Avian relationships with wildfire at two dry forest locations with different historical fire regimes

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Avian relationships with wildfire at two dry forest locations with different historical fire regimes

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Abstract. Wildfire is a key factor influencing bird community composition in western North American forests. We need to understand species and community responses to wildfire and how responses vary regionally to effectively manage dry conifer forests for maintaining biodiversity. We compared avian relationships with wildfire burn severity between two dry forest locations of Arizona and Idaho. We predicted different responses to wildfire between locations due to regional differences in historical fire regime. We conducted point count surveys for 3 yr following wildfire (Arizona: 1997–1999; Idaho: 2008–2010) and used multispecies hierarchical models to analyze relationships of bird occupancy with burn severity. Consistent with our prediction for mixed-severity fire regimes characterizing the Idaho location, we observed proportionately more positive species occupancy relationships and, consequently, a positive species richness relationship with burn severity in Idaho. We also observed the opposite pattern in Arizona, which was congruent with our prediction for the low-severity fire regime characterizing that location. Cavity nesters and aerial insectivores occupied more severely burned sites following wildfire, corresponding with predicted increases in nesting substrate and foraging opportunities for these species. In contrast, canopy-nesting foliage gleaners and pine seed consumers exhibited negative relationships with burn severity. Our results were consistent with predictions based on species life histories and with patterns from the literature, suggesting generality of observed relationships and locational difference in relationships with wildfire. We therefore suggest that optimal management strategies for maintaining avian diversity could differ regionally. Specifically, intensive fuels management may be ecologically less appropriate for promoting biodiversity in areas such as the Idaho location where mixed-severity wildfires and dense forest stands were historically more common.

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Introduction

Wildfire is a major factor shaping the amount and distribution of biodiversity in forested landscapes of western North America. Some species respond positively to recently burned forests, whereas others respond negatively to wildfire resulting in differences in community composition within burned vs. unburned forests (Saab et al. 2005, Kalies et al. 2010, Fontaine

and Kennedy 2012). Species and community responses to a wildfire depend on its burn severity (fire effects on vegetation; Agee 1993, Smith 2000) and time passed since fire (fire history; Nimmo et al. 2014). Stands that vary in fire history will vary in the species they support (Fontaine et al. 2009). Consequently, landscapes containing a diversity of stands varying in fire history are expected to support the greatest array of species (Clarke 2008, Fontaine and Kennedy 2012). Forest managers aiming to conserve and promote biodiversity must recognize the role of wildfire in maintaining overall diversity by supporting fire-adapted species and communities within forested landscapes. A nuanced understanding of species and community responses to wildfire would allow ecologists to better inform forest management decisions.

Such information would particularly inform ongoing research and debate regarding the ecological role of wildfire and related management strategies in lower elevation dry conifer forests. Such forests have generally been characterized historically by frequent low- or mixed-severity fires (Hessburg et al. 2005). In the Inland Northwest, these fires maintained low and variable tree densities, light and patchy ground fuels, simplified forest structure, and favored fire-tolerant trees, such as ponderosa pine (*Pinus ponderosa*), and a low and patchy cover of associated fire-tolerant shrubs (Hessburg et al. 2005, 2007). Historically, in the Southwest, a drier climate has favored forest stands that were relatively homogenous, were lower in both tree and understory density, were heavily dominated by ponderosa pine, and experienced more frequent and lower severity fires (Moir et al. 1997, Bock and Block 2005). In the central west, moister conditions have encouraged denser stands, more landscape-scale heterogeneity in stand structure, more mixed tree species composition, and less frequent and more mixed-severity wildfire (Schoennagel et al. 2004, Saab et al. 2005). The range and scale of spatial and temporal variability characterizing dry conifer forests is currently under investigation and debate (Pierce et al. 2004, Frechette and Meyer 2009, Williams and Baker 2012, Odion et al. 2014). Nevertheless, researchers generally agree that lower density stands associated with higher frequency; lower severity fires were more widespread in the Southwest (Agee 1993, Schoennagel et al. 2004, Nimmo et al. 2014).

Within the last ~100 yr, anthropogenic fire suppression and concurrent logging, development, livestock grazing, and climate change are thought to have reduced fire frequency and increased severity in lower elevation dry conifer forests (Dale et al. 2001, Brown et al. 2004, Schoennagel et al. 2004). Many forest managers implement fuels reduction treatments of low-severity prescribed fire and timber harvest along with continued suppression of wildfires as part of a large-scale effort aimed at restoring historical fire regimes (Fulé et al. 2012). Some expect this approach to be the best possible strategy for maintaining natural processes in managed ponderosa pine-dominated forests (Miller and Thode 2007, Crimmins et al. 2013). This strategy may be more appropriate in the southwestern United States, where biological communities have experienced more frequent lower severity wildfires (Schoennagel et al. 2004, Bock and Block 2005, Illán et al. 2014). In contrast, central Rocky Mountain forests may benefit from use of more high-severity wildfire to restore historical conditions and maximize biodiversity (Schoennagel et al. 2004, Saab et al. 2005). Central to this debate is our understanding of how organisms respond to wildfire. If historical fire regimes shape wildfire responses, biological relationships with wildfire should vary regionally by fire regime, in which case forest management strategies aimed at promoting biodiversity should reflect these differences.

Birds offer useful opportunities for studying biological wildfire relationships. Avian communities can be surveyed without specialized equipment (Sutherland et al. 2004) and are therefore used to evaluate management strategies aimed at biological conservation (Saab and Powell 2005, Saab et al. 2005). Bird species with different ecological and life history traits are affected differentially by wildfire (Saab and Powell 2005, Smucker et al. 2005, Kotliar et al. 2007, Fontaine and Kennedy 2012, Seavy and Alexander 2014). For example, wildfire can create openings to enhance foraging and nesting opportunities for shrub-nesting and ground-foraging species, and create snags that provide important nesting and foraging resources for cavity-nesting species (Hutto 1995, Kotliar et al. 2002, Saab et al. 2009). In contrast, tree mortality after wildfire reduces resources for canopy-

nesting and foliage-gleaning species (Kotliar et al. 2007, Fontaine et al. 2009). Differences among species in relationships with wildfire and consequent changes in community composition have been documented repeatedly (see reviews by Kalies et al. 2010, Fontaine and Kennedy 2012).

Despite numerous studies of avian wildfire relationships, regional variation in these relationships is poorly understood. Individual studies typically examine population or community relationships at one location at a time (e.g., Smucker et al. 2005, Kotliar et al. 2007). Comparisons across studies reveal some consistencies and also differences between studies in different locations. Potential explanations for differences among studies include differences in burn severity, severity measurements, population parameter measurements, study length, spatial scale, and fire regime (Bock and Block 2005, Saab and Powell 2005, Kalies et al. 2010, Fontaine and Kennedy 2012). Recent reviews emphasize burn severity and methodological factors for explaining differences among studies (Kalies et al. 2010, Fontaine and Kennedy 2012). Regional differences in climate, vegetation structure, and historical fire regime, however, could also be important. Studies comparing patterns among regions that control for methodological factors are needed to understand the role of such variation in shaping avian responses to wildfire.

We compared avian relationships with wildfire between two dry coniferous forest locations of the western United States; one in a southwestern forest and the other in the central Rocky Mountains. We surveyed forests following wildfire at sites distributed along a burn severity gradient and compared avian occupancy relationships with burn severity between the two study locations. We used similar survey protocols at both locations and controlled for remaining differences in methodology by estimating and accounting for study-specific detectability. Given differences in historical fire regime and related vegetation structure, we predicted proportionately more bird species at the Idaho location would relate positively with burn severity, and consequently species richness to relate positively. Conversely, we expected the opposite at the Coconino location. We examined how species and community relationships with burn severity were similar and how they differed between the two locations to evaluate this predic-

tion. Additionally, to understand the mechanistic basis for and generality of community-wide patterns, we considered the consistency of observed relationships with species life history traits and patterns reported in the literature. Finally, we discuss the implications of our results for management of dry conifer forests.

METHODS

Study system

We studied avian occupancy in relation to wildfire at the Payette National Forest (NF) in the central Rocky Mountains of western North America and the Coconino NF in southwestern North America. In both forests, fire suppression began ~100 yr prior to this study, and both were managed for multiple uses, including timber harvest, mining, recreation, livestock grazing, wildlife habitat, and watershed management (Hollenbeck et al. 2013).

Payette National Forest

The Payette NF is located in central Idaho (45°00′30″ N 116°02′30″ W; elevation 1127–2075 m). The prefire canopy was dominated by large (≥23 cm dbh) ponderosa pine trees (>65%; Hollenbeck et al. 2013). Other tree species included Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*P. contorta*), and small patches (<10 ha) of quaking aspen (*Populus tremuloides*) in snowmelt drainages. Common understory species include snowberry (*Symphoricarpos albus*), spirea (*Spirea betulifolia*), Saskatoon serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus virginiana*). The prefire overstory consisted of 33% low (<10%), 41% moderate (≥10–40%), and 26% high (>40%) canopy cover and understory shrub cover averaged 24% (Saab et al. 2009).

The East Zone Complex Fire burned the Payette NF on August–September, 2007 (95,100 ha; Fig. 1). Miller and Thode (2007) describe burn severity classes for dry pine forests based on thresholds of change in normalized burned ratios (ΔNBR) as follows: unburned (<41), low severity (41–176), moderate severity (177–366), and high severity (>366). Following this scheme, forests within the East Zone Complex Fire perimeter on the Payette NF were classified as 9% unburned, 19% low severity, 26% moderate severity, and 46% high severity.
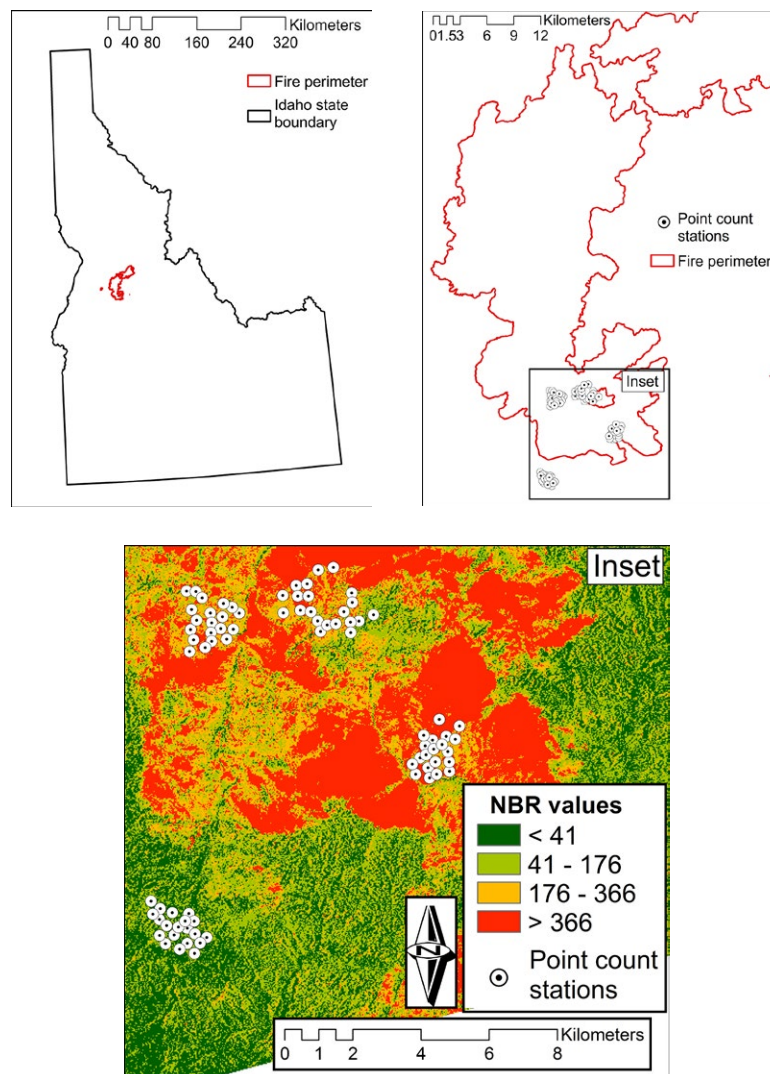
Fig. 1.   Study location, distribution of point count stations, and burn severity map at Payette National Forest, Idaho.

Coconino national forest

The Coconino National Forest is located in north-central Arizona (35°26′00″ N 111°44′49″ W; elevation range 2073–2464 m). The canopy was heavily dominated by large ponderosa pine trees (>80%; Hollenbeck et al. 2013). Other tree species included Gambel oak (*Quercus gambelii*), twoneedle pinyon (*Pinus edulis*), alligator juniper (*Juniperus deppeana*), and one-seed juniper (*J. monosperma*). Understory vegetation included buckbrush (a.k.a. Fendler's Ceanothus; *Ceanothus fendleri*),

rubber rabbitbrush (*Ericameria nauseosa*), and Oregon grape (a.k.a. creeping barberry; *Mahonia repens*). The prefire overstory at the Coconino NF consisted of 1% low (<10%), 61% moderate (≥10–30%), and 38% high (>30%) canopy cover (Coconino National Forest unpublished data accessed October 2014) and understory shrub cover averaged <1% (V. Saab, *unpublished data*). The Horseshoe and Hochderffer fires burned the Coconino NF on May–June, 1996 (3400 and 5300 ha, respectively; Fig. 2). Forests within the two fire
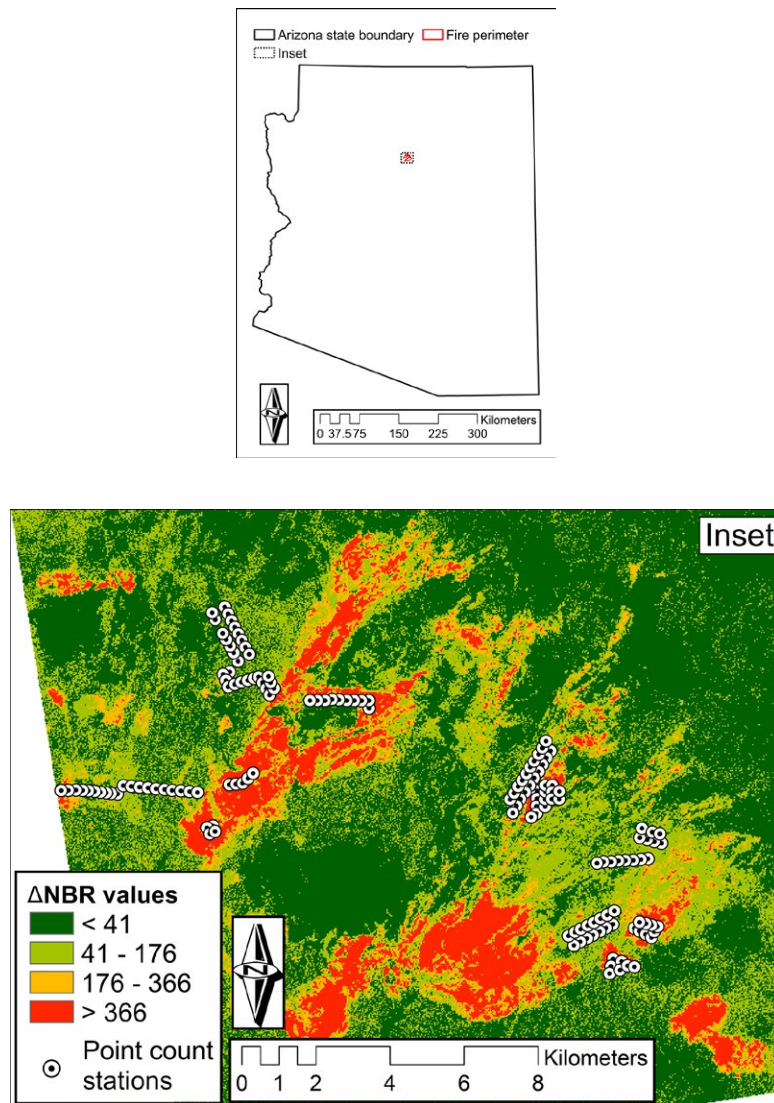
Fig. 2. Study location, distribution of point count stations, and burn severity map at Coconino National Forest, Arizona.

perimeters were 19% unburned, 36% low severity, 20% moderate severity, and 25% high severity.

Data collection

We surveyed bird species using point counts at the Payette and Coconino NFs. We visited point count stations 2–3 times each between 22 May and 3 July over multiple years (twice annually 2008–2010 at Payette NF; thrice annually 1997–1999 at Coconino NF). We began point counts just after the dawn chorus and completed them within 5 h. Observers recorded all birds detected during a 5-min count at the Payette and an 8-min count at the Coconino and estimated distances to each detected individual. Only detections within 100 m of the point were included in this analysis. Our sampling design was a robust design (Pollock 1982) with years as the primary periods and visits within years as the secondary periods.

Table 1. Predicted species-specific responses to fire by life history traits based on published literature (Saab and Powell 2005, Kotliar et al. 2007, Fontaine et al. 2009).

Life history traits	Expected response
Primary cavity-nesting[N], beetle-foragers[F] (i.e., bark-drilling woodpecker species)	Strongly positive due to increases in standing dead wood (snags and dead portions of live trees), in which these species excavate nest cavities and forage for bark- and wood-boring beetle larvae
Secondary cavity-nesting[N]	Positive following increased availability of nest holes excavated by primary cavity nesters (i.e., woodpeckers), assuming other life requisites are present
Foliage and bark-gleaning insectivores[F]	Negative due to desiccation of foliage used for nesting and foraging substrates, especially after high-severity crown fire
Pine seed consumers[F]	Negative due to loss of pine seed production, especially after high-severity crown fire
Shrub- or ground-nesting[N], near-ground insectivores[F]	Positive following regrowth of understory vegetation, which is stimulated by opening of the canopy, particularly at Payette location where shrub understory was prevalent
Aerial insectivores[F]	Positive due to decreases in canopy cover, which provides more space for foraging maneuvers
Open-cup canopy nesting species[N]	Negative due to desiccation of foliage used for nesting, especially after high-severity crown fire

Note: Nesting and foraging traits are indicated by superscript "N" and "F", respectively.

At the Payette location, we established 81 point count stations distributed across five study units (Fig. 1). Point count stations were placed at least 250 m apart and 250 m from study unit boundaries. At the Coconino location, we established 149 point count stations over 15 transect lines with an average of 10 points (range: 3–20) each spaced at 200-m intervals (Fig. 2).

At both locations, point count stations were in areas varying in wildfire burn severity and surveyed for 3 yr following wildfire (2008–2010 at Payette; 1997–1999 at Coconino). We used the ΔNBR index generated from comparison of Landsat TM imagery recorded before (June 14, 1994 at Coconino; August 11, 2005 at Payette) vs. after (June 22, 1997 at Coconino; August 24, 2007 at Payette) wildfire events (MTBS 2012) to quantify burn severity at the point count stations. Raw ΔNBR values were compiled at a 30 × 30 m resolution. We used mean ΔNBR values for 100-m radius neighborhoods centered on point count stations as a covariate of occupancy probabilities during data analysis. In similar habitats, Miller and Thode (2007) found ΔNBR values measured at a resolution similar to those in this study to be closely related with field collected burn severity measurements.

At Payette, two of five study units (31 points) were treated with prescribed fire in 2004 and 2006. Effects of prescribed fire on vegetation are described elsewhere (Saab et al. 2006). The correlation between prescribed fire treatments (1 = treated, 0 = untreated) and wildfire burn severity was low (Pearson's $r = -0.186$, $n = 101$ points), so we had minimal concerns over prescribed fire confounding relationships with burn severity.

Data analysis

We analyzed avian relationships with wildfire using multispecies occupancy models (Gelman and Hill 2007, Royle and Dorazio 2008, Russell et al. 2009). Occupancy models leverage repeat-survey data to estimate species detectability (p) conditional upon occupancy (species occurrence), allowing unbiased estimation of occupancy probabilities (Ψ) given sufficient data (MacKenzie et al. 2002, 2006). We assumed that the occupancy states of species could change among years, but not between visits within a year. We used multispecies occupancy models to estimate species-specific parameters as random variables governed by community-level hyper-parameters. The use of a common distribution among species improves the

precision of species-specific parameter estimates, particularly for rare species (Dorazio et al. 2006, Russell et al. 2009). We excluded raptors, owls, and grouse because they were not readily detectable with our survey methods. We included only species that bred in our study areas. For mobile animals such as birds, detectability (p) estimated with surveys repeated over a season includes information on within-season movement and the observation process (i.e., availability and perceptibility; Chandler and Royle 2013, Amundson et al. 2014). Occupancy probabilities in this study therefore characterize the probability that a surveyed point overlaps at least one home range for a given species.

Predictions for species and communities shaped our analysis. Primarily, because birds have historically experienced more high-severity fire at the Payette compared to the Coconino location, we expected birds would have greater affinity with severely burned forests at Payette. Consequently, we predicted proportionately more positive species relationships and a positive species richness relationship with burn severity at Payette, whereas we predicted the opposite at Coconino. Additionally, to understand the mechanisms underlying community-level patterns, we evaluated predictions for species burn-severity relationships based on life history categories described in the literature (Table 1; Saab and Powell 2005, Kotliar et al. 2007, Fontaine et al. 2009). We expected these predictions to generally describe patterns but recognized that individual species have unique life histories that do not fit perfectly within broad categories. Thus, we considered both general predictions for life history categories and literature on individual species to evaluate the likely generality of observed relationships across locations and regions.

We used a three-dimensional data matrix **y**, where element y_{ijt} was a sum of binary indicators for species detection, rather than the binary indicators of species detection typically used in single- or multispecies occupancy models. When binary indicator of species detection $x_{ijt} = 1$, we detected species i ($i = 1, …, N$) at point count station j ($j = 1, …, J$) during primary sampling occasion year t ($t = 1, …, T$; $T = 3$). Because we did not have covariates that differed for detection between secondary sampling occasions, we analyzed the sum of all binary species i detections over all secondary sampling occasions (s) at each point count station, where $y_{ijt} = \sum_{s=1}^{3} x_{ijts}$ and $y_{ijt} \in \{0,1, …, K\}$ ($K = 2$ at Payette and 3 at Coconino). We modeled the probability of Bernoulli latent variable z_{ijt} for occupancy given probability of occupancy ψ_{ijt} as:

$$[z_{ijt}|\psi_{ijt}] \sim \mathrm{Bern}(\psi_{ijt}) \tag{1}$$

We analyzed relationships between avian occupancy and burn severity for comparisons between our two study locations (Payette and Coconino NFs). For both locations, we modeled occupancy probability ψ_{ijt} for species i at point count station j in year t as a linear function of the covariate for burn severity (ΔNBR). We examined the medians and 95% Bayesian credible intervals (BCI) for this relationship ($\beta_{\Delta\mathrm{NBR}}$) to evaluate statistical support for relationships with burn severity. For numerical reasons, we standardized ΔNBR values using the same scaling constants in both locations to ensure comparability of $\beta_{\Delta\mathrm{NBR}}$ estimates (justified given the similar range of burn severities observed at both locations). We included additional covariates to account for major sources of variation present in each data set. For Coconino data, ψ_{ijt} was partially dependent on the probability of occupancy in the previous year, i.e., we assumed a Markovian process described the current occupancy state. Thus,

$$\mathrm{logit}(\psi_{ijt}) = \begin{cases} \beta_{0,i} + \phi_i \times z_{ij0} + \beta_{\Delta\mathrm{NBR},i} \times \Delta\mathrm{NBR}_j & t = 1 \\ \beta_{0,i} + \phi_i \times z_{ij}(t-1) + \beta_{\Delta\mathrm{NBR},i} \times \Delta\mathrm{NBR}_j & t > 1 \end{cases}$$

$$\tag{2}$$

where $\beta_{0,i}$ is the intercept, ϕ_i is a Markovian parameter for local probability of persistence from the previous year, $z_{ij0} \sim \mathrm{Bern}(\psi_{i0})$ (see Russell et al. 2009), $\beta_{\Delta\mathrm{NBR},i}$ is the burn severity effect, and all three are species-specific normal random effects. The Payette data set contained more inter-annual variability than Coconino data, so we assumed ψ_{ijt} was non-Markovian. Payette sampling was insufficient ($n = 81$ points) to support both year and Markovian effects (a model with both did not converge within a reasonable timeframe and posterior predictive GOF tests (Appendix S1) found little unexplained varia-

tion by a model with only year effects). Thus for Payette data,

$$\text{logit}(\psi_{ijt}) = \beta_{0,it} + \beta_{\Delta\text{NBR},i} \times \Delta\text{NBR}_j \qquad (3)$$

where $\beta_{0,it}$ was a species-specific and a year-specific normal random effect.

We considered parameters describing burn severity relationships ($\beta_{\Delta\text{NBR},i}$, Eqs. 2 and 3) whose 95% BCIs did not overlap zero to be strongly supported and other relationships as either marginally supported (if posterior mass was mainly positive or negative) or unsupported. We compared relationships between locations for species that had strongly supported relationships at one or both locations. We also highlight species whose relationships were marginally supported at both locations but differed in direction. We mainly compared the direction (positive or negative) of species-specific relationships between locations, but we also evaluated overlap of 95% BCIs between parameter estimates to recognize differences in magnitude. Recognizing the potential for sampling error, we tempered interpretation of strongly supported parameters estimated with small sample sizes (species detected during ≤10 point × year occasions).

In addition to species-specific relationships, we report emergent changes in species richness with burn severity. We calculated species richness (N_{jt}) at each point count station j and year t: $N_{jt} = \sum_{i=1}^{\max(i)} z_{ijt}$. Similar to Russell et al. (2009) and unlike others (Dorazio et al. 2006, Kéry et al. 2009), we did not model unobserved species, so community-level inferences were restricted to the subset of members observed at least once during our studies.

For all models, we modeled the probability of observing species i at point count station j during primary period t, y_{ijt}, given K secondary periods, probability of detection p_i, and occupancy latent state z_{ijt} using a binomial distribution with K trials and probability of success $p_i \times z_{ijt}$:

$$[y_{ijt}|p_i,z_{ijt}] \sim \text{Bin}(K,p_i \times z_{ijt}) \qquad (4)$$

Ninety-five percent BCIs for parameters relating burn severity with detection probability overlapped 0 for all species for both data sets, and adding this parameter did not improve mod-

el fit to the Coconino data set (deviance information criterion increased by 2529.9). Therefore, we only modeled detectability as a species-specific normal random effect $b_{0,i}$:

$$\text{logit}(p_i) = b_{0,i} \qquad (5)$$

where p_i is the probability of detecting species i during a survey of a given point count station in a given year when the species was present. 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 and Royle 2005, Kéry et al. 2009). We assumed a multivariate logit-scale normal distribution, where only the non-zero off-diagonal elements of the variance–covariance matrix for occupancy and detection parameters were between $b_{0,i}$ and $\beta_{0,i}$.

We partly accounted for differences in survey protocol between locations (i.e., differences in point count duration and number of surveys per year) by running separate analyses by location and allowing for different numbers of secondary periods with our statistical models. Nevertheless, because we did not model unobserved species, longer point count duration and more repeat surveys increased chances of observing rare species, potentially elevating species richness estimates at Coconino relative to Payette. These differences were of minor importance, however, given our interest in comparing burn severity relationships rather than overall occurrence rates or species richness.

We sampled posterior parameter distributions for all models using either WinBUGS v. 1.4.3 (Lunn et al. 2000) or JAGS v. 3.3.0 (Plummer 2003) programmed with associated packages (R2WinBUGS and R2jags; Sturtz et al. 2005, Su and Yajima 2014) from R (R Core Team 2013). We used independent noninformative priors for all parameters (for priors, see Appendix S2; for model code, see Appendix S3). We ran 3–6 parallel MCMC chains (Coconino: three chains of length 40,000 *it*, burn-in 25,000 *it*, and thinning 10 *it*; Payette: six chains of length 51,000 *it*, burn-in 1000 *it*, and thinning 100 *it*) to sample posterior distributions until $n_{\text{effective}} \geq 100$ and $\hat{R} \leq 1.1$ for all parameters (Gelman and Hill 2007). We ex-

Table 2. Species recorded in either the Payette National Forest, Idaho, or the Coconino National Forest, Arizona.

| Species: common name (taxonomic name) | Code | No. point × year occasions detected | | Traits | | |
		Idaho, postwildfire (max = 243)	Arizona, postwildfire (max = 447)	Forage	Nest layer	Nest type
Mourning Dove (*Zenaida macroura*)	MODO	7	138	OM	SH	O
Common Nighthawk (*Chordeiles minor*)	CONI	2	8	AI	GR	O
Broad-tailed Hummingbird (*Selasphorus platycercus*)	BTAH	3	159	NE	CA	O
Rufous Hummingbird (*Selasphorus rufus*)	RUHU	1	2	NE	CA	O
Lewis' Woodpecker (*Melanerpes lewis*)	LEWO	0	8	AI	CA	Cs
Acorn Woodpecker (*Melanerpes formicivorus*)	ACWO	0	8	OM	CA	Cp
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	WISA	1	1	OM	CA	Cp
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	RNSA	2	0	OM	CA	Cp
Downy Woodpecker (*Picoides pubescens*)	DOWO	1	2	BG	CA	Cp
Hairy Woodpecker (*Picoides villosus*)	HAWO	68	193	BD	CA	Cp
American Three-toed Woodpecker (*Picoides dorsalis*)	ATTW	1	8	BD	CA	Cp
Black-backed Woodpecker (*Picoides arcticus*)	BBWO	6	0	BD	CA	Cp
Northern Flicker (*Colaptes auratus*)	NOFL	23	118	OM	CA	Cp
Pileated Woodpecker (*Dryocopus pileatus*)	PIWO	8	0	OM	CA	Cp
Olive-sided Flycatcher (*Contopus cooperi*)	OSFL	5	37	AI	CA	O
Western Wood-pewee (*Contopus sordidulus*)	WEWP	7	236	AI	CA	O
Hammond's Flycatcher (*Empidonax hammondii*)	HAFL	133	0	AI	CA	O
Dusky Flycatcher (*Empidonax oberholseri*)	DUFL	55	0	AI	SH	O
Cordilleran Flycatcher (*Empidonax occidentalis*)	COFL	0	8	AI	CA	Cs†
Ash-throated flycatcher (*Myiarchus cinerascens*)	ATFL	0	2	AI	SH	Cs
Cassin's Kingbird (*Tyrannus vociferans*)	CAKI	0	2	AI	CA	O
Plumbeous Vireo (*Vireo plumbeus*)	PLVI	0	176	FI	CA	O
Cassin's Vireo (*Vireo cassinii*)	CAVI	39	0	FI	CA	O
Hutton's Vireo (*Vireo huttoni*)	HUVI	0	1	FI	CA	O
Warbling Vireo (*Vireo gilvus*)	WAVI	52	2	FI	CA	O
Gray Jay (*Perisoreus canadensis*)	GRAJ	3	0	OM	CA	O
Pinyon Jay (*Gymnorhinus cyanocephalus*)	PIJA	0	64	OM	CA	O
Steller's Jay (*Cyanocitta stelleri*)	STJA	11	234	OM	CA	O
Clark's Nutcracker (*Nucifraga columbiana*)	CLNU	15	17	PSC	CA	O
American Crow (*Corvus brachyrhynchos*)	AMCR	0	9	OM	CA	O
Common Raven (*Corvus corax*)	CORA	2	22	OM	CA	O
Violet-green Swallow (*Tachycineta thalassina*)	VGSW	0	36	AI	CA	Cs
Mountain Chickadee (*Poecile gambeli*)	MOCH	96	213	FI	CA	Cs
Red-breasted Nuthatch (*Sitta canadensis*)	RBNU	150	0	BG	CA	Cs‡
White-breasted Nuthatch (*Sitta carolinensis*)	WBNU	17	214	BG	CA	Cs
Pygmy Nuthatch (*Sitta pygmaea*)	PYNU	0	116	BG	CA	Cs‡
Brown Creeper (*Certhia americana*)	BRCR	8	34	BG	CA	Cs
Rock Wren (*Salpinctes obsoletus*)	ROWR	16	7	GI	GR§	Cs§
House Wren (*Troglodytes aedon*)	HOWR	14	6	GI	CA	Cs
Golden-crowned Kinglet (*Regulus satrapa*)	GCKI	0	1	FI	CA	O
Ruby-crowned Kinglet (*Regulus calendula*)	RCKI	5	3	FI	CA	O
Western Bluebird (*Sialia mexicana*)	WEBL	1	327	GI	CA	Cs
Mountain Bluebird (*Sialia currucoides*)	MOBL	34	7	AI	CA	Cs

Table 2. Continued

Species: common name (taxonomic name)	Code	No. point × year occasions detected		Traits		
		Idaho, postwildfire (max = 243)	Arizona, postwildfire (max = 447)	Forage	Nest layer	Nest type
Townsend's Solitaire (*Myadestes townsendi*)	TOSO	24	38	AI	GR	O
Swainson's Thrush (*Catharus ustulatus*)	SWTH	21	0	FI	SH	O
Hermit's Thrush (*Catharus guttatus*)	HETH	44	7	GI	SH	O
American Robin (*Turdus migratorius*)	AMRO	99	162	GI	CA	O
Cedar Waxwing (*Bombycilla cedrorum*)	CEDW	0	1	FI	CA	O
Olive Warbler (*Peucedramus taeniatus*)	OLWA	0	1	FI	CA	O
Orange-crowned Warbler (*Oreothlypis celata*)	OCWA	3	0	FI	GR	O
Nashville Warbler (*Oreothlypis ruficapilla*)	NAWA	11	0	FI	GR	O
Virginia's Warbler (*Oreothlypis virginiae*)	VIWA	0	8	GI	GR	O
MacGillivray's Warbler (*Geothlypis tolmiei*)	MGWA	60	0	FI	SH	O
Yellow Warbler (*Setophaga petechia*)	YWAR	1	0	FI	SH	O
Yellow-rumped Warbler (*Setophaga coronata*)	YRWA	185	251	FI	CA	O
Grace's Warbler (*Setophaga graciae*)	GRWA	0	135	FI	CA	O
Townsend's Warbler (*Setophaga townsendi*)	TOWA	34	0	FI	CA	O
Green-tailed Towhee (*Pipilo chlorurus*)	GTTO	0	1	OM	SH	O
Spotted Towhee (*Pipilo maculatus*)	SPTO	1	1	OM	GR	O
Chipping Sparrow (*Spizella passerina*)	CHSP	212	129	OM	SH¶	O
Brewer's Sparrow (*Spizella breweri*)	BRSP	3	1	OM	SH	O
Vesper Sparrow (*Pooecetes gramineus*)	VESP	0	4	OM	GR	O
Lark Sparrow (*Chondestes grammacus*)	LASP	0	12	OM	GR	O
Song Sparrow (*Melospiza melodia*)	SOSP	6	2	GI	SH	O
Lincoln's Sparrow (*Melospiza lincolnii*)	LISP	5	0	OM	GR	O
Dark-eyed Junco (*Junco hyemalis*)	DEJU	119	283	OM	GR	O
Hepatic Tanager (*Piranga flava*)	HETA	0	10	OM	CA	O
Summer Tanager (*Piranga rubra*)	SUTA	0	2	FI	CA	O
Western Tanager (*Piranga ludoviciana*)	WETA	190	283	FI	CA	O
Black-headed Grosbeak (*Pheucticus melanocephalus*)	BHGR	19	24	OM	CA	O
Lazuli Bunting (*Passerina amoena*)	LAZB	71	0	OM	SH	O
Eastern Meadowlark (*Sturnella magna*)	EAME	0	2	GI	GR	O
Western Meadowlark (*Sturnella neglecta*)	WEME	0	26	GI	GR	O
Brown-headed Cowbird (*Molothrus ater*)	BHCO	0	52	OM	–#	–#
Bullock's Oriole (*Icterus bullockii*)	BUOR	0	1	OM	CA	P
House Finch (*Haemorhous mexicanus*)	HOFI	0	12	OM	CA	O
Cassin's Finch (*Haemorhous cassinii*)	CAFI	103	4	OM	CA	O
Red Crossbill (*Loxia curvirostra*)	RECR	59	33	PSC	CA	O
Pine Siskin (*Spinus pinus*)	PISI	94	54	PSC	CA	O
Lesser Goldfinch (*Spinus psaltria*)	LEGO	0	19	OM	CA	O
Evening Grosbeak (*Coccothraustes vespertinus*)	EVGR	0	8	OM	CA	O

Notes: Species were categorized according to life history traits: foraging (aerial insectivore [AI], bark driller [BD], bark gleaner [BG], foliage insectivore [FI], ground insectivore [GI], nectivore [NE], omnivore [OM], or pine seed consumer [PSC]), nest layer (canopy [CA], shrub [SH], or ground [GR]), and nest type (primary cavity [excavator; Cp], secondary cavity [nonexcavator; Cs], open-cup [O], or pendulum [P]; categories modified from Saab and Powell 2005). Life history categorizations reflect primary foraging and nesting modes.

† Cordilleran Flycatchers use a variety of nest sites, including cavities, root wads, and overhangs (Lowther 2000).

‡ Red-breasted and Pygmy nuthatches are facultative excavators.

§ Rock Wren nest structures are typically placed on or in rock outcrops or cliffs.

¶ Chipping Sparrows nest in both trees and shrubs at Coconino (W. Block, *personal observation*).

Brown-headed Cowbirds are obligate brood parasites.

Table 3. Distribution of point count stations among burn severity categories at two study locations in the Payette National Forest (Idaho) and the Coconino National Forest (Arizona).

	% Points	
Severity class	Payette (n = 90)	Coconino (n = 149)
Unburned (ΔNBR† < 41)	26.4	16.1
Low (ΔNBR = 41–176)	12.7	54.4
Moderate (ΔNBR = 176–366)	39.1	8.7
High (ΔNBR > 366)	18.2	20.8

† ΔNBR = the change in remotely sensed normalized burn ratio from before to after wildfire.
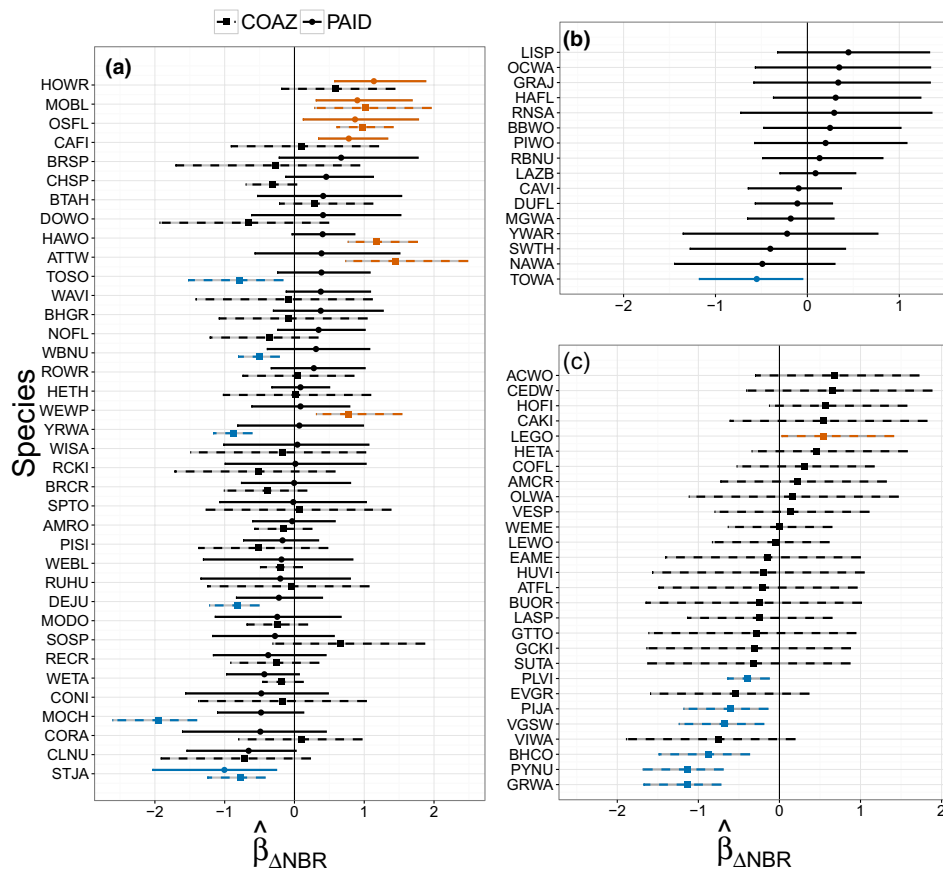
Fig. 3. Posterior parameter estimates (medians and 95% BCIs) describing species occupancy relationships with wildfire burn severity ($\hat{\beta}_{\Delta NBR}$). We compared relationships for the Coconino NF, Arizona (COAZ), and the Payette NF, Idaho (PAID). Panel (a) presents estimates for species observed at both locations. The remaining panels present species only observed at Payette (b) or Coconino (c) locations. Statistically supported positive and negative relationships are colored orange and blue, respectively. We used this information to identify similarities and differences in avian relationships with wildfire between study locations. See Table 2 for common and taxonomic species names.

amined model goodness-of-fit using posterior predictive testing based on both omnibus and targeted descriptions of the data (Appendices S1, S2; Gelman and Hill 2007).
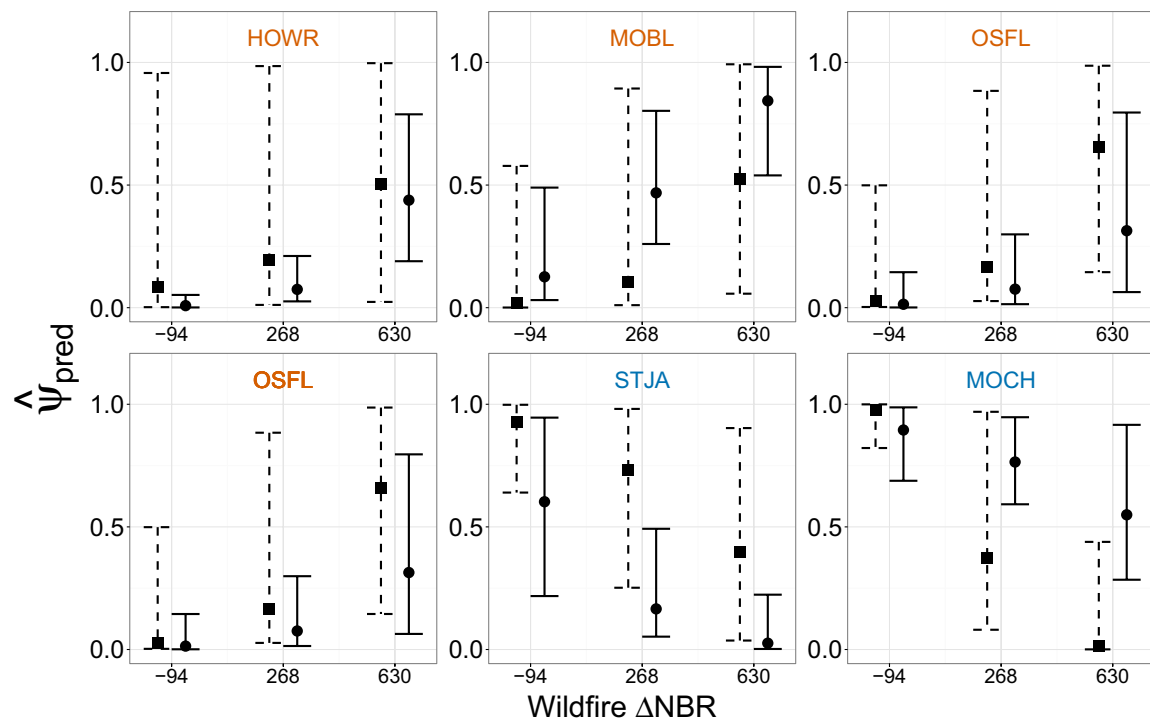
RESULTS

Surveyors detected 81 species: 37 species were

Fig. 4. Predicted occupancy ($\hat{\psi}_{pred}$) relationships with wildfire burn severity (ΔNBR) for six species that exhibited similar relationships at Coconino (squares with dashed lines) vs. Payette (circles with solid lines) locations. Predicted occupancy probabilities are plotted for low burn severity (ΔNBR = −94), average burn severity for Payette sites (ΔNBR = 268), and a high burn severity (ΔNBR = 630). Species plots are arranged to distinguish positive relationships (labeled orange) from negative relationships (labeled blue). Predicted occupancy probabilities are presented to aid interpretation of the magnitude of effect sizes, i.e., how much occupancy changed with varying burn severity. See Table 2 for common and taxonomic species names.

found at both locations, and 16 and 28 species were unique to Payette or Coconino locations, respectively (Table 2). Chipping Sparrow, Western Tanager, Yellow-rumped Warbler, Red-breasted Nuthatch, and Hammond's Flycatcher were detected most frequently (during the most point × year occasions) at the Payette location (see Table 2 for taxonomic names). Western Bluebird, Western Tanager, Dark-eyed Junco, Yellow-rumped Warbler, and Western Wood-peewee were detected most frequently at the Coconino location. Occupancy and detection were correlated at both locations (Payette ρ = 0.71; 95% BCI = 0.37–0.95; Coconino ρ = 0.46; 95% BCI = 0.01–0.74).

Point count stations sampled areas ranging widely in burn severity (Table 3). Detection probability median posterior estimates varied among species (species-specific median poste-

rior p = 0.01–0.49 [min–max] at Coconino sites and 0.02–0.68 at unburned Payette sites; Appendix S4). Posterior predictive tests provided no evidence indicating lack of model fit with respect to differences in apparent occupancy (the proportion of point × year survey occasions a species was detected) among fire conditions. Furthermore, we found evidence for lack of fit with respect to inter-annual variation in apparent occupancy and apparent turnover for only a few species, suggesting our models adequately described the data (Appendices S1, S2).

Relationships with wildfire burn severity

We found both similarities and differences in relationships with wildfire burn severity between the Coconino and Payette locations for the 37 species observed at both locations. Relationships for 21 species (including 13
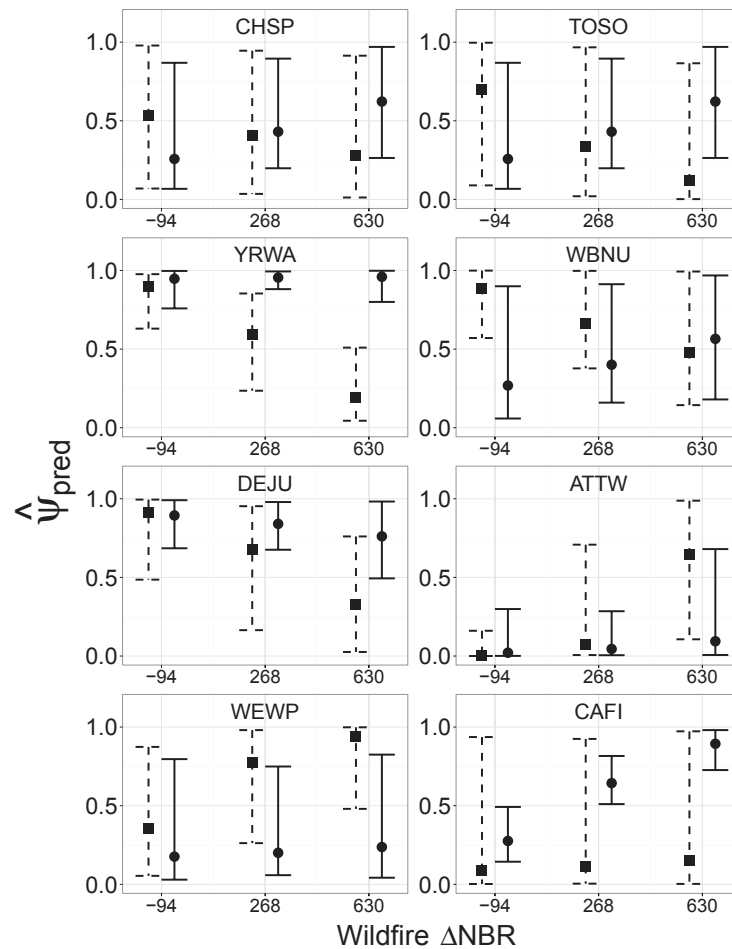
Fig. 5. Predicted occupancy ($\hat{\psi}_{pred}$) relationships with wildfire burn severity (ΔNBR) for eight species that exhibited inconsistent relationships either in direction or magnitude between Coconino (squares with dashed lines) and Payette (circles with solid lines) locations. Predicted occupancy probabilities are plotted for low burn severity (ΔNBR = −94), moderate burn severity (ΔNBR = 268; mean for Payette sites), and high burn severity (ΔNBR = 630). Predicted occupancy probabilities are presented to aid interpretation of the magnitude of effect sizes, i.e., how much occupancy changed with varying burn severity. See Table 2 for common and taxonomic species names.

observed at both locations and 8 observed at only one location) were statistically supported (BCIs did not overlap zero) at one or both locations (Fig. 3). We observed consistently positive relationships with burn severity for House Wren, Mountain Bluebird, Olive-sided Flycatcher, and Hairy Woodpecker, and we observed consistently negative relationships for Steller's Jay and Mountain Chickadee (Figs. 3 and 4).

Other species exhibited relationships that were less consistent between study locations

(Figs. 3 and 5). Townsend's Solitaire exhibited a negative relationship at the Coconino location but a marginally supported positive relationship at the Payette location. Chipping Sparrow exhibited contrasting relationships between locations (negative at Coconino, positive at Payette), although both were marginally supported. Yellow-rumped Warblers, White-breasted Nuthatches, and Dark-eyed Juncos exhibited negative relationships at Coconino, whereas relationships at Payette for these species were weak and unsupported. American Three-toed
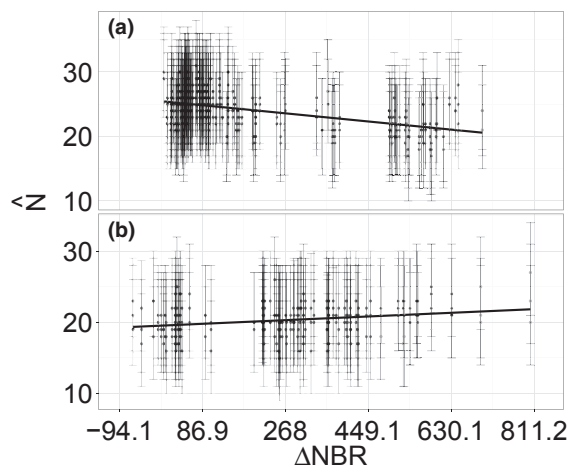
Fig. 6. Species richness posterior estimates ($\hat{N}$; median and 95% BCIs) for point × year survey occasions plotted against wildfire burn severity (ΔNBR). Best-fit lines showing species richness trends are also depicted. We compared species richness trends for sites in the Coconino NF, Arizona (a) vs. the Payette NF, Idaho (b). We used this information to compare community relationships with burn severity between study locations.

Woodpeckers and Western Wood-pewee exhibited positive relationships only at Coconino, although sample sizes were limited at both locations and Payette, respectively. Cassin's Finches were positively related with burn severity only at Payette, but sampling was limited at Coconino. Although consistent in direction, relationships for Hairy Woodpecker and Mountain Chickadee clearly differed in magnitude between locations (Fig. 3).

Of species that were unique to either location, only Lesser Goldfinch at Coconino exhibited a statistically supported positive relationship (Fig. 3). One species only at Payette (Townsend's Warbler) and six species only at Coconino (Plumbeous Vireo, Pinyon Jay, Violet-green Swallow, Brown-headed Cowbird, Pygmy Nuthatch, and Grace's Warbler) exhibited statistically supported negative relationships.

Overall, proportionately more species at the Payette location exhibited statistically supported positive rather than negative relationships with burn severity (four vs. two species, respectively), whereas the opposite was true at the Coconino location (6 positive vs. 12 negative relationships).

Species richness patterns also differed between locations. Species richness tended to increase at the Payette location but decrease at the Coconino location with increasing burn severity (Fig. 6).

DISCUSSION

Observed differences in avian occupancy relationships with burn severity are consistent with expected responses to historical fire regimes and likely reflect life history adaptations to environmental conditions generated by wildfire. Because we used comparable methods and sampled a comparable range of burn severities, variation in observed patterns can be more clearly attributed to differences between locations. Forests of Idaho (i.e., central-northern Rocky Mountains) historically experienced a mixed-severity fire regime (cf. Schoennagel et al. 2004, Saab et al. 2005, Block et al. 2012, Mellen-McLean et al. 2013), whereas those of Arizona (i.e., American Southwest), a low-severity regime (Schoennagel et al. 2004, Bock and Block 2005, Hutto and Belote 2013). Birds in the Payette and Coconino forests likely evolved strategies specific to these locations for when, where, and how to forage and nest. If disturbance (wildfire in this case) results in conditions comparable to what these populations experienced historically, they will likely benefit more from fire. If resulting conditions are not comparable, populations may be reduced or extirpated in affected areas. We predicted that proportionately fewer species would respond positively to severe fire and, consequently, that species richness would decline with increasing burn severity in areas characterized by a low-severity fire regime. In contrast, we predicted the opposite in areas with historically mixed-severity fire regimes. Our results were consistent with these predictions.

Species relationships with burn severity and differences in relationships between locations were generally consistent with species life histories. Wildfire benefits species with certain life history traits, and these species tend to associate with severe burns. In contrast, species with life histories that confer negative responses to wildfire will generally tend to be less prevalent in the most severely burned habitats. The consistency of observed relationships with species life

history traits suggests some generality of species relationships, which are foundational to community patterns.

Consistency with life history and generality of observed patterns

By comparing only two locations, our inferences were limited by lack of replication. Such limitations are pervasive for studies of postfire ecology given the unpredictability of wildfire and infeasibility of experimental study. Nevertheless, species relationships with burn severity observed here were consistent with species life histories and relationships reported in the literature (Smucker et al. 2005, Kotliar et al. 2007, Russell et al. 2009, Fontaine and Kennedy 2012, Seavy and Alexander 2014), suggesting some generality of observed patterns. Because species relationships are foundational to community patterns, consideration of species relationships suggests underlying mechanisms and generality for community patterns.

Hairy and American Three-toed Woodpeckers, both bark-drilling species, tended to relate positively with burn severity, congruent with their reliance on resources enhanced by wildfire: standing dead wood for nesting, and bark and wood-boring beetle larvae (e.g., *Scolytidae* and *Cerambycidae*, respectively) for food (Covert-Bratland et al. 2006). Although sample sizes were limited for American Three-toed Woodpecker, our results were consistent with those from a Colorado study (Kotliar et al. 2008). Positive relationships for bark-drilling species in this and other studies (Kotliar et al. 2008, Saab et al. 2009) suggest generality of the direction of wildfire responses for this group, although the magnitude of responses may vary.

Consistent with our predictions and other studies (Kotliar et al. 2002, Smucker et al. 2005, Russell et al. 2007, Fontaine and Kennedy 2012), secondary cavity-nesting species (House Wren and Mountain Bluebird) and aerial insectivores (Mountain Bluebird and Olive-sided Flycatcher) exhibited positive relationships with burn severity, suggesting generality of these relationships. Western Wood-peewee exhibited a positive relationship at the Payette location only, but sampling was limited at Coconino. Violet-green Swallows forage above the canopy rather than in canopy openings and do not necessarily use woodpecker-excavated cavities for nesting (Brown et al. 2011), so wildfire may affect this species differently than other secondary cavity-nesting aerial insectivores.

Some species that nest in cavities but require live substrate for foraging exhibited negative relationships with burn severity (Mountain Chickadee, White-breasted Nuthatch, and Pygmy Nuthatch). Relationships for these species were more strongly and definitively negative at Coconino, however, and are also mixed across studies (Smucker et al. 2005, Kotliar et al. 2007, Russell et al. 2007, Fontaine and Kennedy 2012, Seavy and Alexander 2014). Mixed responses to wildfire and other natural disturbance may reflect a mix of lost foraging opportunities and gained nesting opportunities (Saab et al. 2007, Norris and Martin 2010). Our results suggest these species may adjust their foraging in response to wildfire more effectively at locations where they are more accustomed to high-severity fire.

Open-cup canopy-nesting species that forage in live trees (Townsend's Warbler at Payette; Yellow-rumped Warbler, Grace's Warbler, and Plumbeous Vireo at Coconino) generally exhibited negative relationships with burn severity. These relationships were consistent with our predictions and other studies (Smucker et al. 2005, Kotliar et al. 2007, Fontaine and Kennedy 2012).

Negative relationships with burn severity also followed predictions for other open-cup canopy-nesting species, Stellar's Jay and Pinyon Jay. Pine seed foraging by Pinyon Jays may also contribute to negative wildfire responses. Pinyon Jays, however, have a diverse diet (Balda 2002) and positive or negative relationships with wildfire are not widely observed (e.g., none reported by Kalies et al. 2010, Fontaine and Kennedy 2012). As generalist foragers, Steller's Jay may take advantage of food resources generated by fire in some cases, possibly explaining positive relationships with relatively moderate burn severity levels reported elsewhere (Kotliar et al. 2007).

Finches as a group tended to exhibit positive relationships with burn severity at the locations where they were relatively common (Cassin's Finch at Payette; House Finch and Lesser Goldfinch at Coconino), a pattern consistent with the literature (Saab et al. 2005, Smucker et al. 2005, Fontaine and Kennedy 2012, Seavy and Alexander 2014). Finches generally favor open-canopy

forests and frequently forage on the ground or on seeds of herbaceous vegetation whose growth is stimulated by fire (Hahn 1996, Hutto et al. 2014, Watt and Willoughby 2014).

Relationships with burn severity exhibited by species that nest and forage in the understory were inconsistent between locations and tended to be more negative at Coconino. A relatively dense understory layer at the Payette location provided for relatively fast regrowth (cf. Saab et al. 2006), potentially providing more nesting and foraging opportunities for species such as Dark-eyed Junco, Chipping Sparrow, and Townsend's Solitaire. In contrast, the relative lack of a substantial shrub layer at the Coconino location (cf. Saab et al. 2006) may explain their more negative relationships with burn severity in the Arizona forest. Positive relationships for shrub-associated species with low-to-moderately burned habitats are reported in other forests with mixed-severity fire regimes (Smucker et al. 2005, Fontaine and Kennedy 2012). Foraging resources for Townsend's Solitaire, however, are not necessarily tied to shrubs (Bowen 1997), so other mechanisms related to food may be more important for this species.

Brown-headed Cowbird, an obligate brood parasite, favors moderately open habitats with tall perches for locating potential hosts (Lowther 1993, Hauber and Russo 2000). Burned forests provide such features, but potential host species (i.e., open-cup nesting birds, Lowther 1993), tended to occupy severely burned sites less at the Coconino location. Analysis of long-term data (1997–2006) from the Coconino location showed mixed relationships with burn severity for this species following relationships exhibited by known host species (J. Sanderlin, W. Block, and B. Strohmeyer, *unpublished manuscript*). A mixed relationship with wildfire for Brown-headed Cowbird was also reported in an aspen forest (Dieni and Anderson 1999).

Locational and regional differences

The Coconino wildfire was less severe and burned less area than the Payette wildfire, consistent with their respective historical fire regimes. Species can evolve plasticity in their responses to disturbances that vary in size and severity, as well as different life histories for different disturbance regimes (Lytle 2001, Lytle and Poff 2004). Such processes could explain patterns observed in this study.

Heterogeneity in severity, size, and configuration of burned patches likely differed in ways that could influence species and community responses (e.g., Cullinane-Anthony et al. 2014, Berry et al. 2015). For example, species experiencing a mix of costs and benefits following wildfire (e.g., secondary cavity-nesting foliage insectivores) may benefit greatest from fires that leave mosaics of burned and unburned forest patches capable of fulfilling different habitat requirements (see also Wightman et al. 2010).

Not all species occurred at both locations, and of those that did, initial population size often differed between locations. Regional differences in historical fire regime and vegetation structure could filter for different sets of species in different locations. Additionally, responses to environmental disturbance by rare species (e.g., Cassin's Finch at Coconino) are difficult to detect due to sampling limitations. Conversely, wildfire may affect abundance without affecting occupancy for common species (e.g., Yellow-rumped Warbler at Payette).

Forest structure and composition may underlie some observed differences between Payette and Coconino locations. The Coconino overstory contained more ponderosa pine and the shrub layer was extremely sparse. In contrast, the Payette forest, although dominated by ponderosa pine, also included other conifer species in the overstory and more shrubs in the understory (cf. Saab et al. 2006). Occurrence and demographics of bark and wood-boring beetle species vary with host tree species and with time since wildfire (Smith 2000, Raffa et al. 2008), potentially influencing responses to wildfire by bark-drilling woodpeckers (e.g., Black-backed, Hairy, and American Three-toed Woodpeckers; Smith 2000). As discussed above, differences in structure and composition of the shrub layer likely contributed to differences in occupancy relationships observed for understory nesting or foraging species.

The landscape context may have influenced observed patterns. Wildfires in the surrounding landscape provide alternative breeding locations for fire associates and thus potentially affect their responses at any one location. The number and severity of wildfires surrounding Payette vs. Coconino locations during sampling therefore

represent unexamined factors that could have contributed to observed patterns.

We cannot completely separate the influence of regional differences in historical fire regime from other location-specific characteristics. Many location-specific characteristics, however, are inter-related with fire regime. Regional variation in vegetation structure parallels variation in fire regimes due to both direct effects of fire on vegetation and shared climatic drivers. Fire size, severity, configuration of burned patches, and the number of fires surrounding a location will likely follow the climatic and vegetation drivers that determine fire regime. Prefire species composition may in part be shaped by the historical wildfire patterns specific to a location. Thus, environmental or biological conditions that consistently differ between regions with different fire regimes may suggest mechanisms for regional differences in wildfire responses. Consistent with our results, a literature review restricted to southwestern studies reported more negative than positive avian relationships with high-severity wildfire (Kalies et al. 2010) but another more geographically extensive review did not (Fontaine and Kennedy 2012).

Considerations for future research

Occupancy only reflects one aspect of population ecology. We did not measure abundance (or territory density), which wildfire can affect independently of occupancy. Detection probability can co-vary with abundance for various reasons (Royle and Nichols 2003, Warren 2011). We implicitly accounted for this relationship by allowing occupancy and detection to co-vary among species. Analyzing abundance explicitly would be beneficial, however, because as a continuous response metric, it can provide additional statistical power for revealing relatively complex relationships with burn severity (e.g., Smucker et al. 2005, Kotliar et al. 2007). In addition to occupancy and abundance, measures of fitness (reproductive success, survivorship) are needed to fully understand wildfire effects on species.

Detection probabilities were low for many species at both locations (Appendix S4). Low detectability induces biased estimation of occupancy probabilities and covariate relationships and is particularly problematic for rare species (MacKenzie et al. 2002, Moreno and Lele 2010, McKann

et al. 2013, Sanderlin et al. 2014). Sanderlin et al. (2014) suggest increased accuracy for rare species could be achieved by sampling more area. More simulation studies examining estimator properties for community occupancy models are needed to guide interpretation of occupancy estimates for rare species.

Studies measuring population shifts from before to after natural disturbance are needed to control for confounding environmental variability among surveyed sites (Wiens and Parker 1995, Popescu et al. 2012). We lacked data necessary to analyze such shifts at the Coconino location. Other studies, however, have found broad consistency between burn severity relationships and population shifts from before to after wildfire (Smucker et al. 2005, Kotliar et al. 2007, Seavy and Alexander 2014). Examining changes in occupancy or abundance with time since disturbance is also necessary for a full understanding of species ecological relationships with wildfire (Saab and Powell 2005, Sitters et al. 2014). Population changes with time since wildfire over a longer timeframe (e.g., 12 yr; Saab et al. 2007) would likely have differed between locations, but we lacked data for verification. Additionally, this study only considered breeding birds. Analysis of fire relationships during the nonbreeding season could reveal additional insights (e.g., Covert-Bratland et al. 2006, Brown et al. 2015).

Depending upon the pace and consistency of natural selection along with biological constraints, current populations may be adapted to current conditions, conditions experienced previously, or conditions experienced elsewhere by past immigrants (Grant and Grant 2002, Lytle and Poff 2004). Given uncertainties about how wildfire severity and associated structural conditions vary (Pierce et al. 2004, Frechette and Meyer 2009, Williams and Baker 2012, Odion et al. 2014), selective pressures influencing avian wildfire responses are not well understood. The relevant spatial scale of variability for understanding natural selection likely varies with species ecology (e.g., home range size, gene flow). In addition to average severity, variability in burn severity at sampling points may be relevant for species with variable resource needs (e.g., foliage- or bark-gleaning insectivores that nest in cavities; see also Wightman et al. 2010). Studying species and communities over a range of locations varying in

current and historical conditions could complement our study for understanding these issues.

Management implications

Large-scale forest restoration efforts currently implemented in western North American dry conifer forests aim to restore natural processes disrupted by anthropogenic activities over the last 100 years (Fulé et al. 2012, Franklin et al. 2014). Fuels reduction typically represents a major component of these efforts. A fundamental assumption of intensive fuels reduction is that recent large-scale severe wildfires are uncharacteristic of historical conditions and therefore harm biodiversity in dry conifer forests, particularly in the Southwest (Lowther 2000, Arno and Fiedler 2005, Miller and Thode 2007). Our results support the growing consensus among avian ecologists that species relationships with wildfire vary not only with life history traits but also regionally in ways that reflect differences in historical fire regime, vegetation, and climate (e.g., Saab and Powell 2005, Hutto et al. 2008). Our results suggest that a greater proportion of bird species in southwestern forests respond negatively than positively to high-severity wildfire (see also Kalies et al. 2010), and these relationships likely differ from dry conifer forests in the central and northern Rocky Mountains. Thus, restoration targets should account for regional differences in historical conditions and consequent differences in the ecological roles of low-, mixed-, and high-severity wildfire. In reality, fire-dependent species occurred at both southwestern and central Rocky Mountain study locations. Even in the Southwest, where wildfires are generally expected to burn at lower severities, some species related positively with severity (Kalies et al. 2010). Thus, in contrast with conventional thought, some mixed-severity fires are likely needed to support the full suite of forest birds throughout dry conifer forests of western North America.

Fire regimes and vegetation structure are fundamentally driven by climate, which is rapidly changing (Agee 1993, Schoennagel et al. 2004). Consequently, recovery of historical fire regimes is likely impossible through forest management alone (Pierce et al. 2004). Nevertheless, historical conditions provide an important reference for designing forest restoration targets (Franklin et al. 2014, Drapeau et al. 2016). Further work examining regional variation in avian fire associations and integrating this information with data on historical conditions could elucidate the optimal distribution of severities for promoting biodiversity within particular landscapes (e.g., Kelly et al. 2015). Such work would benefit from further examination of which life history traits confer fixed vs. variable responses to wildfire across regions and associated fire regimes.

Literature Cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Amundson, C. L., J. A. Royle, and C. M. Handel. 2014. A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts. Auk 131:476–494.

Arno, S. F., and C. E. Fiedler. 2005. Mimicking nature's fire: restoring fire-prone forests in the West. Island Press, Inc., Washington, D.C., USA.

Balda, R. P. 2002. Pinyon Jay (*Gymnorhinus cyanocephalus*). *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/605.

Berry, L. E., D. B. Lindenmayer, and D. A. Driscoll. 2015. Large unburnt areas, not small unburnt patches, are needed to conserve avian diversity in fire-prone landscapes. Journal of Applied Ecology 52:486–495.

Block, W. M., V. A. Saab, and L. F. Ruggerio. 2012. Putting science into action on Forest Service Lands. Pages 49–62 *in* J. P. Sands, S. J. DeMaso, M. J. Schnupp, and L. A. Brennan, editors. Wildlife sci-

ence: connecting research with management. CRC Press, Boca Raton, Florida, USA.

Bock, C. E., and W. M. Block. 2005. Fire and birds in the southwestern United States. Studies in Avian Biology 30:14–32.

Bowen, R. V. 1997. Townsend's Solitaire (*Myadestes townsendi*). *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/269doi:10.2173/bna.269.

Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: principles in the context of place. Conservation Biology 18:903–912.

Brown, C. R., A. M. Knott, and E. J. Damrose. 2011. Violet-green Swallow (*Tachycineta thalassina*). *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/014doi:10.2173/bna.14.

Brown, D. J., J. R. Ferrato, C. J. White, I. Mali, M. R. J. Forstner, and T. R. Simpson. 2015. Short-term changes in summer and winter resident bird communities following a high severity wildfire in a southern USA mixed pine/hardwood forest. Forest Ecology and Management 350:13–21.

Chandler, R. B., and J. A. Royle. 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. Annals of Applied Statistics 7:936–954.

Clarke, M. F. 2008. Catering for the needs of fauna in fire management: science or just wishful thinking? Wildlife Research 35:385–394.

Covert-Bratland, K. A., W. M. Block, and T. C. Theimer. 2006. Hairy woodpecker winter ecology in ponderosa pine forests representing different ages since wildfire. Journal of Wildlife Management 70:1379–1392.

Crimmins, S. M., S. Z. Dobrowski, A. R. Mynsberge, and H. D. Safford. 2013. Can fire atlas data improve species distribution model projections? Ecological Applications 24:1057–1069.

Cullinane-Anthony, B. L., N. E. Seefelt, R. Gregory Corace Iii, D. M. Kashian, and T. M. Gehring. 2014. Influence of residual forest patches on post-fire bird diversity patterns in jack pine-dominated ecosystems of northern Lower Michigan. Forest Ecology and Management 331:93–103.

Dale, V. H., et al. 2001. Climate change and forest disturbances. BioScience 51:723–734.

Dieni, J. S., and S. H. Anderson. 1999. Effects of recent burning on breeding bird community structure in aspen forests. Journal of Field Ornithology 70:491–503.

Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. Journal of the American Statistical Association 100:389–398.

Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87:842–854.

Drapeau, P., M.-A. Villard, A. Leduc, and S. J. Hannon. 2016. Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. Diversity and Distributions, *in press*, http://dx.doi.org/10.1111/ddi.12407.

Fontaine, J. B., and P. L. Kennedy. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22:1547–1561.

Fontaine, J. B., D. C. Donato, W. D. Robinson, B. E. Law, and J. B. Kauffman. 2009. Bird communities following high-severity fire: response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257:1496–1504.

Franklin, J. F., R. K. Hagmann, and L. S. Urgenson. 2014. Interactions between societal goals and restoration of dry forest landscapes in western North America. Landscape Ecology 29:1645–1655.

Frechette, J. D., and G. A. Meyer. 2009. Holocene fire-related alluvial-fan deposition and climate in ponderosa pine and mixed-conifer forests, Sacramento Mountains, New Mexico, USA. Holocene 19:639–651.

Fulé, P. Z., J. E. Crouse, J. P. Roccaforte, and E. L. Kalies. 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? Forest Ecology and Management 269:68–81.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, New York, USA.

Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707–711.

Hahn, T. P. 1996. Cassin's Finch (*Haemorhous cassinii*). *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/240doi:10.2173/bna.240.

Hauber, M. E., and S. A. Russo. 2000. Perch proximity correlates with higher rates of Cowbird parasitism of ground nesting Song Sparrows. Wilson Bulletin 112:150–153.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Hessburg, P. F., R. B. Salter, and K. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences

from landscape patterns of forest structure. Landscape Ecology 22:5–24.

Hollenbeck, J. P., L. J. Bate, V. A. Saab, and J. F. Lehmkuhl. 2013. Snag distributions in relation to human access in ponderosa pine forests. Wildlife Society Bulletin 37:256–266.

Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9:1041–1058.

Hutto, R. L., and R. T. Belote. 2013. Distinguishing four types of monitoring based on the questions they address. Forest Ecology and Management 289:183–189.

Hutto, R. L., C. J. Conway, V. A. Saab, and J. R. Walters. 2008. What constitutes a natural fire regime? Insight from the ecology and distribution of coniferous forest birds in North America. Fire Ecology 4:115–132.

Hutto, R. L., A. D. Flesch, and M. A. Fylling. 2014. A bird's-eye view of forest restoration: do changes reflect success? Forest Ecology and Management 327:1–9.

Illán, J. G., C. D. Thomas, J. A. Jones, W.-K. Wong, S. M. Shirley, and M. G. Betts. 2014. Precipitation and winter temperature predict long-term range-scale abundance changes in Western North American birds. Global Change Biology 20:3351–3364.

Kalies, E. L., C. L. Chambers, and W. W. Covington. 2010. Wildlife responses to thinning and burning treatments in southwestern conifer forests: a meta-analysis. Forest Ecology and Management 259:333–342.

Kelly, L. T., A. F. Bennett, M. F. Clarke, and M. A. McCarthy. 2015. Optimal fire histories for biodiversity conservation. Conservation Biology 29:473–481.

Kéry, M., J. A. Royle, M. Plattner, and R. M. Dorazio. 2009. Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90:1279–1290.

Kotliar, N. B., S. J. Hejl, R. L. Hutto, V. A. Saab, C. P. Mellcher, and M. E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology 25:49–64.

Kotliar, N. B., P. L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. Ecological Applications 17:491–507.

Kotliar, N. B., E. W. Reynolds, and D. H. Deutschman. 2008. American three-toed woodpecker response to burn severity and prey availability at multiple spatial scales. Fire Ecology 4:26–45.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/047doi:10.2173/bna.47.

Lowther, P. E. 2000. Cordilleran Flycatcher (*Empidonax occidentalis*). *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/556b.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS - a Bayesian modeling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Lytle, D. A. 2001. Disturbance regimes and life-history evolution. American Naturalist 157:525–536.

Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19:94–100.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Baily, and J. E. Hines. 2006. Occupancy estimation and modeling. Elsevier Inc., San Diego, CA, USA.

McKann, P. C., B. R. Gray, and W. E. Thogmartin. 2013. Small sample bias in dynamic occupancy models. Journal of Wildlife Management 77:172–180.

Mellen-McLean, K., B. C. Wales, and B. Bresson. 2013. A conservation assessment of the white-headed woodpecker (*Picoides albolarvatus*). USDA forest service, region 6; USDI Bureau of Land Management, Oregon and Washington.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of the Environment 109:66–80.

Moir, W. H., B. Geils, M. A. Benoit, and D. Scurlock. 1997. Ecology of southwestern ponderosa pine forests. RM-GTR-292, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Moreno, M., and S. R. Lele. 2010. Improved estimation of site occupancy using penalized likelihood. Ecology 91:341–346.

MTBS. 2012. Monitoring trends in burn severity. http://mtbs.gov/dataquery/individualfiredata.html (accessed March 2012).

Nimmo, D. G., L. T. Kelly, L. M. Farnsworth, S. J. Watson, and A. F. Bennett. 2014. Why do some species have geographically varying responses to fire history? Ecography 37:805–813.

Norris, A. R., and K. Martin. 2010. The perils of plasticity: dual resource pulses increase facilitation but destabilize populations of small-bodied cavity-nesters. Oikos 119:1126–1135.

Odion, D. C., et al. 2014. Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. PLoS ONE 9:e87852.

Pierce, J. L., G. A. Meyer, and A. J. Timothy Jull. 2004. Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. Nature 432:87–90.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *in* Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22. Vienna, Austria.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752–757.

Popescu, V. D., P. de Valpine, D. Tempel, and M. Z. Peery. 2012. Estimating population impacts via dynamic occupancy analysis of before-after control-impact studies. Ecological Applications 22:1389–1404.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501–517.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology. Elsevier Academic Press, Oxford, UK.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777–790.

Russell, R. E., V. A. Saab, and J. G. Dudley. 2007. Habitat-suitability models for cavity-nesting birds in a postfire landscape. Journal of Wildlife Management 71:2600–2611.

Russell, R. E., J. A. Royle, V. A. Saab, J. F. Lehmkuhl, W. M. Block, and J. R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. Ecological Applications 19:1253–1263.

Saab, V. A., and H. D. W. Powell. 2005. Fire and avian ecology in North America: process influencing pattern. Studies in Avian Biology 30:1–9.

Saab, V. A., H. D. W. Powell, N. B. Kotliar, and K. R. Newlon. 2005. Variation in fire regimes of the Rocky Mountains: implications for avian communities and fire management. Studies in Avian Biology 30:76–96.

Saab, V., L. J. Bate, J. Lehmkuhl, B. G. Dickson, S. Story, S. Jentsch, and W. M. Block. 2006. Changes in downed wood and forest structure after prescribed fire in ponderosa pine forests. *in* Fuels management - how to measure success, Portland, OR, USA. Proceedings RMRS-P-41. USDA, Forest Service, RMRS, Fort Collins, Colorado, USA.

Saab, V. A., W. M. Block, R. E. Russell, J. F. Lehmkuhl, L. Bate, and R. White. 2007. Birds and burns of the Interior West. Pacific Northwest Research Station, U.S. Forest Service, Portland, OR, USA. PNW-GTR-712.

Saab, V. A., R. E. Russell, and J. G. Dudley. 2009. Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. Forest Ecology and Management 257:151–159.

Sanderlin, J. S., W. M. Block, and J. L. Ganey. 2014. Optimizing study design for multi-species avian monitoring programmes. Journal of Applied Ecology 51:860–870.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. BioScience 54:661–676.

Seavy, N. E., and J. D. Alexander. 2014. Songbird response to wildfire in mixed-conifer forest in southwestern Oregon. International Journal of Wildland Fire 23:246–258.

Sitters, H., F. Christie, J. Di Stefano, M. Swan, P. Collins, and A. York. 2014. Associations between occupancy and habitat structure can predict avian responses to disturbance: implications for conservation management. Forest Ecology and Management 331:227–236.

Smith, J. K. (editor). 2000. Wildland fire in ecosystems: effects of fire on fauna. USDA Forest Service General Technical Report RMRS-GTR-vol 1. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Smucker, K. M., R. L. Hutto, and B. M. Steele. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. Journal of Statistical Software 12:1–16.

Su, Y.-S., and M. Yajima. 2014. R2jags: a package for running jags from R. R package version 3.3.0. http://CRAN.R-project.org/package=R2jags.

Sutherland, W. J., I. Newton, and R. E. Green. 2004. Bird ecology and conservation: a handbook of techniques. Oxford University Press, New York, New York, USA.

Warren, C. C. 2011. Singing behavior leads to detection bias in a territorial songbird. M.S. Thesis. Texas State University. https://digital.library.txstate.edu.

Watt, D. J., and E. J. Willoughby. 2014. Lesser Goldfinch (*Spinus psaltria*). *In* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/392doi:10.2173/bna.392.

Wiens, J. A., and K. R. Parker. 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. Ecological Applications 5:1069–1083.

Wightman, C. S., V. A. Saab, C. Forristal, K. Mellen-McLean, and A. Markus. 2010. White-headed Woodpecker nesting ecology after wildfire. Journal of Wildlife Management 74:1098–1106.

Williams, M. A., and W. L. Baker. 2012. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. Global Ecology and Biogeography 21:1042–1052.

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