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Chapter J

Long-Term Post-Wildfire Correlates with Avian Community Dynamics in Ponderosa Pine Forests

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Abstract

We used a 10-year data set to illustrate the long-term correlates of wildfire on avian species richness in the ponderosa pine (*Pinus ponderosa*) forests of northern Arizona. This study was conducted in the vicinity of the Horseshoe and Hochderffer Fires, which occurred in 1996, and sampling began 1 year after the fires. Using point-count data from breeding seasons, we described how avian species richness, local colonization, and local extinction changed over time following the wildfires. We used Bayesian hierarchical models to describe occupancy as a function of burn severity (severe, moderate, or unburned), years since wildfire, and species, while accounting for variables that influenced detection probability, such as species and sampling effort. The avian species from our study followed general patterns predicted from changes in vegetation structure in response to fire based on foraging and nesting requirements. Our results indicated that landscape heterogeneity from a mixture of fire severities and time since fire increased overall species richness across the landscape. Avian species in pine forests evolved with fire. Given that some species demonstrated an affinity to severely burned forests suggests that similar conditions existed historically.

Introduction

Disturbance plays important roles for the conservation of birds by influencing habitat distribution and landscape heterogeneity. Increasing landscape heterogeneity often leads to increased overall species richness with patches having different species compositions (Brawn and others, 2001; Platt and Connell, 2003). Species richness is a common indicator of management success (for example, Russell and others, 2009). Within pine forests in the southwestern United States fire is a common natural disturbance (Covington and Moore, 1994; Moir and others, 1997), and some avian species have evolved as fire specialists (Hutto and others, 2008). Historically, fires in these pine forests tended to be low-severity surface fires. Within the past 20 years, however, fire regimes have changed and have become high-severity, stand-replacing events. An increase in the frequency of large, severe wildfires in the southwestern United States can be attributed to increases in fuel loads and continuity as the result of livestock grazing, logging, and fire suppression (Allen and others, 2002; Covington and Moore, 1994; Moore and others, 1999; Swetnam and others, 1999).

Most information about avian response to wildfire is short-term (<5 years) (Saab and Powell, 2005; Saab and others, 2005). As changes in forest structure occur from fire, we would expect some bird species to respond differently depending on time since fire and the fire regime of the area. Foraging method, nest type, and location all influence a species response to fire (Saab and Powell, 2005). In addition to time since fire, fire severity influences bird response to fire (Kotliar and others, 2002; Smucker and others, 2005). Further, relatively little is known about avian response to southwestern fires extending the need to improve management strategies for avian species (Bock and Block, 2005). One of the primary management tools in southwestern ponderosa pine forests is prescribed fire, so we need to understand how birds respond to wildfire at different burn severities and if we can mimic the historical fire regime with the frequency and severity of prescribed fire.

Our objectives were to quantify wildfire correlates with avian community metrics in Northern Arizona following the Hochderffer and Horseshoe Fires of 1996. Specifically, we were interested in relations of fire burn severity and time since wildfire with species occupancy, species richness, and local colonization and local extinction. We used multispecies occupancy models (Dorazio and others, 2006; MacKenzie and others, 2006) to estimate community metrics, while accounting for imperfect detection. Imperfect detection is important to include in analyses, especially with rare or elusive species or when trying to assess change over time. Estimates of community metrics could be biased if species occupy an area but were never detected during a survey or multiple surveys and could lead to biased study conclusions and management actions.

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Methods

Study Area

Two wildfires (Horseshoe Fire and Hochderffer Fire) occurred in May and June 1996 in the Flagstaff Ranger District of the Coconino National Forest in north-central Arizona. The region of the fires is shown in figure 1.

The Horseshoe Fire encompassed about 3,500 hectares (ha) and the Hochderffer fire encompassed more than 6,600 ha adjacent to the Horseshoe Fire. The predominant vegetation type was ponderosa pine forest. Other tree species included Gambel oak (*Quercus gambelii*), piñon pine (*Pinus edulis*), and alligator (*Juniperus deppeana*) and one-seeded junipers (*J. monosperma*). Understory vegetation included buckbrush (*Ceanothus fendleri*), rabbitbrush (*Chrysothamnus nauseosa*), Oregon grape (*Mahonia repens*), and various grasses and forbs. Burn severity in these areas ranged from high to moderate to low. We used three broad categories of severity (high, moderate, unburned) originally defined by Dwyer and Block (2000) within our analyses. We used the following ranges of the delta normalized burn ratio (dNBR) generated from a comparison of Landsat Thematic Mapper (TM) imagery recorded before and after wildfire (Eidenshink and others, 2007; also see http://www.mtbs.gov/) to define the burn severity categories for each transect. Raw dNBR values were compiled at a 30×30 meter (m) resolution, and a mean dNBR was calculated for a 100-m-radius neighborhood centered on the point count station. Our high severity category represented average dNBR of all points per transect ≥150, moderate severity was <150 and ≥65, and unburned was <65. We used unburned areas for contrasts because pre-wildfire data were unavailable. Unburned areas were similar to burned areas with respect to pre-burn stand structure and species composition but may have deviated from pre-settlement ponderosa pine forest conditions described by Covington and others (1997).

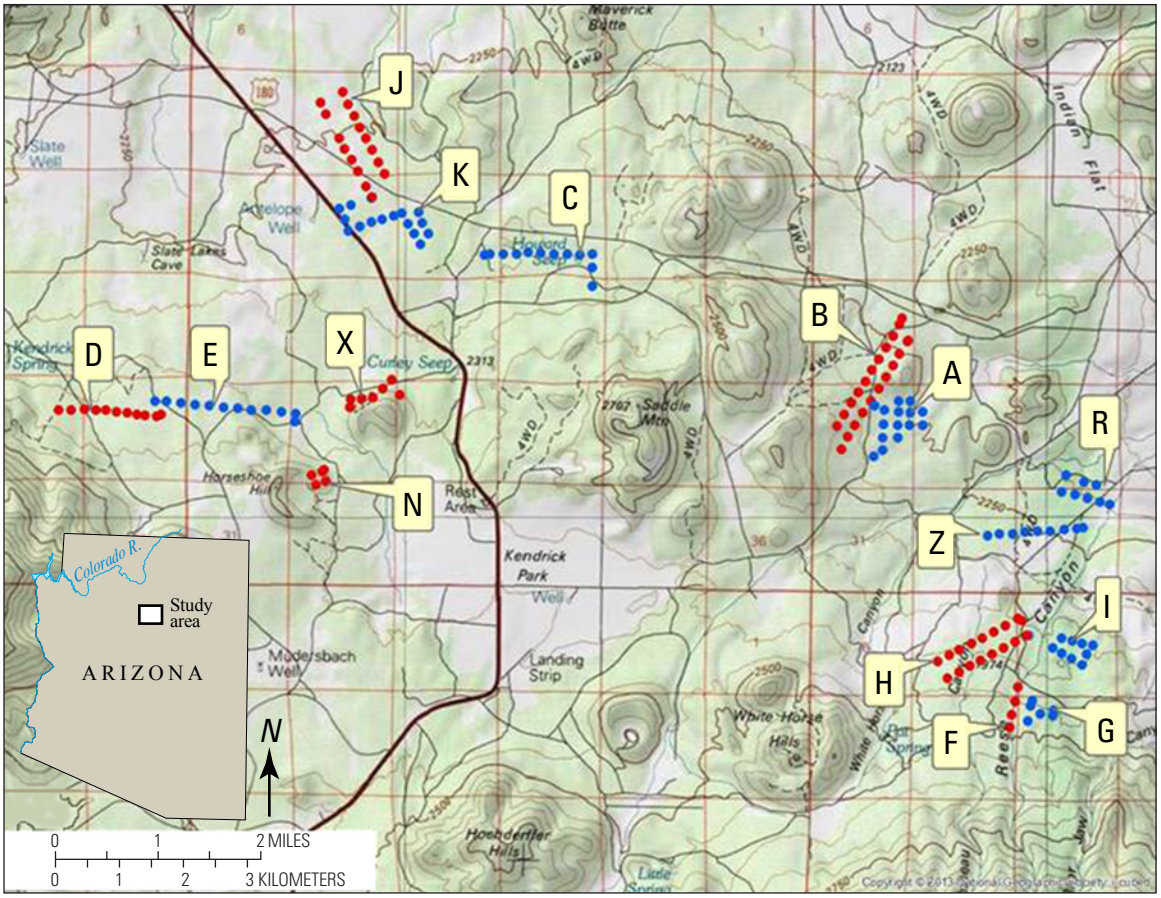

Figure 1. Map showing the avian community study area after the Hochderffer and Horseshoe wildfires that occurred in 1996 in northern Arizona. All 15 avian transects are labeled on the topographic map using different colors to easily distinguish the different transects: blue circles (transects A, C, E, G, I, K, R, Z), red circles (transects B, D, F, H, J, N, X). (Topographic map from Esri ArcGIS Resources online, copyright 2013 National Geographic Society and ʸi-cubed.).

Field

We sampled birds starting 1 year after the fires using the variable-radius point-count method (Reynolds and others, 1980). Sampling occurred during the breeding season over a period of 10 years (primary periods), where each season had as much as three secondary periods (visits). Each transect route consisted of an average of 10 points (range 3–20) spaced at 200 m intervals. The 15 transect lines were categorized as high severity (7 transects with 49 points total), moderate severity (4 transects with 50 points total), and unburned (4 transects with 50 points total). We sampled each point three times during the summer breeding season to sample variation in bird distribution and detectability. Counts began within 30 minutes of sunrise and were completed no later than 4 hours after sunrise to sample points during periods of high bird activity. Observers remained still for 2 minutes after reaching a point to allow birds to resume normal activity patterns after disturbance. The actual point count lasted 8 minutes. The observer recorded weather, windspeed, and temperature in addition to species, age, and sex of all birds detected, mode of detection (audio or visual), and estimated horizontal distance to the bird.

Analytical

We used Bayesian hierarchical models (Gelman and others, 2004) to model detection and occupancy (MacKenzie and others, 2006; Royle and Dorazio, 2008, p. 380–399) and to estimate species richness *N*. We assumed occupancy states of species could change with local extinction and colonization between years, but not during each summer season of each year. We condensed data across points within each transect to increase species detections per year and to reduce model complexity. We used a three-dimensional data matrix **y**, where element y_{ijt} was a sum of binary indicators for species detection of species i (i=1,...,N) at transect j (j=1,…,15) during primary sampling occasion year t (t=1,…, 10), rather than the binary indicators of species detection typically used in single-species or multispecies occupancy models. When binary indicator of species detection x_{ijt}=1, we detected species i at transect j during primary sampling occasion year t. We used the sum of all binary species i detections over all secondary sampling occasions at each transect, where $y_{ijt}=\sum_{s=1}^{3} x_{ijts}$ and $y_{ijt}=\{0, 1, 2, 3\}$. We used species, time since wildfire, and burn severity to model probability of occupancy, and we used species and effort to model detection probability. For numerical reasons, we use standardized covariates of time since wildfire and effort. We defined effort as number of points in each transect (table 1).

Table 1. Number of bird-count points sampled per transect at different burn severities (high, moderate, unburned) after the 1996 Hochderffer and Horseshoe wildfires that occurred in northern Arizona.

Transect	Burn severity	Number of point-count stations
A	High	14
B	Moderate	20
C	High	10
D[1]	High	10
E	Unburned	10
F	High	3
G	High	4
H	Moderate	15
I	High	9
J	Unburned	15
K	Unburned	15
N	High	4
R	Moderate	7
X	High	5
Z	Moderate	8
N	High	4

[1]Transect D was classified as unburned for the first 3 years after wildfire. The Pumpkin Fire went through this area in 2000, so for years 4 through 10 it was classified as high burn severity.

Model

Because we were interested in the whole avian community, not just the species we observed (n_{obs}), we used Bayesian hierarchical models with unknown species richness (Royle and Dorazio, 2008, p. 384–387). We defined w_i as a latent Bernoulli random variable, with probability Ω, indicating whether species i from the supercommunity was available for sampling during all primary sampling seasons:

$$[w_i \mid \Omega] \sim Bern(\Omega). \quad (1)$$

This assumed all of our avian community species were part of the same supercommunity, or regional species pool. To model community change, we assumed a Markovian process described the current occupancy state, whereby probability of occupancy at time t was partially dependent on the probability of occupancy at time t–1. We modeled the probability of Bernoulli latent variable z_{ijt} for occupancy given probability of occupancy ψ_{ijt} and w_i as:

$$[z_{ijt} \mid \Psi_{ijt}, w_i] \sim Bern(\Psi_{ijt} w_i), \quad (2)$$

where probability of occupancy ψ_{ijt} was a function of covariates (indicator of moderate burn severity [*mburn*], indicator of high burn severity [*hburn*], time since wildfire [*time*], time since wildfire squared [$time^2$]) and the previous occupancy state with $z_{ij0} \sim Bern(a_{i1(0)})$:

$$logit(\psi_{ijt}) = \begin{cases} a_{i0} + a_{i1} \times z_{ij0} + a_{i2} \times mburn_j + a_{i3} \times hburn_j + a_{i4} \times time_0 + a_{i5} \times time_0^2 + \\ a_{i6} \times mburn_j \times time_0 + a_{i7} \times hburn_j \times time_0 + a_{i8} \times mburn_j \times time_0^2 & t = 1 \\ a_{i9} \times hburn_j \times time_0^2, \\ a_{i0} + a_{i1} \times z_{ij,t-1} + a_{i2} \times mburn_j + a_{i3} \times hburn_j + a_{i4} \times time_t + a_{i5} \times time_t^2 + \\ a_{i6} \times mburn_j \times time_t + a_{i7} \times hburn_j \times time_t + a_{i8} \times mburn_j \times time_t^2 & t > 1 \\ a_{i9} \times hburn_j \times time_t^2. \end{cases} \quad (3)$$

Value a_{i1} describes a species-specific normal random effect for local probability of survival. These terms also describe species-specific normal random effects: a_{i0} (intercept), a_{i2} (moderate burn severity), a_{i3} (high burn severity), a_{i4} (time since wildfire), a_{i5} (time since wildfire squared), a_{i6} (interaction between time since wildfire and moderate burn severity), a_{i7} (interaction between time since wildfire and high burn severity), a_{i8} (interaction between time since wildfire squared and moderate burn severity), and a_{i9} (interaction between time since wildfire squared and high burn severity). We included quadratic effects of time since wildfire to capture nonlinear responses of species. Occupancy parameter estimates for each species were random variables governed by community-level parameters.

We modeled the probability of observation of species i at transect j during primary period t, y_{ijt}, given secondary periods K, probability of detection p_{ij}, and occupancy latent variable z_{ijt} using a binomial distribution with K trials and probability of success $p_{ij} \times z_{ijt}$:

$$[y_{ijt} \mid p_{ij}, z_{ijt}] \sim Bin(K, p_{ij} \times z_{ijt}). \quad (4)$$

We used species and sampling effort (*eff*) as covariates to model probability of detection p:

$$\text{logit}(p_{ij}) = b_{i0} + b_1 \times eff_j. \quad (5)$$

Covariate b_{i0} was a species-specific normal random effect, whereas b_1 was a fixed effect. Detection parameter estimates for each species were random variables governed by a community-level parameter. We modeled heterogeneity among species using a covariance term (ρ) between species intercepts of occurrence (a_{i0}) and detection probability (b_{i0}) (Royle and Dorazio, 2008, p. 391). We assumed a multivariate logit scale normal distribution, where the only nonzero off-diagonal elements of the variance-covariance matrix with occupancy and detection parameters were between a_{i0} and b_{i0}. This covariance term, our data augmentation step, and the assumption that covariates of species were random variables from a common distribution allowed us to make inferences on occupancy and detection probability of species that we never detected.

We calculated the number of species, species richness, at each transect j and year t:

$$N_{jt} = \sum_{i=1}^{M} z_{ijt}. \quad (6)$$

We also calculated local species colonization, (γ), probability that a species selected at random from the community was not present in the community at time t–1, and local species extinction (ε), or probability that a species selected at random from the community was present at time t-1 but not at time t (Williams and others, 2002):

$$\gamma_{jt} = \frac{\sum_{i=1}^{M} (z_{ijt}) \times (1 - z_{ij,t-1})}{\sum_{i=1}^{M} z_{ij,t-1}} \quad \text{and} \quad (7)$$

$$\varepsilon_{jt} = \frac{\sum_{i=1}^{M} (1 - z_{ijt}) \times (z_{ij,t-1})}{\sum_{i=1}^{M} z_{ij,t-1}}. \quad (8)$$

Inference

We used Bayesian hierarchical models (Gelman and others, 2004) in R2WinBUGS (Sturtz and others, 2005), an R package (R Development Core Team, 2011) that interfaces with WinBUGS (Lunn and others, 2000) to obtain parameter estimates. We used independent non-informative priors because we had no prior knowledge about the parameters: $\Omega \sim Uniform(0,1)$, $\text{expit}(\mu_{a1(0)}) \sim Uniform(0,1)$, $\sigma_{a1(0)} \sim Uniform(0,10)$, $\text{expit}(\mu_{a0}) \sim Uniform(0,1)$, $\sigma_{a0} \sim Uniform(0,10)$, $a_{i1(0)} \sim Uniform(0,1)$, $\mu_{a2} \sim Normal(0,1)$, $\sigma_{a2} \sim Uniform(0,10)$, $\mu_{a3} \sim Normal(0,1)$, $\sigma_{a3} \sim Uniform(0,10)$, $\mu_{a4} \sim Normal(0,1)$, $\sigma_{a4} \sim Uniform(0,10)$, $\mu_{a5} \sim Normal(0,1)$, $\sigma_{a5} \sim Uniform(0,10)$, $\mu_{a6} \sim Normal(0,1)$, $\sigma_{a6} \sim Uniform(0,10)$, $\mu_{a7} \sim Normal(0,1)$, $\sigma_{a7} \sim Uniform(0,10)$, $\mu_{a8} \sim Normal(0,1)$, $\sigma_{a8} \sim Uniform(0,10)$, $\mu_{a9} \sim Normal(0,1)$, $\sigma_{a9} \sim Uniform(0,10)$, $\text{expit}(\mu_{b0}) \sim Uniform(0,1)$, $\sigma_{b0} \sim Uniform(0,10)$, $b_1 \sim Normal\ (0, 1)$, $\rho \sim Uniform(-1,1)$. We used data augmentation (Dorazio and others, 2006) to extend inference to the entire community. We used a sufficiently large supercommunity size M, so the posterior distribution of Ω was centered well below its upper limit ($\Omega \leq 0.5$). We augmented the species observation matrix **y** with (M–n_{obs}) rows of zeros for all transect×primary period sampling sessions. We ran four parallel chains (length 50,000 *it*, burn-in 25,000 *it*, thinning 20 *it*) to estimate the posterior distribution median of model parameters and 95-percent Bayesian Credible Intervals (BCI). We determined statistical significance when 95-percent BCIs did not overlap zero. Convergence was reached ($\hat{R}$ =1.0–1.1; Brooks and Gelman, 1998). We assessed goodness-of-fit (GOF) using two statistics (deviance [–2×log-likelihood], squared

$$\text{loss}\left[\sum_{i=1}^{N}\sum_{j=1}^{15}\sum_{t=1}^{10}\left[Y_{expected,ijt}-Y_{ijt}\right]^2\right],$$

where Y_{ijt} is observed data for species i, at transect j, during year t for a Bayesian p-value (Gelman and others, 2004, p. 162). The Bayesian p-value is the proportion of replicated-data summary values (deviance, squared loss) that were greater than or equal to the observed value (Gelman and others, 2004, p. 162).

Results

Data Summary

We detected 107 bird species (table 2; refer to this table for scientific names of birds discussed in text) over the study period. Total number of species observed on all transects was comparable across years ($n_{obs,yr}$=[59, 54, 57, 57, 60, 72, 60, 60, 63, 65]). There was evidence of overdispersion (Bayesian p-value deviance=0.7112, Bayesian p-value squared loss=1.0). Histograms of median posterior estimates of detection probabilities were bimodal and detection probabilities varied by species, but histograms were similar for all transects (fig. 2). Detection probabilities increased with increased sampling effort (median $\hat{b}_1$=0.4424, 95-percent BCI=0.3938–0.4893).

Table 2. Avian species detected during summer breeding seasons after the 1996 Hochderffer and Horseshoe wildfires of northern Arizona.

Common species name	Scientific name
Wild turkey	*Meleagris gallopavo*
Turkey vulture	*Cathartes aura*
Cooper's hawk	*Accipiter cooperii*
Northern goshawk	*Accipiter gentilis*
Sharp-shinned hawk	*Accipiter striatus*
Red-tailed hawk	*Buteo jamaicensis*
Swainson's hawk	*Buteo swainsoni*
Ferruginous hawk	*Buteo regalis*
Peregrine falcon	*Falco peregrinus*
Merlin	*Falco columbarius*
American kestrel	*Falco sparverius*
Prairie falcon	*Falco mexicanus*
Band-tailed pigeon	*Patagioenas fasciata*
Mourning dove	*Zenaida macroura*
Great horned owl	*Bubo virginianus*
Northern pygmy-owl	*Glaucidium gnoma*
Long-eared owl	*Asio otus*
Flammulated owl	*Otus flammeolus*
Lesser nighthawk	*Chordeiles acutipennis*
Common nighthawk	*Chordeiles minor*
Common poor-will	*Phalaenoptilus nuttallii*
Black-chinned hummingbird	*Archilochus alexandri*
Blue-throated hummingbird	*Lampornis clemenciae*
Broad-tailed hummingbird	*Selasphorus platycercus*
Rufous hummingbird	*Selasphorus rufus*
Northern flicker	*Colaptes auratus*
Acorn woodpecker	*Melanerpes formicivorus*
Lewis's woodpecker	*Melanerpes lewis*
Downy woodpecker	*Picoides pubescens*
American three-toed woodpecker	*Picoides dorsalis*
Hairy woodpecker	*Picoides villosus*
Red-naped sapsucker	*Sphyrapicus nuchalis*
Williamson's sapsucker	*Sphyrapicus thyroideus*
Olive-sided flycatcher	*Contopus cooperi*
Western wood-pewee	*Contopus sordidulus*
Hammond's flycatcher	*Empidonax hammondii*
Dusky flycatcher	*Empidonax oberholseri*
Cordilleran flycatcher	*Empidonax occidentalis*
Gray flycatcher	*Empidonax wrightii*
Ash-throated flycatcher	*Myiarchus cinerascens*
Cassin's kingbird	*Tyrannus vociferans*
Western kingbird	*Tyrannus verticalis*
Warbling vireo	*Vireo gilvus*
Hutton's vireo	*Vireo huttoni*
Plumbeous vireo	*Vireo plumbeous*
Pinyon jay	*Gymnorhinus cyanocephalus*
Western scrub-jay	*Aphelocoma californica*
Stellar's jay	*Cyanocitta stelleri*
Mexican jay	*Aphelocoma wollweberi*
Clark's nutcracker	*Nucifraga columbiana*
American crow	*Corvus brachyrhynchos*
Common raven	*Corvus corax*
Horned lark	*Eremophila alpestris*
Violet-green swallow	*Tachycineta thalassina*
Mountain chickadee	*Poecile gambeli*
Bushtit	*Psaltriparus minimus*
Red-breasted nuthatch	*Sitta canadensis*
White-breasted nuthatch	*Sitta carolinensis*
Pygmy nuthatch	*Sitta pygmaea*
Brown creeper	*Certhia americana*
Rock wren	*Salpinctes obsoletus*
House wren	*Troglodytes aedon*
Blue-gray gnatcatcher	*Polioptila caerulea*
Ruby-crowned kinglet	*Regulus calendula*
Golden-crowned kinglet	*Regulus satrapa*
Mountain bluebird	*Sialia currucoides*
Western bluebird	*Sialia mexicana*
Townsend's solitaire	*Myadestes townsendi*
Red-breasted nuthatch	*Sitta canadensis*
White-breasted nuthatch	*Sitta carolinensis*
Pygmy nuthatch	*Sitta pygmaea*
Brown creeper	*Certhia americana*
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Western bluebird	*Sialia mexicana*
Townsend's solitaire	*Myadestes townsendi*
Hermit thrush	*Catharus guttatus*
American robin	*Turdus migratorius*
Northern mockingbird	*Mimus polyglottos*
American pipit	*Anthus rubescens*
Cedar waxwing	*Bombycilla cedrorum*
Olive warbler	*Peucedramus taeniatus*
Red-faced warbler	*Cardellina rubrifrons*
Yellow-rumped warbler	*Setophaga coronata*
Grace's warbler	*Setophaga graciae*
Black-throated gray warbler	*Setophaga nigrescens*
Townsend's warbler	*Setophaga townsendi*
Orange-crowned warbler	*Oreothlypsis celata*
Virginia's warbler	*Oreothlypsis virginiae*
Green-tailed towhee	*Pipilo chlorurus*
Spotted towhee	*Pipilo maculatus*
Rufous-crowned sparrow	*Aimophila ruficeps*
Black-throated sparrow	*Amphispiza bilineata*
Lark sparrow	*Chondestes grammacus*
Brewer's sparrow	*Spizella breweri*
Chipping sparrow	*Spizella passerina*
Vesper sparrow	*Pooecetes gramineus*
Grasshopper sparrow	*Ammodramus savannarum*
Song sparrow	*Melospiza melodia*
Dark-eyed junco	*Junco phaeonotus*
Hepatic tanager	*Piranga flava*
Western tanager	*Piranga ludoviciana*
Summer tanager	*Piranga rubra*
Black-headed grosbeak	*Pheucticus melanocephalus*
Eastern meadowlark	*Sturnella magna*
Western meadowlark	*Sturnella neglecta*
Brewer's blackbird	*Euphagus cyanocephalus*
Brown-headed cowbird	*Molothrus ater*
Bullock's oriole	*Icterus bullockii*

Species Richness

Avian species richness, on average, increased over the 10-year time period for transects, although 95-percent BCIs overlapped for these transects (fig. 3).

Although patterns were not significant because the 95-percent BCIs overlapped, we describe general patterns of the average posterior median species richness estimates for the transects at different severities below. The average posterior median species richness estimate of moderate severity transects ($\hat{SR}_{\text{median, avg}} = 64, \hat{SR}_{\text{median, sd}} = 5$) was greater than high severity transects ($\hat{SR}_{\text{median, avg}} = 55, \hat{SR}_{\text{median, sd}} = 5$) by 9 species over the 10-year period and greater than unburned transects ($\hat{SR}_{\text{median, avg}} = 50, \hat{SR}_{\text{median, sd}} = 5$) by 14 species over the 10-year period. The average posterior median species richness estimate of high-severity transects was greater than unburned transects by 5 species over the 10-year period. One particular example (unburned for first 3 years and high burn severity for last 7 years for transect D versus unburned for transect E) is of interest. Posterior median estimates of species richness were similar for the first 3 years when transects D and E were both

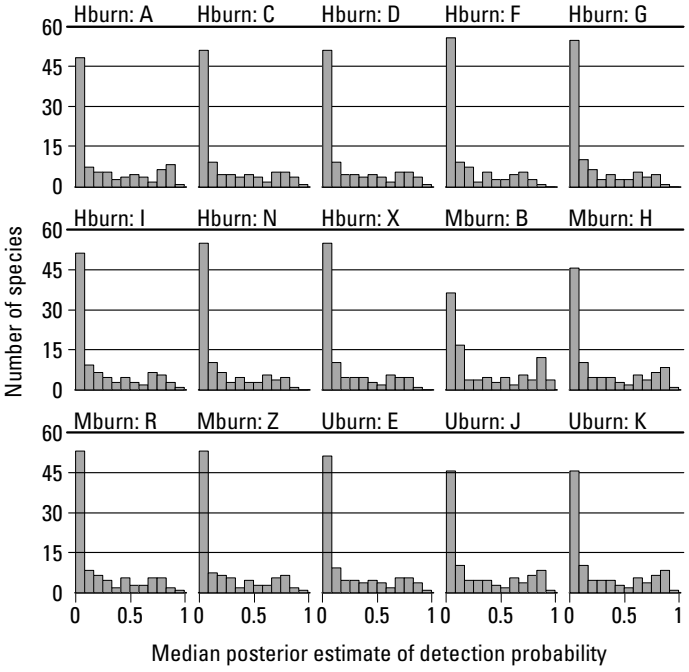

Figure 2. Histograms of median posterior estimates of detection probabilities for avian species at the 15 avian transects (fig. 1) for 10 years after the 1996 Hochderffer and Horseshoe wildfires that occurred in northern Arizona. Subplots are labeled with burn severity and transect name. Note that transect D was classified as unburned for the first 3 years after wildfire and then high severity afterwards. Hburn, high burn severity; Mburn, moderate burn severity; Uburn, unburned.

unburned; however, median posterior estimates of species richness increased for the high-severity transect D with time, while the unburned transect E stayed relatively constant.

Local Colonization and Local Extinction

We found no clear patterns in local colonization and local extinction over all 10 years for unburned, moderate-burn, and high-burn severity transects (fig. 4) because all 95-percent BCIs overlapped.

In general, posterior median estimates of local colonization were greater than posterior median estimates of local extinction of avian species, which is consistent with posterior median estimates of species richness increasing over the 10-year time period for all transects. Local-colonization posterior median estimates tended to be greater than local extinction estimates for the last 5 years, indicating that local colonization was increasing with time, although not significantly.

Responses of Individual Species

Occupancy responses of individual species to time and burn severity were not the same (table 3). Nine species showed an increase in the probability of occupancy (for example, 95-percent BCI did not include zero) over time. One species, western kingbird, exhibited a significantly negative response to the quadratic form of time, indicating that probability of occupancy was greater in the beginning and ending part of the 10-year time period. Six species had significantly greater, and one species, Townsend's solitaire, had significantly lower probability of occupancy in moderate burn severity. Seven species had significantly greater and 14 species had significantly lower probability of occupancy in high burn severity. Three species (American kestrel, rock wren, western meadowlark) had significantly higher and one species had significantly lower (Townsend's solitaire) probability of occupancy for both moderate and high burn severity transects. The only significant interaction between burn severity and time or burn severity and the quadratic form of time was with the American kestrel, which had a positive interaction with high-burn severity and time for probability of occupancy.

Discussion

Burn Severity and Species Richness

Our results indicate that fire severity is an important driver of species richness, supporting research that fire creates landscape heterogeneity (Brawn and others, 2001). Median posterior estimates for avian species richness on transects that had fire were greater than unburned transects over the 10-year period, and species richness median posterior estimates for moderate severity transects were greater than high severity transects, although the credible intervals did overlap. Similarly, Bock and Block (2005) reported more species in severely burned (45) and moderately burned areas (41) than on unburned areas (31) 3 years post-fire on the same transects. Although the numbers of species detected increased over time for all transects, burned areas still exhibited more species than unburned areas 10 years after fire. Other studies (for example, Fontaine and others, 2009) have documented decreased avian

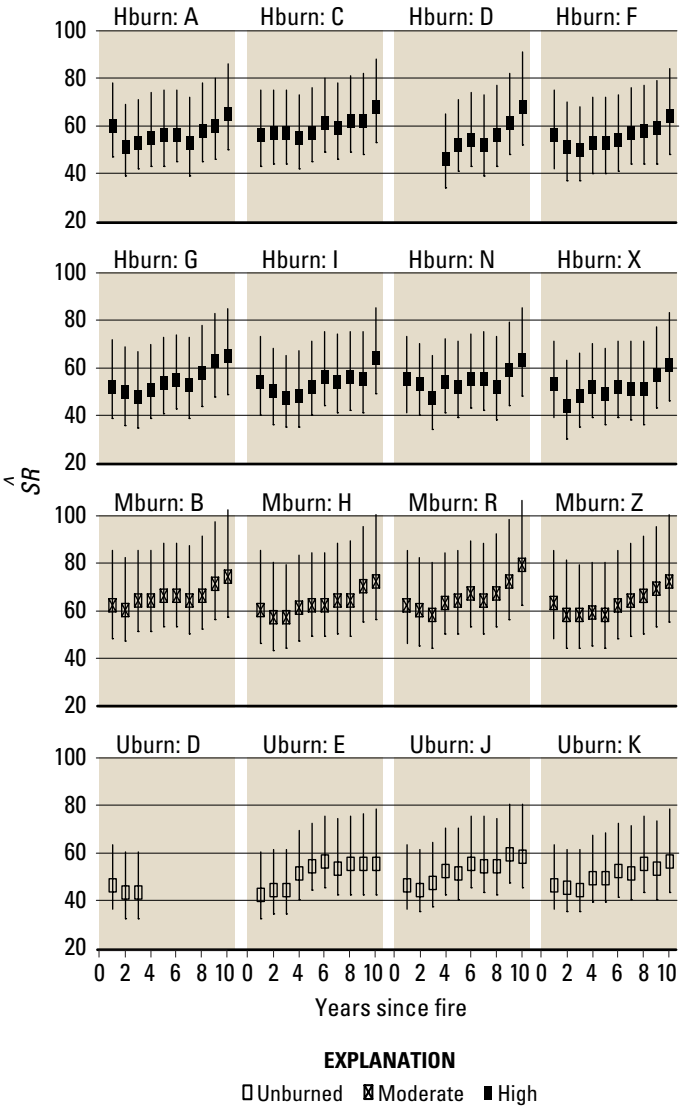

Figure 3. Diagram showing avian community species richness ($\hat{SR}$) posterior estimates and 95-percent Bayesian credible intervals over different burn severity (unburned, white box; moderate burn, box with an x; high burn, black box) transects (fig. 1) for 10 years after the 1996 Hochderffer and Horseshoe wildfires in northern Arizona. Subplots are labeled with burn severity and transect name. Hburn, high burn severity; Mburn, moderate burn severity; Uburn, unburned.

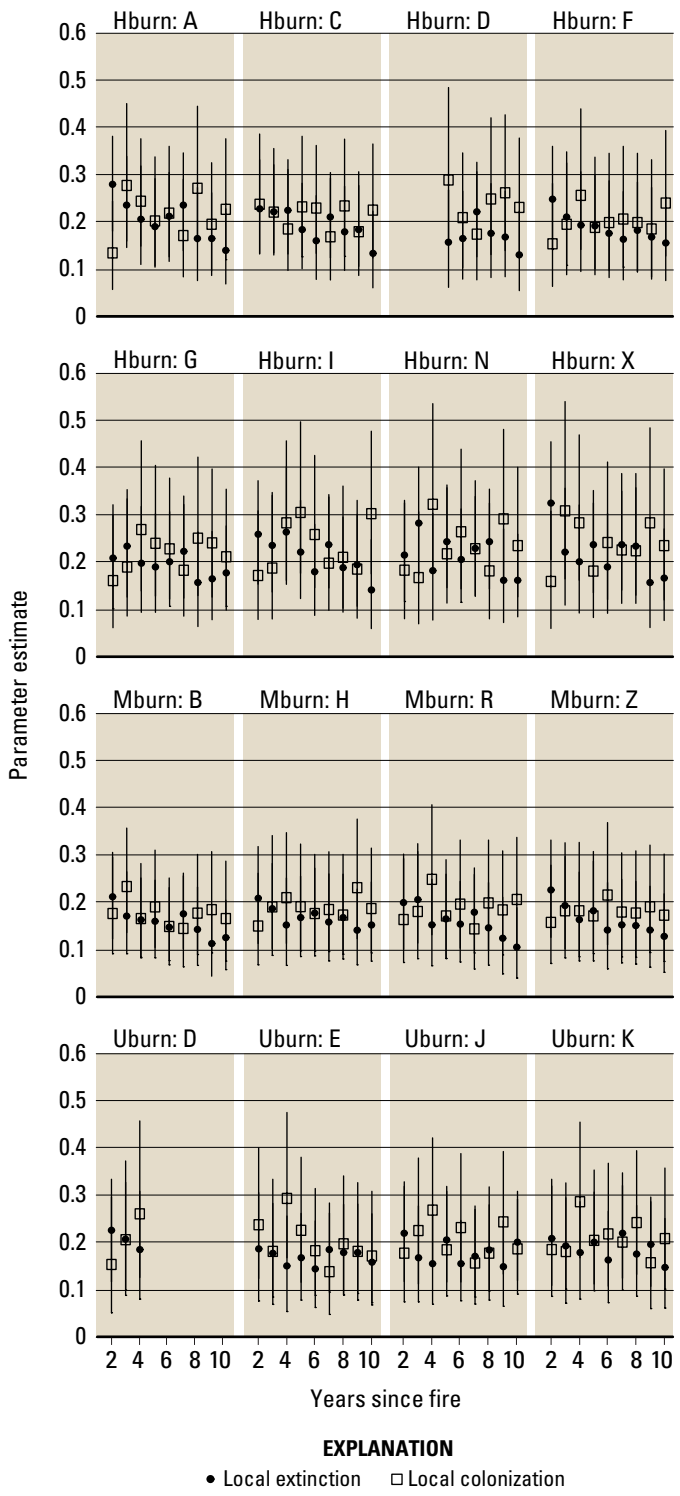

Figure 4. Diagram showing avian community local extinction (black circle) and local colonization (white box) posterior estimates and 95-percent Bayesian credible intervals for all 15 avian transects (fig. 1) for 10 years after the 1996 Hochderffer and Horseshoe wildfires in northern Arizona. Subplots are labeled with burn severity and transect name. Hburn, high burn severity; Mburn, moderate burn severity; Uburn, unburned.

densities with high-severity fire but not necessarily changes in species richness. Hurteau and others (2008) did not detect differences in species richness over different experimental fuel-reduction treatments (thin to reduce stem density and basal area only, prescribed burn only, and thin and prescribed burn).

Local Colonization and Local Extinction

In general, local colonization of avian species was greater than local extinction over the 10-year period for all transects, which is consistent with our result of species richness increasing over the 10-year time period for all transects. This could be the result of other environmental variables not included in this analysis (that is, rainfall, temperature) or even broader regional trends not specific to our study area.

Burn Severity and Time Since Fire for Individual Species

Species that showed significant responses to fire within our study followed the general predictions of Saab and Powell (2005) (table 4). As changes in forest structure occur from fire, we would expect some species to respond differently depending on time since fire. Our study includes how species respond to fire with regards to probability of occupancy; however, in the other studies we reference below, it is important to note that species response could be based on occupancy, counts not adjusted for detection probability, abundance, density, or nest density. Early postdisturbance vegetation structure after fire includes snags and groundcover from herbs. Aerial and ground insectivores, bark and wood foragers, and cavity nesters tend to favor burned habitats. Examples of aerial insectivores that positively responded to fire from our study and other studies included Lewis's woodpecker (Hutto and others, 2008; Saab and Dudley, 1998; Saab and others, 2007) and the olive-sided flycatcher (Kalies and others, 2010; Kotliar and others, 2002; Lowe and others, 1978; Raphael and others, 1987; Smucker and others, 2005). The common nighthawk, also an aerial insectivore, responded positively to fire in other studies (Bock and Bock, 1978; Kalies and others, 2010) but responded negatively to fire in our study. The Cassin's kingbird and western kingbird are also aerial insectivore species that we would expect to positively respond to fire (Bock and Bock, 1978; Kirkpatrick and others, 2006), but we did not detect a significant response to fire in our study. Cassin's kingbird occupancy positively increased and western kingbird occupancy negatively decreased with time for all transects, suggesting that factors not accounted for in our study influenced these species instead. Examples of ground insectivores that positively responded to fire from our study and other studies included house wren (Blake, 1982; Kirkpatrick and others, 2006; Kotliar and others, 2007; Raphael and others, 1987), mountain bluebird (Bock and Bock, 1983; Dieni and Anderson, 1999; Kotliar and others, 2002; Lowe and others,

Table 3. Wildfire responses by individual avian species following the 1996 Hochderffer and Horseshoe wildfires in northern Arizona.

[All significant positive (+) and negative (-) for covariates time, time2, moderate burn severity (Mburn), high burn severity (Hburn), and interactions were noted. Species not listed did not exhibit significant relationships with fire severity, time, or their interaction. There were no significant relations for the interactions of burn severity and time2. Scientific names of species are in table 2]

Common species name	time	time2	Mburn	Hburn	Mburn × time	Hburn × time
Red-tailed hawk			+			
American kestrel			+	+		+
Common nighthawk				-		
Broad-tailed hummingbird	+					
Lewis's woodpecker				+		
Olive-sided flycatcher				+		
Ash-throated flycatcher	+					
Cassin's kingbird	+					
Western kingbird	-					
Warbling vireo	+			-		
Plumbeous vireo				-		
Mountain chickadee				-		
Red-breasted nuthatch	+					
White-breasted nuthatch				-		
Pygmy nuthatch	+			-		
Brown creeper				-		
Rock wren	+		+	+		
House wren				+		
Mountain bluebird				+		
Townsend's solitaire			-	-		
Olive warbler				-		
Yellow-rumped warbler				-		
Grace's warbler				-		
Virginia's warbler				-		
Lark sparrow	+					
Chipping sparrow	+		+			
Western tanager				-		
Western meadowlark			+	+		
Brown-headed cowbird			+	-		

1978; Raphael and others, 1987; Smucker and others, 2005), and rock wren (Blake, 1982; Kotliar and others, 2002). We expected broad-tailed hummingbirds to respond positively to fire due to an increase in flowers as in other studies (Bock and Block, 2005; Kalies and others, 2010; Kotliar and others, 2007), but we did not detect a positive response to fire in our study. We did, however, have a significant increase in occupancy of broad-tailed hummingbirds with time across all transects, suggesting that factors not accounted for in our study influenced this species. The only significant interaction between burn severity and time was with the American kestrel, which had a positive interaction with high-burn severity and time for probability of occupancy, indicating as time increases after fire probability of occupancy increases. This is likely the result of increased prey abundance, availability of nest cavities, and open habitat structure after fire. Similar patterns have been documented with the American kestrel in other studies (Kalies and others, 2010; Lowe and others, 1978; Saab and Dudley, 1998; Saab and others, 2007).

As time progresses, snags fall and the understory develops with more shrubs. We would expect omnivores and shrub nesters to do well when this happens. One example of an omnivore that responded positively to fire in our study and other studies was the chipping sparrow (Bock and Bock, 1983; Lowe and others, 1978; Raphael and others, 1987; Smucker and others, 2005). Finally, as the forest matures, the structure is characterized by a closed canopy with few snags and low understory development, whereas old-growth forests include snags, an open canopy, and an understory that starts to develop. Saab and Powell (2005) found that foliage gleaners preferred unburned habitats, which was true with all our species with significant negative responses to fire. Examples of foliage insectivores with negative responses to fire in our study and other studies included warbling vireo (Dieni and Anderson, 1999; Kotliar and others, 2002) 3 to 6 years after fire (Bagne and Purcell, 2011; Kirkpatrick and others, 2006; Kotliar and others, 2007), yellow-rumped warbler (Kotliar and others, 2007; Raphael and others, 1987; Smucker and others, 2005), western tanager (Raphael and others, 1987; Smucker and others, 2005), and plumbeous vireo (Kotliar and others, 2002). Examples of secondary cavity-nesting species that had negative responses to fire in our study and other studies included mountain chickadee (Dwyer and Block, 2000; Hurteau and others, 2008; Kotliar and others, 2002; Kotliar and others, 2007; Lowe and others, 1978; Saab and Powell, 2005), white-breasted nuthatch (Blake, 1982; Dwyer and Block, 2000), pygmy nuthatch (Blake, 1982; Dickson and others, 2009; Dwyer and Block, 2000; Lowe and others, 1978), and brown creeper (Kotliar and others, 2002; Lowe and others, 1978; Raphael and others, 1987).

We detected only one species that had a mixed response (positive with moderate burn and negative with high severity burn) to wildfire, the brown-headed cowbird. Dieni and Anderson (1999) also found a similar mixed response for the brown-headed cowbird. This is not entirely surprising,

Table 4. Foraging mode, nest layer, and nest type for species, adapted from criteria of Saab and Powell (2005), with significant responses to wildfire in our study in northern Arizona following the 1996 Hochderffer and Horseshoe wildfires.

[Response to fire from our study: positive (+), negative (-), or both. Foraging mode: AI=aerial insectivore, BI=bark insectivore, FI=foliage insectivore, GI=ground insectivore, CA=carnivore, OM=omnivore, and SI=shrub insectivore. Nest layers: GR=ground, SH=shrub, and CA= subcanopy to canopy. Nest types: O=open, C=closed, and P=parasitic. Scientific names of species are in table 2]

Common species name	Response to fire (our study)	Forage mode	Nest layer	Nest type
Red-tailed hawk	+	CA	CA	O
American kestrel	+	CA	CA	C
Common nighthawk	-	AI	GR	O
Lewis's woodpecker	+	AI	CA	C
Olive-sided flycatcher	+	AI	CA	O
Warbling vireo	-	FI	CA	O
Plumbeous vireo	-	FI	CA	O
Mountain chickadee	-	FI	CA	C
White-breasted nuthatch	-	BI	CA	C
Pygmy nuthatch	-	BI	CA	C
Brown creeper	-	FI/BI	CA	C
Rock wren	+	GI	GR	C
House wren	+	GI	CA	C
Mountain bluebird	+	GI/AI	CA	C
Townsend's solitaire	-	AI	GR	O
Olive warbler	-	FI	CA	O
Yellow-rumped warbler	-	FI	CA	O
Grace's warbler	-	FI	CA	O
Virginia's warbler	-	SI	SH	O
Chipping sparrow	+	OM	SH	O
Western tanager	-	FI	CA	O
Western meadowlark	+	GI	GR	O
Brown-headed cowbird	both	OM	-	P

depending on what host species the brown-headed cowbird is targeting for parasitizing. Brown-headed cowbird hosts in the western United States include the plumbeous vireo, western tanager, and warbling vireo (for example, Goguen and others, 2009; Marvil and Cruz, 1989; Ortega and Ortega, 2003), which had negative responses with high-severity burn in our study, mirroring the negative response of high-severity burn with the brown-headed cowbird. Similarly, the chipping sparrow, also a brown-headed cowbird host (for example, Ortega and Ortega, 2001), had a positive response to moderate-severity burn in our study, mirroring the positive response to moderate severity burn with the brown-headed cowbird.

Historical conditions in ponderosa pine forests of northern Arizona were characterized by an open park-like structure (Covington and others, 1997). The unburned areas used as contrasts in our study exhibited higher tree densities than found historically in ponderosa pine forests as the result of livestock grazing, logging, and fire suppression (Allen and others, 2002; Covington and Moore, 1994; Moore and others, 1999; Swetnam and others, 1999). We sampled birds within unburned forest to contrast with areas of moderate and high burn severity. The unburned areas did not represent historical forest conditions.

Our study demonstrates the importance of fire for providing and maintaining habitat for many species. Not all species responded similarly, as some species showed affinity to severely burned forests, whereas others favored moderately burned or unburned forest. We need to fine tune this work by incorporating covariates that may better explain bird-habitat relations. Future research with this study will include the influence of burn severity and patch size (Saab and others, 2005), using dNBR at points instead of broad fire-severity categories and including weather and vegetation covariates. These additions will aid resource managers in characterizing the forest vegetation structure for desired management actions.

Management Implications

Our results indicate the importance of monitoring avian species for longer periods of time following wildfire. Many studies are restricted to 2 to 3 years post-fire, and the results from such studies may not capture long-term effects. At the landscape scale, overall species richness can be maximized by increasing landscape heterogeneity from different fire severities. These patches will have different species compositions, leading to an increase in species richness at the landscape scale. Avian species in pine forests evolved with fire. Given that some species demonstrated an affinity to severely burned forests suggests that similar conditions existed historically. Given behavior of contemporary fire, we envision ample severely burned forest in the foreseeable future. Unknown, however, is information that outlines the amount and distribution of patches across the landscape. Research is needed that addresses the temporal and spatial aspects of fire and fire severity including the size, shape, juxtaposition, and interspersion of patch sizes across the landscape.

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