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Prescribed fire limits wildfire severity without altering ecological importance for birds

Quresh S. Latif^{1*} , Victoria A. Saab² and Jonathan G. Dudley³

Abstract

Background: Fire suppression and anthropogenic land use have increased severity of wildfire in western U.S. dry conifer forests. Managers use fuels reduction methods (e.g., prescribed fire) to limit high-severity wildfire and restore ecological function to these fire-adapted forests. Many avian species that evolved in these forests, however, are adapted to conditions created by high-severity wildfire. To fully understand the ecological implications of fuels reduction treatments, we need to understand direct treatment effects and how treatments modulate subsequent wildfire effects on natural communities. We studied bird population and community patterns over nine years at six study units, including unburned (2002–2003), after prescribed fire (2004–2007), and after wildfire (2008–2010). We used a before-after, control-impact (BACI) approach to analyze shifts in species occupancy and richness in treated units following prescribed fire and again in relation to burn severity following wildfire.

Results: We found examples of both positive and negative effects of wildfire and prescribed fire on bird species occupancy depending on and largely consistent with their life history traits; several woodpecker species, secondary cavity-nesting species, aerial insectivores, and understory species exhibited positive effects, whereas open cup canopy-nesting species and foliage- or bark-gleaning insectivores exhibited negative effects. Wildfire affected more species more consistently through time than did prescribed fire. Wildfire burned units initially treated with prescribed fire less severely than untreated units, but the slopes of wildfire effects on species occupancy were similar regardless of prior prescribed fire treatment.

Conclusions: Our results suggest managers can employ prescribed fire to reduce wildfire severity without necessarily altering the ecological importance of wildfire to birds (i.e., the identity of species exhibiting negative versus positive responses). Additional study of the ecological implications of various fuels reduction practices, representing a range of intensities and fire regimes, would further inform forest management that includes biodiversity objectives.

Keywords: Aves, Birds, Community composition, Dry conifer forest, Fuel management, Occupancy, Prescribed fire, Species richness, Western North America, Wildfire

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Resumen

Antecedentes: La supresión de incendios y el uso antropogénico de la tierra han incrementado la severidad de los incendios en los bosques secos de coníferas del Oeste de los EEUU. Los gestores de recursos usan métodos de reducción del combustible (i.e. quemas prescriptas), para limitar la alta severidad de los incendios y restaurar las funciones de esos bosques adaptados al fuego. Muchas especies de aves que evolucionaron en esos bosques, sin embargo, están adaptadas a condiciones creadas por fuegos de alta severidad. Para comprender totalmente las implicancias ecológicas de los tratamientos de reducción del combustible, necesitamos entender los efectos directos de estos tratamientos y cómo ellos modulan los efectos subsiguientes del fuego sobre las comunidades naturales. Estudiamos las poblaciones de aves y los patrones de la comunidad por nueve años en seis unidades de estudio incluyendo el no quemado (control, 2002-2003), luego de una quema prescripta (2004-2007) y luego de un incendio (2008-2010). Usamos la aproximación de antes-después, y control de impacto (Before-After Control Impact, BACI en inglés) para analizar las desviaciones en la ocupación de especies y riqueza en las unidades tratadas luego de las quemas prescriptas y nuevamente en relación a la severidad de la quema luego de un incendio.

Resultados: Encontramos ejemplos de efectos tanto positivos como negativos del incendio y de las quemas prescriptas en la ocupación del espacio por las aves, dependiendo sobre y consistentemente, de las características de sus historias de vida; muchas especies de pájaros carpinteros, especies secundarias que usan las cavidades para anidar, pájaros insectívoros y especies de sotobosque exhibieron efectos positivos, mientras que aquellas especies que anidan en el dosel superior y aquellas insectívoras que se alimentan de invertebrados del follaje o de la corteza exhibieron efectos negativos. Los incendios afectaron más consistentemente y en el tiempo, más especies que las quemas prescriptas. Las unidades tratadas inicialmente con quemas prescriptas fueron afectadas menos severamente que las no tratadas cuando fueron alcanzadas por incendios, aunque los efectos de la pendiente en la ocupación de las especies fueron similares independientemente del tratamiento previo por las quemas prescriptas.

Conclusiones: Nuestros resultados sugieren que los gestores pueden emplear quemas prescriptas para reducir la severidad sin que necesariamente se altere la importancia ecológica de los incendios sobre las aves (i.e., la identidad de las especies que exhibieron respuestas negativas sobre positivas). Estudios adicionales sobre la implicancia de varias prácticas de reducción del combustible, representando un rango de intensidades y regímenes de fuego, podría informar sobre manejo forestal que incluya objetivos de biodiversidad

Background

Wildfire strongly shapes the amount and distribution of biodiversity in western North American forests. Some species occur more frequently and others less frequently in recently burned forest, causing community composition to vary with burn severity (Saab et al. 2005; Kalies et al. 2010; Fontaine and Kennedy 2012). Landscapes containing a diversity of forest stands varying in history of fire are therefore expected to support the greatest array of species (Clarke 2008; Fontaine et al. 2009; Fontaine and Kennedy 2012). Within the last ~ 100 years, anthropogenic fire suppression, logging, development, livestock grazing, and climate change have caused fuel accumulation and homogenization of vegetation structure in many lower elevation dry conifer forests of the western USA (Covington and Moore 1992; Agee 1993; Brown et al. 2004; Schoennagel et al. 2004). These changes have shifted fire regimes towards less frequent but larger and more severe wildfire, with potential negative consequences for the economic and esthetic values of forests, human safety, and wildlife diversity (Dale et al. 2001; Brown et al. 2004; Schoennagel et al. 2004).

Forest managers widely implement fuel reduction treatments, i.e., prescribed fire, timber harvest, or

some combination of both, to limit wildfire size and severity, with the ultimate goal of restoring historical vegetation structure and composition to mitigate anthropogenic impacts (Fulé et al. 2012). Empirical studies confirm expected reductions in wildfire severity in treated areas for a limited number of years following treatment, particularly when fuel loads are greatly reduced (Pollet and Omi 2002; Fulé et al. 2012; Prichard and Kennedy 2014; Fernandes 2015). Thus, strategically placed treatments could help managers reduce the extent of subsequent wildfire (Stevens et al. 2014). Some expect this approach to restore historical conditions and ecological function to many dry conifer forests (Walker et al. 2018). Desirable historical conditions are difficult to achieve because of climate-induced ecological changes (McKelvey et al. 2021) and because they vary regionally and by spatial scale (Schoennagel et al. 2004; Bock and Block 2005; Illán et al. 2014). Animal ecologists therefore suggest treatments could be ineffective or inappropriate in regions like the central Rocky Mountains where historical levels of diversity were associated with relatively

heterogeneous landscapes maintained by mixed-severity fire (Saab et al. 2005; Latif et al. 2016b).

Birds are valuable as focal organisms for understanding faunal community relationships with wildfire and forest management. Surveys do not require specialized equipment (Sutherland et al. 2004), allowing changes in bird population densities, species distributions, and community structure to readily inform management strategies aimed at biological conservation (Saab and Powell 2005; Saab et al. 2005). Additionally, hierarchical occupancy models facilitate analysis of survey data to evaluate population and community relationships with environmental disturbance and management treatments (Dorazio et al. 2006; Russell et al. 2009; Russell et al. 2015; Latif et al. 2016b). Bird responses to disturbance depend on species ecology and life history traits (Saab and Powell 2005; Smucker et al. 2005; Kotliar et al. 2007; Fontaine and Kennedy 2012; Seavy and Alexander 2014). Wildfire opens the canopy, which can stimulate understory vegetative growth and improve foraging and nesting opportunities for shrub-nesting and ground-foraging species, and creates snags that provide important nesting and foraging resources for cavity-nesting species (Hutto 1995; Kotliar et al. 2002; Saab et al. 2009). In contrast, tree mortality after wildfire reduces resources for canopy-nesting species and species that forage on live trees (Kotliar et al. 2007; Fontaine et al. 2009). As with wildlife communities in general, ecologists expect landscapes representing the historical range of fire conditions to support the greatest array of bird species (see reviews by Kalies et al. 2010; Fontaine and Kennedy 2012).

Fuel reduction treatments could shape bird diversity in various ways. Birds may respond directly to treatment-induced changes in forest structure (Russell et al. 2009; Gaines et al. 2010; Fontaine and Kennedy 2012; White et al. 2013). Managers sometimes look to fuel treatments to provide a surrogate for wildfire (McIver et al. 2013), but severity and scale limit the potential for treatment effects to emulate wildfire effects on birds (Fontaine and Kennedy 2012). Instead, the current debate focuses more on how treatments modulate burn severity and consequent wildfire effects on birds (Hutto et al. 2014). By altering subsequent wildfire behavior, fuel reduction treatments may change the ecological significance of wildfire for birds. For example, by limiting high-severity crown fire, wildfire in treated areas may not generate enough snags to benefit cavity-nesting species or open the canopy sufficiently to benefit understory species (Hutto et al. 2015). Conversely, reduced tree mortality may result in limited negative impacts of wildfire for canopy-nesting and foliage-gleaning species. Studies comparing wildfire behavior and bird responses to wildfire in treated versus untreated stands are needed to test

these hypotheses. Knowledge of how fuel reduction treatments directly and indirectly influence avian populations and communities will inform forest management activities that incorporate habitat conservation for avian diversity.

We studied avian relationships with prescribed fire and wildfire in the Payette National Forest (NF), a lower elevation dry conifer forest in the central Rocky Mountains historically associated with a mixed-severity fire regime. We surveyed birds in paired treatment and control study units before (2002–2003) and after (2004–2007) prescribed fire and following wildfire (2008–2010). We evaluated two primary hypotheses: (1) wildfire burn severity would be lower in units initially treated with prescribed fire, and consequently, (2) birds would respond differently to wildfire in treated compared to untreated units. Secondly, being more severe and extensive, we expected wildfire to have stronger effects on bird populations (inferred from changes in species occupancy) than prescribed fire. We also built on published literature and evaluated hypotheses therein regarding expected responses to wildfire and prescribed fire for particular life histories (Russell et al. 2009; Latif et al. 2016b). We primarily evaluated our hypotheses by looking for temporal shifts in species occupancy of sites varying in burn severity following disturbance, providing relatively strong inference of disturbance effects (Popescu et al. 2012; Russell et al. 2015). We considered implications of observed patterns for forest management with objectives that include conservation of avian diversity.

Methods

Study system

The Payette NF is in the central Rocky Mountains of western North America (45° 00' 30" N 116° 02' 30" W; elevation 1127–2075 m). The East Zone Complex Fire burned the Payette NF in July–October 2007 (95,100 ha; Fig. 1). About 60 years prior to this study, forest managers began suppressing wildfire and managing for multiple uses, including timber harvest, mining, recreation, livestock grazing, wildlife habitat, and watershed management (Hollenbeck et al. 2013). Following the classification scheme of Miller and Thode (2007), burn severity within the East Zone Complex Fire perimeter was classified as 9% unburned, 19% low severity, 26% moderate severity, and 46% high severity (see also Latif et al. 2016b).

The canopy was dominated by large (≥ 23 cm dbh) ponderosa pine (*Pinus ponderosa*) trees ($> 65\%$; Hollenbeck et al. 2013). Other tree species included Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and small patches (< 10 ha) of quaking aspen (*Populus tremuloides*) in snowmelt drainages. Common understory species include snowberry (*Symphoricarpos albus*),

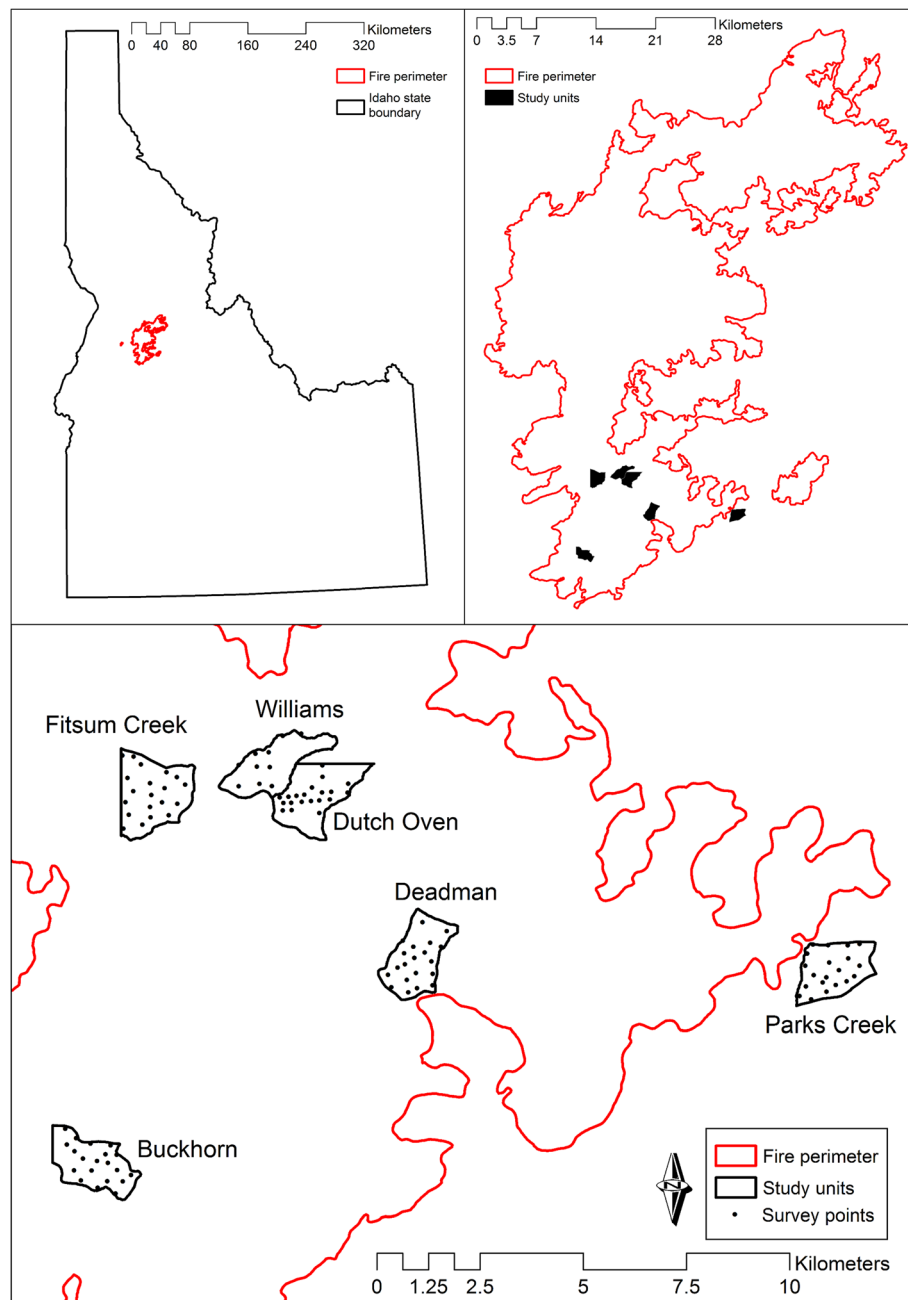


Fig. 1 Study area and units where forest bird data were collected in the Payette National Forest (ID, USA) in relation to prescribed fire treatments and subsequent wildfire. The fire perimeter is for the 2007 East Zone Complex wildfire

spirea (*Spirea betulifolia*), Saskatoon serviceberry (*Aamelanchier alnifolia*), and chokecherry (*Prunus virginiana*).

Study units

We established six study units distributed across ~ 20,000 ha (Fig. 1). Study units were delineated in pairs so that members of each pair were similar in vegetation and topography, and 1 member of each pair was

randomly selected for prescribed fire treatment (Table 1) (for additional details, see Saab et al. (2007)). Forest managers applied prescribed fire treatments in spring prior to the breeding season for most bird species (April–early May); one unit was treated in 2004, and the other two in 2006. The East Zone Complex Fire subsequently burned 5 units (2 treatment, 3 control).

Table 1 Treatment timing and sampling for study units used to examine forest bird occupancy relationships with prescribed fire and wildfire at the Payette National Forest, Idaho. Members of unit pairs represented similar pre-fire environmental conditions

Pair	Study unit	n points	Years surveyed	Prescribed fire timing	Wildfire timing
1	Buckhorn	20	2002–2010	Control	Fall, 2007
	Fitsum Creek	20	2002–2010	Spring, 2006	Fall, 2007
2	Williams	10	2002–2010	Control	Fall, 2007
	Dutch Oven	20	2002–2010	Spring, 2006	Fall, 2007
3	Deadman	20	2002–2006, 2008–2010	Control	Fall, 2007
	Parks Creek	20	2002–2006	Spring, 2004	Not surveyed

Bird surveys

We surveyed birds at 110 point survey stations distributed across the 6 study units (Table 1, Fig. 1). We spaced survey points at least 150 m apart (mean = 277, $SD = 68$) within study unit boundaries. For statistical independence, we space most points ≥ 200 m apart, but we were forced to space a minority of points (32%) in closer proximity due to steep topography with limited access for humans. We surveyed each point twice each between 23 May and 3 July over the years they were surveyed. We began surveys just after the dawn chorus and completed them within 5 h. Observers recorded all birds detected during a 5-min count and estimated distances to each detected individual. We only included detections recorded within 100 m of the surveyor in this analysis. Our sampling design was a robust design (Pollock 1982) with years as the primary periods and visits within years as secondary periods.

We surveyed birds in one unit pair through 2006 and the remaining two pairs through 2007 and then continued monitoring the five units burned by wildfire in 2008–2010. Thus, we obtained data representing 2–4 years before and 2–3 years after prescribed fire treatment and 3 years of post-wildfire (Table 1).

Burn severity measurements and analysis

We measured burn severity using the composite burn severity index (CBI ; Key and Benson 2006) modified to accommodate our study area and objectives. We calculated a CBI value for each survey point (0–3 range) representing the mean of up to 11 components quantifying aspects of canopy structure, understory cover, and downed woody fuels (for details, see Additional file 1: Appendix A). We derived components from field measurements of these attributes before fire (2002–2003), after prescribed fire (2004–2007), and after wildfire (2008–2010). Components represented either changes in these attributes from before to after disturbance or aspects of burn severity apparent after disturbance (e.g., extent of char). We only measured points within burned units and assumed $CBI = 0$ for units that were not burned during our study. Others describe in detail how CBI values correspond with changes in various aspects

of vegetation structure (Key and Benson 2006; Saab et al. 2006). In short, $CBI = 0$, $0 < CBI < 1.25$, $1.25 < CBI < 2.25$, and $CBI > 2.25$ are interpretable as unburned, low severity, moderate severity, and high severity, respectively. In general, low-severity fire primarily affects understory vegetation with minimal canopy mortality ($< 40\%$), whereas high-severity fire results in much greater canopy mortality ($> 70\%$).

We quantified prescribed fire CBI (hereafter CBI_{PF}) using environmental data collected before (2002–2003) versus after (2004–2007) prescribed fire, and wildfire CBI (hereafter CBI_{WF}) with data from immediately before (2004–2007) versus after wildfire (2008–2010). Unfortunately, wildfire burned one treated study unit (Fitsum Creek) before we could measure post-treatment prescribed fire conditions (2004–2007). For this unit, we imputed CBI_{WF} by (1) calculating CBI_{Total} representing overall burn severity (i.e., changes from 2002–2003 to 2008–2010), (2) regressing CBI_{WF} as a linear function of CBI_{Total} at units where both were available (Buckhorn, Dutch Oven, Williams, and Deadman), and (3) using the resulting regression model ($CBI_{WF} = \beta_0 + \beta_1 \times CBI_{Total}$, with estimates β_0 [s.e.] = -0.04623 [0.07653] and $\beta_1 = 0.98415$ [0.04271]) to impute missing data. As a covariate of occupancy, we imputed missing CBI_{WF} values using a normally distributed prior with mean and SD representing model-predicted CBI_{WF} .

Data for calculating CBI_{PF} were relatively limited, so we did not use CBI_{PF} as a covariate of occupancy. Rather, we modeled occupancy with a categorical treatment effect ($TRT_{PF} = 0$ or 1 for survey points in untreated versus treated units, respectively). We then summarized CBI_{PF} values where available (Dutch Oven, Parks Creek) to inform inference and compare with CBI_{WF} . We compared CBI_{WF} between treated and untreated points within treatment-control unit pairs and compared CBI_{WF} with CBI_{PF} where available to evaluate the effect of prescribed fire treatments on subsequent wildfire severity.

Occupancy models

We analyzed avian relationships with prescribed fire using community occupancy models formulated within a

Bayesian hierarchical modeling framework (Dorazio et al. 2006; Russell et al. 2009). Occupancy models leverage repeat-survey data to estimate species detectability (p) conditional upon occupancy (species occurrence within a specified time period), allowing unbiased estimation of occupancy probabilities (ψ) given sufficient data and adherence to model assumptions (MacKenzie et al. 2002; MacKenzie et al. 2006). We assumed that the occupancy states of species could change among years, but not between visits within a year. We estimated 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 (Dorazio et al. 2006; Russell et al. 2009). We excluded raptors, owls, and grouse from analysis because they were not readily detectable with our survey methods. Additionally, we only included species that bred in our study areas. For mobile animals such as birds, detectability (p) estimated with surveys repeated over a season quantifies both within-season movement and the observation process (i.e., availability and perceptibility; sensu Chandler and Andrew Royle 2013; Amundson et al. 2014). In principle, occupancy probabilities thereby estimated the probability of a surveyed point intersecting ≥ 1 home range for a given species (Efford and Dawson 2012; Latif et al. 2016a).

We compiled a 3-dimensional data matrix \mathbf{y} , where element y_{ijt} was the sum of binary indicators for species detection (Sanderlin et al. 2014). Given a binary indicator $x_{ijkt} = 1$, we detected species i ($i = 1, \dots, N$) at survey point j ($j = 1, \dots, J$) during visit k ($k = 1, \dots, K$) in year t ($t = 1, \dots, T$; $T = 4$). 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 survey point j in year t , where $y_{ijt} = \sum_{k=1}^K x_{ijkt}$ and $y_{ijt} \in \{0, 1, \dots, K\}$. We modeled these data given probability of detection p_i and occupancy latent state z_{ijt} using a Bernoulli distribution with probability of success $p_i \times z_{ijt}$:

$$[y_{ijt} | p_i, z_{ijt}] \sim \text{Bin}(K, p_i \times z_{ijt}) \quad (1)$$

where the latent variable z_{ijt} for occupancy given probability of occupancy ψ_{ijt} was modeled as:

$$[z_{ijt} | \psi_{ijt}] \sim \text{Bern}(\psi_{ijt}) \quad (2)$$

We analyzed changes in species occupancy patterns using a model that leveraged our before-after, control-impact (BACI) sampling for examining disturbance effects (Popescu et al. 2012; Russell et al. 2015). For prescribed fire effects, we modeled occupancy (ψ_{ijt}) as a function of treatment ($Trt_{PF,j}$), period ($Per_{jt} = 0$ or 1 for

before or after survey point j was treated, respectively), and the interaction of the two ($Trt_j \times Per_{jt}$). Thus,

$$\begin{aligned} \text{logit}(\psi_{ijt}) = & \beta_{0,i} + \beta_{Per_{PF},i} \times Per_{PF,t} + \beta_{Trt_{PF},i} \\ & \times Trt_{PF,j} + \beta_{Per_{PF} \times Trt_{PF},i} \times Per_{PF,t} \\ & \times Trt_{PF,j} \end{aligned} \quad (3)$$

where $\beta_{0,i}$ is the intercept and $\beta_{Per_{PF},i}$, $\beta_{Trt_{PF},i}$, and $\beta_{Per_{PF} \times Trt_{PF},i}$ describe the additive and interactive effects of covariates $Per_{PF,t}$ and $Trt_{PF,j}$ on occupancy of species i at survey point j in year t . We restricted analysis of prescribed fire effects to data collected before wildfire (2002–2007). For wildfire effects, we analyzed data collected 2 years before and 3 years after wildfire (2006–2010) using two models. The first model analyzed overall wildfire effects:

$$\begin{aligned} \text{logit}(\psi_{ijt}) = & \beta_{0,i} + \beta_{Per_{WF},i} \times Per_{WF,t} + \beta_{CBI_{WF},i} \\ & \times CBI_{WF,j} + \beta_{Per_{WF} \times CBI_{WF},i} \\ & \times Per_{WF,t} \times CBI_{WF,j} \end{aligned} \quad (4)$$

The second model analyzed differences in wildfire effects between units treated versus untreated with prescribed fire:

$$\begin{aligned} \text{logit}(\psi_{ijt}) = & \beta_{0,i} + \beta_{Per_{WF},i} \times Per_{WF,t} + \beta_{Trt_{PF},i} \\ & \times Trt_{PF,t} + \beta_{CBI_{WF},i} \times CBI_{WF,j} \\ & + \beta_{Per_{WF} \times CBI_{WF},i} \times Per_{WF,t} \\ & \times CBI_{WF,j} + \beta_{Trt_{PF} \times CBI_{WF},i} \\ & \times Trt_{PF,j} \times CBI_{WF,j} \\ & + \beta_{Per_{WF} \times Trt_{PF} \times CBI_{WF},i} \times Per_{WF,t} \\ & \times Trt_{PF,j} \times CBI_{WF,j} \end{aligned} \quad (5)$$

As in Eq. 3, $\beta_{0,i}$ is the intercept and all remaining β parameters describe additive and interactive effects of covariates on avian occupancy in Eqs. 4 and 5. All estimated parameters were species-specific normal random effects. For numerical purposes, we rescaled CBI_{WF} values to mean = 0 and $SD = 1$ prior to analysis.

For all three models above (Eqs. 3, 4, and 5), we drew inference of disturbance (prescribed fire or wildfire) effects from the extent to which occupancy shifted towards or away from burned (or unburned) survey points following disturbance. Interaction parameters in Eqs. 3, 4, and 5 quantified these shifts, whereas additive parameters controlled for potentially confounding environmental variation among survey points and time periods (Popescu et al. 2012). We considered statistically supported interaction parameters (90% Bayesian credible interval [BCI] excluded zero) strong evidence for disturbance effects.

We used one additional model to analyze annual changes in bird occupancy and time-dependent

disturbance effects with all available data (2002–2010). This model included a random year effect and year-specific prescribed fire and wildfire effects:

$$\text{logit}(\psi_{ijt}) = \beta_{0,it} + \beta_{Trt_{PF},it_{PF}} \times Trt_{PF,j} + \beta_{CBI_{WF},it_{WF}} \times CBI_{WF,j} \quad (6)$$

The intercept, $\beta_{0,it}$, varied with species and year according to nested normal random effects (year within species). Prescribed fire effects ($\beta_{Trt_{PF},it_{PF}}$) were estimated separately for 4 distinct time periods, pre-treatment ($t_{PF} = 0$) and 1–3 years post-treatment ($t_{PF} = 1-3$, respectively). Similarly, wildfire effects ($\beta_{CBI_{WF},it_{WF}}$) were estimated for 4 time periods, pre-fire (2006–2007; $t_{WF} = 0$) and 1–3 years post-fire (2008–2010; $t_{WF} = 1-3$, respectively). $\beta_{Trt_{PF},it_{PF}}$ was not estimated for 2008–2010 and $\beta_{CBI_{WF},it_{WF}}$ was not estimated for 2002–2005 for comparability with other models (see Eqs. 3, 4, and 5). We used this model to look for time-dependencies in disturbance effects (i.e., where 95% *BCIs* for $\beta_{Trt_{PF},i(t_{PF} \in \{1,2,3\})} - \beta_{Trt_{PF},i(t_{PF}=0)}$ or $\beta_{CBI_{WF},i(t_{WF} \in \{1,2,3\})} - \beta_{CBI_{WF},i(t_{WF}=0)}$ excluded zero, Eq. 6). Additionally, we scanned yearly occupancy estimates for surveyed sites ($\psi'_t = \sum_{j=1}^J z_{ijt} / J$) to identify notable changes among pre-treatment (2002–2003), post-treatment (2004–2007), and post-wildfire (2008–2010) periods. All sites surveyed after wildfire were burned by wildfire to some degree (min *CBI* = 0.39, see the “Results” section), so we expected some changes in overall occupancy for species with similar responses to low- versus high-severity wildfire. We considered inference from changes in overall occupancy weaker, however, because estimates of these changes did not control for potentially confounding factors as did shifts in occupancy with respect to *CBI* (see above).

In addition to species-specific relationships, we plotted emergent changes between species richness with treatment condition. We estimated species richness (N_{jt}) at each survey point j and year t : $N_{jt} = \sum_{i=1}^{\max(i)} z_{ijt}$. Similar to some (Russell et al. 2009, Latif et al. 2016b) and unlike others (Dorazio et al. 2006, Kéry et al. 2009), we did not augment data to represent unobserved species, so community-level inferences were restricted to the subset of species observed at least once during our studies.

We modeled detectability as a species-specific normal random effect $b_{0,i}$:

$$\text{logit}(p_i) = b_{0,i} \quad (7)$$

where p_i is the probability of detecting species i when surveying a given survey point in a given year when the species was present (i.e., ≥ 1 home range intersected the 100-m point neighborhood). Unlike others (Russell et al.

2015), we did not consider treatment effects on detectability. Estimated effects on detectability from preliminary analyses were imprecise (credible intervals overlapped 0 for all species) and model convergence was difficult to achieve, suggesting the additional complexity strained limits of the data (Q. Latif unpublished data). We therefore only modeled heterogeneity in detectability among species and assumed detectability did not change with treatment condition. We modeled heterogeneity among species using a correlation term (ρ) that related species intercepts of detection probability ($b_{0,i}$) with occupancy probability ($\beta_{0,i}$) (Dorazio and Royle 2005, Kéry et al. 2009).

We sampled posterior parameter distributions for all models using JAGS v4 (Plummer 2003) programmed from R (R Core Team 2013; Su and Yajima 2014). We used independent non-informative priors for all parameters (for priors, see Additional file 1: Appendix B). For each model, we ran 6 parallel MCMC chains of length 100,000 *it*, burn-in 10,000 *it*, and thinning 100 *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, where $p < 0.05$ or $p > 0.95$ constituted evidence for lack of fit.

Results

We detected 60 species across all survey points and years (Table 2). The five most frequently detected species were Yellow-rumped Warbler, Western Tanager, Chipping Sparrow, Hammond’s Flycatcher, and Red-breasted Nuthatch. The distributions of *CBIs* for wildfire and prescribed fire at surveyed points broadly overlapped, but on average, wildfire was more severe especially in areas not initially treated with prescribed fire (Fig. 2). Severe wildfire (*CBI* > 2) was extensive at untreated units (10 of 30 points) in contrast with wildfire and prescribed fire at treated units (1 of 40 points for each; Fig. 2). Species-specific detection probability estimates varied and correlated moderately with occupancy (Additional file 1: Appendix C). We found no evidence for lack of fit for community occupancy models (GOF p values ranged 0.49–0.50 for all 4 models).

Overall prescribed fire and wildfire effects

We found statistically supported prescribed fire effects for 2 species and wildfire effects for 7 species (Fig. 3). House Wren, Hairy Woodpecker, Olive-sided

Table 2 Number of detections (no. point × year occasions detected) recorded for species observed 2002–2010 in the Payette National Forest, Idaho. The maximum number of detections possible for each fire condition (unburned, treated units after prescribed fire, and after wildfire) are noted in header parentheses

Common name	Taxonomic name	Code	No. point × year occasions detected (max possible)		
			Unburned (360)	Prescribed fire (260)	Wildfire (270)
Mourning Dove	<i>Zenaida macroura</i>	MODO	0	3	8
Common Nighthawk	<i>Chordeiles minor</i>	CONI	1	3	2
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	BTHU	2	1	3
Rufous Hummingbird	<i>Selasphorus rufus</i>	RUHU	1	0	1
Calliope Hummingbird	<i>Selasphorus calliope</i>	CAHU	18	4	1
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	WISA	6	0	1
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	RNSA	3	1	3
Downy Woodpecker	<i>Dryobates pubescens</i>	DOWO	0	0	1
Hairy Woodpecker	<i>Dryobates villosus</i>	HAWO	64	35	75
American Three-toed Woodpecker	<i>Picoides dorsalis</i>	ATTW	0	5	1
Black-backed Woodpecker	<i>Picoides arcticus</i>	BBWO	2	5	6
Northern Flicker	<i>Colaptes auratus</i>	NOFL	33	17	25
Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO	4	4	10
Olive-sided Flycatcher	<i>Contopus cooperi</i>	OSFL	3	7	5
Western Wood-Pewee	<i>Contopus sordidulus</i>	WEWP	8	2	7
Hammond's Flycatcher	<i>Empidonax hammondii</i>	HAFL	275	178	155
Dusky Flycatcher	<i>Empidonax oberholseri</i>	DUFL	55	37	64
Cassin's Vireo	<i>Vireo cassinii</i>	CAVI	90	42	44
Warbling Vireo	<i>Vireo gilvus</i>	WAVI	72	71	62
Canada Jay	<i>Perisoreus canadensis</i>	CAJA	14	6	3
Steller's Jay	<i>Cyanocitta stelleri</i>	STJA	10	9	12
Clark's Nutcracker	<i>Nucifraga columbiana</i>	CLNU	21	19	16
Common Raven	<i>Corvus corax</i>	CORA	5	3	2
Black-capped Chickadee	<i>Poecile atricapillus</i>	BCCH	4	0	0
Mountain Chickadee	<i>Poecile gambeli</i>	MOCH	165	106	107
Red-breasted Nuthatch	<i>Sitta canadensis</i>	RBNU	235	175	172
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU	25	11	20
Brown Creeper	<i>Certhia americana</i>	BRCR	50	15	9
Rock Wren	<i>Salpinctes obsoletus</i>	ROWR	5	6	16
Canyon Wren	<i>Catherpes mexicanus</i>	CANW	2	0	0
House Wren	<i>Troglodytes aedon</i>	HOWR	2	0	14
Pacific Wren	<i>Troglodytes pacificus</i>	PAWR	10	4	0
Golden-crowned Kinglet	<i>Regulus satrapa</i>	GCKI	2	2	0
Ruby-crowned Kinglet	<i>Regulus calendula</i>	RCKI	25	13	5
Western Bluebird	<i>Sialia mexicana</i>	WEBL	0	1	2
Mountain Bluebird	<i>Sialia currucoides</i>	MOBL	3	1	36
Townsend's Solitaire	<i>Myadestes townsendi</i>	TOSO	73	47	29
Swainson's Thrush	<i>Catharus ustulatus</i>	SWTH	49	46	25
Hermit Thrush	<i>Catharus guttatus</i>	HETH	47	61	48
American Robin	<i>Turdus migratorius</i>	AMRO	171	104	105
Cedar Waxwing	<i>Bombycilla cedrorum</i>	CEDW	1	2	0
Orange-crowned Warbler	<i>Leiothlypis celata</i>	OCWA	8	8	5

Table 2 Number of detections (no. point × year occasions detected) recorded for species observed 2002–2010 in the Payette National Forest, Idaho. The maximum number of detections possible for each fire condition (unburned, treated units after prescribed fire, and after wildfire) are noted in header parentheses (*Continued*)

Common name	Taxonomic name	Code	No. point × year occasions detected (max possible)		
			Unburned (360)	Prescribed fire (260)	Wildfire (270)
Nashville Warbler	<i>Leiothlypis ruficapilla</i>	NAWA	34	28	12
MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	MGWA	67	49	72
Yellow Warbler	<i>Setophaga petechia</i>	YEWA	0	1	1
Yellow-rumped Warbler	<i>Setophaga coronata</i>	YRWA	313	213	209
Townsend's Warbler	<i>Setophaga townsendi</i>	TOWA	64	35	37
Spotted Towhee	<i>Pipilo maculatus</i>	SPTO	4	3	1
Chipping Sparrow	<i>Spizella passerina</i>	CHSP	281	168	233
Brewer's Sparrow	<i>Spizella breweri</i>	BRSP	0	7	3
Song Sparrow	<i>Melospiza melodia</i>	SOSP	4	4	6
Lincoln's Sparrow	<i>Melospiza lincolni</i>	LISP	0	2	6
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU	152	74	127
Western Tanager	<i>Piranga ludoviciana</i>	WETA	306	215	213
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	BHGR	8	3	22
Lazuli Bunting	<i>Passerina amoena</i>	LAZB	3	1	74
Cassin's Finch	<i>Haemorhous cassinii</i>	CAFI	98	89	118
Red Crossbill	<i>Loxia curvirostra</i>	RECR	68	25	67
Pine Siskin	<i>Spinus pinus</i>	PISI	53	14	112
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	EVGR	3	2	1

Flycatcher, and Brewer's Sparrow occupancy shifted towards high-severity burned points following wildfire (Fig. 4). Conversely, Cassin's Vireo, Townsend's Warbler, and Warbling Vireo occupancy shifted towards lower severity burned points (Fig. 5). Rock Wren and American Three-toed Woodpecker shifted towards treated units after prescribed fire (Fig. 6). These prescribed fire effects translated into smaller changes in occupancy than did wildfire effects (compare Fig. 6 with Figs. 4 and 5).

Wildfire effects on species occupancy were similar in units previously treated with prescribed fire compared to untreated units (Fig. 7). The data did not definitively support differences in wildfire effect between treated and untreated units for any species (all 95% $BCIs$ for $\beta_{PerWF \times TrtPF \times CBI_{WF,i}}$ from Eq. 5 included zero). Additionally, species exhibiting the strongest shifts towards or away from high-severity burned points after wildfire were the same in units initially treated versus untreated with prescribed fire (Fig. 7). For certain species, statistical support for wildfire effects differed with prior treatment (see Mountain Chickadee, Cassin's Vireo, and Warbling Vireo). Nevertheless, species never exhibited completely contradictory effects in treated versus untreated units.

Annual changes in occupancy and time-dependent effects

Twenty-four species exhibited disturbance effects that were statistically supported overall or time-dependent, or notable changes in annual occupancy (including the 9 species highlighted above; Figs. 8, 9, and 10). Black-backed Woodpecker, American Three-toed Woodpecker, Rock Wren, and Cassin's Finch exhibited statistically supported shifts towards treated units in year 2 after prescribed fire (Fig. 8; see also similar but less statistically supported pattern for Brewer's Sparrow). Hermit Thrush shifted towards treated units in years 1 and 2 and then shifted back in year 3 following prescribed fire. Hammond's Flycatcher, Chipping Sparrow, Ruby-crowned Kinglet, and Calliope Hummingbird exhibited lagged shifts towards untreated units in years 2 or 3 following prescribed fire.

The 5 species with positive wildfire effects that were statistically supported overall or time-dependent—Hairy Woodpecker, Olive-sided Flycatcher, House Wren, White-breasted Nuthatch, and Brewer's Sparrow—all shifted towards higher severity burned points primarily in years 2–3 after wildfire (Fig. 9). Occupancy for the 3 species with overall negative wildfire effects (Cassin's Vireo, Warbling Vireo, and Townsend's Warbler; see Figs. 3 and 5) shifted immediately towards lower severity burned points and remained there in all 3 years following wildfire (Fig. 9). Red-breasted Nuthatch, White-

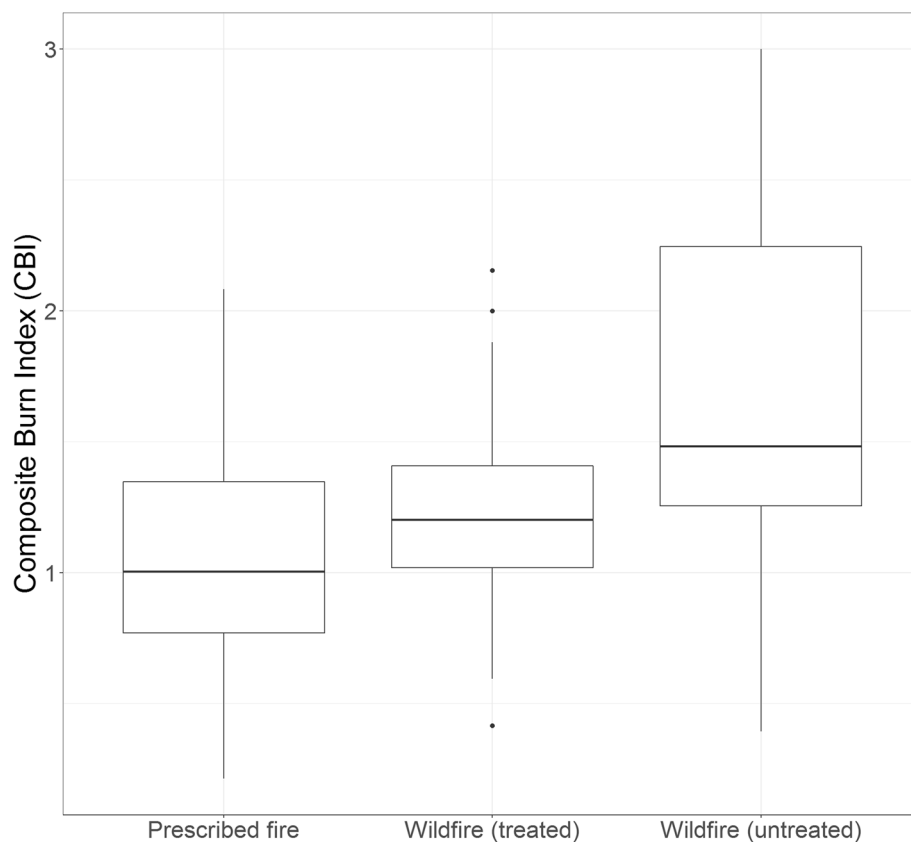


Fig. 2 Box plots depicting distributions of composite burn index (CBI) values for survey points treated by prescribed fire and burned by wildfire. Wildfire CBIs are shown separately for units previously treated versus not treated with prescribed fire. Boxes delineate the 25th, 50th, and 75th percentiles; whiskers denote the distance to observations furthest from the nearest quartiles (i.e., 25th and 75th percentiles) that are also within $1.5 \times$ the inter-quartile range from the nearest quartile; and dots are observations further than $1.5 \times$ the inter-quartile range from the nearest quartile

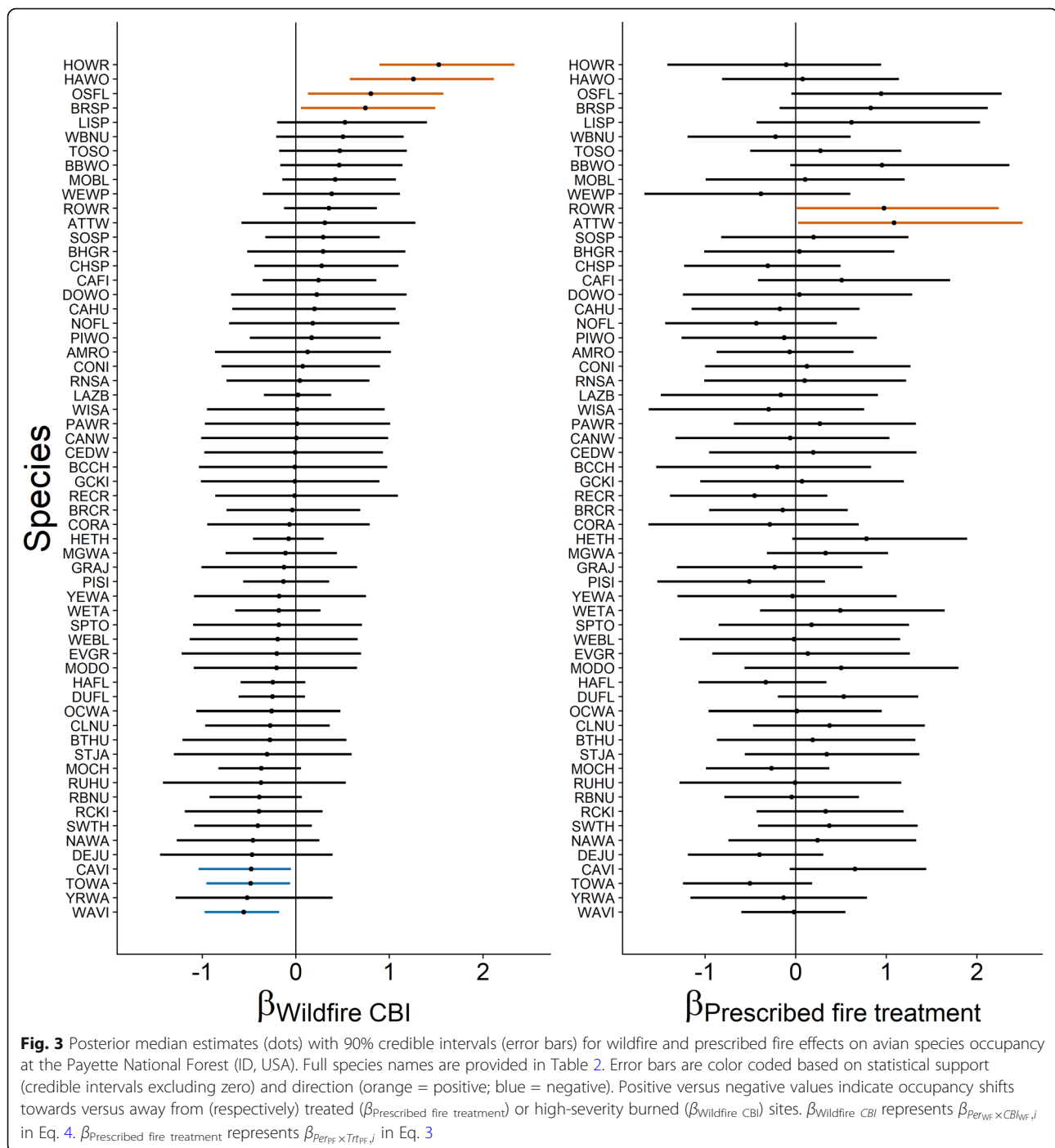
breasted Nuthatch, Hammond's Flycatcher, Lazuli Bunting, and Pine Siskin initially shifted towards lower severity burned points in year 1 but then shifted back in years 2–3 after wildfire. Of particular note, White-breasted Nuthatch occupancy was distributed in completely opposite directions with respect to wildfire burn severity in years 1 (negative) versus 3 (positive). Dusky Flycatcher, Brewer's Sparrow, MacGillivray's Warbler, and Hermit Thrush also exhibited ephemeral shifts towards lower severity burned points in year 1, although these shifts received relatively weak statistical support.

Annual occupancy varied notably among pre-treatment (2002–2003), post-treatment (2004–2007), and post-wildfire years (2008–2010) for many species, providing further insight into disturbance effects (Fig. 10). In addition to shifting towards occupying high-severity burned points, Hairy Woodpecker and House Wren occupancy increased overall after wildfire. Mountain Bluebird, Dusky Flycatcher, Black-headed Grosbeak, Lazuli Bunting, MacGillivray's Warbler, Cassin's Finch, and Pine Siskin also

exhibited notable albeit sometimes lagged increases in occupancy (Fig. 10) despite weak or negative shifts in occupancy with respect to burn severity following disturbance (Figs. 8 and 9). Hammond's Flycatcher and Hermit Thrush exhibited declines in occupancy following disturbance (Fig. 10).

Species richness

We observed no definitive effects of prescribed fire or wildfire on species richness. Species richness increased overall by ~ 5 species following wildfire, but 95% BCIs for site-specific richness estimates overlapped considerably (Fig. 11 top row). Additionally, high-severity burned sites did not become any more or less species rich than lower severity sites following wildfire (i.e., a slight negative relationship with CBI was maintained; Fig. 11 top row). Overall species richness did not substantially change following prescribed fire, nor did the difference in species richness between treated and untreated units (Fig. 11 bottom row).



Discussion

Our results suggest prescribed fire does not necessarily change the short-term ecological importance of wildfire to birds, even with limited wildfire burn severity. Prescribed fire limited subsequent wildfire burn severity within treated units (see also Pollet and Omi 2002; Prichard and Kennedy 2014; Fernandes 2015; Cary et al. 2017) but did not substantially modulate avian responses to wildfire. Species exhibiting the strongest shifts in

occupancy towards or away from high-severity burned points after wildfire were similar in units initially treated versus not treated with prescribed fire.

Our study also highlights the limited ability of prescribed fire to emulate wildfire effects on birds. Wildfire substantially and strongly affected shifts in occupancy in relation to burn severity for multiple bird species. Differing metrics prevented us from quantitatively comparing wildfire with prescribed fire effects. Nevertheless,

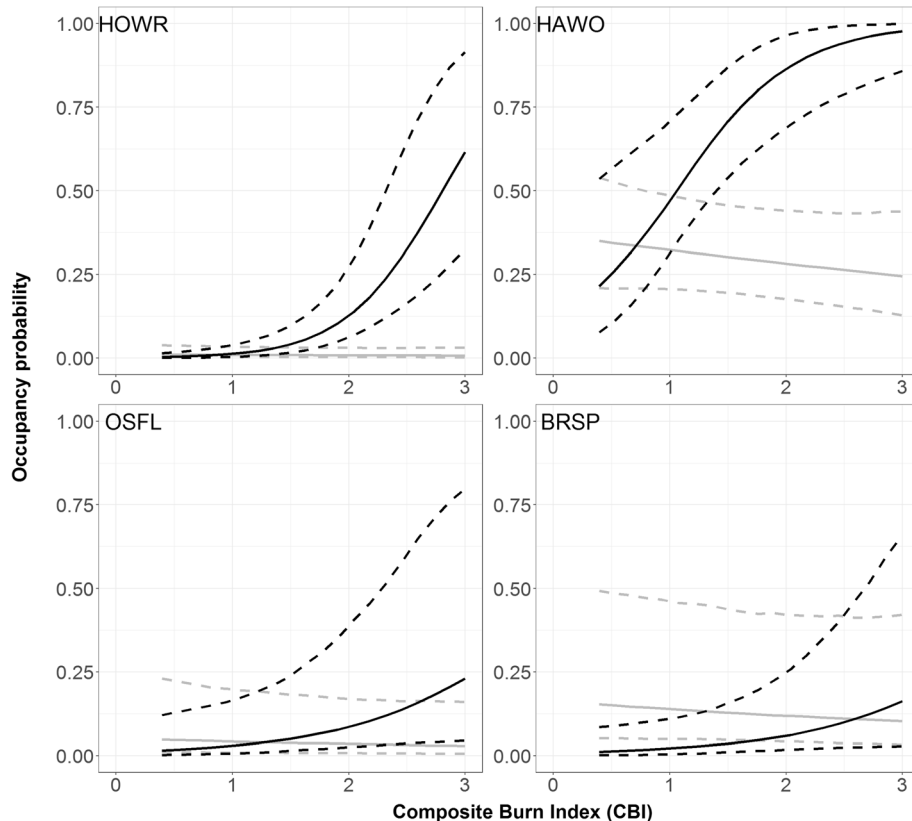


Fig. 4 Predicted occupancy probabilities along a wildfire burn severity gradient (composite burn index; *CBI*) for species exhibiting statistically supported positive wildfire effects, i.e., where occupancy shifted towards high-severity burned sites after wildfire. Occupancy relationships are depicted before (gray) and after (black) wildfire. Species are House Wren (HOWR), Hairy Woodpecker (HAWO), Olive-sided Flycatcher (OSFL), and Brewer's Sparrow (BRSP)

prescribed fire qualitatively affected a different and smaller set of bird species than did wildfire. Several species exhibited dramatic changes in overall occupancy following wildfire but not prescribed fire. Prescribed fire effects tended to be relatively time dependent and brief compared to wildfire effects. Finally, prescribed fire treatments would probably not extend across areas comparable to those burned by wildfire. These differences likely reflected differences in the extent and magnitude of how wildfire versus prescribed fire affected vegetation structure and composition and ultimately habitat conditions for species.

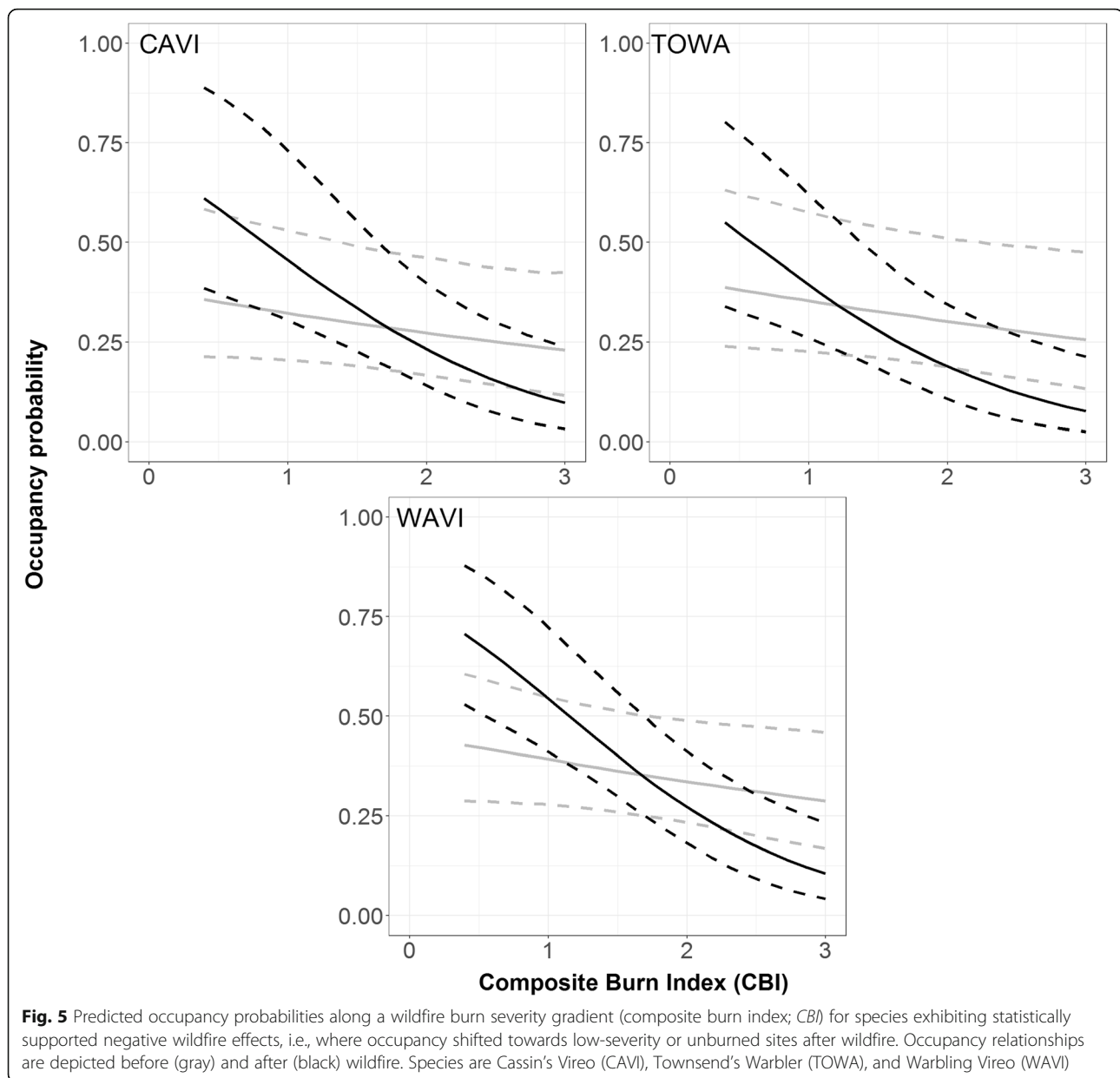
Wildfire affected communities primarily by altering the distribution of individual species rather than overall richness. Species richness increased somewhat after wildfire, but the magnitude of this change was small compared to variation among sites burned at similar severity, and wildfire did not substantially change which sites were most speciose. Rather, wildfire effects were primarily apparent for individual species modulated by life history (discussed further below), implying changes in species composition. Thus, the significance of wildfire

to bird communities and avian diversity depends on the extent, distribution, timing, and severity of wildfire across landscapes (Kalies et al. 2010; Fontaine and Kennedy 2012; Latif et al. 2016b).

We note that although prescribed fire did not substantially alter the slopes of occupancy relationships with wildfire burn severity, prescribed fire did limit subsequent wildfire burn severity. Thus, prescribed fire may limit the magnitude of species occupancy changes following wildfire in so far as those changes depend on burn severity, as they do in our model. Nevertheless, we show that the character of avian responses to wildfire (as represented by slopes of species occupancy relationships) was not substantially altered by previous prescribed fire.

Fire effects depend on species life history, population response, and resource dynamics

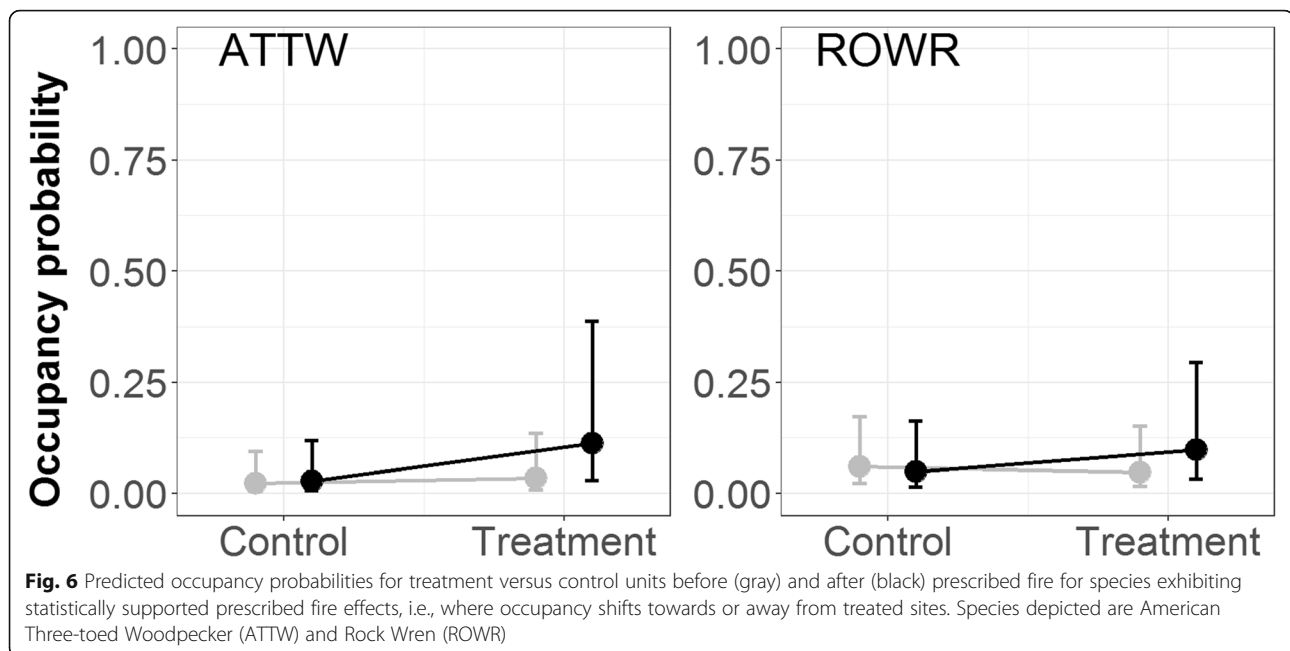
Disturbance effects on species occupancy were generally consistent with species life histories and patterns reported in the literature (Smucker et al. 2005; Kotliar et al. 2007; Russell et al. 2009; Fontaine and Kennedy 2012; Latif et al. 2016b). Positive fire effects (i.e., overall



or time-dependent shifts towards burned sites after wildfire or prescribed fire) on bark-drilling woodpeckers (Hairy, American Three-toed, and Black-backed Woodpecker) were congruent with their reliance on standing dead wood for nesting and bark (e.g., Scolytidae) and wood-boring (Cerambycidae and Buprestidae) beetle larvae for food (Covert-Bratland et al. 2006; Kotliar et al. 2008). More pronounced prescribed fire compared to wildfire effects for disturbance specialist Black-backed and American Three-toed Woodpecker were unexpected, but sample sizes for these species were low and a lack of unburned sites ($CBI = 0$) may have limited power for estimating wildfire effects. Data describing specific life activities (e.g., nesting, foraging, and dispersal) may

more effectively resolve relationships with wildfire for these species (Kotliar et al. 2008; Saab et al. 2009; Latif et al. 2013).

Additional species with positive fire effects included secondary cavity nesters (House Wren, White-breasted Nuthatch), aerial insectivores (Olive-sided Flycatcher), and species that nest or forage in the understory or on the ground (Brewer's Sparrow, Rock Wren). These effects likely reflect increased nesting opportunities in snags generated by wildfire (secondary cavity nesters), increased foraging opportunities in canopy openings (aerial insectivores), and improved habitat quality with understory revegetation (understory species) (Kotliar et al. 2002; Saab et al. 2005; Smucker et al. 2005;



Fontaine and Kennedy 2012; Latif et al. 2016b). Species exhibiting negative fire effects (shifts away from burned sites) included open-cup canopy nesters and bark- and foliage-gleaning insectivores (Mountain Chickadee, Cassin's Vireo, Warbling Vireo, and Townsend's Warbler), reflecting expected net losses in resources for these species (Kotliar et al. 2002; Saab et al. 2005; Smucker et al. 2005; Fontaine and Kennedy 2012; Latif et al. 2016b).

Time-dependent fire effects and overall changes in occupancy suggest some potential nuances in population responses or how fire affects resources. For bark-drilling woodpeckers, wood-boring beetle prey primarily colonize burned forests in year 2 following lags in tree mortality (Ray et al. 2019). Increased cavity availability for secondary cavity-nesting species follows excavation by woodpeckers in initial years (Norris and Martin 2010). More generally, lagged positive effects may reflect greater recruitment of young in subsequent years produced initially by a relatively small number of burned-site colonists or residents. Conversely, site fidelity in the early post-fire years may delay negative population responses for species reliant on green foliage for nesting and foraging.

Following wildfire in temperate forests, soil nutrient releases are typical and herbaceous vegetation regrowth begins within 1 year (Boerner 1982). Shrubs tend to dominate for the next 5–6 years (Schlesinger and Gill 1980; Boerner 1982), a process benefiting a variety of avian species (e.g., Hannon and Drapeau 2005; Saab and Powell 2005; Fontaine and Kennedy 2012). In contrast, brief positive effects of prescribed fire suggest relatively short-lived resource pulses for

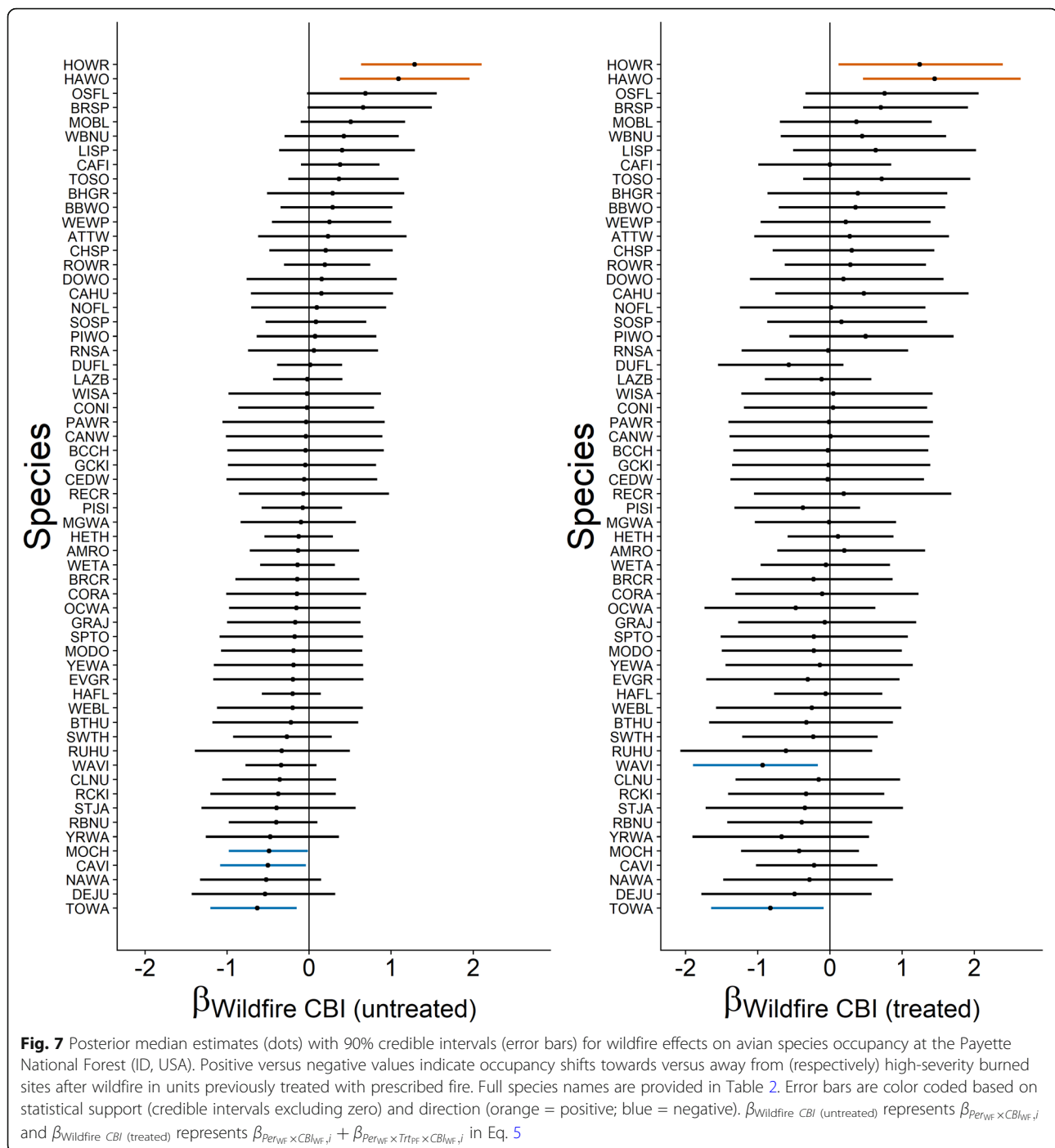
affected species (e.g., Cassin's Finch and Hermit Thrush).

Resources may be greatest initially at lower severity burned sites after wildfire for species that nest or forage in the understory or on the ground. As time since fire progresses, however, resource availability may increase with increasing productivity at high-severity sites. Overall increases in occupancy after wildfire coupled with short-lived negative effects followed by positive effects in subsequent years suggested such resource dynamics for some species (e.g., Lazuli Bunting and Pine Siskin).

Study limitations and future directions

We did not include prescribed fire or wildfire effects on detectability, so fire effects on occupancy reported here do not explicitly control for potential spatial heterogeneity in detectability. In preliminary analyses, we did not find statistical support for such effects (Q. Latif and V. Saab unpublished data), potentially reflecting a lack of such effects or limitations in statistical power. Given our sampling design, however, detectability could include information on movement between replicate surveys (Latif et al. 2016a) or heterogeneity in abundance (Royle and Nichols 2003), both of which are ecologically relevant. By ignoring fire effects on detectability, we forced any fire effects on movement or local abundance to be reflected in occupancy rather than detectability estimates (sensu Latif et al. 2018). Nevertheless, further study of fire or habitat effects on observer error could provide additional insight for interpreting our results.

Unlike others (Russell et al. 2009), we did not include persistence effects relating occupancy with the prior



year's occupancy state (see also Russell et al. 2015). Having used BACI to control for potentially confounding spatial and temporal variation, we sought to avoid including further complexity and maximize information for estimating disturbance effects. Future study employing models representing occupancy dynamics (e.g., colonization, persistence, turnover) may yield additional insights into mechanisms underlying patterns observed here.

Our results are limited to fuel reduction treatments consisting exclusively of prescribed fire of primarily low severity in dry conifer forests characterized by mixed-severity fire regimes. Birds have been shown to respond more strongly to prescribed fire treatments elsewhere likely due to greater treatment severity (e.g., Russell et al. 2009; Bagne and Purcell 2011). Greater treatment severity may elicit responses that more closely resemble responses to wildfire, but such

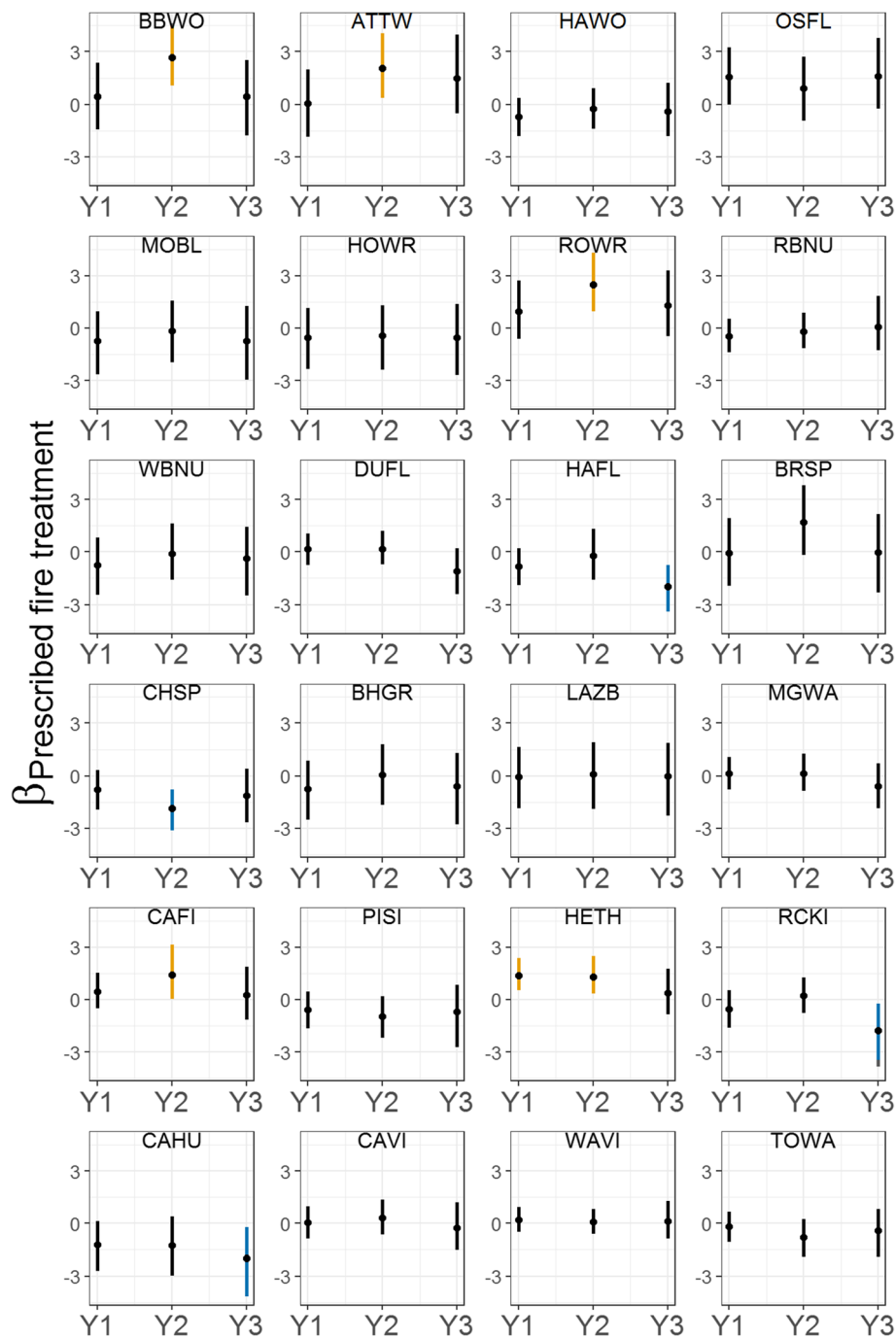


Fig. 8 Posterior median estimates (dots) with 90% credible intervals (error bars) for time-dependent prescribed fire effects on avian species occupancy at the Payette National Forest (ID, USA). Estimates are for all 24 species with statistically supported time-dependent disturbance effects or notable changes in annual occupancy overall (see full species names in Table 2). Error bars are color coded based on statistical support (credible intervals excluding zero) and direction (orange = positive; blue = negative). Positive versus negative values indicate occupancy shifts towards versus away from (respectively) treated sites after treatment. $\beta_{\text{prescribed fire treatment}}$ represents $\beta_{\text{trt}_{\text{PF}},i(t_{\text{PF}} \in \{1,2,3\})} - \beta_{\text{trt}_{\text{PF}},i(t_{\text{PF}} = 0)}$ in Eq. 6, where $t_{\text{PF}} = 1, 2$, and 3 correspond with year 1 (Y1), year 2 (Y2), and year 3 (Y3), respectively, after prescribed fire

treatments may also alter the behavior and ecological significance of subsequent wildfire. In so far as warming temperatures or drought affect prescribed fire treatment severity, patterns observed here may

depend on climate. Selective timber harvest may further alter direct and indirect treatment implications for birds by removing substantial standing woody biomass (Sallabanks et al. 2000; Perry and Thill 2013).

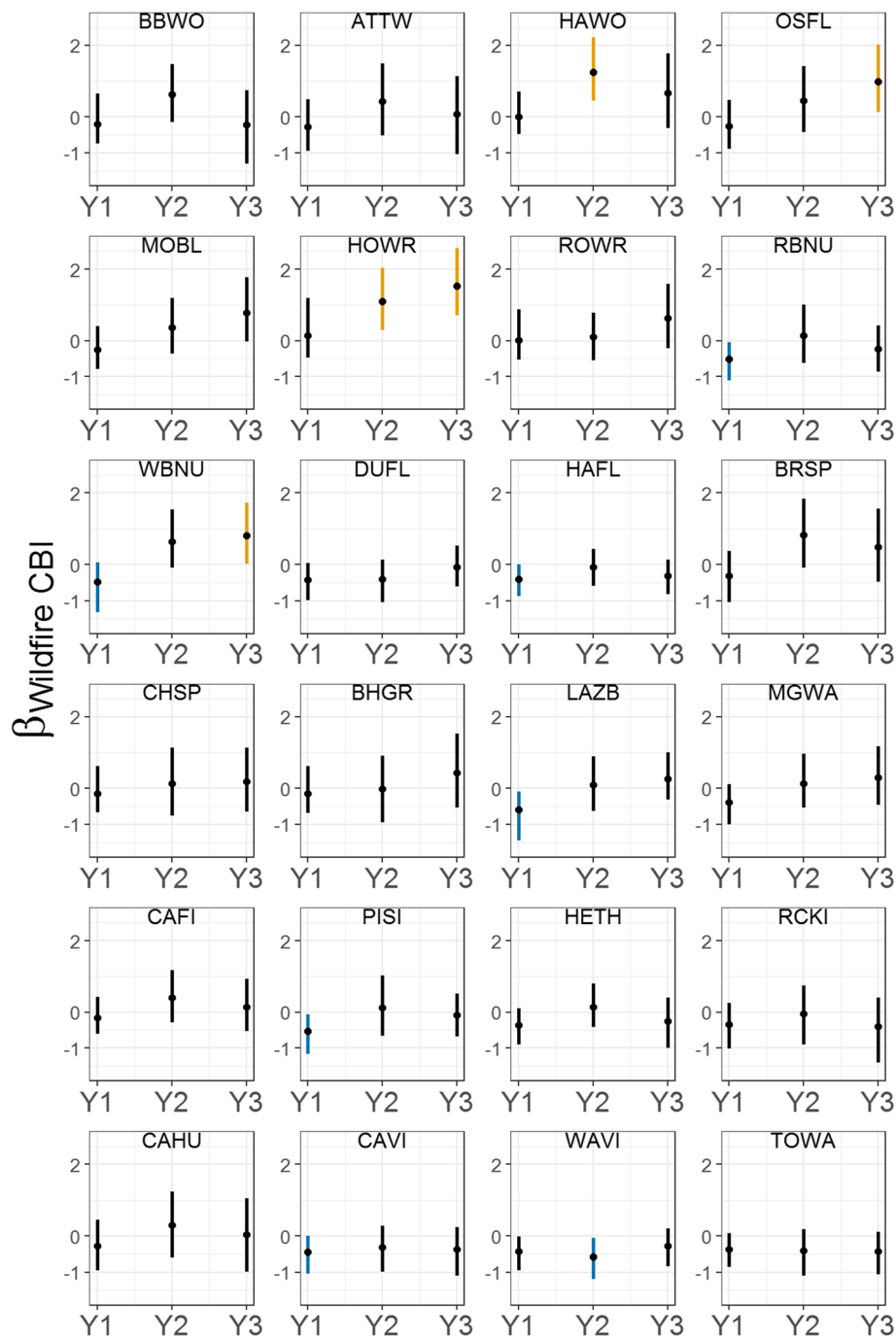


Fig. 9 Posterior median estimates (dots) with 90% credible intervals (error bars) for time-dependent wildfire effects on avian species occupancy at the Payette National Forest (ID, USA). Estimates are for all 24 species with statistically supported time-dependent disturbance effects or notable changes in annual occupancy overall (see full species names in Table 2). Error bars are color coded based on statistical support (credible intervals excluding zero) and direction (orange = positive; blue = negative). Positive versus negative values indicate occupancy shifts towards versus away from (respectively) high-severity burned sites after wildfire. $\beta_{\text{Wildfire CBI}}$ represents $\beta_{\text{CBI}_{WF,j}(t_{WF} \in \{1,2,3\})} - \beta_{\text{CBI}_{WF,j}(t_{WF}=0)}$ in Eq. 6, where $t_{WF} = 1, 2$, and 3 correspond with 2008 (Y1), 2009 (Y2), and 2010 (Y3)

Direct and indirect ecological implications of fuel treatments may further depend on historical fire regime (sensu Latif et al. 2016b). Studies examining interactions of fuel treatments, wildfire, and birds

across a range of treatment severities, types, and sizes are needed to fully inform the management of fire-adapted forests with objectives that include conservation of avian diversity.

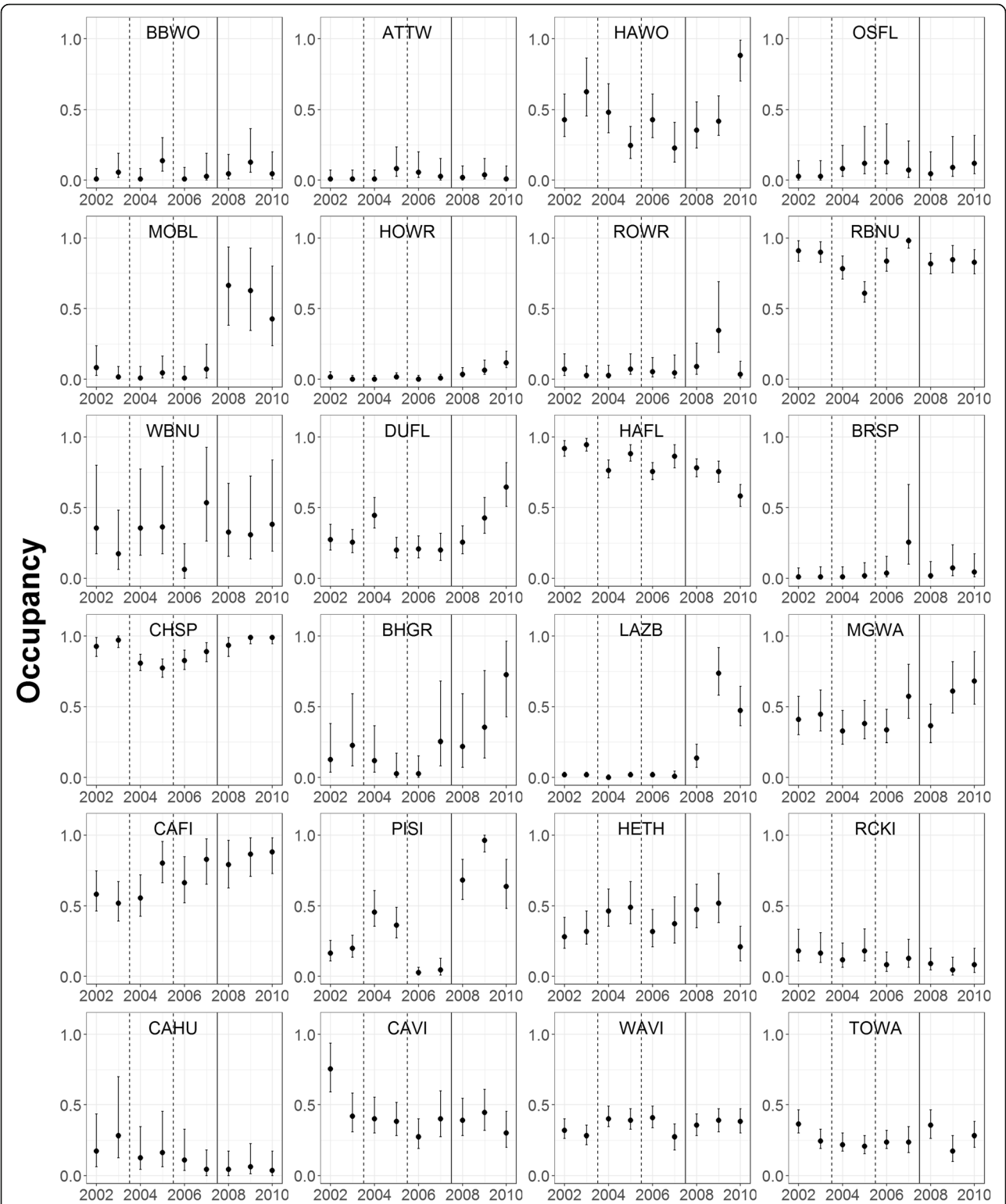
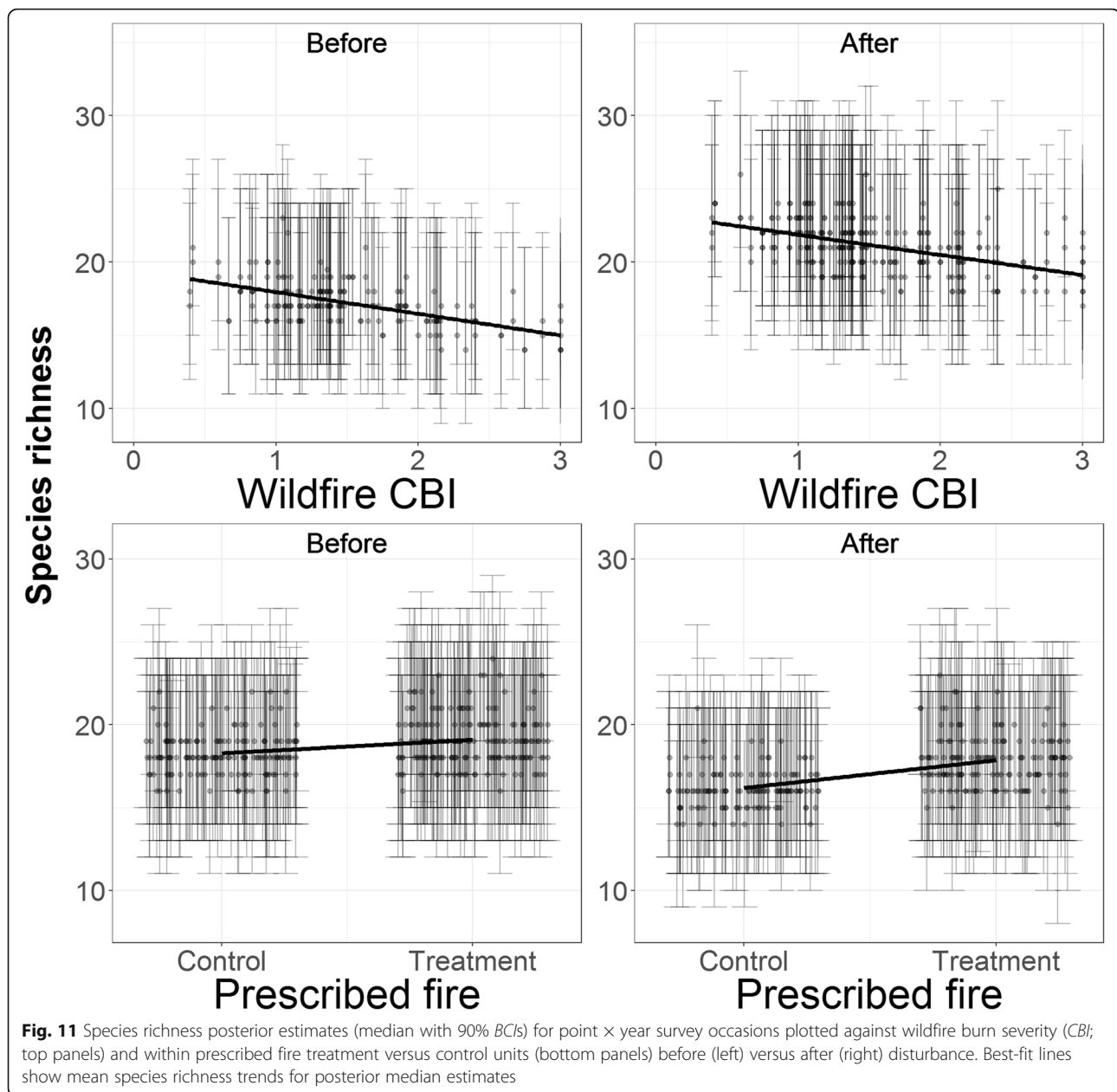


Fig. 10 Posterior median estimates (dots) with 90% credible intervals (error bars) for annual occupancy of surveyed sites for bird species at the Payette National Forest (ID, USA). Estimates are for all 24 species with statistically supported time-dependent disturbance effects or notable changes in annual occupancy overall (see full species names in Table 2). The vertical dashed lines demark when prescribed fire treatments were applied (one unit in 2004; 2 units in 2006), and the vertical solid line demarks when wildfire occurred



Management implications

Our results suggest managers can use prescribed fire to limit burn severity of subsequent wildfire without completely compromising the value of wildfire to fire-associated species (e.g., woodpeckers, secondary cavity-nesting species, aerial insectivores, and understory species) within burned areas. Given similar species relationships with burn severity in areas previously treated with prescribed fire (as observed here), we expect wildfire to generate some habitat for fire-associated species, albeit potentially less than in untreated areas in so far as burn severity is limited. In contrast, prescribed fire is unlikely to resemble wildfire in its ecological value for fire-

associated species, limiting the value of prescribed fire as a surrogate for wildfire. Instead, the implications of prescribed fire for avian diversity in dry conifer forests may hinge more so on whether and how it shapes the spatial extent of subsequent wildfire. Where the extent of treatment units are dwarfed by subsequent wildfire extent (e.g., Fig. 1), treatments may never be extensive enough to limit potential wildfire severity across entire landscapes. Nevertheless, prescribed fire treatments arranged strategically could break up landscapes and limit wildfire spread, particularly in conjunction with other fuel treatments and fire control measures (Arkle et al. 2012; Hunter and Robles 2020). In multiple use forests, such

fire management strategies would ideally allow sufficient wildfire to maintain biodiversity while limiting wildfire extent enough to meet other objectives, such as human safety and infrastructure protection.

Conclusions

We leveraged a rare opportunity to study the serial effects of prescribed fire and subsequent wildfire on small landbirds. To the extent that wildfire affects resources for other species similarly, our study provides evidence that prescribed fire does not necessarily compromise the ecological value of subsequent wildfire for wildlife. Conversely, prescribed fire could help counteract the effects of climate warming by limiting burn severity. To the extent that climate warming compromises the ecological value of wildfire by increasing its extent and severity (e.g., Jones et al. 2021), the effective application of prescribed fire could help mitigate these impacts.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-021-00123-2>.

Additional file 1. Appendices A, B, and C.

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Authors' contributions

VAS 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 and drafted the manuscript. VAS and JGD contributed editorial input during manuscript preparation. The authors read and approved the final manuscript.

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Availability of data and materials

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

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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