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Interacting and non-linear avian responses to mixed-severity wildfire and time since fire

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Abstract. Non-linear and interacting effects of fire severity and time since fire may help explain how pyrodiversity promotes biodiversity in fire-adapted systems. We built on previous research on avian responses to fire by investigating how complex effects of burn severity and time since fire influenced avian community composition across the northern Sierra Nevada, California. We conducted avian point counts from 2009 to 2015 in 10 fires that burned between 2000 and 2014, resulting in a chronosequence of 1–15 yr post-fire. We estimated the effects of burn severity, time since fire, non-linear and interacting effects of fire severity and time since fire, pre-fire forest conditions, and several physiographic parameters on the density of 44 breeding bird species using hierarchical distance sampling models. In addition, we fit separate models to observations of each species in unburned forest to compare species' densities between burned and unburned forests. At least one of the non-linear or interaction fire effects was significant for 27 (61%) of the 44 bird species. The quadratic effect of time since fire was an important predictor of post-fire densities of 20 species, illustrating the dynamic nature of this post-wildfire avian community. Greater maximum densities were estimated at some combination of burn severity and time since fire than in unburned forest for 13 of the 44 (30%) species, only one of which reached maximum density following low-severity fire. In contrast, all of the 12 species that were more abundant in unburned forest reached maximum post-fire densities in fires that burned at low severity. Results from the study suggest that consideration of the non-linear and interacting effects of fire severity and time since fire is important to fully understanding post-wildfire responses for a majority of birds. Moreover, the study supports a growing body of literature that indicates mixed-severity fire is essential for conserving avian diversity in many fire-maintained systems.

Key words: distance sampling; disturbance; pyrodiversity; Sierra Nevada; succession.

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INTRODUCTION

Fire is widely recognized as a fundamental driver of biodiversity in forested systems (Driscoll et al. 2010). Specifically, the components of a fire regime, such as return interval, severity, heterogeneity, and size, directly shape the distribution of species in the post-fire environment (Lindenmayer et al. 2014, Ponisio et al. 2016). As fire regimes change because of increasing human influence on global environmental conditions (Cary and Banks 2000, Miller et al. 2009*b*), mimicking historical fire regimes often is advocated to best conserve biodiversity (Noss et al. 2006). However, considerable uncertainty remains regarding specific characteristics of historical fire regimes for many regions. Recently, studies have emphasized the importance of using ecological responses to fire to inform fire management approaches that support biodiversity (Odion et al. 2014, Kelly et al. 2015, Hutto et al. 2016, Kelly and Brotons 2017). Because birds are diverse and certain species often are associated with specific vegetation conditions that develop in the wake of fire (Smucker et al. 2005, Hutto 2008, Rush et al. 2012, White et al. 2015), this taxon can serve as an indicator of broader responses to pyrodiversity among other wildlife taxa (Hutto et al. 2008).

Though several factors may influence responses by birds to wildfire, including pre-fire forest composition (Nappi and Drapeau 2011), topography (Flatley et al. 2011), and disturbance history (Albanesi et al. 2014), burn severity ranks as one of the most important (Smucker et al. 2005, Hutto 2008, Stephens et al. 2015). The severity of a fire refers to the degree to which a site was altered by fire, usually in regard to changes in both above- and below-ground biomass (Keeley 2009, Miller et al. 2009*a*). Previous studies highlighted the importance of areas that burned at high severity to a number of bird species (Smucker et al. 2005, Kotliar et al. 2007, Hutto and Patterson 2016), and how diversity in burn severity, a component of pyrodiversity (Martin and Sapsis 1992), may promote avian diversity in fire-adapted forests (Tingley et al. 2016).

Although the positive relationship between pyrodiversity and biodiversity is increasingly recognized (Lashley et al. 2014, Hiers et al. 2016, Tingley et al. 2016), changes in species' densities over time may aid in understanding the mechanisms underlying the relationship between pyrodiversity and biodiversity. Because of distinct and predictable associations with successional changes in vegetation (McAthur and McAthur 1961), avian responses to fire over time should aid our understanding of the relationship between pyrodiversity and biodiversity. Though some bird species respond rapidly to fire (Meehan et al. 2003), others may not respond until several years after the fire has burned (Stephens et al. 2015). The amount of time considered by a post-fire study can influence the observed magnitude and direction of bird responses and thus the interpretation of the effects of fire on species (Smucker et al. 2005, Hutto and Patterson 2016). However, few studies of the effects of fire on birds have investigated long-term (i.e., >10 yr) responses to time since fire (Kelly et al. 2015, Rose and Simons 2016). To address this need, we investigated bird responses to 10 fires that burned at different times, effectively substituting space for time. Previous studies have demonstrated the utility of such an approach when longer longitudinal studies or before–after control–impact studies are impractical (Pickett 1989, Adler and Lauenroth 2003, Soininen 2010). Furthermore, space-for-time substitution may underestimate animal responses compared to before–after control–impact designs, thus serving as a conservative estimate of system dynamics (França et al. 2016).

Bird responses to fire severity and time since fire may be complex, and the inclusion of non-linear and interacting terms may elucidate these more nuanced responses. Additional information on the responses of target species can help inform evidence-based land management decisions (Guisan et al. 2013, Latif et al. 2013). Following fire, vegetation composition and structure change rapidly (Moreira et al. 2003), and different bird species may perceive high-quality habitat at different points across this range of vegetation conditions (Rose and Simons 2016, Tingley et al. 2016). Similarly, variation in fire intensity can produce a wide range of post-fire conditions, which may result in non-linear responses by birds to burn severity (Kotliar et al. 2007). Because forest bird communities are closely associated with vegetation composition and structure (Engstrom et al. 1984), these non-linear vegetation responses following fire likely are relevant to avian community dynamics in post-fire environments (Raphael et al. 1987, Watson et al. 2012). In addition to complex responses to each of time since fire and burn severity independently, bird responses to fire may be further complicated by an interaction between these factors. Ecological processes, such as the timing and successional trajectory of plant communities, may occur at different rates across different burn severities within burned areas (Lecomte et al. 2006, Benscoter and Vitt 2008).

A better understanding of avian responses to fire can help inform the debate surrounding the natural range of variability of the fire regime and guide forest management approaches in fire-maintained systems. In dry forests of western North America, there is an ongoing debate regarding historical fire regimes (Williams and

Baker 2014, Hanson and Odion 2015, Miller and Safford 2017), which often serve as restoration targets (Varner et al. 2005, Millar et al. 2007). Mixed-severity fire has long been an important component of the Sierra Nevada Ecosystem (Williams and Baker 2012, Mallek et al. 2013), but the extent of forest burning at high severity is thought to have increased in recent decades (Miller et al. 2009*b*). However, disagreement remains regarding the historical relative contributions of low-, moderate-, and high-severity fire and the current departure from those historical levels (Marlon et al. 2012, Fulé et al. 2014, Hanson and Odion 2014). Yet, characterizing animal responses to fire can provide important insight toward both historical fire regimes and future forest management (Hutto et al. 2016, Latif et al. 2016, Dellasala et al. 2017).

We built on previous research on avian responses to wildfire by investigating the relative importance of non-linear and interacting effects of burn severity and time since fire. This work fills an important information gap on avian responses to fire in forests of western North America by investigating individual species responses in the Sierra Nevada out to 15 yr post-fire. We modeled the densities of 44 bird species across 10 wildfires in the northern Sierra Nevada and southern Cascades, California, USA, over a 15-yr post-fire chronosequence. We predicted that if Sierra Nevada birds evolved under a natural disturbance regime dominated by low-severity fire, then most species would reach their greatest densities in areas burned at low and moderate severities (Hutto et al. 2008). We then compared the maximum post-fire densities for these species to densities in the surrounding unburned forest to determine which species were most affected, positively or negatively, by wildfire.

METHODS

Study location

We conducted the study on the Plumas, Lassen, and Tahoe National Forests in northern California. Pre-fire habitat type was primarily Sierra mixed conifer forest, with areas of montane chaparral, eastside pine, montane hardwood, and true fir forests (USDA Forest Service, 1999). The elevations of sites surveyed ranged from 1079 to 2170 m with a mean of 1649 m.

Site selection

We combined data from three avian monitoring programs with standardized data collection methods, but different site selection protocols, that had sampling stations within a wildfire perimeter that burned between 2000 and 2014. For all three programs, the potential sampling area was limited to US Forest Service land with a slope of <40% and within 1500 m of a navigable road or trail to allow access and safe navigation on foot in a timely manner. The first monitoring program was established to monitor the effects of the Cub, Moonlight, and Storrie fires on birds (Seavy et al. 2012). The second monitoring program was a Sierra-wide National Forest bioregional monitoring project designed to track trends in upland breeding birds (Roberts et al. 2011). Finally, we included stations originally established between 2002 and 2005 in unburned forest, but that subsequently burned in the Chips and Rich fires (Burnett and Roberts 2015, Campos and Burnett 2015). Across all three programs, a minimum spacing of 250 m was maintained between stations. When combined, these three monitoring programs resulted in a sample of 577 stations across 10 fires (Table 1). We then excluded all data from visits to stations that were affected by post-fire silvicultural treatments (e.g., salvage logging, reforestation) or were within 100 m of a subsequent fire, reducing the dataset to 466 of the 577 originally

Table 1. Fire names, National Forest unit, year burned, number of years post-fire that sampling occurred, number of stations, and stacked data sample size.

Fire name	Forest	Year burned	Years post-fire	Stations	N
Storrie	Lassen and Plumas	2000	9–15	71	224
Star	Tahoe	2001	9–14	9	49
Straylor	Lassen	2004	6–11	10	59
Boulder	Plumas	2006	4–9	2	12
Moonlight	Plumas	2007	2–8	94	349
Rich	Plumas	2008	1–7	18	69
Cold	Plumas	2008	3–7	10	45
Cub	Lassen	2008	1–7	66	258
Chips	Lassen and Plumas	2012	1–3	157	439
Bald	Lassen	2014	1	29	29
Total burned				466	1533
Unburned				785	3307

Note: N is stations × years surveyed.

selected stations (Fig. 1). The average number of years surveyed per station was 3.2 (range 1–6 survey years). To provide context to predicted bird densities in burned forest, we selected an additional set of points that were not burned. These unburned stations were comprised of all remaining stations from the same three monitoring programs that were sampled between 2009 and 2015. In addition, we excluded all stations outside of the elevation range of the burned station and

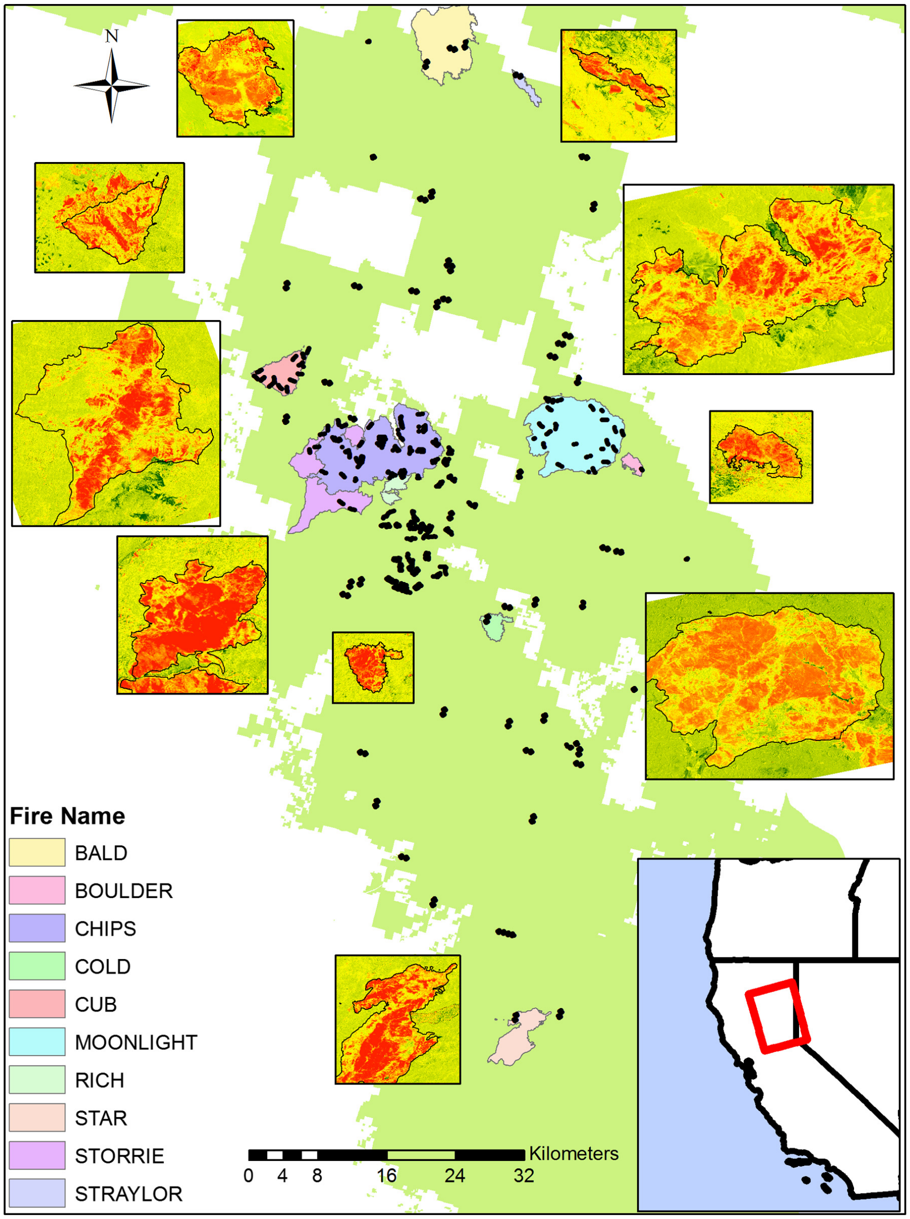

Fig. 1. The bird community was sampled between 2009 and 2015 at 466 point-count stations that were distributed across 10 mixed-severity wildfires in the northern Sierra Nevada and southern Cascades mountains, California, USA, as well as 785 stations in unburned forest within the same latitude and elevation range as the burned stations. Inset maps show fire perimeters as solid black line and burn severity spectrum as green (low severity) to red (high severity).

those that were within 1 km of a fire boundary for all fires that burned since 1984 when standardized, complete record keeping on fire in our study area began, resulting in 785 unburned points (Table 1).

Bird community surveys

During the peak of the breeding season (May 10–June 30) from 2009 to 2015, we surveyed the avian community using 5-min point-count surveys (Reynolds et al. 1980, Ralph et al. 1995). All birds detected during the 5-min survey were recorded according to their initial distance from the observer. Counts began after sunrise, were completed within 4 h of sunrise, and did not occur in inclement weather. We conducted 1–2 visits each year and alternated the observers each visit in a given year.

Habitat variables

We quantified burn severity using the percent change in canopy cover derived from the relative difference normalized burn ratio (Miller et al. 2009*a*, MTBS 2009). We first applied low-pass spatial filter to these data and then averaged across neighboring 30 × 30 m cells by sampling with bilinear interpolation to consider a spatial scale that matches the scale at which we aggregated the bird detections. All spatial processing was done in ArcMAP 10 (ESRI 2011). Values of burn severity for stations ranged from 0 to 100% ($\bar{x}$ = 38). Though we incorporated burn severity as a continuous variable, we used categories of low, moderate, and high severity, corresponding to 0–25%, 26–75%, and >75% canopy cover reduction, respectively, to interpret our findings in the context of other studies (Miller et al. 2009*a*). We did not account for the time of year in which the fire occurred, though all fires burned between late June and the end of September. We incorporated time since fire as the number of growing seasons since the fire burned, which increased by 1 annually for a total range of 1–15 yr.

We used existing vegetation data derived from 1997 to 2002 Landsat imagery, before any of the fires burned, to describe vegetation conditions prior to burning (USDA Forest Service 1999). These data include categorical definitions of forest type, stand density, and tree size across the Sierra Nevada (USDA Forest Service 1981, CDFG 2008). To reduce the degrees of freedom associated with incorporating three separate variables, we combined these variables to create a single, five-category variable of pre-fire forest condition. Specifically, we calculated the mode within 100 m for each of the three variables at each station, and then used these values to assign each station to one of five forest conditions: shrub/chaparral, young forest, open-canopy forest, mid-seral closed-canopy forest, and mature closed-canopy forest (Table 2). We calculated this same forest condition variable for the unburned stations to determine existing forest condition. For these unburned stations, we used an updated version of the vegetation data that more accurately reflected the forest conditions during the period the stations were surveyed (USDA Forest Service 2015). We also calculated the average slope, aspect (converted to Solar Radiation Index as defined in Keating et al. 2007), and elevation within 100 m of each station from a digital elevation model (USGS 2009).

To quantify the influence of vegetation structure surrounding the survey points on the observers' ability to detect birds, we conducted vegetation surveys within 50 m of each station using a relevé-based protocol on one to three occasions during the study. We estimated the percent cover of trees (>5 m tall) and the basal area of snags from these surveys. We did not include the basal

Table 2. Vegetation data collected by the United States Forest Service between 1997 and 1999 was used to estimate the pre-fire forest condition in the northern Sierra Nevada by averaging and combining habitat type, average tree size class, and average tree density class into five pre-fire condition classes.

Condition class	Habitat type	Tree size class (cm)	Forest tree density	N
Shrub	Shrub, chaparral	<15	NA	194
Young forest	Mixed conifer, fir, pine	15–28	All	107
Open canopy	Mixed conifer, fir, pine	>28	10–39%	105
Mid-seral closed-canopy	Mixed conifer, fir, pine	28–61	>40%	431
Mature closed-canopy	Mixed conifer, fir, pine	>61	>40%	696

area of snags as a covariate for the unburned stations, because snags were a trivial component of standing wood in these stands. We then calculated yearly values of these covariates at each station using the value from the nearest prior-year survey to use as covariates on detection. We averaged the values of the previous and new survey to create a transitional value for the years when no vegetation data were collected. We conducted vegetation surveys more frequently in the early post-fire period to account for our presumption of more rapid successional progression.

Analysis

We attempted to evaluate the responses of as many species as possible to better understand how the majority of the avian community responded to fire. We removed species that were inadequately sampled (e.g., nocturnal and wide-ranging species) or those not associated with uplands (e.g., waterbirds). We then fit models for all of the remaining species, but subsequently excluded any species for which we were unable to estimate all model parameters with reasonable precision, resulting in 44 total species (Table 3). These 44 species represent the vast majority of individuals and species of breeding birds in uplands of the northern Sierra Nevada.

We estimated bird density using hierarchical distance models that incorporated all detections within 150 m of observers using the distsamp function in the R package unmarked, version 0.12-2 (Fiske and Chandler 2011, R Core Team 2014). This modeling framework allowed us to estimate the density of each species, corrected for variation in the observers' ability to detect different species as a function of detection distance. Because time since fire changes annually and most sites were sampled in more than one year, we treated each station–year combination as an independent experimental unit. This approach allows bird density to vary over time since fire, but avoids the high computational demand of more explicitly parameterizing population demographics in a distance sampling framework (Sollmann et al. 2015). We acknowledge that this assumption may potentially underestimate error in the model parameter coefficients, but such bias would largely be limited to those parameters that do not vary with time. Furthermore, we are interested in general patterns as opposed to conducting specific hypothesis tests, and as such, believe that the impact of this bias on our conclusions is negligible. Prior to model fitting, all continuous covariates were standardized. We examined the degree of collinearity between all variables using the variable inflation factor (VIF) and detected no evidence for a high degree of collinearity (VIF < 0.4 for all variables).

We included covariates on both density and detection. To estimate detection probability as a function of distance, we fit a model for each of three key functions (half normal, hazard, and uniform) and selected the one with lowest Akaike's Information Criterion. Each of these preliminary detection models included linear effects of burn severity, elevation, slope, and time since fire on density, with no covariates on detection. We then used the best key function to fit a full model for each species, which included linear effects of burn severity, time since fire (TSF), slope, aspect, elevation, and pre-fire condition as covariates on the density at a station in a given year (λ_i; Eq. 1), as well as field-collected, year-specific estimates of tree cover and snag basal area (burned forest observations only) as covariates on the shape parameter of the detection function (σ_i; Eq. 2). In addition, we included quadratic effects of burn severity, time since fire, and elevation, as well as an interaction between burn severity and time since fire, as covariates on density. We used a multiple intercept approach to incorporate pre-fire condition (PFC), rather than estimate the effect of each pre-fire condition category relative to a designated reference condition (Eq. 1). We fit an analogous model to the observations from the unburned stations for each species, but omitted the effects of burn severity and time since fire on density, as well as the effect of snag basal area on detection.

$$\begin{aligned}\log(\lambda_i) \sim \mathrm{PFC}_i &+ (\beta_1 \times \mathrm{Severity}_i) \\ &+ (\beta_2 \times \mathrm{Severity}_i^2) \\ &+ (\beta_3 \times \mathrm{TSF}_i) + (\beta_4 \times \mathrm{TSF}_i^2) \\ &+ (\beta_5 \times \mathrm{Severity}_i \times \mathrm{TSF}_i) \\ &+ (\beta_6 \times \mathrm{Slope}_i) + (\beta_7 \times \mathrm{Aspect}_i) \\ &+ (\beta_8 \times \mathrm{Elevation}_i) \\ &+ (\beta_9 \times \mathrm{Elevation}_i^2)\end{aligned} \tag{1}$$

Table 3. The names of the 44 bird species for which we modeled the effects of burn severity, time since fire, pre-fire forest condition, and topography in the northern Sierra Nevada, California, USA (2009–2012).

Common name	4-letter abbreviation	Scientific name
American Robin	AMRO	*Turdus migratorius*
Black-backed Woodpecker	BBWO	*Picoides arcticus*
Brown-headed Cowbird	BHCO	*Molothrus ater*
Black-headed Grosbeak	BHGR	*Pheucticus melanocephalus*
Brown Creeper	BRCR	*Certhia americana*
Cassin's Finch	CAFI	*Haemorhous cassinii*
Cassin's Vireo	CAVI	*Vireo cassinii*
Chipping Sparrow	CHSP	*Spizella passerina*
Dark-eyed Junco	DEJU	*Junco hyemalis*
Dusky Flycatcher	DUFL	*Empidonax oberholseri*
Evening Grosbeak	EVGR	*Coccothraustes vespertinus*
Fox Sparrow	FOSP	*Passerella iliaca*
Golden-crowned Kinglet	GCKI	*Regulus satrapa*
Gray Flycatcher	GRFL	*Empidonax wrightii*
Green-tailed Towhee	GTTO	*Pipilo chlorurus*
Hammond's Flycatcher	HAFL	*Empidonax hammondii*
Hairy Woodpecker	HAWO	*Leuconotopicus villosus*
Hermit Thrush	HETH	*Catharus guttatus*
Hermit Warbler	HEWA	*Setophaga occidentalis*
House Wren	HOWR	*Troglodytes aedon*
Lazuli Bunting	LAZB	*Passerina amoena*
MacGillivray's Warbler	MGWA	*Geothlypis tolmiei*
Mountain Bluebird	MOBL	*Sialia currucoides*
Mountain Chickadee	MOCH	*Poecile gambeli*
Mourning Dove	MODO	*Zenaida macroura*
Mountain Quail	MOUQ	*Oreortyx pictus*
Nashville Warbler	NAWA	*Leiothlypis ruficapilla*
Northern Flicker	NOFL	*Colaptes auratus*
Olive-sided Flycatcher	OSFL	*Contopus cooperi*
Pine Siskin	PISI	*Carduelis pinus*
Purple Finch	PUFI	*Haemorhous purpureus*
Red-breasted Nuthatch	RBNU	*Sitta Canadensis*
Red-breasted Sapsucker	RBSA	*Sphyrapicus ruber*
Spotted Towhee	SPTO	*Pipilo maculatus*
Steller's Jay	STJA	*Cyanocitta stelleri*
Townsend's Solitaire	TOSO	*Myadestes townsendi*
Warbling Vireo	WAVI	*Vireo gilvus*
White-breasted Nuthatch	WBNU	*Sitta carolinensis*
Western Tanager	WETA	*Piranga ludoviciana*
Western Wood-pewee	WEWP	*Contopus sordidulus*
White-headed Woodpecker	WHWO	*Picoides albolarvatus*
Wilson's Warbler	WIWA	*Cardellina pusilla*
Yellow Warbler	YEWA	*Setophaga petechia*
Yellow-rumped Warbler	YRWA	*Setophaga coronata*

$$\log(\sigma_i) = \beta_1 + (\beta_2 \times \mathrm{Snag}_i) + (\beta_3 \times \mathrm{Tree}_i) \quad (2)$$

We characterized species' responses to fire according to their maximum post-fire densities. We used the "predict" function in the R package *stats* to calculate predicted densities for each species across the range of burn severity and time since fire (with other variables held at their average) and noted at which value of these covariates each species maximum density occurred. For burn severity, we used severity thresholds from Miller et al. (2009*a*) to post hoc categorize responses as low severity (<26%), moderate severity (26–75%), and high severity (>75%). In a similar manner, we categorized responses in terms of time since fire as early (1–5 yr), mid (6–10 yr), and late (11–15 yr).

To evaluate the post-fire response relative to unburned forest for a given species, we compared 95% confidence intervals of the predicted maximum post-fire density to the 95% confidence interval of the predicted density in unburned forest. Preliminary analysis revealed that 16 species reached their maximum density in the first year after low-severity fire. Based on field observations and our existing knowledge of habitat associations, we suspected these high densities were at least partially explained by site fidelity and individuals packing into remnant green forest in the first breeding season after a fire. Thus, for these 16 species that reached their greatest density 1 yr post-fire in low-severity burns, we also calculated the average density across the 15-yr chronosequence and compared the confidence intervals of these average densities to the 95% confidence intervals of the predicted densities in unburned forest. When calculating the predicted densities for all species at the burned and unburned stations, we held all other covariates at their average values. Finally, we examined the effects of pre-fire forest condition by using each species' model to predict the density of that species at each of the five pre-fire condition classes while holding other covariates at mean values.

RESULTS

Wildfires influenced the density of many of the bird species we observed. More species reached maximum density following either high- or low-severity fire (18 and 16 species, respectively) than following moderate-severity fire (10 species; Fig. 2). Regarding temporal responses, 26 species reached a maximum density within the first 5 yr following fire, seven species reached maximum density between 6 and 10 yr, and 11 species reached maximum density between 11 and 15 yr. Greater densities were estimated at some combination of burn severity and time since fire than in unburned forest for 13 of the 44 (30%) species (Fig. 3). Of these species, only dark-eyed junco was predicted to reach maximum density following low-severity fire. Five (11%) species were predicted at significantly greater densities in unburned forest. However, when we averaged predicted densities across time since fire for the 16 species that were predicted to reach maximum post-fire densities in the first year following low-severity fire, the number of species that were predicted to be more abundant following fire changed from 13 to 12 and the number of species more abundant in unburned forest changed from 5 to 12 (Fig. 3).

The interaction between burn severity and time since fire or non-linear effects of either helped explain the post-fire response for the majority of species. At least one non-linear effect or interaction was significant for 27 (61%) of the 44 bird species we modeled (Fig. 4). The quadratic effect of time since fire was significant for more species (20) than either the quadratic effect of burn severity (9) or the interaction (12; Fig. 4). Quadratic parameter estimates were largely negative for both time since fire (80%) and burn severity (66%). Negative values for a quadratic parameter generally reflect an initial increase in density followed by a decrease over time or severity (Fig. 5). However, the realized response pattern depends on the magnitude and direction of the other associated linear and interaction effects. The interaction effect was significant for 12 species, 10 of which reached maximum density following high-severity fire, and parameter estimates of these effects were negative for 10 of these 12 species. As with the quadratic effects, the realized response induced by the interaction depended on the magnitude and sign of the linear and quadratic burn severity and time since fire effects. For example, for some species, like hairy woodpecker, the interaction effect resulted in a stronger, more immediate post-fire response at high severity, compared to a more delayed, smaller density increase at low severity (Fig. 5c).

Avian community composition changed rapidly over the first 15 yr post-fire. Species associated with ephemeral vegetation conditions following fire tended to have negative estimates for the quadratic effect of time since fire, reflecting an initial increase in density, followed by a decrease. For example, the most immediate responders were primary cavity nesters such as hairy and black-backed woodpecker, followed by secondary cavity nesters such as mountain bluebird

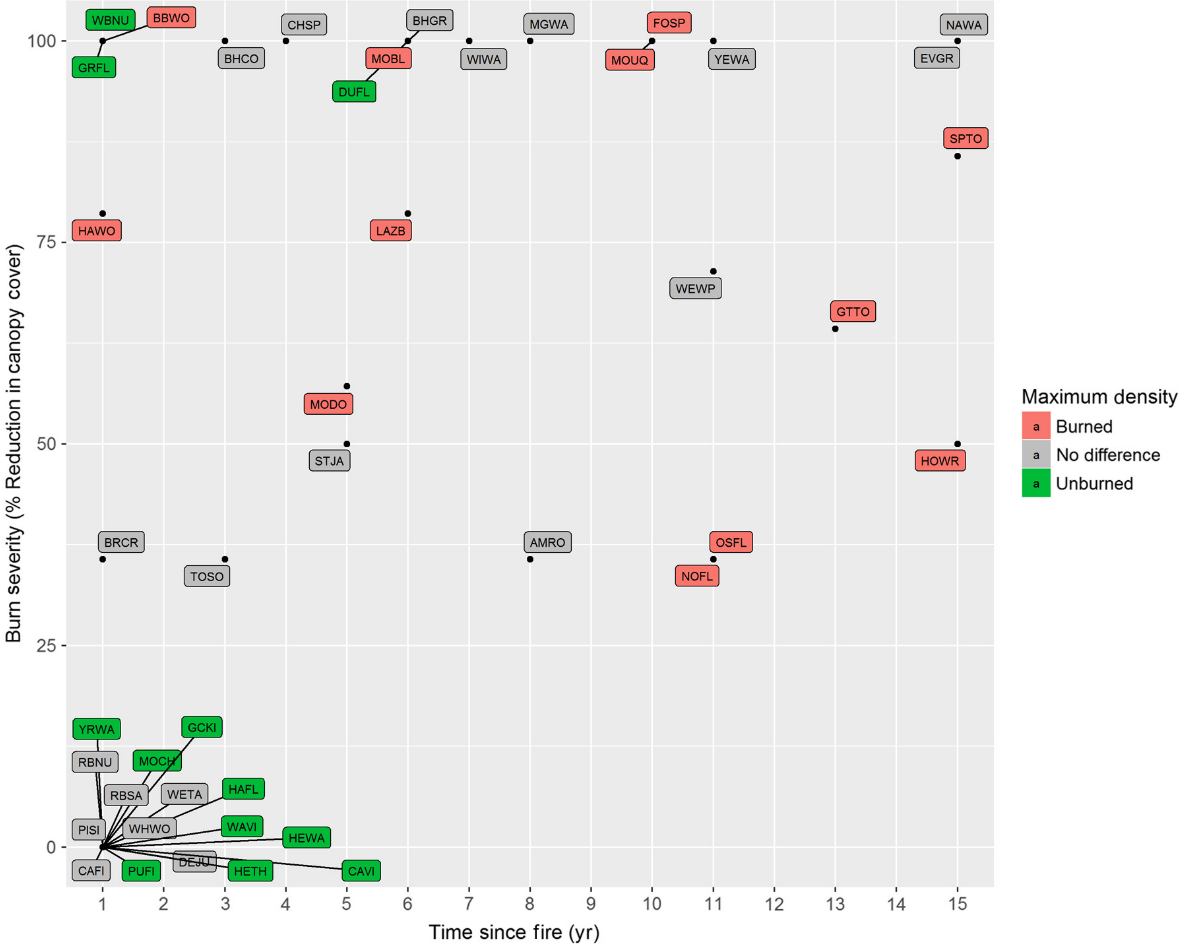

Fig. 2. The 44 most abundant species following wildfire in the northern Sierra Nevada shown at the burn severity and time since fire that each was predicted to reach its maximum density, and colored according to whether the species' maximum predicted density was greater in burned (red) or unburned (green) forest. However, colors reflect the density averaged across time since fire for the 16 species that reached their maximum post-fire density in the first year following low-severity fire (i.e., the species in the lower left corner).

and house wren. Cavity nesters were among the species with the most negative parameter estimates for the interaction between burn severity and time since fire. Species associated with early successional vegetation, such as lazuli bunting and chipping sparrow, increased markedly in the first 5–10 yr following high-severity fire, followed by a rapid decline (Fig. 5b). Despite these declines, some species like lazuli bunting still occurred at greater densities 15 yr following moderate- or high-severity fire than in unburned forest. Responses for these species associated with early seral stages also included a negative interaction between burn severity and time since fire, resulting in a stronger and more immediate response at higher burn severity. Shrub-associated species, including fox sparrow, green-tailed towhee, and spotted towhee, had low predicted densities for the first 5 yr following fire. These species then dramatically increased in density between 5 and 10 yr post-fire, but this increase began to slow toward the end of the 15-yr chronosequence, suggesting they may be reaching maximum densities 15 yr post-fire.

Most of the species that reached maximum density in low-severity burns were associated with mature, closed-canopy forest and were

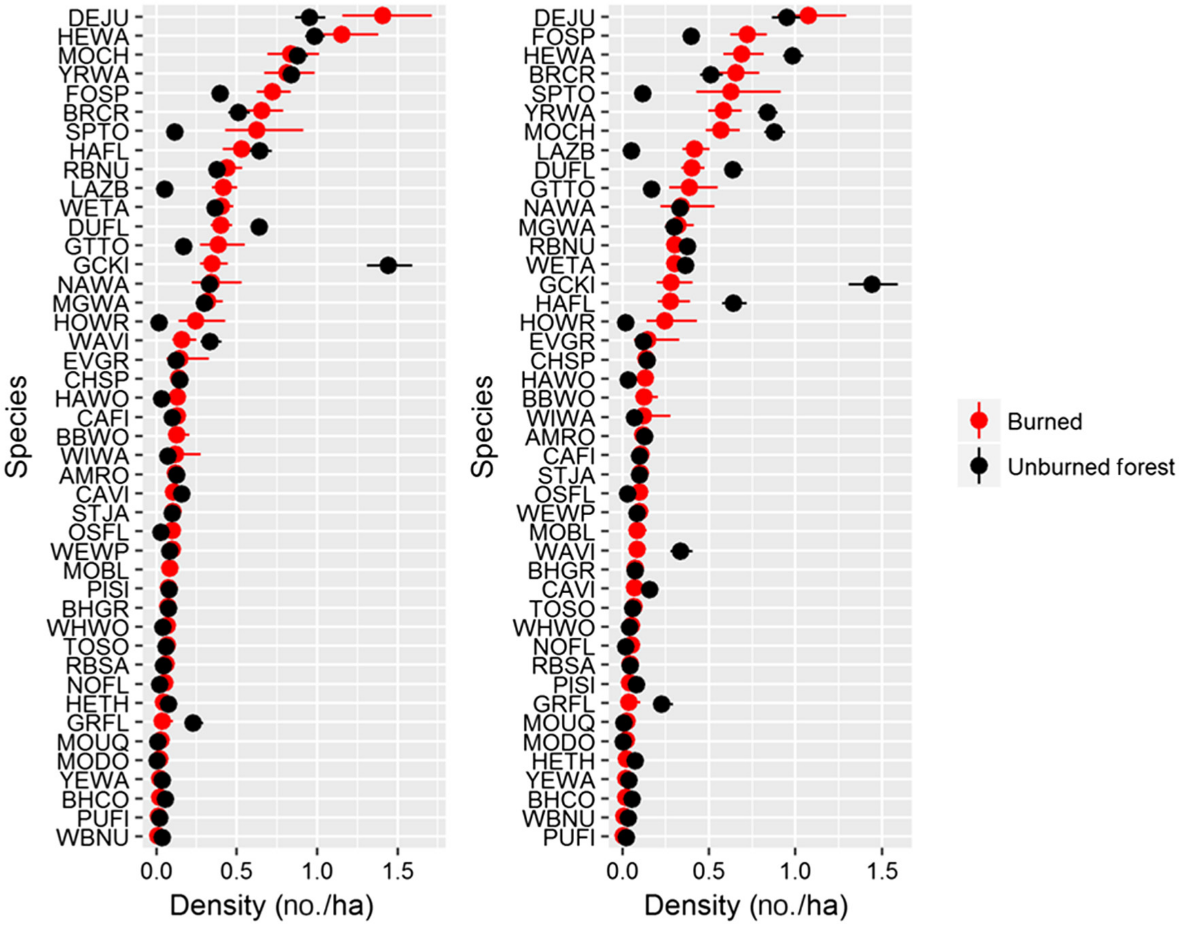

Fig. 3. The predicted densities for each of 44 bird species in unburned forest (black) and the predicted density at the combination of burn severity and time since fire where the species reached its maximum density (left panel) following wildfire (red) in the northern Sierra Nevada, California, USA. Because all 16 species that reached maximum density following low-severity fire were predicted to occur at much greater density 1 yr following fire, the predicted densities for these species averaged across the 15 yr of time since fire are also shown (right panel). There were not enough observations in unburned forest to predict densities of black-backed woodpecker (BBWO) or mountain bluebird (MOBL).

predicted to occur at greater densities in unburned forest. However, some of these species did have greater densities immediately following low-severity fire than in unburned forest, including hermit warbler and Hammond's flycatcher, but these greater densities were limited to the first year post-fire. Several species that reached maximum density following low-severity fire had significant positive quadratic effects of time since fire, reflecting an initial decrease, followed by a gradual recovery in the late post-fire period. Most of these species were cavity nesters (red-breasted nuthatch, red-breasted sapsucker, and white-headed woodpecker), but also included species associated with closed-canopy forest (golden-crowned kinglet). By 15 yr post-fire, both red-breasted sapsucker and white-headed woodpecker rebounded to densities comparable to those predicted in unburned forest.

For most species, we observed little evidence to support the expectation that pre-fire forest condition was important to post-fire responses. For the vast majority of species (>90%), the mean density for the pre-fire condition at which the species was most abundant was within the confidence interval of one of the other four pre-fire

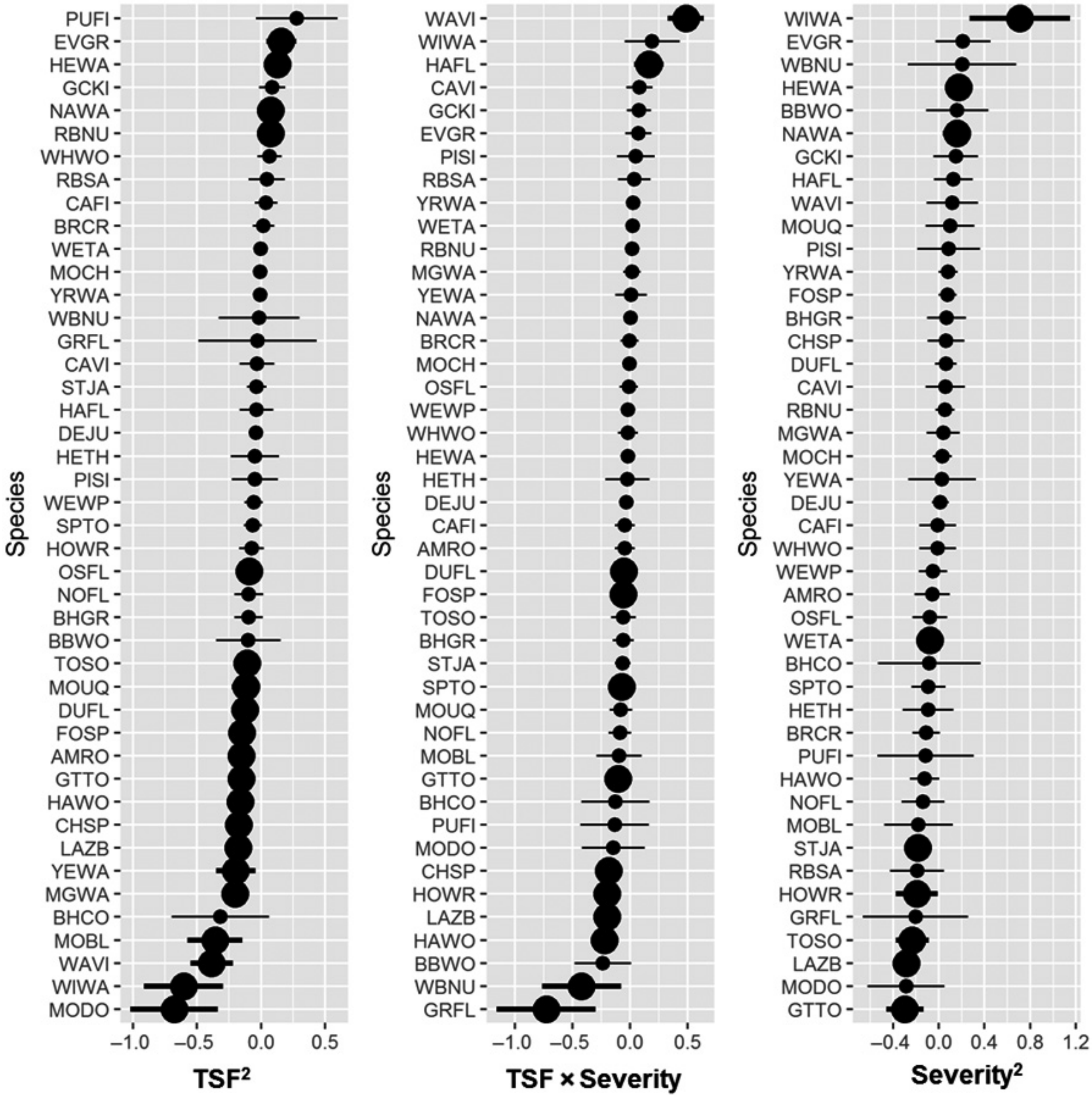

Fig. 4. Parameter estimates and 95% confidence intervals for the interaction between, and quadratic effects of, time since fire and burn severity for 44 bird species (common names can be found in Table 3) following wildfire in the northern Sierra Nevada, California, USA, between 2009 and 2015. Large dots indicate the confidence interval did not overlap 0.

conditions. Of five shrub-associated species that responded to moderate- or high-severity fire, fox sparrow was the only one that we observed at greater density in areas that were shrub-dominated or young forest prior to burning (Fig. 6). In contrast, most (9 of 16) species predicted to reach maximum density following low-severity fire were predicted to reach greater densities in open-canopy forest compared to the other pre-fire conditions, but these differences were not significant (i.e., confidence intervals overlapped).

DISCUSSION

Consideration of the effects of wildfire is fundamental to conserving biodiversity in forests

Fig. 5. The predicted density is shown across the (Fig. 5. *Continued*) range of burn severity and time since fire for three bird species (OSFL, olive-sided flycatcher; LAZB, lazuli bunting; and HAWO, hairy woodpecker) that illustrate quadratic responses to burn severity and time since fire, as well as a severity–time interaction.

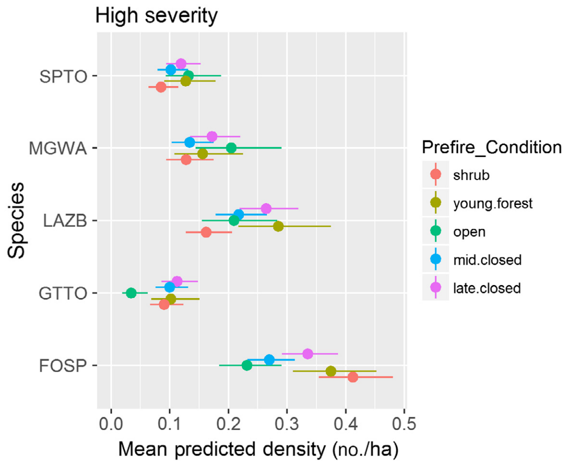

Fig. 6. The predicted densities (and 95% confidence intervals) for the five most common species (common names can be found in Table 3) that reached maximum density following moderate- or high-severity fire of the northern Sierra Nevada, California, USA, as a function of pre-fire forest condition (2009–2015).

historically shaped by fire (Brawn et al. 2001, Driscoll et al. 2010). The varied spatial and temporal responses by birds to wildfire in our study illustrate the diverse conditions created by fire and the importance of these conditions to broader patterns of animal diversity. Specifically, variation in burn severity influenced abundance of several bird species in both the near- and long-term. These lasting effects of wildfire may shape forest communities for at least several decades after a fire.

Non-linear relationships between bird density and time since fire for many bird species in this study highlight the need for managers to consider long temporal windows following fire. Most notably, shrub-associated species did not reach their greatest density until at least 10 yr after fire, when they become the most abundant guild in these burn units. Post-fire management often focuses on snag-associated wildlife but, for activities occurring a decade or more after fire, consideration of the habitat needs of shrub-associated species is important (Fontaine et al. 2009, Betts et al. 2010). Further, our results indicate a fire frequency of greater than 15 yr is needed to allow shrub-associated species to reach maximum densities, unless succession is more rapid following repeat fires (Fontaine et al. 2009). Alternatively, many closed-canopy species occurred at high densities during the first year post-fire, possibly resulting from a combination of breeding site fidelity and low-severity fire serving as a temporary refuge for these species associated with unburned forest (Lindenmayer et al. 2014). However, some of these species may be taking advantage of highly ephemeral conditions following fire, such as exposed ground for foraging. Moreover, some of the species that were more abundant in unburned forest than in burned forest reached densities comparable to or exceeding those in unburned forest approximately a decade after low-severity fire. These results are consistent with previous studies showing that even species associated with mature forest (Burnett and Roberts 2015) are resilient following mixed-severity fire (Seavy and Alexander 2014, Lee and Bond 2015, Hutto and Patterson 2016). Without considering non-linear effects and a longer post-fire period than most previous studies, responses of these species to wildlife could be misinterpreted. Approximately even proportions of the community reached maximum density at early, moderate, and longer time periods post-fire, indicating a highly dynamic post-fire avian community in the first 15 yr after fire with species adapted to exploit habitat conditions across post-fire successional stages. Ensuring the progression through these stages is likely an important consideration for forest managers aiming to conserve birds.

Our results support previous studies that showed the conditions created by mixed-severity fires benefit species associated with early successional stages, resulting in greater densities than in the surrounding unburned forest matrix (Smucker et al. 2005, Rose and Simons 2016, Tingley et al. 2016). A lack of moderate- to high-severity fire, such as that resulting from fire suppression or a fire management approach limited to low-severity prescribed fire would have significant negative implications for the 12 species that were more abundant following high-severity burns than in unburned forest. However, the proportion of the avian community observed to be more abundant at some combination of time since fire and burn severity relative to unburned forest was substantially lower than that observed by Hutto and Patterson (2016), which may reflect a lesser historical role of moderate- and high-severity fire in the Sierra Nevada relative to other regions of western North America (Miller and Safford 2017). Furthermore, our result that birds responding to low-severity fire also appear to be more abundant in burned open-canopy forest compared to other pre-fire conditions may reflect the historical importance of low-severity fire in open-canopy ponderosa pine (*Pinus ponderosa*) forests (Allen et al. 2002). Nonetheless, our results suggest that suppressing high-severity fire would negatively affect a number of species in the Sierra Nevada. Recent studies emphasize the value of mixed-severity fire for snag-associated species (Lorenz et al. 2015, White et al. 2015, Latif et al. 2016), but we show that such conditions are similarly important for species associated with understory vegetation and shrubs, particularly after roughly a decade following fire. Forest managers should consider these lasting effects of high-severity fire on shrub development and supporting shrub-associated birds that are far less abundant in unburned forest. Further study that evaluates the optimization of fire severity and its spatial arrangement will be important to inform the debate over what amount of high-severity conditions should be managed for in these post-fire landscapes (e.g., Kelly et al. 2015).

The incorporation of pre-fire forest condition did not explain variation in bird abundance to the degree we expected based on recent literature (Fontaine et al. 2009, Nappi and Drapeau 2011). In forests with greater pre-fire shrub cover, we assumed re-sprouting would lead to rapid regeneration compared to areas with little or no shrub cover prior to burning. Fontaine et al. (2009) demonstrated that bird community composition was influenced by repeat fires relative to single fires, specifically by benefitting shrub- and ground-nesting birds through rapid regeneration of shrub vegetation. Therefore, it was surprising that we did not observe greater densities of shrub-associated birds in areas with greater pre-fire shrub cover. Because we sampled largely closed-canopy forest, it is possible that we did not sample enough areas with substantial shrub components prior to fire to detect an effect. Alternatively, our categorizations of pre-fire condition were coarse and may not have adequately captured variation in vegetation conditions important to birds. Improvements in the accuracy, frequency, and availability of vegetation classification datasets would greatly aid in understanding the effects of vegetation on species distributions in the Sierra Nevada.

Avian community dynamics following mixed-severity fire are complex. Though non-linear effects of severity and time since fire helped explain responses by most of the species in our study, interpreting these results was challenging, particularly for the interaction between burn severity and time since fire. The relationship between interaction parameter estimate and density depended on the magnitude and direction of the linear effects, so considering the interaction parameter estimate by itself was not informative. Instead, our approach of predicting density across the range of burn severity and time since fire helped to illustrate the overall response of a species, which we could then categorize as responding to a particular range of burn severity or time since fire. Such an approach may be useful for future studies involving interacting and non-linear effects.

In addition to the complex responses to fire that we aimed to highlight in this study, other aspects of the role of fire in shaping avian communities remain uncertain. Climate change will likely have important implications for fire regimes, potentially resulting in larger, more severe fires (Miller et al. 2009*b*.), and our conclusions may not extend to these novel fire conditions. Similarly, the degree to which our results extend to other geographic areas is unknown. Though we aimed to account for among-fire variability by including (Stephens et al. 2013) several fires in our study, the representation of fires during the later stages of time since fire was limited. Future studies that overcome the logistical hurdles of long-term, longitudinal investigations of post-fire bird communities and comparisons across regions and forest types will be important additions to the current body of literature investigating the response of birds to wildfire.

Forest management strategies that widely employ wildfire suppression, rather than incorporating wildfire as a source of avian habitat, will neglect the needs of much of the avian community, potentially leading to reduced biodiversity and ecosystem integrity (Dellasala et al. 2017). Focusing on habitat requirements of short-term fire responders, such as some cavity nesters, also ignores the needs of a number of species for which post-fire vegetation communities become suitable only after a decade or more. For example, the removal or inhibition of broad-leaved shrubs, often intended to reduce fuels and decrease competition with planted and commercially important conifers (e.g., *Pinus* spp.), bypasses the successional stages important to a number of post-fire, shrub-associated birds. Management approaches that attempt to limit fire to low severity, such as many prescribed burns, are unlikely to benefit the many species in the bird community associated with large canopy openings, dense shrub development, and high snag densities that result from high-severity fire (Fontaine and Kennedy 2012, White et al. 2015). Instead, consideration of the complex and lasting effects of mixed-severity fire is appropriate to conserving the high regional bird diversity of fire-prone forests.

Our study contributes to growing consensus about the positive relationships between pyrodiversity and biodiversity. Heterogeneity in fire conditions results in greater diversity of wildlife foods, such as arthropods and fleshy fruits (Ferrenberg et al. 2006, Hulton VantTassel et al. 2015, Lashley et al. 2017). Even for wildlife taxa thought to be vulnerable to the effects of fire, such as some herpetofauna, previous studies did not observe negative responses to fire for these species, and fire contributed to greater herpetofaunal diversity over large spatial and temporal scales (Hossack and Corn 2007, Greenberg et al. 2018). However, some taxa may respond to fire severity and time since fire in unique ways (e.g., small mammals), warranting study of the pyrodiversity–biodiversity relationship across a range of taxa and environmental conditions (Zwolak and Foresman 2007). Nonetheless, wildfires consisting of a broad range of fire conditions are likely to support high levels of wildlife diversity in fire-maintained forests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2291/full