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

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Abstract

Increasingly frequent megafires are dramatically altering landscapes and critical habitats around the world. Across the western United States, 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 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 eight observed mammal species. We used a multispecies occupancy model to quantify the effects of megafire on species' space use, to 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 ha (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; 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 United States generally have experienced their largest and most severe fires in the last 20 years (Li & 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 (Heller & Zavaleta, 2009; Miller et al., 2021). 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 (Ingrisch & Bahn, 2018; Standish et al., 2014). Application is made more difficult by the rarity and dynamic nature of baseline ecological information to compare against recent change (Cammen et al., 2019; Soga & Gaston, 2018). 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, for example, home range size, diet, and trophic level (Jager et al., 2021; Pocknee et al., 2023). 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 et al., 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 aboveground and belowground biomass as a result of fire, is thought to be an important characteristic of fire regimes that directly impacts wildlife (Keeley, 2009). By altering available food resources, megafire may change the distribution of wildlife species in recently burned landscapes (Allred et al., 2011; Cherry et al., 2018). 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 toward shoring up the resistance and resilience of fire-prone ecosystems across the western United States. 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 of California's most biodiverse ecosystems (Hilty & 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 & 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 (Koenig et al., 2013; McShea, 2000), 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 California' recorded history, on the occupancy of eight 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. 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 prefire 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 postfire recovery management, and (2) identifying landscape features that may enhance the resilience and resistance of mammal communities to megafire.

MATERIALS AND METHODS

Study area and fire history

We conducted our study at the 21.54-km^2 University of California 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 m and its highest at 934 m. 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 km² of the HREC (Figure 1). At the time, the Mendocino Complex Fire was the largest fire in California's recorded history, burning 1858 km². 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 & Keeley, 2020). To date, there have been minimal on-site postfire management interventions, providing an opportunity to identify the baseline in how this ecosystem recovers.

Camera survey and study species

To survey mammal species diversity, we created a sampling grid across HREC composed of hexagonal grid cells measuring 750 m 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 m 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 three photos per trigger, with a 0-s 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 1–November 30 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 the 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 min 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 the 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 multispecies 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 eight 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 postfire 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
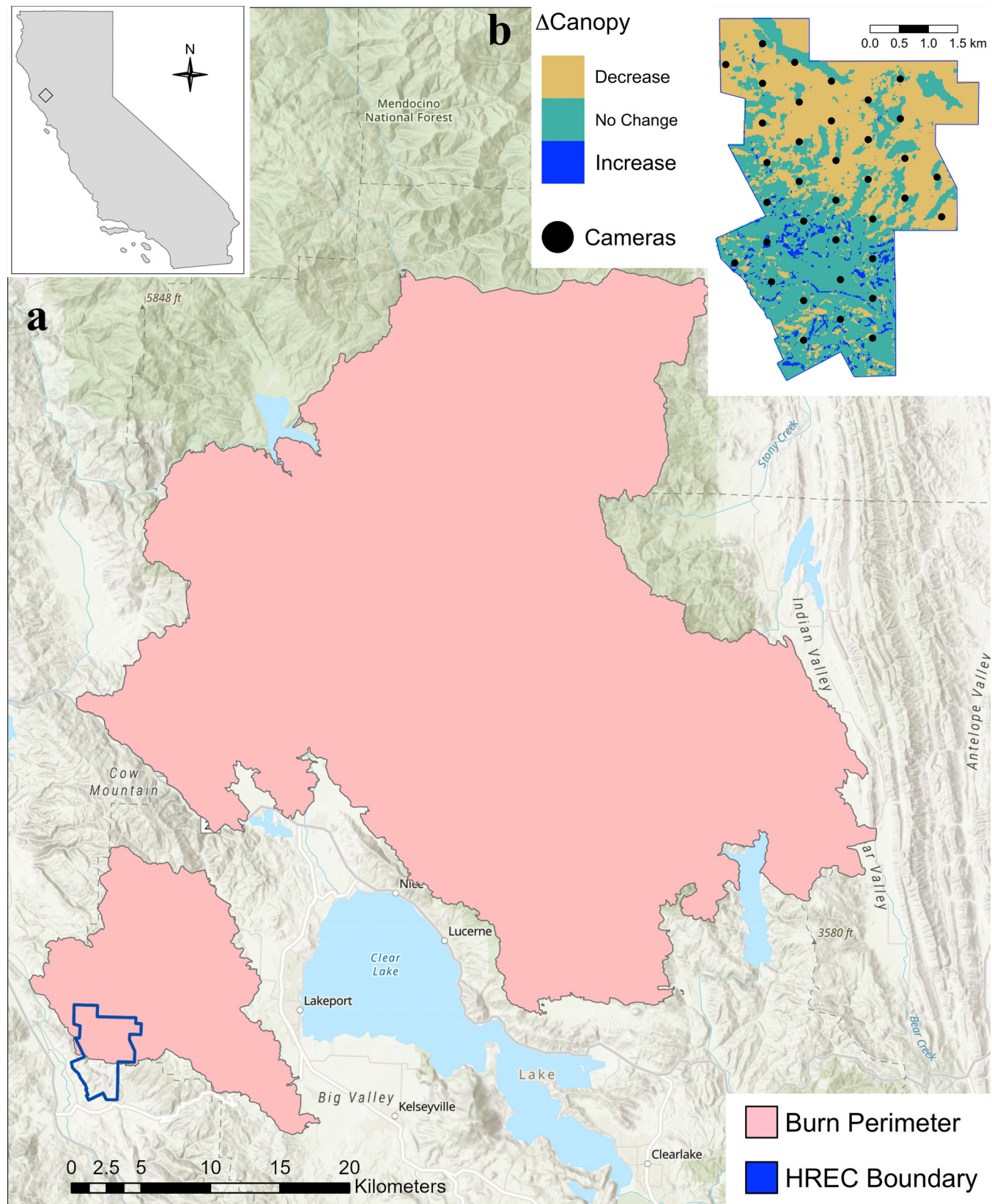
FIGURE 1 Maps of the 2018 Mendocino Complex Fire and the study site, the University of California Hopland Research and Extension Center (HREC) (39°00′ N, 123°04′ W). (a) The total burn perimeter of the Mendocino Complex Fire, composed of the northern Ranch Fire and the southern River Fire. This fire burned into HREC on July 27, 2018. The River Fire burned half of the property. (b) 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.

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-m 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 100-m buffer around each camera site. We estimated canopy cover using 20-m resolution imagery from 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 (Planet Team, 2017; Sunde et al., 2020; Tilahun, 2015). A full description of methods used to create and verify canopy rasters can be found in Appendix S1: Tables S1 and S2. Canopy cover values were extracted from a 100-m 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 five 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 prefire. To estimate how viewshed changed postfire, two independent observers visually estimated viewshed using misfire photographs collected during the study period at each camera station and for each postfire year. Prefire 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 (Hill et al., 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,

TABLE 1 Schematic of five parameterizations of the "time-since-burn" categorical effect, ordered by increasing complexity.

Parameterization	Prefire sites (2016–2017)	Burned sites (2018)	Burned sites (2019)	Burned sites (2020)	Unburned sites postfire (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)[a]	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

Note: After the fire in the summer of 2018, we group sites affected by the fire into one of four 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 postfire, and (4) "Burn Lag 2" for burn sites 2 years postfire. In parameterization 5, "Unburned Lag" represents unburned sites postfire. 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 Watanabe–Akaike information criterion (WAIC). ΔWAIC shows the difference in WAIC values between each parameterization and the selected model.
[a]Selected parameterization based on WAIC.

we created a site-specific "microsite attractant" binary categorical variable that indicated whether a camera was pointed toward the attractants present in our study, for example, 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 multicollinearity would not confound analyses (Appendix S2: Figure S1 and Table S1).

Occupancy modeling framework

We fit a community occupancy model (Devarajan et al., 2020; MacKenzie et al., 2002; Royle & 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 home ranges 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 the study by 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 (Ψ$_{i,j}$):

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

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 & 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 the 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, ($z_{i,j}$):

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

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

$$\begin{aligned} \text{logit}(\Psi_{i,j}) = {} & \alpha 0_i + \alpha 1_i \times \text{Elevation}_j + \alpha 2_i \times \text{Canopy}_j \\ & + \alpha 3_i \times \text{TimeSinceBurn}_j + \alpha 4_i \times \text{Canopy}_j \\ & \times \text{TimeSinceBurn}_j + \text{Site Random Effect}_j. \end{aligned}$$

$$\begin{aligned} \text{logit}(p_{i,j}) = {} & \beta 0_i + \beta 1_i \times \text{Attractant}_j + \beta 2_j \times \text{Viewshed}_j \\ & + \beta 3_i \times \text{TimeSinceBurn}_j \\ & + \text{Site Random Effect}_j. \end{aligned}$$

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" submodels. In the occupancy submodel, we use an interaction term between canopy cover and "time since burn" (Canopy$_j$ × 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 multispecies occupancy models (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 nonindependence 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 SD 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 (Guillera-Arroita et al., 2019; Tingley et al., 2020).

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 three categorical body mass groups from which each had its own group-level hyperparameter: small (<5 kg), medium ($5–15$ kg), and large (>15 kg) (Wilman et al., 2014) (Wilman et al., 2014). Second, to explore the influence of diet, we grouped species into three 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 Appendix S1 (Appendix S2: Table S2).

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 of mean 0 and SD of 2.5, and all random effect and hyperparameter standard deviation priors were half-Cauchy with a scale parameter of 2.5 (Northrup & 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 the most parsimonious model parameterization for the "time-since-burn" covariate, we fit the community multispecies occupancy model using each of the burn category parameterizations and compared their Watanabe–Akaike information criterion (WAIC) values (Gelman et al., 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 no. 5 where unburned sites following the fire received their own category).

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 multispecies occupancy models for 30,000 iterations, with a 2000-iteration burn-in across five chains and used NIMBLE custom samplers to increase the efficiency of MCMC mixing (Gelman et al., 2014). Parameter chains were visually assessed for convergence (Appendix S3: Figures S1–S3). All data and model code used to perform analyses are available within this project's Dryad deposition (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 (Gelman et al., 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 (CI) 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 ($n = 9479$), while brush rabbits (*Sylvilagus bachmani*) were photographed least often ($n = 1$) (Appendix 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 Appendix S4: Figure S1. Summarized detection rates of modeled species can be found in Figure 2.

Model selection and goodness of fit results

Five multispecies occupancy model parameterizations of the effect of fire were compared by the 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 (Appendix 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 six of eight 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.

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 $\pm$ 0.03) and was lowest for black-tailed jackrabbit (mean = 0.28, 90% SD $\pm$ 0.30) (Appendix S2: Table S4). Recently burned sites (i.e., time since burn = "Burned") were associated with increased site use for five of the eight 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.

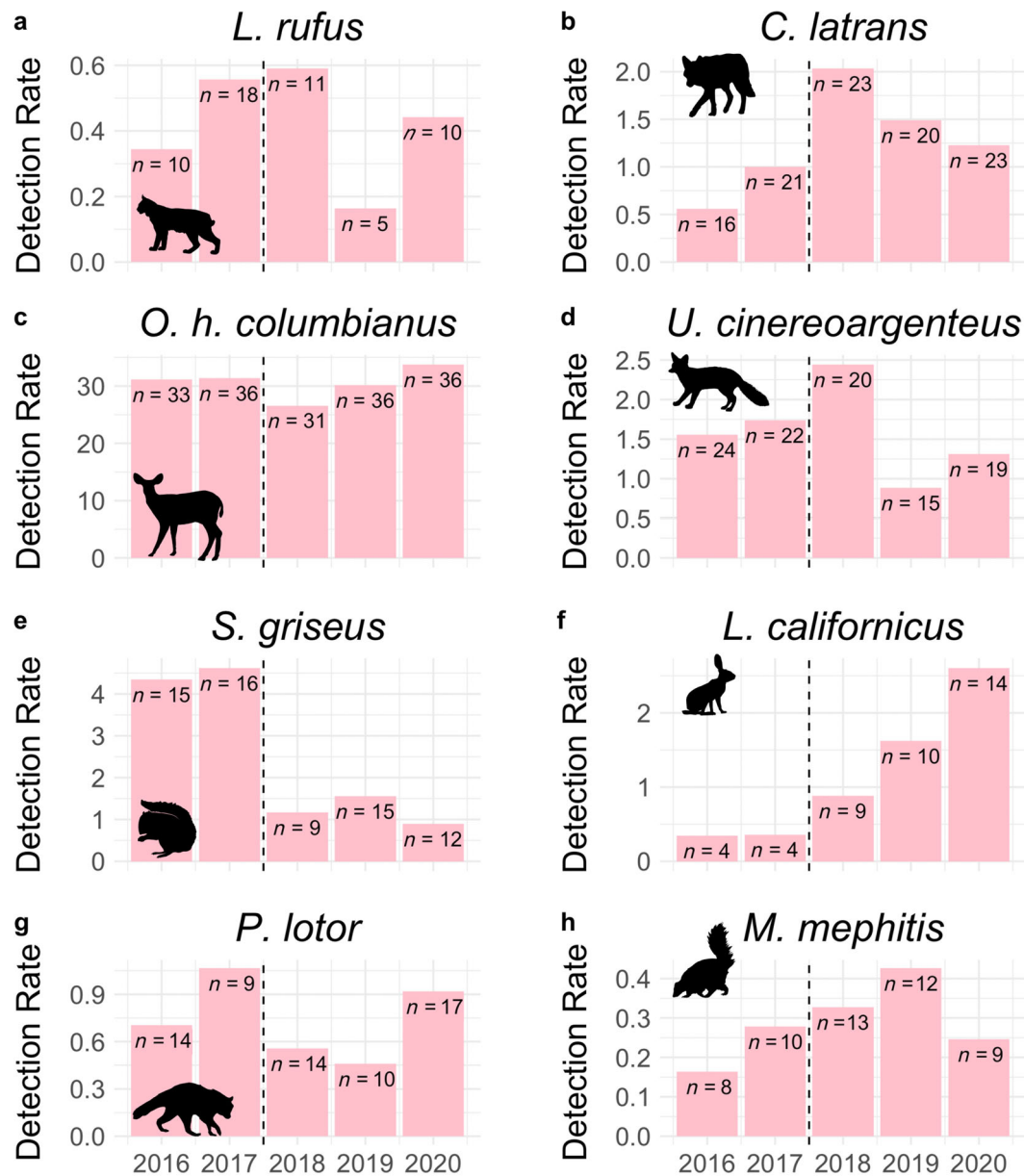Time since burning had a significant effect on the detection probability (including intensity of use) of four

FIGURE 2 Detection rate of modeled mammal species sampled at camera stations during the sampling period (October–November) 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 that the y-axis scale is different between species.

species: black-tailed jackrabbit, coyote, western gray squirrel, and black-tailed deer (90% CI did not overlap zero) (Figure 4, Appendix 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
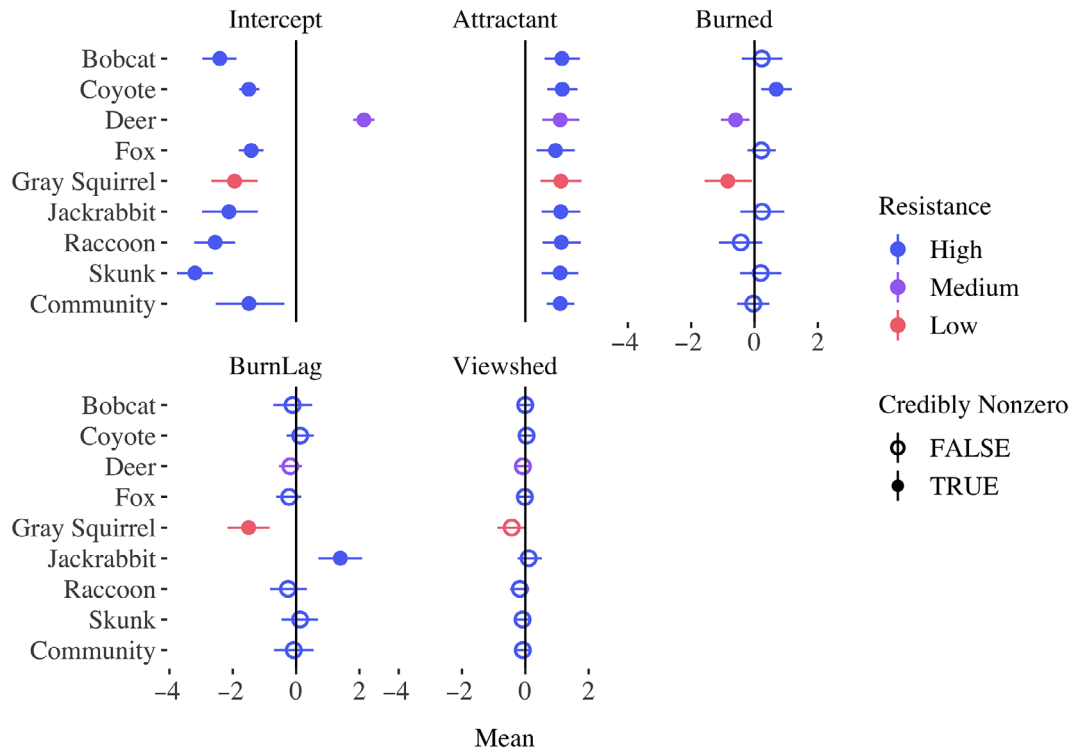
FIGURE 3 Estimated coefficients of all site-specific covariates on probability of site use (Ψ) from the community multispecies occupancy model (MSOM) fit from camera trap data collected from the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Species-specific 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 MSOM 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 (nonresistant in recently burned sites but resistant during the BurnLag), and species with low resistance in red (nonresistant at both Recently Burned and BurnLag sites). All species except deer and gray squirrel showed strong resistance to the initial effects of megafire.

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; Appendix S2: Table S5).

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) (Appendix S2: Figure S3; Appendix S1: Table S6). Intensity of use was

not significantly associated with any burn effects (Appendix S2: Figure S4 and Table S7).

We found no significant effects of burn effects on site use associated with diet groups (Appendix S2: Figure S5 and Table S8). We did find, however, that carnivores had a positive association, albeit nonsignificant, 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 (Appendix S2: Figure S6 and 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
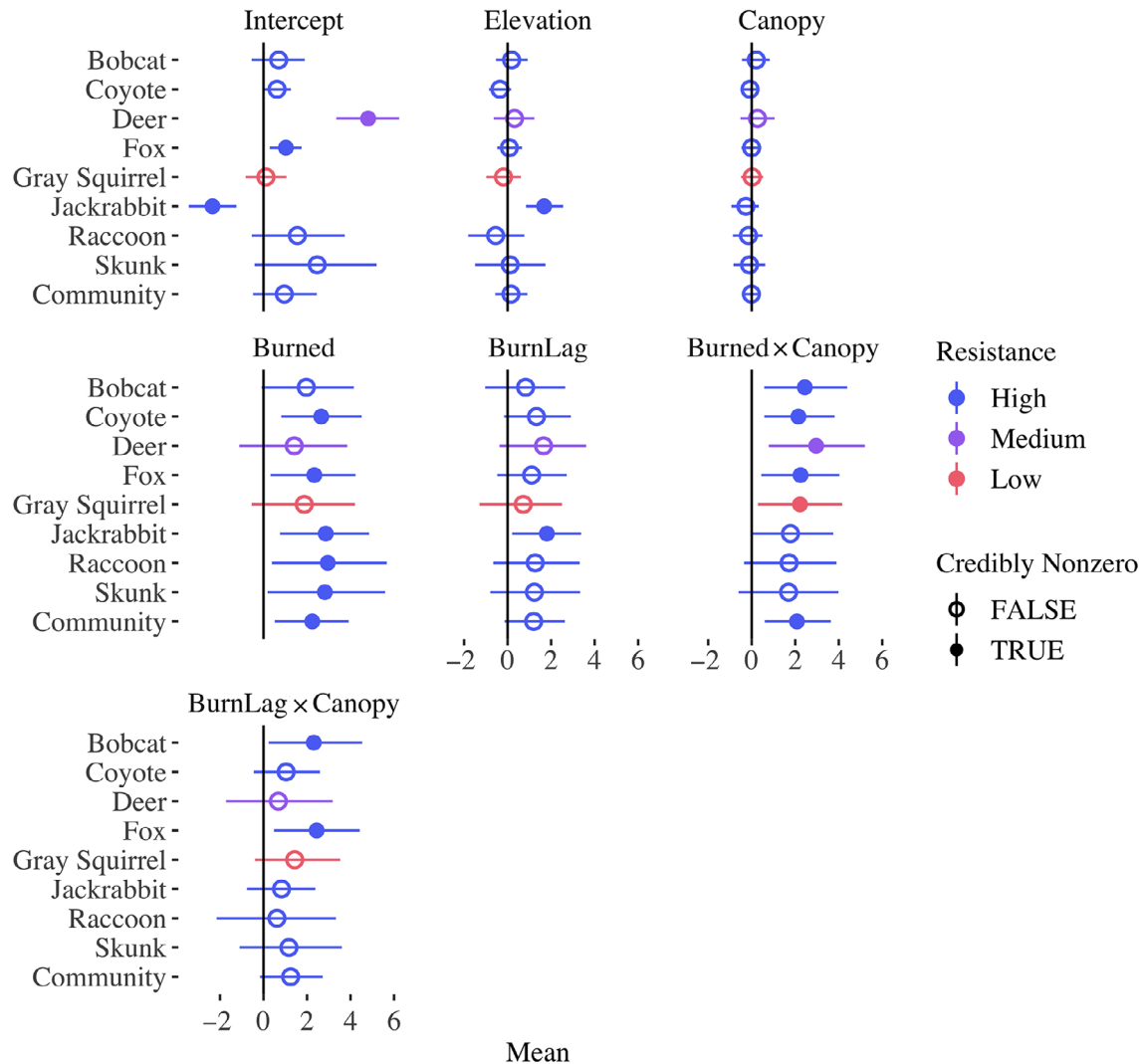
FIGURE 4 Estimated coefficients of all site-specific covariates on intensity of use (p) from the community multispecies occupancy model (MSOM) fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. Species names are 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 MSOM 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 (nonresistant in recently burned sites but resistant during the BurnLag), and species with low resistance in red (nonresistant at both Recently Burned and BurnLag sites).

megafire in this northern California oak woodland, but to a much small degree than we initially hypothesized. Most species were resistant (six of eight) 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 and 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.
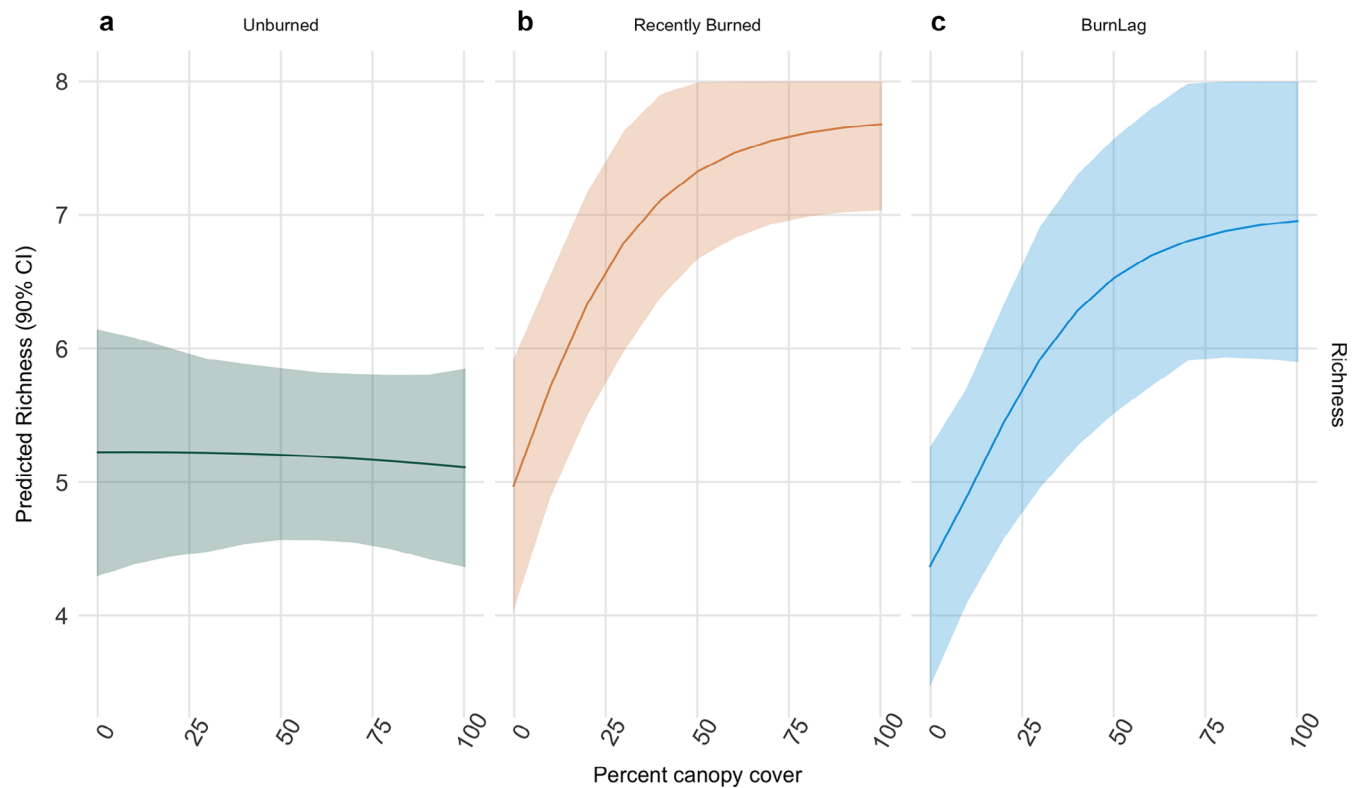
FIGURE 5 Predicted species richness estimates from the multispecies occupancy model (MSOM) across "time-since-burned" categories and canopy cover fit from camera trap data collected at the Hopland Research and Extension Center, CA, USA before and after the 2018 Mendocino Complex Fire. All other occupancy covariates were set to their mean values. (a) All sites that were unburned by the fire; (b) sites that were burned during the year of the fire (2018); (c) burned sites in the years following fire. CI, credible interval.

We observed that most species examined in this study were resistant (six of eight) to the impacts of megafire. This corroborates findings of mammal resistance to wildfire in other ecosystem 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 of 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 nonresistant 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 (Ganz et al., 2022; Kreling et al., 2021) 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 postfire studies performed at broader spatial scales. In our study, we assumed that each species' use of each site was independent from 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 & 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 the study by Pocknee 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 nonresistant 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 raccoon, increased in recently burned areas. These results mirror the response of mesopredators to wildfire observed in similar studies across California (Furnas et al., 2021; Jennings et al., 2016; Schuette et al., 2014). 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 postfire 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 continue 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 (Connor et al., 2022; Jones & Tingley, 2021). 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 postfire (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 interspecies interactions, such as competition and predation, as inter- and intraspecies spatial overlap increases in these limited, intact patches of habitat. Using preemptive 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; Miller et al., 2021). This attractant effect toward canopied areas post-megafire is apparent in 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 (Calhoun et al., 2021; Kelly et al., 2020). Due to the key services and habitat they provide around the world (Eastburn et al., 2017; Veldman et al., 2015), 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 to 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, especially acorns from oak trees, are the primary means of acquiring food resources for most wildlife (Mazur et al., 2013; McShea & 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 postfire 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.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The species record table, species detection histories, camera operation log, taxonomic group information, camera station metadata, and novel code (Calhoun et al., 2023) are available from Dryad: https://doi.org/10.6078/D1W70R.

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SUPPORTING INFORMATION

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