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Patterns of bird species occurrence in relation to anthropogenic and wildfire disturbance: Management implications

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ABSTRACT

We used a chronosequence approach to investigate the relationship between existing conditions of forested land that burned at some point between 1984 and 2014 in western Montana and the abundances of various bird species based on 7533 point-counts. Twelve of 68 bird species occurred significantly more frequently in burned mixed-conifer forest than in any of 13 unburned vegetation types, and most of them reached their greatest abundance in the severely burned portions of those forests. After restricting the analysis to conifer forest types only, 33 of 68 species (49%) were significantly more abundant in burned forest at some combination of time-since-fire and fire severity than in unburned conifer forest. One species, the black-backed woodpecker (*Picoides arcticus*), occurred nearly exclusively in severely and recently burned mixed-conifer forests. Its restricted distribution suggests that it must have evolved in the presence of those burned-forest conditions and, therefore, that it accurately reflects historical post-fire conditions that are critical to maintain on the landscape. This disturbance-dependent species was also affected strongly and negatively by both pre-fire and post-fire tree harvesting. Two important management implications follow directly from these findings: (1) the presence of the full complement of bird species in a landscape cannot be maintained through land management that either suppresses fire or acts to reduce overall fire severity through widespread forest thinning or through the application of homogeneous, low-severity, prescribed burning across the broader landscape—only severe fire can produce the variety of post-fire conditions used by species that are nowhere more abundant than in burned forests; and (2) the presence of many species (especially those most specialized to use burned forest conditions) is incompatible with both pre-fire and post-fire timber harvesting. To maintain the ecological integrity of disturbance-dependent mixed-conifer forest systems, land managers must, therefore, use strategic landscape planning to harvest trees while still retaining both an abundance of minimally disturbed, unburned, mature-forest conditions and an abundance of severely burned forest conditions that emerge from natural fire disturbance events.

1. Introduction

Fire is the most widespread and important agent of natural disturbance in the Rocky Mountains, where 80–90% of all forest types support either a mixed- or high-severity fire regime (Baker, 2009; DellaSala et al., 2015). It has been noted that within the Northern Rocky Mountains, "…a high percentage of vegetation, within all forest zones, is at one stage or another of succession following past fires" (Habeck and Mutch, 1973); indeed, climax forests that have escaped fire or that have experienced only low-severity understory fires are rare in the northern Rockies. The ecological importance of fire as a disturbance agent can be readily exposed through study of one of the most effective biological indicator groups—birds. Two decades ago, Hutto (1995) published the first comparison of published bird survey data collected from a broad range of unburned vegetation types with his own survey data collected from burned conifer forests. The results were striking. Not only were nearly 100 bird species detected in burned forests, but comparative data also suggested that 15 of those species were nowhere more abundant than in burned forest conditions, and a few (most notably, the black-backed woodpecker, *Picoides arcticus*) were nearly restricted in their distribution to burned forests.

Research over the subsequent two decades has only reinforced that original finding. For example, the same patterns emerged from the use of more than 10,000 point-count surveys conducted across a comprehensive range of vegetation types (Hutto, 2008). Fire scientists have also come to understand that an organism's response to fire depends on

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time since fire (Smucker et al., 2005; Saab et al., 2007) and fire severity (Smucker et al., 2005; Hutto, 2008), and that both pre-fire and post-fire tree harvesting have huge impacts on many species, especially those that are relatively restricted in their distribution to burned forest conditions (Kotliar et al., 2002; Hutto and Gallo, 2006; Hutto, 2008; Saab et al., 2011; Rota, 2013; Hutto et al., 2015).

Because most forest lands are actively managed both before and after natural fire events, we need to better understand how fire, as the most widespread form of natural disturbance in conifer forests throughout the West, interacts with the most widespread form of human disturbance (timber harvesting both before and after fire) to affect the suitability of burned forests to the most fire-dependent birds of our western conifer forests. We also need to better understand how any bird species is affected beyond the first few years following fire within any particular combination of fire severity and type of land management preceding and following fire. Unfortunately, long-term data describing changes in ecological conditions in response to land management activities are rare because of the difficulties in maintaining an effective long-term monitoring program (Lindenmayer and Likens, 2010). Indeed, traditional monitoring designs take many years, require large financial investments, and rarely provide the information needed to answer questions about whether there were cumulative impacts of any kind of land-use activity. Therefore, insight into longer-term effects of treatments using monitoring approaches will emerge only from studies that involve repeat visits to the same experimental and control sites for many years after treatment or, as we attempt here, from the use of a chronosequence approach to learning.

A chronosequence is a space-for-time substitution that takes advantage of independent seral stages that have undergone the same natural disturbance and management treatments in the past. This learning approach has been used for at least a century in ecology (Cowles, 1899) to understand long-term ecological phenomena (e.g., succession). Although some (e.g., Johnson and Miyanishi, 2008) have argued that the infinite variety of conditions and processes that drive succession can weaken a chronosequence approach, temporal change can still be successfully explored through judicious use of the approach (Walker et al., 2010). Most importantly, treatment replicates do not depend on conditions being identical in every respect; they only depend on independent applications of a given treatment (Hurlbert, 1984). Accordingly, multiple independent applications of a spraying treatment or a fuel-reduction harvest or a salvage logging operation constitute valuable replicates of those general treatment categories. Because the public and private land mosaic consists of hundreds upon hundreds of past treatments independently applied across the landscape, the number of existing forest stands that fall within each treatment category is large indeed; one could not ask for any better replication or interspersion of treatments if one tried to design a land-use effects study from scratch. Not only are there dozens upon dozens of past fire-condition replicates that vary in age, burn severity, and land-management activity both before and after the fire event in the northern Rocky Mountains, but there is also a large amount of georeferenced bird survey data that have been gathered from within that variety of conditions in the same place. We, therefore, took advantage of this wealth of data to explore the utility of using a chronosequence approach to uncover significant associations between specific post-fire conditions and the occurrence rates of Northern Rocky Mountain bird species on point-count surveys.

2. Methods

2.1. Research design

There are only a few longitudinal studies of the effects of fire on bird species that have been conducted for as long as 10 years after a forest fire event (e.g., Saab et al., 2007; Stephens et al., 2015; Hutto and Patterson, 2016). There are, however, multi-decadal chronosequence studies of birds in response to fires in Australia (Watson et al., 2012; Lindenmayer et al., 2016; Sitters et al., 2016), Yellowstone (Taylor, 1973; Taylor and Barmore, 1980) and the Canadian boreal forest (Zhao et al., 2013), which demonstrate how a chronosequence approach can be used to reach beyond that 10-year window. In the present study, we extended the time-since-fire dimension to 35 years by targeting fires that had burned in western Montana at some point after satellite images became available in 1984. To uncover the relationship between an index of abundance of various bird species and existing burned-forest conditions, we developed a protocol to map a series of locations that together comprised different combinations of four key variables likely to influence bird communities—time-since-fire, fire severity, pre-fire timber harvesting, and post-fire salvage logging. In addition to existence of a wealth of burned, mixed-conifer forest patches representing a complex combination of fire conditions across northern Idaho and western Montana, a wealth of bird survey data were also already available from 52,310 point-counts that were conducted across every major vegetation type in the Northern Rocky Mountains in association with the USFS Northern Region Landbird Monitoring program between 1989 and 2013. A total of 6817 of those point counts were conducted within 107 different fires that had burned within a 35-year period in western Montana prior to when a given bird survey was conducted; most of the remaining counts were conducted within "unburned" forest patches that were generally more than 100 years of age following a stand initiating disturbance event. In 2014 and 2015, we were able to supplement this already existing, large geo-referenced database on bird occurrence with additional point-count data from some of the same (but by then, older) fires and from 10 additional fires to investigate how fire age, fire severity, and timber harvest history affect the probability of occurrence of a variety of bird species, with special attention given those that occur primarily in burned forests. No point was visited more than once in the same year, but there is some inherent pseudoreplication when the same point was visited repeatedly across years. Repeat visits were evenly distributed across the fire severity × time-since-fire combinations, however (Fig. 1), so their occurrence should not bias results even if they affect the accuracy of P-values derived from our statistical analysis.

To work with a manageable number of combinations of forest conditions following a fire, we restricted this study to mixed-conifer forests from 1000 to 2500 m in elevation, and then subdivided each of the 4 land condition variables into a small number of categories to examine existing sample sizes and to target condition combinations that

Fig. 1. Point-count data were collected in each of 15 combinations of fire severity (columns) and time-since-fire (rows). Inside each box, the number of point counts conducted is indicated above the percentage of those counts that were visited only once during that post-fire time interval; the remaining percentage of points were visited on 2 or more years during the time interval. The numbers indicate that at least 25 independent samples were obtained in every severity by time-since-fire combination.

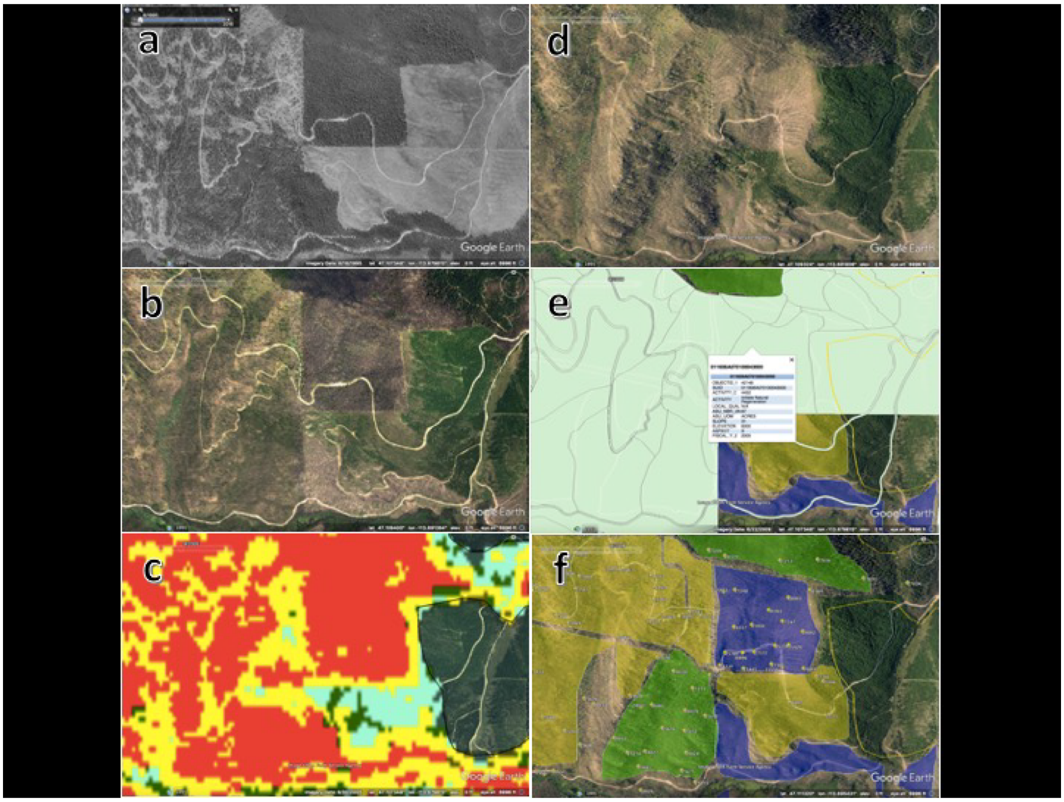

Fig. 2. The routine used to classify land conditions at a survey point included (a) looking at the satellite image from within a few years before a fire occurred to verify locations and types of any pre-fire timber harvests; (b) verifying the fire severity at each point (note the presence of unburned, moderately burned, and severely burned patches; (c) comparing our visual estimates of severity with the MTBS fire severity map; (d) looking for evidence of post-fire salvage logging in satellite images taken within a few years after a fire occurred; (e) verifying our estimates of pre-fire and post-fire timber harvests with a land-use history database provided by the US Forest Service; (f) drawing our own color-coded map of places that were harvested before fire (yellow), after fire (blue), or not harvested at all (green). We used the color-coded maps to determine land conditions surrounding existing bird survey points (apparent in panel f) and to target locations for supplemental survey points. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

most needed additional sampling. Specifically, we used three fire-age categories (1–4, 5–14, 15–35 years after fire), five categories of fire severity (0–20%, 21–40%, 41–60%, 61–80%, and 81–100% tree mortality), and two categories (presence or absence) each for pre-fire and post-fire timber harvesting. Our goal was to attain the recommended (Ralph et al., 1995) minimum of 30 point-count surveys needed to achieve a reliable estimate of bird occurrence rate in each combination of variables.

2.2. Selection of fires and supplementary survey locations

We used the MTBS web site (https://www.mtbs.gov/) to obtain fire perimeter and severity maps for all fires greater than 400 ha in size that occurred between 1984 and 2014 in Montana on lands managed by US Forest Service, National Park Service, Plum Creek, Potlatch, MT Fish, Wildlife and Parks, and Salish and Kootenai tribes. We then used aerial views and elevation information in Google Earth, and field-based vegetation information from the existing landbird monitoring database to restrict our focus to fires that burned within the mid-elevation (1000–2500 m) dry to mesic mixed-conifer zone. We used Google Earth satellite images taken from 1 to 5 years before the date of a given fire to find and map any locations that had been noticeably harvested, and we used images taken from 1 to 5 years after the fire to find and map any locations of post-fire salvage logging activity. Within each fire, we also located and mapped the more severely burned locations that had not been harvested either before or after the fire. Finally, we tallied the number of already existing point-count survey points that occurred within each combination of the 4 variables and chose an additional 10 fires in each of the 3 age categories as potential locations where we could position a minimum of 10 points on roads or trails that would take a field technician through a range of post-fire conditions. In the 2014 field season, we developed field protocols and conducted 162 independent point-counts in different combinations of fire severity and harvest history within the 2003 Black Mountain fire near Missoula, Montana. We also mapped the perimeter of every other fire > 400 ha that had occurred in western Montana from 1984 to 2013, obtained necessary permission to conduct surveys in target fires, and created GIS data layers needed to display road and trail access, fire severity, and land condition both before and after fire within each fire's perimeter. In the 2015 field season, we collected 565 additional point counts in 35 different fires that each provided different combinations of fire severity and harvest history.

2.3. Classifying land conditions surrounding survey points

A growing number of scientists are using remotely sensed fire severity and land condition data in their analyses of fire effects because these GIS data layers are readily available from various sources. Unfortunately, the spatial resolution associated with GIS data layers is not generally fine enough to allow one to simply extract values from these layers and couple those values with on-the-ground, point-based biological data because land conditions within a fire often change dramatically across distances that measure in just tens of meters. Fortunately, for most survey points, we were able to obtain field-based estimates of fire severity, pre-fire harvest condition, and post-fire harvest condition. For bird-survey point counts conducted prior to the 2014 season, however, we could not always determine what the fire severity and immediate pre- and post-fire harvest history were when the count was conducted at an earlier time because (1) already-existing survey points were visited when bird survey crews did not routinely record information on fire severity and history of timber harvesting before and after a fire, or (2) a fire may have burned many years prior to when a bird survey was conducted, making it nearly impossible to reconstruct fire severity accurately. It was also hard to determine whether a harvested area that retained very few live or dead tree boles was harvested shortly before or shortly after a fire that occurred 10–35 years earlier because on-the-ground evidence becomes more and more obscured with time.

Therefore, we proceeded point by point through the entire point-count database and used a variety of sources of information to classify the land condition that we believe was associated with each survey location during the year the point was visited. Specifically, the routine for any given point was to locate that point in Google Earth and superimpose GIS information about vegetation type, fire severity, and land-use history within a 100-m radius around the point, as described in more detail below, and as summarized in Fig. 2.

2.3.1. Fire severity

We used the combination of our field-based estimate of fire severity, MTBS severity map information, and satellite images to classify the fire severity within 100 m of a survey point. A meaningful measure of fire severity (percent canopy tree mortality) can be obtained easily and accurately by visual inspection of tree condition within about 50 m of a survey point, but fire severity is very difficult to discern in the field long after a fire has burned. Therefore, we used a combination of aerial photos from the USFS, aerial imagery in Google Earth (Fig. 2b), MTBS map data (Fig. 2c), and on-the-ground estimates (if they were available) for the year following fire, and necessarily put more weight on the MTBS severity estimates for the older fires. The crosswalk between our field-based fire severity categorization and the MTBS color-coded categories that occurred within 100 m of a point were as follows: 0–20% mortality = none/green; 21–40% mortality = green; 41–60% mortality = green/yellow; 61–80% mortality = yellow; 81–95% mortality = yellow–red; 96–100% mortality = red. The correspondence between MTBS and our own categories was highly significant ($P < 0.001$) and well correlated (Pearson's $R = 0.95$).

2.3.2. Cutting before and after fire

Burned stands within National Parks provided uncut stands only, but for all other locations, we went backward and forward in time in Google Earth to confirm the presence or absence of pre-fire and post-fire cutting. The oldest fires (those that burned prior to about 1990) were problematic because the Google Earth images from before the fire were not available, which made it impossible to distinguish whether a cut stand was the result of pre-fire or a post-fire harvest. In those cases, we relied on the mapped Forest Activity Tracking System (FACTS) codes provided by the USFS Northern Region if the fire occurred on USFS land (Fig. 2e), and on the location of harvest area boundaries in relation to fire severity class boundaries otherwise (assuming that harvests occurring entirely within the higher severity patches were salvage operations). We classified clearcuts, seed-tree cuts, and shelterwood cuts as "cut" forests and considered areas with no recent harvest or with less intensive, selective tree harvesting to be "uncut."

2.4. Bird survey method

We used the standardized point-count method described in Ralph et al., (1995), where observers record numbers of every bird species detected within a fixed distance (100 m) from a given survey point within a 10-min period. Observers practiced locating 50- and 100-m targets during training to ensure accuracy of detection distances during a formal count. Because burned-forest conditions hundreds of meters away from a survey point can be quite different from those immediately surrounding the survey point, we used a 100-m distance cutoff to maximize the probability that every bird detected occurred within the vegetation condition as categorized at the survey point. We used the proportion of counts during which a species was detected as an index of its abundance in that type. By using only those bird detections that were within a fixed distance from the observer, we minimized any potential problem associated with habitat-based detection problems, as demonstrated by comparative data obtained from 3067 points where recording playbacks were used to confirm the presence of black-backs (Hutto, 2008). As described in detail elsewhere (Hutto and Young, 2002, 2003; Johnson, 2008; Hutto, 2016, 2017), the proportion of fixed-radius counts on which a species is detected is likely to be a reliable and biologically meaningful index of abundance that can be gained from point-count data, especially when attempting to uncover habitat associations. Common and scientific bird names follow the AOS Checklist of North and Middle American Birds (Chesser et al., 2018).

2.5. Statistical analysis

We conducted chi-square analyses (with tests adjusted for all pairwise comparisons using the Bonferroni correction) to determine which bird species were significantly ($P < 0.05$) more abundant (had significantly larger percent occurrence rates) in burned conifer forests than in other unburned Northern Rocky Mountain vegetation types. Because the simultaneous consideration of severity and time-since-fire allows one to detect fire effects that are more nuanced than consideration of either variable alone (Stephens et al., 2015; Hutto and Patterson, 2016; Taillie et al., 2018), we also used chi-square analyses (adjusted for all pairwise comparisons using the Bonferroni correction) to determine whether the occurrence rate of a species in any single combination of time-since-fire and fire severity was significantly greater than its occurrence rate in any of the three unburned conifer forest categories. The effect of timber harvesting on each species was evaluated through a simple pairwise comparison of its occurrence rate in burned forest that had been harvested either before or after fire with its occurrence rate in burned forest that had not been recently harvested.

3. Results

We visited a total of 117 fires across 25 post-fire years and conducted a total of 7533 bird point counts within those recently burned mixed-conifer forests. A grand total of 148 bird species were detected on survey points in burned forests, and 68 of those species were detected on more than 50 points, deeming them sufficiently common to explore their patterns of distribution further. Several important bird distribution patterns emerge from these data, as discussed more fully below.

3.1. Bird abundances in burned forest and in unburned vegetation types

Twelve (18%) of the 68 bird species that were adequately sampled were more abundant in burned forest (grouped into a single category) than in any of the 13 unburned Northern Rocky Mountain vegetation types (Table 1); 6 of those 12 were statistically significantly (Bonferroni adjusted chi-square, $P < 0.05$) more abundant in burned forests than anywhere else, as indicated by complete pairwise comparisons of all probabilities of occurrence across vegetation types. As a measure of how restricted a species was to burned forest conditions, we used the Inverse Simpson index of specialization ($1/\Sigma p_i^2$), where p represents the proportionate abundance in the i^{th} vegetation category and the possible values range from 1 (if a species occurs in only a single vegetation category) to 14 (if a species occurs in equal abundance in all 14 vegetation categories). No species is as restricted to burned forest (is as much a burned-forest specialist) as the black-backed woodpecker, which has a calculated habitat niche breadth of 1.08 (Table 1), although the western bluebird (*Sialia mexicana*), American three-toed

Table 1
Numbers represent the percentages of point counts on which a given species was detected in each of 14 vegetation cover types. The twelve species that are highlighted in gray were significantly (Bonferroni corrected chi-square, $P < 0.05$) more abundant in burned forests than in any of the 13 other Rocky Mountain vegetation types shown. The habitat breadth of each species is represented by the inverse Simpson index. Species are listed in alphabetical order.

Species	Urban/Rural n=64	Cropland n=410	Grassland n=4118	Sage/ Greasewood n=2393	Dry shrubfield n=354	Juniper n=630	Dry mixed-conifer n=2662	Mesic mixed-conifer n=24758	Subalpine forest n=6595	Aspen n=296	Cottonwood n=946	Willow n=1241	Streamside riparian n=1029	Burned conifer forest n=7544	Habitat Breadth
American Kestrel, *Falco sparverius*	1.56	2.68	1.04	0.96	1.13	1.27	0.64	0.43	0.17	1.35	4.23	0.64	0.39	0.98	8.39
American Robin, *Turdus migratorius*	56.25	15.37	16.20	21.65	37.57	31.59	32.83	24.00	26.88	36.49	62.05	52.05	40.23	31.65	12.10
American Three-toed Woodpecker, *Picoides dorsalis*	0.00	0.00	0.10	0.00	0.28	0.00	0.19	0.63	0.89	0.00	0.11	0.00	0.00	4.83	2.00
Black-backed Woodpecker, *Picoides arcticus*	0.00	0.00	0.00	0.04	0.00	0.00	0.04	0.08	0.02	0.00	0.00	0.00	0.00	4.43	1.08
Black-capped Chickadee, *Poecile atricapillus*	14.06	1.46	2.14	1.92	5.65	4.44	11.72	7.42	2.41	5.41	19.13	9.99	9.33	3.30	9.21
Black-headed Grosbeak, *Pheucticus melanocephalus*	0.00	0.73	0.78	0.71	4.52	0.63	3.98	3.28	1.15	0.68	14.48	4.67	4.76	3.31	6.04
Brown Creeper, *Certhia americana*	0.00	0.00	0.07	0.08	0.28	0.16	1.05	4.00	2.79	1.35	0.11	0.16	0.39	4.98	4.59
Brown-headed Cowbird, *Molothrus ater*	34.38	21.46	16.93	13.92	8.76	19.84	16.75	5.52	5.72	8.78	34.88	45.77	18.66	6.61	9.91
Calliope Hummingbird, *Selasphorus calliope*	0.00	0.00	0.27	0.00	0.56	0.00	1.77	0.84	0.15	0.00	0.53	1.21	1.75	2.77	5.80
Canada Jay, *Perisoreus canadensis*	0.00	0.00	0.70	0.17	1.69	0.32	2.97	5.96	7.57	3.38	0.00	0.97	0.49	2.40	5.74
Cassin's Finch, *Haemorhous cassinii*	1.56	0.00	1.68	1.21	2.26	5.56	4.58	2.43	3.75	4.05	0.74	2.01	2.62	6.44	9.88
Cassin's Vireo, *Vireo cassinii*	0.00	0.00	0.32	0.04	4.52	0.16	19.72	14.38	2.84	2.36	2.11	1.61	4.47	5.53	4.90
Chipping Sparrow, *Spizella passerina*	14.06	2.44	20.57	21.35	43.22	61.27	54.02	25.62	19.91	25.34	4.97	15.55	26.14	44.30	10.08
Clark's Nutcracker, *Nucifraga columbiana*	0.00	0.00	3.28	2.80	1.69	7.62	5.37	2.27	6.14	3.38	0.63	1.05	2.24	3.02	8.75
Common Raven, *Corvus corax*	0.00	0.98	0.80	0.75	0.85	2.06	1.95	1.87	1.27	0.34	0.74	2.50	1.94	1.37	10.61
Common Yellowthroat, *Geothlypis trichas*	1.56	4.63	4.06	2.17	10.45	3.02	0.19	0.67	1.18	6.76	12.16	21.19	4.37	1.51	6.59
Dark-eyed Junco, *Junco hyemalis*	0.00	0.98	10.51	10.45	26.84	20.63	47.90	51.33	58.71	34.12	3.49	13.54	27.50	60.39	8.66
Dusky Flycatcher, *Empidonax oberholseri*	4.69	0.24	4.47	6.60	26.27	31.27	25.47	12.14	8.04	46.28	8.03	23.53	30.61	18.52	9.11
Dusky Grouse, *Dendragapus obscurus*	0.00	0.00	0.24	1.09	0.56	0.63	0.41	0.34	0.33	1.01	0.00	0.08	0.29	1.19	7.81
Fox Sparrow, *Passerella iliaca*	0.00	0.00	0.29	0.00	0.00	0.16	0.15	3.53	8.08	1.01	0.21	3.87	4.08	3.57	5.05
Golden-crowned Kinglet, *Regulus satrapa*	0.00	0.00	0.41	0.42	3.67	0.32	3.61	21.13	16.21	2.36	0.74	2.58	8.65	2.45	4.72
Hairy Woodpecker, *Dryobates villosus*	0.00	0.24	0.90	0.50	2.82	0.32	4.96	3.73	2.99	5.41	3.07	1.21	1.65	15.67	5.48
Hammond's Flycatcher, *Empidonax hammondii*	0.00	0.00	0.70	1.25	3.39	6.19	12.21	10.80	3.34	4.39	1.59	3.38	14.67	7.49	7.61
Hermit Thrush, *Catharus guttatus*	0.00	0.00	0.90	0.42	0.28	1.90	5.94	4.93	10.28	2.36	0.11	1.13	2.43	2.96	5.91
House Wren, *Troglodytes aedon*	14.06	7.56	12.43	5.06	5.93	6.51	7.66	2.01	1.85	19.59	66.28	9.43	12.83	11.32	5.81
Lazuli Bunting, *Passerina amoena*	9.38	1.71	6.53	2.17	20.90	6.35	3.04	2.59	0.86	12.16	5.92	4.35	8.84	11.52	8.88
Lewis's Woodpecker, *Melanerpes lewis*	0.00	0.00	0.07	0.00	0.00	0.00	0.08	0.03	0.02	0.00	0.21	0.00	0.00	0.74	2.19
Lincoln's Sparrow, *Melospiza lincolnii*	0.00	0.73	1.55	5.14	13.28	1.75	0.34	1.09	5.52	5.41	0.21	23.53	3.40	3.90	5.10
MacGillivray's Warbler, *Geothlypis tolmiei*	1.56	0.00	1.87	1.55	18.64	3.81	12.58	24.48	12.66	18.24	5.60	17.41	31.39	24.03	8.59
Mountain Bluebird, *Sialia currucoides*	0.00	3.41	9.01	8.02	9.32	19.37	3.76	1.70	3.59	4.73	1.16	2.18	3.11	22.19	7.11
Mountain Chickadee, *Poecile gambeli*	1.56	0.24	5.49	6.44	11.86	21.43	24.19	19.93	26.13	25.68	2.11	11.20	14.38	16.95	9.71
Mourning Dove, *Zenaida macroura*	1.56	9.27	9.06	9.61	1.69	12.86	5.37	0.48	0.59	1.01	41.75	4.43	3.89	1.25	4.72
Northern Flicker, *Colaptes auratus*	15.63	5.12	6.70	7.69	8.47	7.94	8.19	7.36	6.97	10.47	25.90	5.16	7.00	16.11	10.72
Northern Waterthrush, *Parkesia noveboracensis*	0.00	0.00	0.24	0.00	0.00	0.00	0.11	1.13	2.02	1.01	2.01	12.17	3.69	2.77	3.52
Olive-sided Flycatcher, *Contopus cooperi*	0.00	0.24	0.19	0.17	0.85	0.32	0.90	3.80	4.18	0.34	0.11	1.13	2.04	8.62	4.61
Orange-crowned Warbler, *Oreothlypis celata*	1.56	0.00	0.85	0.29	3.95	2.06	10.41	9.56	2.94	6.42	1.37	2.01	6.12	7.24	8.14
Pacific Wren, *Troglodytes pacificus*	0.00	0.00	0.00	0.00	0.56	0.16	1.13	10.75	6.99	0.34	0.63	0.64	7.19	2.41	4.23
Pileated Woodpecker, *Dryocopus pileatus*	1.56	0.00	0.02	0.08	0.00	0.00	1.50	2.75	0.64	0.34	0.53	0.56	0.29	0.80	5.84
Pine Grosbeak, *Pinicola enucleator*	0.00	0.00	0.05	0.13	0.00	0.16	0.41	0.65	2.06	0.00	0.11	0.00	0.29	1.06	3.97
Pine Siskin, *Spinus pinus*	12.50	0.98	5.46	5.18	10.73	14.76	17.43	16.34	19.27	22.64	3.59	10.64	16.13	19.50	11.08
Red Crossbill, *Loxia curvirostra*	0.00	0.24	0.95	0.92	1.69	1.43	8.64	3.95	4.53	1.69	0.42	0.81	0.58	3.51	6.44
Red-breasted Nuthatch, *Sitta canadensis*	7.81	0.49	4.66	3.80	7.63	7.30	48.42	39.55	23.29	28.72	2.75	4.59	11.27	26.22	7.41
Red-naped Sapsucker, *Sphyrapicus nuchalis*	1.56	1.46	0.85	1.09	5.37	0.79	1.47	4.29	2.09	10.14	7.08	4.83	5.34	1.72	8.61
Red-tailed Hawk, *Buteo jamaicensis*	1.56	2.20	0.80	0.42	0.85	1.90	0.83	0.71	0.52	1.01	4.44	1.85	0.68	0.97	8.90
Rock Wren, *Salpinctes obsoletus*	1.56	0.24	2.94	8.32	1.98	16.35	1.69	0.24	0.30	1.01	0.85	1.29	4.66	2.47	5.00
Ruby-crowned Kinglet, *Regulus calendula*	3.13	0.49	5.83	6.18	15.25	11.27	17.09	22.03	35.63	31.76	3.49	19.58	21.28	13.51	9.42
Ruffed Grouse, *Bonasa umbellus*	0.00	0.00	0.34	0.63	1.98	0.79	3.91	4.08	1.59	6.76	1.06	2.58	3.60	1.30	7.61
Rufous Hummingbird, *Selasphorus rufus*	0.00	0.00	0.10	0.00	1.98	0.00	0.34	1.04	0.44	0.00	0.32	0.64	0.39	1.31	5.59
Song Sparrow, *Melospiza melodia*	7.81	6.59	3.16	5.77	6.78	8.41	2.03	3.75	2.71	4.73	29.18	49.72	22.74	3.76	5.93
Spotted Towhee, *Pipilo maculatus*	6.25	1.22	22.80	6.23	24.58	13.97	10.41	2.37	0.35	3.04	12.16	1.21	10.30	2.65	7.74

(*continued on next page*)

Table 1 (*continued*)

Species	Urban/Rural n=64	Cropland n=410	Grassland n=4118	Sage/ Greasewood n=2393	Dry shrubfield n=354	Juniper n=630	Dry mixed-conifer n=2662	Mesic mixed-conifer n=24758	Subalpine forest n=6595	Aspen n=296	Cottonwood n=946	Willow n=1241	Streamside riparian n=1029	Burned conifer forest n=7544	Habitat Breadth
Steller's Jay, *Cyanocitta stelleri*	0.00	0.00	0.27	0.21	0.28	0.32	2.18	2.75	2.18	1.01	0.21	0.48	1.46	2.25	7.15
Swainson's Thrush, *Catharus ustulatus*	0.00	0.00	0.78	0.38	8.76	0.48	13.67	33.06	20.73	11.15	4.33	5.48	13.22	16.68	6.87
Townsend's Solitaire, *Myadestes townsendi*	0.00	0.49	1.48	2.05	7.91	4.29	14.61	9.09	9.17	7.77	0.42	1.45	6.71	15.91	7.99
Townsend's Warbler, *Setophaga townsendi*	0.00	0.00	0.19	0.00	6.21	0.16	10.56	36.00	16.62	1.69	0.11	2.10	15.26	6.39	4.53
Tree Swallow, *Tachycineta bicolor*	6.25	3.66	2.04	1.50	3.67	1.90	0.19	0.23	0.24	1.69	19.56	4.59	2.72	6.48	5.63
Varied Thrush, *Ixoreus naevius*	0.00	0.00	0.10	0.00	0.28	0.00	0.30	9.25	10.54	0.34	0.00	0.97	3.50	1.01	3.27
Vesper Sparrow, *Pooecetes gramineus*	6.25	29.27	52.21	42.92	8.19	23.65	4.51	0.59	3.38	5.41	0.74	3.87	3.79	0.87	5.57
Warbling Vireo, *Vireo gilvus*	23.44	0.98	4.76	7.65	29.38	16.19	13.60	18.74	16.13	55.07	25.69	27.64	36.35	16.16	9.91
Western Bluebird, *Sialia mexicana*	0.00	0.00	0.07	0.00	0.00	0.00	0.11	0.06	0.05	0.00	0.00	0.00	0.00	2.45	1.25
Western Tanager, *Piranga ludoviciana*	1.56	0.73	2.23	2.05	11.86	4.44	39.03	32.04	12.90	11.49	4.33	5.32	10.20	28.30	6.98
Western Wood-Pewee, *Contopus sordidulus*	17.19	5.85	1.48	2.21	0.56	2.22	3.94	0.52	1.36	2.70	47.46	5.88	5.34	6.15	3.89
White-breasted Nuthatch, *Sitta carolinensis*	0.00	0.24	0.15	0.04	0.00	0.63	3.83	0.63	0.33	0.68	2.01	0.00	0.29	2.07	4.84
White-crowned Sparrow, *Zonotrichia leucophrys*	0.00	0.49	4.23	8.98	9.89	3.02	0.60	1.16	4.41	3.72	0.63	18.05	2.24	4.32	6.45
Williamson's Sapsucker, *Sphyrapicus thyroideus*	0.00	0.00	0.07	0.17	0.28	0.16	2.10	1.10	0.49	1.35	0.00	0.08	0.19	1.92	5.42
Willow Flycatcher, *Empidonax traillii*	1.56	2.20	0.83	1.00	0.00	1.27	0.23	0.63	1.05	1.01	6.66	22.72	6.22	2.08	3.65
Wilson's Warbler, *Cardellina pusilla*	1.56	0.00	0.15	0.25	1.41	0.79	0.41	4.30	5.44	0.68	0.74	6.20	3.89	3.06	7.11
Yellow Warbler, *Setophaga petechia*	48.44	13.90	13.21	9.11	14.41	12.38	3.49	2.12	2.87	10.14	85.52	67.61	24.39	1.91	6.07
Yellow-rumped Warbler, *Setophaga coronata*	20.31	0.73	6.85	9.90	20.90	17.62	52.03	43.86	46.46	30.07	5.39	14.83	31.68	40.84	9.78

woodpecker (*Picoides dorsalis*), and Lewis's woodpecker (*Melanerpes lewis*) come close (at 1.25, 2.00, and 2.19, respectively).

3.2. Bird occurrence in relation to combinations of time-since-fire and fire severity

To focus greater attention on details surrounding the burned forest condition that is most important to species that are nowhere more abundant, and to species that are at least more abundant in a subset of burned forest conditions than in long-unburned (mature) mixed-conifer forest, we looked at bird distribution patterns across a combined gradient of time-since-fire and fire severity. Even though this constitutes what is certainly one of the largest fire-related databases of its kind in the world, the numbers of survey points are not evenly distributed across categories of each of the four land condition variables because most sampling was accomplished in early post-fire years, in relatively severely burned patches, and in forests that were not recently cut either before or after fire (see sample sizes in Table 2). Nevertheless, there are 11 recognizable patterns of abundance, and nine are represented by sets of species that reach their greatest abundances in one of the nine possible combinations of three levels each of time-since-fire and fire severity (species arranged in groups 1 through 9 in Table 2). The remaining two are represented by sets of species that did not respond noticeably to time-since-fire, but were clearly more abundant in either low or high severity patches (labeled groups 10 and 11 in Table 2). The graded responses to time-since-fire, and the smooth, unimodal responses to severity by most species suggest strongly that the patterns are biologically meaningful and not statistical artifacts. A number of species fit within each of the 11 distribution patterns (Table 2). Specifically, nine species [group 1—American robin (*Turdus migratorius*), American three-toed woodpecker, black-backed woodpecker, dark-eyed junco (*Junco hyemalis*), hairy woodpecker (*Dryobates villosus*), olive-sided flycatcher (*Contopus cooperi*), pine siskin (*Spinus pinus*), Townsend's solitaire (*Myadestes townsendi*), tree swallow (*Tachycineta bicolor*)] are most abundant early on after fire in the most severely burned patches, and the abundance levels of all but the robin are also statistically significantly greater (Bonferroni adjusted chi-square, $P < 0.05$) in one or more burned-forest conditions than in any of the three unburned conifer forest types (Table 2); seven species [group 2—brown creeper (*Certhia americana*), Cassin's finch (*Haemorhous cassinii*), fox sparrow (*Passerella iliaca*), MacGillivray's warbler (*Geothlypis tolmiei*), northern waterthrush (*Parkesia noveboracensis*), rufous hummingbird (*Selasphorus rufus*), Wilson's warbler (*Cardellina pusilla*)] are most abundant early on in locations that burned at moderate rather than high severity, and four of the seven species are significantly more abundant in that type of burned conifer forest than in unburned conifer forest (Table 2); ten species [group 3—black-capped chickadee (*Poecile atricapillus*), black-headed grosbeak (*Pheucticus melanocephalus*), Canada jay (*Perisoreus canadensis*), golden-crowned kinglet (*Regulus satrapa*), pacific wren (*Troglodytes pacificus*), pine grosbeak (*Pinicola enucleator*), ruffed grouse (*Bonasa umbellus*), Swainson's thrush (*Catharus ustulatus*), Townsend's warbler (*Setophaga townsendi*), varied thrush (*Ixoreus naevius*)] are most abundant early on after fire in forests that burned at the lowest fire severity, and none of these species is significantly more abundant in that type of burned conifer forest than in unburned conifer forest (Table 2); seven species [group 4—dusky grouse (*Dendragapus obscurus*), house wren (*Troglodytes aedon*), mountain bluebird (*Sialia currucoides*), northern flicker (*Colaptes auratus*), western bluebird, western wood-pewee (*Contopus sordidulus*), willow flycatcher (*Empidonax traillii*)] are most abundant in the severely burned forest category after about a half-dozen years following fire, and every one of these species is significantly more abundant in that type of burned conifer forest than in unburned conifer forest (Table 2); three species [group 5—calliope hummingbird (*Selasphorus calliope*), white-breasted nuthatch (*Sitta carolinensis*), Williamson's sapsucker (*Sphyrapicus thyroideus*)] are most abundant in burned-forest locations that burned at moderate severity more than about a half-dozen years following fire, and each is significantly more abundant in those conditions than in unburned mixed-conifer forest (Table 2); seven species [group 6—brown-headed cowbird (*Molothrus ater*), Cassin's vireo (*Vireo cassinii*), chipping sparrow (*Spizella passerina*), Hammond's flycatcher (*Empidonax hammondii*), hermit thrush (*Catharus guttatus*), pileated woodpecker (*Dryocopus pileatus*), red crossbill (*Loxia curvirostra*)] are most abundant in forests that burned at the lowest severity after about a half-dozen years following fire, and none of these species is significantly more abundant in that burned-forest condition than in unburned conifer forest (Table 2); six species [group 7—dusky flycatcher (*Empidonax oberholseri*), Lewis's woodpecker, orange-crowned warbler (*Oreothlypis celata*), rock wren (*Salpinctes obsoletus*), warbling vireo (*Vireo gilvus*), white-crowned sparrow (*Zonotrichia leucophrys*)] are most abundant 15–35 years following fire in forest that burned at high severity, and each of those species is more abundant in that type of burned-forest

Table 2
Numbers represent the percentages of point counts on which each of 68 species was present across categories of time-since-fire and fire severity and across categories of unburned conifer forest. Abundances highlighted in gray and noted with an asterisk indicate that the abundance is significantly greater in that particular forest condition than in any of the three unburned conifer forest types (Bonferroni adjusted chi-square, P < 0.05). The names of species that were identified in Table 1 as being more abundant in burned forest than in any other vegetation type are also highlighted in gray; note that most of those species are also most abundant in more severely burned patches in those forests. Species are organized by response group, and then alphabetically within each group.

		1-4 yr after fire					5-14 yr after fire					15-35 yr after fire							
		Fire Severity (% tree mortality)					Fire Severity (% tree mortality)					Fire Severity (% tree mortality)							
		0-20%	21-40%	41-60%	61-80%	81-100%	0-20%	21-40%	41-60%	61-80%	81-100%	0-20%	21-40%	41-60%	61-80%	81-100%	mature, long unburned		
Species	Group	n=619	n=623	n=1080	n=1224	n=1782	n=147	n=234	n=357	n=451	n=589	n=26	n=55	n=104	n=97	n=139	n=2662	n=24758	n=6595
American Robin, *Turdus migratorius*	1--early, high severity	28.9	30.3	34.4	36.2	34.1	32.7	24.4	25.5	23.7	30.4	26.9	25.5	21.2	29.9	26.6	32.8	24.0	26.9
American Three-toed Woodpecker, *Picoides dorsalis*	1--early, high severity	1.9	4.5*	4.9*	6.7*	8.5*	2.7	1.7	3.9*	2.2	0.7	0.0	0.0	1.0	0.0	0.0	0.2	0.6	0.9
Black-backed Woodpecker, *Picoides arcticus*	1--early, high severity	0.6*	2.4*	3.8*	5.3*	7.5*	0.7	4.7*	5.0*	3.5*	4.9*	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Dark-eyed Junco, *Junco hyemalis*	1--early, high severity	57.5	61.3	66.9*	67.6*	75.1*	34.7	45.7	40.3	43.0	44.5	57.7	56.4	35.6	29.9	38.9	47.9	51.3	58.7
Hairy Woodpecker, *Dryobates villosus*	1--early, high severity	8.9	13.2*	15.6*	18.0*	19.1*	9.5	13.7*	16.0*	19.5*	14.3*	0.0	9.1	8.7	9.3	12.2*	5.0	3.7	3.0
Olive-sided Flycatcher, *Contopus cooperi*	1--early, high severity	6.3	9.5*	10.6*	11.9*	10.7*	1.4	3.4	4.8	3.1	6.3	3.9	9.1	8.7	5.2	2.9	0.9	3.8	4.2
Pine Siskin, *Spinus pinus*	1--early, high severity	19.7	20.2	20.7	21.4	26.0*	20.4	17.5	14.9	14.6	7.8	7.7	14.6	10.6	8.3	7.2	17.4	16.3	19.3
Townsend's Solitaire, *Myadestes townsendi*	1--early, high severity	13.4	14.1	14.4	15.8	20.2*	14.3	12.8	18.5	12.9	16.1	0.0	18.2	11.5	13.4	8.6	14.6	9.1	9.2
Tree Swallow, *Tachycineta bicolor*	1--early, high severity	1.9*	3.5*	4.0*	7.1*	14.3*	0.0	0.0	1.7*	4.0*	5.8*	0.0	1.8	1.0	5.2*	3.6*	0.2	0.2	0.2
Brown Creeper, *Certhia americana*	2--early, moderate severity	6.3	8.2*	7.4*	6.9*	5.5	2.7	1.7	2.2	0.0	1.0	0.0	0.0	0.0	1.0	0.0	1.1	4.0	2.8
Cassin's Finch, *Haemorhous cassinii*	2--early, moderate severity	5.0	6.6	7.7*	7.8*	6.8	8.2	9.0	7.8	6.9	2.6	0.0	1.8	1.0	3.1	0.7	4.6	2.4	3.8
Fox Sparrow, *Passerella iliaca*	2--early, moderate severity	4.7	4.2	5.7	5.4	4.4	0.7	0.4	0.0	0.4	0.2	3.9	0.0	0.0	0.0	2.2	0.2	3.5	8.1
MacGillivray's Warbler, *Geothlypis tolmiei*	2--early, moderate severity	25.0	26.3	26.3	24.8	25.0	20.4	22.7	14.6	19.5	25.8	11.5	18.2	14.4	27.8	21.6	12.6	24.5	12.7
Northern Waterthrush, *Parkesia noveboracensis*	2--early, moderate severity	2.3	2.3	4.6	5.6*	3.0	0.0	0.4	1.1	0.4	0.0	0.0	1.8	1.0	0.0	0.0	0.1	1.1	2.0
Rufous Hummingbird, *Selasphorus rufus*	2--early, moderate severity	2.4	1.8	1.4	2.7*	0.3	0.7	1.3	0.8	0.7	0.7	0.0	1.8	1.0	1.0	0.7	0.3	1.0	0.4
Wilson's Warbler, *Cardellina pusilla*	2--early, moderate severity	3.4	2.7	5.0	4.7	3.4	1.4	2.6	0.8	0.4	0.2	0.0	0.0	0.0	3.1	2.2	0.4	4.3	5.4
Black-capped Chickadee, *Poecile atricapillus*	3--early, low severity	7.9	6.1	3.8	3.1	2.3	2.0	1.7	1.4	0.9	1.5	0.0	1.8	2.9	5.2	2.9	11.7	7.4	2.4
Black-headed Grosbeak, *Pheucticus melanocephalus*	3--early, low severity	5.2	4.7	2.7	3.1	3.0	3.4	3.4	2.8	2.7	3.6	0.0	0.0	3.9	4.1	2.9	4.0	3.3	1.2
Canada Jay, *Perisoreus canadensis*	3--early, low severity	4.2	5.1	4.3	2.3	1.2	2.7	1.7	1.1	0.9	0.7	0.0	3.6	1.9	2.1	0.7	3.0	6.0	7.6
Golden-crowned Kinglet, *Regulus satrapa*	3--early, low severity	9.2	5.5	3.4	2.6	0.7	0.7	2.1	0.3	0.2	0.2	3.9	1.8	0.0	0.0	0.7	3.6	21.1	16.2
Pacific Wren, *Troglodytes pacificus*	3--early, low severity	3.1	4.3	3.3	3.6	2.1	4.8	3.4	0.0	0.0	0.5	0.0	1.8	0.0	0.0	0.0	1.1	10.8	7.0
Pine Grosbeak, *Pinicola enucleator*	3--early, low severity	2.1	1.9	0.7	1.6	1.4	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.7	2.1
Ruffed Grouse, *Bonasa umbellus*	3--early, low severity	3.6	2.3	1.6	1.2	0.4	1.4	3.4	0.6	1.3	0.2	0.0	0.0	1.0	3.1	0.0	3.9	4.1	1.6
Swainson's Thrush, *Catharus ustulatus*	3--early, low severity	23.3	23.9	24.0	21.0	13.8	19.1	11.1	7.6	4.4	5.9	23.1	10.9	5.8	12.4	25.2	13.7	33.1	20.7
Townsend's Warbler, *Setophaga townsendi*	3--early, low severity	18.6	15.4	9.1	5.3	2.2	12.2	9.0	2.8	0.7	0.0	11.5	5.5	1.9	2.1	4.3	10.6	36.0	16.6
Varied Thrush, *Ixoreus naevius*	3--early, low severity	2.1	2.3	1.4	0.7	0.9	1.4	0.9	0.3	0.2	0.0	0.0	0.0	0.0	0.0	2.2	0.3	9.3	10.5
Dusky Grouse, *Dendragapus obscurus*	4--short delay, high severity	0.3	0.5	0.7	0.3	0.3	1.4	1.7	4.2*	3.1*	4.9*	0.0	0.0	1.0	0.0	1.4	0.4	0.3	0.3
House Wren, *Troglodytes aedon*	4--short delay, high severity	2.3	4.5	5.6	5.2	4.4	5.4	15.4*	34.5*	41.2*	32.3*	0.0	7.3	11.5	20.6*	22.3*	7.7	2.0	1.9
Mountain Bluebird, *Sialia currucoides*	4--short delay, high severity	3.2	8.7*	12.9*	22.9*	32.5*	4.8	11.1*	26.9*	39.5*	39.2*	0.0	1.8	19.2*	20.6*	16.6*	3.8	1.7	3.6
Northern Flicker, *Colaptes auratus*	4--short delay, high severity	10.5	13.8*	11.6	15.9*	13.1*	14.3	25.6*	24.9*	27.3*	24.8*	11.5	9.1	12.5	20.6*	22.3*	8.2	7.4	7.0
Western Bluebird, *Sialia mexicana*	4--short delay, high severity	0.5	0.8	0.8*	1.7*	1.1*	1.4	2.6*	6.2*	10.4*	7.3	0.0	1.8	0.0	4.1*	2.2*	0.1	0.1	0.1
Western Wood-Pewee, *Contopus sordidulus*	4--short delay, high severity	2.9	2.7	4.4	5.6	3.9	6.1	9.0*	12.3*	16.4*	14.1*	0.0	9.1	1.0	4.1	2.9	3.9	0.5	1.4
Willow Flycatcher, *Empidonax traillii*	4--short delay, high severity	0.8	0.5	1.0	1.5	1.0	0.7	0.4	4.5*	6.0*	6.5*	0.0	1.8	5.8*	6.2*	5.0*	0.2	0.6	1.1
Calliope Hummingbird, *Selasphorus calliope*	5--short delay, moderate severity	2.3	3.5	2.2	1.7	0.7	8.2*	6.8*	3.4	3.8	5.1*	0.0	3.6	3.9	13.4*	5.0	1.8	0.8	0.2
White-breasted Nuthatch, *Sitta carolinensis*	5--short delay, moderate severity	0.7	1.8	0.6	0.6	0.5	4.1	5.6	10.1*	7.5	3.1	3.9	3.6	4.8	3.1	1.4	3.8	0.6	0.3
Williamson's Sapsucker, *Sphyrapicus thyroideus*	5--short delay, moderate severity	2.6	1.9	1.5	0.7	0.3	3.4	7.3*	7.0*	4.4	2.0	0.0	1.8	3.9	3.1	0.7	2.1	1.1	0.5
Brown-headed Cowbird, *Molothrus ater*	6--short delay, low severity	5.5	7.2	5.9	4.9	2.1	22.5	24.8	12.6	7.8	7.3	3.9	12.7	14.4	10.3	5.0	16.8	5.5	5.7
Cassin's Vireo, *Vireo cassinii*	6--short delay, low severity	13.7	9.5	4.7	2.9	1.3	23.8	13.7	4.8	3.3	1.9	23.1	16.4	9.6	10.3	12.2	19.7	14.4	2.8
Chipping Sparrow, *Spizella passerina*	6--short delay, low severity	44.4	44.8	44.3	41.4	41.6	50.3	52.6	48.7	49.2	44.0	46.2	40.0	46.2	59.8	43.9	54.0	25.6	19.9
Hammond's Flycatcher, *Empidonax hammondii*	6--short delay, low severity	12.6	12.4	8.4	7.8	7.1	15.0	15.0	5.6	0.7	1.2	3.9	3.6	1.0	0.0	1.4	12.2	10.8	3.3
Hermit Thrush, *Catharus guttatus*	6--short delay, low severity	4.9	4.2	4.2	3.5	1.7	10.2	4.3	1.1	2.2	0.3	3.9	0.0	6.7	0.0	0.0	5.9	4.9	10.3
Pileated Woodpecker, *Dryocopus pileatus*	6--short delay, low severity	0.3	1.0	1.4	0.6	0.8	2.0	1.3	0.8	0.9	0.0	0.0	0.0	0.0	1.0	0.7	1.5	2.8	0.6
Red Crossbill, *Loxia curvirostra*	6--short delay, low severity	3.7	3.2	3.8	3.4	3.8	6.1	9.8	3.9	2.9	1.5	3.9	3.6	0.0	0.0	0.0	8.6	4.0	4.5
Dusky Flycatcher, *Empidonax oberholseri*	7--long delay, high severity	13.9	14.3	13.3	11.4	7.9	27.9	26.5	30.5	38.6*	35.1*	15.4	29.1	51.9*	59.8*	50.4*	25.5	12.1	8.0
Lewis's Woodpecker, *Melanerpes lewis*	7--long delay, high severity	0.0	0.2	0.0	0.2	0.1	0.0	0.4	1.1*	2.7*	4.4*	0.0	0.0	1.0	0.0	5.8*	0.1	0.0	0.0
Orange-crowned Warbler, *Oreothlypis celata*	7--long delay, high severity	11.0	9.0	3.6	4.8	3.0	11.6	4.7	9.0	12.2	12.9	11.5	12.7	16.4	20.6	21.6*	10.4	9.6	2.9
Rock Wren, *Salpinctes obsoletus*	7--long delay, high severity	1.0	1.4	1.4	2.4	1.6	1.4	1.7	5.0*	5.1*	3.6	0.0	3.6	5.8	9.3*	8.6*	1.7	0.2	0.3

(*continued on next page*)

Table 2 (*continued*)

		1-4 yr after fire					5-14 yr after fire					15-35 yr after fire							
		Fire Severity (% tree mortality)					Fire Severity (% tree mortality)					Fire Severity (% tree mortality)							
		0-20%	21-40%	41-60%	61-80%	81-100%	0-20%	21-40%	41-60%	61-80%	81-100%	0-20%	21-40%	41-60%	61-80%	81-100%	mature, long unburned		
Species	Group	n=619	n=623	n=1080	n=1224	n=1782	n=147	n=234	n=357	n=451	n=589	n=26	n=55	n=104	n=97	n=139	n=2662	n=24758	n=6595
Warbling Vireo, *Vireo gilvus*	7--long delay, high severity	23.6	20.2	16.4	12.4	8.9	24.5	15.8	18.5	19.3	18.7	3.9	18.2	26.0	41.2*	31.7*	13.6	18.7	16.1
White-crowned Sparrow, *Zonotrichia leucophrys*	7--long delay, high severity	1.1	1.1	4.0	5.0	5.7	0.7	1.7	5.0	2.7	8.3	0.0	0.0	0.0	8.3*	10.8*	0.6	1.2	4.4
Common Yellowthroat, *Geothlypis trichas*	8--long delay, moderate severity	0.8	1.1	1.9	1.4	1.2	0.7	0.4	1.4	1.8	2.2	0.0	1.8	7.7*	3.1	2.2	0.2	0.7	1.2
Mourning Dove, *Zenaida macroura*	8--long delay, moderate severity	0.7	1.3	1.1	0.9	0.5	0.7	1.3	2.5	1.3	2.2	0.0	3.6	2.9	4.1	2.9	5.4	0.5	0.6
Red-naped Sapsucker, *Sphyrapicus nuchalis*	8--long delay, moderate severity	1.5	2.7	2.6	1.7	1.1	1.4	1.7	1.4	1.6	0.7	3.9	1.8	4.8	3.1	1.4	1.5	4.3	2.1
Red-tailed Hawk, *Buteo jamaicensis*	8--long delay, moderate severity	1.6	0.8	1.0	1.2	0.6	1.4	0.4	1.4	0.9	0.7	0.0	0.0	1.0	3.1	1.4	0.8	0.7	0.5
Spotted Towhee, *Pipilo maculatus*	8--long delay, moderate severity	1.6	3.5	1.7	1.6	0.5	2.0	3.9	6.4	4.0	1.5	3.9	5.5	11.5	22.7*	13.7	10.4	2.4	0.4
Vesper Sparrow, *Pooecetes gramineus*	8--long delay, moderate severity	1.6	0.3	0.6	0.2	0.1	1.4	1.7	2.8	1.8	1.4	7.7	1.8	3.9	2.1	2.9	4.5	0.6	3.4
Yellow Warbler, *Setophaga petechia*	8--long delay, moderate severity	2.4	1.8	1.5	0.4	0.3	4.1	3.9	3.6	3.1	4.2	0.0	3.6	13.5*	3.1	1.4	3.5	2.1	2.9
Clark's Nutcracker, *Nucifraga columbiana*	9--long delay, low severity	1.5	2.7	3.0	2.5	1.5	1.4	3.4	5.3	7.5	4.9	15.4	10.9	3.9	2.1	2.2	5.4	2.3	6.1
Song Sparrow, *Melospiza melodia*	9--long delay, low severity	2.9	2.6	3.1	4.7	3.5	2.0	2.1	2.2	5.8	5.3	0.0	1.8	13.5	5.2	3.6	2.0	3.8	2.7
American Kestrel, *Falco sparverius*	10--persistent, high severity	0.8	0.3	0.6	1.1	1.5	0.7	0.0	0.8	1.1	1.4	0.0	0.0	1.0	1.0	1.4	0.6	0.4	0.2
Lazuli Bunting, *Passerina amoena*	10--persistent, high severity	10.0*	9.0*	11.9*	11.7*	11.7*	4.8	6.8*	9.2*	12.9*	17.5*	7.7	9.1	10.6*	15.5*	13.7*	3.0	2.6	0.9
Lincoln's Sparrow, *Melospiza lincolnii*	10--persistent, high severity	1.6	2.4	4.0	5.8	5.4	0.0	0.9	4.8	0.4	4.4	0.0	0.0	0.0	5.2	4.3	0.3	1.1	5.5
Common Raven, *Corvus corax*	11--persistent, low severity	2.4	2.4	1.4	1.1	1.1	0.7	0.9	2.0	0.4	1.0	0.0	5.5	1.0	1.0	0.7	2.0	1.9	1.3
Mountain Chickadee, *Poecile gambeli*	11--persistent, low severity	30.5	29.1	22.3	15.5	9.2	19.7	24.8	17.1	11.3	5.4	23.1	25.5	27.9	17.5	12.2	24.2	19.9	26.1
Red-breasted Nuthatch, *Sitta canadensis*	11--persistent, low severity	39.6	41.4	32.4	21.6	16.6	46.9	56.0	31.7	21.5	9.3	30.8	45.5	23.1	24.7	10.1	48.4	39.6	23.3
Ruby-crowned Kinglet, *Regulus calendula*	11--persistent, low severity	28.9	20.7	19.7	11.0	5.7	29.3	28.2	14.3	6.9	1.9	23.1	27.3	17.3	13.4	5.8	17.1	22.0	35.6
Steller's Jay, *Cyanocitta stelleri*	11--persistent, low severity	2.6	4.0	2.1	2.4	1.2	3.4	3.9	2.2	0.7	2.4	3.9	1.8	2.9	7.2	2.9	2.2	2.8	2.2
Western Tanager, *Piranga ludoviciana*	11--persistent, low severity	47.3*	38.7	34.0	26.9	22.6	47.6	43.2	28.6	16.2	6.6	50.0	32.7	26.9	29.9	18.7	39.0	32.0	12.9
Yellow-rumped Warbler, *Setophaga coronata*	11--persistent, low severity	54.0	52.3	46.1	42.7	41.0	57.1	54.7	37.0	20.6	15.1	57.7	54.6	26.0	23.7	32.4	52.0	43.9	46.5

condition than in unburned forest (Table 2); seven species [group 8—common yellowthroat (*Geothlypis trichas*), mourning dove (*Zenaida macroura*), red-naped sapsucker (*Sphyrapicus nuchalis*), red-tailed hawk (*Buteo jamaicensis*), spotted towhee, vesper sparrow (*Pooecetes gramineus*), yellow warbler (*Setophaga petechia*)] are most abundant 15–35 years following fire in forest that burned at moderate severity, and three of those species are more abundant in that type of burned-forest condition than in unburned forest (Table 2); two species [group 9—Clark's nutcracker (*Nucifraga columbiana*), song sparrow (*Melospiza melodia*)] are most abundant 15–35 years following fire in forest that burned at the lowest severity, and neither is more abundant in that type of burned-forest condition than in unburned forest (Table 2); three species [group 10—American kestrel (*Falco sparverius*), lazuli bunting (*Passerina amoena*), Lincoln's sparrow (*Melospiza lincolnii*)] were roughly equally abundant across the three time-since-fire periods we considered in the most severely burned forest patches, and one (lazuli bunting) was significantly more abundant therein than in unburned conifer forest; and seven species [group 11—common raven (*Corvus corax*), mountain chickadee (*Poecile gambeli*), red-breasted nuthatch (*Sitta canadensis*), ruby-crowned kinglet (*Regulus calendula*), Steller's jay (*Cyanocitta stelleri*), western tanager (*Piranga ludoviciana*), yellow-rumped warbler (*Setophaga coronata*)] were also roughly equally abundant across time in the least severely burned forest patches, and one (western tanager) was significantly more abundant therein than in unburned conifer forest.

If we compare the abundances of a species across the various burned-forest conditions with its abundances in the three unburned mixed-conifer forest types (Table 2), 33 of the 68 bird species (49%) were significantly (Bonferroni adjusted chi-square, $P < 0.05$) more abundant in at least one of those burned-forest conditions than in any of the unburned conifer forest types. Nine of the 12 species that were identified as being nowhere more abundant than in burned forests in general, were also most abundant in the more severely burned portions of those burned forests (Table 2).

3.3. *Effects of pre-fire cutting and post-fire salvage logging*

Most bird species are affected by timber harvesting, but the effects vary dramatically among species (compare percent changes in abundance from uncut to cut forests in Table 3). In general, woodpeckers (e.g., American three-toed woodpecker, black-backed woodpecker, pileated woodpecker) and other species (e.g., brown creeper, western wood-pewee, red-breasted nuthatch) that depend on an abundance of tree boles for feeding or nesting purposes were significantly negatively affected (Bonferroni-adjusted chi-square, $P < 0.05$) by cutting. In contrast, bird species that are strongly associated with early successional shrub communities (e.g., black-headed grosbeak, lazuli bunting, orange-crowned warbler) were more abundant in harvested forests, presumably because the additional ground disturbance and increased sunlight tends to speed up the development of such conditions. Exceptions to this general rule include Lewis's woodpecker and mountain bluebird; although these are snag-dependent species, they are not negatively affected by the removal of most standing dead trees because they forage and nest in relatively open conditions with low snag densities anyway (Saab and Dudley, 1998). The effects of tree harvesting on species that most depend on burned forest conditions for their presence are the most important to consider, and the black-backed woodpecker, which is more restricted than any other species to burned forest conditions, was significantly (chi-square, $P < 0.05$) more abundant in uncut than in cut forests. Moreover, if we consider each of the four possible cutting combinations: uncut before/uncut after fire, cut before/cut after fire, uncut before/cut after fire, and cut before/uncut after fire, it appears that the black-backed woodpecker is not only negatively affected by cutting, but is less abundant (although not significantly so) in burned forests that were cut before than in those that were cut after fire (Fig. 3).

4. Discussion

The number of bird species that we detected in burned-forest environments is not only large (148 in this study), but of the 68 species that were adequately sampled, a dozen were more abundant in burned mixed-conifer forest than in any other major vegetation type in the USFS Northern Region, and nearly half (49%) of those 68 were significantly more abundant in some kind of burned conifer forest than in unburned conifer forest. Hutto and Patterson (2016) conducted a similar analysis using data from a single site that had been visited each of 12 years following fire and found that 30 of 50 species (60%) were detected significantly more frequently in burned mixed-conifer forest than in unburned mixed-conifer forest. Kotliar et al., (2002) also found a high proportion of species (56%) to be more abundant in burned than in unburned conifer forest, as evidenced by whether they were either consistently or usually more abundant across three or more studies. Thus, if abundance is any indication, unburned mixed-conifer forests are not nearly as suitable as burned forests for these species. It is not enough, however, to say that burned mixed-conifer forests in general are important environments for native bird species. Forest management requires knowledge of the specific burned-forest conditions associated with each bird species, especially the most fire-dependent species. Below, we provide a biological explanation for each of the nonrandom distributional patterns that emerged upon examining the combination of time-since-fire and fire severity.

Twelve (75%) of the 16 species that were more abundant in the moderate to high severity categories than in the low severity categories soon after fire (patterns labeled 1 and 2 in Table 2) also probably find conditions in the wholly transformed (more severely burned) forest patches to be superior to unburned forest conditions because their abundances are significantly (Bonferroni adjusted chi-square, $P < 0.05$) higher in those burned than in unburned forest conditions. The elevated habitat suitability lasts for only a limited duration, however, as only four species were still significantly more abundant in burned than in unburned conifer forest types 5–14 years after fire, and only one was still significantly more abundant in burned than in unburned conifer forest types 15–35 years following fire (Table 2). The woodpecker species are clearly responding to the explosion in numbers of wood-boring beetle larvae that feed almost exclusively on recently burned and killed trees, as has been described in detail in many previously published reports (Murphy and Lehnhausen, 1998; Powell et al.,

Table 3
Numbers represent the percentages of point counts on which each of 68 species was present in burned forests that were uncut before and uncut after fire, and in burned forests that were cut either before or after fire. Species are ordered by the percent change in abundance from uncut to cut forest. The names of species that were identified in Table 1 as being more abundant in burned forest than in any other vegetation type are highlighted in gray.

	Tree harvest history		
	uncut	cut	
Species	n=5634	n=1875	% change
Northern Waterthrush, *Parkesia noveboracensis*	3.3	1.1	-66
Common Yellowthroat, *Geothlypis trichas*	1.6*	0.6	-64
Hermit Thrush, *Catharus guttatus*	3.4*	1.4	-57
Brown Creeper, *Certhia americana*	5.8*	2.6	-56
Pileated Woodpecker, *Dryocopus pileatus*	0.9*	0.4	-54
Black-backed Woodpecker, *Picoides arcticus*	5.1*	2.4	-53
Common Raven, *Corvus corax*	1.6*	0.8	-53
American Three-toed Woodpecker, *Picoides dorsalis*	5.5*	2.8	-49
Canada Jay, *Perisoreus canadensis*	2.7*	1.4	-47
Varied Thrush, *Ixoreus naevius*	1.1	0.6	-44
Western Wood-Pewee, *Contopus sordidulus*	6.8*	4.2	-38
Golden-crowned Kinglet, *Regulus satrapa*	2.7*	1.8	-34
Townsend's Warbler, *Setophaga townsendi*	7.0*	4.7	-33
White-breasted Nuthatch, *Sitta carolinensis*	2.3	1.6	-31
Pacific Wren, *Troglodytes pacificus*	2.6	1.9	-28
Red-breasted Nuthatch, *Sitta canadensis*	28.1*	20.9	-26
Pine Grosbeak, *Pinicola enucleator*	1.1	0.9	-25
Hammond's Flycatcher, *Empidonax hammondii*	8.0*	6.1	-23
Yellow Warbler, *Setophaga petechia*	1.8	1.4	-22
Brown-headed Cowbird, *Molothrus ater*	6.9*	5.4	-21
Western Bluebird, *Sialia mexicana*	2.6	2.1	-20
Lincoln's Sparrow, *Melospiza lincolnii*	4.1	3.3	-19
Mourning Dove, *Zenaida macroura*	1.2	1.0	-17
Cassin's Finch, *Haemorhous cassinii*	6.7	5.7	-16
Red-naped Sapsucker, *Sphyrapicus nuchalis*	1.8	1.5	-16
American Robin, *Turdus migratorius*	32.7*	28.8	-12
Ruby-crowned Kinglet, *Regulus calendula*	13.9	12.4	-11
Yellow-rumped Warbler, *Setophaga coronata*	42.1*	37.6	-11
Tree Swallow, *Tachycineta bicolor*	6.7	6.0	-10
House Wren, *Troglodytes aedon*	11.6	10.6	-9
Clark's Nutcracker, *Nucifraga columbiana*	3.1	2.8	-8
Red Crossbill, *Loxia curvirostra*	3.6	3.3	-8
Dark-eyed Junco, *Junco hyemalis*	61.5*	58.0	-6
Mountain Chickadee, *Poecile gambeli*	17.2	16.3	-6

(*continued on next page*)

Table 3 (*continued*)

Hairy Woodpecker, *Dryobates villosus*	15.9	15.1	-5
Pine Siskin, *Spinus pinus*	19.8	18.9	-4
White-crowned Sparrow, *Zonotrichia leucophrys*	4.4	4.2	-4
Western Tanager, *Piranga ludoviciana*	28.7	27.4	-4
Swainson's Thrush, *Catharus ustulatus*	16.8	16.4	-2
Olive-sided Flycatcher, *Contopus cooperi*	8.6	8.8	1
Wilson's Warbler, *Cardellina pusilla*	3.0	3.2	5
Cassin's Vireo, *Vireo cassinii*	5.5	5.8	7
Ruffed Grouse, *Bonasa umbellus*	1.3	1.4	9
Townsend's Solitaire, *Myadestes townsendi*	15.6	17.2	10
Northern Flicker, *Colaptes auratus*	15.7	17.6	12
Red-tailed Hawk, *Buteo jamaicensis*	0.9	1.1	13
Willow Flycatcher, *Empidonax traillii*	1.9	2.2	13
Black-capped Chickadee, *Poecile atricapillus*	3.1	3.7	17
Williamson's Sapsucker, *Sphyrapicus thyroideus*	1.8	2.1	17
Chipping Sparrow, *Spizella passerina*	41.8	52.2*	25
Mountain Bluebird, *Sialia currucoides*	20.9	26.6*	27
Fox Sparrow, *Passerella iliaca*	3.3	4.4*	34
Rufous Hummingbird, *Selasphorus rufus*	1.2	1.7	37
Song Sparrow, *Melospiza melodia*	3.3	4.5*	37
Dusky Grouse, *Dendragapus obscurus*	1.1	1.5	38
MacGillivray's Warbler, *Geothlypis tolmiei*	21.4	32.1*	50
Vesper Sparrow, *Pooecetes gramineus*	0.8	1.2	50
Calliope Hummingbird, *Selasphorus calliope*	2.4	3.9*	64
Spotted Towhee, *Pipilo maculatus*	2.2	3.7*	67
Dusky Flycatcher, *Empidonax oberholseri*	15.8	26.6*	69
American Kestrel, *Falco sparverius*	0.8	1.4*	73
Lewis's Woodpecker, *Melanerpes lewis*	0.6	1.2*	94
Warbling Vireo, *Vireo gilvus*	13.0	25.4*	95
Steller's Jay, *Cyanocitta stelleri*	1.8	3.6*	97
Black-headed Grosbeak, *Pheucticus melanocephalus*	2.6	5.4*	105
Lazuli Bunting, *Passerina amoena*	9.0	19.0*	112
Orange-crowned Warbler, *Oreothlypis celata*	5.5	12.6*	130
Rock Wren, *Salpinctes obsoletus*	1.5	5.3*	249

*Indicates that the abundance of the species is significantly greater in that forest condition.

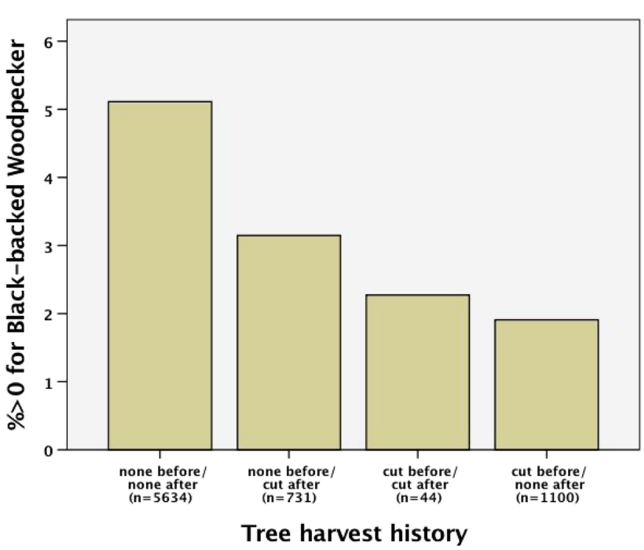

Fig. 3. The percentage of point-counts on which the black-backed woodpecker was detected in each of four tree harvest history categories. The occurrence rate on points in locations where there was no cutting either before or after fire was greater than the occurrence rate on points in locations where there was cutting either before and/or after fire; only the two extreme values differed significantly (Bonferroni adjusted chi-square, $P < 0.05$).

2002; Nappi et al., 2003; Fayt et al., 2005; Kotliar et al., 2008; Rota et al., 2015). The reasons that the other species find severely burned forests to be more suitable than unburned forests is less clear, but the absence of a tree canopy makes foraging conditions better for some (e.g., olive-sided flycatcher, tree swallow) and the short-term increase in abundance of burned-out root wads and uprooted trees that blow down in the first few years following fire make both nesting and foraging conditions better for others (e.g., dark-eyed junco, Townsend's solitaire), as Hutto et al., (2015) discussed in their book chapter on the ecology of birds in severely burned forests.

The species that are more abundant in the more severely burned than in long unburned forest after more than 5 years have passed (patterns labeled 4, 5, 7, and 8 in Table 2) include species that capitalize on the accumulation of woodpecker cavities that become available as nesting sites for secondary cavity nesters (e.g., house wren, mountain bluebird, western bluebird). They also include species that capitalize on the accumulation of new nesting and feeding opportunities as tree tops break and bark begins to sluff off (e.g., Lewis's woodpecker, white-breasted nuthatch, Williamson's sapsucker), and species that respond to increases in shrub, seedling, and sapling cover (e.g., calliope hummingbird, dusky flycatcher, dusky grouse, orange-crowned warbler, spotted towhee (*Pipilo maculatus*), warbling vireo, willow flycatcher). As Hutto and Patterson (2016) emphasized, species that are relatively abundant in burned forests, but not until some years after fire may be no less fire dependent than a species that increases in abundance dramatically within a year or two following fire. Suitable post-fire environmental conditions may take more time to emerge and, as long as no other kind of disturbance creates suitable post-disturbance conditions, a species that is relatively restricted to any stage of succession following fire disturbance (not just the earliest stage) may be relatively dependent upon fires that are severe enough to initiate natural forest succession.

With a single exception (western tanager), none of the 26 species that were most abundant in areas that burned at the lowest of all severity categories (patterns labeled 3, 6, 9, and 11 in Table 2) were also more abundant there than they were in unburned conifer forest. Because these species are less abundant in burned than in unburned conifer forest, and because they are generally common throughout unburned mature forests where they use green-tree sites for nesting and feeding, they probably depend for the most part on the presence of long-unburned forest. The one species that was significantly more abundant in locations that burned at lower severities than in unburned forest locations (western tanager) suggests that it might actually benefit in some way from a low-severity fire. However, the far greater number of species that were significantly more abundant in severely burned than in unburned forest is a good indication that fire-dependent species are much more likely to require high- than low-severity fire.

4.1. Timber harvesting

The effects of timber harvesting vary markedly among species, but consider the pattern displayed by the black-backed woodpecker. This fire-dependent species is clearly less abundant in cut forests, and it appears that the negative effects are even greater in places that were cut before fire than in places that were salvaged logged after fire (Fig. 3). Burned-tree densities are not all that different in places where trees are cut before or cut after fire, so why would black-backed woodpecker abundance be lower in burned forests that were cut before fire than it is in forests salvage logged after fire? As discussed earlier (Hutto, 2008), one possible reason is that the two harvested-forest conditions are not equally attractive to potential colonists. Because salvage logging is frequently delayed for a year or two following fire, birds may be much more attracted to what appears to be a fantastic forest condition and then have to make the best of a bad situation after most of the trees are salvaged, so we still see what are, basically, remnant populations in salvage logged forests (Tarbill et al., 2018). We recognize that not all salvage logging operations are the same, and that there may be a way to salvage log and retain the most fire-dependent species, but even those studies that have considered different levels of salvage logging (e.g., Saab and Dudley, 1998; Hutto, 2008) reveal that any level of salvage harvest has negative effects on the black-backed woodpecker.

The negative responses of other species to either pre-fire or post-fire tree harvest is clearly related to resources that are correlated with burned tree abundance; bird species that rely on wood-boring beetle larvae (e.g., American three-toed woodpecker, black-backed woodpecker, hairy woodpecker) or bark beetle and bark-surface insects (e.g., creeper, red-breasted nuthatch) benefit from higher tree bole densities, as do bird species that rely on seed resources (e.g., pine grosbeak, pine siskin, red crossbill) and on woodpecker cavities, broken-branch, broken-top tree and downed-tree conditions for nesting (e.g., dark-eyed junco, tree swallow, western wood-pewee). In contrast, the positive response by some bird species (e.g., American kestrel, Lewis's woodpecker) to pre-fire or post-fire tree harvest is probably associated with their need for large, relatively decayed trees for nesting, and a lot of open space for foraging, as others have reported (Saab et al., 2007, 2009). The positive response to logging by other species (e.g., house wren, mountain bluebird) may reflect their preference for trees that have accumulated woodpecker cavities or that have broken and developed rapid decay. A final group of species that appears to benefit from tree harvest includes those (e.g., black-headed grosbeak, calliope hummingbird, dusky flycatcher, dusky grouse, lazuli bunting, orange-crowned warbler) that use the shrub understory that develops rapidly after tree harvesting. The relative abundance of these species in the tree-harvested forest conditions clearly reflects an opportunistic use of those conditions, as evidenced by the fact that the same species are broadly distributed across other shrubby vegetation types and early successional forest stages created by other forms of disturbance (Table 1).

4.2. Merits of the chronosequence approach

We found that bird species occur in a variety of combinations of fire severity, time since-fire, and timber harvest history, and that the bird species most restricted in their distribution to burned forest conditions were also most abundant in the more severely burned, uncut patches relatively soon after fire. This result is in complete agreement with every study ever conducted on the effects of fire on birds in western conifer forests, and it underscores how powerful a chronosequence approach can be at uncovering the same significant fire effects that experimental approaches have also exposed. Logistical difficulties associated with work in older burns (e.g., treefall, lack of road maintenance) limited what we were able to accomplish as a small research team, so additional point-count samples will be necessary to uncover the more nuanced effects of severity, time-since-fire, and timber harvest intensity. For example, the previously unreported increase in occurrence rates of several species in burned forests that have reached about 10 years in age (e.g., Williamson's sapsucker, white-breasted nuthatch, willow flycatcher) are intriguing, and signal that we need a broader exploration of time scale in future fire effects studies. Additional samples will also be necessary to avoid the possible conflation of time-since-fire with sampling date. Since most of our older fires were sampled in 2015, any change in bird occurrence rate across fire age could be confused with an unrelated temporal change in bird populations. We suggest that the best way forward is to encourage western bird observatories (e.g., participants in the Avian Knowledge Network) and other conservation partners to work collaboratively across the West to generate, in as little as a single season or two, the bird point-count sample sizes that would allow the collective group to use a chronosequence approach to gain a rapid and more nuanced understanding of the effects of important management-oriented variables on bird occurrence patterns.

4.3. Which distribution patterns carry the most important management implications?

There is huge variation among species in the particular combination of fire severity, time-since-fire, and timber harvest history where each is most abundant, and the range of conditions presumably needed to maintain the presence of each species would appear to be equally broad (Table 2). However, even though the apparent effects of each variable depend heavily on the species in question, not all species are equal in terms of their usefulness as indicators of historical fire regimes and post-fire conditions. Because the black-backed woodpecker occurs nearly exclusively under very narrowly defined burned-forest conditions, it necessarily evolved in the presence of those conditions, and is, therefore, a reliable indicator of conditions that are not only historically important, but necessary to maintain. We detected dozens of other species in burned forests, but they are not reliable indicators of burned forest conditions that must have been historically important because those species also occur in equal or higher abundance outside burned forests and could simply be using burned forests opportunistically instead of relying on burned-forest conditions for their presence and success. Given this logic, the following management implications emerge from an understanding of the habitat distribution pattern of the black-backed woodpecker, which was the most fire-dependent species we detected: (1) time-since-fire—the black-backed woodpecker (and most of the other fire-dependent species that we highlighted in Table 2) needs early successional conditions created by severe fire. Importantly, a variety of studies (Hutto, 1995; Hannon and Drapeau, 2005; Rota et al., 2014; Hutto et al., 2016; Saab et al., 2019; Tingley et al., 2020) have shown that early successional conditions that follow other kinds of severe disturbance (e.g., clearcut logging, beetle kill, blowdown) are entirely unsuitable in the eyes of a black-backed woodpecker; (2) severity—severe fire is necessary to accommodate the needs of the most fire-dependent species early on after fire, and perhaps to accommodate the needs of additional species that occur in later stages of forest succession unique to severe fire disturbance (Stillman et al., 2019). Because severe fires create not only large severely burned forest patches, but also roughly equal proportions in each of the three categories of fire severity (Baker, 2009, Fig. 7.1; Baker and Williams, 2018, Fig. 1a), even species that use (and might even depend on) less severe fire will always benefit from naturally occurring large, wind-driven fires as well; (3) timber harvesting—when they burn, structurally complex, unburned mature forests do a better job of providing for fire-dependent species than do forests that have undergone pre-fire timber harvest. Indeed, the most fire-dependent species (black-backed woodpecker) occurs not only in severely burned forests, but primarily in severely burned forests where tree bole densities and canopy cover prior to fire was high (Hutto, 1995, 2008; Dudley et al., 2012; Hutto et al., 2015; Hutto and Patterson, 2016; Tremblay et al., 2016; Latif et al., 2018). The species that are most restricted to burned-forest conditions are negatively affected by post-fire salvage logging as well. Indeed, no fire-dependent bird species has ever been shown to benefit from salvage logging (Hutto, 2006; Hanson and North, 2008).

The management implications that follow from these findings are profound: uncut burned forests provide the only forest condition that can, through succession following severe natural disturbance, provide for all species that depend on severe natural disturbance. So, what is the best management solution, given these implications? First, management guidelines within mixed-conifer forests throughout the West ought to incorporate ecologically appropriate levels of severe fire and its aftermath (Harvey et al., 2017; Baker and Williams, 2018; Hessburg et al., 2019). Transformed, standing-dead forests that follow severe fire should be left to the myriad plant and animal species that depend on (occur only in) those forest conditions because they are biologically unique, and should be as hands off as old-growth forests are in land management. Fortunately, most western conifer forests are dominated by mixed- to high-severity fire regimes (Noss et al., 2006; Baker et al., 2007; Williams and Baker, 2012; Odion et al., 2014; Williams and Baker, 2014; Baker, 2015; DellaSala and Hanson, 2015; DellaSala et al., 2017; Baker, 2018), so severely burned forest conditions will always be well distributed across the broader landscape. Land managers could use strategic landscape planning to harvest trees while still retaining both an abundance of minimally disturbed, unburned, mature-forest conditions and an abundance of severely burned forest conditions that emerge from natural fire disturbance events. Management solutions are, therefore, more about implementing a landscape tree-harvest prioritization scheme rather than implementing a single-method harvest scheme across the entire landscape.

We can, therefore, have both fire-dependent organisms and timber harvesting by moving recently burned forests close to the bottom of the tree-harvest priority list and moving green-tree harvests that are strategically placed (near human settlements, for example) close to the top of the tree-harvest priority list. Even if the primary motivation to salvage log is an economic one, there are alternative ways that land managers could address that need without conducting any post-fire salvage logging. Specifically, land managers could substitute a green-tree forest harvest near the wildland-urban interface to make up for any short-term loss that a fire might have temporarily removed from the mapped timber base, or they could help local communities promote the ecotourism potential that burned forests provide through the unique wildflower and wildlife viewing opportunities that severely burned forests provide. Paradoxically, managers must also ensure that there is always enough mature forest across the broader landscape to allow for the continual creation of suitable post-fire conditions, and for the longer-term creation of a mosaic of different-aged severe-disturbance induced forest patches across the landscape.

CRediT authorship contribution statement

Richard L. Hutto: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **Russell R. Hutto:** Investigation, Methodology, Writing - review & editing. **Paul L. Hutto:** . **:** Investigation, Methodology.

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