Appendix S3—Figure S3.1, Table S3.1). In contrast, endemic species were less likely to be observed as FRID increased in non-conifer ecosystems than in conifer ecosystems (Appendix S3—Figure S3.2, Table S3.2). A full description of results and their discussion can be found in Appendix S3.

4 | 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 & 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 & 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 & 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 & Syphard, 2015; Keeley & 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 & 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 & 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 (Steel et al., 2019; Wintle et al., 2020; Jones et al., 2020; Pickrell & 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 (Keeley & Syphard, 2018). Recent anthropogenic shifts in the fire return interval in certain ecosystems can change the composition and structure of ecological communities (Brooks & Matchett, 2006; Safford and 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 (Appendix 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 centred primarily on forest fire (Christopher, 2020). As reflected in Appendix S2–Figure S2.2, 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 & 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; USDA Forest Service, 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 et al., 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 (Keeley, 2002; Syphard et al., 2014; Moritz et al., 2014).

5 | CONCLUSIONS

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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CONFLICT OF INTEREST

Authors declare there is no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The datasets for this study are available from the sources listed in Appendix S1, and code for the analyses is available from the authors upon request: https://github.com/KendallCalhoun/CA_Wildfires

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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