Short-Term Benefits of Prescribed Fire to Bird Communities of Dry Forests

Victoria A. Saab (vsaab@fs.fed.us)  
USDA Forest Service Rocky Mountain Research Station  
https://orcid.org/0000-0003-0645-0523

Quresh R. Latif  
Bird Conservancy of the Rockies

William M. Block  
USDA Forest Service Rocky Mountain Research Station

Jonathan G. Dudley  
USDA Forest Service Rocky Mountain Research Station

Research Article

Keywords: BACI, birds, dry conifer forests, fuel treatments, prescribed fire, point count survey, hierarchical Bayes, presence-absence data, ponderosa pine

Posted Date: November 8th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-970162/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License. 
Read Full License
Title: Short-term benefits of prescribed fire to bird communities of dry forests

Authors: Victoria A. Saab¹*, Quresh R. Latif², William M. Block³, Jonathan G. Dudley⁴

*corresponding author: victoria.saab@usda.gov

1 Rocky Mountain Research Station, USDA Forest Service, 1748 South 7th Avenue, MSU Campus, Bozeman, Montana, USA 59717
2 Bird Conservancy of the Rockies, 14500 Lark Bunting Lane, Brighton, Colorado, USA 80603
3 Rocky Mountain Research Station, USDA Forest Service, 2500 South Pine Knoll Drive, Flagstaff, Arizona, USA 86001
4 Rocky Mountain Research Station, USDA Forest Service, 332 East Front Street, Suite 401, Boise, Idaho, USA 83702

Abstract

Background: Low-severity prescribed fire is a tool used for reducing fuel loads on public lands, particularly in dry conifer forests of the western United States characterized by historically mixed- and low-severity fire regimes. Understanding the ecological effects of prescribed fire treatments is important for predicting the impacts of these management actions on wildlife communities. But few studies have estimated small landbird responses to forest treatments at spatial scales relevant to their ecology or have examined potential differences in treatment effects applied within historically mixed- vs. low-severity fire regimes. Therefore, we evaluated prescribed fire treatment effects and relationships with burn severity for avian communities in dry conifer forests dominated by ponderosa pine (Pinus ponderosa) located on seven National
Forests in the interior western United States. We surveyed birds for 1–4 years and 1–3 years before and after prescribed fire treatments at mixed- and low-severity fire regime locations, respectively, following a before-after, control-impact study design – 8 paired control-treatment units in mixed-severity locations (16 total study units with 320 survey points) and 4 paired control-treatment units in low-severity locations (8 total study units with 278 survey points).

Using a Bayesian hierarchical multi-species occupancy model, we analyzed occupancy patterns for 95 species.

Results: We found 33 species with statistically supported treatment effects and/or burn severity relationships primarily in mixed-severity locations. The data supported positive treatment effects at mixed severity locations for 9 species (American Robin [*Turdus migratorius*], Western Bluebird [*Sialia mexicana*], Hairy Woodpecker [*Dryobates villosus*], Black-backed Woodpecker [*Picoides arcticus*], American Three-toed Woodpecker [*Picoides dorsalis*], House Wren [*Troglodytes aedon*], Dusky Flycatcher [*Empidonax oberholseri*], Western Wood-peewee [*Contopus sordidulus*], Gray Flycatcher [*Empidonax wrightii*]), whose occupancy shifted towards more severely burned points after treatment, and a negative effect for one species (Ruby-crowned Kinglet [*Corthylio calendula*]), whose occupancy shifted away from burned points. At low severity locations, only two species exhibited treatment effects, both negative (Red-faced Warbler [*Cardellina rubrifrons*], and Lark Sparrow [*Chondestes grammacus*]). We also found supported occupancy relationships with burn severity post-treatment (i.e., regardless of species distribution before treatment) for 29 species, most of which were consistent with their life histories (e.g., patterns of positive relationships for cavity-nesting, bark insectivores and negative relationships for open-nesting, foliage insectivores). Stronger responses to prescribed fire
treatments at mixed-severity locations were unexpected because prescribed fire applications are more similar to historical wildfires characterizing low-severity fire regimes.

Conclusions: Bird populations in historically low-severity locations may be relatively unresponsive to prescribed fire because fire there is typically more frequent, expected, and regular. By comparison, fire events are relatively rare historically in mixed severity locations, potentially eliciting more responses to an infrequent opportunity, even by species that are strongly associated with recently burned forests by wildfire. Our results suggest that fire management activities intended to reduce fuels and lower the risk of high-severity wildfire can also be effective in creating habitat for some fire specialists at least in the short term.

Keywords
BACI, birds, dry conifer forests, fuel treatments, prescribed fire, point count survey, hierarchical Bayes, presence-absence data, ponderosa pine

Background
Land management agencies have increased use of prescribed fire to reduce fuel loads and restore wildlands to historical conditions in dry conifer forests of the western U.S.A. during the last three decades (Morgan et al. 1994; Ryan et al. 2013; Stephens et al. 2016). Such efforts follow legislative directives designed to reduce fuel loads on public lands (i.e. National Fire Plan [U.S. Department of Agriculture (USDA) 2000], Healthy Forest Restoration Act [USDA 2003], Healthy Forest Initiative [White House 2004], Collaborative Forest Landscape Restoration Program [(Schultz et al. 2012)]). Managers use prescribed fire and mechanical fuel reduction
treatments to reduce risk of high-severity wildfire and to manage changes in forest integrity and ecological functions (Covington and Moore 1994; Covington et al. 1997; McIver et al. 2013). The use of prescribed fire, however, requires careful consideration of treatment effects on wildlife species and communities. In particular, the uncertainty of management outcomes given potentially novel ecological conditions and processes with the interaction of climate change and human disturbance elevate the need for quantifying ecological responses (Millar et al. 2007; Seastedt et al. 2008; McKelvey et al. 2021).

Forest managers pay particular interest to birds in light of policies under the National Forest Management Act (USDA 1976) for the management of biodiversity, protections afforded migratory species through the U.S. Migratory Bird Treaty Act, and requirements under the 2012 Planning Rule and Directives to consider persistence of species of conservation concern (USDA 2012). Additionally, because bird surveys do not require specialized equipment, birds offer useful opportunities for assessing ecological integrity and biodiversity (Sutherland et al. 2004), which represent mandated foci for management under the current U.S. Forest Service planning rule (USDA 2012).

Scientific understanding of avian responses to prescribed fire in Western North American forests includes lasting knowledge gaps (Russell et al. 2009; Bagne and Purcell 2011; Fontaine and Kennedy 2012; McIver et al. 2013). McIver et al. (2013) conducted continent-wide research evaluating forest treatments on avian communities of seasonally dry conifer forests, but small-sized experimental plots (~40 ha) limited their conclusions and inference. Other studies report prescribed fire effects within five years of application that include reduced numbers of ground and shrub nesting birds (Wilson et al. 1995; Artman et al. 2005; Blake 2005) and benefits to cavity-nesting bird populations (Blake 2005; Russell et al. 2009; Bagne and Purcell 2011) and
species that forage in the air and on the ground (Artman et al. 2005; Blake 2005; Russell et al. 2009).

By investigating impacts of fire treatments on individual species at individual sites, however, results of most studies are limited for informing management activities. Single-species management is frequently impractical except for species of conservation concern or status (e.g., threatened or endangered). Studies that synthesize overall treatment impacts on wildlife communities or groups of ecologically similar species across broad geographic extents are therefore particularly informative (Fontaine and Kennedy 2012; McIver et al. 2013). Community metrics like species richness can supplement individual species responses to disturbance for evaluating overall impacts of management actions on birds. In the current era of rapid environmental change, land management agencies are tasked with “managing landscapes for resilience” such that key elements of biodiversity are robust to perturbations (Allen et al. 2011; McKelvey et al. 2021).

Informing forest management that includes avian diversity and habitat conservation objectives requires synthesis of both species-specific and community-wide relationships with fire. Prescribed fire treatments have positive, negative, or mixed effects on individual species (Artman et al. 2005; Saab et al. 2005; Fontaine and Kennedy 2012; McIver et al. 2013). Just like wildfires, the severity of prescribed fires can vary and affect bird distributions (Kuchinke et al. 2020). Additionally, fire timing influences responses by avian species and communities (Smucker et al. 2005; Saab et al. 2007; Bagne and Purcell 2011; Latif et al. 2016b). Managers typically ignite prescribed fires in seasonally dry forests during wet periods to limit burn severity, i.e., spring burning in mixed-severity regimes and fall burning in low-severity regimes.
This timing differs from seasonality of historical wildfires, raising potential conflict with breeding activities of forest birds (Erwin and Stasiak 1979; Bagne and Purcell 2011).

Avian responses to fire depend on burn severity (fire effects on vegetation; Agee 1993; Smith 2000) and time since fire (Saab and Powell 2005). Forested landscapes with a varied fire history are expected to support the greatest diversity of species (Clarke 2008; Fontaine et al. 2009; Fontaine and Kennedy 2012). Varied fire histories are more typical of forests with mixed-severity fire regimes occurring at intermediate frequencies, in contrast to frequent, low-severity regimes of the southwestern United States (Hood et al. 2021). In the central and northern Rocky Mountains, mixed-severity fires that burned principally in late summer maintained landscape-scale heterogeneity in forest structure, and mixed tree species composition, often favored by fire-tolerant ponderosa pine (*Pinus ponderosa*) (Schoennagel et al. 2004; Hessburg et al. 2007) (Hood et al. 2021). Lower density trees associated with higher frequency, lower-severity fires that burned typically in spring were more widespread in the southwestern United States, where a drier climate favored forest patches that were relatively homogenous, lower in tree and shrub densities, and heavily dominated by ponderosa pine (Moir et al. 1997; Schoennagel et al. 2004; Nimmo et al. 2014). Considering this variation in ecological context, birds may respond differently to prescribed fire in locations with historically low- versus mixed-severity fire regimes, with potential implications for the role of prescribed fire in management strategies that include promoting and conserving biodiversity.

Here, we evaluated the influence of prescribed fire treatments on avian species occupancy and richness at locations representing both mixed- and low-severity fire regimes in dry mixed conifer forests across the interior western United States, known as the Birds and Burns Network. Our plot sizes averaged 300 ha, a spatial scale appropriate for drawing inference about
landbirds with varying home range sizes, and we used a before-after-control-impact (BACI) design for rigorous evaluation of treatment effects (Morrison et al. 2008; Popescu et al. 2012).

Low-severity prescribed fire treatments on these study sites increased numbers of dead trees, opened the forest canopy, and reduced shrub cover within two years of treatment (Saab et al. 2006). Based on these habitat changes, we predicted changes in species’ occupancy rates concurring with life history traits (Table 1). We also expected species richness and average species responses to vary regionally depending on the different historical fire regimes (Latif et al. 2016b). Because prescribed fire is intended to burn at low severity, we predicted occupancy changes to be more positive and of stronger magnitude at locations characterized by historically low-severity fire regimes.

Methods

Study system

We selected paired study units (treatments and controls) within areas identified by seven national forests that planned to conduct fuel reduction treatments for the Birds and Burns Network (Figure 1). Each study unit was approximately 200-400 ha (Table 2) and dominated by ponderosa pine. Sixteen study units were located in 3 national forests characterized historically by mixed severity fire regimes: 6 in the Payette National Forest (NF; Idaho), 6 in the Okanogan-Wenatchee NF (Washington), and 4 in the San Juan NF (Colorado). Eight study units were located in 4 national forests characterized historically by low severity fire regimes: 2 in the Gila NF (New Mexico), and 2 each on the Apache-Sitgreaves, Kaibab, and Coconino NFs (Arizona; Figure 1). Thus, we established 12-unit pairs for a total of 24 study units (Table 2). USFS
District fire personnel determined the location and boundary of each prescribed fire treatment unit. Ponderosa pine trees ≥ 23 cm dbh dominated overstory vegetation on all units with both low-severity and mixed-severity historical fire regimes. In low severity locations, the understory was relatively open with few shrubs and dominated by grasses, i.e., Arizona fescue (*Festuca arizonica*) and blue grama (*Bouteloua gracilis*) and elevations ranged from 2072 m to 2500 m. In mixed severity locations, the understory vegetation was comprised of multiple shrub species, including snowberry (*Symphoricarpos albus*), spirea (*Spirea* spp.), ninebark (*Physocarpus* spp.), and serviceberry (*Amelanchier alnifolia*), with Bluebunch wheatgrass (*Pseudoroegenaria spicatus*) and Idaho fescue (*Festuca idahoensis*) as the common grass species and elevations ranging 670 m to 1980 m.

**Study units**

In 2001–2003, we established 320 point count stations in units characterized historically by mixed severity regimes and 278 in low-severity regime units (hereafter mixed-severity and low-severity units, respectively), for a total of 580 point count stations (Table 2). We placed point count stations at least 250 m apart and 250 m from the edge of study unit boundaries and visited each station multiple times (1–4 visits per point) annually between 22 May and 3 July.

**Bird surveys**

We surveyed birds for 1–4 years and 1–3 years before and after prescribed fire treatments at mixed-severity and low-severity units, respectively. For comparability across fire regimes, we restricted our primary analysis to data from 2 years before to 2 years after prescribed fire
treatments (Table 3). A supplemental analysis included all available data from mixed-severity units (Appendix A). We began point counts just after the dawn chorus and completed them within five hours. Only detections within 75 m of the point were included in this analysis. Our sampling design included a robust design (Pollock 1982) with years as primary periods and visits within years as the secondary samples.

**Burn severity measurements and analysis**

Prescribed fire treatments were implemented during 2003–2010 (Table 3). Fires were designed to reduce existing surface and ladder fuels of relatively small diameter (< 15.4 cm dbh), and create small gaps in the upper tree canopy, while retaining large pine trees and snags (>23 cm dbh). We measured burn severity using a composite burn index (CBI) representing a gradient of unburned (min CBI = 0) to severely burned (max CBI = 3; Key and Benson 2006; Appendix B). We assumed CBI = 0 for all survey points in untreated units. One treatment unit in Idaho was burned by wildfire before we could measure post-treatment vegetation. We used the Bayesian approach to missing value imputation for this unit whereby we treated missing values as a parameter to be estimated during model-fitting (Link and Barker 2010). We used a truncated Gaussian prior distribution for missing CBI values in Idaho (mean = 0.32, variance = 0.07, min = 0), approximating the CBI distribution for another unit in the San Juan NF (CO) that burned at a qualitatively similar severity (based on visual assessment). Effects of prescribed fire on vegetation are provided in (Saab et al. 2006). To briefly summarize these effects, overall downed woody material declined by 35% in the Southwest (low-severity fire regime) and 46% in the Northwest (mixed-severity fire regime). Large diameter trees (>23 cm) declined by 19% in
the Southwest with no change in the Northwest. Large diameter snags increased by 72% on the southwestern forests and 29% on the northwestern forests (Saab et al. 2006).

Occupancy models

We used avian point count data in a hierarchical multi-species occupancy model (Dorazio et al. 2006; Russell et al. 2009) to identify changes in occupancy rates in relation to prescribed fire treatments and burn severity. Occupancy models leverage repeat-survey data to estimate species detectability ($p$) conditional upon occupancy (species presence within a specified time period and spatial unit), allowing unbiased estimation of occupancy probabilities ($\psi$) given sufficient data and adherence to model assumptions (MacKenzie et al. 2002; MacKenzie et al. 2018). We assumed that the occupancy states of species could change among years, but not between visits within a year. We used multi-species occupancy models to estimate species-specific parameters as random variables governed by community-level parameters. The use of a common distribution among species improves the precision of species-specific parameter estimates, particularly for rare species, facilitating estimation of species richness (Dorazio et al. 2006; Russell et al. 2009). We excluded raptors, owls, and grouse because they were not readily detectable with our survey methods, and we only included species breeding in our study areas. For mobile animals such as birds, detectability ($p$) estimated with surveys repeated over a season includes information on both within-season movement and surveyor ability (i.e., availability and perceptibility; sensu Chandler and Royle 2013; Amundson et al. 2014). Occupancy probabilities thereby represent the probability of a surveyed point intersecting at least one home range for a given species (Latif et al. 2016a).
We used occupancy patterns estimated from our analysis to evaluate predictions for species based on their individual life histories (Table 1) and on previous research (Russell et al. 2009; Gaines et al. 2010; Bagne and Purcell 2011; Fontaine and Kennedy 2012; McIver et al. 2013). We expected these predictions to describe general patterns while taking into consideration that each individual species has a unique life history that may not fit perfectly within the broad categories for which we had a priori predictions. Thus, we considered both general predictions for life histories and literature on individual species when evaluating whether patterns were consistent with current knowledge.

For each study location, we compiled a 3-dimensional data matrix \( y \), where element \( y_{j i t} \) was the sum of binary indicators for species detection (Sanderlin et al. 2014). Given a binary indicator \( x_{j i k t} = 1 \), we detected species \( i \) (\( i = 1, \ldots, N \)) at point count station \( j \) (\( j = 1, \ldots, J \)) during visit \( k \) (\( k = 1, \ldots, K \)) in year \( t \) (\( t = 1, \ldots, T \); \( T = 4 \)). Because we did not have covariates that differed for detection between visits, we analyzed the sum of all binary detections for species \( i \) over all visits at each point count station \( j \) in year \( t \), where \( y_{j i t} = \sum_{k=1}^{K} x_{j i k t} \) and \( y_{j i t} \in [0,1,\ldots,K] \). We modeled these data given probability of detection \( p_i \), and occupancy latent state \( z_{j i t} \) using a Bernoulli distribution with probability of success \( p_i \times z_{j i t} \):

\[
[y_{j i t} | p_i, z_{j i t}] \sim \text{Bin}(K, p_i \times z_{j i t}) \text{ (Equation 1)},
\]

where the latent variable \( z_{j i t} \) for occupancy given probability of occupancy \( \psi_{j i t} \) was modeled as:

\[
[z_{j i t} | \psi_{j i t}] \sim \text{Bern}(\psi_{j i t}) \text{ (Equation 2)}.
\]

We analyzed changes in species occupancy patterns using a model that fully leverages our BACI sampling design for examining treatment effects (Popescu et al. 2012). Although our study design entailed surveying units with a priori assignments of treatment versus control, treatments did not realize homogenous impacts on vegetation structure and composition. We
therefore measured shifts in occupancy from before to after treatment along a continuous burn severity gradient (contra control-impact categories) represented by CBI to evaluate treatment effects. We modeled occupancy ($\psi_{ijt}$) as a function of burn severity measured after treatment ($CBI_j$), treatment period ($PER_{jt} = 0$ or $1$ for before or after site $j$ was treated, respectively), and the interaction between severity and period ($CBI_j \times PER_{jt}$). Thus,

$$\logit(\psi_{jlt}) = \beta_{0,il} + \beta_{PER,ir} \times PER_{jt} + \beta_{CBI,ir} \times CBI_j + \beta_{PER \times CBI,ir} \times PER_{jt} \times CBI_j$$  (Equation 3),

where $\beta_{0,il}$ is the intercept and $\beta_{ir}$ parameters described additive or interactive effects of covariates $PER_{jt}$ and $CBI_j$ on occupancy of species $i$ at site $j$ in year $t$. All estimated parameters were species-specific normal random effects, $\beta_{0,il}$ was estimated separately by location ($l = 1, \ldots, L; L = 7$), and covariate effects ($\beta_{ir}$) were estimated separately by fire regime ($r = 1, \ldots, R; R = 2$). For numerical purposes, $CBI_j$ values were centered at the mean for point count stations in treated units (0.76) prior to all analyses. Unlike others (Russell et al. 2009), we did not model persistence as a Markovian process in our primary model to avoid stretching the limits of our data at low-severity locations. We did include Markovian species persistence, however, in a supplemental analysis of data from mixed-severity locations (described further below and in Appendix A).

We primarily inferred species-specific prescribed fire effects from the extent to which occupancy shifted towards or away from severely burned (or unburned) points following treatment (hereafter treatment effect = $\beta_{PER \times CBI,ir}$). We considered the evidence for prescribed fire effects to be definitive for species with statistically supported treatment effects (90% BCI excluded zero). We also examined support for differences in treatment effects between fire regimes by deriving the 90% BCI for
\[ \beta_{\text{diff}} = \beta_{\text{mixed}} - \beta_{\text{low}} \] (Equation 4),

where \( \beta_{\text{mixed}} \) and \( \beta_{\text{low}} \) represent estimated treatment effects in mixed- and low-severity regimes, respectively.

Our sampling design afforded inferences that were stronger than purely observational studies but not equivalent to a fully controlled experiment (see Popescu et al. 2012 and literature referenced therein). We controlled for potentially confounding factors by randomly designating members of paired units as treatment versus control in most cases, replicating sampling (i.e., sampling multiple units and locations in each fire regime), and explicitly separating treatment effects (\( \beta_{\text{PER} \times \text{CBI}, ir} \)) from potentially confounding sources of variation (\( \beta_{\text{PER}, ir}, \beta_{\text{CBI}, ir}; \) Equations 3) during analysis (Popescu et al. 2012). Nevertheless, burn severity within treated units was likely influenced by factors for which we did not explicitly control (e.g., vegetation structure, moisture levels, and topography). Furthermore, some species whose life histories typically confer effects of prescribed fire may exhibit subdued treatment effects if occupancy already favors desirable sites prior to treatment. Finally, our timeframe of sampling (2 years pre-, 2 years post-treatment) potentially limited the scope and strength of inference, especially because we expected some species to exhibit delayed effects of treatment.

Considering these limitations, we supplemented our evaluation of BACI treatment effects (\( \beta_{\text{PER} \times \text{CBI}, ir}; \) hereafter treatment effects) by also evaluating post-treatment CBI-occupancy relationships (hereafter burn severity relationships = \( \beta_{\text{CBI}, ir} + \beta_{\text{PER} \times \text{CBI}, ir} \)). We drew strongest inference from treatment effects, and we also drew weaker but substantive inference from burn severity relationships that were consistent with our predictions based on species life histories.

We also followed up our primary analysis with two supplemental analyses. For one, we included data from additional years at mixed severity locations and a Markovian persistence parameter to
better account for variability among years (hereafter “extended sampling model”; Appendix A). For the other, we analyzed data from each fire regime separately and estimated separate treatment effects for each post-treatment year (hereafter “yearly effect model”; Appendix A). We examined species with statistically supported treatment effects or CBI relationships from our primary analysis, and/or statistically supported treatment effects in supplemental analyses. We evaluated the strength of evidence for prescribed fire effects based on the consistency of patterns estimated across analyses and with biologically based predictions (Table 1).

We modeled detectability separately by location (fixed effect) and as a species-specific normal random effect $b_{0,i}$:

$$\text{logit}(p_{il}) = b_{0,il} \text{ (Equation 5)},$$

where $p_{il}$ is the probability of detecting species $i$ at location $l$ during a survey of a given point count station in a given year when the species was present. We modeled heterogeneity in detectability among species and assumed detectability did not change with treatment condition (preliminary models with treatment effects on detection converged poorly and were therefore abandoned). We modeled heterogeneity among species using a correlation term ($\rho$) between species intercepts of detection probability ($b_{0,i}$) with occupancy probability ($\beta_{0,i}$) (Dorazio et al. 2006; Kéry et al. 2009).

In addition to species-specific relationships, we calculated and plotted emergent changes between species richness with treatment condition. We estimated species richness ($N_{jt}$) at each point count station $j$ and year $t$: $N_{jt} = \sum_{l=1}^{\text{max}(l)} z_{ijt}$. Community-level inferences were restricted to the subset of members observed at least once during our studies (cf. Russell et al. 2009; Latif et al. 2016b).
We sampled posterior parameter distributions for all models using JAGS v. 3.3.0 (Plummer 2003) programmed from R (Team 2013) (Su and Yajima 2014). We used independent non-informative priors for all parameters (for priors, see Appendix C; for model code, see Appendix D). We ran 6 parallel MCMC chains of length 100,000 \( it \), burn-in 10,000 \( it \), and thinning 10 \( it \) to sample posterior distributions. We verified that \( n_{\text{effective}} \geq 100 \) and \( \hat{R} \leq 1.1 \) for all parameters (Gelman and Hill 2007). We examined model goodness-of-fit (GOF) using posterior predictive testing (Gelman and Hill 2007). Specifically, we calculated a Bayesian \( p \)-value representing the proportion of simulated datasets drawn from model posterior predictive distributions with deviance higher than deviance for observed datasets from each location, whereby \( p < 0.05 \) or \( p > 0.95 \) constitutes evidence for lack of fit.

**Results**

Ninety-five species were detected across all point count stations and years (Appendix E). Forty-seven species were detected in both fire regimes, 19 unique to low-severity locations, and 29 at only mixed-severity locations. The five most commonly detected species at the three mixed-severity locations were Western Tanager, Yellow-rumped Warbler, Chipping Sparrow, Red-breasted Nuthatch, and Mountain Chickadee. The five most commonly detected species at low-severity locations were Dark-eyed Junco, Pygmy Nuthatch, Mountain Chickadee, Western Bluebird, and Grace’s Warbler. Burn severity measured at points within treated units was variable (mean [SD] CBI = 0.92 [0.40], \( n = 274 \) points) and broadly overlapped among locations (Figure 2). Detection probability estimates varied among species (median posterior \( p \) ranged 0.008–0.637; Appendix F) and were highly correlated with occupancy (median estimate [90%
BCLs] for \( \rho = 0.80 [0.75–0.85] \). We found no evidence for lack of model fit (location-specific GOF \( p \) values from primary model ranged 0.34–0.42).

Species-level prescribed fire effects and burn severity relationships

We identified 33 species for which we found statistically supported treatment effects and/or burn severity (CBI) relationships (Figures 3, 4, 5). Treatment effects were supported for 4 species in our primary analysis (American Robin, Western Bluebird, Hairy Woodpecker, and Ruby-crowned Kinglet) and 8 additional species in supplementary analyses (Black-backed Woodpecker, American Three-toed Woodpecker, House Wren, Dusky Flycatcher, Western Wood-peewee, Gray Flycatcher, Red-faced Warbler, and Lark Sparrow). Supported treatment effects for these species were primarily positive and observed at locations characterized by mixed severity regimes (9 species). We found one negative treatment effect in mixed severity locations (Ruby-crowned Kinglet) and two in low severity locations (Red-faced Warbler and Lark Sparrow). We also found 36 statistically supported CBI relationships for 29 species (primary analysis), including relationships for 8 of 12 species listed above with supported treatment effects (Figures 4, 5). Supported CBI relationships included 11 positive and 12 negative at mixed-severity regime locations, and 9 positive and 4 negative at low-severity regime locations.

Evidence for treatment effects varied with time since treatment and fire regime. We found the most evidence for positive treatment effects in the mixed severity fire regime (e.g., for American Robin, Western Bluebird, and Hairy Woodpecker; Figures 3, 4). For some species, treatment effects and CBI relationships were not unequivocally supported in every analysis (i.e.,
90% BCIs sometimes included zero) but were nevertheless consistent in direction (e.g., Black-backed Woodpecker and Ruby-crowned Kinglet; Figure 4).

Positive treatment effects were also statistically supported for several species in the mixed severity regime when data from additional years were considered (Black-backed Woodpecker, American Three-toed Woodpecker, Brown Creeper, Western Wood-peewee, House Wren, Dusky Flycatcher, and Gray Flycatcher; Figure 4). The yearly effect model showed treatment effects primarily arose in the second year following treatment (Figure 4D, 4E). For Dusky and Gray Flycatchers occupancy changes became apparent only in the second year after treatment, suggesting lagged treatment effects.

For 21 species exhibiting 24 CBI relationships, we never found statistically supported treatment effects (Figures 4, 5). For some of these species, estimated treatment effects were nevertheless consistent in direction with CBI relationships and with predictions for aspects of their life histories (e.g., Pine Siskin, Pygmy Nuthatch, Orange-crowned Warbler; Table 1). Several species exhibited positive CBI relationships in the low severity fire regime, but these relationships were not clearly reflected as a treatment effect (e.g., Hairy Woodpecker and Western Bluebird; Figures 5, 6). Although consistent with species life histories, some supported CBI relationships followed very low-magnitude treatment effects, supporting relatively weak inference (e.g., Nashville Warbler, Yellow-rumped Warbler, Warbling Vireo, and Townsend’s Warbler in the mixed severity regime; White-breasted Nuthatch, Northern Flicker, and Western Wood-peewee in the low severity regime; Mountain Chickadee in both regimes). Other species exhibited CBI relationships that were not accompanied by notable treatment effects (e.g., Black-throated Gray Warbler, Western Tanager, Green-tailed Towhee) or were not necessarily
consistent with their life histories (e.g., Ash-throated Flycatcher, and Townsend’s Solitaire), suggesting they were possibly spurious.

Community-level patterns

Community-wide patterns and differences between regimes were also apparent but limited. Treatment effects were generally stronger in magnitude (i.e., deviated further from zero) in the mixed severity regime, where effects were more positive than negative (Figures 3, 4, 5). Despite the apparent difference between regimes, we found no statistically supported difference in treatment effect between regimes for any one species (BCIs for $\beta_{Diff}$ all overlapped zero; Equation 4). In burn severity relationships, however, we found differences between regimes for two species (Gray flycatcher and Spotted Towhee). Although treatment effects were more positive in the mixed severity regime (see above), treatment did not have a notable effect on species richness (Figure 7). Instead, species richness varied much more among locations within and between fire regimes than with burn severity or treatment application. Treatment effects were generally stronger in year 2 compared to year 1 following treatment in both fire regimes (Figures 4, 5).

Discussion

Changes in avian occupancy related to prescribed fire treatments and relationships with burn severity generally supported our predictions. Accordingly, our findings followed conclusions of previous prescribed fire studies (e.g., Hurteau et al. 2008; Dickson et al. 2009; Russell et al. 2009; Bagne and Purcell 2011; Fontaine and Kennedy 2012; White et al. 2016) and supported our predictions that prescribed fires benefit cavity-nesting, bark and ground insectivores. We
found increases in occupancy related to post-fire treatments or burn severity for many cavity-
nesting birds, including bark-insectivores (American three-toed, hairy, black-backed
woodpeckers, white-breasted nuthatch, brown creeper, and pygmy nuthatch) and ground
insectivores (American robin, Western bluebird, house wren). Increases in available snags
created soon after fire likely increased nesting substrate and food resources (bark beetle larvae
[Scolytidae]) for cavity-nesting, bark insectivores (Saab and Powell 2005; Saab et al. 2006;
Russell et al. 2009). Notably, we recorded positive changes in occupancy related to low-severity
prescribed fire for species known to favor higher severity wildfires (e.g., Black-backed
woodpecker, Saab et al. 2007), suggesting that fire management can be an effective tool to create
habitat for some fire specialist species at least for a few years.

Further reductions in post-fire ground cover may have increased foraging opportunities
across both fire regimes for open-ground feeding species (American robin, Western bluebird,
house wren), including Northern flicker (Bagne and Purcell 2011; White et al. 2016). Although
we expected occupancy increases by several aerial foragers in relation to fire (Bagne and Purcell
2011), we detected few positive trends (Western wood-pewee [both regimes], dusky and gray
flycatchers [mixed fire-regime]), suggesting that effects of low-severity fire treatments are
variable for aerial insectivores. Habitat changes resulting from higher severity burns are likely
more beneficial to aerial insectivores (Kotliar et al. 2002; Smucker et al. 2005; Russell et al.
2006; Kotliar et al. 2007; Latif et al. 2016b). Compared to low-severity fire, moderate- to high-
severity burns potentially create more openings in the forest canopy, allowing efficiency in
flycatching for insects, and release more soil nutrients that allow for shrub growth and increased
abundance of associated arthropods (cf. Certini 2005), followed by increases of insect prey
availability for aerial insectivores.
Negative relationships with burn severity followed our predictions for canopy foliage-gleaners (mixed severity: Cassin’s and warbling vireos; ruby-crowned kinglet, Nashville, yellow-rumped and Townsend’s warblers, mountain chickadee; low severity: red-faced warbler and mountain chickadee) and were consistent with other prescribed-fire studies (Bagne and Purcell 2011; Fontaine and Kennedy 2012; White et al. 2016). These species forage in live trees, contributing to their negative relationships with fires of various severities that can damage or kill portions of live trees. A negative percent change of live trees across our study locations averaged 45% (Saab et al. 2006), likely promoting the negative relationships between foliage insectivores and burn severity.

Unexpectedly, prescribed fire treatments provoked stronger responses, including lagged effects, at mixed-severity locations. Sampling effort could have played a role in the observed differences but we restricted the primary analysis to 1-2 years before and after prescribed fire in both regimes, thus standardizing the number of years of data collection. Differences in timing of burns (spring at mixed severity locations vs. primarily fall at low severity locations) could also contribute, although the timing of prescribed burns intentionally and consistently avoided historical wildfire seasons across both fire regimes. Spring burning at mixed severity locations could have interfered with breeding the first year, although we did not find strong evidence for immediate interference of fire on breeding bird behavior. Rather, we found more lagged responses in the years subsequent to burning applications within both regimes.

Perhaps bird populations occurring in historically low-severity locations had fewer occupancy changes because fire is typically more frequent, expected, and regular. By comparison, fire events are relatively rare historically in mixed severity locations, potentially eliciting more responses to an infrequent opportunity, even by species that are strongly
associated with recently burned forests by wildfire (e.g., Black-backed and American three-toed woodpeckers). This pattern suggests that fire management activities intended to reduce fuels and lower the risk of high-severity wildfire can be effective in creating habitat for some fire specialists at least in the short term. Historical conditions are especially meaningful when they encompass evolutionary relationships such as the role fire regimes play in structuring bird communities and species distributions (cf. Hutto et al. 2008).

We found no definitive evidence for either short-term prescribed fire treatment effects or burn severity relationships for many bird species (61 of 95 species). For many species that were rarely detected, lack of evidence likely reflects low statistical power. Additionally, a lack of rapid responses to habitat changes after prescribed fire may be related to time lags created by site tenacity of breeding birds (Wiens and Rotenberry 1985), as indicated by our data for lagged positive responses by dusky and gray flycatchers at mixed severity locations, and lagged negative responses by red-faced warbler and lark sparrow at low severity locations. Longer-term data may be necessary to quantify the timeframe of negative and positive impacts of prescribed fire on foliage gleaners and bark insectivores, respectively.

Our findings that species richness was affected little by prescribed fire treatments concurs with previous literature (George and Zack 2008; Hurteau et al. 2008; Russell et al. 2009). Post-fire bird communities may contain the same number of species as the pre-fire community, but nevertheless contain different species, including those not prevalent outside of recently disturbed forests, such as Black-backed and American three-toed woodpeckers. Assessing both individual species responses to management practices and the overall contribution of a species to biodiversity on a larger regional scale (such as a forested area containing burned and unburned portions) is important for addressing specific management goals. Additionally, treatments on a
study unit may affect shifts in species distributions only observable with a BACI study design
that clarify species responses. For example, consistent with their life history, House Wren shifted
their distribution toward burned/treated units, although this shift was not strong enough to
completely negate or reverse their greater prevalence at unburned compared to burned units prior
to treatment.

Our study design was unprecedented by the combination of large spatial scale,
replication, multiple years, assessment of burn severity, and experimental plot sizes (173 – 486
ha). By designing our study to estimate changes in avian species occupancy and species richness
at appropriate spatial scales, our study supports inference more relevant to landbirds than
previous continent-wide research (e.g, McIver et al. 2013).

We evaluated occupancy changes for individual species and for trends in species grouped
by life history traits. Although limitations apply to evaluating species grouped by traits (Fontaine
and Kennedy 2012), we found evidence of changes in occupancy for many species that matched
our life-history trait predictions (e.g., patterns of positive changes for cavity-nesting, bark
insectivores and negative changes for open-nesting, foliage insectivores). Most occupancy
changes occurred at mixed-fire regime locations. Some species exhibited changes with treatment
overall, but lagged effects were more pronounced two years post-treatment, particularly in the
mixed-severity fire regime locations. Evaluating post-treatment occupancy relationships with
burn severity (i.e., disregarding pre-treatment distributions) revealed additional species that at
least maintained distributions relative to treatment that were consistent with their life histories.

Management Implications
Our results revealed primarily short-term benefits and limited negative effects of prescribed fire practices to the avifauna of seasonally dry forests across the Interior Western United States. Our data suggest that the longer-term potential benefits of prescribed fire for ecosystem resilience likely outweigh any potential near-term costs to avian diversity.

Unprecedented, extreme fire behavior resulting in rapid and extensive tree mortality is expected to be more common under changing climate conditions (Fettig et al. 2013), raising concerns by ecologists worldwide (Pickrell and Pennisi 2020). Prescribed fire and other fuel reduction treatments potentially reduce the risk of future severe wildfires, decrease tree mortality, and increase forest resilience to climate change (Stephens et al. 2018). Prescribed fire treatments are also potentially useful for creating near-term habitats for fire specialists that are more frequently found after wildfires. Fire suppression in the long-term does not benefit avian species or biodiversity overall (Bagne and Purcell 2011). For example, broadscale contiguous tree mortality can result in homogeneity produced by fire suppression, reducing the fine-scale heterogeneity of forest conditions that contribute to resilience and biodiversity (Stephens et al. 2018). Prescribed fire and forest thinning could enhance adaptation to climate-induced stress if resources are focused on creating spatially and temporally variable patterns in seasonally dry forests that are aligned with local fire patterns (cf. North et al. 2009), accordingly supporting local avian communities.

Dry forested landscapes of the interior western United States support a diverse avifauna, including species of concern that rely on recent disturbance (e.g., Black-backed Woodpecker), old/mature forest specialists (e.g., Red-faced Warbler), and species that require multiple seral stages (e.g., White-headed Woodpecker; Latif et al. 2015). Our results indicate that fire management practices promoting a mosaic of habitat conditions will best support the full suite of
avian species native to seasonally dry conifer forests of western North America (Saab et al. 2005; Veech and Crist 2007; Fontaine et al. 2009; Fontaine and Kennedy 2012).

Conclusions

We implemented a regional Interior Western U.S. study to estimate small landbird responses to prescribed fire treatments at spatial scales relevant to their ecology. We examined differences in treatment effects applied within historically mixed- vs. low-severity fire regimes. Bird populations in historically low-severity locations were relatively unresponsive to prescribed fire possibly because fire there is typically more frequent, expected, and regular. By comparison, fire events were relatively infrequent historically in mixed severity locations, potentially eliciting more responses to an occasional opportunity, even by species that are strongly associated with recently burned forests by wildfire. Fire treatments intended to reduce fuels and lower the risk of high-severity wildfire potentially can be effective in creating habitat for some fire specialists over the short term.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable
Data availability

The datasets used and/or analyzed here are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests

Funding

Joint Fire Science Program (#01-1-3-25), National Fire Plan (02.RMS.C.2 and 01.PNW.C.2), and the USDA Forest Service Rocky Mountain Research Station, Pacific Northwest Research Station, and Intermountain and Pacific Northwest Regions provided funding. The Payette, Okanogan-Wenatchee, San Juan, Kaibab, Coconino, Apache-Sitgreaves, and Gila National Forests and Montana State University, Ecology Department also contributed funds and logistical support.

Author contributions

VAS and WMB designed the study and obtained funding. VAS and JGD organized and oversaw data collection. QSL and VAS developed the analysis approach. QSL implemented the analysis. VAS drafted the manuscript. QSL and JGD contributed editorial input during manuscript preparation.

Acknowledgements


We thank field crews for conducting bird surveys and measuring vegetation. We are grateful to field crew supervisors at each location for overseeing the data collection, including Kent Woodruff, Scott Story, Gary Vos, Brett Dickson, Stephanie Jentsch, and Anthony Garcia. Brett Dickson provided essential data for Kaibab, Coconino, Apache-Sitgreaves, and Gila National Forests.

References

Agee, J. K. 1993. Ponderosa pine and lodgepole pine forests. In Fire Ecology of Pacific Northwest Forests, ed. J. K. Agee, 320-350. Island Press.

Allen, Craig R, Graeme S Cumming, Ahjond S Garmestani, Phillip D Taylor, and Brian H Walker. 2011. Managing for resilience. Wildlife Biology 17 (4):337-349, 13.

Amundson, Courtney L., J. Andrew Royle, and Colleen M. Handel. 2014. A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts. Auk 131 (4):476-494. https://doi.org/10.142/AUK-14-11.1.

Artman, Vanessa L, Todd F Hutchinson, and Jeffrey D Brawn. 2005. Fire ecology and bird populations in eastern deciduous forests. Studies in Avian Biology 30:127-138.

Bagne, Karen E., and Kathryn L. Purcell. 2011. Short-term responses of birds to prescribed fire in fire-suppressed forests of California. Journal of Wildlife Management 75 (5):1051-1060. https://doi.org/10.1002/jwmg.128.

Billeman, S. M., B. K. Keeney, P. G. Rodewald, and T.S. Schulenberg. 2020. "Birds of the World." Cornell Laboratory of Ornithology. https://birdsoftheworld.org/bow/home.

Blake, John G. 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. Biological Conservation 121 (4):519-531. https://doi.org/https://doi.org/10.1016/j.biocon.2004.06.021.

Certini, Giacomo. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143 (1):1-10. https://doi.org/10.1007/s00442-004-1788-8.

Chandler, Richard B., and J. Andrew Royle. 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. Annals of Applied Statistics 7:936-954. https://doi.org/10.1214/12-AOAS610.

Clarke, Michael F. 2008. Catering for the needs of fauna in fire management: science or just wishful thinking? Wildlife Research 35 (5):385-394. https://doi.org/https://doi.org/10.1071/WR07137.

Covington, W., P. Fule, M. Moore, S. Hart, T. Kolb, J. Mast, S. Sackett, and M. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the southwest Journal of Forestry 95 (4):23-29.

Covington, W., Wallace, and Margaret M. Moore. 1994. Southwestern ponderosa forest structure. Journal of Forestry January:39-47.

Dickson, Brett G., Barry R. Noon, Curtis H. Flather, Stephanie Jentsch, and William M. Block. 2009. Quantifying the multi-scale response of avifauna to prescribed fire experiments in the southwest United States. Ecological Applications 19 (3):608-621. https://doi.org/10.1890/08-0905.1.

Dorazio, Robert M., J. Andrew Royle, Bo Söderström, and Anders Glimskär. 2006. ESTIMATING SPECIES RICHNESS AND ACCUMULATION BY MODELING SPECIES OCCURRENCE AND
DETECTABILITY. Ecology 87 (4):842-854. https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2.

Erwin, William J., and Richard H. Stasiak. 1979. Vertebrate Mortality During the Burning of a Reestablished Prairie in Nebraska. The American Midland Naturalist 101 (1):247-249. https://doi.org/10.2307/2424922.

Fettig, Christopher J., Mary L. Reid, Barbara J. Bentz, Sanna Sevanto, David L. Spittlehouse, and Tongli Wang. 2013. Changing Climates, Changing Forests: A Western North American Perspective. Journal of Forestry 111 (3):214-228. https://doi.org/10.5849/jof.12-085.

Fontaine, Joseph B., Daniel C. Donato, W. Douglas Robinson, Beverly E. Law, and J. Boone Kauffman. 2009. Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257 (6):1496-1504.

Fontaine, Joseph B., and Patricia L. Kennedy. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22 (5):1547-1561. https://doi.org/10.1890/12-0009.1.

Fettig, Christopher J., Mary L. Reid, Barbara J. Bentz, Sanna Sevanto, David L. Spittlehouse, and Tongli Wang. 2013. Changing Climates, Changing Forests: A Western North American Perspective. Journal of Forestry 111 (3):214-228. https://doi.org/10.5849/jof.12-085.

Fontaine, Joseph B., Daniel C. Donato, W. Douglas Robinson, Beverly E. Law, and J. Boone Kauffman. 2009. Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257 (6):1496-1504.

Fontaine, Joseph B., and Patricia L. Kennedy. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22 (5):1547-1561. https://doi.org/10.1890/12-0009.1.

Gaines, William, Maryellen Haggard, James Begley, John Lehmkuhl, and Andrea Lyons. 2010. Short-Term Effects of Thinning and Burning Restoration Treatments on Avian Community Composition, Density, and Nest Survival in the Eastern Cascades Dry Forests. Washington. Forest Science 56 (1):88-99.

Gelman, Andrew, and Jennifer Hill. 2007. Data analysis using regression and multilevel/hierarchical models, Analytical methods for social research. New York, NY: Cambridge University Press.

George, T. Luke, and Steve Zack. 2008. Bird occupancy and richness in ponderosa pine forests with contrasting forest structure and fire history. Canadian Journal of Forest Research 38 (5):936-942. https://doi.org/10.1139/x07-238.

Hessburg, P.F., R. B. Salter, and K. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecology 22:25-24.

Hurteau, Sarah R., Sisk Thomas D., William M. Block, and Brett G. Dickson. 2008. Fuel-reduction treatment effects on avian community structure and diversity. The Journal of Wildlife Management 72 (5):1168-1174. https://doi.org/doi:10.2193/2007-351.

Hutto, Richard L., Courtney J. Conway, Victoria A. Saab, and Jeffrey R. Walters. 2008. What Constitutes a Natural Fire Regime? Insight from the Ecology and Distribution of Coniferous Forest Birds in North America. Fire Ecology 4 (2):115-132. https://doi.org/10.4996/fireecology.0402115.

Kéry, Marc, J. Andrew Royle, Matthias Plattner, and Robert M. Dorazio. 2009. Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90 (5):1279-1290. https://doi.org/10.1890/07-1794.1.

Key, Carl H., and Nathan C. Benson. 2006. Landscape assessment. Sampling and analysis Methods. USDA Forest Service General Technical Report RMRS-GTR-164-CD. 55p.

Kotliar, Natasha B., Sallie J. Heji, Richard L. Hutto, Victoria A. Saab, Cynthia P. Melcher, and Mary E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western united states. Studies in Avian Biology 25:49-64.

Kotliar, Natasha B., Patricia L. Kennedy, and Kimberly Ferree. 2007. AVIFAUNAL RESPONSES TO FIRE IN SOUTHWESTERN MONTANE FORESTS ALONG A BURN SEVERITY GRADIENT. Ecological Applications 17 (2):491-507. https://doi.org/10.1890/06-0253.

Kuchinke, Diana, Julian Di Stefano, Holly Sitters, Richard Loyn, Peter Gell, and Grant Palmer. 2020. Prescribed burn severity has minimal effect on common bird species in a fire-prone forest ecosystem. Forest Ecology and Management 475:118437. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118437.
Latif, Quresh S., Martha M. Ellis, and Courtney L. Amundson. 2016a. A broader definition of occupancy: Comment on Hayes and Monfils. *The Journal of Wildlife Management* 80 (2):192-194. https://doi.org/10.1002/jwmg.1022.

Latif, Quresh S., Victoria A. Saab, Kim Mellen-Mclean, and Jonathan G. Dudley. 2015. Evaluating habitat suitability models for nesting white-headed woodpeckers in unburned forest. *The Journal of Wildlife Management* 79 (2):263-273. https://doi.org/10.1002/jwmg.842.

Latif, Quresh S., Jamie S. Sanderlin, Victoria A. Saab, William M. Block, and Jonathan G. Dudley. 2016b. Avian relationships with wildfire at two dry forest locations with different historical fire regimes. *Ecosphere* 7 (5):e01346. https://doi.org/10.1002/ecs2.1346.

Link, William A., and Richard J. Barker. 2010. *Bayesian Inference with Ecological Applications*: Elsevier.

MacKenzie, Darryl I., James D. Nichols, G.B. Lachman, S. Droegge, J. Andrew Royle, and C.A. Langlimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248-2255.

MacKenzie, Darryl I., James D. Nichols, J. Andrew Royle, Kenneth H. Pollock, Larissa L. Baily, and James E. Hines. 2018. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. 2 ed. London, UK: Academic Press.

McIver, James D., Scott L. Stephens, James K. Agee, Jamie Barbour, Ralph E. J. Boerner, Carl B. Edminster, Karen L. Erickson, Kerry L. Farris, Christopher J. Fettig, Carl E. Fiedler, Sally Haase, Stephen C. Hart, Jon E. Keeley, Eric E. Knapp, John F. Lehmkuhl, Jason J. Moghaddas, William Otrosina, Kenneth W. Outcalt, Dylan W. Schwilk, Carl N. Skinner, Thomas A. Waldrop, C. Phillip Weatherspoon, Daniel A. Yaussy, Andrew Youngblood, and Steve Zack. 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogate study (FFS). *International Journal of Wildland Fire* 22 (1):63-82. https://doi.org/http://dx.doi.org/10.1071/WF11130.

McKelvey, Kevin S., William M. Block, Theresa B. Jain, Charles H. Luce, Deborah S. Page-Dumroese, Bryce A. Richardson, Victoria A. Saab, Anna W. Schoettle, Carolyn H. Sieg, and Daniel R. Williams. 2021. Adapting research, management, and governance to confront socioecological uncertainties in novel ecosystems. *Frontiers in Forests and Global Change* 4 (14). https://doi.org/10.3389/ffgc.2021.644696.

Millar, Constance I., Nathan L. Stephenson, and Scott L. Stephens. 2007. *CLIMATE CHANGE AND FORESTS OF THE FUTURE: MANAGING IN THE FACE OF UNCERTAINTY*. Ecological Applications 17 (8):2145-2151. https://doi.org/doi:10.1890/06-1715.1.

Moir, William H., Brian Geils, Mary Ann Benoit, and Dan Scurlock. 1997. Ecology of southwestern ponderosa pine forests. edited by William M. Block and Deborah M. Finch. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.

Morgan, Penelope, Gregory H. Aplet, Jonathan B. Hautler, Hope C. Humphries, Margaret M. Moore, and W. Dale Wilson. 1994. Historical range of variability. *Journal of Sustainable Forestry* 2 (1-2):87-111. https://doi.org/10.1300/J091v02n01_04.

Morrison, Michael L., William M. Block, M. Dale Strickland, B. A. Collier, and M. J. Peterson. 2008. *Wildlife study design*. New York, New York, USA: Springer.

Nimmo, D. G., L. T. Kelly, L. M. Farnsworth, S. J. Watson, and A. F. Bennett. 2014. Why do some species have geographically varying responses to fire history? *Ecography* 37 (8):805-813. https://doi.org/https://doi.org/10.1111/ecog.00684.

North, M., P. Stine, K. O’Hara, W. Zielinski, and S.L. Stephens. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. edited by US Department of Agriculture. Albany, CA: Forest Service, Pacific southwest Research Station.

Pickrell, John, and Elizabeth Pennisi. 2020. Record U.S. and Australian fires raise fears for many species. *Science* 370 (6512):18-19. https://doi.org/10.1126/science.370.6512.18.

Plummer, M. 2003. *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). Vienna, Austria, March 20-22, 2003.
Pollock, Kenneth H. 1982. A Capture-Recapture Design Robust to Unequal Probability of Capture. The Journal of Wildlife Management 46 (3):752-757. https://doi.org/10.2307/3808568.

Popescu, Viorel D., Perry de Valpine, Douglas Tempel, and M. Zachariah Peery. 2012. Estimating population impacts via dynamic occupancy analysis of Before-After Control-Impact studies. Ecological Applications 22 (4):1389-1404. https://doi.org/10.1890/11-1669.1.

Russell, Robin E., J. Andrew Royle, Victoria A. Saab, John F. Lehmkuhl, William M. Block, and John R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. Ecological Applications 19 (5):1253-1263. https://doi.org/10.1890/08-0910.1.

Russell, Robin E., Victoria A. Saab, Jonathan G. Dudley, and Jay J. Rotella. 2006. Snag longevity in relation to wildfire and postfire salvage logging. Forest Ecology and Management 232:179-187.

Ryan, Kevin C, Eric E Knapp, and J Morgan Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Frontiers in Ecology and the Environment 11 (s1):e15-e24. https://doi.org/https://doi.org/10.1890/120329.

Saab, V. A., R.E. Russell, and J.G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor 109:97-108.

Saab, V.A., and Hugh D. W. Powell. 2005. Fire and avian ecology in North America: process influencing pattern. Studies in Avian Biology 30:1-13.

Saab, Victoria A., Hugh D. W. Powell, Natasha B. Kotliar, and Karen R. Newlon. 2005. Variation in fire regimes of the Rocky Mountains: implications for avian communities and fire management. Studies in Avian Biology 30:76-96.

Sanderlin, Jamie S., William M. Block, and Joseph L. Ganey. 2014. Optimizing study design for multi-species avian monitoring programmes. Journal of Applied Ecology 51 (4):860-870. https://doi.org/10.1111/1365-2664.12252.

Seastedt, Timothy R, Richard J Hobbs, and Katharine N Suding. 2008. Management of novel ecosystems: are novel approaches required? Frontiers in Ecology and the Environment 6 (10):547-553. https://doi.org/https://doi.org/10.1890/070046.

Smucker, Kristina M., Richard L. Hutto, and Brian M. Steele. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15 (5):1535-1549.

Stephens, Scott L, Brandon M Collins, Christopher J Fettig, Mark A Finney, Chad M Hoffman, Eric E Knapp, Malcolm P North, Hugh Safford, and Rebecca B Wayman. 2018. Drought, Tree Mortality, and Wildfire in Forests Adapted to Frequent Fire. BioScience 68 (2):77-88. https://doi.org/10.1093/biosci/bix146.

Sutherland, William J., Ian Newton, and Rhys E. Green. 2004. Bird ecology and conservation: a handbook of techniques. New York, New York, USA.: Oxford University Press.
Team, R Core. 2013. "R: A language and environment for statistical computing." In. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

USDA. 2012. United States Department of Agriculture (USDA). 2012. National Forest System land management planning. Federal Register 77:21162 - 21276.

Veech, Joseph A., and Thomas O. Crist. 2007. Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. Global Ecology and Biogeography 16 (5):650-656. https://doi.org/https://doi.org/10.1111/j.1466-8238.2007.00315.x.

White, A. M., P. N. Manley, G. L. Tarbill, T. W. Richardson, R. E. Russell, H. D. Safford, and S. Z. Dobrowski. 2016. Avian community responses to post-fire forest structure: implications for fire management in mixed conifer forests. Animal Conservation 19 (3):256-264. https://doi.org/10.1111/acv.12237.

Wiens, J. A., and J. T. Rotenberry. 1985. Response of Breeding Passerine Birds to Rangeland Alteration in a North American Shrubsteppe Locality. Journal of Applied Ecology 22 (3):655-668.

Wilson, Christopher W., Ronald E. Masters, and George A. Bukenhofer. 1995. Breeding bird response to pine-grassland community restoration for red-cockaded woodpeckers. The Journal of Wildlife Management 59 (1):56-67. https://doi.org/10.2307/3809116.
Table 1. Predicted species-specific responses to fire by life history traits based on published literature and reviewed in Birds of the World (Billerman et al. 2020).

| Life History Trait      | Foraging          | Nesting          |
|-------------------------|-------------------|------------------|
|                         | Cavity            | Open-cup         |
| Aerial insectivore      | Prediction: positive  
                      | Rationale: increased foraging opportunities due to reduction in forest canopy and increase in available nesting cavities.  
                      | Species: ash-throated flycatcher, purple martin, tree swallow, violet-green swallow, mountain bluebird, white-throated swift, western flycatcher  |
| Bark insectivore        | Prediction: strong positive  
                      | Rationale: increased availability of nest substrates (i.e. snags and dead portions of live trees) for all species and food (i.e. beetle larvae) for beetle foraging species.  
                      | Species: hairy woodpecker, American three-toed woodpecker, black-backed woodpecker, downy woodpecker, white-breasted nuthatch, brown creeper, red-breasted nuthatch, pygmy nuthatch, Pacific wren  |
| Canopy foliage insectivore | Prediction: mixed  
                      | Rationale: increased nest availability with increases in dead portions of trees, but reductions in food resources of live foliage and bark.  |
|                         | Prediction: negative  
                      | Rationale: reduced nesting and foraging substrate due to desiccation of foliage  |
| Species: black-capped chickadee, mountain chickadee |
| Species: gray vireo, plumbeous vireo, Cassin's vireo, warbling vireo, golden-crowned kinglet, ruby-crowned kinglet, olive warbler, Nashville warbler, yellow warbler, yellow-rumped warbler, Grace's warbler, Townsend's warbler, Virginia's warbler, black-throated gray warbler, red-faced warbler, olive warbler, western tanager, bushtit |

| Shrub or ground insectivore |
| **Prediction:** positive  
**Rationale:** increased nest availability with increases in dead portions of trees, increased foraging substrate of open ground.  
**Species:** rock wren, house wren, western bluebird |
| **Prediction:** mixed  
**Rationale:** positive following regrowth of understory vegetation, which is stimulated by opening of the canopy, but negative for species reliant on ground litter  
**Species:** American robin, Swainson's thrush, orange-crowned warbler, MacGillivray's warbler, Wilson's warbler, vesper sparrow, Lincoln's sparrow |

| Omnivore |
| **Prediction:** Mixed  
**Rationale:** Generalist foraging strategies for these species will result in minimal distributional changes, despite a potential increase in nesting habitat  
**Species:** Northern flicker, pileated woodpecker, red-naped sapsucker |
| **Prediction:** Neutral  
**Rationale:** generalist foraging strategies for these species were expected to result in minimal changes  
**Species:** band-tailed pigeon, mourning dove, Hermit thrush, cedar waxwing, green-tailed towhee, spotted towhee, black-headed grosbeak, lazuli bunting, western meadowlark, Bullock's oriole, Cassin's finch, red crossbill, pine siskin, lesser goldfinch, song sparrow, brown-headed cowbird, chipping sparrow, Brewer's sparrow, lark sparrow, dark-eyed junco, hepatic tanager |
Table 2. Locations, areas, sampling distributions, and historical fire regime, for study units where avian community changes in relation to prescribed fire were studied on 7 National Forests in the Interior West.

| National Forest, State          | Unit pair | Number of survey points; unit area (ha) | Historical fire regime |
|---------------------------------|-----------|-----------------------------------------|------------------------|
|                                 |           | Treatment | Control |                         |
| Payette, Idaho                  | 1         | 20; 210   | 20; 224 | mixed severity          |
|                                 | 2         | 20; 280   | 20; 220 |                         |
|                                 | 3         | 11; 248   | 10; 216 |                         |
| Okanogan-Wenatchee, Washington  | 4         | 20; 400   | 20; 369 | mixed severity          |
|                                 | 5         | 20; 392   | 20; 342 |                         |
|                                 | 6         | 20; 253   | 20; 351 |                         |
| San Juan, Colorado              | 7         | 32; 179   | 25; 265 | mixed severity          |
|                                 | 8         | 21; 186   | 21; 173 |                         |
| Kaibab, Arizona                 | 9         | 40; 396   | 50; 486 | low severity            |
| Gila, New Mexico                | 10        | 25; 261   | 25; 244 | low severity            |
| Apache-Sitgreaves, Arizona      | 11        | 29; 247   | 29; 285 | low severity            |
| Coconino, Arizona               | 12        | 40; 402   | 40; 404 | low severity            |
Table 3. Treatment and sampling timing at 24 study units established for the primary analysis of avian community changes with prescribed fire at 7 National Forests in the Interior West.

| National Forest, State | Unit | Mean visits per season (range) | Burn Timing (S = Spring, F = Fall) | Number seasons (survey years) |
|------------------------|------|--------------------------------|-----------------------------------|------------------------------|
|                        |      |                                | Before                            | After                        |
| Payette, Idaho         | 1    | 1.99 (1–2)                     | S2004                             | 2 (2002–2003) 2 (2004–2005)  |
|                        | 2    | 1.98 (1–2)                     | S2006                             | 2 (2004–2005) 2 (2006–2007)  |
|                        | 3    | 1.98 (1–2)                     | S2006                             | 2 (2004–2005) 2 (2006–2007)  |
| Okanogan-Wenatchee,    | 4    | 2.98 (2–3)                     | S2004                             | 2 (2002–2003) 2 (2004–2005)  |
| Washington             | 5    | 2.99 (2–3)                     | S2004                             | 2 (2002–2003) 2 (2004–2005)  |
|                        | 6    | 2.98 (2–3)                     | S2005                             | 2 (2003–2004) 2 (2005–2006)  |
| San Juan, Colorado     | 7    | 1.99 (1–2)                     | S2008                             | 2 (2004–2005) 2 (2008–2009)  |
|                        | 8    | 1.99 (1–2)                     | S2010                             | 2 (2004–2005) 1 (2010)      |
| Kaibab, Arizona        | 9    | 3.35 (1–4)                     | F2003 & S2004                     | 2 (2002–2003) 2 (2004–2005)  |
| Gila, New Mexico       | 10   | 3.63 (1–4)                     | F2003 & S2004                     | 2 (2002–2003) 2 (2004–2005)  |
| Apache-Sitgreaves,     | 11   | 3.79 (2–4)                     | F2003                             | 1 (2003) 2 (2004–2005)      |
| Arizona                | 12   | 3.90 (2–4)                     | F2003                             | 1 (2003) 2 (2004–2005)      |
Figure Legends

Figure 1. Study areas of the Birds and Burns Network located on 7 National Forests of the interior western United States.

Figure 2. Composite burn index (CBI) frequency distributions by national forest study location: Okanagan-Wenatchee in Washington (OKWA), Payette NF in Idaho (PAID), San Juan NF in Colorado (SJCO), Apache-Sitgreaves NF in Arizona (ASA AZ), Coconino NF in Arizona (COAZ), Gila NF in New Mexico (GINM), and Kaibab NF in Arizona (KAAZ). Sample sizes (n) represent the number of point count stations where birds were surveyed. Vertical solid lines denote mean values and vertical dashed lines denote 1 SD above and below the mean.

Figure 3. Parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\hat{\beta}_{CBI \times PER}$ from Equation 3). Estimates are for locations with historically mixed-severity (circles with solid lines) and low-severity (squares with dashed lines) fire regimes. The 47 species observed in both fire regimes (left), 29 species observed only in mixed-severity regime locations (upper right), and 19 species observed only in low-severity regime locations (lower right) are shown. Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with treatment application.

Figure 4. Statistically supported occupancy parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\hat{\beta}_{CBI \times PER}$) and post-treatment CBI relationships ($\hat{\beta}_{CBI} + \hat{\beta}_{CBI \times PER}$) for 25 species observed at locations with historically mixed-severity fire regimes.
Estimates from a primary model (A, B) are compared with those from supplemental models that included data from additional years and a Markovian persistence effect (C) or separated effects by post-treatment year (D, E). Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with treatment application, whereas CBI (composite burn index) relationships quantify the post-treatment correlation only.

Figure 5. Statistically supported occupancy parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\hat{\beta}_{CBI\times PER}$) and CBI relationships ($\hat{\beta}_{CBI} + \hat{\beta}_{CBI\times PER}$) for 17 species observed at locations with historically low-severity fire regimes. Estimates from our main model (A, B) are compared with those from a supplemental model that separated effects by post-treatment year (C, D). Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with treatment application, whereas CBI (composite burn index) relationships quantify the post-treatment correlation only.

Figure 6. Predicted occupancy with burn severity (CBI) for example species showing treatment responses statistically supported in historically mixed severity regimes but not supported in low severity regimes. Relationships with CBI were estimated before (grey) and after (black) treatment in mixed severity regimes (left) and low severity regimes (right), and treatment responses are inferred from the change in slope between the two. Intercept terms for calculating model predictions were averaged (mean) across locations within each regime. Full species names are listed in Appendix E.

Figure 7. Species richness estimates and 90% BCIs for surveyed points along burn severity (CBI) gradients estimated before (left column) and after (right column) prescribed fire
treatments. Locations appearing in the top row historically experienced mixed-severity fire regimes (Okanagan-Wenatchee [OKWA], Payette [PAID], and San Juan [SJCO] National Forests), whereas locations in the bottom panels experienced low-severity regimes (Apatchee-Sitgreaves [ASA], Coconino [COAZ], Gila [GINM], and Kaibab [KAAZ] National Forests). Best-fit lines show trends in posterior median estimates. The change in slope of trend lines from left to right indicates treatment effect on estimated species richness at surveyed point count stations.
Figures

Figure 1

Study areas of the Birds and Burns Network located on 7 National Forests of the interior western United States.
Composite burn index (CBI) frequency distributions by national forest study location: Okanagan-Wenatchee in Washington (OKWA), Payette NF in Idaho (PAID), San Juan NF in Colorado (SJCO), Apache-Sitgreaves NF in Arizona (ASAZ), Coconino NF in Arizona (COAZ), Gila NF in New Mexico (GINM), and Kaibab NF in Arizona (KAAZ). Sample sizes (n) represent the number of point count stations.
Parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\beta$ CBI×PER) from Equation 3). Estimates are for locations with historically mixed-severity (circles with solid lines) and low-severity (squares with dashed lines) fire regimes. The 47 species observed in both fire regimes (left), 29 species observed only in mixed-severity regime locations (upper right), and 19 species observed only in
low-severity regime locations (lower right) are shown. Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with treatment application.

Figure 4

Statistically supported occupancy parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\beta_{\text{CBI} \times \text{PER}}$) and post-treatment CBI relationships ($\beta_{\text{CBI}} + \beta_{\text{CBI} \times \text{PER}}$) for 25 species observed at locations with historically mixed-severity fire regimes. Estimates from a primary model (A, B) are compared with those from supplemental models that included data from additional years and a Markovian persistence effect (C) or separated effects by post-treatment year (D, E).

Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with
treatment application, whereas CBI (composite burn index) relationships quantify the post-treatment correlation only.

Figure 5

Statistically supported occupancy parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\beta_{\text{CBI} \times \text{PER}}$) and CBI relationships ($\beta_{\text{CBI}} + \beta_{\text{CBI} \times \text{PER}}$) for 17 species observed at locations with historically low-severity fire regimes. Estimates from our main model (A, B) are compared with those from a supplemental model that separated effects by post-treatment year (C, D). Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with
treatment application, whereas CBI (composite burn index) relationships quantify the post-treatment correlation only.

**Figure 6**

Predicted occupancy with burn severity (CBI) for example species showing treatment responses statistically supported in historically mixed severity regimes but not supported in low severity regimes. Relationships with CBI were estimated before (grey) and after (black) treatment in mixed severity regimes.
Species richness estimates and 90% BCIs for surveyed points along burn severity (CBI) gradients estimated before (left column) and after (right column) prescribed fire treatments. Locations appearing in the top row historically experienced mixed-severity fire regimes (Okanagan-Wenatchee [OKWA], Payette [PAID], and San Juan [SJCO] National Forests), whereas locations in the bottom panels experienced low-severity regimes (Apache-Sitgreaves [ASAZ], Coconino [COAZ], Gila [GINM], and Kaibab [KAAZ] National Forests).
Forests). Best-fit lines show trends in posterior median estimates. The change in slope of trend lines from left to right indicates treatment effect on estimated species richness at surveyed point count stations.

**Supplementary Files**

This is a list of supplementary files associated with this preprint. Click to download.

- MSappendices2.pdf