

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

Victoria A. Saab (✉ [vsaab@fs.fed.us](mailto:vsaab@fs.fed.us))

USDA Forest Service Rocky Mountain Research Station <https://orcid.org/0000-0003-0645-0523>

Quresh R. Latif

Bird Conservancy of the Rockies

William M. Block

USDA Forest Service Rocky Mountain Research Station

Jonathan G. Dudley

USDA Forest Service Rocky Mountain Research Station

---

## Research Article

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

**Posted Date:** November 8th, 2021

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

**License:**  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

**Version of Record:** A version of this preprint was published at Fire Ecology on April 12th, 2022. See the published version at <https://doi.org/10.1186/s42408-022-00130-x>.

1 **Front Material**

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

3

4 Authors: Victoria A. Saab<sup>1\*</sup>, Quresh R. Latif<sup>2</sup>, William M. Block<sup>3</sup>, Jonathan G. Dudley<sup>4</sup>

5 \*corresponding author: [victoria.saab@usda.gov](mailto:victoria.saab@usda.gov)

6 <sup>1</sup> Rocky Mountain Research Station, USDA Forest Service, 1748 South 7<sup>th</sup> Avenue, MSU

7 Campus, Bozeman, Montana, USA 59717

8 <sup>2</sup> Bird Conservancy of the Rockies, 14500 Lark Bunting Lane, Brighton, Colorado, USA 80603

9 <sup>3</sup> Rocky Mountain Research Station, USDA Forest Service, 2500 South Pine Knoll Drive,

10 Flagstaff, Arizona, USA 86001

11 <sup>4</sup> Rocky Mountain Research Station, USDA Forest Service, 332 East Front Street, Suite 401,

12 Boise, Idaho, USA 83702

13

14 **Abstract**

15 Background: Low-severity prescribed fire is a tool used for reducing fuel loads on public lands,

16 particularly in dry conifer forests of the western United States characterized by historically

17 mixed- and low-severity fire regimes. Understanding the ecological effects of prescribed fire

18 treatments is important for predicting the impacts of these management actions on wildlife

19 communities. But few studies have estimated small landbird responses to forest treatments at

20 spatial scales relevant to their ecology or have examined potential differences in treatment

21 effects applied within historically mixed- vs. low-severity fire regimes. Therefore, we evaluated

22 prescribed fire treatment effects and relationships with burn severity for avian communities in

23 dry conifer forests dominated by ponderosa pine (*Pinus ponderosa*) located on seven National

24 Forests in the interior western United States. We surveyed birds for 1–4 years and 1–3 years  
25 before and after prescribed fire treatments at mixed- and low-severity fire regime locations,  
26 respectively, following a before-after, control-impact study design – 8 paired control-treatment  
27 units in mixed-severity locations (16 total study units with 320 survey points) and 4 paired  
28 control-treatment units in low-severity locations (8 total study units with 278 survey points).  
29 Using a Bayesian hierarchical multi-species occupancy model, we analyzed occupancy patterns  
30 for 95 species.

31  
32 Results: We found 33 species with statistically supported treatment effects and/or burn severity  
33 relationships primarily in mixed-severity locations. The data supported positive treatment effects  
34 at mixed severity locations for 9 species (American Robin [*Turdus migratorius*], Western  
35 Bluebird [*Sialia mexicana*], Hairy Woodpecker [*Dryobates villosus*], Black-backed Woodpecker  
36 [*Picoides arcticus*], American Three-toed Woodpecker [*Picoides dorsalis*], House Wren  
37 [*Troglodytes aedon*], Dusky Flycatcher [*Empidonax oberholseri*], Western Wood-peewee  
38 [*Contopus sordidulus*], Gray Flycatcher [*Empidonax wrightii*]), whose occupancy shifted towards  
39 more severely burned points after treatment, and a negative effect for one species (Ruby-  
40 crowned Kinglet [*Corthylio calendula*]), whose occupancy shifted away from burned points. At  
41 low severity locations, only two species exhibited treatment effects, both negative (Red-faced  
42 Warbler [*Cardellina rubrifrons*], and Lark Sparrow [*Chondestes grammacus*]). We also found  
43 supported occupancy relationships with burn severity post-treatment (i.e., regardless of species  
44 distribution before treatment) for 29 species, most of which were consistent with their life  
45 histories (e.g., patterns of positive relationships for cavity-nesting, bark insectivores and negative  
46 relationships for open-nesting, foliage insectivores). Stronger responses to prescribed fire

47 treatments at mixed-severity locations were unexpected because prescribed fire applications are  
48 more similar to historical wildfires characterizing low-severity fire regimes.

49

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

57

58 **Keywords**

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

61

62 **Background**

63 Land management agencies have increased use of prescribed fire to reduce fuel loads and restore  
64 wildlands to historical conditions in dry conifer forests of the western U.S.A. during the last  
65 three decades (Morgan et al. 1994; Ryan et al. 2013; Stephens et al. 2016). Such efforts follow  
66 legislative directives designed to reduce fuel loads on public lands (i.e. National Fire Plan [U.S.  
67 Department of Agriculture (USDA) 2000], Healthy Forest Restoration Act [USDA 2003],  
68 Healthy Forest Initiative [White House 2004], Collaborative Forest Landscape Restoration  
69 Program [(Schultz et al. 2012)]). Managers use prescribed fire and mechanical fuel reduction

70 treatments to reduce risk of high-severity wildfire and to manage changes in forest integrity and  
71 ecological functions (Covington and Moore 1994; Covington et al. 1997; McIver et al. 2013).  
72 The use of prescribed fire, however, requires careful consideration of treatment effects on  
73 wildlife species and communities. In particular, the uncertainty of management outcomes given  
74 potentially novel ecological conditions and processes with the interaction of climate change and  
75 human disturbance elevate the need for quantifying ecological responses (Millar et al. 2007;  
76 Seastedt et al. 2008; McKelvey et al. 2021).

77 Forest managers pay particular interest to birds in light of policies under the National  
78 Forest Management Act (USDA 1976) for the management of biodiversity, protections afforded  
79 migratory species through the U.S. Migratory Bird Treaty Act, and requirements under the 2012  
80 Planning Rule and Directives to consider persistence of species of conservation concern (USDA  
81 2012). Additionally, because bird surveys do not require specialized equipment, birds offer  
82 useful opportunities for assessing ecological integrity and biodiversity (Sutherland et al. 2004),  
83 which represent mandated foci for management under the current U.S. Forest Service planning  
84 rule (USDA 2012).

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

93 species that forage in the air and on the ground (Artman et al. 2005; Blake 2005; Russell et al.  
94 2009).

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

106 Informing forest management that includes avian diversity and habitat conservation  
107 objectives requires synthesis of both species-specific and community-wide relationships with  
108 fire. Prescribed fire treatments have positive, negative, or mixed effects on individual species  
109 (Artman et al. 2005; Saab et al. 2005; Fontaine and Kennedy 2012; McIver et al. 2013). Just like  
110 wildfires, the severity of prescribed fires can vary and affect bird distributions (Kuchinke et al.  
111 2020). Additionally, fire timing influences responses by avian species and communities  
112 (Smucker et al. 2005; Saab et al. 2007; Bagne and Purcell 2011; Latif et al. 2016b). Managers  
113 typically ignite prescribed fires in seasonally dry forests during wet periods to limit burn  
114 severity, i.e., spring burning in mixed-severity regimes and fall burning in low-severity regimes.

115 This timing differs from seasonality of historical wildfires, raising potential conflict with  
116 breeding activities of forest birds (Erwin and Stasiak 1979; Bagne and Purcell 2011).

117 Avian responses to fire depend on burn severity (fire effects on vegetation; Agee 1993;  
118 Smith 2000) and time since fire (Saab and Powell 2005). Forested landscapes with a varied fire  
119 history are expected to support the greatest diversity of species (Clarke 2008; Fontaine et al.  
120 2009; Fontaine and Kennedy 2012). Varied fire histories are more typical of forests with mixed-  
121 severity fire regimes occurring at intermediate frequencies, in contrast to frequent, low-severity  
122 regimes of the southwestern United States (Hood et al. 2021). In the central and northern Rocky  
123 Mountains, mixed-severity fires that burned principally in late summer maintained landscape-  
124 scale heterogeneity in forest structure, and mixed tree species composition, often favored by fire-  
125 tolerant ponderosa pine (*Pinus ponderosa*) (Schoennagel et al. 2004; Hessburg et al. 2007)  
126 (Hood et al. 2021). Lower density trees associated with higher frequency, lower-severity fires  
127 that burned typically in spring were more widespread in the southwestern United States, where a  
128 drier climate favored forest patches that were relatively homogenous, lower in tree and shrub  
129 densities, and heavily dominated by ponderosa pine (Moir et al. 1997; Schoennagel et al. 2004;  
130 Nimmo et al. 2014). Considering this variation in ecological context, birds may respond  
131 differently to prescribed fire in locations with historically low- versus mixed-severity fire  
132 regimes, with potential implications for the role of prescribed fire in management strategies that  
133 include promoting and conserving biodiversity.

134 Here, we evaluated the influence of prescribed fire treatments on avian species  
135 occupancy and richness at locations representing both mixed- and low-severity fire regimes in  
136 dry mixed conifer forests across the interior western United States, known as the Birds and Burns  
137 Network. Our plot sizes averaged 300 ha, a spatial scale appropriate for drawing inference about

138 landbirds with varying home range sizes, and we used a before-after-control-impact (BACI)  
139 design for rigorous evaluation of treatment effects (Morrison et al. 2008; Popescu et al. 2012).  
140 Low-severity prescribed fire treatments on these study sites increased numbers of dead trees,  
141 opened the forest canopy, and reduced shrub cover within two years of treatment (Saab et al.  
142 2006). Based on these habitat changes, we predicted changes in species' occupancy rates  
143 concurring with life history traits (Table 1). We also expected species richness and average  
144 species responses to vary regionally depending on the different historical fire regimes (Latif et al.  
145 2016b). Because prescribed fire is intended to burn at low severity, we predicted occupancy  
146 changes to be more positive and of stronger magnitude at locations characterized by historically  
147 low-severity fire regimes.

148

## 149 **Methods**

### 150 *Study system*

151 We selected paired study units (treatments and controls) within areas identified by seven national  
152 forests that planned to conduct fuel reduction treatments for the Birds and Burns Network  
153 (Figure 1). Each study unit was approximately 200-400 ha (Table 2) and dominated by  
154 ponderosa pine. Sixteen study units were located in 3 national forests characterized historically  
155 by mixed severity fire regimes: 6 in the Payette National Forest (NF; Idaho), 6 in the Okanagon-  
156 Wenatchee NF (Washington), and 4 in the San Juan NF (Colorado). Eight study units were  
157 located in 4 national forests characterized historically by low severity fire regimes: 2 in the Gila  
158 NF (New Mexico), and 2 each on the Apache-Sitgreaves, Kaibab, and Coconino NFs (Arizona;  
159 Figure 1). Thus, we established 12-unit pairs for a total of 24 study units (Table 2). USFS

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

162 Ponderosa pine trees  $\geq 23$  cm dbh dominated overstory vegetation on all units with both  
163 low-severity and mixed-severity historical fire regimes. In low severity locations, the understory  
164 was relatively open with few shrubs and dominated by grasses, i.e., Arizona fescue (*Festuca*  
165 *arizonica*) and blue gramma (*Bouteloua gracilis*) and elevations ranged from 2072 m to 2500 m. In  
166 mixed severity locations, the understory vegetation was comprised of multiple shrub species,  
167 including snowberry (*Symphoricarpos albus*), spirea (*Spirea* spp.), ninebark (*Physocarpus* spp.),  
168 and serviceberry (*Amelanchiar alnifolia*), with Bluebunch wheatgrass (*Pseudoroegenaria spicatus*)  
169 and Idaho fescue (*Festuca idahoensis*) as the common grass species and elevations ranging 670 m  
170 to 1980 m.

171

#### 172 *Study units*

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

178

#### 179 *Bird surveys*

180 We surveyed birds for 1–4 years and 1–3 years before and after prescribed fire treatments at  
181 mixed-severity and low-severity units, respectively. For comparability across fire regimes, we  
182 restricted our primary analysis to data from 2 years before to 2 years after prescribed fire

183 treatments (Table 3). A supplemental analysis included all available data from mixed-severity  
184 units (Appendix A). We began point counts just after the dawn chorus and completed them  
185 within five hours. Only detections within 75 m of the point were included in this analysis. Our  
186 sampling design included a robust design (Pollock 1982) with years as primary periods and visits  
187 within years as the secondary samples.

188

### 189 *Burn severity measurements and analysis*

190 Prescribed fire treatments were implemented during 2003–2010 (Table 3). Fires were designed  
191 to reduce existing surface and ladder fuels of relatively small diameter (< 15.4 cm dbh), and  
192 create small gaps in the upper tree canopy, while retaining large pine trees and snags (>23 cm  
193 dbh). We measured burn severity using a composite burn index (CBI) representing a gradient of  
194 unburned (min CBI = 0) to severely burned (max CBI = 3; Key and Benson 2006; Appendix B).  
195 We assumed CBI = 0 for all survey points in untreated units. One treatment unit in Idaho was  
196 burned by wildfire before we could measure post-treatment vegetation. We used the Bayesian  
197 approach to missing value imputation for this unit whereby we treated missing values as a  
198 parameter to be estimated during model-fitting (Link and Barker 2010). We used a truncated  
199 Gaussian prior distribution for missing CBI values in Idaho (mean = 0.32, variance = 0.07, min =  
200 0), approximating the CBI distribution for another unit in the San Juan NF (CO) that burned at a  
201 qualitatively similar severity (based on visual assessment). Effects of prescribed fire on  
202 vegetation are provided in (Saab et al. 2006) . To briefly summarize these effects, overall  
203 downed woody material declined by 35% in the Southwest (low-severity fire regime) and 46% in  
204 the Northwest (mixed-severity fire regime). Large diameter trees (>23 cm) declined by 19% in

205 the Southwest with no change in the Northwest. Large diameter snags increased by 72% on the  
206 southwestern forests and 29% on the northwestern forests (Saab et al. 2006).

207

### 208 *Occupancy models*

209 We used avian point count data in a hierarchical multi-species occupancy model (Dorazio et al.  
210 2006; Russell et al. 2009) to identify changes in occupancy rates in relation to prescribed fire  
211 treatments and burn severity. Occupancy models leverage repeat-survey data to estimate species  
212 detectability ( $p$ ) conditional upon occupancy (species presence within a specified time period and  
213 spatial unit), allowing unbiased estimation of occupancy probabilities ( $\psi$ ) given sufficient data  
214 and adherence to model assumptions (MacKenzie et al. 2002; MacKenzie et al. 2018). We  
215 assumed that the occupancy states of species could change among years, but not between visits  
216 within a year. We used multi-species occupancy models to estimate species-specific parameters  
217 as random variables governed by community-level parameters. The use of a common distribution  
218 among species improves the precision of species-specific parameter estimates, particularly for  
219 rare species, facilitating estimation of species richness (Dorazio et al. 2006; Russell et al. 2009).  
220 We excluded raptors, owls, and grouse because they were not readily detectable with our survey  
221 methods, and we only included species breeding in our study areas. For mobile animals such as  
222 birds, detectability ( $p$ ) estimated with surveys repeated over a season includes information on  
223 both within-season movement and surveyor ability (i.e., availability and perceptibility; sensu  
224 Chandler and Royle 2013; Amundson et al. 2014). Occupancy probabilities thereby represent the  
225 probability of a surveyed point intersecting at least one home range for a given species (Latif et  
226 al. 2016a).

227 We used occupancy patterns estimated from our analysis to evaluate predictions for  
 228 species based on their individual life histories (Table 1) and on previous research (Russell et al.  
 229 2009; Gaines et al. 2010; Bagne and Purcell 2011; Fontaine and Kennedy 2012; McIver et al.  
 230 2013). We expected these predictions to describe general patterns while taking into consideration  
 231 that each individual species has a unique life history that may not fit perfectly within the broad  
 232 categories for which we had *a priori* predictions. Thus, we considered both general predictions  
 233 for life histories and literature on individual species when evaluating whether patterns were  
 234 consistent with current knowledge.

235 For each study location, we compiled a 3-dimensional data matrix  $\mathbf{y}$ , where element  $y_{jit}$   
 236 was the sum of binary indicators for species detection (Sanderlin et al. 2014). Given a binary  
 237 indicator  $x_{jikt} = 1$ , we detected species  $i$  ( $i = 1, \dots, N$ ) at point count station  $j$  ( $j = 1, \dots, J$ ) during  
 238 visit  $k$  ( $k = 1, \dots, K$ ) in year  $t$  ( $t = 1, \dots, T$ ;  $T = 4$ ). Because we did not have covariates that differed  
 239 for detection between visits, we analyzed the sum of all binary detections for species  $i$  over all  
 240 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  
 241 modeled these data given probability of detection  $p_i$ , and occupancy latent state  $z_{ijt}$  using a  
 242 Bernoulli distribution with probability of success  $p_i \times z_{ijt}$ :

$$243 \quad [y_{jit} | p_i, z_{ijt}] \sim \text{Bin}(K, p_i \times z_{ijt}) \text{ (Equation 1),}$$

244 where the latent variable  $z_{ijt}$  for occupancy given probability of occupancy  $\psi_{jit}$  was modeled as:

$$245 \quad [z_{ijt} | \psi_{jit}] \sim \text{Bern}(\psi_{jit}) \text{ (Equation 2).}$$

246 We analyzed changes in species occupancy patterns using a model that fully leverages  
 247 our BACI sampling design for examining treatment effects (Popescu et al. 2012). Although our  
 248 study design entailed surveying units with *a priori* assignments of treatment versus control,  
 249 treatments did not realize homogenous impacts on vegetation structure and composition. We

250 therefore measured shifts in occupancy from before to after treatment along a continuous burn  
251 severity gradient (*contra* control-impact categories) represented by CBI to evaluate treatment  
252 effects. We modeled occupancy ( $\psi_{ijt}$ ) as a function of burn severity measured after treatment  
253 ( $CBI_j$ ), treatment period ( $PER_{jt} = 0$  or  $1$  for before or after site  $j$  was treated, respectively), and  
254 the interaction between severity and period ( $CBI_j \times PER_{jt}$ ). Thus,

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

257 where  $\beta_{0,il}$  is the intercept and  $\beta_{ir}$  parameters described additive or interactive effects of  
258 covariates  $PER_{jt}$  and  $CBI_j$  on occupancy of species  $i$  at site  $j$  in year  $t$ . All estimated parameters  
259 were species-specific normal random effects,  $\beta_{0,il}$  was estimated separately by location ( $l =$   
260  $1, \dots, L; L = 7$ ), and covariate effects ( $\beta_{ir}$ ) were estimated separately by fire regime ( $r = 1, \dots, R; R$   
261  $= 2$ ). For numerical purposes,  $CBI_j$  values were centered at the mean for point count stations in  
262 treated units (0.76) prior to all analyses. Unlike others (Russell et al. 2009), we did not model  
263 persistence as a Markovian process in our primary model to avoid stretching the limits of our  
264 data at low-severity locations. We did include Markovian species persistence, however, in a  
265 supplemental analysis of data from mixed-severity locations (described further below and in  
266 Appendix A).

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

273  $\beta_{diff} = \beta_{mixed} - \beta_{low}$  (Equation 4),

274 where  $\beta_{mixed}$  and  $\beta_{low}$  represent estimated treatment effects in mixed- and low-severity regimes,  
275 respectively.

276 Our sampling design afforded inferences that were stronger than purely observational  
277 studies but not equivalent to a fully controlled experiment (see Popescu et al. 2012 and literature  
278 referenced therein). We controlled for potentially confounding factors by randomly designating  
279 members of paired units as treatment versus control in most cases, replicating sampling (i.e.,  
280 sampling multiple units and locations in each fire regime), and explicitly separating treatment  
281 effects ( $\beta_{PER \times CBI,ir}$ ) from potentially confounding sources of variation ( $\beta_{PER,ir}$ ,  $\beta_{CBI,ir}$ ;  
282 Equations 3) during analysis (Popescu et al. 2012). Nevertheless, burn severity within treated  
283 units was likely influenced by factors for which we did not explicitly control (e.g., vegetation  
284 structure, moisture levels, and topography). Furthermore, some species whose life histories  
285 typically confer effects of prescribed fire may exhibit subdued treatment effects if occupancy  
286 already favors desirable sites prior to treatment. Finally, our timeframe of sampling (2 years pre-,  
287 2 years post-treatment) potentially limited the scope and strength of inference, especially because  
288 we expected some species to exhibit delayed effects of treatment.

289 Considering these limitations, we supplemented our evaluation of BACI treatment effects  
290 ( $\beta_{PER \times CBI,ir}$ ; hereafter treatment effects) by also evaluating post-treatment CBI-occupancy  
291 relationships (hereafter burn severity relationships =  $\beta_{CBI,ir} + \beta_{PER \times CBI,ir}$ ). We drew strongest  
292 inference from treatment effects, and we also drew weaker but substantive inference from burn  
293 severity relationships that were consistent with our predictions based on species life histories.  
294 We also followed up our primary analysis with two supplemental analyses. For one, we included  
295 data from additional years at mixed severity locations and a Markovian persistence parameter to

296 better account for variability among years (hereafter “extended sampling model”; Appendix A).  
297 For the other, we analyzed data from each fire regime separately and estimated separate  
298 treatment effects for each post-treatment year (hereafter “yearly effect model”; Appendix A). We  
299 examined species with statistically supported treatment effects or CBI relationships from our  
300 primary analysis, and/or statistically supported treatment effects in supplemental analyses. We  
301 evaluated the strength of evidence for prescribed fire effects based on the consistency of patterns  
302 estimated across analyses and with biologically based predictions (Table 1).

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

305 
$$\text{logit}(p_{il}) = b_{0,il} \text{ (Equation 5),}$$

306 where  $p_{il}$  is the probability of detecting species  $i$  at location  $l$  during a survey of a given point  
307 count station in a given year when the species was present. We modeled heterogeneity in  
308 detectability among species and assumed detectability did not change with treatment condition  
309 (preliminary models with treatment effects on detection converged poorly and were therefore  
310 abandoned). We modeled heterogeneity among species using a correlation term ( $\rho$ ) between  
311 species intercepts of detection probability ( $b_{0,i}$ ) with occupancy probability ( $\beta_{0,i}$ ) (Dorazio et al.  
312 2006; Kéry et al. 2009).

313 In addition to species-specific relationships, we calculated and plotted emergent changes  
314 between species richness with treatment condition. We estimated species richness ( $N_{jt}$ ) at each  
315 point count station  $j$  and year  $t$ :  $N_{jt} = \sum_{i=1}^{\max(i)} z_{ijt}$ . Community-level inferences were restricted to  
316 the subset of members observed at least once during our studies (cf. Russell et al. 2009; Latif et  
317 al. 2016b).

318 We sampled posterior parameter distributions for all models using JAGS v. 3.3.0  
319 (Plummer 2003) programmed from R (Team 2013)(Su and Yajima 2014). We used independent  
320 non-informative priors for all parameters (for priors, see Appendix C; for model code, see  
321 Appendix D). We ran 6 parallel MCMC chains of length 100,000 *it*, burn-in 10,000 *it*, and  
322 thinning 10 *it* to sample posterior distributions. We verified that  $n_{\text{effective}} \geq 100$  and  $\hat{R} \leq 1.1$  for all  
323 parameters (Gelman and Hill 2007). We examined model goodness-of-fit (GOF) using posterior  
324 predictive testing (Gelman and Hill 2007). Specifically, we calculated a Bayesian *p*-value  
325 representing the proportion of simulated datasets drawn from model posterior predictive  
326 distributions with deviance higher than deviance for observed datasets from each location,  
327 whereby  $p < 0.05$  or  $p > 0.95$  constitutes evidence for lack of fit.

328

## 329 **Results**

330 Ninety-five species were detected across all point count stations and years (Appendix E). Forty-  
331 seven species were detected in both fire regimes, 19 unique to low-severity locations, and 29 at  
332 only mixed-severity locations. The five most commonly detected species at the three mixed-  
333 severity locations were Western Tanager, Yellow-rumped Warbler, Chipping Sparrow, Red-  
334 breasted Nuthatch, and Mountain Chickadee. The five most commonly detected species at low-  
335 severity locations were Dark-eyed Junco, Pygmy Nuthatch, Mountain Chickadee, Western  
336 Bluebird, and Grace's Warbler. Burn severity measured at points within treated units was  
337 variable (mean [SD] CBI = 0.92 [0.40],  $n = 274$  points) and broadly overlapped among locations  
338 (Figure 2). Detection probability estimates varied among species (median posterior *p* ranged  
339 0.008–0.637; Appendix F) and were highly correlated with occupancy (median estimate [90%

340 BCLs] for  $\rho = 0.80$  [0.75–0.85]). We found no evidence for lack of model fit (location-specific  
341 GOF  $p$  values from primary model ranged 0.34–0.42).

342

### 343 *Species-level prescribed fire effects and burn severity relationships*

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

358 Evidence for treatment effects varied with time since treatment and fire regime. We  
359 found the most evidence for positive treatment effects in the mixed severity fire regime (e.g., for  
360 American Robin, Western Bluebird, and Hairy Woodpecker; Figures 3, 4). For some species,  
361 treatment effects and CBI relationships were not unequivocally supported in every analysis (i.e.,

362 90% BCIs sometimes included zero) but were nevertheless consistent in direction (e.g., Black-  
363 backed Woodpecker and Ruby-crowned Kinglet; Figure 4).

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

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

384 consistent with their life histories (e.g., Ash-throated Flycatcher, and Townsend's Solitaire),  
385 suggesting they were possibly spurious.

386

### 387 *Community-level patterns*

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

400

## 401 **Discussion**

402 Changes in avian occupancy related to prescribed fire treatments and relationships with burn  
403 severity generally supported our predictions. Accordingly, our findings followed conclusions of  
404 previous prescribed fire studies (e.g., Hurteau et al. 2008; Dickson et al. 2009; Russell et al.  
405 2009; Bagne and Purcell 2011; Fontaine and Kennedy 2012; White et al. 2016) and supported  
406 our predictions that prescribed fires benefit cavity-nesting, bark and ground insectivores. We

407 found increases in occupancy related to post-fire treatments or burn severity for many cavity-  
408 nesting birds, including bark-insectivores (American three-toed, hairy, black-backed  
409 woodpeckers, white-breasted nuthatch, brown creeper, and pygmy nuthatch) and ground  
410 insectivores (American robin, Western bluebird, house wren). Increases in available snags  
411 created soon after fire likely increased nesting substrate and food resources (bark beetle larvae  
412 [Scolytidae]) for cavity-nesting, bark insectivores (Saab and Powell 2005; Saab et al. 2006;  
413 Russell et al. 2009). Notably, we recorded positive changes in occupancy related to low-severity  
414 prescribed fire for species known to favor higher severity wildfires (e.g., Black-backed  
415 woodpecker, Saab et al. 2007), suggesting that fire management can be an effective tool to create  
416 habitat for some fire specialist species at least for a few years.

417 Further reductions in post-fire ground cover may have increased foraging opportunities  
418 across both fire regimes for open-ground feeding species (American robin, Western bluebird,  
419 house wren), including Northern flicker (Bagne and Purcell 2011; White et al. 2016). Although  
420 we expected occupancy increases by several aerial foragers in relation to fire (Bagne and Purcell  
421 2011), we detected few positive trends (Western wood-pewee [both regimes], dusky and gray  
422 flycatchers [mixed fire-regime]), suggesting that effects of low-severity fire treatments are  
423 variable for aerial insectivores. Habitat changes resulting from higher severity burns are likely  
424 more beneficial to aerial insectivores (Kotliar et al. 2002; Smucker et al. 2005; Russell et al.  
425 2006; Kotliar et al. 2007; Latif et al. 2016b). Compared to low-severity fire, moderate- to high-  
426 severity burns potentially create more openings in the forest canopy, allowing efficiency in  
427 flycatching for insects, and release more soil nutrients that allow for shrub growth and increased  
428 abundance of associated arthropods (cf. Certini 2005), followed by increases of insect prey  
429 availability for aerial insectivores.

430 Negative relationships with burn severity followed our predictions for canopy foliage-  
431 gleaners (mixed severity: Cassin's and warbling vireos; ruby-crowned kinglet, Nashville, yellow-  
432 rumped and Townsend's warblers, mountain chickadee; low severity: red-faced warbler and  
433 mountain chickadee) and were consistent with other prescribed-fire studies (Bagne and Purcell  
434 2011; Fontaine and Kennedy 2012; White et al. 2016). These species forage in live trees,  
435 contributing to their negative relationships with fires of various severities that can damage or kill  
436 portions of live trees. A negative percent change of live trees across our study locations averaged  
437 45% (Saab et al. 2006), likely promoting the negative relationships between foliage insectivores  
438 and burn severity.

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

449 Perhaps bird populations occurring in historically low-severity locations had fewer  
450 occupancy changes because fire is typically more frequent, expected, and regular. By  
451 comparison, fire events are relatively rare historically in mixed severity locations, potentially  
452 eliciting more responses to an infrequent opportunity, even by species that are strongly

453 associated with recently burned forests by wildfire (e.g., Black-backed and American three-toed  
454 woodpeckers). This pattern suggests that fire management activities intended to reduce fuels and  
455 lower the risk of high-severity wildfire can be effective in creating habitat for some fire  
456 specialists at least in the short term. Historical conditions are especially meaningful when they  
457 encompass evolutionary relationships such as the role fire regimes play in structuring bird  
458 communities and species distributions (cf. Hutto et al. 2008).

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

468         Our findings that species richness was affected little by prescribed fire treatments concurs  
469 with previous literature (George and Zack 2008; Hurteau et al. 2008; Russell et al. 2009). Post-  
470 fire bird communities may contain the same number of species as the pre-fire community, but  
471 nevertheless contain different species, including those not prevalent outside of recently disturbed  
472 forests, such as Black-backed and American three-toed woodpeckers. Assessing both individual  
473 species responses to management practices and the overall contribution of a species to  
474 biodiversity on a larger regional scale (such as a forested area containing burned and unburned  
475 portions) is important for addressing specific management goals. Additionally, treatments on a

476 study unit may affect shifts in species distributions only observable with a BACI study design  
477 that clarify species responses. For example, consistent with their life history, House Wren shifted  
478 their distribution toward burned/treated units, although this shift was not strong enough to  
479 completely negate or reverse their greater prevalence at unburned compared to burned units prior  
480 to treatment.

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

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

496

497 *Management Implications*

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

502 Unprecedented, extreme fire behavior resulting in rapid and extensive tree mortality is  
503 expected to be more common under changing climate conditions (Fettig et al. 2013), raising  
504 concerns by ecologists worldwide (Pickrell and Pennisi 2020). Prescribed fire and other fuel  
505 reduction treatments *potentially* reduce the risk of future severe wildfires, decrease tree  
506 mortality, and increase forest resilience to climate change (Stephens et al. 2018). Prescribed fire  
507 treatments are also potentially useful for creating near-term habitats for fire specialists that are  
508 more frequently found after wildfires. Fire suppression in the long-term does not benefit avian  
509 species or biodiversity overall (Bagne and Purcell 2011). For example, broadscale contiguous  
510 tree mortality can result in homogeneity produced by fire suppression, reducing the fine-scale  
511 heterogeneity of forest conditions that contribute to resilience and biodiversity (Stephens et al.  
512 2018). Prescribed fire and forest thinning could enhance adaptation to climate-induced stress if  
513 resources are focused on creating spatially and temporally variable patterns in seasonally dry  
514 forests that are aligned with local fire patterns (cf. North et al. 2009), accordingly supporting  
515 local avian communities.

516 Dry forested landscapes of the interior western United States support a diverse avifauna,  
517 including species of concern that rely on recent disturbance (e.g., Black-backed Woodpecker),  
518 old/mature forest specialists (e.g., Red-faced Warbler), and species that require multiple seral  
519 stages (e.g., White-headed Woodpecker; Latif et al. 2015). Our results indicate that fire  
520 management practices promoting a mosaic of habitat conditions will best support the full suite of

521 avian species native to seasonally dry conifer forests of western North America (Saab et al. 2005;  
522 Veech and Crist 2007; Fontaine et al. 2009; Fontaine and Kennedy 2012).

523

## 524 **Conclusions**

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

535

## 536 **Declarations**

537

## 538 **Ethics approval and consent to participate**

539 Not applicable

540

## 541 **Consent for publication**

542 Not applicable

543

544 **Data availability**

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

547

548 **Competing interests**

549 The authors declare that they have no competing interests

550

551 **Funding**

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

558

559 **Author contributions**

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

564

565 **Acknowledgements**

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

571

## 572 **References**

- 573  
574 Agee, J. K. 1993. Ponderosa pine and lodgepole pine forests. In *Fire Ecology of Pacific Northwest*  
575 *Forests*, ed. J. K. Agee, 320-350. Island Press.
- 576 Allen, Craig R, Graeme S Cumming, Ahjond S Garmestani, Phillip D Taylor, and Brian H Walker.  
577 2011. Managing for resilience. *Wildlife Biology* 17 (4):337-349, 13.
- 578 Amundson, Courtney L., J. Andrew Royle, and Colleen M. Handel. 2014. A hierarchical model  
579 combining distance sampling and time removal to estimate detection probability during  
580 avian point counts. *Auk* 131 (4):476-494. <https://doi.org/10.1642/AUK-14-11.1>.
- 581 Artman, Vanessa L, Todd F Hutchinson, and Jeffrey D Brawn. 2005. Fire ecology and bird  
582 populations in eastern deciduous forests. *Studies in Avian Biology* 30:127-138.
- 583 Bagne, Karen E., and Kathryn L. Purcell. 2011. Short-term responses of birds to prescribed fire in  
584 fire-suppressed forests of California. *Journal of Wildlife Management* 75 (5):1051-1060.  
585 <https://doi.org/10.1002/jwmg.128>.
- 586 Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T.S. Schulenberg. 2020. "Birds of the World."  
587 Cornell Laboratory of Ornithology. <https://birdsoftheworld.org/bow/home>.
- 588 Blake, John G. 2005. Effects of prescribed burning on distribution and abundance of birds in a  
589 closed-canopy oak-dominated forest, Missouri, USA. *Biological Conservation* 121 (4):519-  
590 531. <https://doi.org/https://doi.org/10.1016/j.biocon.2004.06.021>.
- 591 Certini, Giacomo. 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143 (1):1-  
592 10. <https://doi.org/10.1007/s00442-004-1788-8>.
- 593 Chandler, Richard B., and J. Andrew Royle. 2013. Spatially explicit models for inference about  
594 density in unmarked or partially marked populations. *Annals of Applied Statistics* 7:936-  
595 954. <https://doi.org/10.1214/12-AOAS610>.
- 596 Clarke, Michael F. 2008. Catering for the needs of fauna in fire management: science or just  
597 wishful thinking? *Wildlife Research* 35 (5):385-394.  
598 <https://doi.org/https://doi.org/10.1071/WR07137>.
- 599 Covington, W., P. Fule, M. Moore, S. Hart, T. Kolb, J. Mast, S. Sackett, and M. Wagner. 1997.  
600 Restoring ecosystem health in ponderosa pine forests of the southwest *Journal of Forestry*  
601 95 (4):23-29.
- 602 Covington, W. Wallace, and Margaret M. Moore. 1994. Southwestern ponderosa forest structure.  
603 *Journal of Forestry* January:39-47.
- 604 Dickson, Brett G., Barry R. Noon, Curtis H. Flather, Stephanie Jentsch, and William M. Block. 2009.  
605 Quantifying the multi-scale response of avifauna to prescribed fire experiments in the  
606 southwest United States. *Ecological Applications* 19 (3):608-621.  
607 <https://doi.org/10.1890/08-0905.1>.
- 608 Dorazio, Robert M., J. Andrew Royle, Bo Söderström, and Anders Glimskär. 2006. ESTIMATING  
609 SPECIES RICHNESS AND ACCUMULATION BY MODELING SPECIES OCCURRENCE AND

610 DETECTABILITY. *Ecology* 87 (4):842-854. [https://doi.org/https://doi.org/10.1890/0012-9658\(2006\)87\[842:ESRAAB\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2).

611

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

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

618 Fontaine, Joseph B., Daniel C. Donato, W. Douglas Robinson, Beverly E. Law, and J. Boone  
619 Kauffman. 2009. Bird communities following high-severity fire: Response to single and  
620 repeat fires in a mixed-evergreen forest, Oregon, USA. *Forest Ecology and Management*  
621 257 (6):1496-1504.

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

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

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

632 George, T. Luke, and Steve Zack. 2008. Bird occupancy and richness in ponderosa pine forests  
633 with contrasting forest structure and fire history. *Canadian Journal of Forest Research* 38  
634 (5):936-942. <https://doi.org/10.1139/x07-238>.

635 Hessburg, P.F., R. B. Salter, and K. James. 2007. Re-examining fire severity relations in pre-  
636 management era mixed conifer forests: inferences from landscape patterns of forest  
637 structure. *Landscape Ecology* 22:5-24.

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

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

645 Kéry, Marc, J. Andrew Royle, Matthias Plattner, and Robert M. Dorazio. 2009. Species richness  
646 and occupancy estimation in communities subject to temporary emigration. *Ecology* 90  
647 (5):1279-1290. <https://doi.org/10.1890/07-1794.1>.

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

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

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

656 Kuchinke, Diana, Julian Di Stefano, Holly Sitters, Richard Loyn, Peter Gell, and Grant Palmer. 2020.  
657 Prescribed burn severity has minimal effect on common bird species in a fire-prone forest  
658 ecosystem. *Forest Ecology and Management* 475:118437.  
659 <https://doi.org/https://doi.org/10.1016/j.foreco.2020.118437>.

660 Latif, Quresh S., Martha M. Ellis, and Courtney L. Amundson. 2016a. A broader definition of  
661 occupancy: Comment on Hayes and Monfils. *The Journal of Wildlife Management* 80  
662 (2):192-194. <https://doi.org/10.1002/jwmg.1022>.

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

666 Latif, Quresh S., Jamie S. Sanderlin, Victoria A. Saab, William M. Block, and Jonathan G. Dudley.  
667 2016b. Avian relationships with wildfire at two dry forest locations with different historical  
668 fire regimes. *Ecosphere* 7 (5):e01346. <https://doi.org/10.1002/ecs2.1346>.

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

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

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

677 McIver, James D., Scott L. Stephens, James K. Agee, Jamie Barbour, Ralph E. J. Boerner, Carl B.  
678 Edminster, Karen L. Erickson, Kerry L. Farris, Christopher J. Fettig, Carl E. Fiedler, Sally  
679 Haase, Stephen C. Hart, Jon E. Keeley, Eric E. Knapp, John F. Lehmkuhl, Jason J.  
680 Moghaddas, William Otrosina, Kenneth W. Outcalt, Dylan W. Schwilk, Carl N. Skinner,  
681 Thomas A. Waldrop, C. Phillip Weatherspoon, Daniel A. Yaussy, Andrew Youngblood, and  
682 Steve Zack. 2013. Ecological effects of alternative fuel-reduction treatments: highlights of  
683 the National Fire and Fire Surrogate study (FFS). *International Journal of Wildland Fire* 22  
684 (1):63-82. <https://doi.org/http://dx.doi.org/10.1071/WF11130>.

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

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

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

696 Morgan, Penelope, Gregory H. Aplet, Jonathan B. Haufler, Hope C. Humphries, Margaret M.  
697 Moore, and W. Dale Wilson. 1994. Historical range of variability. *Journal of Sustainable*  
698 *Forestry* 2 (1-2):87-111. [https://doi.org/10.1300/J091v02n01\\_04](https://doi.org/10.1300/J091v02n01_04).

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

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

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

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

709 Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs  
710 sampling. . Proceedings of the 3rd International Workshop on Distributed Statistical  
711 Computing (DSC 2003), Vienna, Austria, March 20-22, 2003.

- 712 Pollock, Kenneth H. 1982. A Capture-Recapture Design Robust to Unequal Probability of  
713 Capture. *The Journal of Wildlife Management* 46 (3):752-757.  
714 <https://doi.org/10.2307/3808568>.
- 715 Popescu, Viorel D., Perry de Valpine, Douglas Tempel, and M. Zachariah Peery. 2012. Estimating  
716 population impacts via dynamic occupancy analysis of Before-After Control-Impact  
717 studies. *Ecological Applications* 22 (4):1389-1404. <https://doi.org/10.1890/11-1669.1>.
- 718 Russell, Robin E., J. Andrew Royle, Victoria A. Saab, John F. Lehmkuhl, William M. Block, and John  
719 R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife  
720 communities: avian responses to prescribed fire. *Ecological Applications* 19 (5):1253-  
721 1263. <https://doi.org/doi:10.1890/08-0910.1>.
- 722 Russell, Robin E., Victoria A. Saab, Jonathan G. Dudley, and Jay J. Rotella. 2006. Snag longevity  
723 in relation to wildfire and postfire salvage logging. *Forest Ecology and Management*  
724 232:179-187.
- 725 Ryan, Kevin C, Eric E Knapp, and J Morgan Varner. 2013. Prescribed fire in North American forests  
726 and woodlands: history, current practice, and challenges. *Frontiers in Ecology and the*  
727 *Environment* 11 (s1):e15-e24. <https://doi.org/https://doi.org/10.1890/120329>.
- 728 Saab, V. A., R.E. Russell, and J.G. Dudley. 2007. Nest densities of cavity-nesting birds in relation  
729 to postfire salvage logging and time since wildfire. *Condor* 109:97-108.
- 730 Saab, V.A., and Hugh D. W. Powell. 2005. Fire and avian ecology in North America: process influencing  
731 pattern. *Studies in Avian Biology* 30:1-13.
- 732 Saab, Victoria A., Hugh D. W. Powell, Natasha B. Kotliar, and Karen R. Newlon. 2005. Variation in  
733 fire regimes of the Rocky Mountains: implications for avian communities and fire  
734 management. *Studies in Avian Biology* 30:76-96.
- 735 Saab, Victoria, Lisa Bate, John Lehmkuhl, Brett Dickson, Scott Story, Stephanie Jentsch, and  
736 William Block. 2006. Changes in downed wood and forest structure after prescribed fire in  
737 ponderosa pine forests. Fuels management -- How to measure success, Portland, OR.
- 738 Sanderlin, Jamie S., William M. Block, and Joseph L. Ganey. 2014. Optimizing study design for  
739 multi-species avian monitoring programmes. *Journal of Applied Ecology* 51 (4):860-870.  
740 <https://doi.org/10.1111/1365-2664.12252>.
- 741 Schoennagel, T., T.T. Veblen, and William H. Romme. 2004. The interaction of fire, fuels, and  
742 climate across Rocky Mountain forests. *Bioscience* 54:661-676.
- 743 Schultz, Courtney A., Theresa Jedd, and Ryan D. Beam. 2012. The Collaborative Forest  
744 Landscape Restoration Program: A History and Overview of the First Projects. *Journal of*  
745 *Forestry* 110 (7):381-391.
- 746 Seastedt, Timothy R, Richard J Hobbs, and Katharine N Suding. 2008. Management of novel  
747 ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment* 6  
748 (10):547-553. <https://doi.org/https://doi.org/10.1890/070046>.
- 749 Smucker, Kristina M., Richard L. Hutto, and Brian M. Steele. 2005. Changes in bird abundance  
750 after wildfire: importance of fire severity and time since fire. *Ecological Applications* 15  
751 (5):1535-1549.
- 752 Stephens, Scott L, Brandon M Collins, Christopher J Fettig, Mark A Finney, Chad M Hoffman, Eric E  
753 Knapp, Malcolm P North, Hugh Safford, and Rebecca B Wayman. 2018. Drought, Tree  
754 Mortality, and Wildfire in Forests Adapted to Frequent Fire. *BioScience* 68 (2):77-88.  
755 <https://doi.org/10.1093/biosci/bix146>.
- 756 Stephens, Scott L., Brandon M. Collins, Eric Biber, and Peter Z. Fulé. 2016. U.S. federal fire and  
757 forest policy: emphasizing resilience in dry forests. *Ecosphere* 7 (11):e01584.  
758 <https://doi.org/https://doi.org/10.1002/ecs2.1584>.
- 759 Su, Yu-Sung, and Masanao Yajima. 2014. R2jags: A package for running jags from R. R package  
760 version 3.3.0.
- 761 Sutherland, William J., Ian Newton, and Rhys E. Green. 2004. *Bird ecology and conservation: a*  
762 *handbook of techniques*. New York, New York, USA.: Oxford University Press.

763 Team, R Core. 2013. "R: A language and environment for statistical computing." In. Vienna,  
764 Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.

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

767 Veech, Joseph A., and Thomas O. Crist. 2007. Habitat and climate heterogeneity maintain beta-  
768 diversity of birds among landscapes within ecoregions. *Global Ecology and*  
769 *Biogeography* 16 (5):650-656. [https://doi.org/https://doi.org/10.1111/j.1466-](https://doi.org/https://doi.org/10.1111/j.1466-8238.2007.00315.x)  
770 [8238.2007.00315.x](https://doi.org/https://doi.org/10.1111/j.1466-8238.2007.00315.x).

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

775 Wiens, J. A., and J. T. Rotenberry. 1985. Response of Breeding Passerine Birds to Rangeland  
776 Alteration in a North American Shrubsteppe Locality. *Journal of Applied Ecology* 22  
777 (3):655-668.

778 Wilson, Christopher W., Ronald E. Masters, and George A. Bukenhofer. 1995. Breeding bird  
779 response to pine-grassland community restoration for red-cockaded woodpeckers. *The*  
780 *Journal of Wildlife Management* 59 (1):56-67. <https://doi.org/10.2307/3809116>.

781

782

783 **Tables**

784 Table 1. Predicted species-specific responses to fire by life history traits based on published

785 literature and reviewed in Birds of the World (Billerman et al. 2020).

<b>Life History Trait</b>		
<b>Foraging</b>	<b>Nesting</b>	
	<i>Cavity</i>	<i>Open-cup</i>
Aerial insectivore	<p><i>Prediction:</i> positive</p> <p><i>Rationale:</i> increased foraging opportunities due to reduction in forest canopy and increase in available nesting cavities.</p> <p><i>Species:</i> ash-throated flycatcher, purple martin, tree swallow, violet-green swallow, mountain bluebird, white-throated swift, western flycatcher</p>	<p><i>Prediction:</i> moderate positive</p> <p><i>Rationale:</i> decreases in canopy cover, which provides more space for foraging maneuvers.</p> <p><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</p>
Bark insectivore	<p><i>Prediction:</i> strong positive</p> <p><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.</p> <p><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</p>	None in study.
Canopy foliage insectivore	<p><i>Prediction:</i> mixed</p> <p><i>Rationale:</i> increased nest availability with increases in dead portions of trees, but reductions in food resources of live foliage and bark.</p>	<p><i>Prediction:</i> negative</p> <p><i>Rationale:</i> reduced nesting and foraging substrate due to desiccation of foliage</p>

	<p><i>Species:</i> black-capped chickadee, mountain chickadee</p>	<p><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, bushtit</p>
Shrub or ground insectivore	<p><i>Prediction:</i> positive <i>Rationale:</i> increased nest availability with increases in dead portions of trees, increased foraging substrate of open ground.</p> <p><i>Species:</i> rock wren, house wren, western bluebird</p>	<p><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</p> <p><i>Species:</i> American robin, Swainson's thrush, orange-crowned warbler, MacGillivray's warbler, Wilson's warbler, vesper sparrow, Lincoln's sparrow</p>
Omnivore	<p><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</p> <p><i>Species:</i> Northern flicker, pileated woodpecker, red-naped sapsucker</p>	<p><i>Prediction:</i> Neutral <i>Rationale:</i> generalist foraging strategies for these species were expected to result in minimal changes</p> <p><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</p>

787 Table 2. Locations, areas, sampling distributions, and historical fire regime, for study units  
 788 where avian community changes in relation to prescribed fire were studied on 7 National Forests  
 789 in the Interior West.

National Forest, State	Unit pair	Number of survey points; unit area (ha)		Historical fire regime
		Treatment	Control	
Payette, Idaho	1	20; 210	20; 224	mixed severity
	2	20; 280	20; 220	
	3	11; 248	10; 216	
Okanogan-Wenatchee, Washington	4	20; 400	20; 369	mixed severity
	5	20; 392	20; 342	
	6	20; 253	20; 351	
San Juan, Colorado	7	32; 179	25; 265	mixed severity
	8	21; 186	21; 173	
Kaibab, Arizona	9	40; 396	50; 486	low severity
Gila, New Mexico	10	25; 261	25; 244	low severity
Apache-Sitgreaves, Arizona	11	29; 247	29; 285	low severity
Coconino, Arizona	12	40; 402	40; 404	low severity

Table 3. Treatment and sampling timing at 24 study units established for the primary analysis of avian community changes with prescribed fire at 7 National Forests in the Interior West.

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

## Figure Legends

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

Figure 2. Composite burn index (CBI) frequency distributions by national forest study location: Okanagan-Wenatchee in Washington (OKWA), Payette NF in Idaho (PAID), San Juan NF in Colorado (SJCO), Apache-Sitgreaves NF in Arizona (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.

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

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

Estimates from a primary model (A, B) are compared with those from supplemental models that included data from additional years and a Markovian persistence effect (C) or separated effects by post-treatment year (D, E). Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with treatment application, whereas CBI (composite burn index) relationships quantify the post-treatment correlation only.

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

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

Figure 7. Species richness estimates and 90% BCIs for surveyed points along burn severity (CBI) gradients estimated before (left column) and after (right column) prescribed fire

treatments. Locations appearing in the top row historically experienced mixed-severity fire regimes (Okanagan-Wenatchee [OKWA], Payette [PAID], and San Juan [SJCO] National Forests), whereas locations in the bottom panels experienced low-severity regimes (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.

# Figures



**Figure 1**

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

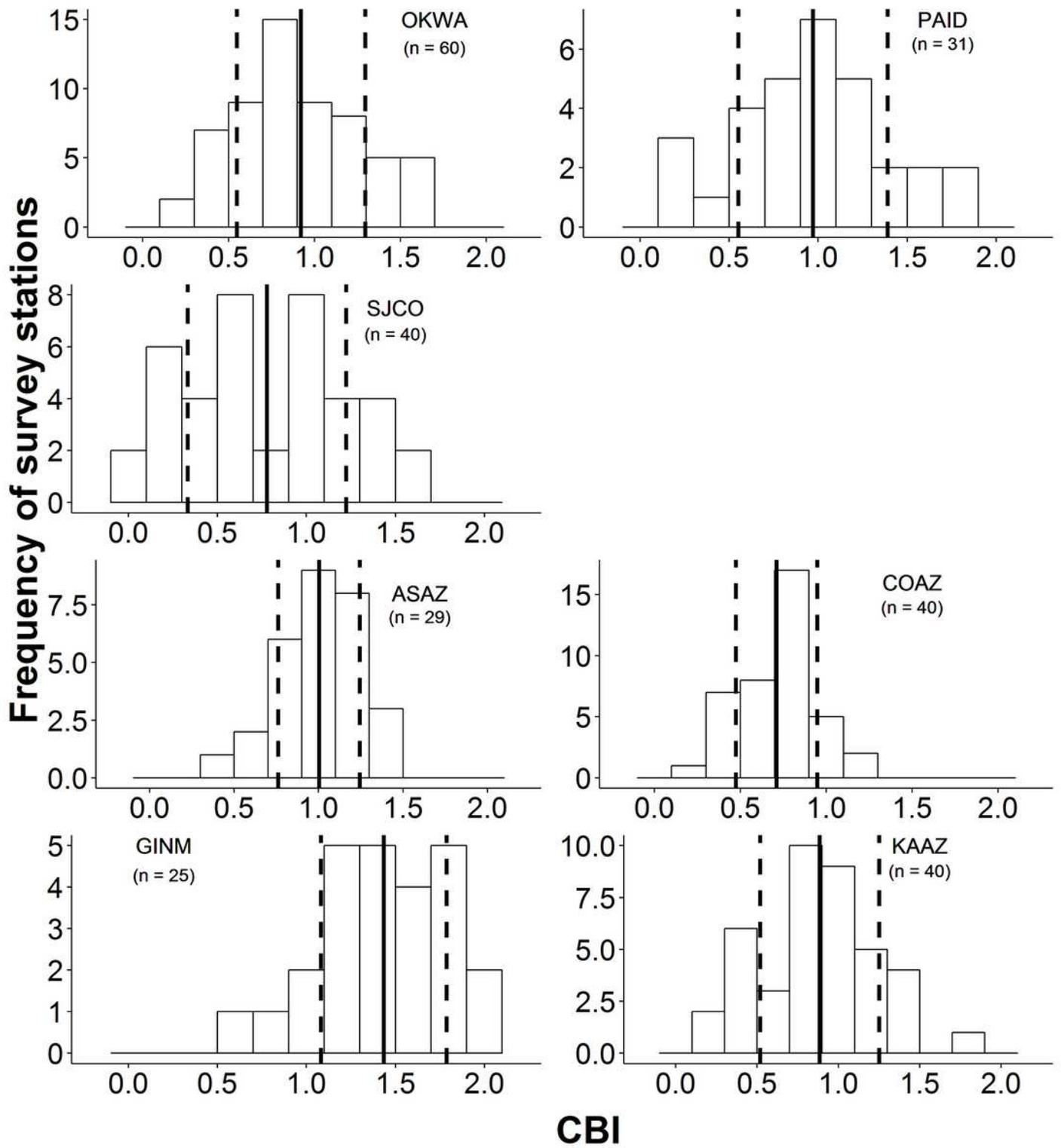


Figure 2

Composite burn index (CBI) frequency distributions by national forest study location: Okanagan-Wenatchee in Washington (OKWA), Payette NF in Idaho (PAID), San Juan NF in Colorado (SJCO), Apache-Sitgreaves NF in Arizona (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.

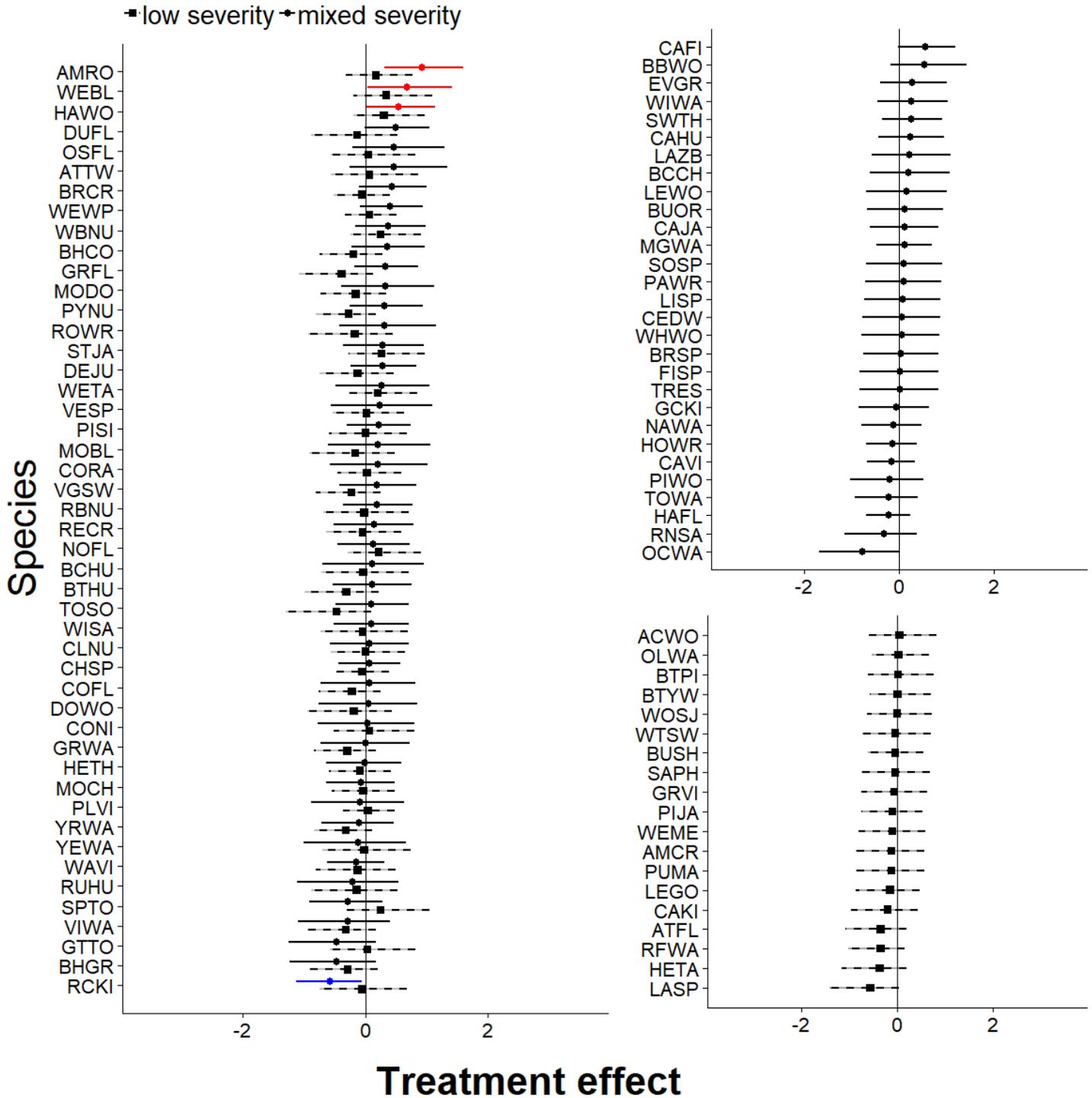
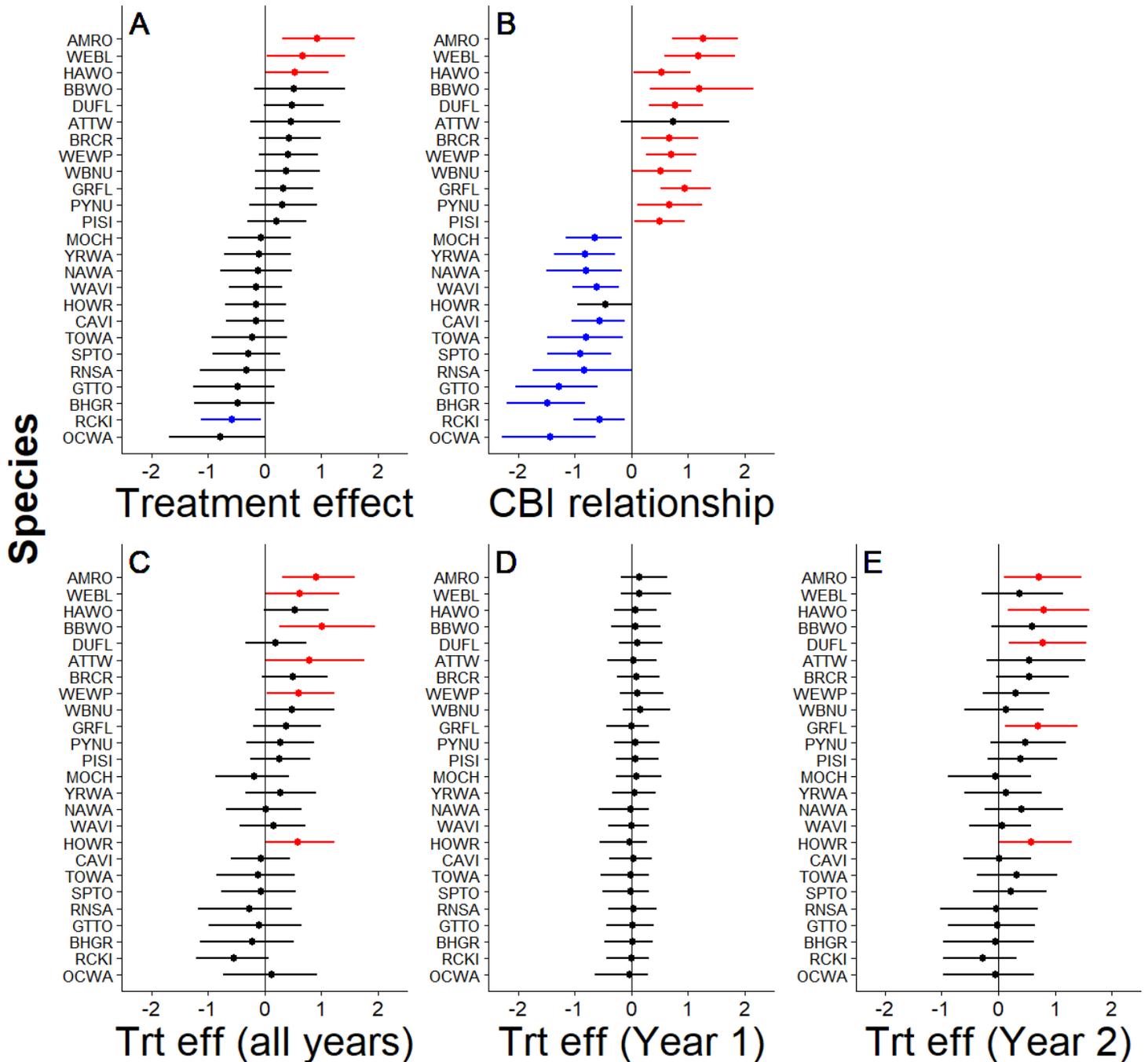


Figure 3

Parameter estimates (posterior median) and 90% BCIs describing treatment effects ( $\beta_{(CBI \times PER)}$  from Equation 3). Estimates are for locations with historically mixed-severity (circles with solid lines) and low-severity (squares with dashed lines) fire regimes. The 47 species observed in both fire regimes (left), 29 species observed only in mixed-severity regime locations (upper right), and 19 species observed only in

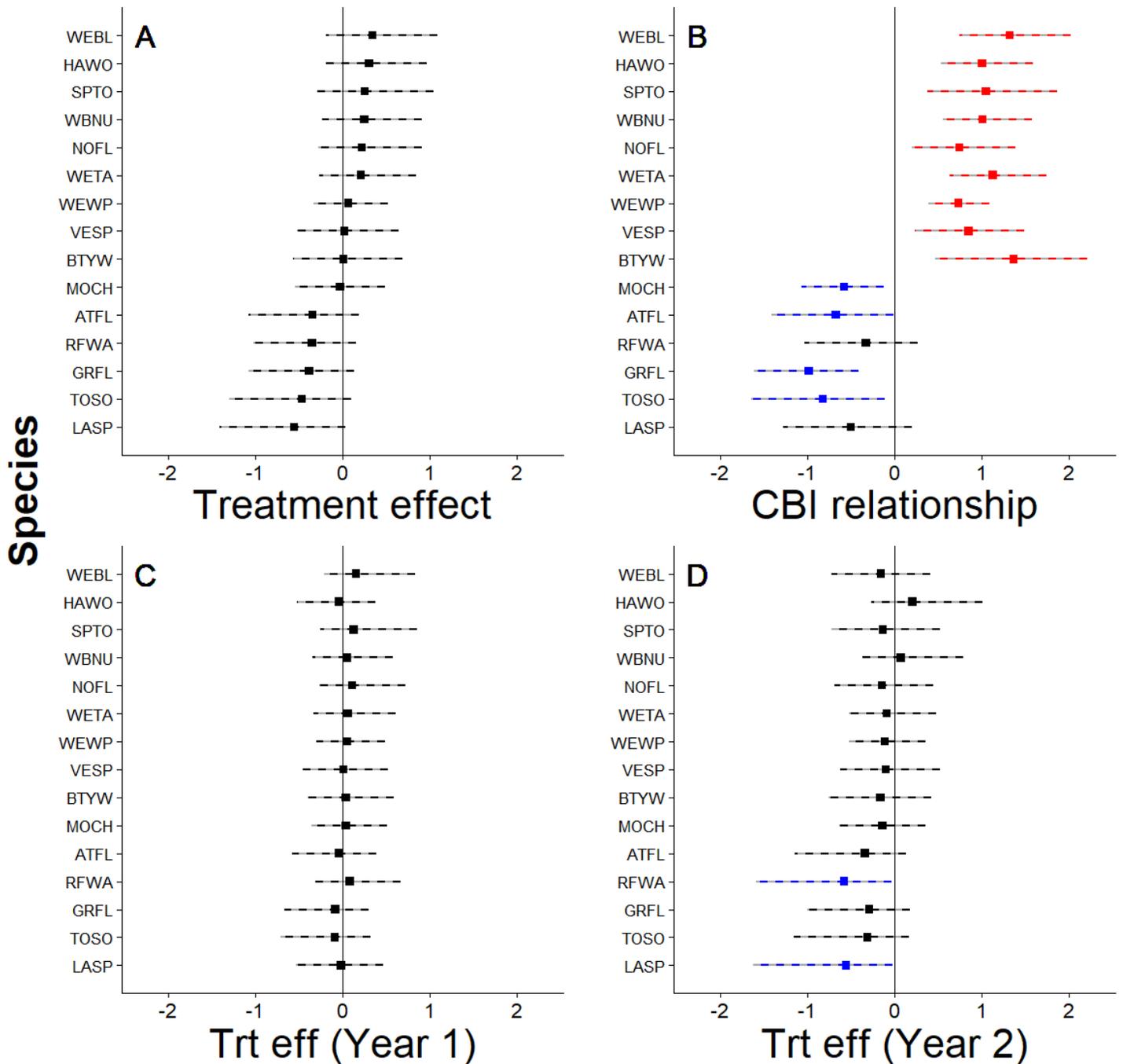
low-severity regime locations (lower right) are shown. Treatment effects describe the extent to which occupancy shifted towards or away from burned sites with treatment application.



**Figure 4**

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

treatment application, whereas CBI (composite burn index) relationships quantify the post-treatment correlation only.



**Figure 5**

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

treatment application, whereas CBI (composite burn index) relationships quantify the post-treatment correlation only.

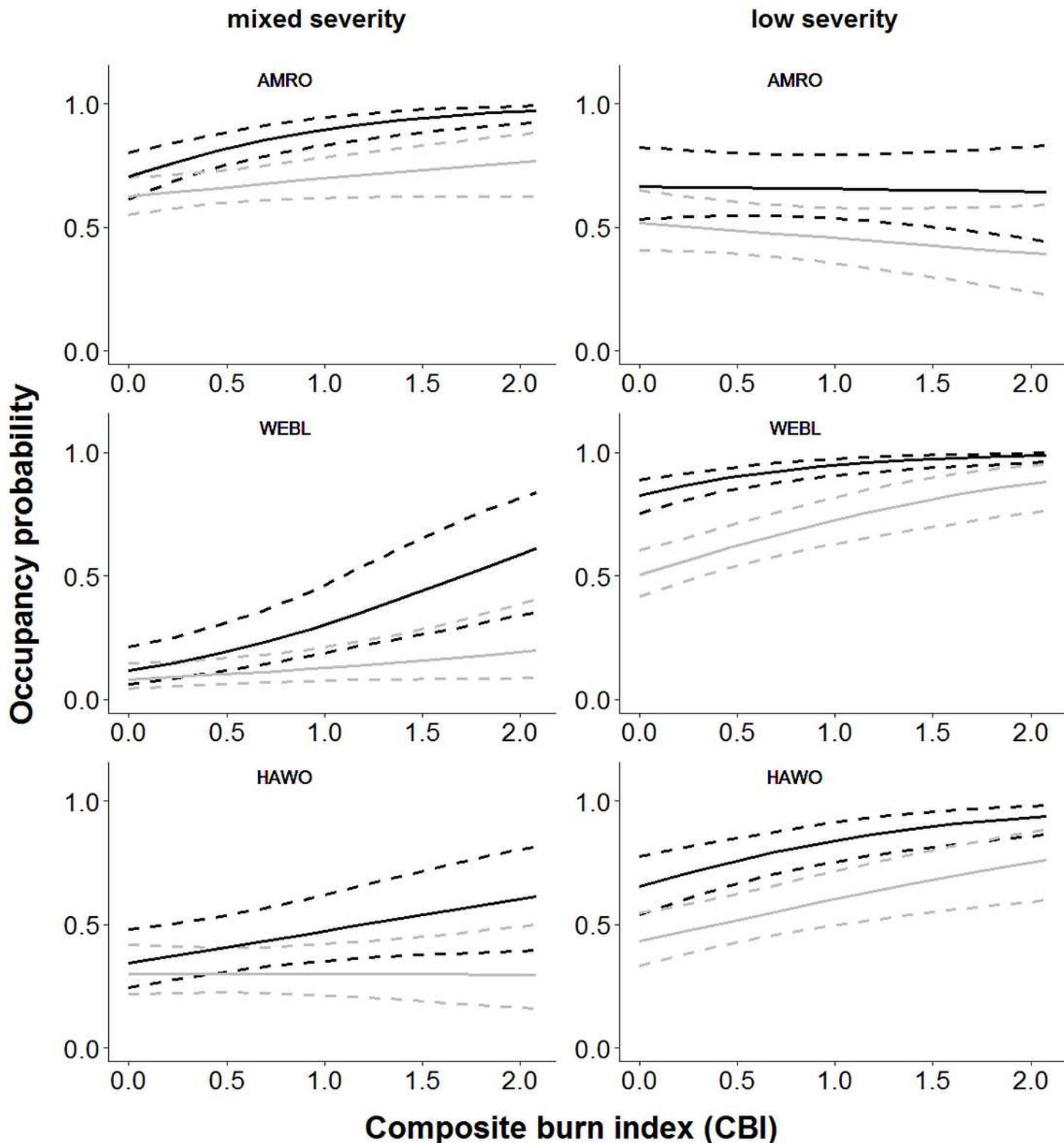
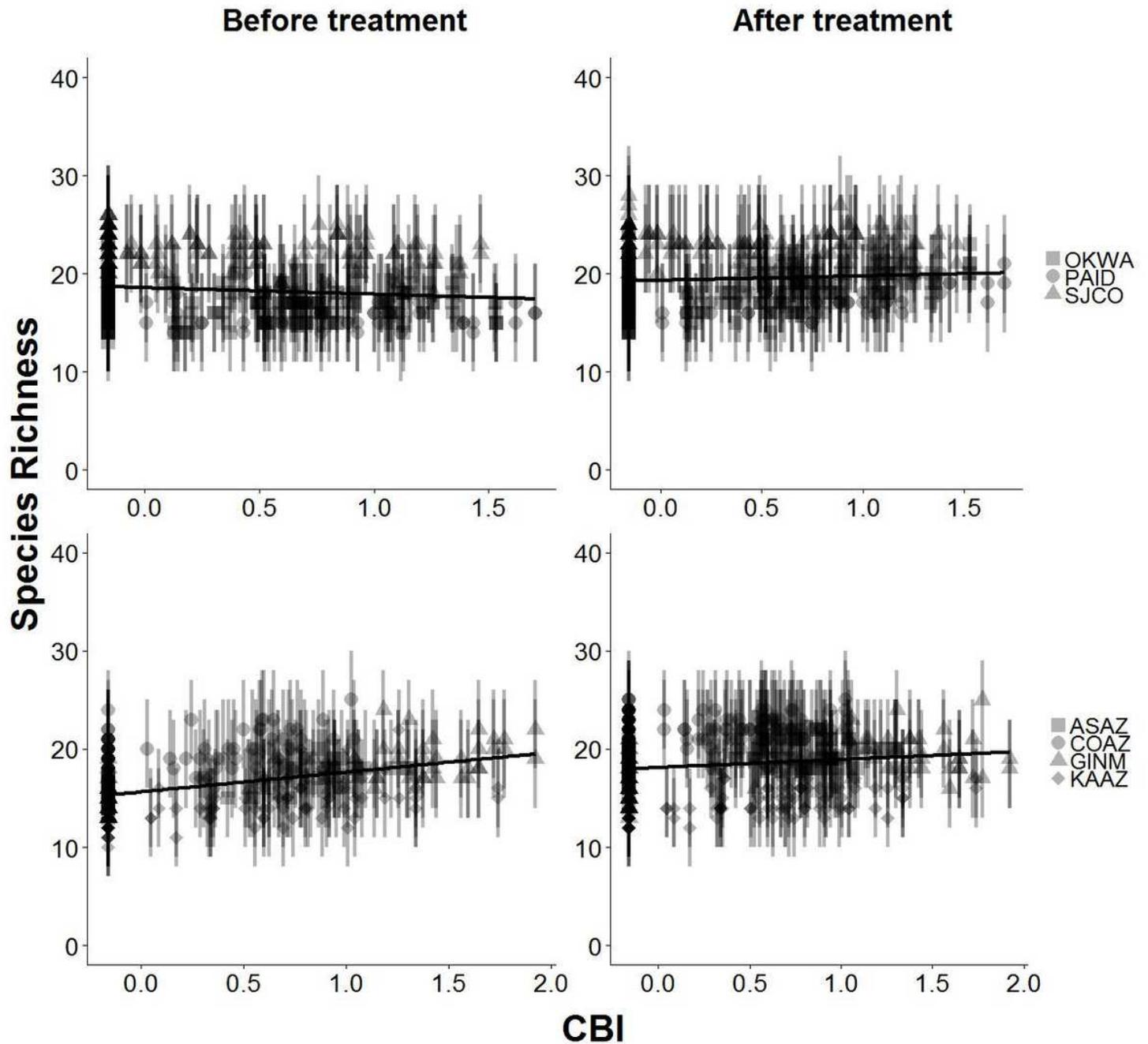


Figure 6

Predicted occupancy with burn severity (CBI) for example species showing treatment responses statistically supported in historically mixed severity regimes but not supported in low severity regimes. Relationships with CBI were estimated before (grey) and after (black) treatment in mixed severity regimes

(left) and low severity regimes (right), and treatment responses are inferred from the change in slope between the two. Intercept terms for calculating model predictions were averaged (mean) across locations within each regime. Full species names are listed in Appendix E.



**Figure 7**

Species richness estimates and 90% BCIs for surveyed points along burn severity (CBI) gradients estimated before (left column) and after (right column) prescribed fire treatments. Locations appearing in the top row historically experienced mixed-severity fire regimes (Okanagan-Wenatchee [OKWA], Payette [PAID], and San Juan [SJCO] National Forests), whereas locations in the bottom panels experienced low-severity regimes (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.

## Supplementary Files

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

- [MSappendices2.pdf](#)