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Short-term benefits of prescribed fire to bird communities of dry forests

Victoria A. Saab^{1*} , Quresh R. Latif², William M. Block³ and Jonathan G. Dudley⁴

Abstract

Background: Low-severity prescribed fire is an important tool to manage fire-maintained forests across North America. In dry conifer forests of the western USA, prescribed fire is often used to reduce fuel loads in forests characterized historically by 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. Few studies, however, 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 USA. 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 (10 total study units with 278 survey points). Using a Bayesian hierarchical multi-species occupancy model, we investigated responses to prescribed fire treatments by a community of 95 bird species.

Results: We found statistically supported treatment effects and/or burn severity relationships for 33 species 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-pewee [*Contopus sordidulus*], gray flycatcher [*Empidonax wrightii*]), whose occupancy was more likely after treatment at the most severely burned units, and a negative effect for one species (ruby-crowned kinglet [*Corthylio calendula*]), whose occupancy was less likely after treatment at the most severely burned units. 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 were more similar to historical wildfires characteristic of 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 and regular. By comparison, fire events in forests characterized by a

*Correspondence: victoria.saab@usda.gov

¹ Rocky Mountain Research Station, USDA Forest Service, 1748 South 7th Avenue, MSU Campus, Bozeman, MT 59717, USA

Full list of author information is available at the end of the article

mixed-severity regime are less common, 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

Resumen

Antecedentes: Las quemas prescritas de baja severidad son una herramienta importante para manejar bosques dependientes de fuegos periódicos a través de América del Norte. En bosques secos de coníferas del oeste de los EEUU, las quemas prescritas son usadas frecuentemente para reducir la carga de combustible en aquellos bosques caracterizados históricamente por tener regímenes de fuego mixtos y de baja severidad. Entender los efectos ecológicos de los tratamientos con quemas prescritas es importante para poder predecir los impactos de estas acciones de manejo en las comunidades de fauna silvestre. Pocos estudios, sin embargo, han estimado las respuestas de pequeñas aves terrestres a los tratamientos de bosques a escala espacial relevantes para su ecología, o han examinado las diferencias potenciales en los efectos de los tratamientos aplicados dentro de regímenes de fuego mixtos versus otros de baja severidad. Para ello, evaluamos los efectos de los tratamientos de quemas y sus relaciones con la severidad para comunidades aviares en bosques de coníferas secos dominados por pino ponderosa (*Pinus ponderosa*) ubicados en siete Bosques Nacionales interiores del oeste de los EEUU. Relevamos estas aves por 1-4 años y 1-3 años antes y después de tratamientos en ubicaciones de quemas prescritas de severidad mixta y baja, siguiendo un diseño de estudio de control de impacto de antes y después de los tratamientos, que involucraban 8 pares de unidades de tratamientos de control en ubicaciones de severidad mixta (un total de 16 unidades de estudio con 320 puntos de relevamientos), y 4 pares de unidades de tratamientos de control en ubicaciones de severidad baja (10 unidades de estudio en total con 278 puntos de relevamiento). Utilizando un modelo jerárquico Bayesiano de ocupación múltiple de especies, investigamos las respuestas a las quemas prescritas en una comunidad compuesta por 95 especies de aves.

Resultados: Encontramos efectos estadísticamente validados en los tratamientos de severidad y/o relaciones con las quemas prescritas para 33 especies ubicadas primariamente en tratamientos de quemas mixtas. Los datos respaldan los efectos positivos de los tratamientos en ubicaciones de severidad mixta para 9 especies (*Turdus migratorius*, *Sialia mexicana*, *Dryobates villosus*, *Picoides arcticus*, *Picoides dorsalis*, *Troglodytes aedon*, *Empidonax oberholseri*, *Contopus sordidulus*, y *Empidonax wrightii*), cuya ocupación fue probablemente muy rápida luego del tratamiento en las unidades quemadas con mayor severidad, y el efecto negativo sobre otra especie (*Corthylio calendula*), cuya ocupación del sitio fue muy poco probable luego del tratamiento en las unidades quemadas a mayor severidad. En ubicaciones quemadas a baja severidad, solo dos especies exhibieron efectos de los tratamientos, y ambos negativamente (*Cardellina rubrifrons*, y *Chondestes grammacus*). También encontramos relaciones de ocupación consistentes con la severidad post tratamiento (i. e. independientemente de la distribución de especies antes del tratamiento) para 29 especies, la mayoría de las cuales era consistente con sus historias de vida (p. ej. patrones de relaciones positivas para los excavadores de nidos, aves insectívoras de la corteza, y relaciones negativas para aquellas con nidos en lugares abiertos, o insectívoras del follaje). Las respuestas más fuertes para las quemas prescritas en unidades de severidad mixta fueron las menos esperadas, dado que las aplicaciones de quemas prescritas de baja severidad fueron más parecidas a las quemas naturales históricas características de bosques con regímenes de fuego de baja severidad.

Conclusiones: Las poblaciones de aves ubicadas en lugares caracterizados históricamente por regímenes de baja severidad pueden ser relativamente poco reactivas a las quemas prescritas dado que los fuegos en esos lugares son típicamente frecuentes y regulares. En comparación, los eventos de fuego en bosques caracterizados por un régimen de severidad mixta son menos comunes, dando potencialmente más respuestas a una oportunidad infrecuente, aun para especies que están fuertemente asociadas a incendios naturales recientes en estos bosques. Nuestros resultados sugieren que las actividades de manejo del fuego tendientes a reducir los combustibles y disminuir el riesgo de incendios de alta severidad pueden ser también efectivas para crear hábitat para algunas aves habituadas a fuegos severos, al menos en el corto plazo.

Background

Managers use prescribed fire and mechanical fuel reduction treatments to reduce the 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). Following a century of fire suppression, land management agencies have increased the use of prescribed fire in recent decades to reduce fuel loads and restore wildlands to desired conditions in dry conifer forests of the western USA (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 [US 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)]). 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).

Understanding wildlife responses to prescribed fire is needed to assess the consequences of forest management practices intended to reduce fuels. Avifauna offer useful opportunities for assessing ecological integrity and biodiversity in relation to forest management actions (Sutherland et al. 2004). 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 US Migratory Bird Treaty Act, and requirements under the 2012 Planning Rule and Directives to consider persistence of species of conservation concern (USDA 2012). Birds, in particular, serve as an appropriate taxon for investigating the effects of fire because they have varied and predictable relationships with vegetation structure.

Scientific understanding of avian responses to prescribed fire in Western North American forests includes persistent 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. Consistent patterns have been reported in other prescribed fire studies, including reduced numbers of ground and shrub nesting birds (Wilson et al.

1995; Artman et al. 2005; Blake 2005), benefits to cavity-nesting bird populations (Blake 2005; Russell et al. 2009; Bagne and Purcell 2011), and increases in aerial insectivore and ground-foraging species (Artman et al. 2005; Blake 2005; Russell et al. 2009). Knowledge is lacking on response differences among different fire regimes. Additionally, sparse information exists from studies conducted at appropriate spatial scales for drawing inference about landbirds with varying home range sizes.

Avian responses to fire depend on burn severity (fire effects on vegetation; Agee 1993; Fontaine and Kennedy 2012) 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 USA (Hood et al. 2021).

In the central and northern Rocky Mountains, mixed-severity fires burned principally in late summer and maintained heterogeneity in forest structure with mixed tree species composition, often favored by ponderosa pine (*Pinus ponderosa*) (Schoennagel et al. 2004; Hessburg et al. 2007) (Hood et al. 2021). In the southwestern USA, forests with lower tree densities were more widespread and associated with higher frequency, lower-severity fires that burned typically in spring. A drier climate in the Southwest 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 USA, known as the Birds and Burns Network. We used a before-after-control-impact (BACI) design with plot sizes averaging 300 ha for rigorous evaluation of treatment effects (Morrison et al. 2008; Popescu et al. 2012). Based on habitat changes expected within 5 years of low-severity prescribed fire treatments (Saab et al. 2006), we predicted changes in species' occupancy rates concurring with life history traits (Table 1), including reductions of ground and shrub nesting birds (Wilson et al. 1995; Artman et al. 2005; Blake 2005), benefits to cavity-nesting bird populations (Blake 2005; Russell et al.

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	<i>Prediction:</i> positive <i>Rationale:</i> increased foraging opportunities due to reduction in forest canopy and increase in available nesting cavities <i>Species:</i> ash-throated flycatcher, purple martin, tree swallow, violet-green swallow, mountain bluebird, white-throated swift, western flycatcher	<i>Prediction:</i> moderate positive <i>Rationale:</i> decreases in canopy cover, which provides more space for foraging maneuvers <i>Species:</i> common nighthawk, Cassin's kingbird, olive-sided flycatcher, western wood-pewee, Hammond's flycatcher, gray flycatcher, dusky flycatcher, Townsend's solitaire, Say's phoebe
	<i>Prediction:</i> strong positive <i>Rationale:</i> 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 <i>Species:</i> hairy woodpecker, American three-toed woodpecker, black-backed woodpecker, downy woodpecker, white-breasted nuthatch, brown creeper, red-breasted nuthatch, pygmy nuthatch, Pacific wren	None in study
Bark insectivore	<i>Prediction:</i> mixed <i>Rationale:</i> increased nest availability with increases in dead portions of trees, but reductions in food resources of live foliage and bark <i>Species:</i> black-capped chickadee, mountain chickadee	<i>Prediction:</i> negative <i>Rationale:</i> reduced nesting and foraging substrate due to desiccation of foliage <i>Species:</i> 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, bush-tit
Shrub or ground insectivore	<i>Prediction:</i> positive <i>Rationale:</i> increased nest availability with increases in dead portions of trees, increased foraging substrate of open ground <i>Species:</i> rock wren, house wren, western bluebird	<i>Prediction:</i> mixed <i>Rationale:</i> positive following regrowth of understory vegetation, which is stimulated by opening of the canopy, but negative for species reliant on ground litter <i>Species:</i> American robin, Swainson's thrush, orange-crowned warbler, MacGillivray's warbler, Wilson's warbler, vesper sparrow, Lincoln's sparrow
Omnivore	<i>Prediction:</i> mixed <i>Rationale:</i> generalist foraging strategies for these species will result in minimal distributional changes, despite a potential increase in nesting habitat <i>Species:</i> Northern flicker, pileated woodpecker, red-naped sapsucker	<i>Prediction:</i> neutral <i>Rationale:</i> generalist foraging strategies for these species were expected to result in minimal changes <i>Species:</i> 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

2009; Bagne and Purcell 2011), and advantages to species that forage in the air and on the ground (Artman et al. 2005; Blake 2005; Russell et al. 2009).

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 (Fig. 1). Each study unit was approximately 100–400 ha (Table 2) and dominated by ponderosa pine that had not burned by wild-fire for nearly 100 years or prescribed fire for more than 10 years. 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). Ten study units were located in 4 national forests characterized historically by a low-severity fire regime: 2 each in the Gila (New Mexico) and Coconino NFs (Arizona) and 3 each in the Apache-Sitgreaves and Kaibab NFs (Arizona; 1 treatment unit “paired” with 2 smaller control units at each location; Fig. 1). Thus, we established 12 treatment-control pairs consisting of 26 study units (Table 2). USFS District fire

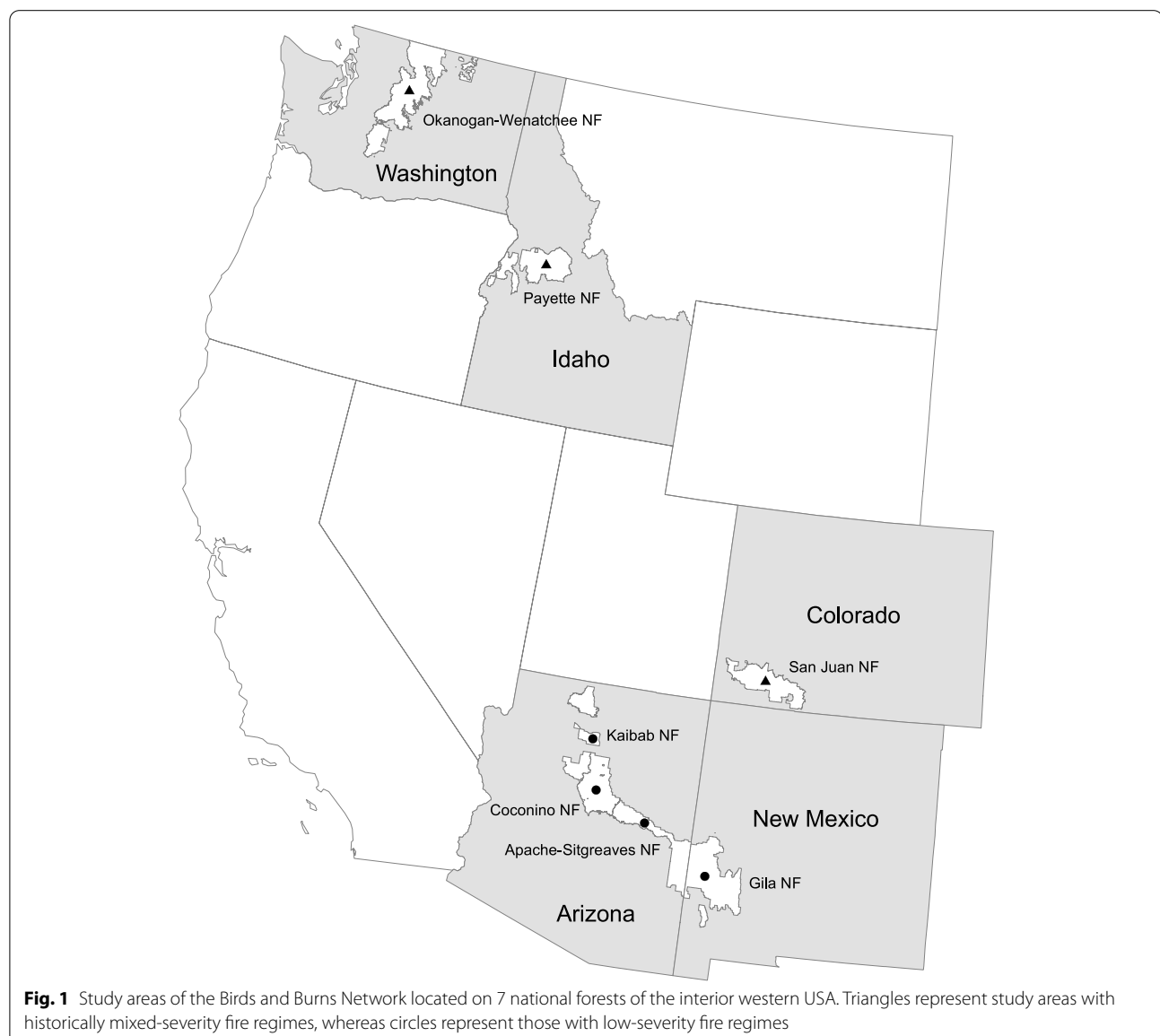


Table 2 Locations, areas, sampling distributions, and historical fire regime, for study units where avian community changes in relation to prescribed fire were studied on 7 national forests in the Interior West

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	40; 359 10; 127	Low severity
Gila, New Mexico	10	25; 261	25; 244	Low severity
Apache-Sitgreaves, Arizona	11	29; 247	20; 186 9; 99	Low severity
Coconino, Arizona	12	40; 402	40; 404	Low severity

personnel determined the location and boundary of each prescribed fire treatment unit.

Ponderosa pine trees ≥ 23 cm diameter-at-breast-height (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 gramma (*Bouteloua gracilis*), and elevations ranged from 2072 to 2500 m. In mixed-severity locations, the understory vegetation was comprised of multiple shrub species, including snowberry (*Symphoricarpos* spp.), spirea (*Spirea* spp.), ninebark (*Physocarpus malvaceus*), and serviceberry (*Amelanchiar alnifolia*), with Bluebunch wheatgrass (*Pseudoroegneria spicatus*) and Idaho fescue (*Festuca idahoensis*) as the common grass species and elevations ranged from 670 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 598 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 the BACI design, we collected data in control units that were never burned but measured during the same timeframe, i.e., before and after prescribed fire applied to the treatment units. Control and treated points were surveyed in the same years. 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 (Additional file 1: Appendix A). We began point counts just after the dawn chorus and completed them within 5 h. 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; Additional file 1: 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

Table 3 Treatment and sampling timing at 26 study units established for the primary analysis of avian community changes with prescribed fire at 7 national forests in the Interior West. In mixed-severity locations where fire treatments occurred in spring of the same year as post-treatment bird surveys, fire treatments were always applied *prior* to the breeding season, in contrast with bird surveys, which always occurred *during* the breeding season

National forest, state	Unit pair	Mean visits per season (range)	Burn timing (S = spring, F = fall)	Number of seasons (survey years)	
				Before	After
Payette, Idaho ^a	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, Washington ^a	4	2.98 (2–3)	S2004	2 (2002–2003)	2 (2004–2005)
	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 ^a	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 ^b	9	3.35 (1–4)	F2003 and S2004	2 (2002–2003)	2 (2004–2005)
Gila, New Mexico ^b	10	3.63 (1–4)	F2003 and S2004	2 (2002–2003)	2 (2004–2005)
Apache-Sitgreaves, Arizona ^b	11	3.79 (2–4)	F2003	1 (2003)	2 (2004–2005)
Coconino, Arizona ^b	12	3.90 (2–4)	F2003	1 (2003)	2 (2004–2005)

^a Mixed-severity locations

^b Low-severity locations

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). Saab et al. (2006) reported effects of prescribed fire on vegetation. 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 (ψ) 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 Andrew 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 $\mathbf{y}$, where element y_{jit} was the sum of binary

indicators for species detection (Sanderlin et al. 2014). Given a binary indicator $x_{jikt} = 1$, we detected species i ($i = 1, \dots, N$) at point count station 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 point count station j in year t , where $y_{jit} = \sum_{k=1}^K x_{jikt}$ and $y_{jit} \in [0, 1, \dots, K]$. We modeled these data given probability of detection p_i and occupancy latent state z_{ijt} using a Bernoulli distribution with probability of success $p_i \times z_{ijt}$:

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

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 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 represented by CBI to evaluate treatment effects (CBI = 0 for unburned control units). We modeled occupancy (ψ_{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,

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

where $\beta_{0,il}$ is the intercept and β_{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 ($l = 1, \dots, L$; $L = 7$), and covariate effects (β_{ir}) were estimated separately by fire regime ($r = 1, \dots, R$; $R = 2$). 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 Additional file 1: 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 refers to $\beta_{PER \times CBI, ir}$ in Eq. 3). We considered 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

$$\beta_{diff} = \beta_{mixed} - \beta_{low} \quad (4)$$

where β_{mixed} and β_{low} represent estimated treatment effects (i.e., $\beta_{PER \times CBI, ir}$ in Eq. 3) 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 ($\beta_{PER \times CBI, ir}$) from potentially confounding sources of variation ($\beta_{PER, ir}$, $\beta_{CBI, ir}$; Eq. 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 (e.g., Taillie et al. 2018).

Considering these limitations, we supplemented our evaluation of BACI treatment effects ($\beta_{PER \times CBI, ir}$; hereafter treatment effects) by also evaluating post-treatment CBI-occupancy relationships (hereafter burn severity relationships = $\beta_{CBI, ir} + \beta_{PER \times CBI, ir}$). We drew the 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 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”; Additional file 1: 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”; Additional file 1: 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 $b_{0,i}$:

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

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 (ρ) 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 : $N_{jt} = \sum_{i=1}^{\max(i)} z_{ijt}$. 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 Additional file 1: Appendix C; for model code, see Additional file 1: 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 (Additional file 1: 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 (Fig. 2). Detection probability estimates varied among species (median posterior p ranged 0.008–0.637; Additional file 1: 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 the 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 (Figs. 3, 4, and 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-pewee, 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 (Figs. 4 and 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; Figs. 3 and 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; Fig. 4).

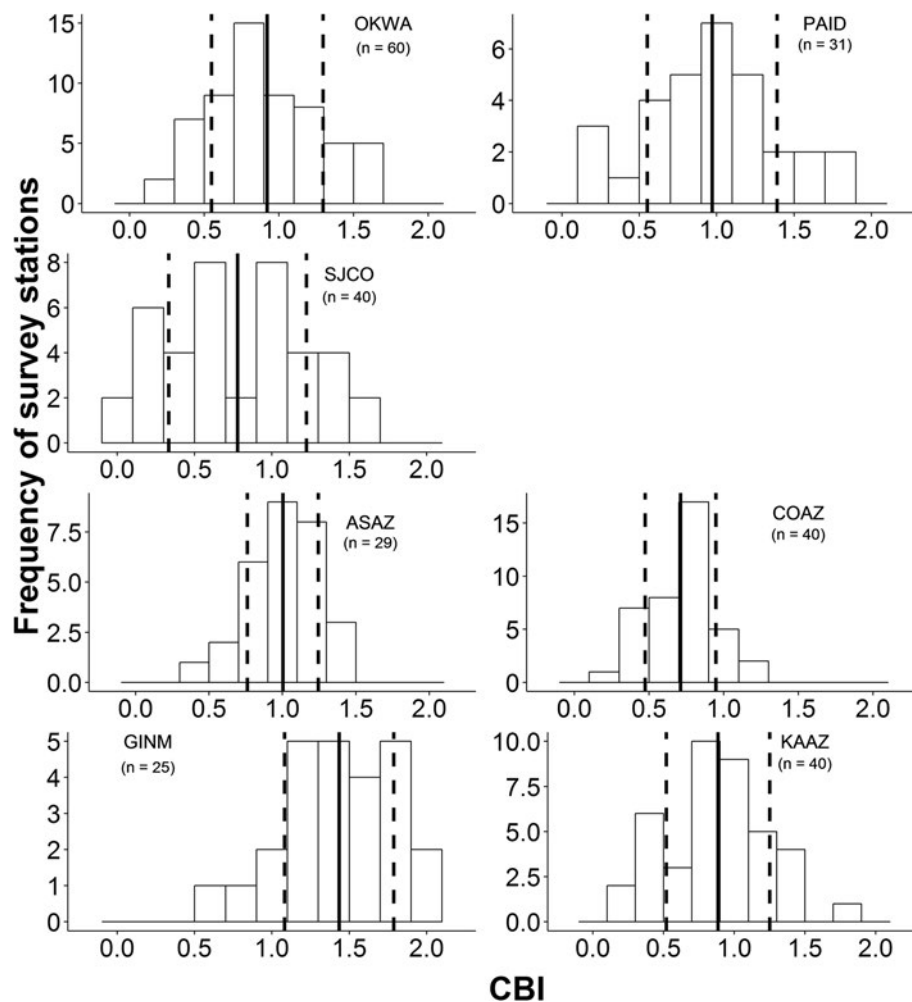


Fig. 2 Composite burn index (CBI) frequency distributions by national forest study location: Okanogan-Wenatchee in Washington (OKWA), Payette NF in Idaho (PAID), San Juan NF in Colorado (SJCO), Apache-Sitgreaves NF in Arizona (ASAZ), Coconino NF in Arizona (COAZ), Gila NF in New Mexico (GINM), and Kaibab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

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-pewee, house wren, dusky flycatcher, and gray flycatcher; Fig. 4). The yearly effect model showed treatment effects primarily arose in the second year following treatment (Fig. 4D, E). 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 (Figs. 4 and 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; Figs. 5 and 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-pewee 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

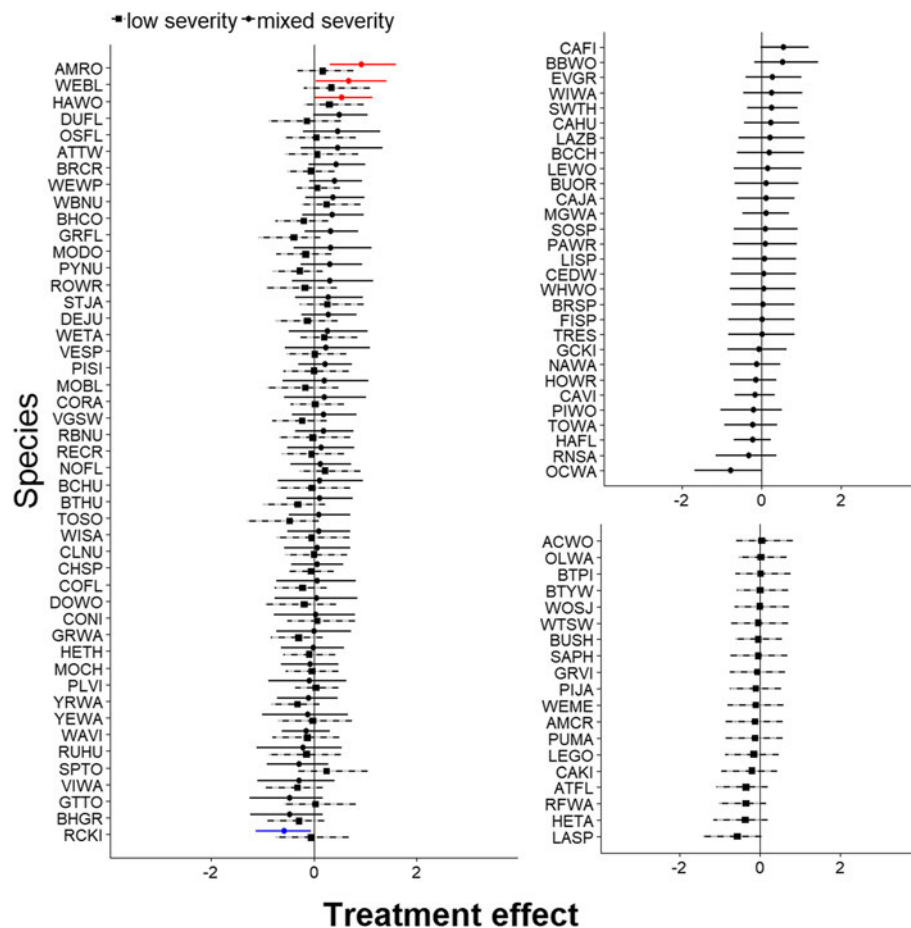


Fig. 3 Parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\hat{\beta}_{CBI \times PER}$ from Eq. 3). Estimates are for locations with historically mixed-severity (circles with solid lines) and low-severity (squares with dashed lines) fire regimes. The 47 species observed 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

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 (Figs. 3, 4, and 5). Despite the apparent difference between regimes, we found no statistically supported difference in treatment effect between regimes for any one species (BCIs for β_{Diff} all overlapped zero; Eq. 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 (Fig. 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 (Figs. 4 and 5).

Discussion

Changes in avian occupancy related to prescribed fire treatments and relationships with burn severity generally supported our predictions. Accordingly, our findings followed the 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

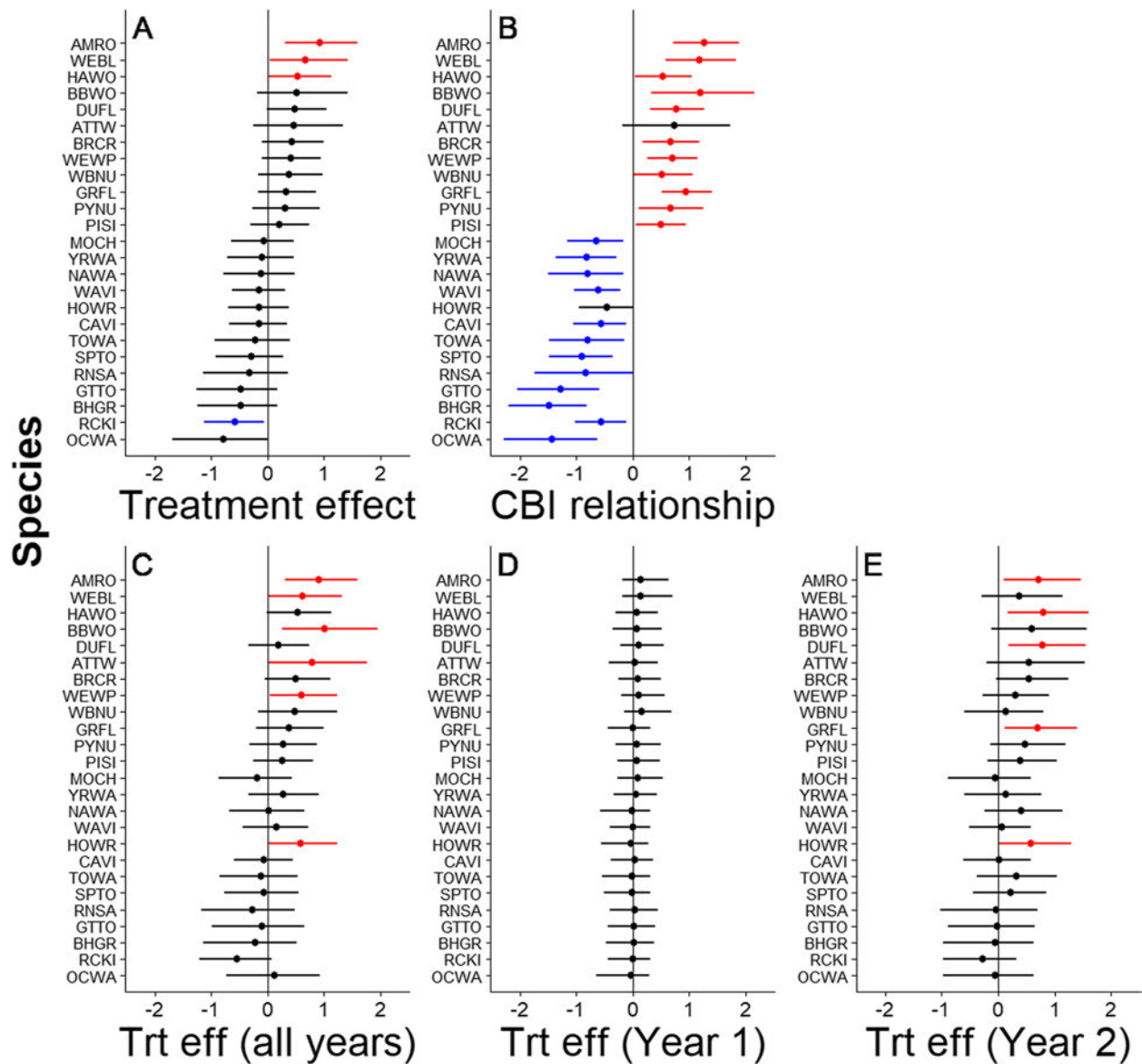
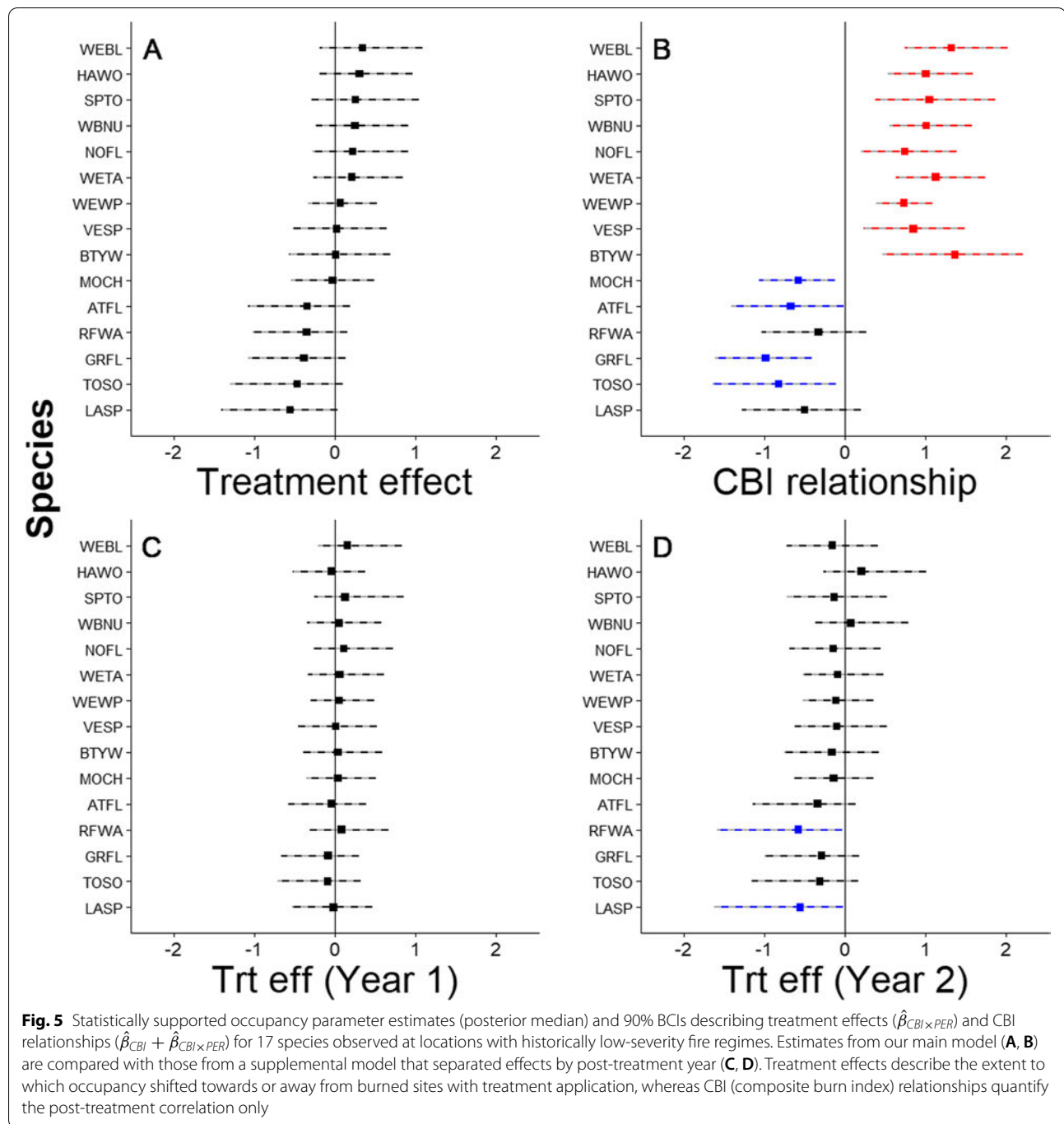


Fig. 4 Statistically supported occupancy parameter estimates (posterior median) and 90% BCIs describing treatment effects ($\hat{\beta}_{CBI \times PER}$) and post-treatment CBI relationships ($\hat{\beta}_{CBI} + \hat{\beta}_{CBI \times PER}$) for 25 species observed at locations with historically mixed-severity 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

that prescribed fires benefited 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

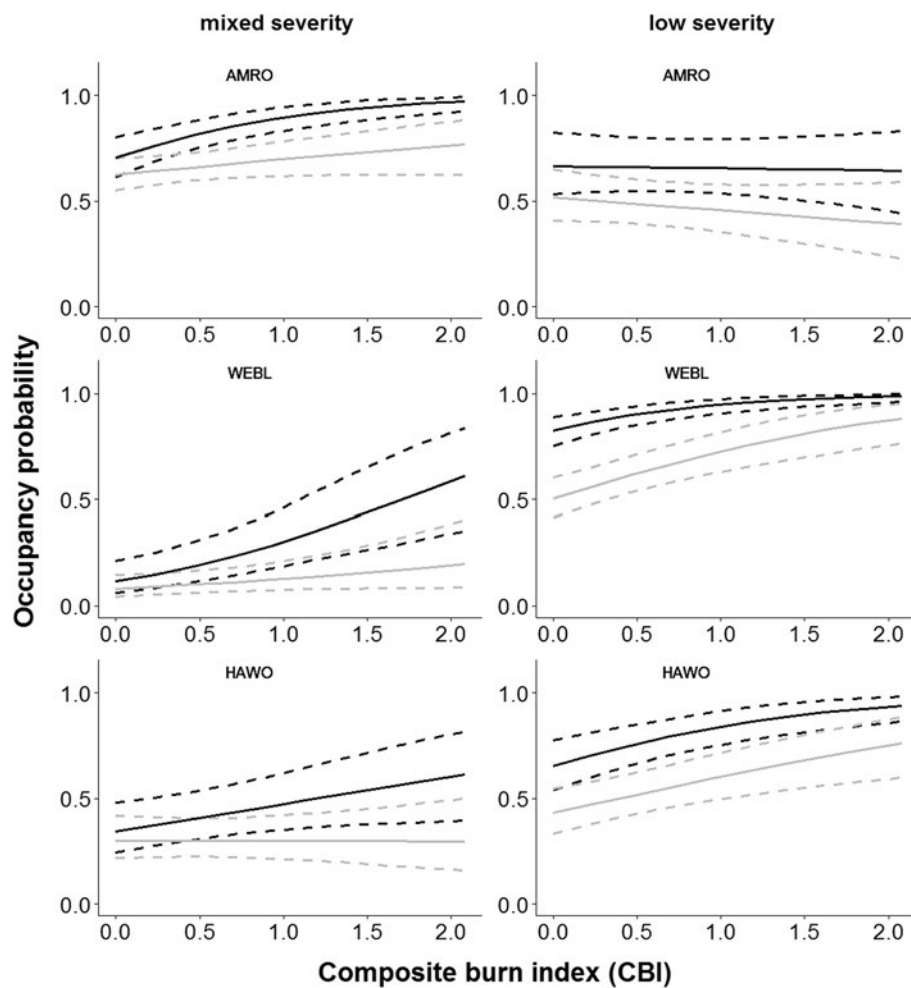


Fig. 6 Predicted occupancy with burn severity (CBI) for example species showing treatment responses statistically supported in historically mixed-severity regimes but not supported in low-severity regimes. Relationships with CBI were estimated before (gray) and after (black) treatment in mixed-severity 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 Additional file 1: Appendix E

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. Live tree densities were reduced by 37% (Additional file 1: Appendix B Table 3) to 45% across our study locations (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

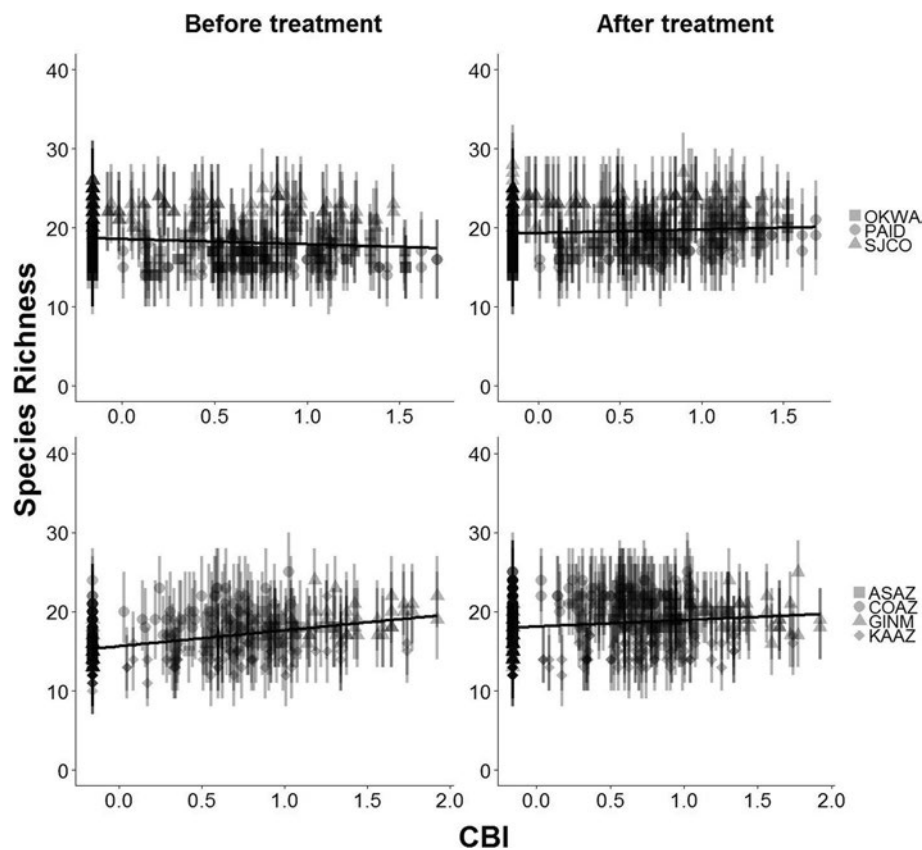


Fig. 7 Species richness estimates and 90% BCIs for surveyed points along burn severity (CBI) gradients estimated before (left column) and after (right column) prescribed fire treatments. Locations appearing in the top row historically experienced mixed-severity fire regimes (Okanogan-Wenatchee [OKWA], 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). 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

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 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 the majority of 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 concur 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 clarifies 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 (179–402 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 2 years post-treatment. This was particularly evident in the mixed-severity fire regime locations, where the understory vegetation had greater potential to influence changes in occupancy. 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 USA. 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 USA 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 US 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, regular, and expected by the avifauna. 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.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-022-00130-x>.

Additional file 1.

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Authors' 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. 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.

Author details

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

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