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ARTICLE

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Severity outweighs pyrodiversity in shaping avian and bat species distributions following an oak woodland megafire

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Abstract

Anthropogenic pressures have altered fire regimes across the western United States. These altered fire regimes, and the megafires they often produce, threaten ecologically and economically critical ecosystems and biodiversity across this region. Oak woodland savannas may be particularly sensitive to altered fire regimes, but there remains a significant gap in our understanding of how different characteristics of wildfire impact these ecosystems and the wildlife species that reside within them. In this study, we used an occupancy modeling framework to investigate how fire severity and pyrodiversity, the diversity of severity patches, impact the distributions of bird and bat species assemblages following a major wildfire in northern California. We used acoustic monitors deployed across the Hopland Research and Extension Center following the 2018 Mendocino Complex Fire and compared how patterns of fire severity and pyrodiversity influence habitat preferences across a diverse community of woodland bird and bat species. We found that fire enhances habitat use and increases occupancy for several species and species groups across both taxonomic groups. Specifically, low-to-moderate severity fire increased occupancy for several species and species groups. Pyrodiversity had smaller, negligible effects on species distributions relative to fire severity. Fires that reproduce the natural heterogeneity of oak woodland landscapes are likely key to sustaining high biodiversity across oak woodland ecosystems.

KEYWORDS
bats, birds, oak woodland, occupancy, pyrodiversity, severity, wildfire

INTRODUCTION

Fire plays a major role in shaping patterns of species distributions and diversity in many ecosystems across the world (McLauchlan et al., 2020; Viljur et al., 2022). The historical and contemporary anthropogenic use of fire is an important tool for managing ecosystems in ways that benefit wildlife use and ecosystem services (Christianson et al., 2022). However, researchers continue to debate the exact mechanisms by which fire produces some of these observed effects (He et al., 2019; Jager et al., 2021; Jones & Tingley, 2021). Simultaneously,

land-use change and climate change have greatly increased the frequency of fires that exceed 100 km^2, also known as megafires (Linley et al., 2022), which greatly surpass the severity (Williams et al., 2023) and size (Safford et al., 2022) of historical wildfires. These megafires threaten large landscapes, potentially altering resource availability for wildlife across both space and time by removing critical habitat (Jones et al., 2016; Ward et al., 2020) and dramatically altering food resources (Kreling et al., 2021).

Fire severity and pyrodiversity are key mechanisms that shape biodiversity in fire-prone landscapes. Fire severity, or the measured change in living vegetation in response to fire, may play a significant role in driving the distributions of wildlife species following fire. For example, high severity fires remove food, nesting, and other habitat resources for certain species (Chia et al., 2016; Franklin et al., 2022; Roberts et al., 2011), but open new resources for others (Tingley et al., 2018). The presence of varying burn severities may therefore support the presence of a broader variety of species (Novoa et al., 2021). The dynamics of fire severity also vary across time and space. This variation is measured by pyrodiversity, or the variation in fire regime characteristics across landscapes (Martin & Sapsis, 1992; Steel, Collins, et al., 2021). Variation in fire severity across space ("spatial pyrodiversity") and variation in the timing of burns ("temporal pyrodiversity") across landscapes may produce a diverse mosaic of vegetation types. Greater habitat heterogeneity created by pyrodiversity is expected to support greater species diversity at the community scale (Beale et al., 2018; Ponisio et al., 2016) and may even enhance community resistance to future disturbances (Ponisio, 2020). Theoretically, wildlife communities are adapted to the historical regimes of an area, and deviations from these historical patterns (e.g., uncharacteristically frequent or severe fire or reduced pyrodiversity) may have negative effects on wildlife communities (Jones & Tingley, 2021). Understanding how severity and pyrodiversity shape wildlife communities in burned landscapes will be key to informing conservation actions that support wildlife species in our current era of global change (Steel et al., 2023). These insights are especially critical in non-forested fire-prone ecosystems, like woodland savannas and shrublands, where we have relatively limited research on the impacts of fire on ecological communities (Calhoun et al., 2021).

A better understanding of the role fire regimes play in non-forested ecosystems can help guide the implementation of fire and wildlife management. Amidst ongoing global change pressures, fire continues to play a key role in many ecosystems (McLauchlan et al., 2020), including ecologically diverse oak woodland savannas in the Western United States. Oak woodlands serve as important working landscapes by providing critical ecosystem services to human communities while simultaneously supporting wildlife (Huntsinger & Oviedo, 2014; Kremen & Merenlender, 2018). Oak woodland landscapes typically consist of a patchwork of vegetation types, including oak woodland savannas, grasslands, and chaparral shrubland (Eastburn et al., 2017). These mixed-regime landscapes are characterized by semi-frequent, low severity fires in the understory of oak savannas and relatively infrequent, high-severity crown fires in the chaparral (Perry et al., 2011). Historically, Indigenous communities used fire in woodland-scrublands to burn the understory in order to facilitate hunting and resource acquisition (Anderson, 2006). Shifting fire regimes caused by the exclusion of Indigenous burning, a century of fire suppression, and other anthropogenic pressures such as climate change may cause significant damage to the short- and long-term composition and functioning of these landscapes. These changes lead to increased fuel loads that contribute to higher severity fires (Parks et al., 2018) which cause mortality of mature oaks (Williams et al., 2023), exhaust chaparral regeneration (Syphard et al., 2006), and increase the presence of introduced annual grasses (Keeley, 2000). Furthermore, changes in fire regimes are predicted to have greater consequences for biodiversity in savanna-type ecosystems, such as oak woodlands, than in other fire-prone ecosystems (Kelly et al., 2020).

Bird and bat communities provide key ecological functions that support broader ecosystem services in oak woodland communities, such as agricultural pest removal (López-Hoffman et al., 2010) and oak regeneration (Martínez-Baroja et al., 2021). However, the potential positive and negative effects of wildfire on these species' distributions in these ecosystems remain poorly understood. The effects of fire on Californian bird and bat communities are nuanced and vary across specific environmental contexts. Previous work in conifer forest ecosystems suggests that large, high severity patches of fire negatively influence the presence of trees and primary cavity nesting birds (Steel, Fogg, et al., 2021) and certain insectivorous and granivorous birds (Latif et al., 2016). Simultaneously, the presence of some high severity patches following fires can create new habitat niches for fire-specialist species such as the Black-backed woodpecker (*Picoides arcticus*) which uses high severity areas located near low severity edges preferentially to establish nesting sites (Stillman et al., 2019). Ongoing work and theory suggest that the presence of a variety of different severity patches can facilitate increased biodiversity across landscapes by encouraging a diversity of different vegetation types (Jorge et al., 2022; Steel et al., 2019; Tingley et al., 2016). For example, pyrodiversity may create new roosting and nesting habitat in one burned severity patch and enhance food resources in another nearby

patch, thereby providing multiple resources for use (Steel et al., 2023). To date, these dynamics of pyrodiversity and severity are largely understudied in oak woodland, shrubland, and savanna ecosystems (Jones & Tingley, 2021). Oak woodland ecosystems historically consisted of a mixed-severity fire regime. Thus, pyrodiversity may underlie much of the biodiversity they are able to sustain. Changes in oak woodland fire regimes, specifically fires with increasingly large patches of contiguous high severity burns, could threaten to erase these supposed benefits. This omission in our understanding of pyrodiversity and novel fire regimes in oak woodlands leaves a profound gap in our collective approach to manage both wildlife and wildfire in oak woodland systems as fire regimes continue to change.

In this study, we compared the roles fire severity and pyrodiversity play in shaping patterns of diversity in bird and bat communities following a major oak woodland megafire in Northern California. We use automatic recording units (ARUs) to survey the presence of bird and bat species across a large oak woodland–shrubland savanna in Mendocino County, USA, following the historic 2018 Mendocino Complex Fire, the edge of which burned a substantial portion of the Hopland Research and Extension Center (HREC). We predicted that high severity burns would decrease the presence of tree nesting and granivorous birds by top-killing oak trees that could be used for nesting as well as by decreasing overall acorn production (a major food resource in this system [Koenig et al., 2013; McShea, 2000]). We predicted that moderate severity fire would increase the presence of bats and insectivorous birds by increasing the abundance of insects via the presence of dead wood (Nappi et al., 2010) and by leaving some remnant habitat structure. We also predicted that moderate severity fire would increase occupancy of primary and secondary nesters by weakening trees that could be used for nesting without removing them from the landscape (Tarbill et al., 2015). We predicted that increased pyrodiversity, or the diversity of severity patches, would increase diversity in bird and bat communities by creating variation in vegetation types over time that can support a greater diversity of bird and bat species. In teasing apart how each of these characteristics of fire (severity and pyrodiversity) influences bird and bat communities in this system, we help inform future management objectives in using fire to benefit wildlife and mitigate the impacts of future megafires.

METHODS

Study site

We conducted our study at the 21.54 km^2 U.C. HREC in Mendocino County, northern California (39°00′ N, 123°04′ W). HREC is composed of a diverse range of habitat types, including open grassland, oak woodland, and chaparral shrubland, providing habitat to a diversity of bird and bat species. HREC is situated at an important intersection of wildlands and ranchlands; it provides habitat for a diverse group of wildlife and serves as pastoral land for people and livestock. HREC consists of a combination of rolling valleys and peaks with its lowest elevation being 164 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 River Fire, part of the much larger Mendocino Complex Fire, burned over 13.76 km^2, or roughly half, of the HREC (Figure 1). At the time, the Mendocino Complex Fire was the largest fire in California's recorded history, burning 1858 km^2. The edge of this megafire was the first wildfire that burned a significant portion of HREC in over 60 years. The scale and severity of this fire contrasted with the historical fire regime in this region, which is characterized by frequent, lower severity fires in woodlands (5–10 years) and infrequent, more severe burns in shrubland habitats (30–80+ years) (Syphard & Keeley, 2020).

Acoustic monitoring and data management

To sample bird diversity following the 2018 Mendocino Complex Fire, we developed a sampling grid across HREC composed of hexagonal grid cells measuring 750 m across (Figure 1). Starting 2 years after the Mendocino Complex Fire, we deployed and randomly rotated a set of acoustic ARUs (Audiomoths model v1.1.0) across 36 sites near the centroid of each hexagonal grid from 2020 to 2022 (3 years total). Of these 36 sites, 25 sites were located within the burn perimeter of the Mendocino Complex Fire and 11 were located in unburned areas serving as controls. We conducted acoustic monitoring surveys during the spring–early summer (March 15–July 6) each year, which corresponded with the core nesting season when most passerines sing for the breeding season. ARUs were placed in a plastic Ziploc bag with a small desiccant pack and fastened to a tree or fence post at least 2 m off the ground. As demonstrated by Furnas and Callas (2015), we programmed ARUs to record three 5-min recording clips: one 30 min before sunrise, one at sunrise, and one 30 min after sunrise (15 min per day total, sampling frequency = 32 kHz) to sample the dawn chorus, when songbirds are most dependably active. These aggregated 15-min surveys were conducted at each site for a minimum of 4 days (range = 4–62 days, median = 8 days).

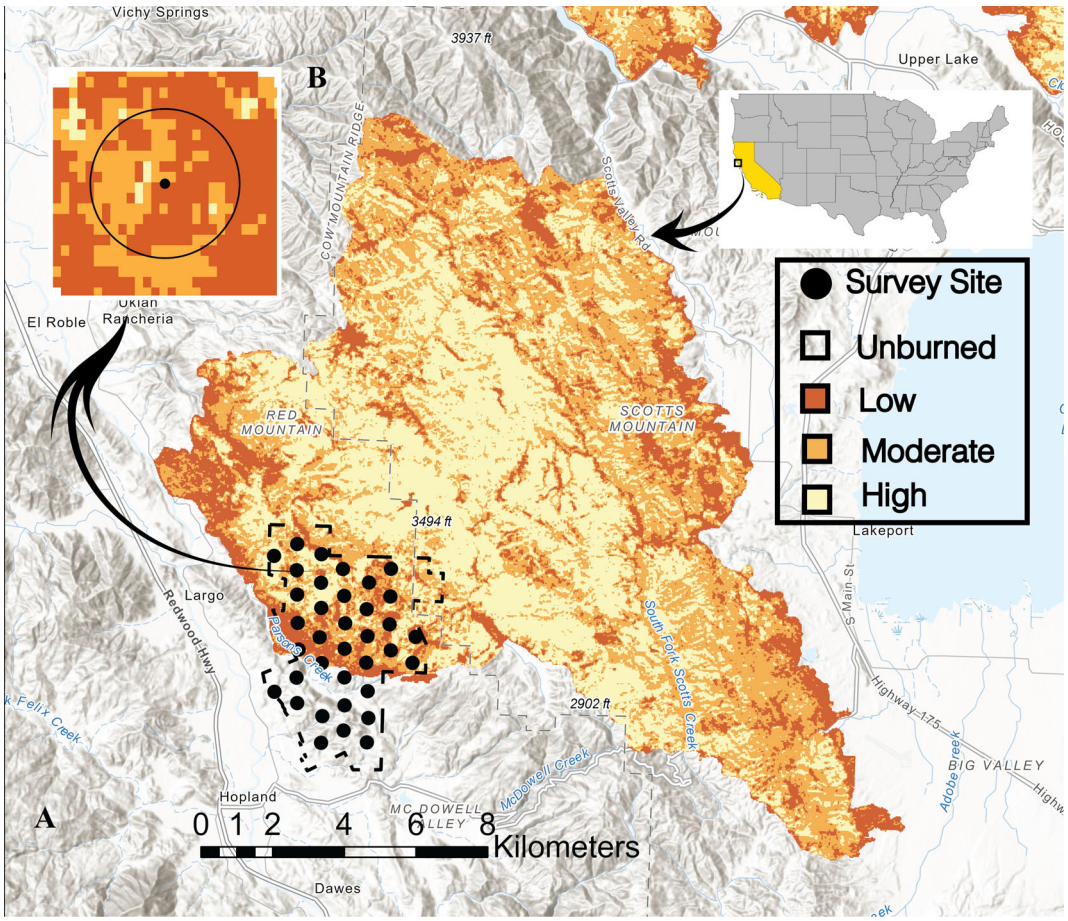


FIGURE 1 Map of study region and study site, the University of California Hopland Research and Extension Center (HREC) (39°00′ N, 123°04′ W) in Mendocino County, CA, USA. (A) The total coverage and severity of the Mendocino Complex Fire and where it overlapped with HREC (outlined in a dashed black line). (B) Binned categories of fire severity based on the Composite Burned Index (CBI) surrounding a single site at the 500-m buffer scale used to examine pyrodiversity in this study.

To classify species recorded at each sampling site, we used BirdNet (Kahl et al., 2021) to auto-classify each detected bird vocalization within our recorded acoustic data. BirdNet detects and auto-classifies birdsong in 3-s segments to species-level identifications, which can then be used as presence/absence data for modeling. To guide BirdNet auto-classification, we created a custom species list generated from eBird sightings of birds at HREC (Appendix S2: Table S1). Consistent point counts of birds are performed at HREC annually by researchers and community science activities that support these up-to-date species lists (Newman et al., 2018; Pascoe et al., 2023). For initial classification purposes only, we set the confidence threshold for auto-classifications at 0.01 to include as many detections as possible and left all other BirdNet settings as default.

For analyses, we followed the established guidance of Toenies and Rich (2021) and Cole et al. (2022) to process the collected acoustic data using a set of validation and tiered filtering methods to remove probable false positive detections (Cole et al., 2022; Toenies & Rich, 2021). Whereas in bat ultrasonic call validation (see *Ultrasonic monitoring and data management*) we were able to conservatively validate the presence of species for each sampling night per site, we were unable to vet the presence of every detected bird species for each site and each occasion due to the much larger number of bird species and sampling occasions. For the birds, we first removed all detections with confidence scores <0.50 across all detected species. We randomly selected 50 of the remaining 3-s calls annotated by BirdNet from each detected bird species and validated whether the detection was a true or false positive. At least two team members validated a subset of the 50 total auditory detections for each species. For species with <50 calls, all calls detected by BirdNet were validated ($n = 25$ species). We created a species-specific confidence threshold by selecting the false positive detection with the highest confidence score (as generated by BirdNet) and adding a buffer of 0.05, filtering out all detection calls with confidence scores

lower than this threshold (Cole et al., 2022). For species with no false positives in their 50 validated calls, we set the threshold to be 0.05 greater than the lowest true positive score for that species. After validation-based filtering, we only included bird species detected at five or more sites for modeling to ensure each modeled species had enough detections to obtain accurate estimates from our models ($n = 40$ species). Once complete, we produced a record table of these bird detections for analyses in R (R Core Team, 2021) using "camtrapR" (Niedballa et al., 2016) (v.2.2.0).

Ultrasonic monitoring and data management

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

We used SonoBat West (v.4.4.1) and western regional library with reference calls for all 12 detected bat species to classify, visualize, and vet recorded bat calls by species (www.sonobat.com). First, we used the "SonoBat Batch Scrubber" feature to filter out non-bat ultrasonic calls from the recorded data. Next, we used the "SonoBatch" classifier feature to classify detected calls as recorded bat species. We set the classifier region setting to "Western US" to guide these classifications. We set the acceptable quality threshold for bat calls to 0.80, the sequence decision threshold to 0.90, and allowed a maximum of eight calls to be considered per file. SonoBat automated classification is purposefully conservative to reduce the likelihood of false positive detections across species. Once classified by SonoBat, we vetted species classifications at each site, conservatively ensuring that at least one detected call for each species was a true positive for each monitoring night at each site. False positive species detections during specific monitoring nights were removed. Once complete, we produced a record table of all bat species detections across all sites and years.

Fire covariates

To quantify fire severity on the landscape, we used the Composite Burn Index (CBI) layer of the 2018 Mendocino Complex Fire generated using pre- and post-fire LandSat imagery following Parks et al. (2019) at a 30 m resolution. CBI is a characterization of burn severity based on the impact of fire on aboveground vegetation (litter, herbs, shrubs, and trees) and thus provides an ecologically relevant quantification of fire's effects on wildlife habitat. From this raster, we extracted the average severity value from a 500 m buffer surrounding each acoustic sampling site predicting that fire severity would drive species occupancy (Figure 1B). We predicted that species' responses to fire severity may be non-linear, with some species potentially attracted to moderately burned sites, and therefore included a quadratic term for CBI in the occupancy sub-model. To calculate pyrodiversity, we quantified the diversity of categorical fire severity cells within a 500 m buffer of each sampling site using the Inverse Simpson's Diversity Index in the landscapemetrics (v.1.5.6) package (Hesselbarth et al., 2019) of R, where $D =$ the diversity index, $n_i =$ the number of cells in each severity category, and $N =$ the total number of cells within the buffer:

$$D = 1 - \Sigma \frac{n_i(n_i - 1)}{N(N-1)}.$$

$$\text{Inverse Simpson's Diversity Index} = \frac{1}{D}.$$

Categorical patches of severity were binned from the CBI, where severity of 0 was categorized as "unburned," 0–1 as "low severity," 1–2 as moderate severity, and 2–3 as high severity.

Environmental covariates

In addition to fire severity and pyrodiversity, we also expected that vegetation cover type (woodland and shrubland) and elevation would influence bird and bat species presence. The presence of woodland or shrub cover has been found to influence bird and bat communities at broad regional scales by providing specific resources, including food, nesting, roosting, and microhabitats for different species (Fuentes-Montemayor et al., 2013; Herrando & Brotons, 2002; Mendelsohn et al., 2008).

We estimated vegetation cover surrounding sampling sites by classifying the study site into broad land cover categories including woodland, grassland, and shrubland (chaparral). To do this, we hand-digitized vegetation layers using high resolution (<1 m) aerial imagery from

the National Agriculture Imagery Program (2014–2015). We ground-truthed these digitizations by checking 50 randomly generated points across the study site to validate classifications (results were 98% accurate). We extracted percent (%) woodland and chaparral cover within a 500-m buffer of each sampling site. We obtained elevation for each site using the ASTER Global Digital Elevation Model at a 10 m resolution (NASA and METI, 2011) and extracted average elevation values from a 500 m buffer around each sampling site as well.

We predicted date, wind speed, temperature, and canopy cover would affect the detectability of bird and bat species at recording stations. To account for certain birds and bats being more or less active during the beginning, middle, or end of the spring season (Furnas & McGrann, 2018), we incorporated Julian day and its quadratic term for each detection in our occupancy models. Similarly, daily temperatures may impact the activity and call rate of both birds (Puswal et al., 2021) and bats (Jorge et al., 2021), so we extracted daily temperature data across HREC to account for this. Detections of bird song and bat calls may be further influenced by ambient noise caused by wind or the density of vegetation in the surrounding area ("canopy cover"). HREC contains six weather stations located across the property that record wind speed and temperature once per hour. We downloaded both logs to calculate average daily temperatures (in degrees Celsius) and wind speeds (in kilometers per hour) across the property for each sampling day of our study.

We estimated post-fire 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 the year 2020 (Calhoun et al., 2023). These rasters were visually verified using fine scale, 3-m resolution imagery via Planet Labs (Planet Team, 2017; Sunde et al., 2020; Tilahun, 2015). We extracted percent (%) canopy cover from a 100 m buffer surrounding each sampling site to examine how canopy cover and openness influence detectability.

All continuous covariates were checked for non-collinearity and standardized to have a mean of 0 and a SD of 1. Fire severity and pyrodiversity were highly correlated. We therefore ran separate model parameterizations for (1) severity-only and (2) pyrodiversity-only to compare the individual effects of fire severity and pyrodiversity on species occupancy. See Table 1 for the mean, range, and resolution of all covariates and Appendix S2: Figure S1 for a correlation matrix of all continuous covariates.

Occupancy modeling framework

We use an occupancy modeling framework to describe species distributions over time, which predicts the probability of a species occurring at a site ("occupancy") (ψ) given how detectable it is at that site ("detection probability") (p) (MacKenzie et al., 2002). We fit two multi-species community occupancy models (Devarajan et al., 2020;

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

Covariate	Mean	Range	Resolution
Detection covariates			
Julian date	...	74–187[a]	...
Wind speed (km h^{-1})	4.80	1.93–10.46	Daily average across HREC
Temperature (°C)	15.45	4.28–29.06	Daily average across HREC
Post-fire canopy cover (%)	77.23	0–100	100 m buffer
Sampling effort (days)			
Birds	11.13	4–62	...
Bats	4.84	3–10	...
Occupancy covariates			
Elevation (m)	487.93	221.97–878.78	500 m buffer
Composite Burn Index (CBI)	0.95	0.00–1.98	500 m buffer
Pyrodiversity[b]	1.77	1.00–2.93	500 m buffer
Woodland Cover (%)	46	7–81	500 m buffer
Chaparral Cover (%)	16	0–78	500 m buffer

Note: An ellipsis indicates not applicable.
[a]March 15–July 6.
[b]Inverse Simpson's Diversity Index.

MacKenzie et al., 2002; Royle & Dorazio, 2008), one for each taxonomic group, to investigate the effects of fire severity and pyrodiversity on patterns of species' distributions and species richness. Our acoustic sampling methodology was designed to sample across a diversity of bird and bat species to inform our assessment of community composition. We followed standard practices of ARU deployment to maximize the detectability of bat and bird species at each monitored site to reduce model bias (Loeb et al., 2015; Toenies & Rich, 2021). We defined a binary latent true occupancy variable, $z_{i,j}$, where $z_{i,j} = 1$ indicates that at least one individual of the species (i) occupied the area covered by the acoustic sampling station in year (j) and $z_{i,j} = 0$ indicates that no individual of the species (i) occupied the area covered by the acoustic sampling site-year (j). We assumed that occupancy was drawn from a Bernoulli distribution with probability ($\psi_{i,j}$):

$$Z_{i,j} \sim \text{Bernoulli}\left(\psi_{i,j}\right).$$

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

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

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

$$\begin{aligned}\text{Logit}\left(\psi_{i,j}\right) = {} & \alpha 0_i + \alpha 1_i \times \text{Elevation}_j + \alpha 2_i \times \%\text{Woodland}_j \\ & + \alpha 3_i \times \%\text{Chaparral}_j + \alpha 4_i \times \text{Severity}_j + \alpha 5_i \\ & \times \text{Severity}_j^2 + \text{Site Random Effect}_{i,j} \\ & + \text{Year Random Effect}_{i,m}.\end{aligned}$$

$$\begin{aligned}\text{Logit}\left(\psi_{i,j}\right) = {} & \alpha 0_i + \alpha 1_i \times \text{Elevation}_j + \alpha 2_i \times \%\text{Woodland}_j \\ & + \alpha 3_i \times \%\text{Chaparral}_j + \alpha 4_i \times \text{Pyrodiversity}_j \\ & + \text{Site Random Effect}_{i,j} \\ & + \text{Year Random Effect}_{i,m}.\end{aligned}$$

$$\begin{aligned}\text{Logit}\left(p_{i,j}\right) = {} & \beta 0_i + \beta 1_i \times \text{Date}_{j,k} + \beta 2_i \times \text{Date}_{j,k}^2 + \beta 3_i \\ & \times \text{WindSpeed}_{j,k} + \beta 4_i \times \text{Temperature}_{j,k} + \beta 5_i \\ & \times \text{PostFireCanopy}_{j,k} + \text{Site Random Effect}_{i,j} \\ & + \text{Year Random Effect}_{i,m}.\end{aligned}$$

We treated each site-year as a unique site to allow occupancy and detection to vary across years. We included species-specific site random effects within the occupancy and detection sub-models to account for non-independence between surveys at sites. We chose not to represent data collected across years as a dynamic occupancy model because we did not need to explicitly estimate extinction and colonization rates, which require large amounts of data. To control for environmental differences in annual resource availability caused by changes in rainfall, acorn masting, and other sources of variation, we also included species-specific year random effects (m) within the occupancy and detection sub-models.

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

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

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

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

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

We fit two additional multi-species occupancy models using the bird occurrence data and with identical model parameterizations as the community-level multi-species occupancy model, this time assigning hyperparameters to groups of species as defined by nesting (tree, primary cavity, secondary cavity, ground, shrub) and diet (granivore, insectivore, omnivore, nectarivore) guilds, rather than the entire community. These guilds were assigned to modeled species according to their known life histories (Wilman et al., 2014). Birds whose diets were composed of greater than 60% of plant material were grouped as "granivores" and birds whose diets were composed of greater than 60% of invertebrates were grouped as "insectivores." Bird species whose diets were composed of less than 60% of either plant material or invertebrates were grouped as "omnivores." Only one observed species was present in the nectarivore diet group, Anna's Hummingbird (*Calypte anna*), so this diet group was removed from the analysis. Species-level coefficients for each model (nesting guild

model and diet guild model) were drawn from group-level (g) hyperparameters from a group mean of μ_g and SD of σ_g following the community model framework given above. See Appendix S2: Table S1 for groupings of individual species into nesting and diet groups.

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

Model implementation and fit

We implemented and estimated all multi-species occupancy models with Markov chain Monte Carlo (MCMC) using the R packages nimble (v.0.11.1) and nimbleEcology (v.0.4.0) (de Valpine et al., 2017; Goldstein et al., 2021). We ran all multi-species models for 60,000 iterations with a 10,000 iteration burn-in for a total of 50,000 samples across three chains and used nimble custom samplers to increase the efficiency of MCMC mixing (Gelman et al., 2004). We assessed parameter chains for all models for convergence and that R-hat values for each parameter were estimated to be less than 1.1 (Gelman et al., 2004). We then compared the fit of the severity-only and pyrodiversity-only parameterizations using their Watanabe–Akaike information criterion (WAIC) values (Gelman et al., 2014). We considered a model to fit significantly better if its WAIC score was ≤2 points lower than the other model parameterization.

We assessed model fit for both the bat and bird community multi-species occupancy models using posterior predictive checks. We simulated a new dataset using the parameters in each MCMC sampling iteration and sampled the deviance of each from the true model. We compared observed model deviances to these posterior checks for evidence that the data do not correspond to the fit models (Gelman et al., 1996; MacKenzie et al., 2017). We assessed a covariate as being a "significant" predictor of occupancy or detection if the 90% credible interval for that variable did not overlap zero and used this definition to describe significance under Bayesian inference (McElreath, 2016). By definition, 5% of the posterior distribution is above and below a 90% credible interval; thus, a "significant" result has a 5% or lower chance of representing a false positive or false negative result. Additionally, we used model posterior samples to estimate exact probabilities of covariates having positive (P(+)) or negative (P(−)) effects at the species level by dividing the number of samples with positive (or negative) coefficients by the total number of samples taken ($n = 50{,}000$).

RESULTS

Bird acoustic survey results

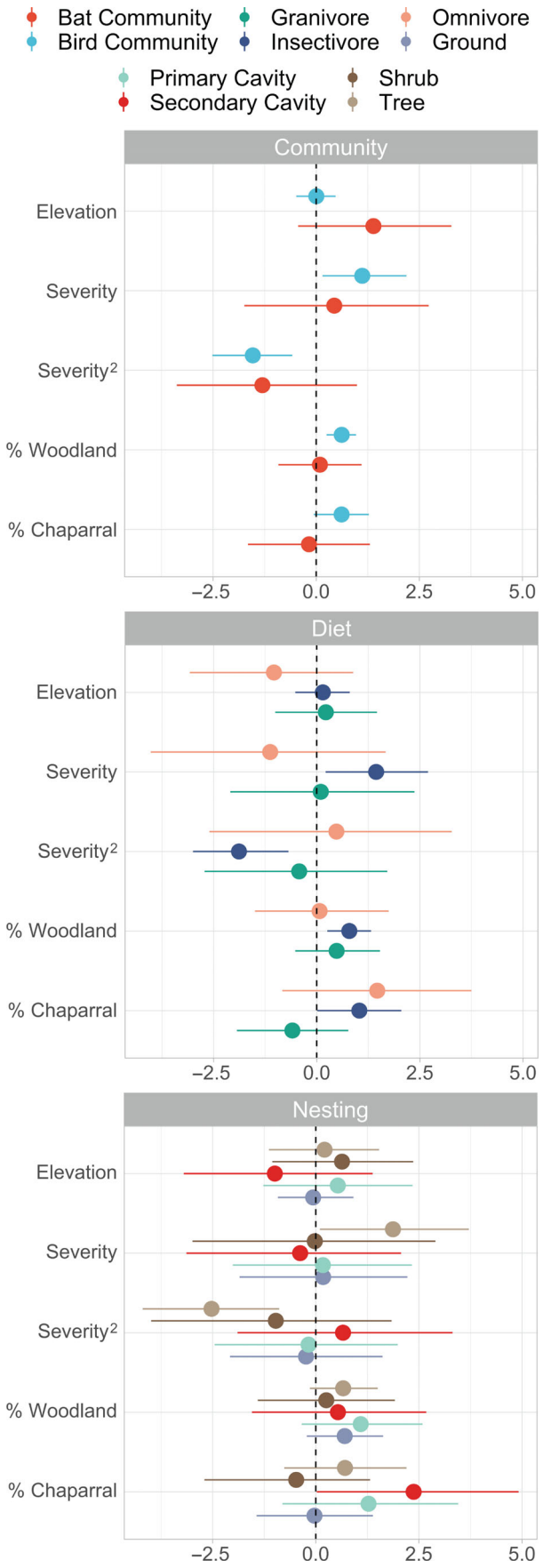
We collected 17,190 h of avian acoustic recordings over the course of 1146 sampled mornings and across 103 site-years at 36 locations (2020–2022). From these recordings, BirdNet annotated over 800,000 individual detections of bird song. We validated the presence of 67 detected species (listed in Appendix S2: Table S1). Ultimately, 39 species known to breed during the study period had enough validated detections, post confidence-threshold filtering (see *Acoustic monitoring and data management*), to be included in the multi-species occupancy model. Across modeled species, Acorn Woodpecker (*Melanerpes formicivorus*) was the most detected species ($n = 8422$) and Brown-headed Cowbird (*Molothrus ater*) was the least commonly detected species ($n = 10$) (Appendix S2: Table S2).

Bat ultrasonic survey results

We collected over 190,000 ultrasonic bat detections over 1146 sampled nights and across 99 site-years (2020–2022) at 36 unique locations. Of these detections, we subset a total of 14,916 bat detections that were vetted to the species level, which included 13 different bat species (Appendix S2: Table S3). The Mexican free-tailed bat (*Tadarida brasiliensis*) was the most detected species ($n = 5645$) and Townsend's big-eared bat (*Corynorhinus townsendii*) was the least detected species ($n = 3$) (Appendix S2: Table S3). We ultimately did not include Townsend's big-eared bat in multi-species occupancy models due to too few detections but incorporated the remaining 12 species into the bat multi-species community model.

Bird multi-species occupancy community- and group-level model results

We used the community-level multi-species bird occupancy model to examine the species-specific effects of fire and other environmental covariates on detection and occupancy (Appendix S2: Tables S4 and S5). The bird severity-only model parameterization fit significantly better than the pyrodiversity-only parameterization (ΔWAIC = 20.32, Appendix S1: Table S1) and demonstrated



goodness-of-fit within acceptable bounds (Appendix S1: Figure S1). We therefore used the better-fitting severity-only model parameterization to assess the effects of fire on bird occupancy. Bird community-level occupancy (Ψ) was significantly (90% CI does not overlap zero) negatively associated with the quadratic severity term (concave-down) (mean = −1.54 [−2.52, −0.58]), indicating a peak in occupancy at low to moderate severity fire (Figure 2). Percent (%) woodland had a significant positive correlation with bird community-level occupancy (mean = 0.62 [0.25, 0.97]).

Fire effects influenced species-group habitat preferences as well (Appendix S2: Tables S6–S9). The quadratic burn severity term was a significant negative predictor of occupancy for one bird nesting group, tree nesters (mean = −2.53 [−4.20, −0.89]) and one diet group, insectivorous birds (mean = −1.88 [−3.00, −0.69]), indicating both groups were more likely to occupy sites that burned at low to moderate severities (Figure 2).

As indicated by a significant negative quadratic term, moderate severity fire was associated with higher rates of species-specific occupancy for 23 of 39 modeled bird species, including Violet-green Swallow (*Tachycineta thalassina*) (Severity^2 parameter mean = −1.59 [−2.79, −0.34]), California Quail (*Callipepla californica*) (mean = −1.95 [−3.36, −0.63]), and House Finch (*Haemorhous mexicanus*) (mean = −2.71 [−4.54, −0.96]) (Appendix S2: Figure S3). Additionally, occupancy increased linearly with fire severity for six additional species, including Spotted Towhee (*Pipilo naculatus*) (mean = 1.36 [0.01, 2.67]), Dark-eyed Junco (*Junco hyemalis*) (mean = 1.44 [0.08, 2.80]), and Blue-gray Gnatcatcher (*Polioptila caerulea*) (mean = 1.43 [0.09, 2.69]) (Appendix S2: Figure S2).

Using the pyrodiversity-only model parameterization, we found that pyrodiversity was not a significant predictor of community-level, group-level, or species-level occupancy (Appendix S2: Figure S4). However, pyrodiversity had a greater than 80% probability of at least being positively associated with the occupancy of 3 of 39 bird species, including Lazuli Bunting (*Passerina amoena*) (P(+) = 92%), Oak Titmouse (P(+) = 89%), and Mountain Quail (*Oreotryx pictus*) (P(+) = 82%) indicating a small effect may be detectable with greater sample sizes.

FIGURE 2 Model coefficients for the effects of covariates from the severity-only model on occupancy from the bat and bird community, bird diet group, and bird nesting group multi-species occupancy models following the 2018 Mendocino Complex Fire in Mendocino County, CA, USA.

Bat multi-species occupancy community model results

We used the bat multi-species occupancy model to examine the species-specific effects of fire severity and pyrodiversity on bat occupancy (Appendix S2: Tables S10 and S11). The bat severity-only model parameterization fit significantly better than the pyrodiversity-only parameterization (ΔWAIC = 5.10) but had poorer goodness of fit relative to the bird data (Appendix S1: Figure S2). We used the better-fitting severity-only model parameterization to assess the effects of fire on bat occupancy. Fire severity (Severity and Severity^2) was not a significant predictor of occupancy for the bat community mean hyperparameter (90% credible interval overlapped zero) (mean = −1.31 [−3.38, 0.99]) (Figure 2).

Similarly, we found that fire severity was not a significant predictor of bat species-specific occupancy across sites (Appendix S2: Figure S6). However, 4 of 12 bat species had a greater than 80% probability of having a negative association with the quadratic severity term indicating a likely positive association with moderate severity fire (Figure 3). These species included the Canyon bat (*Parastrellus hesperus*) (mean = −3.29 [−6.77, 0.24]), the Pallid bat (*Antrozous pallidus*) (mean = −3.14 [−7.03, 0.63]), the Mexican Free-tailed bat (*T. brasiliensis*) (mean = −1.82 [−4.31, 0.57]), and the Hoary bat (*Lasiurus cinereus*) (mean = −1.62 [−4.37, 1.07]) (Appendix S2: Figure S5).

Using the pyrodiversity-only model parameterization, we found that pyrodiversity was also not a significant predictor of community-level or species-level occupancy across bats (Appendix S2: Figure S7). Using our posterior samples, we found that all bat species had <80% probability of being positively associated with pyrodiversity (Figure 3).

DISCUSSION

As in other ecosystems, we found the effects of fire on bird and bat species in oak woodlands to vary across individual species, taxonomic groups, and species-trait groups. Within this variation, we also find a compelling trend of evidence supporting the overall benefits of fire for a variety of individual species and species groups.

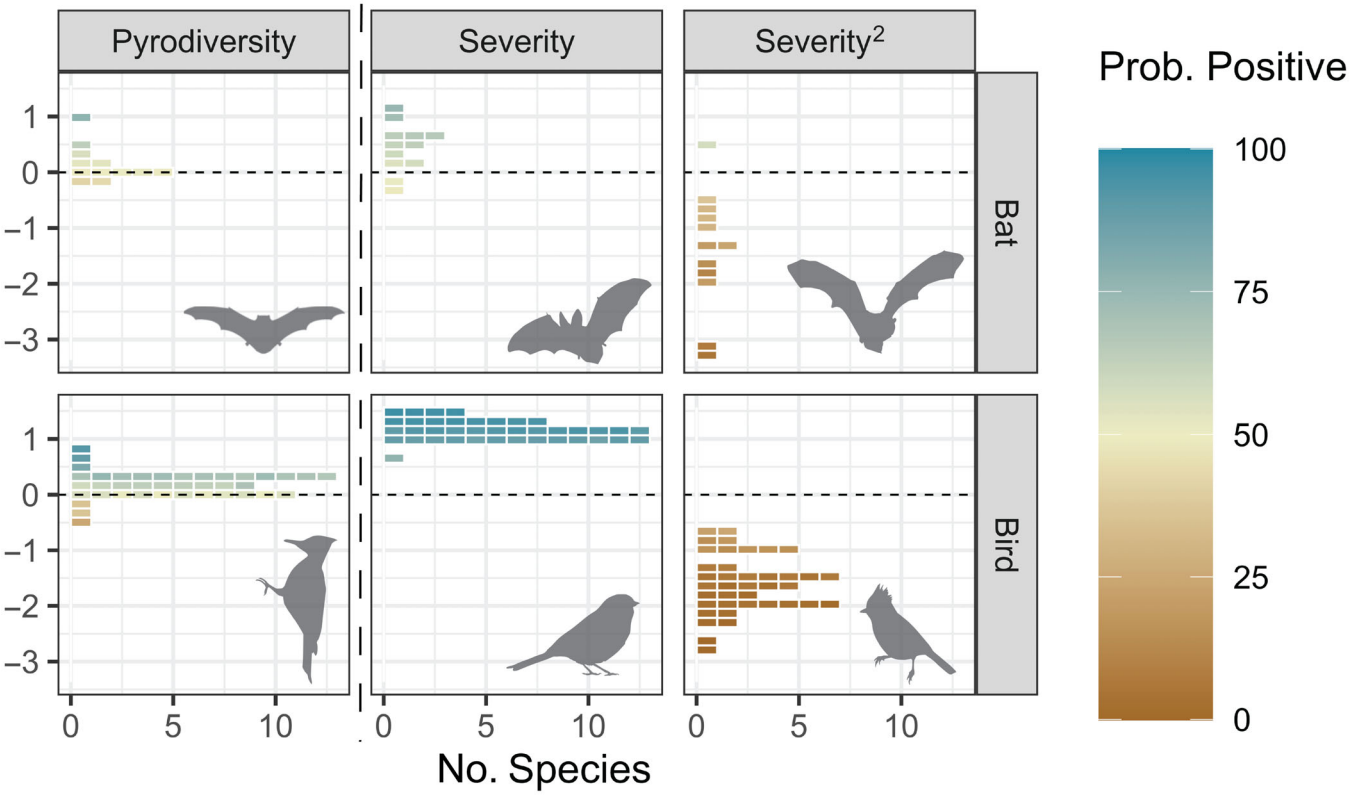


FIGURE 3 Species-specific coefficient means of fire covariates on occupancy derived from bird and bat community multi-species occupancy models following the Mendocino Complex Fire in Mendocino County, CA, USA. Each square represents one of the modeled species (12 bats, 39 birds, and 51 total species). The color of the square represents the probability that the fire covariate has a positive effect on occupancy. Coefficients from the pyrodiversity-only and severity-only models are separated by a dashed line.

At the community level, bird community occupancy (community-level hyperparameters) was strongly positively correlated with low-to-moderate severity fire. At finer species-specific and group-specific scales, we found that severity did influence habitat preferences positively for several groups (insectivorous birds, tree nesters, and several bat species). We did not find compelling evidence to support the pyrodiversity-biodiversity hypothesis as pyrodiversity was not a significant predictor of community, group, or species-level occupancy, and its model generally performed poorer than the severity-only parameterization. This may be influenced by the overall recentness of this study relative to the fire event or the limited sample size within our study preventing us from detecting the full realized effect of pyrodiversity. For example, Tingley et al. (2016) found the positive effect of pyrodiversity for montane birds increased over time within the first decade post-fire. Our results underline how wildlife communities in oak woodlands remain resilient to, and can even benefit from, a broad range of wildfire effects across oak woodland landscapes.

Fire severity was a strong, non-linear predictor of occupancy for many species. As found across a variety of other studies examining the impact of fire severity on wildlife habitat usage (Albanesi et al., 2014; Furnas et al., 2021), we found species among both the bird and bat communities were most likely to occupy sites that burned at low to moderate severities. We found no evidence that unburned patches and low severity fire significantly increased the occupancy of any bird or bat species. Therefore, these low and moderately burned areas may create new habitat conditions that certain species are able to take advantage of without excluding species that may be more sensitive. The majority of birds (37 of 39 species) likely (>80% probability) had some positive association with low and moderate severity burning, potentially driving the community-level mean response across the bird community specifically.

Occupancy for some bat species (4 of 12) in our study showed a positive correlation (albeit statistically non-significant) and large effect sizes with sites that burned at moderate severities. In more forested ecosystems, studies have found bat species' occupancy increased with sites that burned at higher severities in the Sierra Nevada (Steel et al., 2019). Higher severity fires may introduce greater heterogeneity to the landscape relative to unburned fire-suppressed forests, thus increasing accessibility to foraging habitat. This preference, however, may be dependent on the interaction between species-specific foraging strategies and fire severity (Blakey et al., 2019). In oak woodlands that are naturally more open, moderate and mixed-severity fires may be the most appropriate fire regime to emulate and sustain the natural heterogeneity of the ecosystem (Agee, 2005; Perry et al., 2011). We found little variation in bat presence across sites; the majority of bat species were present across most sampling sites regardless of fire severity and other predictor covariates. Our lack of numerous sample sites may limit our ability to disentangle whether the effects of severity on bat populations and foraging groups are just weaker in oak woodlands than in conifer systems or whether we lack the statistical power to estimate this relationship precisely. Future efforts expanding the scope of this work to consider additional burned oak woodland sites at a regional scale could generate the statistical power needed for greater precision.

Fire severity had varied effects on bird occupancy depending on species trait groupings. Insectivorous birds were more likely to occupy sites that burned at moderate severities. As shown in previous work (Taillie et al., 2018), moderate severity fires may benefit both insectivorous bats (all bat species in this study) and insectivorous birds that are able to take advantage of insects attracted to areas with dead wood following the initial burn. We did not find support for our hypothesis that primary and secondary cavity nesters would be more likely to be present at sites that burned at moderate severities. Time since burning is likely an important interacting term with fire severity that influences species' habitat preferences over time that we were unable to appropriately model given the short window of our study (Hutto & Patterson, 2016; Tingley et al., 2016). Over longer periods of time, primary and secondary nesters may eventually take advantage of snags and weakened trees to create nests (Tarbill et al., 2015). Unexpectedly, moderate severity fire increased occupancy of tree nesting species. The mechanism of this response remains unclear, but other underlying trait responses, such as diet, may be driving this result. For example, 7 of 12, or over half, of the tree nesting species are also insectivores that were expected and observed to increase occupancy in moderately burned areas. We did not find support for our hypothesis that granivorous birds would be less likely to occupy severely burned areas due to an immediate decrease in plant-based food following high severity burning. Altogether, these suggest that the effects of fire severity on potentially vulnerable groups may play out differently in oak woodlands compared to forest-dominated landscapes. Pre-existing heterogeneity in landscape composition and vegetation within oak woodlands may help prevent large, homogenous burn patches that greatly alter community assemblages as observed in other studies such as Steel, Fogg, et al. (2021). Maintaining this natural heterogeneity could be essential for sustaining the resilience of some of the species that could be potentially more vulnerable.

We did not find evidence to support our hypothesis that ground-nesting birds would be more likely to occupy

higher severity sites. However, we did find that severity was a significant, linear positive predictor of occupancy for two bird guilds (insectivores and tree nesters) and some specific bird species (6 of 39 birds), including Mountain Quail, a species of increasing conservation concern. As a limitation of our sampling design, we were unable to test for the effects of high severity fire (CBI $\geq$ 2.4; see Table 1) on occupancy, but these results suggest that moderate to high severity fire could increase occupancy for these species and species groups. High severity patches may provide pulses of resources that are distinct from those found in other burned patches. Certain species such as Mountain Quail are known to preferentially select these high severity areas to hone in on these initial resources and use the shrubs and other plants that regenerate in high severity patches over time (Brunk et al., 2023). Future studies that capture the full extent of severity effects on oak woodland landscapes by incorporating multiple fires with varying extents and severities could more accurately estimate the relationship between high severity fire and optimal occupancy for these bird and bat communities.

We found important differences in the relative responses to fire severity across taxonomic groups as well as life-history trait types (e.g., diet vs. nesting strategies). Overall, individual bat species showed variable responses to fire severity, with generally larger model uncertainty. This level of uncertainty in our estimated relationship between bat occupancy and fire severity was likely attributable to a relatively small sample size, which translated to poorer model fit and larger CIs. Within birds, we found that severity and pyrodiversity had largely negligible effects in predicting nesting group occupancy relative to the diet group results. Certain life-history traits, such as diet in this case, may be more directly linked to species' responses to certain disturbances (Pausas & Parr, 2018). Developing our understanding of the relative importance of these different traits in responding to disturbances such as fire (Pocknee et al., 2023) across different taxonomic groups such as birds and bats could help identify potentially vulnerable species and improve our predictions of the anticipated effects of fire.

Pyrodiversity had generally negligible effects on occupancy for both taxonomic community-level means, all bird species trait groups, and most individual species. Both the pyrodiversity hypothesis and the intermediate disturbance hypothesis (IDH) predict increased biodiversity in landscapes with high pyrodiversity and moderate levels of disturbance, respectively (Steel et al., 2023). These predicted impacts, however, are difficult to disentangle due to the fact that moderate severity fire is often correlated with variation in fire severity across space (pyrodiversity). Our results suggest that moderate severity fire (IDH) and not pyrodiversity plays a greater role in shaping species distributions within the given timescale of our study. However, the observed impacts of pyrodiversity may be dependent on the temporal scale and pyrodiversity metric employed (Jones & Tingley, 2021; Steel, Collins, et al., 2021). As observed in other work (Stillman et al., 2023; Tingley et al., 2016), the effects of pyrodiversity may become more pronounced with time. The limited timescale of our own study (3–5 years post-fire) may prevent us from observing the realized effects of pyrodiversity in shaping species distributions over time. Furthermore, we are only able to consider a single dimension of pyrodiversity within our study ("spatial pyrodiversity") when a combination of both "spatial" and "temporal" (variance in fire age classes across landscapes) pyrodiversity likely influences species diversity and distributions over time (Kelly et al., 2017). Finally, fire may also have varying impacts on species presence depending on the vegetation type that is burned and how that vegetation typically regenerates over time (Keeley et al., 2006). These differences may contribute to varying species responses to fire severity immediately following fire and to varying responses to pyrodiversity over time.

Our findings in comparing the effects of severity and pyrodiversity are also likely influenced by the tools available to measure both fire regime components. The realized ecological effects of these metrics have been thoroughly studied in systems such as California's mixed-conifer forests (Miller et al., 2009; Miller & Thode, 2007), but a large gap remains in our understanding of how these metrics translate to non-forested systems such as woodland savannas and shrublands. The same severity metrics (low, medium, or high severity burning) may have variable realized effects across different ecosystem types (Huang et al., 2020; Stambaugh et al., 2015). For example, green-up in many oak woodland systems occurs much more rapidly following fire than in many forested systems, even in high severity patches (Huerta et al., 2022). Developing improved tools to quantify both severity and pyrodiversity may help future studies better discern the effects of fire characteristics on patterns of biodiversity in oak woodland savannas.

Within the timeframe of our study, our findings further demonstrate the natural resilience of many bat (Ancillotto et al., 2021; Loeb & Blakey, 2021) and bird (Lindenmayer et al., 2022) species to fire, as well as the ways fire may enhance habitat for several of these species, that have been established in past work. No species in our study exhibited a decrease in occupancy associated with increasing fire severity or pyrodiversity. In fact, most species (36 of 39 bird species and 8 of 12 bat species) appeared to prefer some form of burned habitat relative to unburned sites. The species that showed no strong positive or negative preference toward fire effects were likely

resistant, able to withstand the initial impacts of the disturbance (Pimm, 1984), or resilient, able to recover quickly following the disturbance (Holling, 1973), to the initial impacts of the fire. This resilience may, again, be dependent on the sustained natural heterogeneity of oak woodlands to produce pockets of refugia for species that prefer unburned and/or lower severity burned areas (Calhoun et al., 2023). Fire management that takes this into account to produce a diversity of burned effects that maintain this heterogeneity would be critical for maximizing species diversity at a broader landscape scale (Prowse et al., 2017). In this way, considering regional pyrodiversity would be key in producing these intended effects with prescribed burning in oak woodland systems.

CONCLUSION

Fire in oak woodlands played an important role in enhancing habitat for several bird and bat species across our study. Mixed-regime fires (at least first-entry fires) in oak woodlands may sustain the heterogeneity characteristic of these ecosystems that is able to support high levels of biodiversity. Therefore, fire and land management that encourages the sustainability of these mosaic landscapes is essential to supporting a diversity of bat and bird species from different functional groups. We believe there is significant opportunity to employ these findings in existing structures of fire and land management in rangelands and woodland savannas. Fire has and will continue to play a pivotal role in these landscapes. Thus, finding and maximizing the co-benefits of using fire management to enhance wildlife habitat and reduce the risk of more extreme fire that may change these ecosystems is vital.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Species record tables, detection histories, taxonomic group information, site metadata, and novel code (Calhoun et al., 2025) are available from Dryad: https://doi.org/10.5061/dryad.wwpzgmsqx. Sentinel-2 satellite imagery was downloaded from USGS EarthExplorer (https://earthexplorer.usgs.gov).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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