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Source: *The Condor*, 117(3):430-446.

Published By: Cooper Ornithological Society

DOI: <http://dx.doi.org/10.1650/CONDOR-14-58.1>

URL: <http://www.bioone.org/doi/full/10.1650/CONDOR-14-58.1>

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RESEARCH ARTICLE

Fire severity affects mixed broadleaf–conifer forest bird communities: Results for 9 years following fire

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Submitted April 5, 2014; Accepted June 2, 2015; Published August 12, 2015

ABSTRACT

Wildfire is an important disturbance regime that can structure wildlife communities and their habitats for many years. Using a before-after-control-impact framework, we evaluated the effect of the Quartz Fire on a mixed broadleaf–conifer forest and associated bird community in southwestern Oregon, USA, over 10 yr. To assess whether fire severity explained changes better than simply whether an area was burned, we used a tiered sampling approach by comparing unburned control points with either all burned points combined (burned) or those same points partitioned by severity level (low, moderate, high). As expected, overall tree cover decreased while cover of shrubs increased in response to greater fire severity. This pattern was most pronounced in high-severity areas, where tree cover declined by 40% and remained depressed, but shrub cover recovered from 10% the year following fire to 75% by year 6. Ordinations of bird species density showed turnover in community composition in all burned areas combined, as well as in moderate-severity areas, shifting to a shrub-associated community 9 yr postfire. For individual species, annual density variations were best explained by fire for 14 of 37 species, with fire severity providing the best-fitting model for 7 species. Of those 7 species, 3 declined and 4 increased with greater severity. When grouped into guilds, flycatching foragers and shrub nesters increased with greater fire severity. Our results illustrate the importance of mixed-severity wildfire in creating diverse vegetation structure and composition that supports distinct bird communities for at least a decade following fire.

Keywords: bird density, community composition, fire severity, guilds, vegetation, wildfire

La severidad del fuego afecta a las comunidades de aves de bosques mixtos de hoja ancha y coníferas: Resultados de nueve años posteriores al fuego

RESUMEN

El fuego silvestre es un régimen de disturbio importante que puede estructurar por muchos años a las comunidades de vida silvestre y sus hábitats. Usando un marco de impacto antes-después-control, evaluamos el efecto del Fuego Cuarzo sobre un bosque mixto de hoja ancha y coníferas y sobre la comunidad de aves asociada en el sudoeste de Oregón a lo largo de 10 años. Para evaluar si la severidad del fuego explicaba mejor los cambios que simplemente si el área había sido quemada, usamos un modo de muestreo pareado comparando puntos de control no quemados ya sea con todos los puntos quemados juntos (quemado) o con aquellos mismos puntos agrupados por nivel de severidad (bajo, moderado, alto). Como esperábamos, la cobertura total disminuyó, mientras que la cobertura de arbustos aumentó en respuesta a una mayor severidad del fuego. Este patrón en áreas de alta severidad fue más pronunciado en donde la cobertura de los árboles disminuyó en un 40% y permaneció baja, pero la cobertura de arbustos se recuperó desde un 10% durante el año posterior al fuego hasta un 75% al año 6. El ordenamiento de la densidad de las especies de aves mostró un recambio en la composición de la comunidad en todas las áreas quemadas combinadas, lo mismo que en áreas de severidad moderada, cambiando hacia una comunidad asociada con arbustos luego de nueve años del fuego. Considerando las especies individualmente, la variación en la densidad anual fue explicada mejor por el fuego para 14 de las 37 especies, y la severidad del fuego brindó el mejor modelo ajustado para 7 especies. De estas 7 especies, 3 disminuyeron y 4 aumentaron con una severidad mayor. Al agrupar a las aves en gremios, los atrapamoscas y los que nidifican en arbustos aumentaron con una mayor severidad del fuego. Nuestros resultados muestran la importancia de la severidad de los fuegos silvestres en crear diversas estructuras y composiciones de la vegetación que albergan diferentes comunidades de aves por al menos una década luego del fuego.

Palabras clave: densidad de aves, composición de la comunidad, fuegos silvestres, severidad del fuego, gremios, vegetación

INTRODUCTION

Natural disturbance is an important process that alters forest structure and composition (Brawn et al. 2001, Noss et al. 2006, Donato et al. 2009). Across western North America, wildfire acts as a significant disturbance regime, producing complex forest mosaics that vary structurally in relation to the frequency, severity, and intensity of fire (Agee 1998). Bird communities, in particular, can change dramatically in response to wildfire, and species-specific patterns in distribution have been linked to postfire habitat succession and composition (Raphael et al. 1987, Brawn et al. 2001, Huff et al. 2005).

Both fire severity and time since fire influence the response of bird communities to wildfire (Saab and Powell 2005, Smucker et al. 2005, Kotliar et al. 2007, Vierling and Lentile 2008). Although short-term temporal patterns of avian response to fire in the western United States have been well documented, longer-term studies are limited (Raphael et al. 1987, Bock and Block 2005, Schieck and Song 2006, Seavy and Alexander 2014), and few have examined fire severity (Fontaine and Kennedy 2012). In a review of 22 studies, Kotliar et al. (2002) found strong and consistent responses for some species—for example, Black-backed Woodpecker (*Picoides arcticus*) increasing and Hermit Thrush decreasing after fire—and mixed responses for nearly half the species analyzed (scientific names of species included in the present study are given in Appendix Table 5). Smucker et al. (2005) found that fire severity helped explain some of the variation within species, including some of the species with mixed responses in Kotliar et al. (2002). Additionally, the failure of most studies to incorporate longer time intervals (>4 yr) across fire severity gradients likely confounds our ability to make consistent inference (Kotliar et al. 2002, Smucker et al. 2005).

Concerns about the ecological impacts of fire suppression, fire risk at the wildland–urban interface, and projections of larger and more severe fires as a result of climate change are driving management decisions about fire and vegetation structure. This has prompted fuel reduction and prescribed burning in western forests to reduce wildfire risk, techniques that have generally been successful, with few unintended consequences (Agee and Skinner 2005, Stephens et al. 2012). Fuel-reduction treatments and prescribed low-intensity fire have had only modest effects on bird richness, abundance, and productivity (Alexander et al. 2007, Hurteau et al. 2008, Stephens and Alexander 2011), which suggests that although these management techniques may be effective in reducing risk of fire, they likely mimic only low-severity fire and will not create habitat for bird species that benefit from moderate- and high-severity fire (Stephens et al. 2012). An improved understanding of the response of bird communities and

individual species to fire severity is needed to inform both fire-management policies and fuel-reduction programs.

An example of a mixed-severity wildfire, the Quartz Fire, burned in the Little Applegate Valley of southwest Oregon, USA, during the summer of 2001 in an area where bird and vegetation surveys had been completed earlier in the same year as part of a larger inventory study. In the first 4 yr after this fire, 6 of 27 species exhibited decreased occurrence in burned areas, while only Lazuli Bunting increased (Seavy and Alexander 2014). These authors hypothesized that over a longer period, shrub-associated species would increase in occurrence, a pattern that is supported by other chronosequence studies of postfire changes in bird abundance (Schieck and Song 2006, Fontaine et al. 2009).

Here, we revisit the Quartz Fire to quantify changes in vegetation, bird community composition, and individual species and guild densities 9 yr after the fire. This study builds upon the previous analysis by extending the time series and incorporating fire severity. We applied a before-after-control-impact (BACI) study design with a single year of prefire data and 7 yr of data collected in the 9 yr after the fire. Typically, wildfire reduces vegetation structure and alters vegetation composition; increasing severity enhances the shift to early-successional and broadleaf species (Ireland and Petropoulos 2015). Corresponding to vegetation change, we expected that bird density and community composition would vary among unburned areas and low-, moderate-, and high-severity burned areas. We evaluated vegetation structure, bird community structure, nesting guilds, foraging guilds, and abundance of individual species. We asked whether variation in these metrics was described adequately by simply comparing burn status, or whether fire severity (low, medium, or high) was important for understanding vegetation and bird responses.

METHODS

Study Area

We studied bird response to fire in and adjacent to the Quartz Fire in the Little Applegate Valley of southwestern Oregon (Figure 1). Elevation of the sampling locations ranged from 695 to 1,975 m above sea level. The mixed broadleaf–conifer forest was dominated by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and hardwoods including tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), canyon live oak (*Quercus chrysolepis*), California black oak (*Q. kelloggii*), Oregon white oak (*Q. garryana*), and bigleaf maple (*Acer macrophyllum*). The relative composition of these species varied with elevation, aspect, soils, and disturbance history. Generally, these forest types correspond

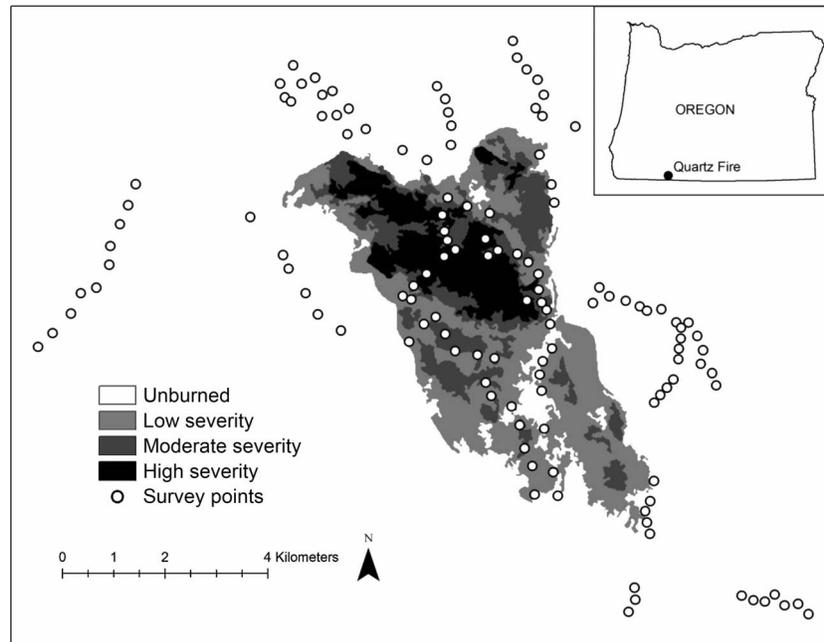


FIGURE 1. Bird and vegetation surveys were conducted in and adjacent to the Quartz Fire, Oregon, USA, 1 yr prefire (2001) and during 9 yr postfire (2002–2006, 2007, 2010) in unburned controls ($n = 83$) and in low-severity ($n = 17$), moderate-severity ($n = 21$), and high-severity ($n = 9$) burned areas.

to the Douglas-fir, mixed evergreen hardwood, or white fir types (Franklin and Dyrness 1988, Huff et al. 2005).

The Quartz Fire burned $\sim 2,500$ ha between August 9 and 31, 2001. Fire severity was mapped by the Burned Area Emergency Rehabilitation (BAER) team of the U.S. Forest Service and classified as low, moderate, or high on the basis of crown scorch and consumption and changes in soil structure (USDA Forest Service 2002; Figure 1). The Quartz Fire was classified as 23% low-severity, 36% moderate-severity, and 41% high-severity (Alexander et al. 2006). Areas at higher elevation and with larger-diameter trees were more likely to have burned at low severity or moderate severity, and areas with southern aspects tended to burn with high severity; a detailed description of fire severity patterns is provided by Alexander et al. (2006).

Sampling Design

The Quartz Fire burned in an area where bird and vegetation data had been collected earlier that year as part of a larger ecological inventory. Forty-seven sampling points were burned in the fire (Figure 1); 17 were located in low-severity burn areas (elevation 975–1,860 m), 21 in moderate-severity areas (elevation 1,000–1,505 m), and 9 in high-severity areas (elevation 1,075–1,220 m). An additional 83 unburned sampling points, also surveyed prior to the fire, were used as controls. They were located

within 5 km of the fire and were of similar elevation (700–1,975 m) and general vegetation classification (Figure 1; Seavy and Alexander 2014). Sampling points were spaced 250 m apart on transects of 10–18 points along secondary and tertiary roads and trails. Although bird sampling on roads may increase detection rates of birds associated with edges, it generally does not have large effects on the ability to detect patterns of habitat association with stand-level vegetation characteristics (Hanowski and Niemi 1995).

Both unburned and burned points were surveyed once per year, prior to the fire (2001) and after the fire (2002–2005, 2007, 2009, and 2010); thus, unburned points were not burned in either 2001 or subsequent years, whereas burned points were not yet burned in 2001 but were burned in subsequent years. The study design applies a tiered approach, including all burned sampling points combined, regardless of severity (hereafter “burned”) and subsets of those sampling points for each BAER severity level (low, moderate, high); both burned points and severity levels are compared with unburned sampling points. Thus, the BACI study design controls for potential spatial differences prior to the fire, as well as annual variation in abundance for individual species (Appendix Table 5).

Field Surveys

Vegetation structure and composition. Vegetation data were collected using standard *relevé* methodology

(Ralph et al. 1993). Within a circular plot defined by a 50-m radius, we recorded total cover of 2 strata—the tree stratum (all vegetation typically ≥ 5 m) and shrub stratum (all vegetation typically ≥ 0.5 m and < 5 m) as the midpoint of 1 of 5 cover classes (0–2.5, 2.5–25, 25–50, 50–75, and 75–100%). The percent cover of individual tree and shrub taxa were also recorded independently of the strata estimates, using the 5 cover classes described above.

Birds. Community composition and bird density were measured using standard point-count methodologies between May 11 and July 2 in a given year (Ralph et al. 1993). Five-minute point counts were conducted between sunrise and 1000 hours, during which all individuals detected by sight or sound were recorded and distance was estimated to each individual. Surveys were conducted on days with wind < 20 km hr⁻¹ and without rain. All observers were proficient with species identification and trained in distance estimation. Prior to the onset of field surveys, observers estimated distances to standing objects until estimates were consistently within $\pm 10\%$ of actual measures. Following this, training included estimating distances to singing birds, locating the birds, and measuring exact distances with a rangefinder to refine estimates by song volume. Throughout the field surveys, a rangefinder was used before each point-count survey to calibrate distance to several standing objects (Stephens et al. 2010).

Before analyzing the bird data, we used Program Distance to calculate point-level densities for 37 species for which we had adequate sample sizes ($n \geq 60$ individuals of a species; Buckland et al. 2001; Appendix Table 5). Program Distance produces density estimates that account for detection probability via detection functions that incorporate variance associated with factors such as observer bias or habitat heterogeneity. Because detection probability likely varies among vocalization types for many species, we used only songs—with the exception of Bushtit, chickadees, and Western Wood-pewee, for which we used songs and calls; and woodpeckers and Steller's Jay, for which we used calls. In building our detection functions, we pooled observations across years and unburned and burned (all severity levels) because sample sizes were small when parsing both by year and by burn status ($n < 60$). We then ranked 8 competing models using Akaike's Information Criterion (AIC) and extracted density estimates from the highest-ranking model that converged correctly. Because variation in observer behavior and habitat structure caused by fire can presumably produce bias in calculating detection probabilities, we included models that incorporated observer and severity level (including unburned) as covariates in estimating the detection functions. First, our models were divided equally between the hazard-rate and half-normal functions, all incorporating the cosine key. Second, for each function type, we included 2 univariate models (observer or

severity), 1 additive model (observer + severity), and 1 model with no covariates. The top model from which density estimates were used was either $< 2 \Delta AIC$ from the subsequent model or the most parsimonious when multiple models were equally ranked. Detections with distance estimates in the lower 5% and upper 5% were truncated for all models to eliminate influential outliers (Buckland et al. 2001).

Analysis

Bird community composition. To examine changes in community composition due to the fire, we ordinated species-specific density estimates by burned (all severities combined) and unburned and also by severity level for 1 yr prefire (2001) and 9 yr postfire (2010). Analyses were performed in PC-ORD 6 (McCune and Mefford 2011) using nonmetric multidimensional scaling (NMS), following procedures outlined by Fontaine et al. (2009). Species for which $< 5\%$ of the points had a nonzero value were censored (McCune et al. 2002). Point-count survey locations were ordinated in species space using species-specific density estimates; ordinated points represent unique bird communities in species space as defined by multiple axes that explain variation in the ordination space. MRPP (multi-response permutation procedure) analysis was conducted to statistically test for differences between the 2 groups (2001 and 2010). MRPP is a nonparametric procedure that tests the hypothesis that there is no difference between groups and produces an A statistic that estimates the effect size and within-group heterogeneity; theoretically, when $A = 1.0$ the groups are completely dissimilar; $A = 0.0$ represents the random expectation (McCune et al. 2002). Ordination plots of point axis scores for each fire severity level and unburned controls were also examined visually for divergence in species space between 2001 and 2010. Vegetation structure and composition (i.e. total tree, total shrub, *Arctostaphylos* spp., *Ceanothus* spp., and Pacific madrone), and nesting and foraging guild density estimates, were correlated with each axis to provide mechanistic explanations for observed patterns in the ordinations.

Vegetation-cover and bird-density response to fire. To evaluate the response of vegetation and bird density to the fire, our analysis used a BACI framework with 1 yr of prefire (before impact) data and 7 yr of postfire (after impact) data collected at the same sites over a 9-yr period following the fire. This included both sites that were burned by the fire (impact), and others that were not (controls). For the models with an effect of fire, we described the affected sites simply as burned (all severities combined) or categorized the affected sites by fire severity (low, moderate, high; hereafter "severity"). To evaluate the effect of fire, we ranked the following 6 competing models within an AIC framework:

(1) Response = 1

The “null model” suggests that variation in the response variable is not explained by year, burn status, or severity. If this model is well supported, it implies there is little evidence for any effect of fire or time on the response variable.

(2) Response = year

This “temporal model” describes annual variation in the response variable regardless of burn status or severity. Like the null model, this model provides no evidence for an effect of fire on the response variable.

(3) Response = year + burned

This “burned additive model” describes the variation in the response variable as changing differently by burn status, but without an interaction with time that would indicate that fire created the difference. However, because we had only a single year of prefire data, it is possible that extreme differences in postfire bird density could overpower that year of prefire data, making this model better supported than the interaction model for some species that did respond to the fire. We visually inspected the data for all cases in which this model was the best supported and based our inference on the visual inspection.

(4) Response = year + burned + year*burned

The “burned interaction model” describes the response variable as changing differently among years by burn status. This model provides the strongest evidence for a fire effect regardless of severity level.

(5) Response = year + severity

The “severity additive model” describes variation in the response variable as changing differently among severity levels, but without an interaction with time that would indicate that the fire created the difference, with the caveats described for model 3.

(6) Response = year + severity + year*severity

The “severity interaction model” describes the response variable as varying in distinct ways across years, dependent on severity levels. This model provides the strongest evidence that the effect of fire varies with the degree of fire severity.

Vegetation cover was analyzed for overall tree and shrub cover, as well as cover of 2 dominant shrub genera (*Arctostaphylos* spp., *Ceanothus* spp.) and 1 species (Pacific madrone). For these variables, we fit generalized linear models using a Gaussian distribution, and cover estimates were square-root transformed when needed to meet assumptions of normality.

For the bird response, we converted density data to integers by multiplying species-specific densities by 3.14 to approximate an estimate of birds per 100-m circle and then rounding to the nearest integer. This allowed us to

use generalized linear models with Poisson distribution. Guild density was calculated as the summed density of individual species that contribute to each of the nesting (Ehrlich et al. 1988) and foraging guilds (Cornell Lab of Ornithology 2014) (Appendix Table 5). Because the models displayed moderate overdispersion ($\hat{c} < 6$ for 36 of 37 species), we ranked the models with QAIC, which incorporates the overdispersion parameter \hat{c} to account for extra-Poisson variance.

We determined the best-supported model for vegetation cover, species-specific bird densities, and nesting and foraging guilds on the basis of AIC rank ($< 2 \Delta AIC$ or $\Delta QAIC$ from the subsequent model or the most parsimonious model when multiple models were equally ranked) and model weights. All analyses were conducted in R using the functions “glm” and “ICtab.”

We displayed the differences between prefire and postfire vegetation cover and bird density values graphically to (1) visually assess whether a fire effect was apparent when an additive model was best (models 3 and 5) and (2) interpret whether the fire effect was positive or negative when an interaction model was best (models 4 and 6). First, we plotted annual percent cover by unburned and each severity level for the 5 vegetation metrics. Second, we compared differences in mean bird density between 1 yr prefire (t_0) and each year postfire (t_i) by unburned, burned, and low, moderate, and high severity levels for the species whose variation in density was best explained by models 3–6. We calculated bootstrapped means and 90% confidence intervals for each difference $t_i - t_0$ in R using the “boot” and “boot.ci” functions (“basic” interval method; 1,000 iterations). Means with confidence intervals not including zero indicate significant changes in density compared with the prefire year.

Of the 6 models, the burned interaction model (4) and severity interaction model (6) provide the strongest evidence of the effect of the fire. Similarly, the null model (1) and temporal model (2) provide the strongest evidence of no effect of the fire. In a typical BACI framework that has multiple years of pre- and post-impact data, the severity additive (5) and burned additive (3) models would not provide evidence of an impact. With only a single year of prefire data, we cautiously interpreted results supporting these models, because they may also have been driven by scant sampling before the fire.

RESULTS

Vegetation Cover

Vegetation structure and composition changed dramatically after the fire and continued to change over the following 9 yr. Both total tree cover and total shrub cover were best explained by the severity interaction model (Table 1). Tree cover decreased with increasing severity

TABLE 1. Generalized linear models (see text) for vegetation cover estimates using Akaike's Information Criterion (AIC), with number of parameters (K), log likelihood ratio (LL), the difference between each model and the best-fitting one (Δ AIC), and the model weight (w_i). Models are reported where $w_i > 0.01$. Abbreviations: Y = year, B = burned, S = severity.

	K	LL	Δ AIC	w_i
Tree cover ^a				
Y + S + Y*S	33	305.1	0	1.00
Shrub cover ^b				
Y + S + Y*S	33	198.5	0	1.00
<i>Arctostaphylos</i> spp. ^c				
Y + S	12	1,064.5	0	0.61
Y + B	10	1,061.8	1.5	0.29
Y	9	1,059.7	3.6	0.10
<i>Ceanothus</i> spp. ^d				
Y + S + Y*S	33	343.9	0	1.00
Pacific madrone ^e				
Y + S + Y*S	33	804.1	0	1.00

^a Minimum AIC = -544.1

^b Minimum AIC = -330.9

^c Minimum AIC = -2,105.1

^d Minimum AIC = -621.7

^e Minimum AIC = -1,542.1

and remained depressed over the 9-yr period (Figure 2). Shrub cover decreased immediately postfire and increased steadily in subsequent years and at a greater rate in moderate- and high-severity areas (Figure 2). Changes in cover of 2 dominant shrubs, *Ceanothus* spp. and Pacific madrone, were also best explained by the severity interaction model; both decreased in the first year postfire and increased gradually in subsequent years, exceeding prefire cover in high-severity areas 6 yr postfire (Table 1 and Figure 2). *Arctostaphylos* spp. cover increased in high-severity areas only in year 9 and was best explained by the burned additive model (Table 1 and Figure 2).

Bird Community Composition

Variation in bird community structure was best explained by 2 axes for unburned points and 3 axes for burned points and all severity levels, with the first axis explaining over half the variation for all 5 ordinations (Figure 3). All ordinations passed their stress tests with $P < 0.05$.

Bird communities shifted significantly across species space 9 yr after the fire in burned areas (all severities combined; $A = 0.03$, $P < 0.001$; Figure 3B) and at the moderate severity level ($A = 0.06$, $P < 0.001$; Figure 3D). For burned areas in general, the dominant axis 1 ($R^2 = 0.64$) was strongly aligned with tree nesters ($r = -0.72$), ground nesters ($r = -0.58$), foliage gleaners ($r = -0.81$), and ground foragers ($r = -0.46$) (Table 2). Environmental gradients were less clear for axis 1, however, given that only shrub cover was moderately correlated ($r = -0.30$) (Table 2). Axis 2 was positively aligned with gradients in

the cover of 2 shrubs, *Arctostaphylos* spp. ($r = 0.335$) and Pacific madrone ($r = 0.318$). Accordingly, ground nesters ($r = 0.32$), shrub nesters ($r = 0.47$), and ground foragers were positively aligned, and tree nesters were negatively aligned ($r = -0.42$) (Table 2). Axis 3 was positively aligned with tree cover ($r = 0.36$), cavity nesters ($r = 0.44$), and ground nesters ($r = 0.44$) and negatively aligned with shrub nesters ($r = -0.43$), flycatching foragers ($r = -0.41$), and ground foragers ($r = -0.32$) (Table 2). For moderate-severity burns (Figure 3D), the dominant axis 1 ($R^2 = 0.64$) was strongly aligned with tree nesters ($r = -0.67$), ground nesters ($r = -0.57$), foliage gleaners ($r = -0.77$), and ground foragers ($r = -0.44$), likely reflecting gradients in overall tree cover ($r = -0.40$). Conversely, shrub nesters ($r = -0.70$) and ground foragers ($r = -0.62$) were aligned oppositely with tree nesters ($r = 0.57$) and foliage gleaners ($r = 0.42$) along the remaining axes that were moderately correlated with overall shrub cover ($r = -0.36$), specifically *Ceanothus* spp. ($r = -0.33$) (Table 2). In summary, prior to the fire, bird communities were predominantly composed of arboreal and ground associates, whereas the postfire community was strongly influenced by shrub-associated species (Figure 3).

Surprisingly, bird communities within high-severity burns showed no significant shifts across species space ($A = -0.01$, $P = 0.60$; Figure 3E), which may be due to small sample size. Likewise, communities within low-severity burns were similar between years ($A = 0.01$, $P = 0.16$; Figure 3C). The statistically significant shift for communities within unburned points ($A = 0.02$, $P < 0.001$) appears to be anomalous; when inspecting the ordination plot, the 2001 and 2009 communities largely overlap. This result may reflect the MRPP's extreme sensitivity with large sample sizes (McCune et al. 2002).

Bird Density

The 2 interaction models that suggested the strongest evidence for a response of bird density to fire were the best-supported models for 11 of the 37 species we analyzed (Table 3). Of these, the burned interaction model was best supported for 7 species and the burned severity model for 4 (Table 3 and Figure 4A-4D).

The burned additive model was the best-supported model for 6 species. For all these species, our examination of differences in mean bird density between 1 yr prefire and each year postfire illustrated no clear response to the fire. These species were Chipping Sparrow, Golden-crowned Kinglet, Mountain Chickadee, Pileated Woodpecker, Western Wood-Pewee, and Western Tanager (Figure 4E). The severity additive model was the best-supported model for 9 species (Table 3). For 3 of these species—Black-headed Grosbeak, House Wren, and Lesser Goldfinch—our visual examination of prefire and postfire density by severity level showed a directional change different from the unburned

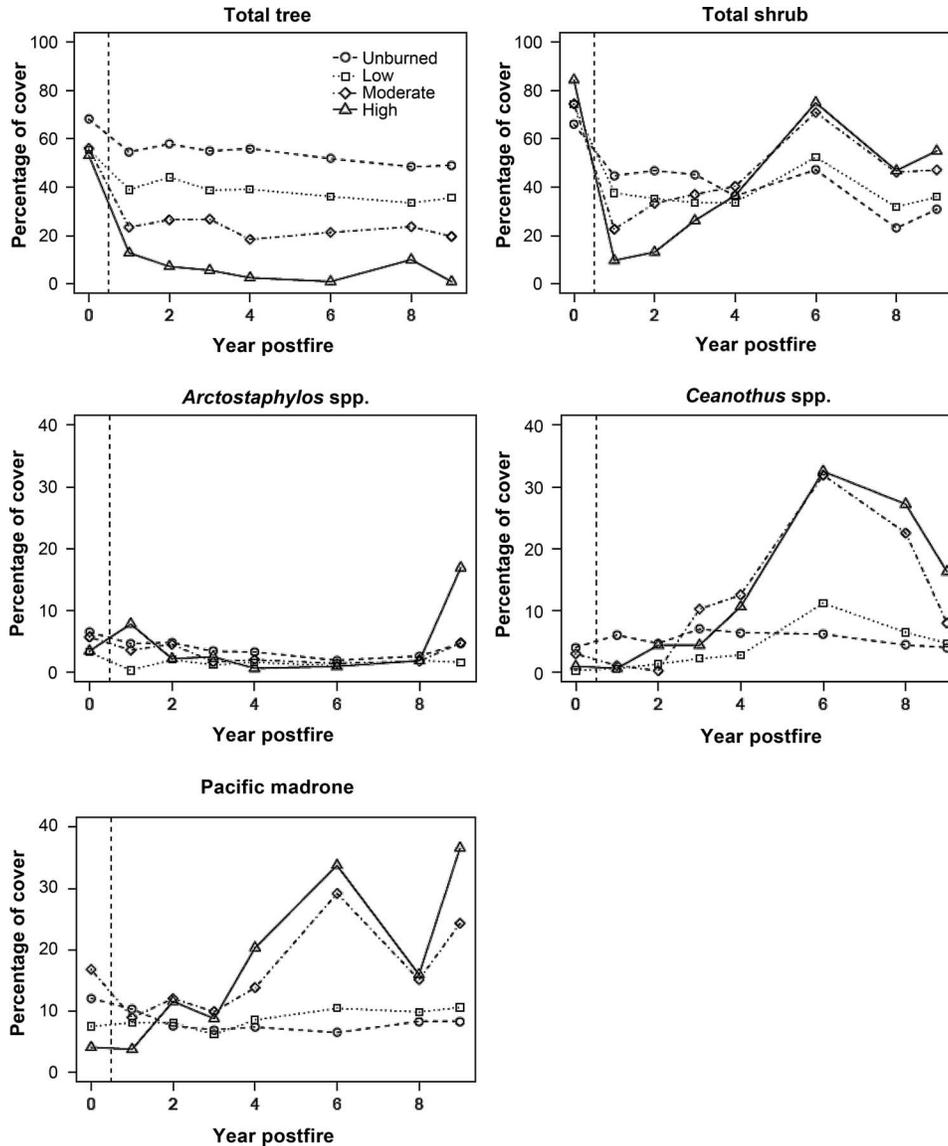


FIGURE 2. Percent cover of total tree and shrub vegetative layers, 2 shrub genera, and 1 shrub species, 1 yr prior to the Quartz Fire (2001; dashed line) and during 9 yr postfire (2002–2006, 2007, 2010), at unburned controls ($n = 83$) and in low-severity ($n = 17$), moderate-severity ($n = 21$), and high-severity ($n = 9$) burned areas.

control; for these species the additive model was explained by a difference in magnitude of change by severity, and species were classified as declining or increasing with greater severity (Figure 4C, 4D). Hairy Woodpecker, Nashville Warbler, Northern Flicker, Pacific-slope Flycatcher, Spotted Towhee, and Wilson's Warbler did not show a clear pattern of increase or decrease and were classified as "no response by severity" (Figure 4F). The null model or the temporal model was the best supported model for 11 species, which suggests that these species were not affected by the fire (Table 3). Based on the interaction and additive model results, in combination with our examination of differences in mean bird density between 1 yr prefire and

each year postfire, we described the species' response to the fire as follows.

Declined in burned areas. Five species decreased in response to fire, but without variation attributed to fire severity. These included Chestnut-backed Chickadee, Hermit Thrush, Hutton's Vireo, MacGillivray's Warbler, and Red-breasted Nuthatch (Figure 4A).

Increased in burned areas. Two species increased after fire without variation attributed to fire severity. These were Dusky Flycatcher and Wrentit, the latter increasing in years 6–9 (Figure 4B).

Declined with greater severity. Three species decreased in response to greater severity (Figure 4C). This

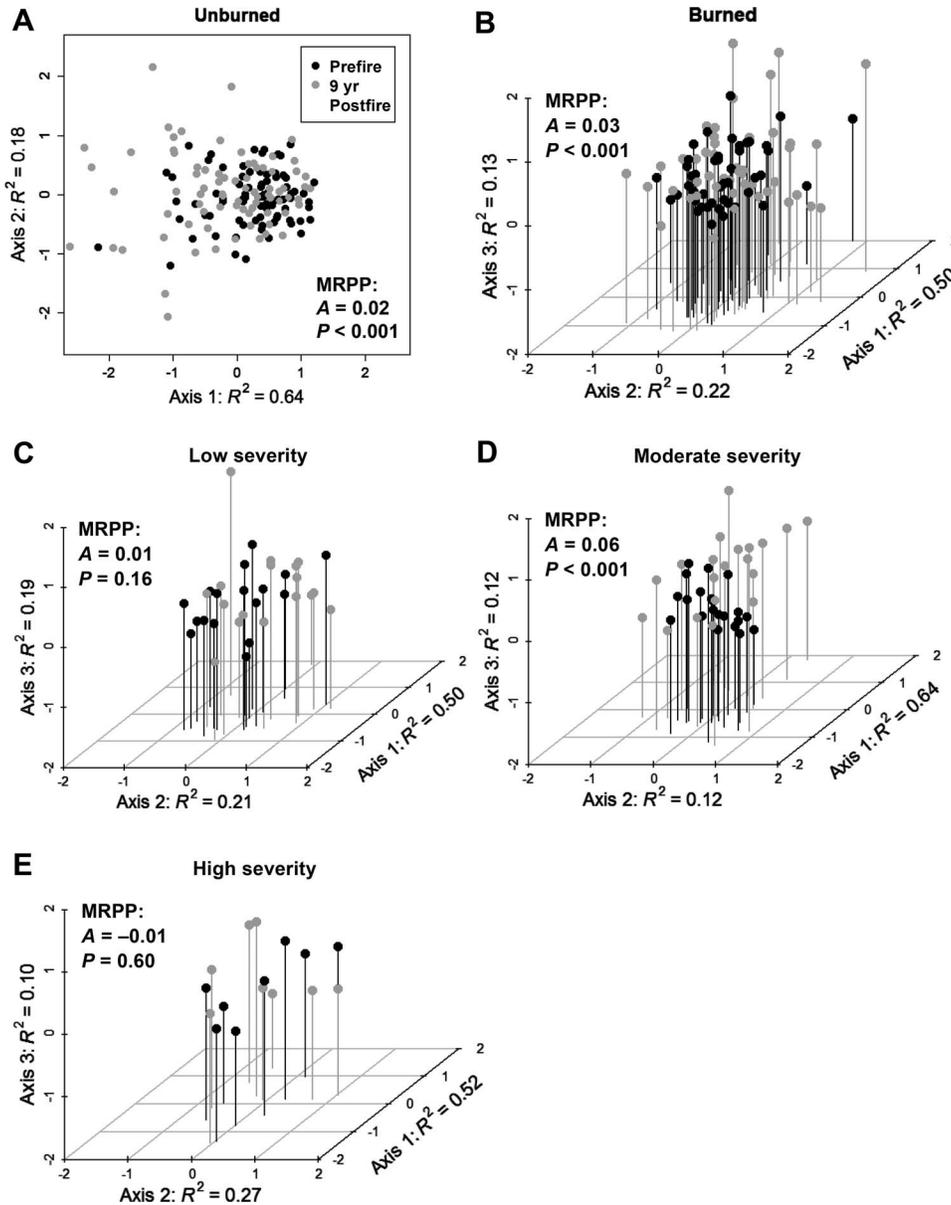


FIGURE 3. NMS (nonmetric multidimensional scaling) ordination of bird communities in the Quartz Fire, 1 yr prefire (2001) and 9 yr postfire (2010), in (A) unburned controls ($n = 83$), (B) burned ($n = 47$), (C) low-severity ($n = 17$), (D) moderate-severity ($n = 21$), and (E) high-severity ($n = 9$) areas. Points represent survey locations ordinated in species space. Axis correlations are reported in Table 2.

response was best explained by the severity interaction model for Hermit Warbler and Yellow-rumped Warbler. Of the 9 species for which the severity additive model was best supported, our visual examination of the data suggested that 1 species, Black-headed Grosbeak, declined with greater fire severity.

Increased with greater severity. Four species increased in response to severity (Figure 4D). The responses of Lazuli Bunting and Olive-sided Flycatcher were best explained by the severity interaction model; the Olive-sided Flycatcher showed a positive response beginning in year 4 (Figure

4D). Of the 9 species for which the severity additive model was best supported, our visual inspection of the data suggested that House Wren and Lesser Goldfinch responded positively to greater fire severity.

Avian Guilds

Of the 2 interaction models that would suggest the strongest evidence of a guild response to fire, only the burned interaction model was best supported and only for a single guild; bark-gleaning foragers declined in burned areas (Table 4 and Figure 5A). The burned additive model

TABLE 2. Axis correlations (r) for 5 vegetation metrics and 8 bird guilds from NMS (nonmetric multidimensional scaling) ordination of bird communities at unburned ($n = 83$), burned ($n = 47$), low-severity ($n = 17$), moderate-severity ($n = 21$), and high-severity ($n = 9$) points. For details on ordination procedure, see text.

	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
	Unburned			Burned			Low-severity		
Total tree	0.31	-0.10	-	-0.23	-0.24	0.36	-0.08	-0.10	-0.34
Total shrub	0.39	-0.31	-	-0.30	0.29	0.12	-0.42	-0.40	-0.03
Pacific madrone	0.39	-0.21	-	-0.20	0.32	-0.05	-0.38	-0.16	0.07
<i>Arctostaphylos</i> spp.	0.19	-0.01	-	-0.17	0.34	-0.04	-0.18	-0.28	0.00
<i>Ceanothus</i> spp.	0.17	-0.05	-	-0.07	0.24	-0.17	-0.14	0.03	0.25
Cavity nesters	0.09	0.40	-	-0.02	-0.12	0.44	0.06	-0.60	-0.24
Ground nesters	0.51	-0.39	-	-0.58	0.32	0.44	-0.38	-0.69	0.16
Shrub nesters	0.39	-0.38	-	-0.37	0.47	-0.43	-0.40	0.19	0.24
Tree nesters	0.74	0.13	-	-0.72	-0.42	-0.06	-0.70	0.01	-0.57
Bark foragers	-0.07	0.35	-	-0.09	-0.23	0.22	0.39	-0.30	-0.50
Foliage gleaners	0.85	0.10	-	-0.81	-0.19	0.23	-0.80	-0.48	-0.27
Flycatching foragers	0.27	-0.22	-	-0.09	-0.22	-0.41	-0.21	0.65	0.02
Ground foragers	0.26	-0.44	-	-0.46	0.43	-0.32	-0.19	-0.24	-0.05
	Moderate-severity			High-severity					
Total tree	-0.40	0.26	-0.11	-0.20	0.08	-0.04			
Total shrub	-0.21	-0.07	-0.36	0.15	0.20	0.28			
Pacific madrone	-0.09	-0.06	-0.25	-0.06	0.21	0.33			
<i>Arctostaphylos</i> spp.	-0.25	0.01	-0.04	0.22	0.51	-0.03			
<i>Ceanothus</i> spp.	-0.08	-0.33	-0.14	0.10	0.02	0.25			
Cavity nesters	0.08	-0.07	-0.12	0.06	-0.31	-0.45			
Ground nesters	-0.57	0.17	-0.60	-0.70	0.09	-0.28			
Shrub nesters	-0.29	-0.70	-0.20	-0.35	0.60	-0.39			
Tree nesters	-0.67	0.32	0.57	-0.91	-0.17	0.05			
Bark foragers	-0.30	-0.12	0.22	-0.01	0.23	0.62			
Foliage gleaners	-0.77	0.42	0.07	-0.89	-0.26	-0.19			
Flycatching foragers	-0.10	-0.30	0.09	-0.33	-0.31	0.11			
Ground foragers	-0.44	-0.62	0.13	-0.37	0.69	-0.17			

was the best-supported model for cavity nesters; visual examination of density between 1 yr prefire and each year postfire indicated that this guild declined in burned areas. The severity additive model was the best-supported model for 6 guilds (Table 4). Visual examination of prefire and postfire density suggested that 2 guilds increased in response to greater severity: flycatching foragers and, following a short-term decline, shrub nesters (Figure 5B). The other 4 guilds—ground and tree nesters and gleaning and ground foragers—showed no clear response to the fire (Figure 5C).

DISCUSSION

We found that vegetation response to the Quartz Fire over 9 yr following the fire was best explained by time and burn severity, not simply by whether or not the plot was burned. Bird responses were more complex; some community metrics and species responses were explained adequately by burn status alone, whereas others were explained best by considering severity, and still others were unaffected by the fire. Shifts in community composition and changes in density for 7 species and 2 guilds were best explained by burn status, regardless of severity level. Shifts in commu-

nity composition in moderate-severity burns and changes in density for 7 species and 2 guilds were best explained by increasing fire severity level.

Our results build upon earlier efforts to quantify the changes in bird occurrence in the first 4 yr following the Quartz Fire (Seavy and Alexander 2014). In that study, 6 of 27 species exhibited decreased occurrence in burned areas, while only a single species (Lazuli Bunting) increased (Seavy and Alexander 2014). With our longer time series, we found evidence of postfire dynamics for a larger proportion of species: 14 of 37, with 7 explained by burn status and 7 best explained by fire severity level. Six of the 14 species increased with burn or with greater severity. The larger proportion of species showing a response in our study can likely be attributed to 2 factors: (1) our analysis considered severity and thereby allowed us to detect species responses in low-, moderate-, and high-severity areas that would not necessarily have been apparent in a burn-only analysis; and (2) our analysis included a longer time series, which allowed us to detect fire effects on species that experienced delayed responses.

In combination, our results for vegetation, community composition, and species-specific and guild densities suggest that severity is an important factor in understand-

TABLE 3. Generalized linear models (see text) for species-specific density estimates using Akaike's Information Criterion corrected for overdispersion (QAIC) using the parameter \hat{c} , with number of parameters (K), log likelihood ratio (LL), the difference between each model and the best-fitting one (Δ QAIC), and the model weight (w_i). Models are reported where $w_i > 0.01$. Abbreviations: Y = year, B = burned, S = severity.

	K	LL	Δ QAIC	w_i		K	LL	Δ QAIC	w_i
Mountain Quail					Dusky Flycatcher				
Y + S	11	-511.9	0	0.50	Y + B + Y*B	16	-934	0	0.89
Y	8	-515	1.6	0.23	Y + S + Y*S	32	-897	4.1	0.11
Y + B	9	-514.3	1.8	0.20	Minimum QAIC = 734 ($\hat{c} = 2.7$)				
Y + B + Y*B	16	-509.4	4	0.07	Pacific-slope Flycatcher				
Minimum QAIC = 1,273.1 ($\hat{c} = 1$)					Y + S	11	-1,014.9	0	0.86
Hairy Woodpecker					Y + B	9	-1,030.2	4.6	0.09
Y + S	11	-584.3	0	1.00	Y	8	-1,036.3	6	0.04
Minimum QAIC = 505.8 ($\hat{c} = 2.4$)					Minimum QAIC = 594.3 ($\hat{c} = 3.5$)				
Northern Flicker					Cassin's Vireo				
Y + S	11	-519.3	0	0.71	Null	1	-1,799	0	0.57
Y + B	9	-522.4	2.2	0.23	Y	8	-1,776.7	2.1	0.20
Null	1	-531.9	5.4	0.05	Y + B	9	-1,774.2	2.8	0.14
Minimum QAIC = 1,068.7 ($\hat{c} = 1$)					Y + B + Y*B	16	-1,750.7	4.3	0.07
Pileated Woodpecker					Y + S	11	-1,772.9	6.1	0.03
Y + B	9	-218.8	0	0.78	Minimum QAIC = 959.8 ($\hat{c} = 3.8$)				
Y + S	11	-218.4	3.1	0.17	Hutton's Vireo				
Null	1	-227.8	6.9	0.03	Y + B + Y*B	16	-325.1	0	1.00
Minimum QAIC = 574.9 ($\hat{c} = 1$)					Minimum QAIC = 484.0 ($\hat{c} = 1.4$)				
Olive-sided Flycatcher					Warbling Vireo				
Y + S + Y*S	32	-188.2	0	0.84	Y	8	-1,384.7	0	0.57
Y + S	11	-205.3	4.9	0.07	Y + B	9	-1,384.4	1.9	0.23
Y + B + Y*B	16	-201.9	5.6	0.05	Y + S	11	-1,377.5	2.4	0.17
Y + B	9	-207.3	6.4	0.04	Y + B + Y*B	16	-1,365.3	6.3	0.02
Minimum QAIC = 578.7 ($\hat{c} = 1$)					Minimum QAIC = 706.8 ($\hat{c} = 4.0$)				
Western Wood-Pewee					Steller's Jay				
Y + B	9	-599.9	0	0.67	Y + B	9	-791.5	0	0.60
Y + S	11	-597.4	1.4	0.33	Y	8	-793.4	1.6	0.28
Minimum QAIC = 611.4 ($\hat{c} = 2.0$)					Y + S	11	-791.1	3.3	0.11
Mountain Chickadee					Minimum QAIC = 1,467.9 ($\hat{c} = 1.1$)				
Y + B	9	-1,118.4	0	0.79	American Robin				
Y + S	11	-1,116.2	2.7	0.20	Y + S	11	-685.8	0	0.47
Minimum QAIC = 630.9 ($\hat{c} = 3.6$)					Y	8	-694.7	1.2	0.27
Chestnut-backed Chickadee					Y + B + Y*B	16	-676.6	2.5	0.13
Y + B + Y*B	16	-1,503.8	0	1.00	Y + B	9	-694.1	2.7	0.12
Minimum QAIC = 522.3 ($\hat{c} = 6.13$)					Minimum QAIC = 577.4 ($\hat{c} = 2.5$)				
Bushtit					Wrentit				
Y + S	11	-3,356.9	0	0.36	Y + S + Y*S	32	-137.1	0	0.59
Y + B + Y*B	16	-3,249	0.1	0.33	Y + B + Y*B	16	-147.2	0.9	0.38
Null	1	-3,587	1.1	0.21	Y + S	11	-151.7	5.7	0.03
Y	8	-3,464.2	3.8	0.05	Minimum QAIC = 510.8 ($\hat{c} = 1$)				
Y + B	9	-3,444.4	4	0.05	Nashville Warbler				
Minimum QAIC = 329.1 ($\hat{c} = 21.9$)					Y + S	11	-3,086.2	0	0.99
Red-breasted Nuthatch					Minimum QAIC = 1,494.3 ($\hat{c} = 1$)				
Y + B + Y*B	16	-1,255.2	0	1.00	Yellow-rumped Warbler				
Minimum QAIC = 995.0 ($\hat{c} = 2.6$)					Y + S + Y*S	32	-1,903.3	0	0.99
Brown Creeper					Minimum QAIC = 1,509.9 ($\hat{c} = 2.6$)				
Y + B	9	-598.8	0	0.57	Hermit Warbler				
Y	8	-603.5	1.4	0.28	Y + S + Y*S	32	-2,410	0	1.00
Y + S	11	-597	2.8	0.14	Minimum QAIC = 1,539.2 ($\hat{c} = 3.3$)				
Minimum QAIC = 447.9 ($\hat{c} = 2.79$)					MacGillivray's Warbler				
House Wren					Y + B + Y*B	16	-1,806.8	0	1.00
Y + S	11	-1,247	0	1.00	Minimum QAIC = 1,058.5 ($\hat{c} = 3.5$)				
Minimum QAIC = 800.8 ($\hat{c} = 3.2$)					Wilson's Warbler				
					Y + S	11	-892.7	0	0.76

TABLE 3. Continued.

	K	LL	Δ QAIC	w_i		K	LL	Δ QAIC	w_i
Townsend's Solitaire					Y	8	-914.4	3.5	0.13
Y + B + Y*B	16	-525.9	0	0.42	Y + B	9	-911.9	4.4	0.08
Y + S	11	-535.5	0.4	0.35	Null	1	-952.9	6.5	0.03
Y	8	-542.5	1.9	0.16	Minimum QAIC = 415.4 (\hat{c} = 4.5)				
Y + B	9	-542.2	3.7	0.07	Western Tanager				
Minimum QAIC = 602.1 (\hat{c} = 1.8)					Y + B	9	-1,182.2	0	0.82
Hermit Thrush					Y + S	11	-1,181.8	3.6	0.14
Y + B + Y*B	16	-409.6	0	0.93	Y	8	-1,190.4	6.2	0.04
Y + S + Y*S	32	-397.4	5.1	0.07	Minimum QAIC = 1,207.6 (\hat{c} = 1.99)				
Minimum QAIC = 937.2 (\hat{c} = 1)					Brown-headed Cowbird				
Spotted Towhee					Null	1	-1,170.1	0	0.82
Y + S	11	-1,463.6	0	1.00	Y + S	11	-1,123.8	4.4	0.09
Minimum QAIC = 811.0 (\hat{c} = 3.7)					Y	8	-1,144.2	5.3	0.06
Chipping Sparrow					Y + B	9	-1,143.3	7	0.03
Y + B	9	-337.1	0	0.62	Minimum QAIC = 396.6 (\hat{c} = 5.93)				
Y + S	11	-336	2.6	0.17	Purple Finch				
Y + B + Y*B	16	-328.5	2.6	0.17	Y	8	-616.6	0	0.35
Y	8	-342.5	5.2	0.05	Null	1	-629.8	0.5	0.27
Minimum QAIC = 465.3 (\hat{c} = 1.5)					Y + B	9	-615.6	0.9	0.22
Dark-eyed Junco					Y + B + Y*B	16	-604.3	2.6	0.10
Y + B	9	-2,280	0	0.48	Y + S	11	-614.3	3.5	0.06
Y	8	-2,285.4	0.6	0.35	Minimum QAIC = 693.6 (\hat{c} = 1.8)				
Y + S	11	-2,276.3	2.2	0.16	Lesser Goldfinch				
Minimum QAIC = 1,134.5 (\hat{c} = 4.1)					Y + S	11	-766.9	0	0.98
Black-headed Grosbeak					Y + B + Y*B	16	-764.8	8.8	0.01
Y + S	11	-2,553	0	1.00	Y + S + Y*S	32	-711.4	9.7	0.01
Minimum QAIC = 1,875.2 (\hat{c} = 2.76)					Minimum QAIC = 468.0 (\hat{c} = 3.4)				
Lazuli Bunting									
Y + S + Y*S	32	-1,205.2	0	0.97					
Y + S	11	-1,285.2	6.9	0.03					
Minimum QAIC = 800.9 (\hat{c} = 3.3)									

ing response to wildfire. Moderate-severity fire altered the bird community as a whole, and both moderate and high severity benefited select individual species as well as shrub-nesting species and flycatching foragers. The changes in individual bird species' densities that we found are consistent with several studies that have emphasized the importance of fire severity in understanding changes in bird abundance (Smucker et al. 2005, Kotliar et al. 2007). The number of species included in our analysis was similar to that in Smucker et al. (2005; $n = 40$) and notably more than included by Kotliar et al. (2007; $n = 15$), but the proportions of species responses in all 3 studies were quite similar. We found an effect of burn status for 19% of species and an effect of severity level for 19% of species. Smucker et al. (2005) found 22% of species affected by burn status and an additional 25% affected when considering severity level; Kotliar et al. (2007) examined only a severity effect and found changes for 26% of species analyzed.

The strong positive response by shrub nesters, which was not found by Seavy and Alexander (2014) in the earlier Quartz Fire study, in combination with the shifts in

community composition in burned and moderate severity, suggest that time since fire was important even over the relatively short time frame of our study. Nine years postfire, the bird community had shifted from mature-forest species associated with tree cover to early-successional species associated with shrub cover. This is consistent with the findings of Fontaine et al. (2009) in a high-severity fire in the same region, where the bird community differed between mature forest, recent burn, older burn, and repeat burn, with the lowest density 2 yr after fire. Burned communities were driven by reduced conifer cover, increased shrub volume, and increased numbers of snags (Fontaine et al. 2009). In this region, mixed-severity fire regimes play an important role in maintaining the presence of hardwoods, most of which show rapid basal sprouting postfire (Halofsky et al. 2011). Hardwoods form much of the shrub and subcanopy layers and provide structural diversity important to wildlife (Hagar 2007). However, fire-generated early-successional habitat in the western United States is limited, compared with historical conditions, and is a limiting factor for a number of management-relevant species (Noss et al. 2006,

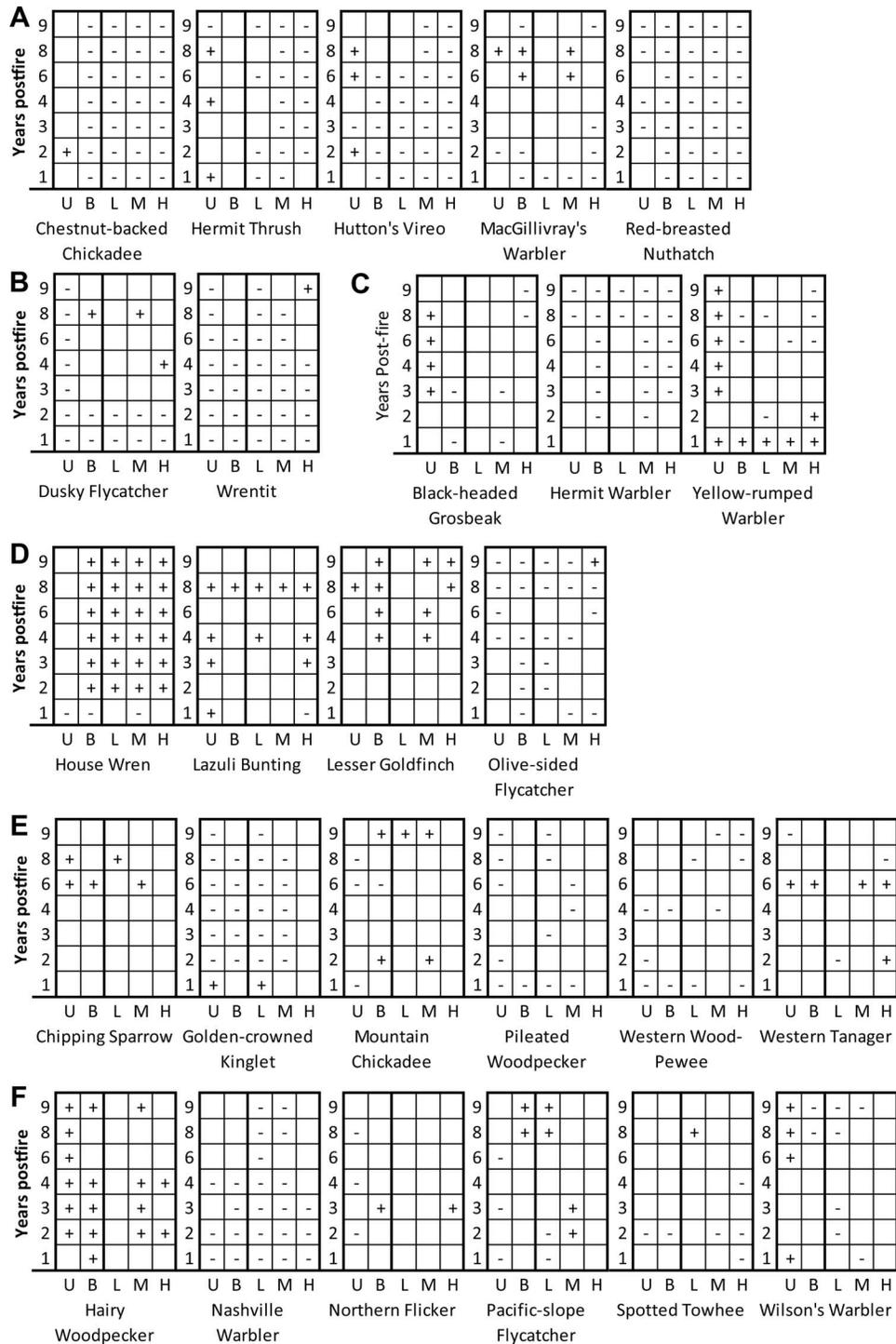


FIGURE 4. We compared differences in mean density between 1 yr prefire (t_0) and each year postfire (t_i) for the 26 species whose variation in density was best explained by the burn-status or severity model sets. We bootstrapped means and 90% confidence intervals (1,000 repetitions) for each year by burn status or severity level. Mean density between years t_i and t_0 are significantly greater (+) or lower (-) when confidence intervals do not overlap zero. White squares indicate no significant difference in densities between years t_i and t_0 . Results were visually examined to organize species by postfire response: (A) declined in burned areas, (B) increased in burned areas, (C) declined with greater severity, (D) increased with greater severity, (E) no response by burn, and (F) no response by severity. Abbreviations and sample sizes: U = unburned control ($n = 83$), B = burned ($n = 47$), L = low-severity ($n = 17$), M = moderate-severity ($n = 21$), and H = high-severity ($n = 9$).

TABLE 4. Generalized linear models (see text) for density estimates of (A) nesting and (B) foraging guilds using Akaike's Information Criterion corrected for overdispersion (QAIC) using the parameter \hat{c} , with number of parameters (K), log likelihood ratio (LL), the difference between each model and the best-fitting one (Δ QAIC), and the model weight (w_i). Models are reported where $w_i > 0.01$. Abbreviations: Y = year, B = burned, S = severity.

(A)				
Guild	K	LL	Δ QAIC	w_i
Cavity nesters ^a				
Y + B	9	-2,519.5	0	0.80
Y + S	11	-2,518.8	3.7	0.13
Y + B + Y*B	16	-2,498.6	4.9	0.07
Ground nesters ^b				
Y + S	11	-3,452.6	0	0.65
Y	8	-3,468	2.2	0.22
Y + B	9	-3,466.5	3.4	0.12
Shrub nesters ^c				
Y + S	11	-2,922.7	0	1.00
Tree nesters ^d				
Y + S	11	-5,050.1	0	0.92
Y + B + Y*B	16	-5,040.4	6.7	0.03
Y	8	-5,088.2	6.8	0.03
Y + B	9	-5,085.4	7.9	0.02

^a Minimum QAIC = 1,121.4 (\hat{c} = 4.6).

^b Minimum QAIC = 1,865.1 (\hat{c} = 3.7).

^c Minimum QAIC = 1,497.9 (\hat{c} = 4.0).

^d Minimum QAIC = 1,719.2 (\hat{c} = 6.0).

(B)				
Guild	K	LL	Δ QAIC	w_i
Bark foragers ^a				
Y + B + Y*B	16	-1,853.3	0	0.97
Y + B	9	-1,888.9	8.2	0.02
Gleaning foragers ^b				
Y + S	11	-5,409.6	0	0.92
Y + B + Y*B	16	-5,395.2	5.4	0.06
Y + S + Y*S	32	-5,302.6	7.7	0.02
Flycatching foragers ^c				
Y + S	11	-1,862.8	0	0.75
Y + B + Y*B	16	-1,852.3	2.7	0.20
Y + B	9	-1,876.4	5.4	0.05
Ground foragers ^d				
Y + S	11	-3,314.1	0	1.00

^a Minimum QAIC = 1,187.3 (\hat{c} = 3.2).

^b Minimum QAIC = 1,757.4 (\hat{c} = 2.9).

^c Minimum QAIC = 1,310.5 (\hat{c} = 6.2).

^d Minimum QAIC = 1,816.4 (\hat{c} = 3.7).

Fontaine and Kennedy 2012). Hence, reduction in broadleaf-dominated early seral forest due to fire suppression, forest management, postfire forest management, and succession has led to population declines for birds associated with this habitat (Betts et al. 2010).

The complex mosaic created by the Quartz Fire, including low-, moderate-, and high-severity burned points

within 2,500 ha surrounded by extant forest, represents the naturally occurring heterogeneity that was prominent historically in forests with mixed-severity fire regimes (Agee 1998). Although both local vegetation and the amount and distribution of habitat at larger scales have been shown to be important for individual bird species (Lichstein et al. 2002, Taillie et al. 2015) the importance of the juxtaposition of patches of varying fire severity is still not well understood (Lindenmayer et al. 2014). Birds will move among fire severity stages, perhaps influenced by availability of snags or other features (e.g., Tingley et al. 2014). This may be another important driver of postfire bird abundance and community composition. Future study incorporating patch size and heterogeneity of vegetation structure and composition characteristics, including those that are driven by disturbance severity, would be informative.

Management Implications

Our results illustrate the importance of mixed-severity wildfire in shaping bird communities. In western forest landscapes, where wildfire is regularly suppressed, development of forest-management practices that maintain heterogeneous vegetative composition and seral stages to support a diversity of bird communities and maintain species-specific populations and guilds is an important consideration. Land managers charged with maintaining biodiversity as well as achieving management priorities should consider how both natural disturbance events and land-management actions cumulatively affect wildlife. The potential for wildfire to benefit select bird species and guilds should be considered among more typical management objectives when designing postfire management. Common postfire management actions that alter natural succession, such as planting of conifer trees and control of broadleaf shrubs, may not be necessary to achieve objectives (Shatford et al. 2007, Halofsky et al. 2011). Furthermore, our results add to a growing body of literature suggesting that bird communities and individual bird species respond differently to fire severity levels, supporting the need for all fire severities to be represented within management of western forests that historically experienced mixed-severity fire regimes (Saab and Powell 2005, Hutto et al. 2008). Although some forest-management techniques (e.g., thinning and fuel reduction) provide disturbance, most techniques applied independently will likely not achieve the gradient of change that resulted from historical fire events (Rush et al. 2012, Stephens et al. 2012)—which emphasizes the important ecological role of wildfire and subsequent natural succession, and the potential role that managed wildfire could play in achieving forest-management goals.

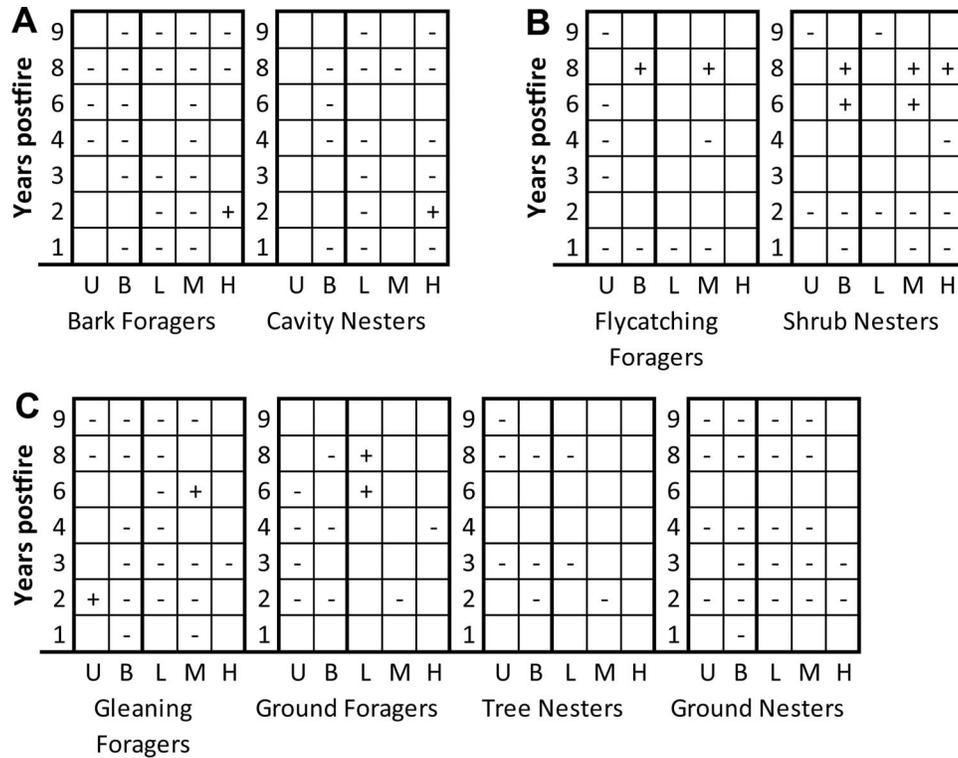


FIGURE 5. We compared differences in mean density between 1 yr prefire (t_0) and each year postfire (t_i) for the 8 foraging and nesting guilds whose variation in density was best explained by the burn-status or severity model sets. We bootstrapped means and 90% confidence intervals (1,000 repetitions) for each year by burn status or severity level. Mean density between years t_i and t_0 are significantly greater (+) or lower (–) when confidence intervals do not overlap zero. White squares indicate no significant difference in densities between years t_i and t_0 . Results were visually examined to organize guilds by postfire response: (A) declined in burned areas, (B) increased with greater severity, and (C) no response by severity. Abbreviations and sample sizes are the same as in Figure 4.

ACKNOWLEDGMENTS

This paper was strengthened by the reviews of J. DeJulio, B. McCune, C. J. Ralph, and two anonymous reviewers. We also thank C. Spinosa for her vision and support of management-relevant bird monitoring in the Applegate Valley. Thanks to the many people who completed fieldwork for this project, including D. Van den Broek, B. Chapman, M. Clegg, E. Crosson, A. Darlak, J. DeStaebler, K. Glueckert, S. Kies, I. Koski, J. Lawrence, F. Lospalluto, and L. Sutherlin.

Funding statement: Funding for this project was provided by the Joint Fire Sciences Program project 01B-3-2-10, Rogue River-Siskiyou National Forest, Bureau of Land Management Medford District, and Secure Rural Schools and Community Self-Determination Act of 2000 Title II. None of the funders had any influence on the content of this manuscript and none required approval for publication.

Ethics statement: No permits or approvals were necessary for this field study, and all land accessed was publicly owned.

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APPENDIX TABLE 5. Average density (individuals ha⁻¹) and standard error for (A) species and (B) guilds 1 yr prior to the fire (2001) in unburned areas and sites that would later burn during the Quartz Fire (all severities combined). Guild classifications are based on Ehrlich et al. (1988) (nesting) and Cornell Lab of Ornithology 2014 (foraging). The analysis was restricted to these species, which had sufficient sample size ($n > 60$) across all years and burn statuses for calculating density. Species with zero detections in 2001 were detected in later years.

(A)					
Common name	Scientific name	Foraging guild	Nesting guild	Unburned	Burned
Mountain Quail	<i>Oreortyx pictus</i>	Ground	Ground	0.09 (0.01)	0.06 (0.02)
Hairy Woodpecker	<i>Picoides villosus</i>	Bark	Cavity	0.00 (0.00)	0.00 (0.00)
Northern Flicker	<i>Colaptes auratus</i>	Ground	Cavity	0.07 (0.02)	0.07 (0.02)
Pileated Woodpecker	<i>Dryocopus pileatus</i>	Bark	Cavity	0.03 (0.01)	0.01 (0.01)
Olive-sided Flycatcher	<i>Contopus cooperi</i>	Flycatching	Tree	0.02 (0.01)	0.10 (0.02)
Western Wood-Pewee	<i>Contopus sordidulus</i>	Flycatching	Tree	0.06 (0.02)	0.14 (0.04)
Dusky Flycatcher	<i>Empidonax oberholseri</i>	Flycatching	Shrub	0.18 (0.05)	0.25 (0.07)
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	Flycatching	Tree	0.17 (0.05)	0.03 (0.03)
Cassin's Vireo	<i>Vireo cassinii</i>	Foliage-gleaning	Tree	0.35 (0.07)	0.39 (0.09)
Hutton's Vireo	<i>Vireo huttoni</i>	Foliage-gleaning	Tree	0.02 (0.01)	0.08 (0.03)
Warbling Vireo	<i>Vireo gilvus</i>	Foliage-gleaning	Tree	0.28 (0.06)	0.25 (0.09)
Steller's Jay	<i>Cyanocitta stelleri</i>	Ground	Tree	0.16 (0.03)	0.13 (0.03)
Mountain Chickadee	<i>Poecile gambeli</i>	Foliage-gleaning	Cavity	0.27 (0.07)	0.02 (0.02)
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	Foliage-gleaning	Cavity	0.13 (0.07)	0.46 (0.14)
Bushtit	<i>Psaltriparus minimus</i>	Foliage-gleaning	Tree	0.25 (0.15)	0.56 (0.33)
Golden-crowned Kinglet	<i>Regulus satrapa</i>	Foliage-gleaning	Tree	0.50 (0.14)	0.25 (0.14)
Red-breasted Nuthatch	<i>Sitta canadensis</i>	Bark	Tree	0.37 (0.06)	0.56 (0.09)
Brown Creeper	<i>Certhia americana</i>	Bark	Tree	0.05 (0.03)	0.07 (0.04)
House Wren	<i>Troglodytes aedon</i>	Foliage-gleaning	Cavity	0.04 (0.03)	0.22 (0.06)
Townsend's Solitaire	<i>Myadestes townsendi</i>	Flycatching	Ground	0.05 (0.02)	0.04 (0.02)
Hermit Thrush	<i>Catharus guttatus</i>	Ground	Ground	0.04 (0.01)	0.13 (0.03)
American Robin	<i>Turdus migratorius</i>	Ground	Tree	0.20 (0.05)	0.09 (0.04)
Wrentit	<i>Chamaea fasciata</i>	Foliage-gleaning	Shrub	0.04 (0.02)	0.06 (0.02)
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	Foliage-gleaning	Ground	1.16 (0.17)	1.55 (0.17)
Yellow-rumped Warbler	<i>Setophaga coronata</i>	Foliage-gleaning	Tree	0.24 (0.05)	0.33 (0.07)
Hermit Warbler	<i>Setophaga occidentalis</i>	Foliage-gleaning	Tree	1.04 (0.11)	0.75 (0.12)
MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	Foliage-gleaning	Shrub	0.26 (0.06)	0.37 (0.08)
Wilson's Warbler	<i>Cardellina pusilla</i>	Ground	Ground	0.02 (0.02)	0.07 (0.05)
Western Tanager	<i>Piranga ludoviciana</i>	Foliage-gleaning	Tree	0.24 (0.05)	0.11 (0.04)
Spotted Towhee	<i>Pipilo maculatus</i>	Ground	Shrub	0.17 (0.06)	0.50 (0.12)
Chipping Sparrow	<i>Spizella passerina</i>	Ground	Tree	0.02 (0.01)	0.00 (0.00)
Dark-eyed Junco	<i>Junco hyemalis</i>	Ground	Ground	0.46 (0.07)	0.38 (0.10)
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	Foliage-gleaning	Tree	0.76 (0.09)	0.90 (0.11)
Lazuli Bunting	<i>Passerina amoena</i>	Ground	Shrub	0.06 (0.03)	0.16 (0.05)
Brown-headed Cowbird	<i>Molothrus ater</i>	Ground	Tree	0.12 (0.05)	0.09 (0.06)
Purple Finch	<i>Haemorhous purpureus</i>	Foliage-gleaning	Tree	0.06 (0.02)	0.07 (0.03)
Lesser Goldfinch	<i>Spinus psaltria</i>	Foliage-gleaning	Tree	0.03 (0.02)	0.00 (0.00)
(B)				Unburned	Burned
Guild					
Bark foragers				0.46 (0.07)	0.64 (0.1)
Flycatching foragers				0.47 (0.07)	0.56 (0.11)
Foliage-gleaning foragers				5.68 (0.37)	6.43 (0.47)
Ground foragers				1.40 (0.13)	1.61 (0.22)
Cavity nesters				0.55 (0.10)	0.60 (0.14)
Ground nesters				1.77 (0.18)	2.18 (0.2)
Shrub nesters				0.71 (0.12)	1.34 (0.2)
Tree nesters				5.00 (0.28)	5.12 (0.42)