Received: 7 September 2024 | Revised: 9 January 2025 | Accepted: 1 April 2025

DOI: 10.1111/cobi.70079

Conservation Biology

CONTRIBUTED PAPER

Finding floral and faunal species richness optima among active fire regimes

Zachary L. Steel[1,2] | **Alissa M. Fogg**[3] | **Raphaela Floreani Buzbee**[2] | **Kate Wilkin**[4] | **Brandon M. Collins**[3,5] | **Ryan Burnett**[3] | **Marc D. Meyer**[6] | **Amarina Wuenschel**[7] | **Scott L. Stephens**[3]

[1]USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA

[2]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, California, USA

[3]Point Blue Conservation Science, Petaluma, California, USA

[4]Department of Biological Sciences, San Jose State University, San Jose, California, USA

[5]USDA Forest Service, Pacific Southwest Region, Vallejo, California, USA

[6]USDA Forest Service, Region 5 Ecology Program, Southern Sierra Province, Bishop, California, USA

[7]USDA Forest Service, Region 6 Ecology Program, Blue Mountains Area, Baker City, Oregon, USA

Correspondence
Zachary L. Steel, USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect Rd., Fort Collins, CO 95826, USA. Email: zachary.steel@usda.gov

Article impact statement: Biodiversity peaks under nonhistorical fire conditions, indicating history is an imperfect surrogate for ecological integrity.

Funding information
California Department of Forestry and Fire Protection, Grant/Award Number: 8GG21823

Abstract

Changing fire regimes have important implications for biodiversity and challenge traditional conservation approaches that rely on historical conditions as proxies for ecological integrity. This historical-centric approach becomes increasingly tenuous under climate change, necessitating direct tests of environmental impacts on biodiversity. At the same time, widespread departures from historical fire regimes have limited the ability to sample diverse fire histories. We examined 2 areas in California's Sierra Nevada (USA) with active fire regimes to study the responses of bird, plant, and bat communities to a broad spectrum of temporal, spatial, and severity patterns of fire. Bird and plant species richness peaked in the first decade following fire. Species richness was highest with moderate burn severity for birds and with low burn severity for plants. Bat richness increased with longer mean fire-return intervals and was greatest in landscapes that included predominantly unburned areas or moderate to high burn severity patches. All taxa responded positively to pyrodiversity, with effect sizes varying with the metric used to assess variation in fire patterns. Our results suggest that restoring historical fire regimes would benefit biodiversity relative to most contemporary dry forests in California, but that total species richness would be highest under somewhat more frequent and varied severity fires than historical targets would indicate. Given the variable optima among taxa, managing for a range of complementary conditions that create local and landscape heterogeneity would best accommodate diverse flora and fauna and other forest conservation objectives.

KEYWORDS
biodiversity, conservation management, ecological integrity, fire ecology, fire regimes, pyrodiversity, wildfire

INTRODUCTION

Fire drives the ecology of individual species and greatly influences biological communities globally (He et al., 2019; Viljur et al., 2022). When the long-term spatial and temporal patterns of fires shift, the composition and richness of an ecosystem's flora and fauna likely change in response. In many ecosystems, including the dry forests of the western United States, departures from the historical fire regimes due to past and ongoing forest management and climate change are pervasive (Collins et al., 2016; Margolis et al., 2022; Stephens et al., 2007; Williams et al., 2023). The effects of long-term fire exclusion and recent large and severe wildfires in many western U.S. landscapes are especially widespread, resulting in major changes in the structure, composition, and function of ecosystems throughout the region (Hagmann et al., 2021; Safford et al., 2022; Seidl & Turner, 2022). As a result, few contemporary reference areas characterized by the full range of historical fire patterns remain, limiting our ability to observe the entirety of fire's impact on biodiversity and inform successful conservation management.

Fire predominantly affects populations and biodiversity indirectly through alterations of the abiotic or biotic habitat conditions (Turner et al., 1998). Whether such changes are beneficial or detrimental to individual species or assemblages is dependent on the spatial, temporal, and magnitude characteristics of one or multiple fires (van Wagtendonk et al., 2018). Often, fire-induced changes benefit species associated with early-successional conditions to the detriment of those dependent on mature forests (Taillie et al., 2018). Repeated fires create both a visible mosaic represented by changes evident from the most recent disturbance and an invisible mosaic where physical or biological legacies from prior disturbances persist and may continue to influence biological communities (Brown & York, 2017). When biodiversity is sensitive only to the visible mosaic and successional processes following the most recent disturbance, we may consider the ecological memory of the biological community to be low. In contrast, if the invisible mosaic that includes disturbance characteristics from previous events drives community dynamics, the level of ecological memory in the system would be considered high (Johnstone et al., 2016). Further, groups of species with different life history characteristics (e.g., sessile plants vs. highly vagile bats) respond to environmental heterogeneity at different spatial scales. Maximizing the variation in fire regime characteristics (i.e., pyrodiversity) is a promising approach for accommodating species with diverse responses to fire (Martin & Sapsis, 1992; Steel et al., 2024). However, theory and mixed empirical support globally suggest that the hypothesis that pyrodiversity begets biodiversity is not universally true or is nonlinear (Jones & Tingley, 2022). For example, high levels of pyrodiversity may result in habitat fragmentation to the detriment of species that need large patch sizes (He et al., 2019). More generally, for ecosystems that historically had low levels of pyrodiversity, the native ecological community may not be adapted to conditions of high pyrodiversity (Steel et al., 2024).

Conservation and restoration ecology often use historical reference conditions to inform ecosystem management targets and improve ecological integrity (McClenachan et al., 2024). Ecological integrity is defined by Wurtzebach and Schulz (2016) as "The ability of an ecological system to support and maintain a community of organisms that has species composition, diversity, and functional organization comparable to those of natural habitats within a region." The use of "natural" or "historical" (when including Indigenous stewardship) targets inherently assumes that ecological integrity is maximized or at least achieves high levels under conditions in which species evolved and communities assembled prior to broad ecological changes associated with Euro-American colonization and global change (Wiens et al., 2012). However, this predominant assumption is often untested.

Directly testing what fire regime conditions maximize biodiversity and ecological integrity is often challenged by filtering bias where only a portion of the relevant environmental variation is observed due to dramatic shifts from historical conditions (Prichard et al., 2017). In historically frequent-fire forests (fire return interval <35 years) of the western United States, widespread timber harvest of large, fire-resistant trees and a century of exclusion of Indigenous burning and fire suppression have led to high forest density and reduced landscape heterogeneity (Eisenberg et al., 2024; Lydersen & Collins, 2018). The resulting fuel buildup plus a warming climate are driving uncharacteristically large and severe megafires (Stephens et al., 2022; Williams et al., 2023). Consequently, much of the fire and biodiversity research to date has focused on landscapes of extremes composed of forests in great deficit of fire and areas recently affected by these megafires (e.g., Steel et al., 2019; Tarbill et al., 2023). Fire ecology and conservation science are left with few intact reference sites in which to test the assumption that historical conditions are equivalent to high ecological integrity and a full relationship between fire and biodiversity. Further, managing for historical conditions is increasingly challenging given the large discrepancies between historical and contemporary climate. Understanding the conditions that maximize biodiversity is an important step in defining a desired range of variability and in determining whether such desired conditions differ from historical references and whether either target is feasible under shifting disturbance regimes (Jackson & Hobbs, 2009).

For the past several decades, federal land management agencies in the western United States have used managed wildfires (i.e., naturally ignited fires managed primarily for resource benefits in predetermined areas) to reduce hazardous fuels and restore fire as an essential and natural ecological process (van Wagtendonk, 2007). Recent policy changes (i.e., 2009 Guidance for Implementation of Federal Wildland Fire Management Policy) have increased the number of managed wildfires, but the total burned area remains largely unchanged because the practice is constrained to a select number of wilderness areas and remote landscapes in the western United States (Iniguez et al., 2022; Young et al., 2020). Yet, in these wilderness areas, the repeated use of this fire management strategy has been successful at reestablishing frequent-fire regimes, restoring ecosystems, building resilience to subsequent fires, and achieving a broad range of fire histories and pyrodiversity (Miller & Aplet, 2016; Steel et al., 2021; Stephens et al., 2021; van Wagtendonk, 2007). Additionally, these pyrodiverse landscapes serve as contemporary reference areas that can either supplement or refine historical understanding, particularly at larger landscape scales where quantitative historical information is often lacking (Meyer, 2015). For our purposes, these landscapes also provide the best available opportunity to test the impacts of a wide range of fire histories on the diversity of multiple taxonomic groups.

To identify optimal wildfire characteristics for biodiversity, we leverage 2 wilderness areas in the Sierra Nevada of California that are the subject of a long-term experiment of restoring the historical frequent-fire regime of the region. By analyzing multiyear biodiversity survey efforts in these areas, we considered the following questions: how do the taxa respond to different spatial scales, levels of ecological memory, and measures of pyrodiversity (Question 1); how does bird, plant, and bat species richness vary across gradients of burn severity, fire frequency, and pyrodiversity (2); and how does the fire regime that

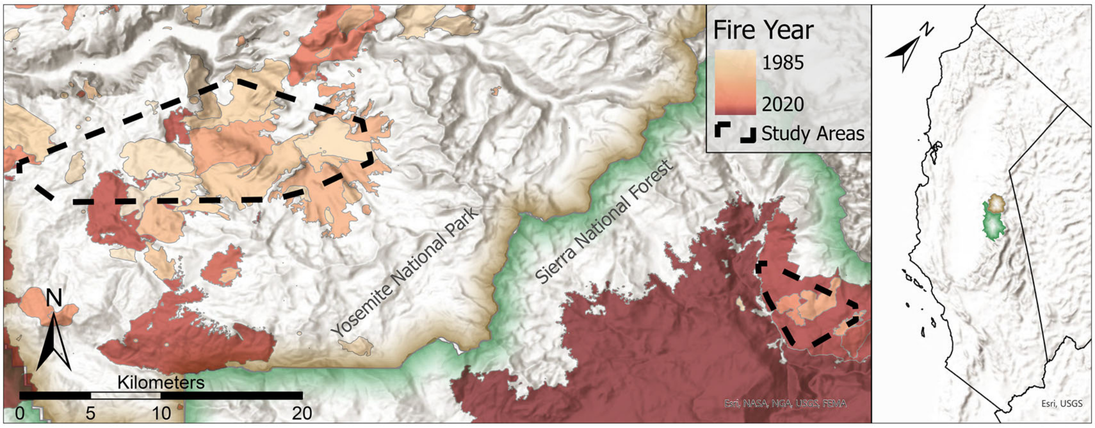

FIGURE 1 Yosemite National Park (brown boundaries) and Sierra National Forest (green boundaries) study areas in the Sierra Nevada of California, USA. Polygons of fires between 1985 and 2020 are shown to illustrate the fire history of the area.

supports the greatest total species richness compare with historical fire regime (3)?

METHODS

Study areas

Our study areas included 2 landscapes managed as wilderness in the Sierra Nevada of California (USA) (Figure 1). The first study area was in Yosemite National Park and included a watershed where managed wildfire has been employed since the 1970s and a contiguous area with long-unburned patches. The second study area was to the southeast in the Ansel Adams Wilderness in the Sierra National Forest, where the use of managed wildfire for resource benefit was implemented starting in 2003.

Survey locations in the Yosemite study area had 0–4 fires since 1985. Locations in the Sierra National Forest study area had one or 2 fires during this time, most notably the 2018 Lion's Fire (Figure 1). Study areas were primarily composed of Jeffrey pine (*Pinus jeffreyi*), mixed conifer, and red fir (*Abies magnifica*) forests intermixed with patches of meadows and shrublands. Before Euro-American colonization, fire regimes of yellow pine (including *P. jeffreyi* and *P. ponderosa*) and mixed conifer forests were characterized by frequent fires (5- to 15-year return intervals), primarily of low to moderate severity. High severity patches were estimated to occur over 8% of the landscape on average in a salt-and-pepper pattern in which patch sizes were typically small (Collins & Stephens, 2010; Safford & Stevens, 2017). In comparison, red fir forests (occurring above the mixed conifer zone) historically supported moderately frequent-fire regimes (40- to 50-year mean return intervals) that burned primarily at low to moderate severity. On average, 11% of burn areas were of high severity (Meyer & North, 2019). Relative to contemporary fire-suppressed forests, managed wildfires in these landscapes have resulted in increased fire frequencies, greater structural and landscape heterogeneity, reduced fuels, improved watershed function, and forest structural features similar to historical conditions (Boisramé et al., 2017; Collins et al., 2016; Meyer & North, 2019).

Biodiversity surveys and environmental data

Bird, plant, and bat surveys were conducted during the summers of 2021 and 2022 in both study areas. Plant surveys conducted in 2012 in Yosemite with the same sampling method were also included. The bird community was surveyed using a 5-min point count protocol in which experienced observers recorded each detected individual bird and its initial distance from the point center (Ralph et al., 1993). Morning surveys were conducted during the peak breeding season (late May to early July) in both years, and repeat surveys were conducted by different observers, where possible, to reduce the likelihood of observer bias. The plant community was sampled by a trained botanist using a timed area search where all plant species were identified when possible. Bat surveys were conducted using acoustic recording units (SMMBAT—Wildlife Acoustics) with microphones that provide full-spectrum recordings of bat echolocation calls. Recorded calls were classified using SonoBat 4.3 and the western regional library. SonoBat-corrected counts were used to determine whether a species was observed during each survey night. Corrected counts exclude low-quality or ambiguous calls to minimize misclassifications. Recording units were elevated approximately 2 m above the ground and were located away from immediate sources of clutter (e.g., branches) and sound-reflective surfaces that might distort recordings. Detectors were deployed for approximately 2-week survey periods from May to September, recording each night.

An interagency fire perimeter database was used to calculate fire frequency (https://www.fire.ca.gov). Burn severity as measured by the composite burn index (CBI) was estimated using Google Earth Engine (Gorelick et al., 2017) and the Parks et al. (2019) model. Pyrodiversity was calculated as the functional dispersion of severity, frequency, and patch size across the local landscape. Functional dispersion is similar to the median absolute deviation statistic when applied to a single variable but can be calculated for multiple variables (up to 3 in our case) with equal or differing variable weights (Laliberté & Legendre, 2010). To test the relative importance of different aspects of the fire regime when calculating pyrodiversity, functional dispersion was calculated using all unique combinations (10 total) of severity, frequency, and patch size with weights of 0%, 33%, 67%, or 100%. Elevation, which correlates with species distributions (Siegel et al., 2011), was extracted using the elevatr R package (Hollister & Shah, 2017). Patches of distinct fire effects were defined by discretizing fire severity into 4 classes—unchanged, low, moderate, and high—based on thresholds defined by Miller and Thode (2007) for each fire year. Patch size was subsequently calculated in log hectares. Habitat structural characteristics and soil type were collected in the field at each survey point as local model covariates.

Fire regime variables were summarized at different spatial extents (radius size) and levels of ecological memory. Ecological memory, or the strength of the invisible matrix, was measured as the relative weight of fire characteristics of burns that occurred prior to the most recent event. When calculating fire regime traits, values are often averaged across the period of record (100% memory) or values from only the most recent disturbance are used (0% memory). For example, fire frequency can be calculated as the mean interval between all recorded fires or as the time since the last fire, respectively. In addition to these extremes, intermediate levels of ecological memory can be calculated using a recency-weighted average where the weight of older fires decays in order (Steel et al., 2021).

Site selection

We sought to sample evenly across the range of fire regime characteristics represented in our study area. Initially, a 250-m grid of potential sample sites was created across the Yosemite and Sierra National Forest Wilderness areas for 2021 and 2022 surveys. For each grid point and the existing 2012 Yosemite plant survey locations, values were calculated for fire return interval, severity, and severity class patch size of the most recent fire. For each point, the mean and standard deviation of each variable were calculated within 500 m. The point elevation and dominant forest type were also extracted. These values were used to characterize the multidimensional environmental space of the potential sample point population. Starting with all potential points (n), functional evenness was calculated using the FD R package (Laliberté & Legendre, 2010), where each environmental variable was considered a functional trait. Each individual point was then removed from the sample population, and functional evenness was recalculated for the $n - 1$ subpopulation. The removed point for which the $n - 1$ sample population had the highest evenness value was dropped, and the removal process was repeated i times until $n - i$ was sufficiently small that functional evenness could no longer be calculated (i.e., when the number of traits considered exceeded the sample population size). The reverse point drop order was used as the site sample priority so that data collection maximized the sampled environmental heterogeneity across the variables of interest (Appendix S1). This prioritization process was done separately for each study taxa. For birds, the drop process was done at the transect level where all points in a transect were dropped together. The 2012 plant surveys followed a systematic sampling design that stratified across forest type and number of previous fires.

During the 2012, 2021, and 2022 survey seasons, unique survey locations totaled 313 for birds, 144 for plants, and 53 for bats. Of these, 304 bird, 28 plant, and 5 bat locations were sampled in 2 of the survey years, with the remaining locations surveyed in only one year. On average, bird locations were surveyed 1.3 times in a season, and bat locations were surveyed during 9.2 nights per season to aid in detection rate estimation. The elevational range of all sample points was 1854–2696 m. Points had experienced 0–4 fires since 1985. For those points that had at least one burn, the mean time since last fire was 16 years. The full range of fire severity was sampled, from unburned to high severity (0–3 CBI). No points included 100% high severity within 1000 m, which resulted in CBI values of <3 mean severity at broader spatial scales.

Statistical analyses

Our study objectives required models that maximized predictive performance and statistical inference. Because these 2 goals often require different model structures (McElreath, 2016), we fit 2 classes of models for each taxa, hereafter referred to as *prediction* and *inference* models. Specifically, prediction models were used to assess how different taxa respond to variable spatial scales, levels of ecological memory, and measures of pyrodiversity (Question 1). Inference models were used to test fire effects on species richness (Question 2). Prediction models were also used to compare fire regimes in areas of high species richness to our reference landscapes overall (Question 3). The analyses were carried out in 3 steps (prediction model selection, inference model fitting, and spatial predictions and comparison) described below and visualized in Appendix S2.

Prediction models were fit first and were used to compare different spatial scales and levels of ecological memory. In the case of birds and bats where detection rates were imperfect, we fit multispecies occupancy models (MSOMs) consisting of occurrence and detection submodels with the spOccupancy R package (Doser et al., 2022). Observation data are binary, and $y_{s,i,j} = 1$ when species s was detected at point i and survey j, or $y_{s,i,j} = 0$ when a species was not detected. For birds, replicate surveys j consisted of one or 2 visits per year. For bats, each recording night was considered a replicate survey for a point. We assumed the detection–nondetection data arose from a Bernoulli process:

$$y_{s,i,j} \sim \text{Bernoulli}\left(p_{s,i,j} Z_{s,i}\right),$$

$$\text{logit}\left(p_{s,i,j}\right) = \mathbf{v}_{s,i,j}\ \mathbf{ff}_s, \tag{1}$$

where $p_{s,i,j}$ is the probability of detecting species s at site i during replicate j. Detection probability was modeled as a function of site or replicate covariates $\boldsymbol{\nu}$ and species-specific coefficients $\boldsymbol{\alpha}_s$. The latent occurrence variable Z_s is assumed to arise from a Bernoulli process:

$$Z_{s,i} \sim \text{Bernoulli}\left(\Psi_{s,i}\right), \tag{2}$$

$$\text{logit}\left(\Psi_{s,i}\right) = \mathbf{x}_i \mathbf{fi}_s,$$

where $\Psi_{s,i}$ is the probability of occurrence of species s at site i. This was modeled as a function of site-specific covariates $\boldsymbol{\chi}$ and species-specific coefficients $\boldsymbol{\beta}_s$. Regression parameters $\boldsymbol{\alpha}_s$ and $\boldsymbol{\beta}_s$ were estimated as random effects arising from community-level distributions.

Occurrence covariates $\boldsymbol{\chi}$ included the fire regime measures of pyrodiversity, burn severity, fire frequency, patch size, and mean elevation of a site. Linear and quadratic terms were included for these variables, allowing the models to find occurrence optima or nadirs. Because many sites were sampled in both study years, point identity (ID) was included as a random effect, as we expect occurrence rates to be similar between survey years at the same location. This can be considered a correlative multiseason model because we did not model extinction and colonization rates as is done in dynamic multiseason models. Bird occurrence covariates also included transect ID as a random effect to account for the spatial structure of our sampling design. Detection covariates ($\boldsymbol{\nu}$) for the bird model included Julian day (and its quadratic), time of day, canopy cover, and shrub cover. The bat detection covariates included Julian day (and its quadratic), mean temperature during the sampling night, a measure of noise during the sampling night (number of recordings of bat passes/number of triggered recordings), lunar illumination during the sampling night (calculated using the Lunar R package; Lazaridis, 2022), site canopy cover, and shrub cover. For the plant prediction models, we fit a generalized linear model with site species richness as the response variable and a Poisson error structure. We included the same fixed effects as the MSOM occurrence submodels above as predictors, plus point ID and soil type (sensu Wilkin et al., 2021) as random intercepts.

We used a model selection approach to test whether prediction of richness was sensitive to spatial scale and ecological memory. For spatial scale, we fit models for each taxa that varied by the radius in which predictors were summarized (100, 500, and 1000 m). Additional spatial scales were subsequently added for the plant (50-m radius) and bat (2500-m radius) model sets to ensure the optimal scale for each was included within the range of radii tested. Fire covariates were also calculated at 3 levels of ecological memory where values from only the most recent fire were included (0%, full amnesia), the weight of older fires decayed by 50%, and all overlapping fires at a pixel received equal weight (100%, perfect memory). Models were also fit for each of the 10 versions of the pyrodiversity metric, resulting in a total of 90 (birds) or 120 (plants and bats) candidate models per taxa. Each candidate model was fit with 5-fold cross-validation (with consistent folds across model runs) to calculate out-of-sample predictive performance. When running cross-validation for the MSOMs and plant models, we followed the recommendations of the spOccupancy and BRMS packages, respectively. As such, for MSOM cross-validation, we used deviance as the scoring rule (Doser et al., 2022). For the plant models, we used a k-fold information criterion score (Bürkner, 2017). All model scores are included in the associated github repository (link below). The best-performing predictive models were used to identify the optimal spatial scale and level of ecological memory (Question 2).

A second set of models were fit specifically for inferring the influence of burn frequency, severity, and pyrodiversity on species richness. These inference models differed from the predictive models in 2 ways. First, to avoid statistical confounding of related fire regime metrics, separate models were fit for each of the 3 fire regime metrics of interest (linear and quadratic terms), and potentially confounding fire regime metrics were excluded a priori. For example, when seeking to test the effect of fire frequency on species richness, fire severity was excluded as it would constitute a posttreatment effect (Grace & Keeley, 2006) because the probability of severe fire increases with time since fire (Steel et al., 2015). Second, the bird and bat inference models used estimates of species richness with fully propagated uncertainty calculated from MSOM posteriors of each species' predicted occurrence rates as part of a 2-step MSOM (Steel et al., 2022; Tingley et al., 2016). Specifically, for each sample point, the model response included the mean and standard deviation of MSOM-estimated richness as parameters in a measurement error model run with the BRMS R package (Bürkner, 2017). To test the sensitivity of the pyrodiversity effect to different trait weights, models were run for each of the 10 pyrodiversity metrics, and the linear effect estimates were compared for each taxon. The pyrodiversity metric with the highest absolute effect was included in the final inference model that also included a quadratic term to allow for pyrodiversity optima or nadir. Inference models had predictor variables calculated with the scale and level of ecological memory selected through cross-validation of the predictive models. For all models, continuous covariates were scaled with a mean of 0 and a standard deviation of 1.

The best-performing predictive models were also used to make spatially explicit predictions of species richness with respect to fire across our study area based on the realized fire conditions as of 2020 (Question 3). Elevation was kept at its mean value; thus, predictive surfaces were conditional on the fire histories only. Predicted species richness was normalized from 0 to 1, where 1 represented the maximum predicted value for a taxon. The 3 normalized richness rasters were summed to create an index of multitaxa richness ranging from 0 to 3. Fire variable values were extracted from the 20% most speciose pixels (i.e., richness hotspots) to assess the fire conditions expected to create the highest overall richness. The distribution of burn severity, frequency, and pyrodiversity in these richness hotspots was compared with the available landscape as determined by the geographic convex hull of sample points. Additionally, we quantified under which fire regime conditions hotspots occurred more often than would be expected from a random sampling of the study areas by calculating the difference in the proportion of each fire characteristic distribution in 6 quantiles between the available landscape and the hotspot areas.

Spatial autocorrelation is a potential problem, especially for wide-ranging species, such as birds and bats. To minimize statistical challenges associated with spatial autocorrelation, we made the following adjustments: large-ranging birds, such as raptors, were excluded from the analysis; avian point count transect ID was included as a random effect to model any residual correlation among clustered point count locations; cross-validation was used to compare different spatial scales rather than information criteria approach, which can be sensitive to shared predictor information when broadscale radii (e.g., 1000 m) around sample points overlap; and bat survey locations were spaced farther apart than plants and birds (approximately 500 m at minimum). Proper mixing of model sampling chains was checked using traceplots, and community-level parameter estimates had R-hat values of <1.1, indicating convergence. Posterior predictive check Bayesian p values (spOccupancy models) and visualizations (BRMS models) indicated adequate fit. All analyses were conducted in the R statistical environment (R Core Team, 2024). Code and data are available at https://github.com/zacksteel/FireBioOptima.

RESULTS

Spatial scale and ecological memory

The best-performing predictive models for each taxa showed that plants responded to fire effects at fine scales, whereas bird and bat communities responded to fire at increasingly broad scales (Appendix S3). The highest performing plant model included variables summarized within a 100-m radius, although models trained on 50-m radii performed nearly as well. The best-performing bird models included predictor variables summarized within a 500-m radius, and the best bat models included predictor variables summarized within a 1000-m radius. When considering different levels of ecological memory, the best plant and bird models included information on only the most recent fire event (0% memory), and the top bat model included equal weighting of all past fire events (100% memory) (Appendix S3).

Pyrodiversity effects

The linear relationship between species richness and pyrodiversity was highly sensitive to the choice of fire regime component included in the pyrodiversity metric. Of the 10 versions of pyrodiversity assessed for each taxa, the majority had positive relationships with species richness as well as some instances of negative or neutral effect estimates. In the case of birds, 5 pyrodiversity effects were positive, 3 were negative, and 2 had 95% credible intervals (CIs) that included 0, indicating weak or imprecise effect estimates (Figure 2a). The strongest absolute effect of pyrodiversity for birds was positive and represented by a functional dispersion metric composed of two-thirds severity and one-third frequency ($\beta_{\mathrm{fdis}} = 0.896$, 95% CI 0.645 to 1.143). The strongest negative effect of pyrodiversity for birds was composed of 100% fire frequency ($\beta_{\mathrm{fdis}} = -0.652$, 95% CI −0.863 to −0.420). In the case of plants, 8 out of 10 pyrodiversity effects were positive, and 2 showed weak or uncertain effects (Figure 2b). The strongest absolute pyrodiversity effects were positive and came from 2 metrics composed of two-thirds severity and one-third frequency and a fully balanced version (one-third severity, frequency, and patch size) ($\beta_{\mathrm{fdis}} = 0.102$, 95% CI 0.068 to 0.137). No pyrodiversity metric resulted in a clear negative effect on plants. For bats, 6 out of the 10 tests of pyrodiversity showed positive effects, one negative, and 3 weak or neutral effects (Figure 2c). The strongest absolute effect was positive, resulting from a functional dispersion metric composed of two-thirds patch size and one-third frequency ($\beta_{\mathrm{fdis}} = 0.852$, 90% CI 0.548 to 1.145). The strongest negative effect on bats was a pyrodiversity metric composed of 100% burn severity ($\beta_{\mathrm{fdis}} = -0.642$, 95% CI −0.954 to −0.313).

Species richness and fire regime traits

Our inference models showed clear responses of birds, bats, and plants to different aspects of the region's fire regime and often indicated peaks or nadirs at certain levels of severity, frequency, and pyrodiversity. The 3 taxa responded quite differently to burn severity. Bird richness peaked at moderate levels (approximately 1.5 CBI), as estimated by positive linear ($\beta_{\mathrm{sev}} = 1.384$, 95% CI 1.077 to 1.699) and negative quadratic ($\beta_{\mathrm{sev2}} = -1.107$, 95% CI −1.351 to −0.858) parameters. Plant richness declined as fire severity increased ($\beta_{\mathrm{sev}} = -0.069$, 95% CI −0.121 to −0.017), and bat richness showed a U-shaped response ($\beta_{\mathrm{sev2}} = 0.641$, 95% CI 0.126 to 1.129). The lowest bat species richness was expected at low to moderate severity sites (approximately 1 CBI) (Figure 3a; Appendices S4 & S5). Species richness declined as years since fire increased for birds ($\beta_{\mathrm{freq}} = -1.646$, 95% CI −2.000 to −1.259) and plants ($\beta_{\mathrm{freq}} = -0.187$, 95% CI −0.231 to −0.143). For the bird and plant models, frequency was equivalent to years since fire because the models were fit with 0% ecological memory. Bird richness leveled off after approximately 25 years since fire, reflecting a positive quadratic term ($\beta_{\mathrm{freq2}} = 1.874$, 95% CI 1.450 to 2.323). The bat model showed the opposite effect, with species richness expected to increase as fire return intervals lengthened ($\beta_{\mathrm{freq}} = 1.218$, 95% CI 0.657 to 1.743) (Figure 3b). The effect of pyrodiversity was positive for final models of all 3 taxa with no indication of a pyrodiversity maxima. Quadratic parameters were also positive for both birds ($\beta_{\mathrm{fdis2}} = 0.237$, 95% CI 0.034 to 0.435) and bats ($\beta_{\mathrm{fdis2}} = 0.637$, 95% CI 0.319 to

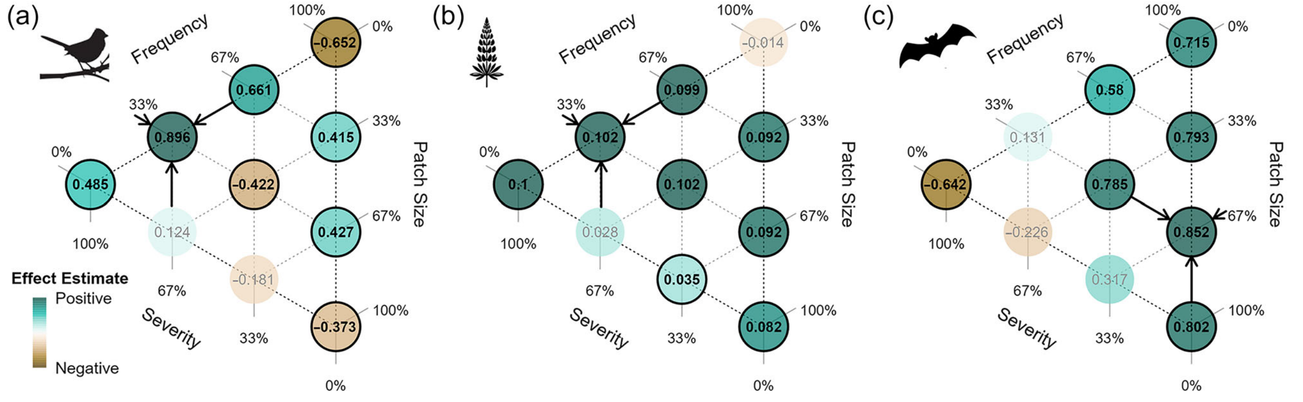

FIGURE 2 Linear effect estimates of different pyrodiversity metrics for (a) birds, (b) plants, and (c) bats. Circle position along the three axes indicate the relative weight of the severity, frequency, and patch size in the three-trait measure of functional dispersion. Arrows point to the largest absolute effect for each taxa; bold numbers and circle outlines indicate estimates where 95% credible intervals do not include zero. For example, the strongest pyrodiversity effect for birds is a metric that is weighted 67% severity (reading up from the bottom axis), 33% frequency (from the top axis), and 0% patch size (from the right axis). Models were fit using the scale and level of ecological memory for each species identified during the cross-validation process.

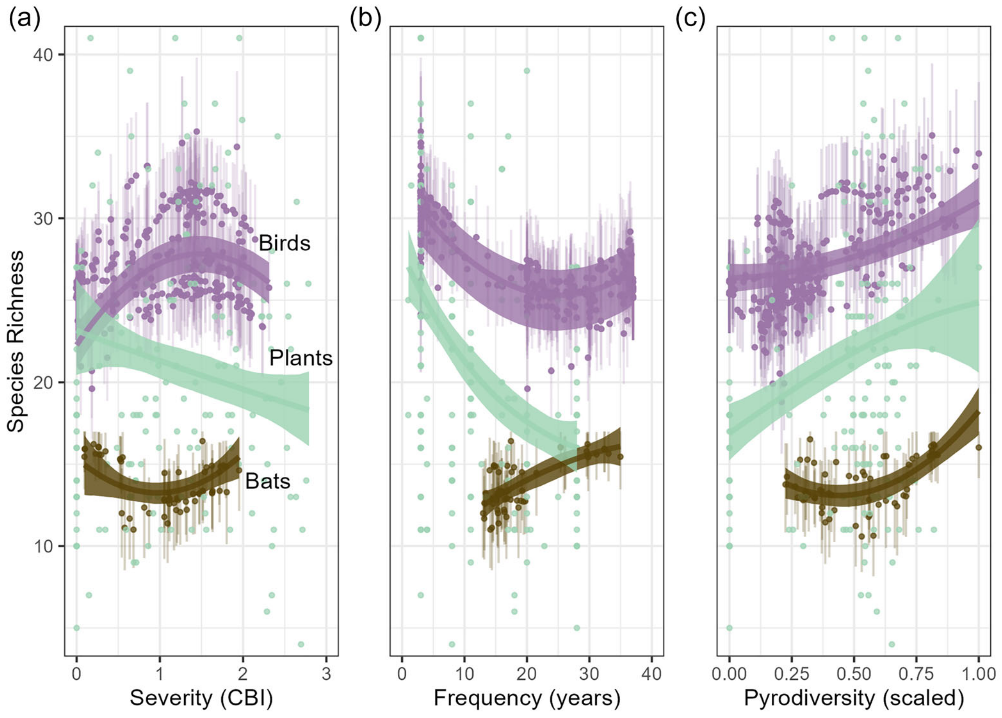

FIGURE 3 Marginal effects of (a) mean burn severity, (b) mean burn frequency, and (c) pyrodiversity (scaled from 0 to 1) for the final bird (purple), plant (green), and bat (brown) inferential models. The bird and plant models are fit with predictors for which values are from the last fire (i.e., frequency is equal to years since fire). The bat model was fit with predictors representing the mean of all fires since 1985 (i.e., frequency is equal to the mean fire return interval). For birds and bats, points represent the median and lines the 95% prediction intervals of richness from the final multispecies occupancy model.

0.949), indicating increasingly positive effects at higher levels of pyrodiversity (Figure 3c; Appendix S5).

Areas of high overall species richness with respect to fire regime conditions showed clear spatial clustering across our 2 study areas (Figure 4a,b). The richness hotspots largely encompassed low to moderate severity fire areas (Figure 4c). The median and interquartile range of this optimal severity for biodiversity (CBI median = 1.36, IQR = 0.53–1.9) was higher than the landscapes overall (CBI median = 0.86, IQR = 0–1.61). Hotspots occurred less often in unburned areas or areas of very low severity fires and more often in moderate severity areas than would be expected by random chance (Figure 4d). Thirteen percent of hotspots fell in high severity (CBI > 2.24) fire areas, which was somewhat higher than the full landscape (9%) and historical mean estimates for yellow pine and mixed conifer (8%) and red fir (11%) forests (Meyer & North, 2019;

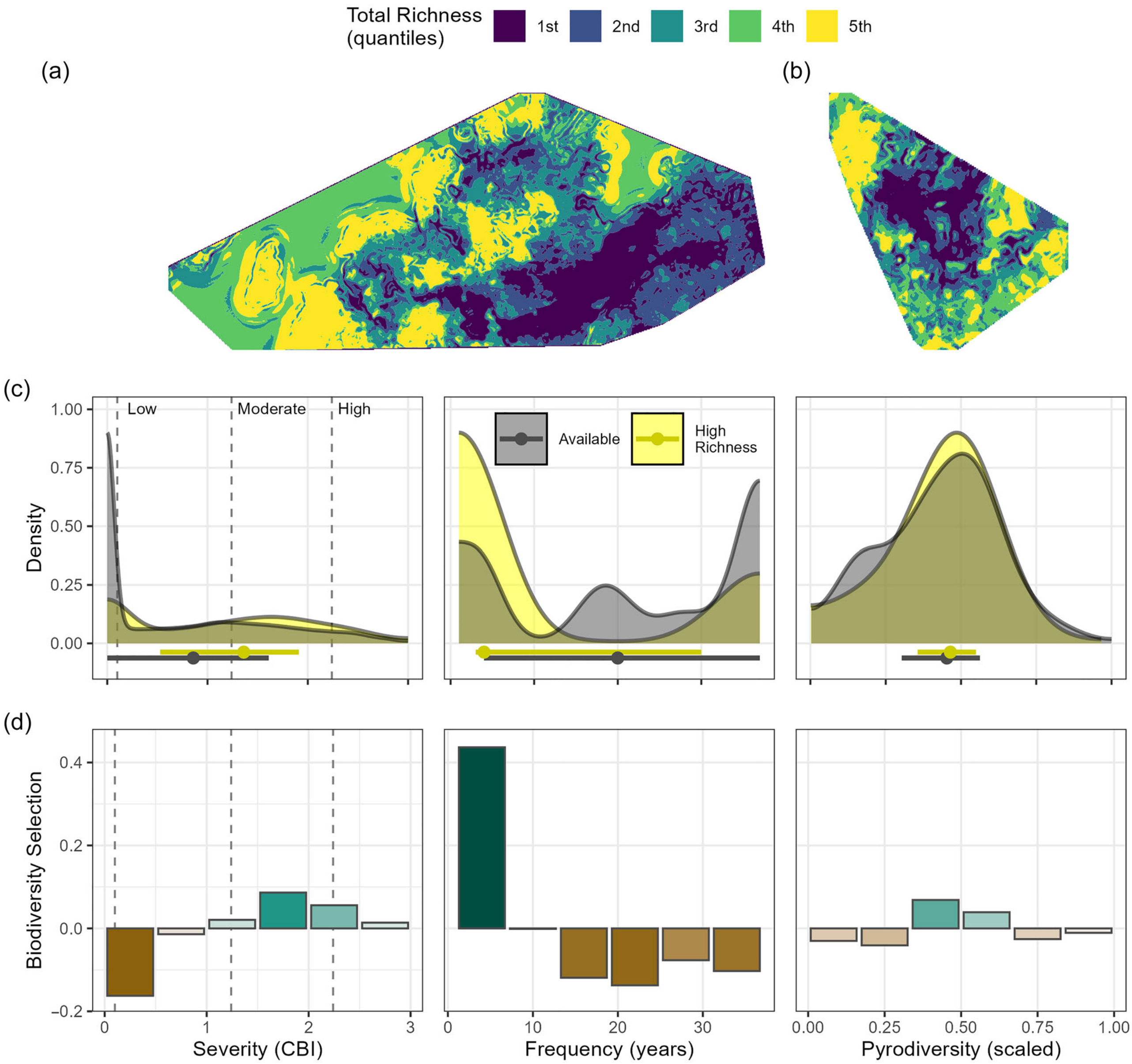

FIGURE 4 Total species richness across study areas in (a) Yosemite National Park and (b) Ansel Adams Wilderness area; (c) density distributions of burn severity, frequency, and pyrodiversity (i.e., frequency of each fire regime characteristic) across the combined study areas (gray) and the species richness hotspots (yellow) (top 20% of pixels) (bars and points represent interquartile ranges and medians of each distribution); and (d) biodiversity hotspot selection relative to available fire regime conditions (brown, hotspots occurred less often than random [negative values]; green, hotspots occurred more often than random [positive values]; vertical dashed lines indicate composite burn index [CBI] severity level cutoffs).

Safford & Stevens, 2017). The richness hotspots primarily fell in recently burned areas (median = 4 years, IQR = 1–30). This was far more often than was typical across the study areas (median = 20 years, IQR 1–37) and historical estimates of 5- to 15-year return intervals for yellow pine and mixed conifer and 40–50 years for red fir forests (Meyer & North, 2019; Safford & Stevens, 2017). Although some hotspots were found in areas that had not burned in at least 30 years, this occurred less often than expected given a random sample. Areas with moderate burn frequency did not contain any richness hotspots (Figure 4c,d). Pyrodiversity in hotspot areas (median normalized value = 0.46, IQR = 0.36–0.55) was largely characteristic of the landscape overall (median = 0.45, IQR = 0.30–0.56), but pyrodiversity in hotspots had a slightly more constricted range.

DISCUSSION

Our results revealed complex relationships between fire regimes and biodiversity in California's Sierra Nevada and highlight some important differences between reference conditions and areas of realized species richness optima. This work builds on earlier studies by examining how multiple taxa respond to complex fire patterns across multiple scales. Biodiversity responses to fire varied among birds, plants, and bats, underscoring the challenges in managing fire for multiple taxa simultaneously, especially under a changing climate and fire regimes. Both bird and plant richness peaked in recently burned areas, although birds benefited from moderate severity fire, whereas plant richness declined with increasing fire severity. In contrast, bat richness was maximized in areas with longer fire return intervals and was lowest in areas dominated by low Past research has shown severity fire. Pyrodiversity was beneficial for all 3 taxa, suggesting a focus on variation in fire history may present a broadly successful conservation strategy. Predicted biodiversity hotspots occurred in somewhat more frequently and severely burned areas than was typical across the 2 reference landscapes and relative to historical estimates.

Variable fire impacts on biodiversity

The variable responses to fire among birds, plants, and bats reflect their distinct life histories and habitat requirements. For birds, the preference for recently burned areas with moderate severity and high pyrodiversity likely reflects the diverse nesting and foraging requirements of different bird species (Taillie et al., 2018; Tingley et al., 2016). These fire conditions create a mix of open forest and early-seral vegetation, including meadows and montane chaparral, as well as diverse structures that simultaneously support species associated with live canopy, cavities excavated from snags, and understory vegetation (Beedy & Pandolfino, 2013; Roberts et al., 2021). Plants showed a similar preference for recently burned areas, which may be attributed to reduced competition and increased resource availability following fire (Bond & Wilgen, 2012). However, the negative relationship with burn severity indicates that extreme fire events can be detrimental to plant diversity, particularly as time since fire increases (Weeks et al., 2023). This result contrasts somewhat with previous studies that showed a moderate severity peak in similar forests (Richter et al., 2019). One clear difference is that Richter et al. (2019) examined single, full-suppression wildfires (i.e., forests burned once following a period of long-term fire exclusion) compared with the pyrodiverse landscapes of this study. Bat preference for areas with longer fire return intervals and depressed richness levels in low-severity areas presents an interesting contrast to the other 2 taxa. Past research has shown a positive relationship between burn severity and bat richness—with the lowest diversity in unburned areas (Steel et al., 2019). Steel et al. (2019) hypothesized that fire suppression and subsequent forest densification decrease habitat quality to an extent that even "clutter-adapted" bat species prefer more disturbed areas. Unburned areas in our current study area were embedded in a more pyrodiverse landscape and forests that had not experienced extensive harvest of large trees, as is common outside of wilderness areas (Collins et al., 2017), potentially making these old-growth forests more appealing bat habitat than unburned forests elsewhere. The bimodal peak in bat richness here likely better reflects the diversity of bat functional groups that forage and roost in both open- and closed-canopy forested habitats (Blakey et al., 2019, 2021).

Our results support the pyrodiversity–biodiversity hypothesis (Martin & Sapsis, 1992; Steel et al., 2024). Although we found positive relationships between pyrodiversity and species richness across taxa, the specific components of fire regimes that drove these relationships varied. This highlights the importance of considering multiple aspects of fire history when assessing pyrodiversity's effects on biodiversity (Steel et al., 2021; Wilkin et al., 2021) and hints at one reason the observed effect of pyrodiversity varies among studies in the literature (Jones & Tingley, 2022). We found little evidence of diminishing returns or negative impacts of high levels of pyrodiversity, contrary to some previous hypotheses (He et al., 2019). This suggests that in our study areas, which have a wide range of fire conditions, even high levels of pyrodiversity continue to benefit biodiversity. However, this relationship may not hold true for all taxa or in landscapes not adapted to frequent fire or in landscapes with substantial habitat loss (Jones & Tingley, 2022).

Our analyses revealed important differences in how birds, plants, and bats respond to spatial scale and ecological memory. Predictive model performance improved with increasingly broader spatial scales for plants, birds, and bats, respectively. This ordered result aligns with the life histories of these taxa. Plants, being sessile, are most affected by local fire conditions (Wilkin et al., 2021). Birds and bats, being mobile, respond to habitat features across broader landscapes, with bats showing the largest scale of response. The concept of ecological memory, or the lasting effects of past disturbances, also varied among taxa. Plants and birds showed little sensitivity to fires prior to the most recent event, suggesting a relatively limited memory of fire effects. In contrast, bat models performed best when incorporating the full fire history, indicating a stronger ecological memory. This may reflect the importance of habitat features created by earlier fires, such as high-quality snag or injured tree roost sites, which maintain or increase in value through subsequent burns (Campos et al., 2020; Loeb & Blakey, 2021).

We tested fire regime components, which are indirect drivers of biodiversity. Many factors determine habitat quality, including vegetation structural and compositional characteristics. These characteristics are directly influenced by fire, but they are also a product of the underlying edaphic and biophysical environment (Collins et al., 2016). The ability to manage for conditions that optimize biodiversity would benefit from additional studies assessing these direct drivers—perhaps by taking advantage of advances in remotely sensed data acquisitions (lidar, Unmanned Aircraft System imagery). Further, to gain a fuller understanding of ecological integrity, other aspects of biodiversity (e.g., evenness, functional diversity, and beta diversity) should be assessed, along with the responses of individual species of conservation concern (Miller-ter Kuiler et al., 2025).

History as an imperfect surrogate for ecological integrity

Conditions maximizing species richness across the 3 taxa studied represent somewhat more frequent and severe fire patterns than the estimated historical fire regime. These results perhaps represent some good news for biodiversity in this system, as fire regimes are trending toward higher frequency and greater severity. However, much of the recent megafires experienced in fire-suppressed forests overshoot these optima with very large high severity patches that result in low local pyrodiversity and lower biodiversity (Steel et al., 2022), large-scale vegetation type conversion (Guiterman et al., 2022), and diminished ecosystem integrity and services (Stephens et al., 2020). Our results, showing greater bird and plant diversity in recently burned areas, may reflect historical filters of the species pool whereby early successional species are represented by more species-rich clades (Betts et al., 2019). Management efforts that push conditions toward historical targets appear to benefit biodiversity relative to the contrasting landscapes of fire-suppressed forests and megafires that dominate dry forests of the western United States (Fontaine & Kennedy, 2012). However, by examining biodiversity maxima in these landscapes, one can refine and update the understanding of desirable fire patterns beyond what is inferred from historical estimates alone. Importantly, our results and those of others (e.g., Fontaine & Kenney, 2012) suggest that biodiversity conservation may require greater flexibility in fire management, potentially accepting somewhat more frequent and severe fires than occurred historically, at least during initial, first-entry fires (i.e., fires that followed a long period of exclusion) (Meyer, 2015). This is particularly relevant as land management agencies work to reestablish primarily low to moderate severity fire regimes at broad scales and increase the pace of beneficial wildland fire (especially managed wildfires) on the landscape (North et al., 2021; USDA, 2022). Management frameworks that focus on ecosystem resilience and direct measures of biodiversity may be necessary supplements to traditional ecosystem restoration under changing disturbance regimes (Falk, 2017).

Managing frequent-fire forests for biodiversity presents a complex challenge that requires balancing the needs of multiple taxa and practical barriers. Our results indicated that frequent moderate severity fire creating pyrodiverse landscapes maximizes species richness, but this condition alone may not benefit all species. Patches of infrequently burned mature forest embedded in a heterogeneous frequent-fire landscape appear important for part of the montane bat community as well as other mature forest specialists, such as the California spotted owl (*Strix occidentalis occidentalis*) and pacific fisher (*Pekania pennanti*) (Doty et al., 2023; Kramer et al., 2021; Thompson et al., 2021). Frequent moderate severity fire may also appear at odds with other management objectives, including maintaining large amounts of vegetative carbon on the landscape (Bernal et al., 2022) to partially offset fossil fuel emissions and mitigate climate change. However, continued exclusion of fire makes mature forest habitats and carbon stocks increasingly susceptible to loss from severe disturbance (Steel et al., 2023). Managers are faced with the difficult but necessary task of building resilience of mature forests and carbon stocks through the careful use of fire or fire surrogates (Stephens et al., 2024) while minimizing negative impacts on sensitive species (Eisenberg et al., 2024; Halofsky et al., 2024). Our results support continued and expanded use of managed wildfire and a broader acceptance of mixed-severity fire effects in prescribed burning where applicable. Further, pyric landscapes conducive to high biodiversity can be maintained or enhanced in low to moderate severity areas of unplanned wildfires.

Although historical fire regimes provide valuable context, our results demonstrated that tying ecological integrity directly to observed biodiversity optima offers a more nuanced and potentially more effective approach for setting conservation targets. This method allows the adaptation of management strategies to current ecological realities, including changing climate and fire regimes, rather than relying solely on historical estimates that may no longer be achievable or optimal. By embracing this outcome-centric approach to ecological integrity, managers can develop more flexible, data-driven strategies that promote resilient, diverse ecosystems while navigating the challenges of contemporary forest management.

ACKNOWLEDGMENTS

A long list of field technicians contributed to data collection over multiple years. Their hard work and tolerance for long days of hiking and counting made this work possible. This research was funded in part by the California Department of Forestry and Fire Protection (grant 8GG21823).

ORCID

Zachary L. Steel https://orcid.org/0000-0002-1659-3141
Brandon M. Collins https://orcid.org/0000-0002-1282-7502
Scott L. Stephens https://orcid.org/0000-0001-7703-4485

REFERENCES

Beedy, E. C., & Pandolfino, E. R. (2013). *Birds of the Sierra Nevada: Their natural history, status, and distribution*. University of California Press.

Bernal, A. A., Stephens, S. L., Collins, B. M., & Battles, J. J. (2022). Biomass stocks in California's fire-prone forests: Mismatch in ecology and policy. *Environmental Research Letters*, *17*, Article 044047.

Betts, M. G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D. B., Barlow, J., Eigenbrod, F., Faria, D., Fletcher, R. J., Hadley, A. S., Hawes, J. E., Holt, R. D., Klingbeil, B., Kormann, U., Lens, L., Levi, T., Medina-Rangel, G. F., Melles, S. L., … Ewers, R. M. (2019). Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*, *366*, 1236–1239..

Blakey, R. V., Webb, E. B., Kesler, D. C., Siegel, R. B., Corcoran, D., Cole, J. S., & Johnson, M. (2021). Extent, configuration and diversity of burned and forested areas predict bat richness in a fire-maintained forest. *Landscape Ecology*, *36*, 1101–1115.

Blakey, R. V., Webb, E. B., Kesler, D. C., Siegel, R. B., Corcoran, D., & Johnson, M. (2019). Bats in a changing landscape: Linking occupancy and traits of a diverse montane bat community to fire regime. *Ecology and Evolution*, *9*, 5324–5337..

Boisramé, G., Thompson, S., Collins, B., & Stephens, S. (2017). Managed wildfire effects on forest resilience and water in the Sierra Nevada. *Ecosystems*, *20*, 717–732.

Bond, W. J., & van Wilgen, B. W. (2012). *Fire and plants*. Springer Science & Business Media.

Brown, J., & York, A. (2017). Fly and wasp diversity responds to elements of both the visible and invisible fire mosaic. *International Journal of Wildland Fire*, *26*, 434–443.

Bürkner, P-C. (2017). Brms: An R Packagefor Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28.

Campos, B. R., Latif, Q. S., Burnett, R. D., & Saab, V. A. (2020). Predictive habitat suitability models for nesting woodpeckers following wildfire in the Sierra Nevada and Southern Cascades of California. *The Condor*, *122*, Article duz062. https://academic.oup.com/condor/article/122/1/duz062/5696652

Collins, B. M., Fry, D. L., Lydersen, J. M., Everett, R., & Stephens, S. L. (2017). Impacts of different land management histories on forest change. *Ecological Applications*, *27*, 2475–2486.

Collins, B. M., Lydersen, J. M., Fry, D. L., Wilkin, K., Moody, T., & Stephens, S. L. (2016). Variability in vegetation and surface fuels across mixed-conifer-dominated landscapes with over 40 years of natural fire. *Forest Ecology and Management*, *381*, 74–83.

Collins, B. M., & Stephens, S. L. (2010). Stand-replacing patches within a 'mixed severity' fire regime: Quantitative characterization using recent fires in a long-established natural fire area. *Landscape Ecology*, *25*, 927–939.

Doser, J. W., Finley, A. O., Kéry, M., & Zipkin, E. F. (2022). spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, *13*, 1670–1678.

Doty, A. C., Crawford, R. D., & Blakey, R. V. (2023). Bat roosting strategies and torpor expression in a wildfire-affected landscape during summer. *Fire Ecology*, *19*, Article 39.

Eisenberg, C., Prichard, S., Nelson, M. P., & Hessburg, P. (2024). *Braiding Indigenous and western knowledge for climate-adapted forests: An ecocultural state of science report*. https://depts.washington.edu/flame/mature_forests/pdfs/BraidingSweetgrassReport.pdf

Falk, D. A. (2017). Restoration ecology, resilience, and the axes of change. *Annals of the Missouri Botanical Garden*, *102*, 201–216.

Fontaine, J. B., & Kennedy, P. L. (2012). Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecological Applications*, *22*, 1547–1561.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27.

Grace, J. B., & Keeley, J. E. (2006). A structural equation model analysis of postfire plant diversity in California shrublands. *Ecological Applications*, *16*, 503–514.

Guiterman, C. H., Gregg, R. M., Marshall, L. A. E., Beckmann, J. J., Van Mantgem, P. J., Falk, D. A., Keeley, J. E., Caprio, A. C., Coop, J. D., Fornwalt, P. J., Haffey, C., Hagmann, R. K., Jackson, S. T., Lynch, A. M., Margolis, E. Q., Marks, C., Meyer, M. D., Safford, H., Syphard, A. D., … Stevens, J. T. (2022). Vegetation type conversion in the US Southwest: Frontline observations and management responses. *Fire Ecology*, *18*, Article 6.

Hagmann, R. K., Hessburg, P. F., Prichard, S. J., Povak, N. A., Brown, P. M., Fulé, P. Z., Keane, R. E., Knapp, E. E., Lydersen, J. M., Metlen, K. L., Reilly, M. J., Sánchez Meador, A. J., Stephens, S. L., Stevens, J. T., Taylor, A. H., Yocom, L. L., Battaglia, M. A., Churchill, D. J., Daniels, L. D., … Waltz, A. E. M. (2021). Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecological Applications*, *31*, Article e02431.

Halofsky, J. S., Donato, D. C., Singleton, P. H., Churchill, D. J., Meigs, G. W., Gaines, W. L., Kane, J. T., Kane, V. R., Munzing, D., & Hessburg, P. F. (2024). Reconciling species conservation and ecosystem resilience: Northern spotted owl habitat sustainability in a fire-dependent forest landscape. *Forest Ecology and Management*, *567*, Article 122072.

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews*, *94*, 1983–2010.

Hollister, J. W., & Shah, T. (2017). *elevatr: Access elevation data from various APIs*. http://github.com/usepa/elevatr

Iniguez, J. M., Evans, A. M., Dadashi, S., Young, J. D., Meyer, M. D., Thode, A. E., Hedwall, S. J., McCaffrey, S. M., Fillmore, S. D., & Bean, R. (2022). Comparing geography and severity of managed wildfires in California and the Southwest USA before and after the implementation of the 2009 Policy Guidance. *Forests*, *13*, Article 793.

Jackson, S. T., & Hobbs, R. J. (2009). Ecological restoration in the light of ecological history. *Science*, *325*, 567–569.

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, *14*, 369–378.

Jones, G. M., & Tingley, M. W. (2022). Pyrodiversity and biodiversity: A history, synthesis, and outlook. *Diversity and Distributions*, *28*, 386–403.

Kramer, H. A., Jones, G. M., Whitmore, S. A., Keane, J. J., Atuo, F. A., Dotters, B. P., Sawyer, S. C., Stock, S. L., Gutiérrez, R. J., & Peery, M. Z. (2021). California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. *Forest Ecology and Management*, *479*, Article 118576.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Lazaridis, E. (2022). *lunar: Lunar phase & distance, seasons and other environmental factors*. R package.

Loeb, S. C., & Blakey, R. V. (2021). Bats and fire: A global review. *Fire Ecology*, *17*, Article 29.

Lydersen, J. M., & Collins, B. M. (2018). Change in vegetation patterns over a large forested landscape based on historical and contemporary aerial photography. *Ecosystems*, *21*, 1348–1363.

Margolis, E. Q., Guiterman, C. H., Chavardès, R. D., Coop, J. D., Copes-Gerbitz, K., Dawe, D. A., Falk, D. A., Johnston, J. D., Larson, E., Li, H., Marshall, J. M., Naficy, C. E., Naito, A. T., Parisien, M.-A., Parks, S. A., Portier, J., Poulos, H. M., Robertson, K. M., Speer, J. H., … Weisberg, P. J. (2022). The North American tree-ring fire-scar network. *Ecosphere*, *13*, Article e4159.

Martin, R., & Sapsis, D. B. (1992). Fires as agents of biodiversity: Pyrodiversity promotes biodiversity. In *Proceedings of the Conference on Biodiversity of Northwest California Ecosystems*. Cooperative Extensions, University of California, Berkeley.

McClenachan, L., Rick, T., Thurstan, R., Trant, A., Alagona, P. S., Alleway, H. K., Armstrong, C., Bliege Bird, R., Rubio-Cisneros, N. T., Clavero, M., Colonese, A. C., Cramer, K., Davis, A. O., Drew, J., Early-Capistrán, M. M., Gil-Romera, G., Grace, M., Hatch, M., Higgs, E., … Van Houtan, K. S. (2024). Global research priorities for historical ecology to inform conservation. *Endangered Species Research*, *54*, 285–310.

McElreath, R. (2016). *Statistical rethinking: A Bayesian course with examples in R and Stan*. https://www.crcpress.com/Statistical-Rethinking-A-Bayesian-Course-with-Examples-in-R-and-Stan/McElreath/p/book/9781482253443

Meyer, M. D. (2015). Forest Fire severity patterns of resource objective wildfires in the southern Sierra Nevada. *Journal of Forestry*, *113*, 49–56.

Meyer, M. D., & North, M. P. (2019). *Natural range of variation of red fir and subalpine forests in the Sierra Nevada bioregion* (Gen Tech. Rep. PSW-GTR-263). U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. https://www.fs.fed.us/psw/publications/documents/psw_gtr263/index.shtml

Miller, C., & Aplet, G. H. (2016). Progress in wilderness fire science: Embracing complexity. *Journal of Forestry*, *114*, 373–383.

Miller, J. D., & Thode, A. E. (2007). Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of Environment*, *109*, 66–80.

Miller-ter Kuiler, A., Sanderlin, J. S., Ayars, J. S., Chmura, H. E., Dressen, M., Golding, J. D., Jones, G. M., Kirby, R., Norman, K. E., Steel, Z. L., & Foster, V. S. (2025). Functionalizing ecological integrity: using functional ecology to monitor animal communities. *Frontiers in Ecology and the Environment*, e2852. https://doi.org/10.1002/fee.2852

North, M. P., York, R. A., Collins, B. M., Hurteau, M. D., Jones, G. M., Knapp, E. E., Kobziar, L., Mccann, H., Meyer, M. D., Stephens, S. L., Tompkins, R. E., & Tubbesing, C. L. (2021). Pyrosilviculture needed for landscape resilience of dry western United States forests. *Journal of Forestry*, *119*, 520–544.

Parks, S., Holsinger, L., Koontz, M., Collins, L., Whitman, E., Parisien, M.-A., Loehman, R., Barnes, J., Bourdon, J.-F., Boucher, J., Boucher, Y., Caprio, A., Collingwood, A., Hall, R., Park, J., Saperstein, L., Smetanka, C., Smith, R., & Soverel, N. (2019). Giving ecological meaning to satellite-derived fire severity metrics across North American forests. *Remote Sensing*, *11*, Article 1735.

Prichard, S. J., Stevens-Rumann, C. S., & Hessburg, P. F. (2017). Tamm Review: Shifting global fire regimes: Lessons from reburns and research needs. *Forest Ecology and Management*, *396*, 217–233.

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E., & DeSante, D. F. (1993). *Handbook of field methods for monitoring landbirds* (Gen. Tech. Rep. PSW-GTR-144). U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. https://www.fs.usda.gov/treesearch/pubs/3639

Roberts, L. J., Burnett, R., & Fogg, A. (2021). Fire and mechanical forest management treatments support different portions of the bird community in fire-suppressed forests. *Forests*, *12*, Article 150.

Richter, C., Rejmánek, M., Miller, J. E. D., Welch, K. R., Weeks, J., & Safford, H. (2019). The species diversity × fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. *Ecosphere*, *10*, e02882.

Safford, H. D., Paulson, A. K., Steel, Z. L., Young, D. J. N., & Wayman, R. B. (2022). The 2020 California fire season: A year like no other, a return to the past or a harbinger of the future? *Global Ecology and Biogeography*, *31*, 2005–2025. https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.13498

Safford, H. D., & Stevens, J. T. (2017). *Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA* (General Technical Report PSW-GTR-256). U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Seidl, R., & Turner, M. G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world. *Proceedings of the National Academy of Sciences of the United States of America*, *119*, Article e2202190119.

Siegel, R., Wilkerson, R. L., Saracco, J. F., & Steel, Z. L. (2011). Elevation ranges of birds on the Sierra Nevada's west slope. *Western Birds*, *42*, 2–26.

Steel, Z. L., Campos, B., Frick, W. F., Burnett, R., & Safford, H. D. (2019). The effects of wildfire severity and pyrodiversity on bat occupancy and diversity in fire-suppressed forests. *Scientific Reports*, *9*, Article 16300.

Steel, Z. L., Collins, B. M., Sapsis, D. B., & Stephens, S. L. (2021). Quantifying pyrodiversity and its drivers. *Proceedings of the Royal Society B: Biological Sciences*, *288*, Article 20203202.

Steel, Z. L., Fogg, A. M., Burnett, R., Roberts, L. J., & Safford, H. D. (2022). When bigger isn't better—Implications of large high-severity wildfire patches for avian diversity and community composition. *Diversity and Distributions*, *28*, 439–453.

Steel, Z. L., Jones, G. M., Collins, B. M., Green, R., Koltunov, A., Purcell, K. L., Sawyer, S. C., Slaton, M. R., Stephens, S. L., Stine, P., & Thompson, C. (2023). Mega-disturbances cause rapid decline of mature conifer forest habitat in California. *Ecological Applications*, *33*, Article e2763.

Steel, Z. L., Miller, J. E. D., Ponisio, L. C., Tingley, M. W., Wilkin, K., Blakey, R., Hoffman, K. M., & Jones, G. (2024). A roadmap for pyrodiversity science. *Journal of Biogeography*, *51*, 280–293.

Steel, Z. L., Safford, H. D., & Viers, J. H. (2015). The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere*, *6*, 1–23.

Stephens, S. L., Bernal, A. A., Collins, B. M., Finney, M. A., Lautenberger, C., & Saah, D. (2022). Mass fire behavior created by extensive tree mortality and high tree density not predicted by operational fire behavior models in the southern Sierra Nevada. *Forest Ecology and Management*, *518*, Article 120258.

Stephens, S. L., Foster, D. E., Battles, J. J., Bernal, A. A., Collins, B. M., Hedges, R., Moghaddas, J. J., Roughton, A. T., & York, R. A. (2024). Forest restoration and fuels reduction work: Different pathways for achieving success in the Sierra Nevada. *Ecological Applications*, *34*, Article e2932.

Stephens, S. L., Martin, R. E., & Clinton, N. E. (2007). Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. *Forest Ecology and Management*, *251*, 205–216.

Stephens, S. L., Thompson, S., Boisramé, G., Collins, B. M., Ponisio, L. C., Rakhmatulina, E., Steel, Z. L., Stevens, J. T., van Wagtendonk, J. W., & Wilkin, K. (2021). Fire, water, and biodiversity in the Sierra Nevada: A possible triple win. *Environmental Research Communications*, *3*, Article 081004.

Stephens, S. L., Westerling, A. L., Hurteau, M. D., Peery, M. Z., Schultz, C. A., & Thompson, S. (2020). Fire and climate change: Conserving seasonally dry forests is still possible. *Frontiers in Ecology and the Environment*, *18*, 354–360.

Taillie, P. J., Burnett, R. D., Roberts, L. J., Campos, B. R., Peterson, M. N., & Moorman, C. E. (2018). Interacting and non-linear avian responses to mixed-severity wildfire and time since fire. *Ecosphere*, *9*, Article e02291.

Tarbill, G. L., White, A. M., & Sollmann, R. (2023). Response of pollinator taxa to fire is consistent with historic fire regimes in the Sierra Nevada and mediated through floral richness†. *Ecology and Evolution*, *13*, Article e10761.

Thompson, C. M., Smith, H., Green, R., Wasser, S., & Purcell, K. (2021). Fisher use of postfire landscapes: Implications for habitat connectivity and restoration. *Western North American Naturalist*, *81*, 225–242.

Tingley, M. W., Ruiz-Gutiérrez, V., Wilkerson, R. L., Howell, C. A., & Siegel, R. B. (2016). Pyrodiversity promotes avian diversity over the decade following forest fire. *Proceedings of the Royal Society B: Biological Sciences*, *283*, Article 20161703.

Turner, M. G., Baker, W. L., Peterson, C. J., & Peet, R. K. (1998). Factors influencing succession: Lessons from large infrequent natural disturbances. *Ecosystems*, *1*, 511–523.

United States Department of Agriculture (USDA). (2022). *Confronting the wildfire crisis: A strategy for protecting communities and improving resilience in America's forests* (FS-1187a). USDA Forest Service. https://www.fs.usda.gov/sites/default/files/fs_media/fs_document/Confronting-the-Wildfire-Crisis.pdf

van Wagtendonk, J. W. (2007). The history and evolution of wildland fire use. *Fire Ecology*, *3*, 3–17.

van Wagtendonk, J. W., Sugihara, N. G., Stephens, S. L., Thode, A. E., Shaffer, K. E., & Fites-Kaufman, J. A. (2018). *Fire in California's ecosystems*. University of California Press.

Viljur, M.-L., Abella, S. R., Adámek, M., Alencar, J. B. R., Barber, N. A., Beudert, B., Burkle, L. A., Cagnolo, L., Campos, B. R., Chao, A., Chergui, B., Choi, C.-Y., Cleary, D. F. R., Davis, T. S., Dechnik-Vázquez, Y. A., Downing, W. M., Fuentes-Ramirez, A., Gandhi, K. J. K., Gehring, C., … Thorn, S. (2022). The effect of natural disturbances on forest biodiversity: An ecological synthesis. *Biological Reviews*, *97*, 1930–1947.

Weeks, J., Miller, J. E. D., Steel, Z. L., Batzer, E. E., & Safford, H. D. (2023). High-severity fire drives persistent floristic homogenization in human-altered forests. *Ecosphere*, *14* e4409.

Wiens, J. A., Hayward, G. D., Safford, H. D., & Giffen, C. M. (2012). *Historical environmental variation in conservation and natural resource management*. John Wiley & Sons, Ltd.

Wilkin, K., Ponisio, L., Fry, D. L., Collins, B. M., Moody, T., & Stephens, S. L. (2021). Drivers of understory plant communities in Sierra Nevada mixed conifer forests with pyrodiversity. *Fire Ecology*, *17*, Article 30.

Williams, J. N., Safford, H. D., Enstice, N., Steel, Z. L., & Paulson, A. K. (2023). High-severity burned area and proportion exceed historic conditions in Sierra Nevada, California, and adjacent ranges. *Ecosphere*, *14*, Article e4397.

Wurtzebach, Z., & Schultz, C. (2016). Measuring ecological integrity: History, practical applications, and research opportunities. *Bioscience*, *66*, 446–457.

Young, J. D., Evans, A. M., Iniguez, J. M., Thode, A., Meyer, M. D., Hedwall, S. J., McCaffrey, S., Shin, P., & Huang, C.-H. (2020). Effects of policy change on wildland fire management strategies: Evidence for a paradigm shift in the western US? *International Journal of Wildland Fire*, *29*, 857–877.

SUPPORTING INFORMATION

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

How to cite this article: Steel, Z. L., Fogg, A. M., Buzbee, R. F., Wilkin, K., Collins, B. M., Burnett, R., Meyer, M. D., Wuenschel, A., & Stephens, S. L. (2025). Finding floral and faunal species richness optima among active fire regimes. *Conservation Biology*, e70079. https://doi.org/10.1111/cobi.70079