When bigger isn't better – implications of large high-severity wildfire patches on avian diversity and community composition

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Abstract

Aim:

Modern wildfires increasingly create large high-severity patches with interior areas far from less disturbed habitats. We evaluated how these trends impact montane bird communities by investigating the effect of internal distance to lower severity areas, high-severity patch size, and years since fire on avian alpha and beta diversity.

Location:

Sierra Nevada Mountains, California, USA

Methods:

Bird occurrence data were collected during 2009-2017 within high-severity patches of 27 wildfires representing 1-30 years since disturbance. A two-step multispecies occupancy method was used to account for imperfect detection of 94 species and estimate effects of high-severity patch characteristics on community richness and dissimilarity as well as richness of nesting guilds.

Results:

Community richness decreased with distance from patch edge and with high-severity patch size. Richness increased with years since fire, but this pattern was mediated by distance to edge with higher peak richness (23 species) on the patch edges than interiors (18 species). Community dissimilarity was not explained by distance from edge or patch area indicating that interiors of large high-severity patches contain a subset of rather than a complement to the edge community. Guild richness of tree and primary cavity nesters was negatively associated with distance and patch size. Richness of ground and shrub nesters was insensitive to these metrics but due to declines among other species, the groups made up a greater percentage of the avian community within patch interiors.

Main conclusions:

As fire activity increases due to accumulating forest fuels and accelerating climate change, high-severity patches and their resulting early-seral habitats are becoming more extensive with less edge and more interior area. Such changes are likely to decrease avian diversity locally and shift community composition away from forest-associated species. Management actions that promote the full range of fire effects but limit the size of high-severity patches may best conserve bird diversity within fire-adapted ecosystems.

Keywords

Avian diversity, fire ecology, fire suppression, heterogeneity, landscape ecology, multispecies occupancy model, patch size, pyrodiversity, wildfire

Introduction

Wildfire is a fundamental ecological process that influences the distribution of ecosystems (Whittaker 1975, Bond and Keeley 2005, McLauchlan et al. 2020), landscape pattern (Turner 2010), and vegetation structure (Agee 1996). Wildfire patterns are shifting globally (Flannigan et al. 2009, Bowman et al. 2011) and especially in fire-prone forests of California where increasingly large wildfires are creating ever larger patches of high-severity effects (Miller et al. 2012, Westerling 2016, Abatzoglou and Williams 2016), and post-fire habitats far from less disturbed areas (Steel et al. 2018). Such shifts influence landscape heterogeneity and bird habitat availability, potentially driving patterns of species diversity and community composition. A greater understanding of how changes in the spatial pattern of high-severity fire are impacting bird communities is necessary to effectively manage fire-adapted ecosystems and conserve biodiversity.

Bird species vary widely in their response to wildfire and in their associations with post-fire habitats (Fontaine and Kennedy 2012). When low- to moderate-severity fires burn conifer forests, tree and understory density is reduced but the majority of the mature canopy is maintained (Miller et al. 2009). In contrast, most vegetation is killed by high-severity fire, leaving fire-killed trees (snags) in the short-term, with early-successional habitats such as herbaceous plants and montane chaparral developing in the years immediately following the fire (White et al. 2016). If reestablishment of conifer species or hardwood trees are successful and in the absence of repeated severe disturbance, the habitat will transition back to a forested state in the decades following fire (Agee 1996, van Wagtendonk et al. 2018). Many bird species in the Sierra Nevada are adapted to particular combinations of burn severity and time since fire, including early-successional habitats created by high-severity fire (Fontaine et al. 2009, White et al. 2016, Taillie et al. 2018). Indeed peak abundance of at least a quarter of the bird community occurs in recently burned forests (≤ 15 years) across the severity gradient with an equivalent number most abundant in unburned forests (Taillie et al. 2018). Because bird occurrence and diversity are strongly associated with vegetation structure and landscape pattern (MacArthur and MacArthur 1961, McGarigal and McComb 1995) that are directly manipulated by fire, we might expect many species to respond to high-severity wildfire according to common functional traits such as nest site preference, while other's respond idiosyncratically. Further, wildfire spatial pattern is an important determinant of vegetation succession and landscape heterogeneity (Turner 2010), with likely consequences for bird diversity in the decades following disturbance. In these fire-adapted landscapes bird diversity may maximize in areas characterized by heterogeneous fire histories (aka pyrodiversity) where variation in burn severity and other fire regime characteristics is high, and where a mix of habitat types and ecological niches are maintained in the local landscape (Steel et al. In Review, Martin and Sapsis 1992, Tingley et al. 2016).

Historically, the Sierra Nevada frequently experienced fire dominated by low- to moderate-severity, but legacies of past fire and forest management as well as accelerating climate change are causing shifts in fire patterns across the region (Van de Water and Safford 2011, Mallek et al. 2013). Following Euro-American colonization and genocide of native peoples in the 1800s traditional fire management ceased and naturally-ignited wildfires were suppressed (Stephens et al. 2007, Anderson and Keeley 2018, van Wagtendonk et al. 2018). Forest structure was further altered in many areas by 19th and 20th century timber harvest and silvicultural practices

(McKelvey and Johnston 1992, Safford and Stevens 2017). These changes led to a large increase in tree density and surface fuels and consequently an elevated risk of high-severity fire effects (Stephens et al. 2015, Steel et al. 2015, Lydersen and Collins 2018). Apart from vegetation pattern and structure, climate change is lengthening fire seasons and increasing instances of extreme fire weather (Westerling 2016, Williams et al. 2019). Contemporary wildfires that escape suppression efforts are consequently burning larger, with a greater proportion of high-severity, larger high-severity patches, and more high-severity area far from patch edges (Parks and Abatzoglou n.d., Miller et al. 2012, Steel et al. 2018). Increased fire activity including high-severity fire can increase pyrodiversity at the landscape scale, especially within fire-suppressed forests (Steel et al. In Review). However, the interiors of large high-severity patches likely contain lower habitat heterogeneity and slower conifer regeneration relative to patch edges (Greene and Johnson 1995, Welch et al. 2016, Shive et al. 2018), potentially driving differences in bird diversity immediately following disturbance and over time.

To assess how increasingly large high-severity patches influence avian community diversity and composition we use a two-step multispecies occupancy model analysis along with 2044 bird community surveys conducted within high-severity patches of 27 wildfires. Specifically, we address the following questions: 1) How does location within a high-severity patch (i.e. distance to lower severity areas) and patch size influence occupancy of individual species, as well as avian alpha and beta diversity? 2) How does diversity change 1-30 years after fire and are these changes mediated by distance to lower severity areas? 3) Do these factors influence species richness of functional groups (i.e. nesting guilds), and their relative prevalence in the bird community?

Methods

Study system

We surveyed birds within previously burned conifer forests of the Sierra Nevada and Southern Cascade ranges in California (Figure 1). Sample locations span an elevation gradient of 1050 – 2200 m, and a latitudinal gradient of 35.8 – 41.4 degrees, which encompasses the lower and upper montane zones of the range. Along this gradient, dominant tree species transition from *Pinus ponderosa, P. lambertiana, Abies concolor, Pseudotsuga menziesii, Calocedrus decurrens* and *Quercus spp* in the lower montane to *A. magnifica,* and *Pinus jeffreyi* in the upper montane. Shrubs, including *Arctostaphylos* spp., *Ceanothus* spp., *Prunus* spp., *Q. vaccinifolia*, *Chrysolepis sempervirens* and *Ribes* spp., are also found in conifer stands or as the dominant vegetation in areas characterized by xeric conditions, poor soils, or past disturbance (van Wagtendonk et al. 2018). Historically, the lower montane yellow pine and mixed conifer forests were characterized by a 10-20 year mean fire return interval with 5-8% of burned area experiencing high-severity effects on average. At higher elevations red fir forests burned slightly less frequently (40 year mean fire return interval) and with greater percentage of high-severity (20%; Van de Water and Safford 2011, Mallek et al. 2013). The historic spatial patterns of fire severity is less certain, but high-severity patches were likely relatively small (mostly < 10 ha) in the yellow pine and mixed conifer forests (Safford and Stevens 2017), and contemporary reference sites show 86% of high-severity patches in red fir and subalpine forests are less than 15 ha in size (Meyer and North 2019).

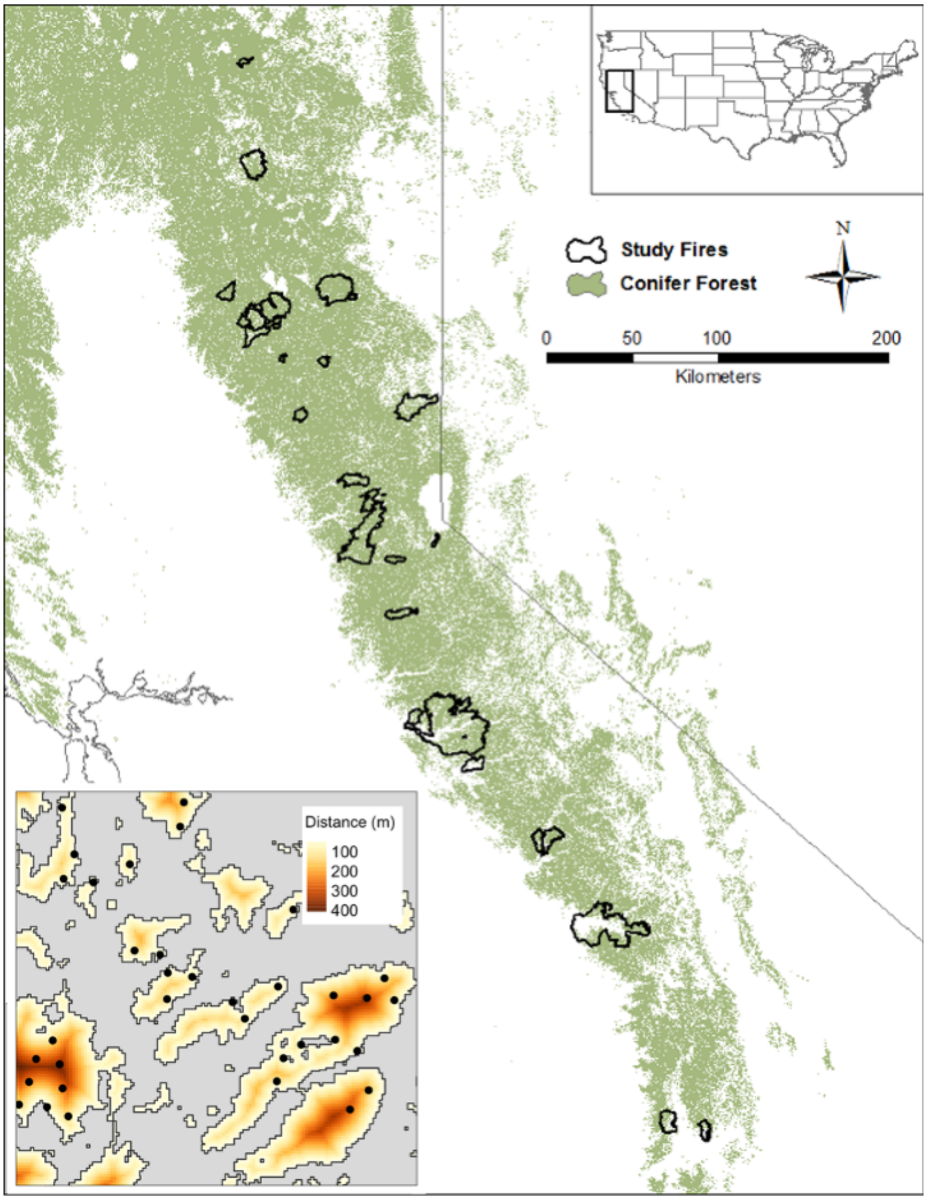

Figure 1. *California's conifer forests with perimeters of 27 wildfires where post-fire bird communities were surveyed in the Sierra Nevada and southern Cascade Mountains. Displayed conifer extent represents predicted climax conditions under historic climate and disturbance regime rather than existing vegetation (LANDFIRE 2013). The inset map provides an example of survey locations at various distances from edge within high-severity patches. Grey areas represent habitat that burned at less than high-severity.*

Bird surveys and environmental data

We combined avian point count survey data from multiple monitoring programs in the Sierra Nevada and Southern Cascade Mountains. The majority of surveys (62%) were conducted as part of a post-fire monitoring program in eight fires of the central and northern part of the study region. To extend the temporal and geographic scope of our analysis, we also draw from a region-wide monitoring program where survey locations were coincident with areas that previously experienced high-severity fire (Figure 1; Roberts et al. 2011, Burnett and Roberts 2015, Taillie et al. 2018). Survey sites were spaced a minimum of 250 m apart and were located on US Forest Service lands. A standard 5-min point count survey protocol was used where each individual bird was recorded along with its initial distance from point center (Ralph et al. 1993). Surveys were conducted during the peak breeding season (May - June), with repeat visits conducted by different observers. Sites used in analysis were limited to locations classified as conifer forests prior to the most recent fire, had not experienced a previous high-severity event since at least 1984, and where no major management actions (e.g. salvage logging, herbicide or reforestation treatments) had occurred since the fire either at the location of the survey or between survey points and the nearest high-severity patch edge. The Forest Service Activity Tracking System database (available at https://www.fs.usda.gov/main/r5/landmanagement/gis) was used to identify post-fire management and was verified with historical Google Earth aerial imagery. In total, 746 point count sites were surveyed in multiple years during the 2009-2017 seasons. Sites were located within one of 130 high-severity patches and 27 fires. Sampled wildfires burned between 1987 and 2015, with surveys conducted 1-30 years post-fire (median = 3 years; mean = 6 years). Sample distributions of distance from edge and patch size were log-normal with distance from lower severity areas ranging between 1 m and 1090 m (median = 81 m; mean = 125 m) and high-severity patch size ranging between 0.1 and 21,000 ha (median = 42 ha; mean = 680 ha). Stand structure data were also collected at point count locations during some years using a modified relevè protocol (Ralph et al. 1993), and used for modeling variation in bird detectability. For years where birds were surveyed but not vegetation, the most proximate (before or after) vegetation data was used.

Fire severity data were obtained from a Forest Service maintained database, which includes fires that occurred at least partially on Forest Service or National Park Service land in California since 1984 (available at http://www.fs.usda.gov/detail/r5/landmanagement/gis/). The database was derived from LANDSAT-TM satellite multispectral imagery. The Relativized differenced Normalized Burn Ratio was calculated as a measure of vegetation change resulting from each fire, and was subsequently used to quantify basal area mortality (Miller and Thode 2007, Miller et al. 2009). We define high-severity patches as contiguous areas (i.e. connected by at least one 900 m^2 pixel) where a minimum of 75% of the pre-fire tree basal area was killed. This threshold is often used to designate high-severity fire effects (e.g. Steel et al. In Review, Tingley et al. 2016, Welch et al. 2016, Jones et al. 2020), although other thresholds have also been used in the literature (e.g. Lydersen et al. 2016, Collins et al. 2017). Patch size and the distance from each site location within a high-severity patch to areas with < 75% pre-fire mortality (i.e. patch edge) was calculated using R (R Core Team 2020).

Statistical Analysis

Of the 122 species observed during at least one survey occasion, we restricted our analysis to 94 species that are effectively surveyed using the point count protocol and are known to breed within the study area (see Appendix S1 in Supporting Information). Species were classified into nesting guilds according to known life-histories as breeding bird territories and occurrence are tightly linked to nesting sites (Steel et al. 2012, Beedy and Pandolfino 2013). Specifically, each species was classified as predominantly a tree, primary cavity, secondary cavity, shrub, or ground nester (Appendix S1). We consider each survey season and site combination as a primary survey occasion (*i*), and within season visits as temporal replicates (*j*). The community is assumed to be closed during each season, allowing for formal estimation of rates of detection and true occupancy. On average, each site was surveyed for 2.7 years, for a total of 2044 primary survey occasions; most (90%) composed of two visits per year. Observation data are binary with $y_{s,i,j} = 1$ when species s is detected during survey i and visit j within 100 m of the observer, or $y_{s,i,j} = 0$, when a species was not detected. Because detection is imperfect, we utilize an occupancy modeling framework $y_{s,i,j} = Bernoulli(p_{s,i,j} * z_{s,i})$ where $p_{s,i,j}$ is the probability of detection given a site is occupied (i.e. $z_{s,i} = 1$). A species' true occurrence is modeled as $z_{s,i} = Bernoulli(\psi_{s,i})$ where $\psi_{s,i}$ is the probability of occurrence, and $z_{s,i}$ is a binary latent variable of a species' true occurrence state.

We assumed detection and occurrence probabilities vary by species and survey and are functions of habitat and survey characteristics. The detection process is modeled using the following logit-linear function:

[1]

$$\begin{aligned} logit(p_{s,i,j}) \quad &= \alpha 0_s \\ &+\alpha_{day,s} * X1_{i,j} + \alpha_{day^2,s} * X2_{i,j} \\ &+\alpha_{snag,s} * X3_i + \alpha_{shrub,s} * X4_i \end{aligned}$$

where the Julian day (α_{day} and α_{day^2}) of each visit, snag basal area (α_{snag}), and percentage shrub cover (α_{shrub}) are predictors of detection probability. The occurrence process is modeled using the following logit-linear function:

[2]

$$\begin{aligned} logit(\psi_{s,i}) \quad &= \beta 0_s + \beta site[i]_s + \beta patch[i]_s + \beta fire[i]_s \\ &+\beta_{YSF,s} * X5_i + \beta_{YSF^2,s} * X6_i \\ &+\beta_{dist,s} * X7_i + \beta_{dist*YSF,s} * X7_i * X5_i \\ &+\beta_{area,s} * X8_i + \beta_{lat,s} * X9_i \\ &+\beta_{elev,s} * X10_i + \beta_{elev^2,s} * X11_i \end{aligned}$$

Where $\beta site$, $\beta patch$, and $\beta fire$ are random intercepts for site, patch, and fire ID for species *s*. For each species, occupancy probability is a function of number of years since fire (β_{YSF} and β_{YSF^2}), distance (log m; β_{dist}) from high-severity patch edge, the interaction of years since fire and distance to patch edge ($\beta_{dist*YSF}$), patch area (log ha; β_{area}), latitude (degrees; β_{lat}), and elevation (m; β_{elev} and β_{elev^2}). Among the detection or occupancy model variables correlations were low (< | 0.6 |).

The primary predictor variables of interest are distance from patch edge, years since fire, their interaction, and high-severity patch size. The additional predictors in equations 1 and 2 were chosen based on previous work assessing species occurrence in the Sierra Nevada Mountains (e.g. Burnett and Roberts 2015, Tingley et al. 2016, White et al. 2016). We utilize a multispecies occupancy model where each species-specific parameter α_s or β_s is modeled as a random sample from a community-level hyperparameter. This allows for more precise estimates for rare species, which can be challenging to model using single-species approaches, and improves estimates of community metrics with appropriate propagation of model uncertainty (Zipkin et al. 2010). We allow intercepts of ψ_s to vary by fire and patch ID to help account for spatial clustering of points within fires. Site ID is modeled as a varying intercept to account for variation in occupancy probability due to unmodeled habitat characteristics and other local influences unique to each point. This approach may be considered a correlated multispecies model as it makes explicit the assumption that occupancy at a site is not fully independent between years. This model differs from a dynamic multispecies model (Dorazio et al. 2010) in that correlations are bi-directional (e.g. information in survey year two informs estimates of year one and vice versa) and does not estimate rates of local extinction and colonization, which are not of interest here. All continuous predictors were standardized with a mean of zero and standard deviation of one, and random intercepts are estimated with a group population mean of zero. The multispecies occupancy model was estimated using Hamiltonian Monti Carlo sampling in Stan via the rstan package (Stan Development Team 2020). We specified weakly regularizing priors to prevent model over-fitting (McElreath 2016).

To estimate alpha and beta diversity at the community level we used a two-step (aka Bayesian meta-analysis) modeling process (Tingley and Beissinger 2013, Kery and Royle 2015) where the detection-corrected estimates of occupancy ($z_{s,i}$) from the multispecies occupancy model were used to calculate diversity metrics for each primary survey occasion. Richness (alpha diversity) is calculated as the sum of $z_{s,i}$ for the full community or for a subset of species when conducting nesting guild analysis. Beta diversity is calculated as the compositional dissimilarity from the group centroid (multidimensional median), where groups are defined as each of the 27 sampled fire areas. We use the Raup-Crick Index (Raup and Crick 1979) because it adjusts for differences in species richness by evaluating dissimilarity between each survey and randomly generated communities based on the group's species pool (Chase et al. 2011). Alpha and beta diversity calculations were conducted for each draw of the model posterior creating derived distributions for each metric and each primary survey occasion. By using the full multispecies model posterior, model uncertainty is properly propagated to the community models (Tingley and Beissinger 2013, Kery and Royle 2015). Community models were fit using the BRMS and rstan packages (Bürkner 2017, Stan Development Team 2020) with the same set of predictors as equation 2 as well as a gaussian error structure and log-link. All models were run with 4 chains, each for 1000 samples with a burn in of 500, resulting in 2000 post-warmup samples. Proper mixing of sampling chains was checked using traceplots, and all parameters received R-hat values of less than 1.1. Model code can be found in Appendix S2 with additional supporting code found at https://github.com/zacksteel/High_Severity_Birds.

To quantify the interaction of distance to patch edge and years since fire we calculated marginal effects of years since fire at three distance levels (10, 50, and 250 m). We limit projected effects to 250 m because surveys conducted at greater distances from patch edge were limited to the first two decades since fire. The use of a linear and quadratic effect of years since fire assumes a parabolic form with an average peak or nadir at some vertex year following disturbance. We solved for the location of the vertex of each richness model by calculating the expected year since fire when the derivative of the parabola is equal to zero (i.e. when the rate of change is zero; $-\beta_{YSF}/2 * \beta_{YSF^2}$). To evaluate the degree to which distance mediates changes in species richness over time we calculated the expected difference between year one and the vertex year with respect to the three distance levels. Probabilistic statements as well as derived model estimates and credible intervals were calculated using model posterior distributions. For example, the probability an effect was positive (or negative) was calculated as the proportion of the parameter posterior distribution above (or below) zero.

Results

Species-level effects

Individual bird species differed greatly in how occupancy was affected by the environmental variables tested (Figure 2 & Appendix S3). Among the primary variables of interest, years since fire showed the widest range of standardized effects, with 26% of species showing clear (probability [Pr.] > 95%) positive and 20% showing clear negative associations with occupancy. 14% of species showed a concave (positive quadratic effect) and 26% showed a convex (negative quadratic effect) functional relationship between occupancy and years since fire. Occupancy of 14% of species showed clear positive associations with internal distance to patch edge, while 24% showed a clear negative relationship. The species with the strongest positive effect of distance from edge included European Starling (*Sturnus vulgaris*), Bullock's Oriole (*Icterus bullockii*), Sooty Grouse (*Dendragapus fuliginosus*), and Lewis' Woodpecker (*Melanerpes lewis*), while those with the strongest negative effect included Red-breasted Nuthatch (*Sitta canadensis*), Hermit Warbler (*Setophaga occidentalis*), Mountain Chickadee (*Poecile gambeli*), and Brown Creeper (*Certhia americana*). Occupancy of 7% of species showed either a positive or negative interaction between years since fire and distance indicating the rate of change following fire is mediated by within-patch location. Occupancy of only 1% of species (i.e. Lazuli Bunting; *Passerina amoena*) showed a positive association between high-severity patch size, while 9% of species occurred more often in smaller patches (Figure 2). Those species with the strongest negative effect of patch size included Red-breasted Nuthatch, Western Wood-pewee (*Contopus sordidulus*), Hutton's Vireo (*Vireo huttoni*), and Yellow-rumped Warbler (*S. coronate*). Estimates of all multispecies model parameters can be found in Appendix S3.

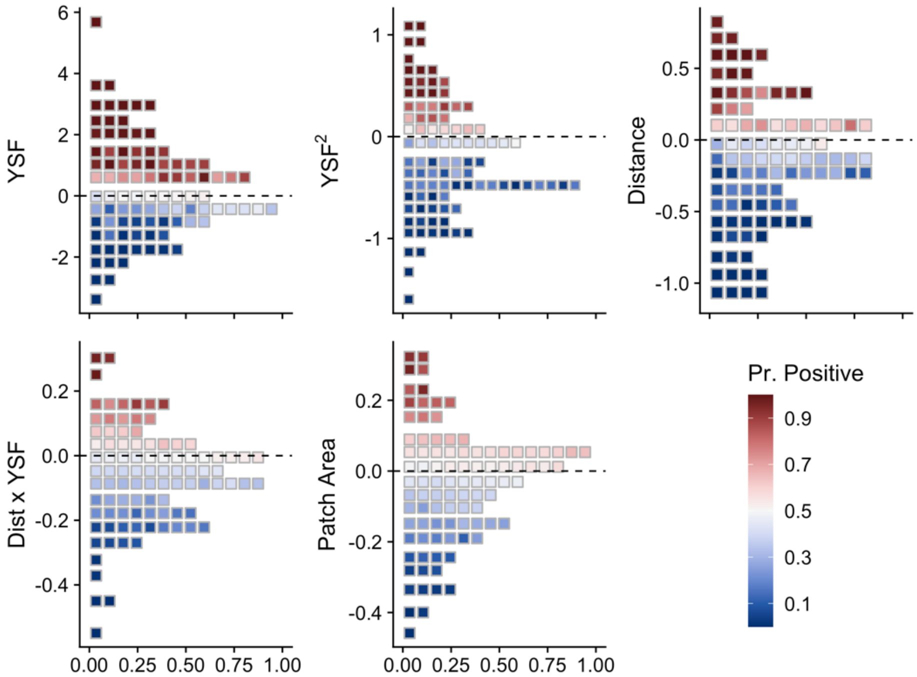

***Figure 2**. Coefficient estimates for avian multispecies occupancy model parameters of interest. Each square represents a single species with its location on the y-axis indicating the mean parameter estimate and color indicating probability of a positive or conversely negative (1 – Pr. Positive) effect. The x-axis indicates the count of species in a given effect size bin relative to the bin with the maximum count. Estimates are for bird species of the Sierra Nevada, California.*

Community richness and dissimilarity

The community richness model estimated very clear (Pr. ≥ 99%) effects of all parameters describing internal distance to patch edge, years since fire, latitude, and patch area (Figure 3a). Richness was positively associated with years since fire with a negative quadratic term indicating a convex (humped-shaped) relationship with time. Richness was negatively associated with internal distance to high-severity patch edge. The interaction of years since fire and distance to patch edge was negative indicating that the positive effect of years since fire diminished with distance, and conversely that the negative effect of distance grew stronger with time. Richness declined with latitude and with increasing patch size, and likely increased with elevation but with greater model uncertainty (Pr. = 94%; Figure 3a). The combined effects of years since fire, distance from patch edge, and patch size resulted in the most speciose communities occurring near patch edges (Figure 4a) and within relatively small patches (Figure 5a). After accounting for differences in species richness, community dissimilarity was negatively associated with the linear elevation term and positively with the quadratic elevation term (Pr. > 99%), indicating a concave (U-shaped) relationship with points located at low and high elevations were most different from the average community (Figure 3b). Community dissimilarity was also negatively associated with the quadratic term of years since fire and likely positively related to linear term of years since fire (Pr. = 92%; Figures 3b & 4b). The direction of all other effects in the community dissimilarity model were less certain (Pr. < 89%; Figure 3b).

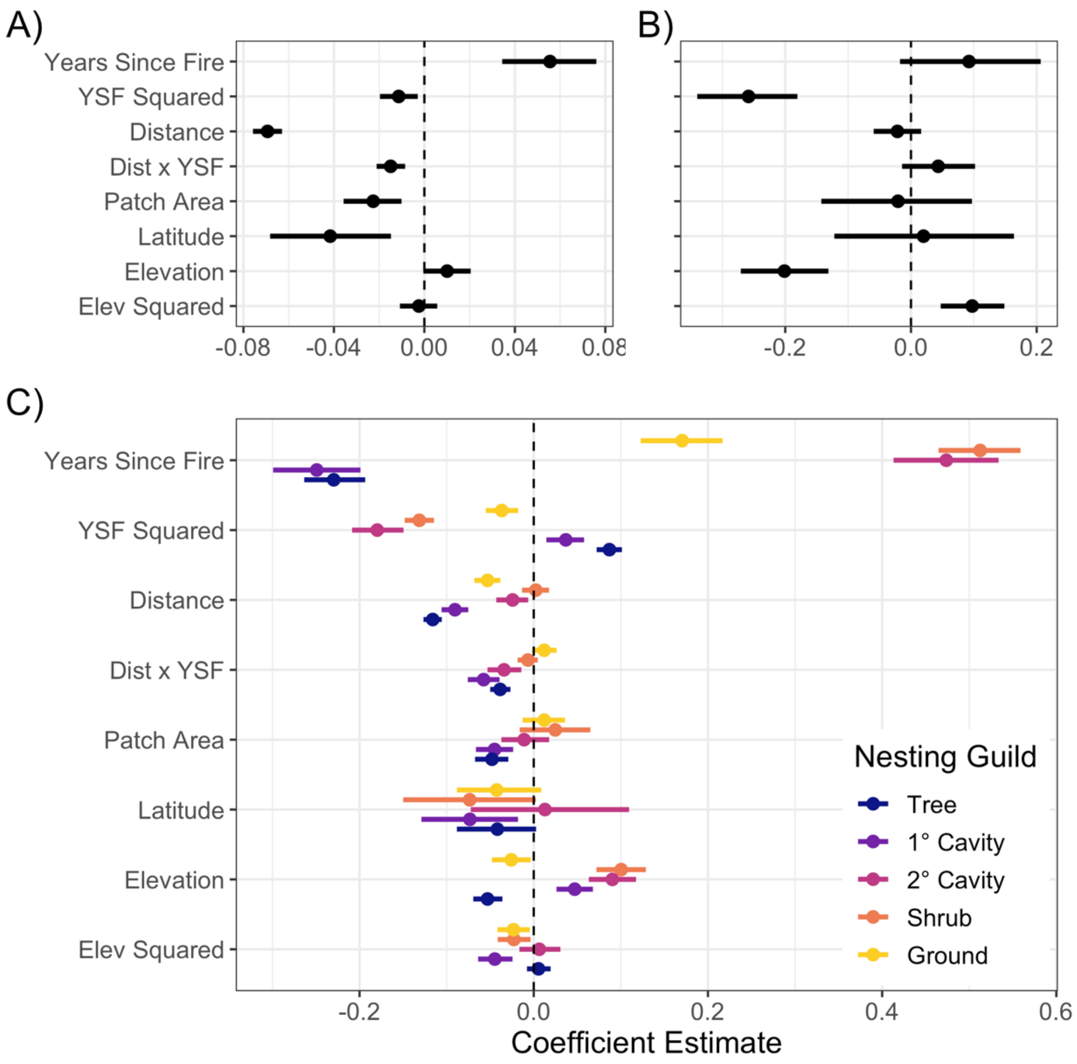

Figure 3. *Coefficient dotplots for avian A) community richness, B) community dissimilarity, and C) guild richness in the Sierra Nevada, CA. Points represent median parameter estimates and bars represent 90% credible intervals. Tabulated parameter estimates can be found in Appendix S4.*

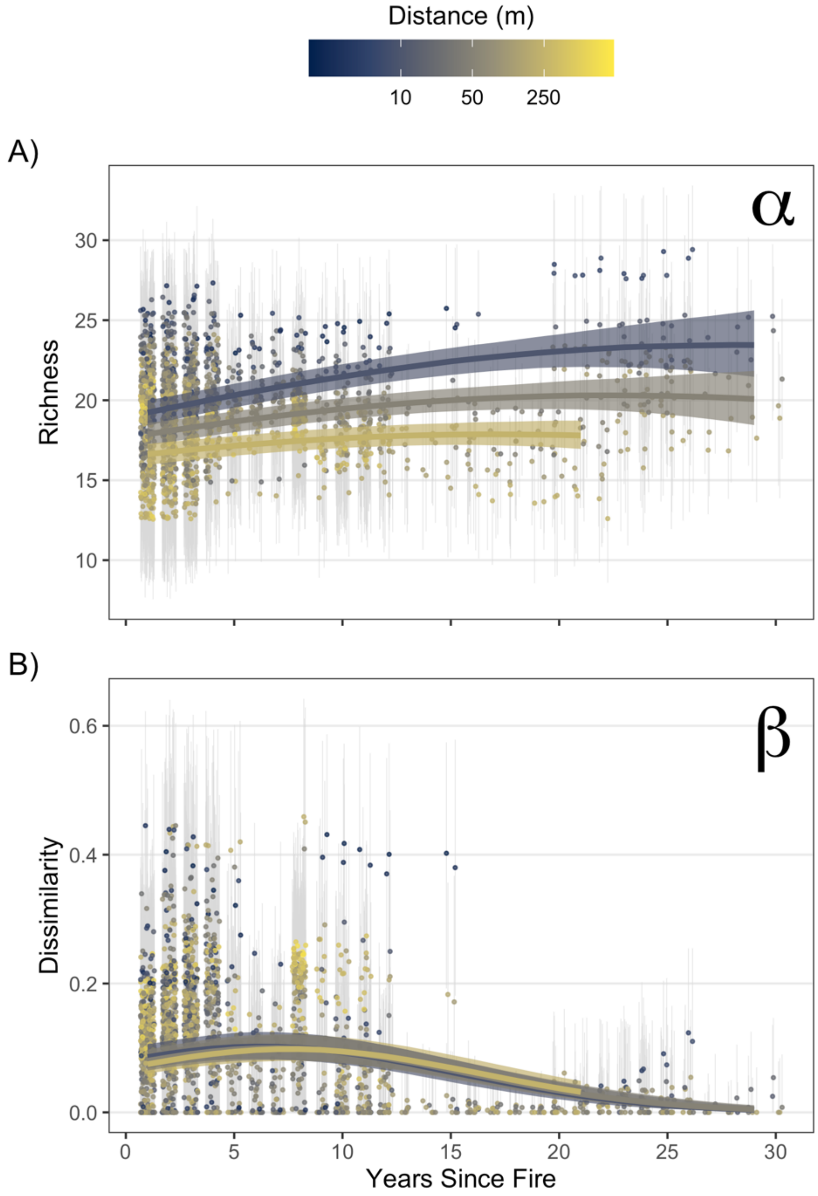

Figure 4. *Marginal effects of years since fire and distance from edge on bird community alpha and beta diversity in the Sierra Nevada, CA. A) Alpha diversity is quantified as species richness. B) Beta diversity is quantified using the Raup-Crick Index, where groups (species pools) are defined by each individual fire area. Model fits are shown as median lines and 90% credible interval bands for 10 (blue), 50 (grey) and 250 m (yellow) from patch edge with other predictor variables held at their mean values. After accounting for imperfect detection, estimated medians and 90% credible intervals of sampled communities are shown as jittered points and vertical bars.*

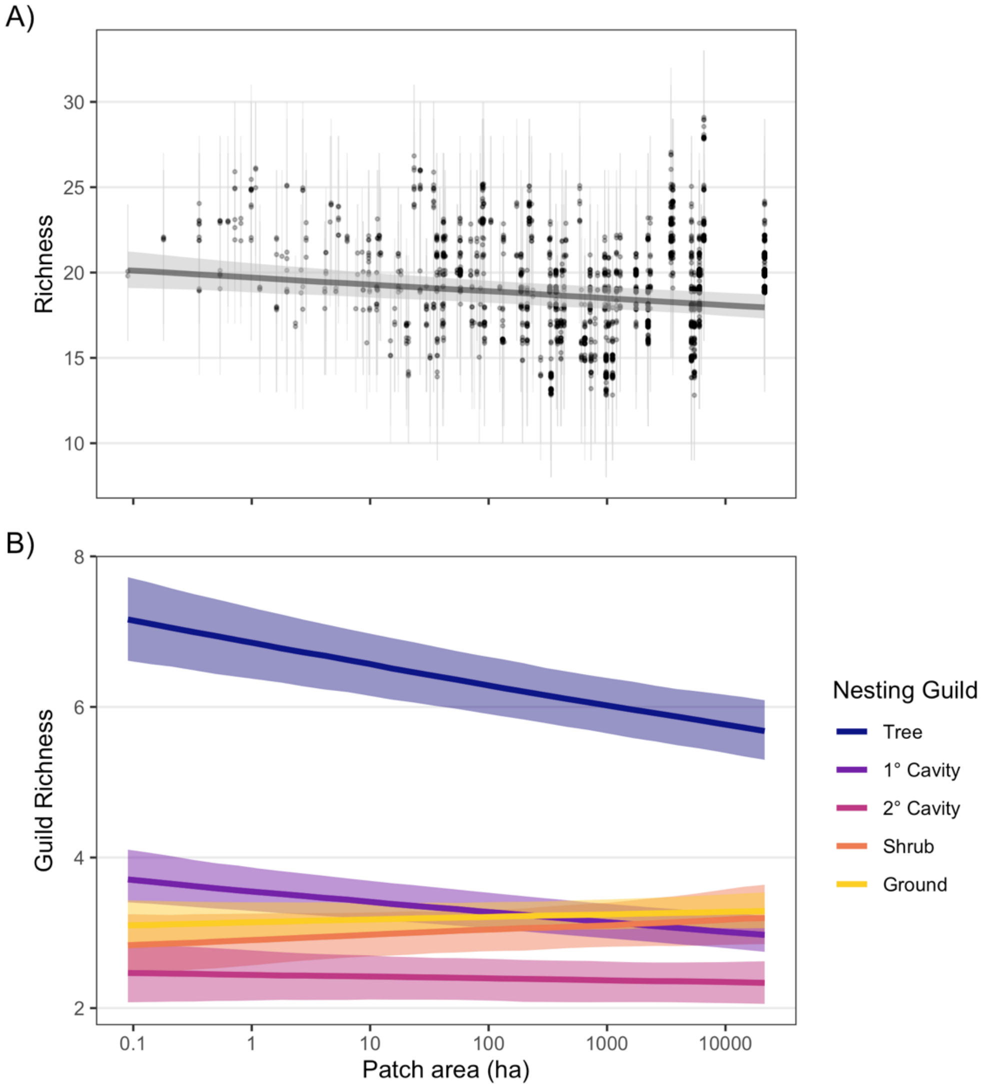

***Figure 5**. Marginal effects of patch area on A) bird community richness and B) nesting guild richness in the Sierra Nevada, CA. Model fits are shown as median lines and 90% credible interval bands with other predictor variables held at their mean values (e.g., 6 years since fire). For A), after accounting for imperfect detection, estimated medians and 90% credible intervals of sampled communities are shown as jittered points and bars.*

Nesting Guilds

The direction and magnitude of model effects varied considerably among nesting guilds (Figure 2c). Tree and primary cavity nester richness was very clearly (Pr. ≥ 99%) negatively associated with years since fire and positively associated with years since fire quadratic term resulting in concave (U-shaped) relationships over time (Figure 6a & b). Conversely, secondary cavity, shrub, and ground nesters richness was positively associated with years since fire and negatively associated with the years since fire quadratic term resulting in a convex (hump-shaped) relationship over time (Figure 6c-e). Distance from patch edge had a negative effect on richness for all guilds with the exception of shrub nesters; the magnitude of the effect was strongest for tree nesters, followed by primary cavity nesters. The interaction of distance and years since fire had a negative effect on richness of for tree, primary cavity, and secondary cavity nesters (Pr. > 99%), while likely positive for ground nesters (Pr. 92%). High-severity patch area was negatively associated with richness of tree and primary cavity nesters (Pr. > 99%) but showed no clear effect on other guilds (Pr. < 85%; Figure 4b). Latitude was negatively associated with richness of primary cavity nesters (Pr. > 98%), and likely negatively with shrub and tree nesters (Pr. 94%). Elevation was positively associated with richness of primary cavity, secondary cavity, and shrub nesters (Pr. > 99%), and negatively with tree and ground nesters (Pr. > 97%). The quadratic term of elevation was negative for primary cavity, ground, and shrub nesters (Pr. > 97%; Figure 3c). While guild-level patterns were often apparent, there were within-guild exceptions. For example, in contrast to the guild overall Hairy (*Dryobates villosus*), Lewis', and Acorn (*M. formicivorus*) woodpeckers occurred more often with increasing distance to patch edge, while the Black-backed woodpecker (*Picoides arcticus*; an important species for post-fire management) showed a neutral response (Appendix S3).

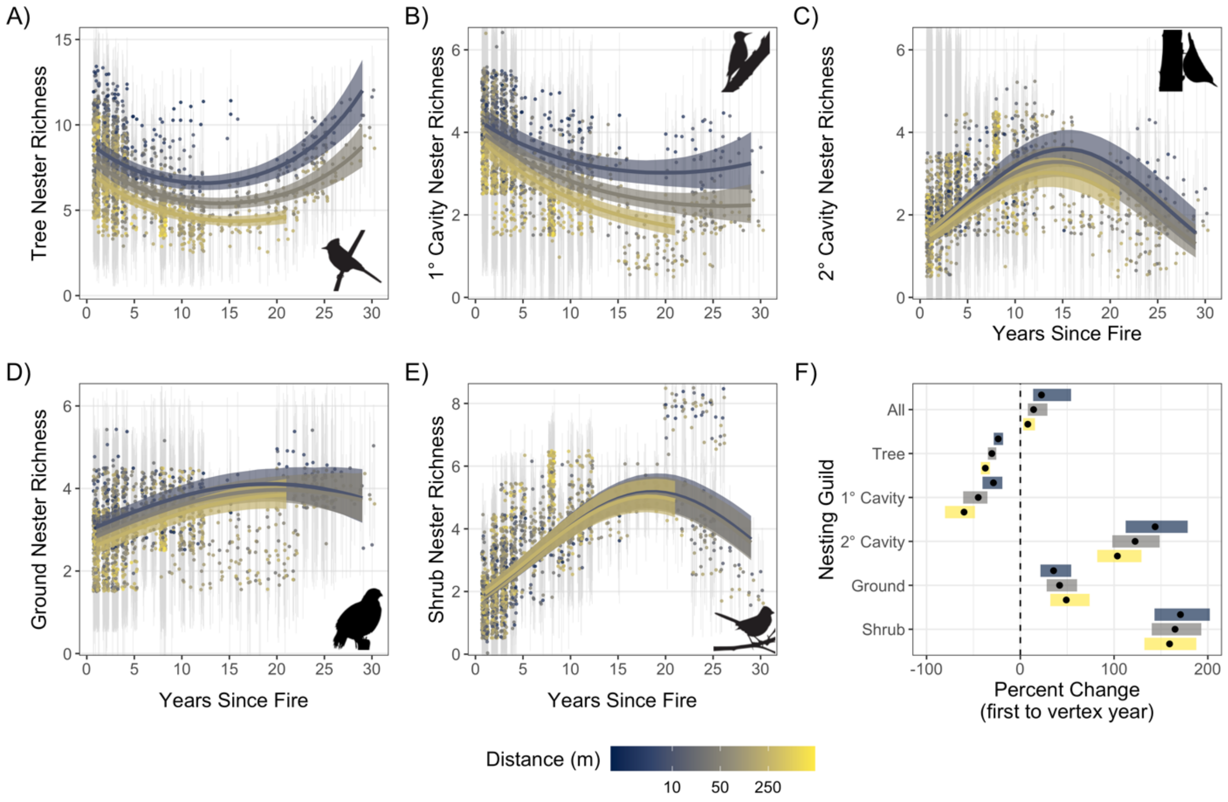

Figure 6. *Marginal effects of years since fire and internal distance from high-severity patch edge on avian guild richness in the Sierra Nevada, CA. Panels represent A) tree, B) primary cavity, C) secondary cavity, D) ground, E) shrub nester richness, and F) percent change in richness from one year since fire to the median vertex (peak or nadir) year. Model fits are shown as median lines and 90% credible interval bands for 10 (blue), 50 (grey), and 250 m (yellow) from patch edge with other predictor variables held at their mean values. After accounting for imperfect detection, estimated medians and 90% credible intervals of sampled communities are*

shown as jittered points and vertical bars. Bird silhouettes from www.allaboutbirds.org, © Cornell Lab of Ornithology.

Distance-mediated avian succession

For the avian community overall and for some nesting guilds, distance from patch edge mediated the rate at which species richness changed following wildfire (Figure 3c; 6f). For the full community, more species occurred along patch edges than interiors, but edges also saw greater growth in richness with time since fire. Between one year since fire and the year of peak richness, richness increased by a median of 23% at 10 m from patch edge and 8% at 250 m from edge. The declines in richness experienced by the tree and primary cavity nesting guilds were more pronounced in patch interiors than edges. Between one year since fire and the guild's nadir, tree nesters declined by a median of 24% 10 m from edge and 37% 250 m from edge, while primary cavity nesters declined by 29% along edges and 60% in patch interiors. Similar to the overall community, between year one and the year of peak richness secondary cavity nester richness increased more along edges (median = 144%) than interiors (median = 104%). Temporal changes in ground and shrub guild richness were largely unaffected by distance to edge (Figure 6f). The strength of the interactions of distance and years since fire ultimately influences the relative composition of communities along edges and interiors. Approximately two decades following a fire when guilds reached their richness peak or nadir, tree and primary cavity nesters represented greater percentages of the full community along edges than interiors, while the ground and shrub guilds saw the opposite pattern. Specifically, the relative number of tree nesters decreased from a median of 28% of the community at 10 m from edge to 24% at 250m from edge. Similarly, the relatively number of primary cavity nesters decreased from 13% to 8%. Conversely, the median percentage of the community composed of ground nesters increases from 18% at 10 m from edge to 22% at 250m from edge, while the relative number of shrub nesters increases from 22% to 28%. Secondary cavity nesters maintained approximately the same percentage of the community regardless of distance from edge. These mediating effects of distance to patch edge were weaker in the years immediately following a fire, and likely continued or strengthened into the third decade since fire, although our sampling of patch interiors (e.g., > 250 m) beyond 20 years since fire was limited (Figure 6).

Discussion

As fire activity increases across the western United States and patches of high-severity effects increase in size, it is important to understand how bird communities will respond in the decades follow disturbance. Here we show that as compared to small patches or patch edges, interiors of large patches support fewer species and a lower rate of increase in species richness within the first three decades following wildfire. Further, this lower richness is not compensated by an increase in compositional dissimilarity, indicating that patch interiors contain a subset of those species found at patch edges, rather than species unique to patch interiors. These differences within and among high-severity patches are largely attributable to tree and primary cavity nesting species, which were more common in small patches and along patch edges. Neither ground nor shrub nesting guilds had higher species richness in large patch interiors despite the greater cover of early-seral habitat in the local landscape. However, differential responses to distance to patch edge and its interaction with time since fire resulted in relative shifts in community composition where ground and shrub nesting species made up a greater percentage of interior communities with greater time since fire, while tree and primary cavity nesters experienced declines. Taken together these results suggest that small high-severity patches or large patches with high edge-area ratios support higher levels of bird diversity than large high-severity patches containing extensive interior habitat.

These findings further our understanding of how montane bird communities respond to high-severity wildfire but also highlight areas of future research. Species occupancy is generally correlated with abundance (Kery and Royle 2015), but the latter along with fecundity data can provide a more nuanced picture than occupancy of how individual species respond to their environment. Further, our data was limited to 30 years since fire with relatively few surveys in the oldest fires conducted far from edges of high-severity patches (e.g. > 250 m). More extensive sampling of older fires would allow for a more complete understanding of the relationship between fire patterns, vegetation succession and bird diversity. We also limit our assessment of patch dynamics to one local-level metric (distance to edge) and one patch-level metric (size). Assessments of other landscape metrics and the broader landscape context may complement this work and our understanding of post-fire habitats. As burn severity data accumulate (first available starting in 1984) and recent large wildfires age, future studies can further elucidate the relationship between high-severity patch dynamics and long-term avian succession.

High-severity patches and pyrodiversity

Pyrodiversity, or the variation in a landscape's history of fire severity, patch sizes, frequency, and seasonality likely plays an important role in maintaining biodiversity in fire-adapted ecosystems (Steel et al. In Review, Martin and Sapsis 1992, Tingley et al. 2016). Due to their proximity to lower-severity areas, the local landscape surrounding edges of high-severity patches contain greater variation in fire severity than patch interiors. Thus, our finding that edges of high severity patches support greater species richness is consistent with past research showing many western bird species are tolerant or even benefit from creation of habitat edges (McGarigal and McComb 1995, Sisk and Battin 2002), and that variation in burn severity is positively associated with bird diversity (Tingley et al. 2016). Diversity of other taxa in the Sierra Nevada including bats (Steel et al. 2019) and plant-pollinator communities (Ponisio et al. 2016) also increase with variation in burn severity suggesting that pyrodiversity likely promotes biodiversity generally. Although a landscape composed of a variety of patch sizes may promote biodiversity, many of the large patches assessed in this study far exceeded the estimated natural range of variation where the majority of high-severity patches were likely less than 10 ha (Safford and Stevens 2017). The availability of habitat features such as snags and montane chaparral necessary for early-seral birds may be sufficient in much smaller high-severity patches than the largest patches in the fires we studied. The relatively strong influence of distance to patch edge suggests that shape complexity (i.e., the amount of edge per unit area) may also be an important consideration as large patches may accommodate high bird diversity if most of its area is near less disturbed habitats. Additionally, edges of high-severity patches appear to accommodate individual bird species of conservation concern with otherwise contrasting habitat needs. While we found little effect of distance to patch edge on occupancy of breeding Black-backed Woodpeckers, other studies have found juveniles of the snag specialist preferred patch edges to interiors (Stillman et al. 2019) and nest site suitability was lower toward the center of large patches (Campos et al.

2020). On the other hand, the mature forest specialist Spotted Owl (*Strix occidentalis*) selects small high-severity patches (i.e., < 115 ha) and uses patch edges but avoids large patches and interior areas beyond approximately 100 m (Kramer et al. 2020, Jones et al. 2020).

The temporal components of pyrodiversity have been less explicitly studied but our findings that individual species and guild richness peak at different years reinforces previous findings that a variety of fire ages within a landscape would promote overall bird diversity (Smucker et al. 2005, Taillie et al. 2018). Both absolute richness and the post-fire rate of change was dependent on distance to patch edge, perhaps reflecting that proximity to residual live trees and greater natural regeneration of conifers near patch edges (Greene and Johnson 1995, Welch et al. 2016) might be important for the bird community in this region. We suspect that the relatively high richness of tree nesters soon after fire is indicative of high site fidelity for some species as well as delayed tree mortality providing temporary residual habitat (Hood et al. 2007). Primary cavity nesters also showed greater richness soon after fire and a decline with years since fire, likely reflecting woodpecker food resources associated with recently killed trees and subsequent losses of snag habitat as fire-killed trees decay and fall (Raphael et al. 1987, Smucker et al. 2005, Ritchie et al. 2013, White et al. 2016). This decline was less pronounced along edges where woodpeckers can switch to using residual live trees (Dudley and Saab 2007). Richness peaked at later times since fire for the other three nesting guilds. Slightly more secondary cavity nesters were found near patch edges and mean guild richness is expected to reach a higher peak as compared to patch interiors, but distance to patch edge had little influence on either ground or shrub guild richness. Overall, high-severity patches of a range of ages contribute to montane bird diversity with edges producing greater species richness across the gradient of years since fire.

Changing fire regimes and outlook for the future

Montane bird communities face opposing but interconnected changes to habitats shaped by fire or its absence. A century of fire exclusion in western forests has led to over-densification and in some areas and a loss or degradation of early-seral habitats (Betts et al. 2010). Due to these changes and factors associated with climate change (Parks and Abatzoglou n.d., Westerling 2016), contemporary fires are becoming more severe with larger patches of high-severity effects all while a deficit of low- to moderate-severity fire persists in these fire-adapted ecosystems (Mallek et al. 2013). As fires continue to grow larger and more severe, we are likely to see directional shifts from conifer forests to montane chaparral or forests dominated by resprouting oaks (Coppoletta et al. 2016, Tepley et al. 2017, Safford and Vallejo 2019, Coop et al. 2020). Such shifts would have mixed consequences for the montane bird community. Increases in chaparral habitat will benefit shrub-associated bird species, but when conversions are primarily concentrated in large patches with proportionally less edge, overall diversity is likely to decline at least within the first 30 years after fire. On the other hand, yellow pine and mixed conifer forests of the Sierra Nevada have experienced a massive reduction in acres burned since the onset of modern fire suppression (Stephens et al. 2007, Mallek et al. 2013) and large modern wildfires can help alleviate this fire deficit when they contain extensive areas of low- to moderate-severity which can also promote forest resilience (Steel et al. In Review, Collins et al. 2018, Kane et al. 2019). Thus, increasing prevalence of uncharacteristically large fires promise both positive and negative impacts with some areas representing degraded ecosystem resilience and biodiversity while others supporting partially restored ecological communities.

Management implications

High-severity patches, which represent the greatest ecosystem change within a wildfire footprint, are also frequently the targets of post-fire management. To reforest a burned area quickly, practices include removing snags, controlling shrubs mechanically or chemically, and planting desired tree species (Lindenmayer et al. 2012, North et al. 2019). These management actions themselves impact the local bird community, particularly species that rely on snags, shrubs, and herbaceous vegetation as habitat (Saab et al. 2009, Lindenmayer et al. 2012). Consequently, reforestation may eventually benefit late-seral species by accelerating forest succession, whereas high-severity wildfire without intensive post-fire management may benefit early seral species for decades. When attempting to balance multiple objectives with limited funds, reforestation on public lands may be conducted in some areas with natural succession left to proceed in others (North et al. 2019). These tradeoffs are accentuated in modern wildfires, which are progressively more likely to be large and severe with increasingly large and simply shaped high-severity patches (Miller et al. 2012, Westerling 2016, Steel et al. 2018). If reforestation efforts occur, managers concerned with avian diversity can prioritize interiors of large high-severity patches where average bird diversity is lowest and where natural conifer reforestation is least likely to succeed (Welch et al. 2016, Shive et al. 2018). In contrast, avoiding intensive management along patch edges and within high-severity patches of sizes that fall within the natural range of variation can retain pyrodiversity and diversity of the broader avian community. Further, prescribed fire and managed wildfire that increase pyrodiversity in both previously burned and fire suppressed forests can help restore fire-adapted habitats and promote bird diversity as the avian community responds to accelerating global change.

Acknowledgments

We thank the National Forests in the Sierra-Cascades region, especially the Eldorado, Lassen and Plumas National Forests and the Region 5 staff for their support and coordination with data collection. We are indebted to numerous dedicated field staff, in particular B. Campos, M. Preston, J. Stagner, P. Taillie, and J. Tietz. We also thank Mark Schwartz and Malcolm North for providing critiques of early versions of this article, and Matt Williamson with assistance with Stan. Funding was provided by the USDA Forest Service, the Richard Grand Foundation and the University of California, Davis.

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