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Birds of the Burn: Avian Community and Functional Guild Variation Five Years Post-Fire in Warm–Dry Mixed Conifer, Southwest Colorado

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Abstract: Birds contribute to the trophic interactions within mixed conifer ecosystems and provide a suite of services, such as nutrient transport, seed dispersal, habitat creation, and insect regulation. Avian communities vary in response to the structure and composition of their habitat, which may be drastically altered by fire, the predominant disturbance of western mixed conifer forests. We conducted avian point count surveys during the peak breeding season, five years post-fire, across four burn severities (unburned, low, moderate, and high) within the 416 Fire perimeter, a 55,000-acre mixed-severity fire that burned near Durango, Colorado in 2018. Avian communities in each burn severity were evaluated for richness, diversity, differentiation, indicator species, and functional guild composition. Species assemblages were significantly different across all burn severities, excluding the low to moderate areas comparison, with differentiation driven by live tree and snag density. Avian species' richness and diversity were not significantly different across burn severities, highlighting the importance of utilizing multivariate community analysis. Unburned and high-burn areas had significant variation in functional guilds and numerous indicator species. This study provides evidence of avian community differentiation by burn severity, suggesting that management practices promoting heterogenous stand structure in warm–dry mixed conifer will positively influence avian biodiversity.

Keywords: mixed conifer; fire; avian community; avian assemblages; functional guild; indicator species; birds; southwest Colorado

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1. Introduction

Mixed conifer forests are a diverse, prominent habitat type covering approximately 20% of forested lands in the Southwestern United States, at elevations 2270–3030 m [1,2]. The disturbance regimes, habitat characteristics, and species present in mixed conifer forests represent a transition zone between lower elevation ponderosa pine forests and higher elevation spruce–fir forests [1]. Mixed conifer forests may be categorized as warm–dry to cool–moist [1]. Warm–dry mixed conifer forests occur predominantly on south-facing aspects at lower elevations and, in the Southwest, are composed primarily of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), aspen (*Populus tremuloides*), and Gambel oak (*Quercus gambelii*) [1]. These forests are valuable ecological systems that are home to dozens of resident and migratory birds, including species of management concern, such as the Mexican Spotted Owl, Northern Goshawk, Williamson's Sapsucker, Dusky Flycatcher, and the Olive-Sided Flycatcher [3]. Avian species contribute to the trophic interactions within a forest ecosystem and provide a suite of ecosystem services such as nutrient transport, seed dispersal, habitat creation, and insect regulation [4,5]. These birds form communities that vary in response to the structure and composition of the forest, which may be drastically altered by fire, the predominant disturbance in the Southwest [6–9]. Recognizing the variation in avian community assemblages within a post-fire environment may aid in understanding the resilience of mixed conifer ecosystems following fire, as avian diversity is often correlated with the diversity of other taxa [10,11].

Fires in warm–dry mixed conifer forests were historically of mixed severity: low- to moderate-intensity surface fires burned at multi-decadal frequencies, with occasional high-severity patches of crown fires [1,12]. Low- to moderate-severity burn areas generally are characterized by removal and then regrowth of resprouting surface fuels (grass, forbs and shrubs), with losses of the tree canopy in areas with moderate burn severity and long burning residence times. High-severity fires cause tree mortality and create open areas with snags and regrowth of herbaceous plants and shrubs. Mixed-severity fires generate a heterogeneous mosaic of stands that vary in their vertical and horizontal structure and composition [13,14]. Following European settlement in the Southwest, fire suppression altered the recurrent mixed-severity fire regime [15]. The absence of fire promoted the growth of shade-tolerant, mesic species such as *Pseudotsuga menziesii* and *Abies concolor* in warm–dry mixed conifer forests, altering stand characteristics such as density and canopy cover, serving to homogenize the horizontal and vertical structure of mixed conifer forests on a landscape scale [16,17]. The homogenization of forests and increased drought conditions in the Southwest have increased fire severity, frequency, and area burned, influencing avian species assemblages post-fire [15,18–23].

Post-fire conditions vary based on the severity of the fire and provide alternate resources used by different bird species. A greater complexity of post-fire habitat in a region should correlate to a greater diversity of birds, assuming the habitat is suitable for local species [11,14,24,25]. In regions with prominent deciduous forests, diversity is often positively correlated with the presence of broadleaf trees, due to their structural complexity and foraging opportunities [11]. In western conifer ecosystems, this same principle may be tested in post-fire successional stands that gain complexity from shrub cover, snags, and the resprouting of aspen. Quantifying post-fire diversity is increasingly relevant due to warming climate trends and increased fire frequency in the Southwest, necessitating active forest management strategies [22,23]. Diversity is an important measure of ecosystem and community health; however, it is important to consider other measures when evaluating communities, as an area with high diversity may not have high ecological value [26]. Likewise, areas with low diversity may have distinct features that are utilized by unique specialist species. Specialists often have narrow habitat requirements and may be significantly impacted by successional changes in post-fire vegetation and forest management activities [9]. These specialist species may be considered positive indicator species, species that have special habitat needs and are representative of the habitat in which they are found [26,27]. For wildfire, a species may be considered a positive indicator of a post-burn habitat if they are strongly associated with one burn severity. In addition to diversity indices and indicator species, the composition of avian communities is of interest, to illustrate how interrelated taxa form assemblages in a habitat. Variations in environmental conditions in different burn areas may drive divergent community assemblages with unique compositions [9].

To provide a generalized approach in understanding avian communities, species may be grouped into functional guilds based on a variety of life history habits such as feeding substrate, feeding technique, nesting sites, and migratory patterns [6]. These are useful ways to measure how changes in habitat influence not just species, but community dynamics [6]. The variety of habitats in post-burn forests provides diverse opportunities for functional guilds. High-burn severity areas typically have a high snag density, which favors cavity-nesting species such as woodpeckers and insectivorous species that eat insects associated with recently deceased trees [28]. Aerial insectivores, such as flycatchers, are known to respond favorably to moderately open canopies that favor their hunting strategies [29]. The successional growth of shrubs and aspen following low- and moderate-severity fire favors shrub-nesting species [29]. In low- and moderate-severity fires, large trees may produce more cones when released from pressure from surrounding small trees. This increase in cone production may favor granivorous species such as Clark's Nutcracker and Red Crossbill [29]. The evaluation of functional guilds can illuminate the type and quantity of resources available in different post-fire environments, and how different resources reflect avian community structure.

Avian communities in post-burn mixed conifer forests have been studied extensively in some regions of the country, but there is little recent information about these systems in Southwest Colorado [3,9,13,28,30]. When researchers first began studying the effects of fire on birds in USA, studies often focused on the difference between burned and unburned forest [30,31]. It quickly became clear that some birds respond favorably to fire and others unfavorably. Indeed, Bock and Lynch reported more species unique to burned areas than unburnt in 1970 [30]. However, the lack of distinction between burn severities caused many birds to be listed as mixed responders [28,31]. Around 2004, researchers began to include burn severity into studies, making the response of avian species more predictable and informative [28,32]. This study addresses the variation in burn severities by stratifying burn areas by change in percent canopy cover, according to RAVG data (Rapid Assessment of Vegetation Condition after Wildfire). The time since fire has also been revealed to be a crucial component to post-burn avian communities, as many groups follow successional trajectories initiated by fire and continue to be influenced by fire up to a decade post-burn [24,29,33]. Many studies in mixed conifer areas post-fire have been conducted three years or less following a burn, with studies five years post-fire lacking in the Southwest [9,25]. Five years post-fire is sufficient time for shrub regeneration and the secondary colonization of snags, following the dispersal of wood-boring insects [13,31].

Previous studies in mixed conifer forests have demonstrated changes in the abundance and/or density of avian species in response to fire [25,28]. This study aims to build on previous work by evaluating avian community differentiation and changes in functional guild abundance across burn severities, as well as identifying indicator species. This can inform management decisions, such as forest thinning, prescribed fire treatments, and species monitoring, to help forest managers promote biodiversity when considering the effects of fire in the Southwest. We used the 416 Fire in Southwest Colorado as a model to quantify the differences in avian community composition following mixed severity fire in warm–dry mixed conifer forests. The objectives were as follows: (1) to determine how avian richness, abundance, and diversity vary among burn severities (unburned, low, moderate, and high); and (2) to quantify variations in avian community assemblages and functional guild associations and to identify indicator species (e.g., species that are uniquely associated with burn severity) for different burn severities in warm–dry mixed conifer forests in Southwest Colorado. We hypothesized that, firstly, high burn severities would significantly differ in their community and functional guild composition from other burn areas, due to the greater density of snags, lower density of live trees, and increased presence of herbaceous plants; and, secondly, that indicator species would be found in unburned and high-severity areas, as some birds rely on snags and others on undisturbed old growth.

2. Materials and Methods

The 416 Fire was ignited on 1 June 2018, and burned 223 km^2 in the Southern San Juan National Forest in the Hermosa Special Management Area and Hermosa Wilderness [33]. The area burned was primarily mixed conifer [33]. The approximate distribution of burn severities was 44% low, 20% moderate, 19% high, and 17% unburned [34]. The study site is located approximately 21 km north of Durango, Colorado, in the southern portion of the San Juan National Forest adjacent to Hermosa Creek within the Hermosa Special Management Area and Hermosa Wilderness [33]. The study area ranges in elevation from 2277 m to 2470 m on slopes that range from 30 to 45 degrees with diverse aspects. The average daily temperatures range from a maximum of 30 °C in July to a minimum of −9.7 °C in January [35]. The average annual precipitation is 53.2 cm, with the greatest amounts occurring in July and August due to summer thunderstorm activity [35]. Precipitation from November to March is dominated by snowfall. Forest types in the study area vary from pine oak forest and warm–dry mixed conifer in the southern section of the burn to cool–moist mixed conifer and subalpine in the northern section of the burn area [34]. Aspen is present in the study area and continuous stands of aspen exist adjacent to plots; however, aspen is only a minor component of the overstory trees present in plots. The study area has never been logged and has a high proportion of large diameter trees for all species present, with many stands having old growth characteristics [34]. *Pinus ponderosa*, *Pseudotsuga menziesii*, *Abies concolor*, *Abies lasiocarpa* (subalpine fir), *Pinus flexilis* (limber pine), *Picea pungens* (blue spruce), and *Populus tremuloides* are the common tree species. Common sprouting shrubs include *Quercus gambelii*, *Symphoricarpos oreophilus* (snowberry), *Prunus virginiana* (chokecherry), and *Amelanchier alnifolia* (Utah serviceberry). In 2008, portions of the study area were burned in a broadcast prescribed fire using aerial ignitions [34]. Ten years later in 2018, the study area was burned by an unplanned, artificial ignition that burned a total of 223 km^2 (the 416 Fire). The 416 Fire burned during an extreme drought year, resulting in mixed burn severities from overall moderate fire behavior, driven primarily by available fuels and topography. Suppression efforts focused on the wildland urban interface and no slurry drops or direct attack measures were taken in the study area (from communication with the Incident Section Chief).

Forty random points were stratified across burn severities in the southern area of the burn using RAVG data (low, moderate, and high). Ten plots in each burn severity were established in burned patches no less than 180 m from burn severity boundaries, as well as ten unburned control plots adjacent to the 416 Fire burn perimeter in the Junction Creek drainage area (Figure 1). Unburned plots were established outside of the burn perimeter due to a lack of suitable, accessible unburned warm–dry mixed conifer sites within the 416 Fire perimeter. While stringent experimental design is ideal, it is not always possible in ecological studies of isolated large-scale disturbance, such as the 416 Fire [36]. The absence of pre-fire data in the area eliminates our ability to draw inference on the effect of divergent environmental variables observed between burned and unburned plots. To compare burned areas with unburned areas, we established unburned plots as spatially segregated pseudoreplicates and reported environmental variables that were significantly different. Plots were spaced, on average, 409 m apart, with a standard error of 19.5 m [37]. Points were selected within a 100 m buffer of existing trails to ensure accessibility to sites, given the steep slopes of the drainage. Plots were aggregated near accessible trailheads and roads due to the steep, inaccessible terrain within the burn perimeter and the temporal limitations of the study.

Starting in May 2023, we established 40 plots, and collected vegetation data. We counted live trees and snags (>2.64 m height) within a 22.6 m diameter or 400 m^2 circle plot [34]. Gambel oak with a diameter at breast height (dbh) of >3 cm and a height of >1.5 m were considered trees [38,39]. Aspen with a dbh of >10 cm were considered trees. We estimated basal area using 15 and 20 Basal Area Factor (BAF) wedge prisms and averaged the prism scores. We measured the understory cover and aspen regeneration on a 30 m belt transect along the elevational gradient, 15 m above and below the center point of the plot. We divided the understory cover into two classes: greater than and less than 1.4 m. We counted conifer saplings (<2.64 m height) and seedlings along the 30 m transect, extending 5 m to both sides of the belt (300 m^2) [33]. We established four 1 m^2 subplots evenly along the 30 m transect to quantify herbaceous cover and divided the cover into grass and forbs [34]. We recorded slope, aspect, and elevation for each plot.

From May 25 to July 15, we conducted standard point count surveys at the center of each plot for 10 min [40,41]. We identified species and individuals by visual and vocal detection. We began our surveys 30 min before sunrise and ended five hours later [40]. We visited each of the 40 plots three times to ensure suitable sample size (Appendix A, Figure A1) [42].

We converted shrubs, aspen regeneration, forbs, and grasses to percentage surface cover. We summed point count data for each plot and grouped species into functional guilds based on foraging technique, foraging substrate, nest placement, and migratory pattern [6,11,14,43,44] (see Appendix A, Table A2). Species that fell into more than two guilds were classified as generalists; species that fell into two guilds were classified on a per-species basis, based on the best available information. We compared environmental, vegetation structure, avian functional guilds, abundance, richness, and diversity data among the four study sites with a Kruskal–Wallis test ($p < 0.05$), followed by a post hoc Bonferroni pairwise test [45]. We used non-metric multi-dimensional scaling (NMDS) to examine avian community assemblages among all four study sites in R versions 4.2.1 using the metaMDS function in the package vegan [46–48]. We ran the NMDS ordination using a Bray–Curtis distance measure, random starting configurations, and a minimum of 50 runs. Differences in avian assemblages among the four burn severities were determined using a permutational multivariate analysis of variance (Permanova), using adonis in the R package vegan [47,49,50]. Permanova uses common ecological distance measures (Bray–Curtis for this study) to examine multivariate data sets and calculate p-values using permutations, rather than tabled p-values that assume normality. We used a one fixed factor design with burn severity as our main effect [51]. We performed Pearson and Kendall correlation tests between avian and environmental/vegetation data using combined Permanova in PC-ORD software version 5.10 [52]. We performed an indicator species analysis, which uses richness and associated abundance values of species, to identify species that were particularly faithful indicators for a particular burn severity [52]. A comparison between the maximum indicator value (0–100) and random trials for occurrence of a given species (1000 Monte Carlo randomizations) provided an approximate p-value [51]. Species with $p < 0.05$ and indicator values (INDVAL) > 25 (INDVAL = relative abundance × relative frequency; INDVAL ranges from 0 to 100) were accepted as indicator species for a particular burn severity [26].

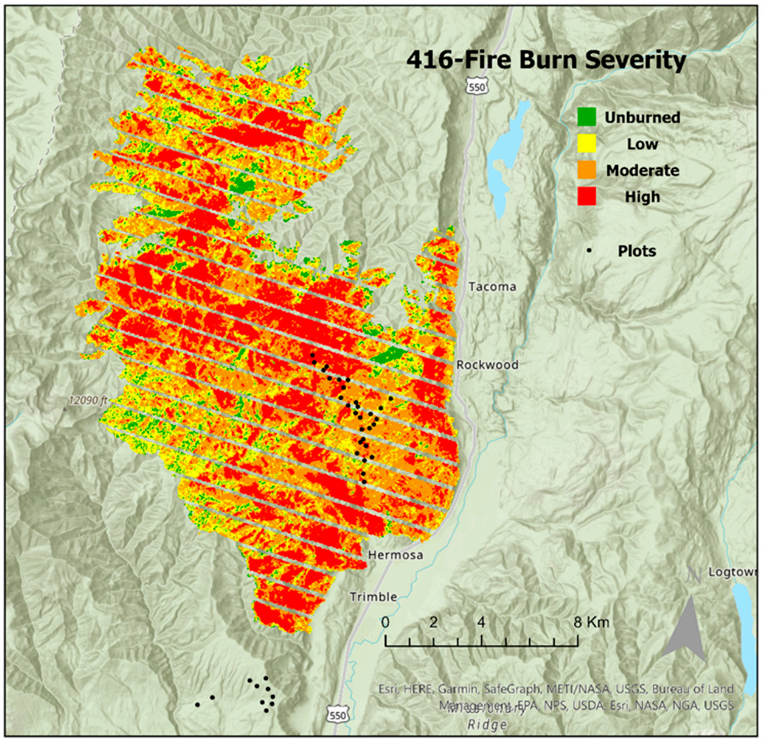

Figure 1. Study area map of the 416 Fire burn perimeter. Burn severity classified using Rapid Assessment of Vegetation Condition after Wildfire (RAVG) Composite Burn Index data. Unburned plots were established southwest of the burn perimeter adjacent to Junction Creek Road. Colorless diagonal bands were caused by satellite imaging error.

3. Results

3.1. Environmental, Vegetation, and Forest Characteristics

Unburned areas had significantly lower slope gradients and higher elevation than all three burn severities ($p < 0.05$, Table 1). Aspect, basal area, and total tree density (live + snag) were not different across burn severities ($p > 0.05$, Tables 1 and 2). The density of snags was significantly greater across burn areas ($H = 16.1$, $p < 0.01$, Figure 2, Table 2). Pairwise comparisons found that high burn areas had significantly more snags than unburned and low-burn areas ($p < 0.01$, Figure 2, Table 2). Snag density was marginally greater in high-burn areas than in moderate-burn areas ($p = 0.067$, Figure 2, Table 2). Live tree density was significantly different across burn severities ($H = 23.8$, $p < 0.01$, Figure 2, Table 2). Live tree density was significantly greater in unburned, low-burn, and moderate-burn areas than in high-burn areas ($p < 0.01$, Figure 2, Table 2). Live *P. ponderosa* abundance was significantly less in high-burn areas than all other areas ($p < 0.05$, Figure 3, Table 3). Live *A. concolor* abundance was significantly greater in unburned areas than in moderate- and high-burn areas ($p < 0.05$) (Figure 3, Table 3). Live *P. tremuloides* abundance was marginally greater in unburned areas than in moderate- and high-burn areas ($p = 0.056$, Figure 3, Table 3). Low shrub (<1.4 m) cover, high shrub (>1.4 m) cover, and forb cover were not significantly different across burn severities ($p > 0.05$, Table 4). Aspen regeneration was marginally greater in high-burn areas than moderate-burn areas ($p = 0.07$, Table 4). Conifer regeneration was marginally greater in unburned areas than in high-burn areas ($p = 0.078$, Table 4).

Table 1. Environmental site characteristics by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (N = 10/burn severity). Mean values (±standard error of the mean). Differences were determined using Kruskal–Wallis tests, followed by pairwise comparisons using a Bonferroni correction. Significant differences among burn severities for a specific environmental site characteristic is denoted by different letters and highlighted in bold. ($p < 0.05$).

Burn Severity	Slope	Aspect	Elevation
Unburned	**20.8 (2.12) a**	205.6 (12.74) a	**2673.0 (35.83) a**
Low	38.2 (4.14) b	254.0 (23.80) a	2436.9 (28.65) b
Moderate	42.0 (4.76) b	229.9 (15.85) a	2404.3 (23.84) b
High	45.4 (4.22) b	254.2 (17.59) a	2407.4 (23.83) b

Table 2. Forest stand structure characteristics by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (N = 10/burn severity). Mean values (±standard error of the mean). Differences were determined using Kruskal–Wallis tests, followed by pairwise comparisons using a Bonferroni correction. Significant differences among burn severities are denoted by different letters and highlighted in bold. ($p < 0.05$).

Burn Severity	Basal Area	Snags/Ha	Live Trees/Ha	Total Trees/Ha
Unburned	89.5 (11.7) a	76.3 (28.8) a	283.2 (46.4) a	359.5 (52.1) a
Low	90.3 (11.4) a	76.3 (26.9) a	416.1 (126.3) a	492.5 (130.2) a
Moderate	130.0 (22.5) a	147.7 (54.6) ab	275.8 (98.9) a	423.5 (97.6) a
High	91.5 (10.8) a	**421.0 (66.2) b**	**4.9 (4.7) b**	426.0 (65.1) a

Table 3. Tree species density by burn severity (unburned, low, moderate, high) within the 416 Fire perimeter, five years post-fire (N = 10/burn severity). Mean values (±standard error of the mean). Differences were determined using Kruskal–Wallis tests followed by pairwise comparisons using a Bonferroni correction. Significant differences among burn severities are denoted by different letters ($p < 0.05$). (PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABCO) = *Abies concolor*; PSME = *Pseudotsuga menziesii*; JUOS = *Juniperus osteosperma*; QUGA = *Quercus gambelii*).

Burn Severity	PIPO/Ha	POTR/Ha	ABCO/Ha	PSME/Ha	JUOS/Ha	QUGA/Ha
Unburned	113.3 (49.5) a	24.6 (10.4) a	68.9 (25.1) a	9.8 (7.1) a	2.5 (2.3) a	64.0 (22.1) a
Low	101.0 (25.7) a	22.2 (21.0) ab	24.6 (12.6) ab	29.5 (17.0) a	9.8 (7.1) a	229.0 (123.4) a
Moderate	93.6 (24.1) a	0 (0) b	0 (0) b	4.9 (3.1) a	2.5 (2.3) a	174.8 (101.5) a
High	0 (0) b	0 (0) b	0 (0) b	0 (0) a	0 (0) a	4.9 (4.7) a

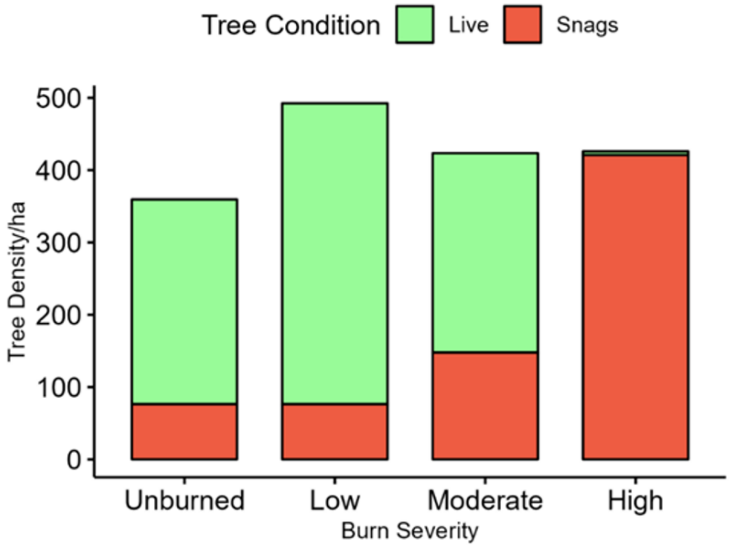

Figure 2. Mean live tree and snag density by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (N = 10/burn severity). Differences were determined using Kruskal–Wallis tests, followed by pairwise comparisons using a Bonferroni correction. Snag density was significantly greater in high-severity burn areas than in unburned and low-burn areas ($p < 0.05$). Snag density was marginally greater in high-burn areas than in medium-burn areas ($p = 0.067$). Live tree density was significantly lower in high-severity burn areas than all other burn severities ($p < 0.05$).

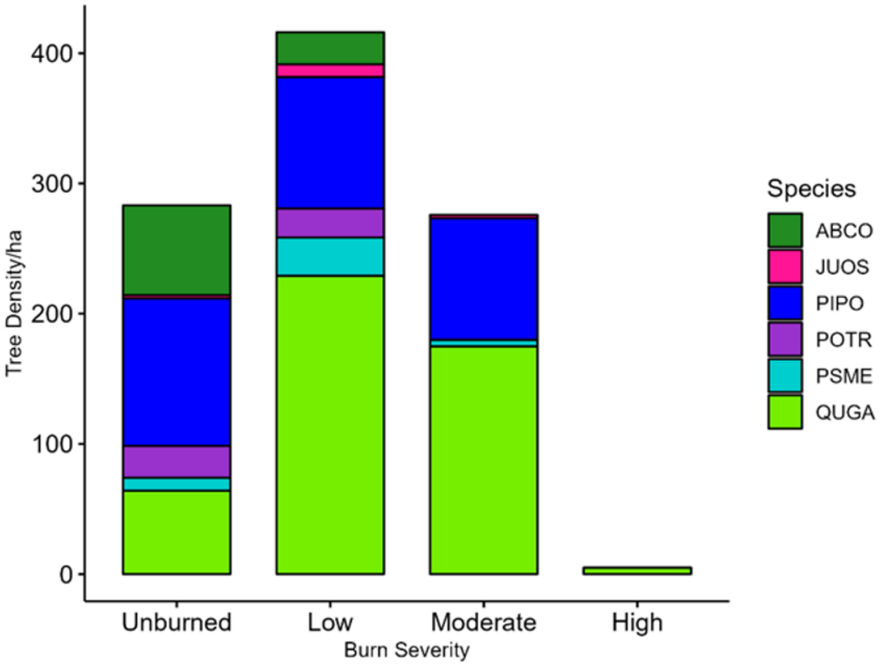

Figure 3. Mean live tree species density by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (N = 10/burn severity). Differences were determined using Kruskal–Wallis tests, followed by pairwise comparisons using a Bonferroni correction. Abundance of *Pinus ponderosa* (PIPO), *Abies concolor* (ABCO) and *Populus tremuloides* (POTR) were significantly different between high-burn areas and all other burn areas based on Kruskal–Wallis tests with a Bonferroni correction, excluding ABCO and POTR in moderate-severity burns ($p < 0.05$). Other tree species' abundance was not significantly different. (PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABCO = *Abies concolor*; PSME = *Pseudotsuga menziesii*; JUOS = *Juniperus osteosperma*; QUGA = *Quercus gambelii*).

Table 4. Vegetation characteristics by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (N = 10/burn severity). Mean values (±standard error of the mean). Differences were determined using Kruskal–Wallis tests, followed by pairwise comparisons using a Bonferroni correction. Significant differences among burn severities are denoted by different letters and highlighted in bold. ($p < 0.05$). Low and high shrub cover are defined as less than or greater than 1.4 m.

Burn Severity	% Low Shrub Cover	% High Shrub Cover	% Aspen Regeneration	Mean Forbs %	Mean Grass %	Conifer Regeneration/Ha
Unburned	46.3 (6.9) a	19.3 (7.8) a	4.7 (3.3) a	21.0 (2.1) a	**43.3 (4.8) a**	116.7 (42.2) a
Low	31.9 (6.1) a	17.6 (5.0) a	2.8 (2.7) a	24.7 (2.3) a	24.9 (6.3) ab	70.0 (46.5) a
Moderate	51.9 (9.2) a	13.5 (5.6) a	2.7 (2.7) a	33.8 (2.5) a	48.0 (6.0) ab	40.0 (36.5) a
High	50.8 (7.6) a	10.2 (3.5) a	17.3 (6.3) a	34.8 (6.6) a	10.5 (2.6) b	50.0 (50.0) a

3.2. Avian Univariate

We detected 1697 individual birds, consisting of 53 species, during our point count surveys in the 416 Fire perimeter and the adjacent unburned Junction Creek drainage (see Appendix A). Mean total abundance (424 birds/burn severity; 42 birds/plot), richness (40 species/burn severity; 17 species/plot), and Shannon diversity across burn severities were not significantly different (Table 5, Appendix A Table A1).

Table 5. Avian species richness, diversity, and abundance per plot by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (N = 10/burn severity). Mean values (±standard error of the mean). Differences were determined using Kruskal–Wallis tests. No measures were significantly different.

Burn Severity	Richness	Shannon Diversity	Abundance
Unburned	17.8 (1.26)	2.67 (0.07)	39.5 (4.35)
Low	18.0 (0.96)	2.69 (0.06)	42.0 (2.71)
Moderate	18.5 (1.56)	2.65 (0.12)	44.0 (4.27)
High	16.4 (1.42)	2.49 (0.11)	44.2 (4.02)

3.3. Avian Community

We quantified avian community assemblages in the 416 Fire perimeter to be significantly different among all burn severities (F = 3.01, $p = 0.0002$). Pairwise comparisons between burn severities were all significant ($p < 0.01$), except between low- and moderate-severity burn areas ($p = 0.19$, Figure 4). Live tree and snag density were the best correlates of variation in species assemblages (Kendall's Tau = −0.4, 0.27). Multivariate comparison of species composition weighted by bird abundance showed strong separation between unburned and high-burn-severity areas (Figure 4). Indicator species analysis detected species that were consistent positive indicators for all burn severities, with the most occurring in unburned and high-burn areas (Table 6). Unburned indicator species include Mountain Chickadee (IV = 57.9, $p < 0.01$), Ruby-crowned Kinglet (IV = 32, $p < 0.05$), Virginia's Warbler (IV = 40, $p < 0.05$), Evening Grosbeak (IV = 40.5, $p < 0.05$), and Williamson's Sapsucker (IV = 30, $p = 0.05$). High-burn indicator species include Broad-tailed Hummingbird (IV = 46.7, $p < 0.01$), House Wren (IV = 55.2, $p < 0.01$), Green-tailed Towhee (IV = 38.8, $p < 0.05$), and Dusky Flycatcher (IV = 35.3, $p = 0.05$). Low-burn indicator species were Yellow-rumped Warbler (IV = 40.5, $p < 0.05$) and Hammond's Flycatcher (IV = 42.9, $p < 0.01$). The American Robin was found to be the only indicator species in moderate-burn areas (IV = 41.9, $p < 0.01$).

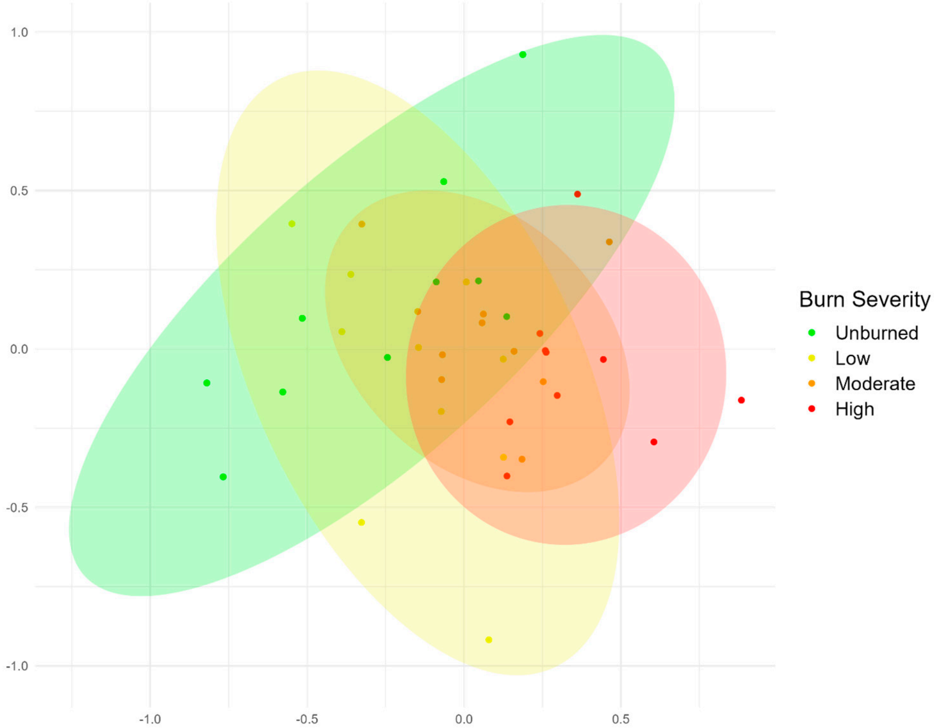

Figure 4. Non-metric multi-dimensional scaling (NMDS) of avian community assemblages by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire. Community assemblage variation was driven by live tree density (Kendall's tau: −0.40) and snag density (Kendall's tau: 0.27). Species assemblages were significantly different across burn severities, according to a Permanova analysis of variance (F = 3.01, $p = 0.0002$). Pairwise comparisons found significant differences between all burn severities ($p < 0.01$), except between low- and moderate-severity ($p = 0.19$). Each point represents one plot (abundance combined across three sampling times, N = 40, 10 plots per burn severity). Ellipses indicate 95% confidence intervals of plots by burn severity. Stress = 0.15, k = 3, distance measure = Bray–Curtis.

Table 6. Indicator species by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-burn (N = 10/burn severity). A comparison between the maximum indicator value (0–100) and random trials for occurrence of a given species (1000 Monte Carlo randomizations) provided an approximate *p*-value [50]. Species with $p < 0.05$ and indicator values (INDVAL) > 25 (INDVAL = relative abundance x relative frequency; INDVAL ranges from 0 to 100) were accepted as indicator species for a particular burn severity [26].

Burn Severity	Species	Indicator Value	*p*-Value
Unburned	Williamson's Sapsucker	30	0.05
	Mountain Chickadee	57.9	0.0006
	Ruby-crowned Kinglet	32	0.03
	Virginia's Warbler	40	0.02
	Evening Grosbeak	40.5	0.01
Low	Hammond's Flycatcher	42.9	0.01
	Yellow-rumped Warbler	40.5	0.02
Moderate	American Robin	41.9	0.007
High	Broad-tailed Hummingbird	46.7	0.003
	Dusky Flycatcher	35.3	0.05
	House Wren	55.2	0.0002
	Green-tailed Towhee	38.8	0.04

3.4. Avian Functional Guilds

We grouped avian species by functional guild into categories (Appendix A, Tables A2 and A3) [6]. We compared the mean abundance of functional guild categories across burn severities, and the most evident trend was the difference between unburned and high-burn areas. Specifically, air foragers were significantly more abundant in high-burn areas than in unburned areas, while bark foragers were more abundant in unburned than high-burn areas ($p < 0.05$, Figure 5). We observed the same pattern in short- and medium-distance migratory species, who were both more abundant in high-burn areas than in unburned areas ($p < 0.05$, Figure 6). In the foraging technique category, salliers (flycatchers) were significantly more abundant in high-burn areas than unburned ($p < 0.05$, Figure 7). Shrub nesting species were also significantly more abundant in high-burn areas than in unburned areas ($p < 0.05$, Figure 8). Additionally, the percent composition of guilds within burn severities were significantly different for all categories ($p < 0.01$, Figure 9, Appendix A Tables A4–A8).

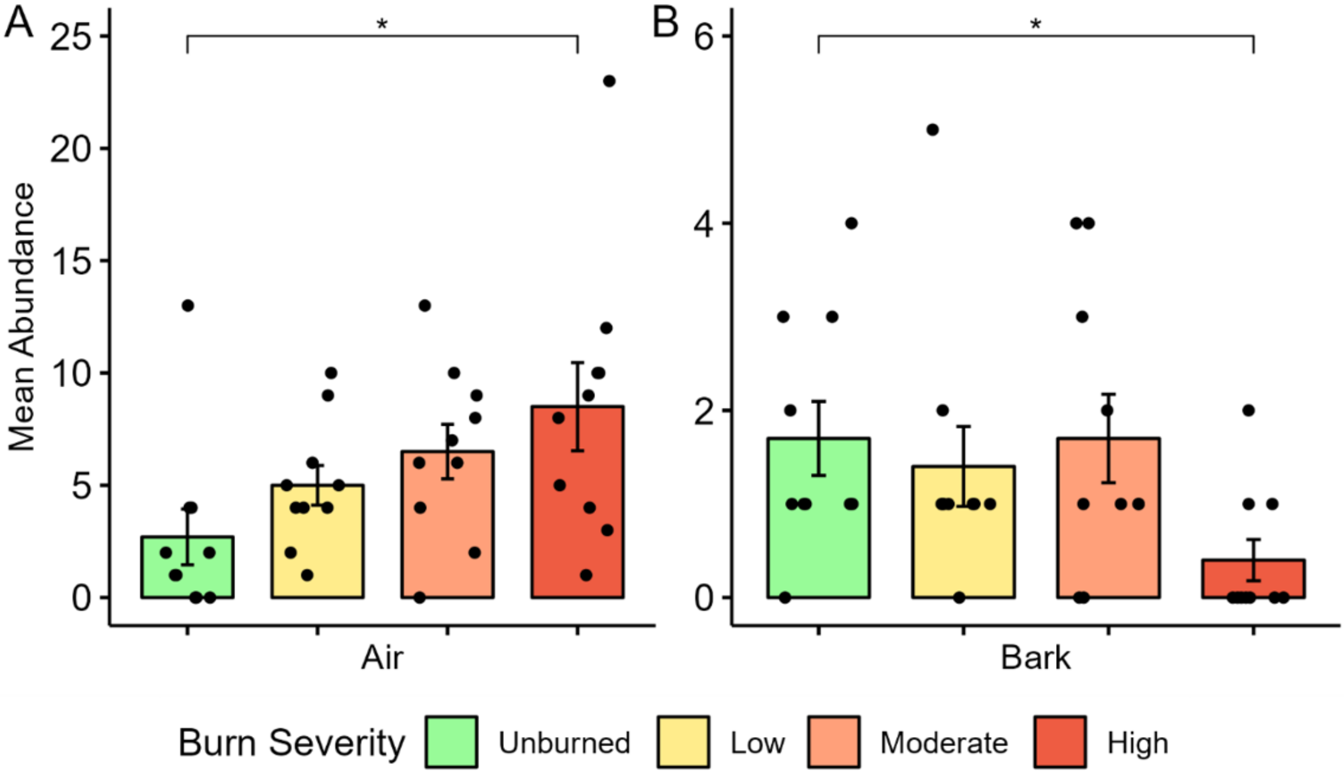

Figure 5. Mean abundance of (**A**) air and (**B**) bark foragers in the foraging substrate functional guild category by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (abundance combined across three sampling times, N = 10/burn severity). Mean values (±standard error of the mean). Dots represent the actual abundance per plot. Differences were determined using Kruskal–Wallis tests, followed by pairwise Dunn tests and Bonferroni corrections. Significant differences among burn severities are denoted by an asterisk ($p < 0.05$). Air foragers find their food in the air and are usually salliers (flycatchers) and hawkers (birds of prey). Significantly more air foragers were detected in the high-burn areas than in unburned areas. Bark foragers find their food (usually insects and/or sap) on or under the bark of trees. Significantly more bark foragers were detected in the unburned than in high-severity burn areas. Marginally more bark foragers were detected in moderate-burn areas than in high-burn areas ($p < 0.08$).

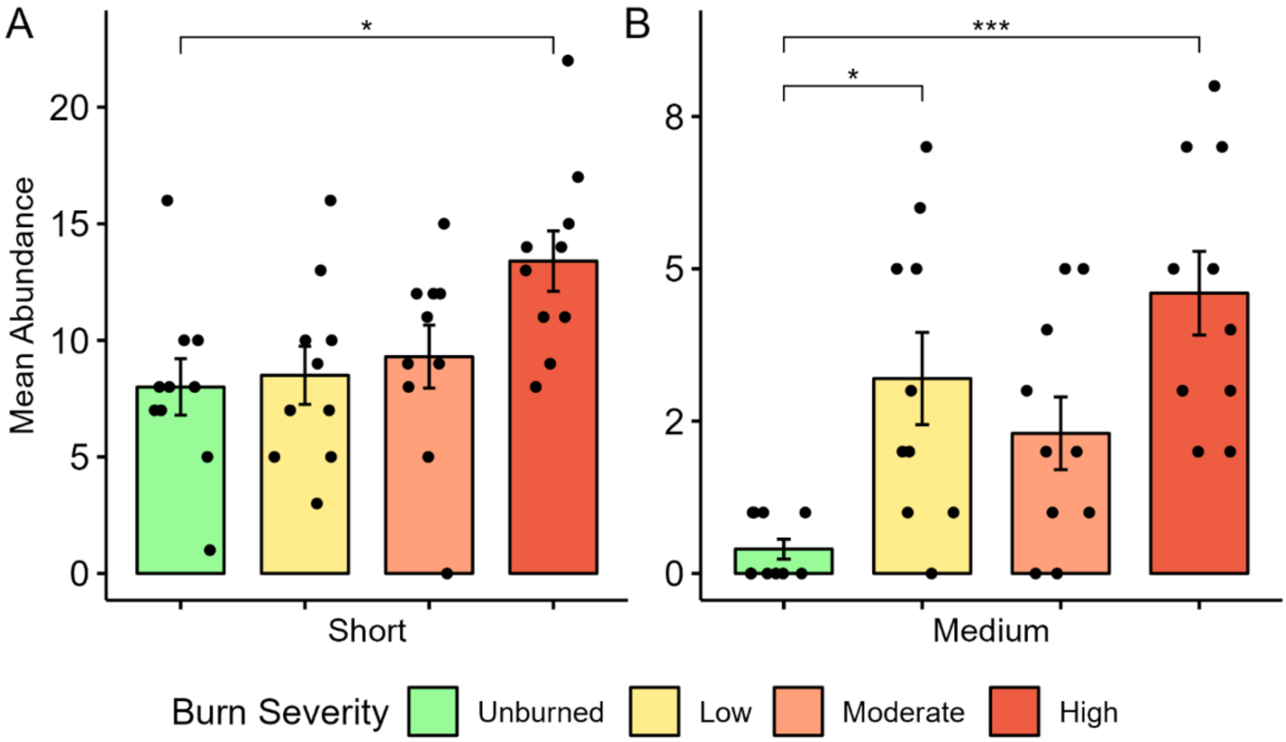

Figure 6. Mean abundance of (**A**) short- and (**B**) medium-distance migratory guilds by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (abundance combined across three sampling times, N = 10/burn severity). Mean values (±standard error of the mean). Dots represent the actual abundance per plot. Differences were determined using Kruskal–Wallis tests, followed by pairwise Dunn tests and Bonferroni corrections. Significant differences among burn severities are denoted by asterisks (* = $p < 0.05$, *** = $p < 0.001$). Short-distance migratory species travel altitudinally and winter near their breeding grounds. Significantly more short-distance migrants were detected in high-burn areas than in unburned areas. Marginally more short-distance migrants were detected in high-burn areas than low-burn areas ($p < 0.07$). Medium-distance migratory species travel regionally, up to several hundred miles from their breeding ground. Significantly fewer medium-distance migrants were detected in unburned areas than in low- and high-burn areas.

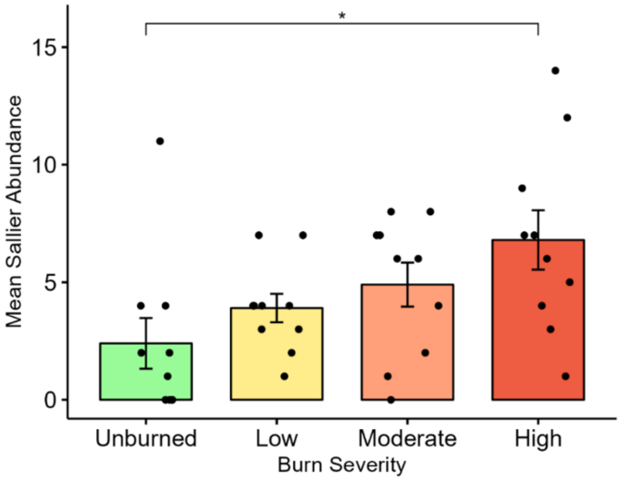

Figure 7. Mean abundance of sallier species (flycatchers) in the foraging technique functional guild category by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (abundance combined across three sampling times, N = 10/burn severity). Mean values (±standard error of the mean). Dots represent the actual abundance per plot. Differences were

determined using Kruskal–Wallis tests, followed by pairwise Dunn tests and Bonferroni corrections. Significant differences among burn severities are denoted by an asterisk ($p < 0.05$). Salliers perch on a branch and fly out to catch prey in the air before returning to their perch. Significantly more salliers were detected in high-burn areas than in unburned areas. Abundances of other foraging technique guilds were not significantly different across burn severities.

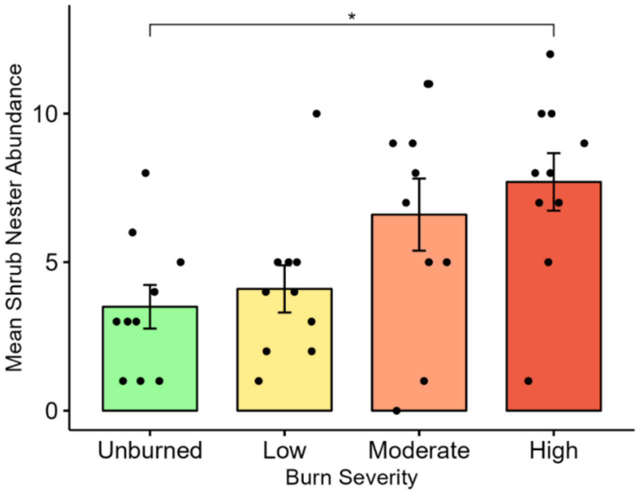

Figure 8. Mean abundance of shrub nesting species in the nesting location functional guild category by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (abundance combined across three sampling times, N = 10/burn severity). Mean values (±standard error of the mean). Dots represent the actual abundance per plot. Differences were determined using Kruskal–Wallis tests, followed by pairwise Dunn tests and Bonferroni corrections. Significant differences among burn severities are denoted by an asterisk ($p < 0.05$). Significantly more shrub nesters were detected in high-burn areas than in unburned areas. Abundances of other nesting location guilds were not significantly different across burn severities.

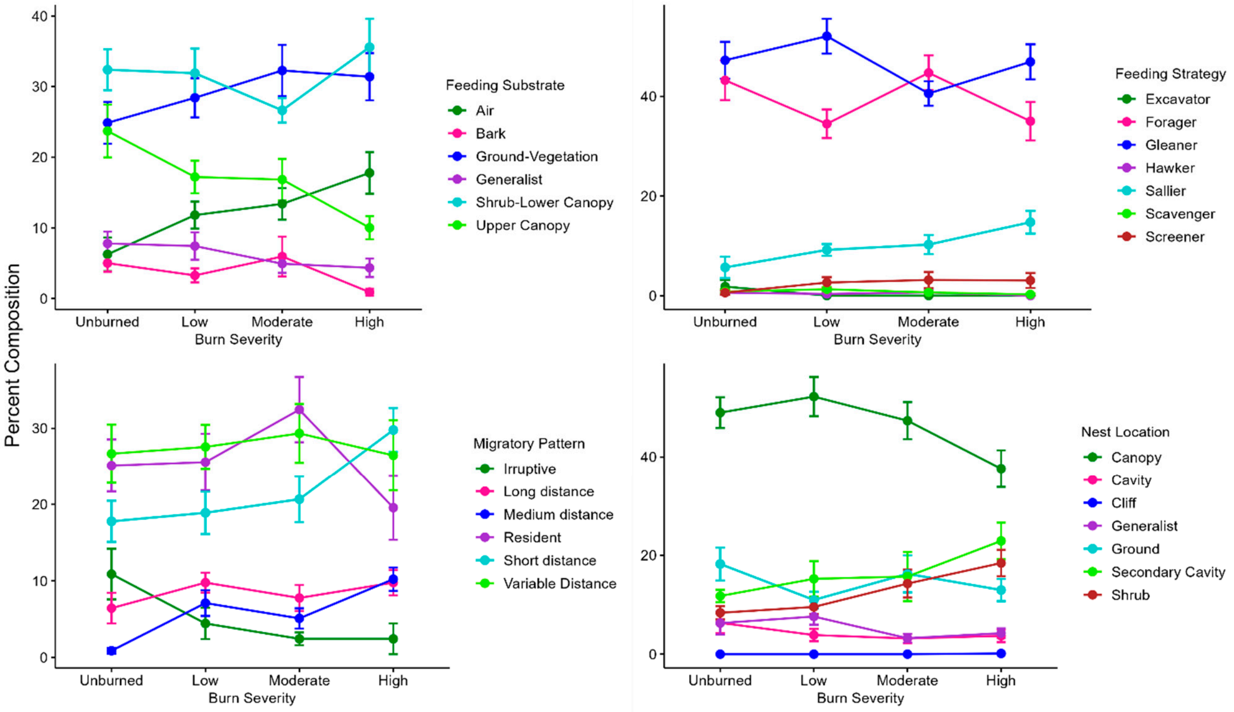

Figure 9. Percent composition of functional guilds by burn severity (unburned, low, moderate, and high) within the 416 Fire perimeter, five years post-fire (abundance combined across three sampling

times, N = 10/burn severity). Mean values (±standard error of the mean). Differences were determined using Kruskal–Wallis tests, followed by pairwise Dunn tests and Bonferroni corrections. Percentage composition of functional guilds was significantly different within each burn severity, for every category ($p < 0.01$, Table A4).

4. Discussion

The varying vegetation characteristics of the different burn severity areas indicate ecological succession is occurring five years post-fire; the five years were ample time for the regeneration of *Q. gambelii* throughout the study area, irrespective of burn severity, as well as other low-growing shrub species. Low shrub cover (<1.4 m) averaged 30–50% in all burn areas, benefiting the diversity of shrub-using birds in all burn severities. Aspen regeneration was more prevalent in high-burn areas, while mesic tree species were absent from these areas, illustrating that differential succession patterns are creating spatially heterogenous habitats. Live tree species were predominantly xeric-adapted species, including *P. ponderosa* and *Q. gambelii*. Conifer regeneration was not significantly different among burn severities but was more prominent in unburned and low-burn areas, which is likely associated with the predominance of *P. ponderosa* in the overstory for these two burn severities [53].

Univariate measures of richness, diversity, and abundance were not significantly different across burn severities. In this study, abundance was not considered per-species, but as a measure of total birds observed; this study focused on community composition, as opposed to other studies that have shown fine-scale changes in relative abundance, occupancy, or density pre- and post-fire [8,25,32]. One study that compared average species abundance identified four response patterns that correlated to burn severity, reinforcing that individual species' response to burn severity, as well as community structure, may change, while overall abundance may not, as demonstrated in our study [8]. Other recent studies on avian species' richness responses have reported similar results within burn severities [25,54]. A 1970 study found that species richness was greater in burned forest than unburned, without considering burn severity; this is unsurprising, given the complexity of post-fire habitat in mixed conifer forests [30]. A study in montane forests in California found that, at a landscape scale, a greater diversity of fire behavior (pyrodiversity) promoted avian diversity, while, within a single fire, diversity tended to decrease with increasing fire severity [24]. The lack of significant difference in avian species diversity across burn severities in our study reinforces the importance of uniquely burned habitats and suggests that assessing diversity over larger landscape scales across different wildfires, rather just within one fire, may more accurately reflect the importance of mixed-severity fire in promoting biodiversity.

Distinct avian community differentiation between unburned and burned forest was observed in this study, as well as finer scale differences among burn severities established by mixed-severity fire. The significant divergence of species assemblages between burn severities and lack of variation in univariate richness and diversity exemplify the ecological benefits of mixed-severity fire in promoting biodiversity at a landscape scale. Indeed, this study highlights the importance of community analysis at multiple levels; the results of univariate analyses of abundance, richness, and diversity were not different across burn severities, but multivariate community analysis identified significantly divergent species assemblages across all burn severities, except between low- and moderate-burn areas. This is consistent with other studies that found fine-scale patterns of avian response to wildfire when evaluated by burn severity [8,24]. While significant divergence was identified, there was some overlap in assemblages that represent a gradient of species present from unburned to high-burn areas. This gradient is most convergent at the low- to moderate-burn severities and most divergent between unburned and high-burn areas. A study of Mediterranean pine forests also observed significantly divergent avian communities between recently burned and unburned areas for >40 years [55]. The variation in species assemblages was best correlated with the density of live trees and snags, indicating the importance of these variables for promoting avian biodiversity and predicting species' response to wildfire [8,9]. This builds on previous work that demonstrated the importance of snag and live tree density for avian communities three years post-burn and reinforces that these factors are still relevant five years post-burn [9].

The strong correlation of avian assemblages with live and dead tree density in this study is well supported [9]. The presence of more indicator species in unburned and high-burn areas than in low- and moderate-burn areas reflects the importance of managing for mixed-severity fire that allows for patchy high-severity burns. Broad-tailed Hummingbird and House Wren were unsurprising indicators of high-burn severities; the two species are known to flourish in areas that experience high tree mortality [9,25,54]. Green-tailed Towhee was another indicator species of high-burn severity areas, whose association with live shrubs has been documented and shown to provide nest sites and foraging opportunities [56]. Contrary to our findings, one study demonstrated that Green-tailed Towhees were associated with unburned areas following prescribed fire, three to five years post-fire, in montane shrublands [56]. Differential shrub regeneration between mixed conifer and montane shrubland likely account for the difference in Green-tailed Towhee fire response, as five years post-fire was adequate time for shrub cover to regenerate in high-severity burn areas in our study, such that Green-tailed Towhees were exceedingly associated with high-severity fire. The Dusky Flycatcher's high-burn severity indicator status is of interest because although they have been found to respond positively to generalized mixed-severity fire, some studies have reported a negative association with fire [8,25]. Dusky Flycatchers typically nest in shrubs and given the ubiquitous shrub cover in the study area, other factors such as predation and open canopy space may be influencing their association with the high-severity portions of the 416 Fire area [57].

The Mountain Chickadee was an expected indicator species for unburned areas as they are associated with live tree density and absence of fire [31,54]. Virginia's Warbler are sometimes associated with low- or moderate-burn severities, but are also a shrub-associated species, and in this study the percentage of shrub cover was consistent across all burn severities, which may have influenced it being an indicator species for unburned areas [54]. Ruby-crowned Kinglet was another expected indicator of unburned areas, whose reliance on unburned forest has been documented [25,31]. Additionally, Evening Grosbeak's indicator status in unburned areas is consistent with a study that found that this species was more likely to occur in areas with high densities of live trees [9]. Indicator species of low-severity burn areas are interesting because they accentuate the fine scale differences between unburned and low-burn areas, despite the similar forest structure 5 years post-fire. This is demonstrated by Hammond's Flycatcher, which was an indicator species for low-burn areas in our study area five years post-fire but is known to have mixed post-fire responses [28,31]. The Yellow-rumped Warbler is an expected indicator, as they utilize small forest openings but typically avoid areas with high tree mortality [8,54]. The presence of indicator species in low-burn areas emphasizes the importance of analyzing avian communities using multiple methods, especially given the convergent species assemblages in low- and moderate-burn severities. Moderate-burn areas are a unique habitat within mixed conifer systems, in that they have a substantial density of snags and live trees. This combination, however, did not correlate with many indicator species, with the American Robin being the only indicator species. This species is frequently considered a generalist in habitat preference, but has been shown to respond positively to fire, and more specifically, moderate-severity fire [8,25,54]. Indeed, although American Robins were found to be an indicator of moderate-burn areas, they were relatively abundant in all burn severities.

We observed evident trends in avian functional guilds between unburned and high-severity burns. The percent composition of functional guilds within burn severities was significantly different for all burn severities and guild categories, however, some of the differences may be attributed to low abundances of some specialist guild species (cliff nesters, excavators, scavengers, hawkers, and screeners). The prominence of sallier species (flycatchers), such as the Western Wood Pewee, Dusky Flycatcher, and Olive-sided Flycatcher in high-burn areas is consistent with other studies [8,25,54]. These aerial insectivores are known to utilize high-burn areas with ample inter-canopy space for flycatching. An unexpected finding was the association of bark foraging species with unburned habitats. Some bark feeding species, such as woodpeckers, are cavity nesters, which are associated with high-burn areas that provide suitable nest sites and an abundance of wood-boring insects [9,31]. High-burn areas are frequently associated with an increase in insects that colonize dead and dying trees immediately following fire, providing food for the bark feeding species [31,58]. In our study, five years post-fire was sufficient time for the pulse of insects to subside, followed by the subsequent dispersal of bark feeding species and the colonization of cavities by secondary cavity nesters [58]. Williamson's Sapsucker detections account for the association of bark foragers with unburned areas, as Sapsuckers feed primarily on tree sap and are therefore associated with living trees; Williamson's Sapsucker was also an unburned indicator species in our study [59]. Other woodpecker species were either generalists (Hairy and Downy) or ground–vegetation foragers (Northern Flicker) and did not contribute to the bark foraging guild. Similarly, bark foraging species have been observed to be more abundant in long-unburned areas of dry Australian woodlands [60]. Significantly more shrub nesting species were detected in high-severity burns than unburned areas, largely due to the abundance of Green-tailed Towhees and Dusky Flycatchers in high-burn areas. This is interesting, due to the widespread shrub cover in all burned areas and considering the indicator status of Virginia's Warbler in unburned areas. As previously expressed, other environmental variables are likely contributing to the association of these species with specific burn severities.

The influence of wildfire on migratory guilds in mixed conifer forests is not well studied, so this study aimed to evaluate migration distance in addition to simply residency status. Short- and medium-distance migrants were both significantly more abundant in high-burn than unburned areas. This is corroborated by a study of Chilean temperate forests that found migrants and partial migrants to be more associated with burned forest than unburned, however, partial migrants required forest that had several years to regenerate post-fire [14]. Partial migrants may be related to the short- and medium-distance guilds in this study, groups that travel altitudinally or up to several hundred miles, respectively. Interestingly, in this study, medium-distance migrants were significantly more abundant in low-burn than unburned areas and residents were more associated with unburned forest than burned forest [14]. These findings indicate that migratory birds may be more resilient to disturbance than resident species. However, another study in dry Australian forests found that migrant species were associated with unburned forest [61]. In our study, the distinction between unburned and burned forest is not sufficient to describe resident species as residents were most abundant in moderate burn severities, least abundant in high burn severities, and equally abundant in unburned and low burn severities. These findings illustrate that distinctions among migratory guilds involving their resiliency and response to fire necessitate further study. We also found irruptive migrants most associated with unburned areas, which may be attributed to the predominance of Red Crossbill and Evening Grosbeak, birds that follow fluctuating tree food-crops and lack site fidelity [62]. This trend suggests further post-fire avian research at a species-specific scale, including the study of food-crop response to fire severity. The response of migratory guilds to fire is of particular interest, due to its management relevance and fine-scale changes among species. Focusing on this may assist forest managers in predicting migratory stopover and regional movements of species of interest.

5. Conclusions

The 416 Fire burned through a warm–dry mixed conifer forest with a heterogeneous stand structure and old growth characteristics that had been largely unaltered by logging, fire mitigation, or development. As such, the 416 Fire was an ideal area in which to study the impacts of a large-scale mixed-severity fire. Implementing heterogeneous landscapes using tree thinning and/or prescribed fire in a spatially explicit restoration approach may mimic wildfires and create varied forest stand structure with diverse age classes to promote stand complexity and ecosystem function, promoting unique avian community assemblages as demonstrated in our study findings [8,9,25,63]. This kind of spatially explicit restoration should approach fire mitigation and post-fire salvage conservatively, with snag removal only occurring when it is a safety issue, as numerous bird species are strongly associated with snag density and require specific post-fire habitats that may not be replicated unless mixed-severity fires are allowed to burn [28]. Additionally, the post-fire salvage of snags should be minimized to promote the abundance of snag-associated species [28]. Despite the possible similarities in fire behavior outcome following homogenous fuels reduction and spatially explicit restoration treatments, management strategies that promote habitat heterogeneity are likely to promote a greater diversity of species assemblages [8,24,63]. Fuels reduction treatments favor the removal of younger trees and understory that may act as ladder fuels when ignited, leading to possible crown fires. In spatially explicit restoration treatments, the maintenance of various age classes of trees to promote increased vertical and horizontal complexity can promote a wide range of ecosystem functionality such as succession, resilience, diverse understory communities, more wildlife habitat, and resource availability [63]. Unburned and high-severity burn areas were the most important in supporting high numbers of indicator species and significant functional guild variation in our study, and as such, management for these habitats should be prioritized [9,64]. The strong association of species with high-severity burn areas provides evidence of historical patches of high-severity burns on the landscape of the Southern Rockies in mixed conifer forests. This same finding was reflected in a study of the Black-Backed Woodpecker in Idaho and Montana, illustrating the importance of high-severity burns [64]. This study demonstrates that unique avian communities respond to vegetational successional processes post-fire and reinforces the importance of managing forests for heterogenous forest structure [24,28,32].

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Data Availability Statement: Data and code presented and used in this study are openly available at https://github.com/lukescottarthur/Birds-of-the-Burn (accessed on 1 February 2024). Note: Pearson and Kendall correlations, vegetation Kruskal–Wallis tests, and indicator species analysis were performed in PC-ORD; results can be provided by request.

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Appendix A

Table A1. Total bird count by species detected across four burn severities within the 416 Fire perimeter, 5 years post-burn.

Species		**Unburned**	**Low**	**Medium**	**High**
Dusky Grouse	*Dendragapus obscurus*	2	1		1
Mourning Dove	*Zenaida macroura*			1	2
White-throated Swift	*Aeronautes saxatalis*				1
Broad-tailed Hummingbird	*Selasphorus platycercus*	2	16	14	28
Cooper′s Hawk	*Accipiter cooperii*	2			
Red-tailed Hawk	*Buteo jamaicensis*	1			
Northern Pygmy Owl	*Glaucidium gnoma*		1		
Williamson′s Sapsucker	*Sphyrapicus thyroideus*	4			
Red-naped Sapsucker	*Sphyrapicus nuchalis*	1			
Downy Woodpecker	*Dryobates pubescens*				1
Hairy Woodpecker	*Dryobates villosus*	1	2	3	4
Northern Flicker	*Colaptes auratus*	15	13	12	13
American Kestrel	*Falco sparverius*			3	
Olive-sided Flycatcher	*Contopus cooperi*	3	6	5	15
Western Wood Pewee	*Contopus sordidulus*	13	9	30	25
Hammond′s Flycatcher	*Empidonax hammondii*	2	15	2	2
Dusky Flycatcher	*Empidonax oberholseri*	6	6	12	19
Cordilleran Flycatcher	*Empidonax occidentalis*		3		7
Plumbeous Vireo	*Vireo plumbeus*	1	6	5	
Warbling Vireo	*Vireo gilvus*	23	24	23	17
Steller′s Jay	*Cyanocitta stelleri*	15	12	10	5
American Crow	*Corvus brachyrhynchos*		1		
Common Raven	*Corvus corax*	3	6	3	1
Mountain Chickadee	*Poecile gambeli*	21	7	1	
Violet-green Swallow	*Tachycineta thalassina*	3	11	16	16
Ruby-crowned Kinglet	*Corthylio calendula*	12	2		1
Red-breasted Nuthatch	*Sitta canadensis*	3	1	1	
White-breasted Nuthatch	*Sitta carolinensis*	6	7	8	4
Pygmy Nuthatch	*Sitta pygmaea*	3	4	8	
Brown Creeper	*Certhia americana*		2		
House Wren	*Troglodytes aedon*	11	29	24	79
Gray Catbird	*Dumetella carolinensis*	1			
Western Bluebird	*Sialia mexicana*	1		5	2
Townsend′s Solitaire	*Myadestes townsendi*			2	1
Hermit Thrush	*Catharus guttatus*	20	24	11	9
American Robin	*Turdus migratorius*	17	24	49	27
Evening Grosbeak	*Coccothraustes vespertinus*	17	2	2	
Cassin′s Finch	*Haemorhous cassinii*	1	8	4	1
Red Crossbill	*Loxia curvirostra*	20	2	4	3
Pine Siskin	*Spinus pinus*	12	16	5	8
American Goldfinch	*Spinus tristis*			1	1
Chipping Sparrow	*Spizella passerina*	8	17	15	6
Dark-eyed Junco	*Junco hyemalis*	14	18	19	11
Lincoln′s Sparrow	*Melospiza lincolnii*		1		1
Green-tailed Towhee	*Pipilo chlorurus*	17	8	29	41
Spotted Towhee	*Pipilo maculatus*	16	9	25	22
Orange-crowned Warbler	*Leiothlypis celata*	21	14	8	17
Virginia′s Warbler	*Leiothlypis virginiae*	14	3	8	3
MacGillivray′s Warbler	*Geothlypis tolmiei*	2	12	9	10
Yellow-rumped Warbler	*Setophaga coronata*	20	32	15	12
Grace′s Warbler	*Setophaga graciae*	5	19	20	

Table A1. *Cont.*

Species		Unburned	Low	Medium	High
Western Tanager	*Piranga ludoviciana*	17	17	16	8
Black-headed Grosbeak	*Pheucticus melanocephalus*	19	10	12	18
	Total Abundance	395	420	440	442
	Richness	42	41	39	38

Table A2. Functional guild classifications, adapted from DeGraaf and Cornell Birds of the World [6,65].

Species	Feeding Substrate	Feeding Technique	Migration	Nesting Location
Dusky Grouse	ground–vegetation	forager	resident	ground
Mourning Dove	ground–vegetation	gleaner	variable	generalist
White-throated Swift	air	screener	variable	cliff
Broad-tailed Hummingbird	ground–vegetation	gleaner	medium	canopy
Cooper's Hawk	generalist	hawker	variable	canopy
Red-tailed Hawk	ground–vegetation	hawker	resident	generalist
Northern Pygmy Owl	ground–vegetation	hawker	resident	secondary cavity
Williamson's Sapsucker	bark	excavator	variable	cavity
Red-naped Sapsucker	bark	excavator	short	cavity
Downy Woodpecker	generalist	gleaner	resident	cavity
Hairy Woodpecker	generalist	gleaner	resident	cavity
Northern Flicker	ground–vegetation	gleaner	resident	cavity
American Kestrel	generalist	hawker	variable	secondary cavity
Olive-sided Flycatcher	air	sallier	long	canopy
Western Wood Pewee	air	sallier	variable	canopy
Hammond's Flycatcher	air	sallier	long	canopy
Dusky Flycatcher	air	sallier	long	shrub
Cordilleran Flycatcher	air	sallier	medium	generalist
Plumbeous Vireo	shrub–lower canopy	gleaner	variable	canopy
Warbling Vireo	upper canopy	gleaner	variable	canopy
Steller's Jay	generalist	forager	resident	canopy
American Crow	ground–vegetation	forager	resident	canopy
Common Raven	ground–vegetation	scavenger	resident	generalist
Mountain Chickadee	shrub–lower canopy	gleaner	resident	secondary cavity
Violet-green Swallow	air	screener	variable	secondary cavity
Ruby-crowned Kinglet	shrub–lower canopy	gleaner	short	canopy
Red-breasted Nuthatch	bark	gleaner	resident	cavity
White-breasted Nuthatch	bark	gleaner	resident	secondary cavity
Pygmy Nuthatch	bark	gleaner	resident	secondary cavity
Brown Creeper	bark	gleaner	resident	canopy
House Wren	shrub–lower canopy	gleaner	short	secondary cavity
Gray Catbird	generalist	forager	long	shrub
Western Bluebird	ground–vegetation	gleaner	resident	secondary cavity
Townsend's Solitaire	generalist	forager	resident	ground
Hermit Thrush	ground–vegetation	gleaner	short	generalist
American Robin	shrub–lower canopy	forager	resident	canopy
Evening Grosbeak	upper canopy	forager	irruptive	canopy
Cassin's Finch	ground–vegetation	forager	resident	canopy
Red Crossbill	upper canopy	forager	irruptive	canopy
Pine Siskin	generalist	forager	irruptive	canopy
American Goldfinch	generalist	forager	short	shrub
Chipping Sparrow	ground–vegetation	forager	resident	shrub
Dark-Eyed Junco	ground–vegetation	forager	variable	ground
Lincoln's Sparrow	ground–vegetation	forager	medium	ground
Green-tailed Towhee	ground–vegetation	forager	short	shrub
Spotted Towhee	ground–vegetation	forager	resident	ground
Orange-crowned Warbler	shrub–lower canopy	gleaner	variable	ground
Virginia's Warbler	shrub–lower canopy	gleaner	short	ground

Table A2. *Cont.*

Species	**Feeding Substrate**	**Feeding Technique**	**Migration**	**Nesting Location**
MacGillivray's Warbler	shrub–lower canopy	gleaner	medium	shrub
Yellow-rumped Warbler	shrub–lower canopy	gleaner	variable	canopy
Grace's Warbler	upper canopy	gleaner	short	canopy
Western Tanager	upper canopy	forager	long	canopy
Black-headed Grosbeak	upper canopy	forager	variable	canopy

Table A3. Functional guild descriptions adapted from DeGraaf's guild assignments [6] and Cornell Birds of the World [65]. Guild placement based on breeding season designations, or year-round designations if no specific breeding season guilds were described. Asterisk indicates guild groupings that were significantly different across burn severities.

Feeding Substrate	
ground–vegetation	Finds food on ground or in low vegetation
shrub–lower canopy	Finds food in shrubs, small trees, or in low canopies
upper canopy	Finds food in upper canopy of trees
air *	Catches food in the air or in flight
bark *	Finds food on or in the bark of trees
generalist	Finds food in variable places
Feeding Technique	
gleaner	Selects particular food items from substrate
excavator	Locates food in bark by drilling holes
forager	Takes variety of foods from a substrate
hawker	Flies after prey catching in air or on ground
sallier *	Perches on branch, flies out to catch prey, and returns
scavenger	Takes various food, refuse, or carrion
screener	Flies with bill open and screens food from air
Migratory Pattern	
short *	Short or altitudinal movements, wintering near breeding grounds
medium *	Regional movements up to several hundred miles
long	Movements from North America to Central and South America
resident	Lives in region year-round
irruptive	Sporadic movements typically related to food supply
variable	Populations exhibit different migratory patterns
Nesting Location	
cavity	Excavates cavities in trees
secondary cavity	Uses previously excavated cavities
ground	Nests on ground
shrub *	Nests in shrubs
canopy	Nests in tree canopy
cliff	Nests on cliffs
generalist	Nests in various places; opportunist

Table A4. Functional guild percent composition test statistic values within a given burn severity, calculated with Kruskal–Wallis tests and Bonferroni corrections. H-values (p-values). All burn severities had significantly different compositions of functional guilds.

Burn Severity	**Migratory Pattern**	**Nest Location**	**Feeding Substrate**	**Foraging Strategy**
Unburned	34.6 ($p < 0.01$)	48.3 ($p < 0.01$)	39.3 ($p < 0.01$)	51.1 ($p < 0.01$)
Low	37.3 ($p < 0.01$)	49.2 ($p < 0.01$)	42.8 ($p < 0.01$)	60.4 ($p < 0.01$)
Moderate	40 ($p < 0.01$)	48.8 ($p < 0.01$)	38.9 ($p < 0.01$)	57.6 ($p < 0.01$)
High	36.9 ($p < 0.01$)	54.4 ($p < 0.01$)	46.4 ($p < 0.01$)	62.3 ($p < 0.01$)

Table A5. Pairwise feeding strategy (technique) guild percent composition significance (*p*-values), calculated with pairwise Dunn tests and Bonferroni corrections.

Unburned	Excavator	Forager	Gleaner	Hawker	Scavenger	Sallier	Screener
Excavator	-	<0.01	<0.01	NS	NS	NS	NS
Forager	-	-	NS	<0.01	<0.01	NS	<0.01
Gleaner	-	-	-	<0.01	<0.01	<0.05	<0.01
Hawker	-	-	-	-	NS	NS	NS
Scavenger	-	-	-	-	-	NS	NS
Sallier	-	-	-	-	-	-	NS
Low Burn	Excavator	Forager	Gleaner	Hawker	Scavenger	Sallier	Screener
Excavator	-	<0.01	<0.01	NS	NS	<0.05	NS
Forager	-	-	NS	<0.01	<0.01	NS	<0.05
Gleaner	-	-	-	<0.01	<0.01	NS	<0.01
Hawker	-	-	-	-	NS	<0.05	NS
Scavenger	-	-	-	-	-	NS	NS
Sallier	-	-	-	-	-	-	NS
Moderate Burn	Excavator	Forager	Gleaner	Hawker	Scavenger	Sallier	Screener
Excavator	-	<0.01	<0.01	NS	NS	NS	NS
Forager	-	-	NS	<0.01	<0.01	NS	<0.01
Gleaner	-	-	-	<0.01	<0.01	NS	<0.01
Hawker	-	-	-	-	NS	NS	NS
Scavenger	-	-	-	-	-	NS	NS
Sallier	-	-	-	-	-	-	NS
High Burn	Excavator	Forager	Gleaner	Hawker	Scavenger	Sallier	Screener
Excavator	-	<0.01	<0.01	NS	NS	<0.05	NS
Forager	-	-	NS	<0.01	<0.01	NS	<0.01
Gleaner	-	-	-	<0.01	<0.01	NS	<0.01
Hawker	-	-	-	-	NS	<0.05	NS
Scavenger	-	-	-	-	-	NS	NS
Sallier	-	-	-	-	-	-	NS
Screener	-	-	-	-	-	-	-

Table A6. Pairwise nest location guild percent composition significance (*p*-values), calculated with pairwise Dunn tests and Bonferroni corrections.

Unburned	Canopy	Cavity	Cliff	Generalist	Ground	Secondary Cavity	Shrub
Canopy	-	<0.01	<0.01	<0.01	NS	NS	<0.01
Cavity	-	-	NS	NS	NS	NS	NS
Cliff	-	-	-	NS	<0.01	<0.01	NS
Generalist	-	-	-	-	NS	NS	NS
Ground	-	-	-	-	-	NS	NS
Secondary Cavity	-	-	-	-	-	-	NS
Low Burn	Canopy	Cavity	Cliff	Generalist	Ground	Secondary Cavity	Shrub
Canopy	-	<0.01	<0.01	<0.01	NS	NS	<0.05
Cavity	-	-	NS	NS	NS	NS	NS
Cliff	-	-	-	NS	<0.01	<0.01	<0.05
Generalist	-	-	-	-	NS	NS	NS
Ground	-	-	-	-	-	NS	NS
Secondary Cavity	-	-	-	-	-	-	NS
Moderate Burn	Canopy	Cavity	Cliff	Generalist	Ground	Secondary Cavity	Shrub
Canopy	-	<0.01	<0.01	<0.01	NS	NS	NS
Cavity	-	-	NS	NS	NS	NS	NS

Table A6. *Cont.*

Cliff	-	-	-	NS	<0.01	<0.01	<0.01
Generalist	-	-	-	-	NS	NS	NS
Ground	-	-	-	-	-	NS	NS
Secondary Cavity	-	-	-	-	-	-	NS
High Burn	Canopy	Cavity	Cliff	Generalist	Ground	Secondary Cavity	Shrub
Canopy	-	<0.01	<0.01	<0.01	NS	NS	<0.01
Cavity	-	-	NS	NS	NS	<0.05	NS
Cliff	-	-	-	NS	<0.05	<0.01	<0.01
Generalist	-	-	-	-	NS	<0.05	NS
Ground	-	-	-	-	-	NS	NS
Secondary Cavity	-	-	-	-	-	-	NS

Table A7. Pairwise feeding substrate guild percent composition significance (*p*-values), calculated with pairwise Dunn tests and Bonferroni corrections.

Unburned	Air	Bark	Generalist	Ground–Vegetation	Shrub–Lower Canopy	Upper Canopy
Air	-	NS	NS	<0.01	<0.01	<0.05
Bark	-	-	NS	<0.01	<0.01	<0.01
Generalist	-	-	-	NS	<0.01	NS
Ground–Vegetation	-	-	-	-	NS	NS
Shrub–Lower Canopy	-	-	-	-	-	NS
Low Burn	Air	Bark	Generalist	Ground–Vegetation	Shrub–Lower Canopy	Upper Canopy
Air	-	NS	NS	NS	<0.05	NS
Bark	-	-	NS	<0.01	<0.01	NS
Generalist	-	-	-	<0.01	<0.01	NS
Ground–Vegetation	-	-	-	-	NS	NS
Shrub–Lower Canopy	-	-	-	-	-	NS
Moderate Burn	Air	Bark	Generalist	Ground–Vegetation	Shrub–Lower Canopy	Upper Canopy
Air	-	NS	NS	<0.05	NS	NS
Bark	-	-	NS	<0.01	<0.01	NS
Generalist	-	-	-	<0.01	<0.01	NS
Ground–Vegetation	-	-	-	-	NS	NS
Shrub–Lower Canopy	-	-	-	-	-	NS
High Burn	Air	Bark	Generalist	Ground–Vegetation	Shrub–Lower Canopy	Upper Canopy
Air	-	<0.05	NS	NS	NS	NS
Bark	-	-	NS	<0.01	<0.01	NS
Generalist	-	-	-	NS	<0.01	NS
Ground–Vegetation	-	-	-	-	NS	NS
Shrub–Lower Canopy	-	-	-	-	-	<0.05

Table A8. Pairwise migratory pattern guild percent composition significance (*p*-values), calculated with pairwise Dunn tests and Bonferroni corrections.

Unburned	Irruptive	Long	Medium	Resident	Short	Variable
Irruptive	-	NS	NS	NS	NS	NS
Long	-	-	NS	<0.05	NS	<0.05
Medium	-	-	-	<0.05	<0.05	<0.05
Resident	-	-	-	-	NS	NS
Short	-	-	-	-	-	NS
Low Burn	Irruptive	Long	Medium	Resident	Short	Variable
Irruptive	-	NS	NS	<0.01	<0.05	<0.01
Long	-	-	NS	<0.05	NS	<0.05
Medium	-	-	-	<0.01	NS	<0.01

Table A8. *Cont.*

Resident	-	-	-	-	NS	NS
Short	-	-	-	-	-	NS
Moderate Burn	Irruptive	Long	Medium	Resident	Short	Variable
Irruptive	-	NS	NS	<0.01	<0.05	<0.01
Long	-	-	NS	<0.05	NS	<0.05
Medium	-	-	-	<0.01	NS	<0.01
Resident	-	-	-	-	NS	NS
Short	-	-	-	-	-	NS
High Burn	Irruptive	Long	Medium	Resident	Short	Variable
Irruptive	-	NS	NS	<0.05	<0.01	<0.01
Long	-	-	NS	NS	<0.01	NS
Medium	-	-	-	NS	<0.05	NS
Resident	-	-	-	-	NS	NS
Short	-	-	-	-	-	NS

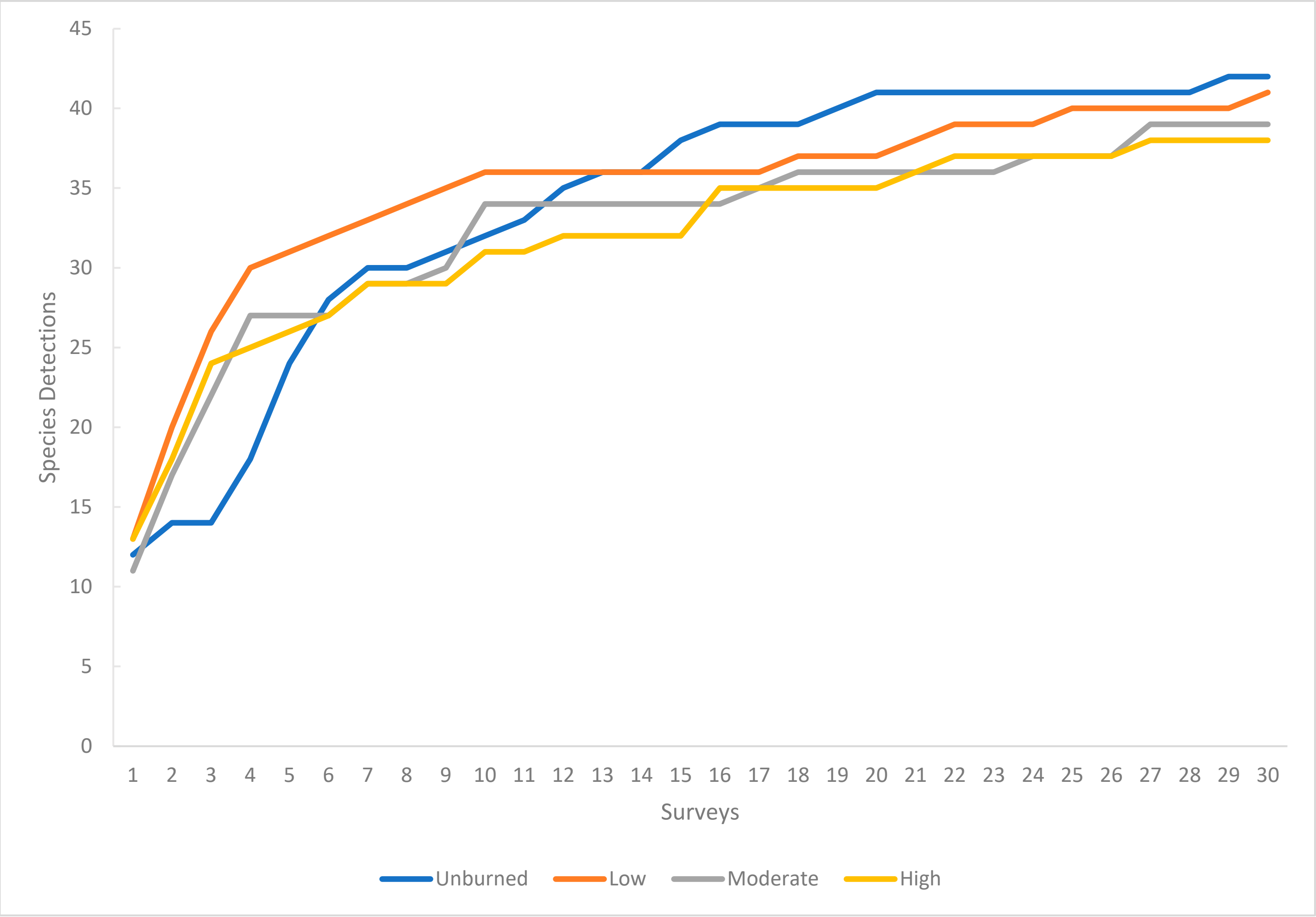

Figure A1. Species accumulation curve depicting the number of surveys required to first detect a species, by burn severity.

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