Breeding bird changes during 50 years of post-fire succession in the Sierra Nevada

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***Abstract*:** Wildfire has substantial immediate effects on vegetation structure and composition. Those changes and subsequent vegetation succession alter nesting and foraging habitats of birds. In 1960, the stand-replacing Donner Ridge Fire burned 18,000 ha in California's northern Sierra Nevada. Subsequent bird-population studies in this area provided us an opportunity to investigate both short-term and long-term responses of birds to vegetation change following fire. Almost 50 years of periodic breeding bird surveys document bird-community changes in response to vegetation succession after this large wildfire. On the basis of intermittent breeding bird counts and vegetation sampling from 1966 to 2014, we describe and compare changes in bird-community structure on one burned and one nearby unburned plot (each 8.5 ha) of mixed-conifer forest within the Sagehen basin of the Tahoe National Forest. We used spot-mapping to estimate bird abundance (number of territories) and diversity during 4 sampling periods: 1966–1968, 1975–1979, 1981–1985, and 2010–2014. Most changes in the avian community were those expected from the post-fire changes in vegetation structure. These changes were most marked on the burned plot: shrub cover increased from 22% to 71%, tree-canopy cover increased from 7% to 27%, basal area of conifers increased about three-fold, and the density of larger snags decreased from 26 to 1.5 per ha. During this same time, numbers of foliage-searching birds increased about six-fold (from 2 to 13 territories per plot), whereas timber-drilling birds decreased from 1.3 to 0.3 territories, likely reflecting the loss of snags. On the unburned plot, changes during the period were subtler: tree-canopy cover decreased slightly, basal area of conifers increased by at least 25%, and shrub cover remained low. Notably, snag density on the unburned plot increased from 9 to 31 stems per ha, perhaps explaining the increase in timber-drilling birds on that plot (from 0.5 to 1.3 territories) over the five decades. The increase in snags and volume of conifers (basal area) on the unburned plot may also have contributed to the observed increase in bark-gleaning birds (from 2.0 to 5.5 territories). Finally, on the unburned plot, foliage-searching birds increased in abundance from 9 to 17 territories from 1966 to 2014. In general, changing vegetation structure, and the foraging and nesting habitat associations of the plots' birds, explained most of the observed trends in the avian communities. Some changes may have been associated with the 2010–2014 period being drier and warmer, which appears to be part of a broader climatic trend. The average annual temperature increased markedly and the date of last freezing shifted earlier, which could have facilitated increases of some species, including the Hermit Warbler (*Setophaga occidentalis*), which was detected for the first time during the 2010–2014 sampling period, when it was abundant.

***Keywords*:** bird-community structure, conifer forest, fire, foraging group, nesting group, vegetation succession

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High-intensity wildfire is increasing in many forested areas of western North America in response to woody materials accumulating from fire exclusion, exacerbated by increased temperatures and reduced moisture resulting from climate change (Mote et al. 2003, Millar et al. 2006, Littell et al. 2009, Miller et al. 2009, van Mantgem et al. 2009, Stephens et al. 2015). Wildfire has substantial effects on avian and other wildlife communities (Saab and Powell 2005) by modifying vegetation structure and composition (Haney et al. 2008, Stephens et al. 2009, Fontaine and Kennedy 2012, Lowe et al. 2012, Seavy and Alexander 2014). Following wildfire, animal communities change as vegetation structure and communities change through plant succession, typically to reestablish ultimately some semblance of pre-fire conditions (Seavy and Alexander 2011, White et al. 2015). Immediately after a fire the ground is often bare, and, where the fire is intense, the number of standing dead trees (snags) and downed logs is large (Raphael and White 1984).

The effects of habitat changes resulting from wildfire on avian populations have received substantial attention (e.g., Saab and Powell 2005). Typically, studies have been of two types: (1) those documenting conditions within the same plots over a short duration post-fire, illustrating the effects of the most extreme fire-induced vegetation changes (Hutto 1995, Russell et al. 2009, Bagne and Purcell 2011), or (2) those describing conditions over a short period across a set of plots representing conditions at different times post-fire (Huff et al. 1985, Venier and Pearce 2005, Watson et al. 2012). Few studies have monitored the vegetation and avian community at the same site over decades following fire (Engstrom et al. 1984, Raphael et al. 1987, Haney et al. 2008), but such studies are necessary to illustrate subtleties of site-specific changes in vegetation composition and structure and birds' responses to these changes. The information from such research has important implications for land-management policy, yet most research results available to land managers reflect only short periods after fire. Relying on only near-term results could lead to poor policy decisions and unintended consequences. Here we report on site-specific study of changes in an avian community over a period of nearly 50 years after a fire. This study is an extension of that of Raphael et al. (1987), which reported changes in vegetation and bird populations during the first 25 years following fire. Here we describe changes on the same plots after another 25 years.

In 1960, the Donner Ridge Fire burned nearly 18,000 ha that supported primarily mixed-conifer forest in Placer and Nevada counties in the northern Sierra Nevada of California. In 1965, Bock and Lynch (1970) established two permanent 8.5-ha plots within this area, one in burned forest and the other in a nearby unburned forest area. Both plots are within the Pacific Southwest Research Station's Sagehen Creek Experimental Forest, which remained unburned. The plots, but not surrounding areas, were protected from any vegetation treatment, to allow natural vegetation succession on both the burned and unburned plots. Lands surrounding the plots were managed under a variety of treatments designed to accelerate recovery of conifer forest, including site preparation, tree planting, herbicide spraying for brush control, and thinning. In some years, sheep were also allowed to graze. Vegetation conditions and bird communities had been surveyed to track their changes in three periods: 1966–1968 (Bock and Lynch 1970), 1975–1979 (Raphael and White 1984), and 1981–1985 (Raphael et al. 1987). In this study, we returned to the plots 25 years later and repeated vegetation and bird monitoring over the 5-year period of 2010–2014 to encompass nearly 50 years of intermittent monitoring of the study plots.

Our primary objectives were to describe and contrast vegetation structure and composition on the burned and unburned plots, compare the plots' bird abundance and diversity, and relate changes in bird communities to changes in vegetation over the 50-year study period. Although climate effects were not an initial objective of the study, we also considered the potential effects on bird communities of conditions during the years of our study. We considered changes in the bird community in the context of climatic change over the 50-year period and in light of the recognition in recent decades of climate change as an agent of ecological change (Tingley et al. 2009, Seavy et al. 2018).

METHODS

STUDY AREA

The burned and unburned study plots are located on a broad ridgetop east of the Sierra Nevada crest at an elevation of about 2100 m, 13 km north of Truckee, California, within a 39-km^2 basin of Sagehen Creek in the Sagehen Creek Experimental Forest, managed by the Truckee Ranger District of the Tahoe National Forest in cooperation with the Pacific Southwest Research Station and the University of California, Berkeley

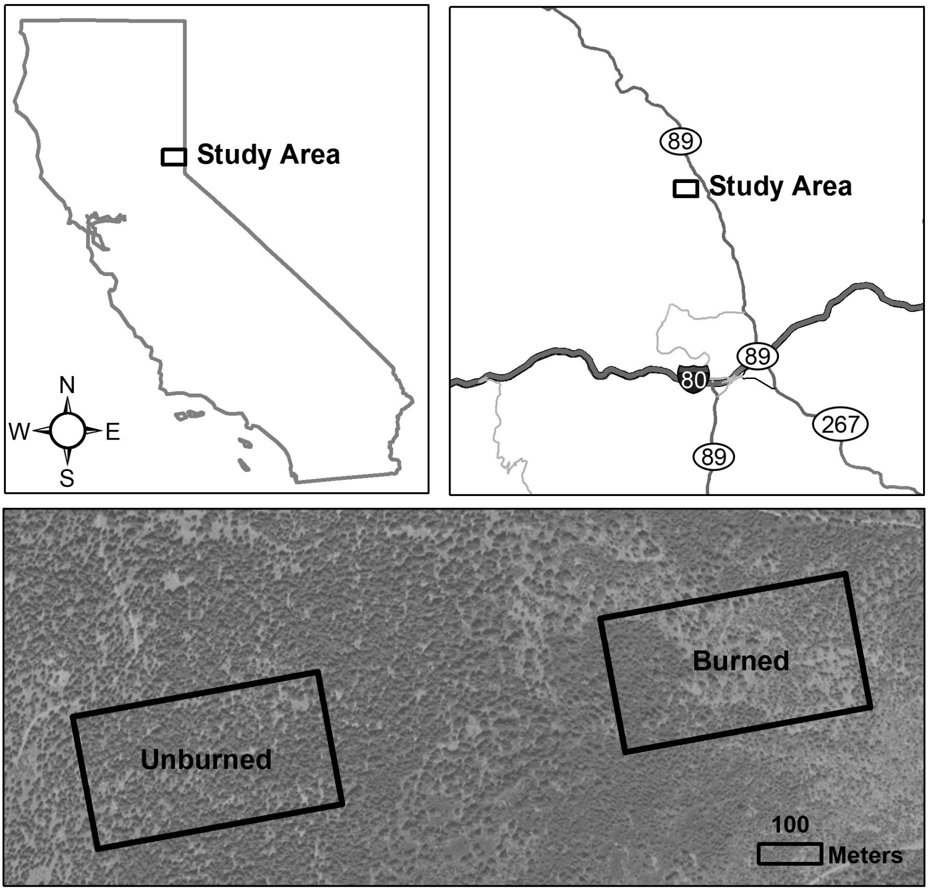

Figure 1. Location of study area and study plots.

(39° N, 120° W, Figure 1). The basin is dominated by second-growth mixed-conifer forest of yellow pine (a complex of *Pinus jeffreyi* and *P. ponderosa washoensis*), sugar pine (*P. lambertiana*), and white fir (*Abies concolor*). Meadows and stands of lodgepole pine (*P. contorta* var. *murrayana*) occur near springs and streams in the basin; red fir (*Abies magnifica*) and mountain hemlock (*Tsuga mertensiana*) occur at higher elevations. Bock and Lynch (1970), Raphael and White (1984), and Raphael et al. (1987) described the study area further.

Two 8.5-ha study plots, each measuring 214 × 397 m and located about 400 m apart, were established in 1965 (Figure 1). Each was marked at 30.5-m intervals with permanent metal stakes to form a grid. On the unburned plot, vegetation consisted of second-growth mixed-conifer forest that was largely undisturbed following regrowth from harvest of selected mature trees from 1890 to 1920. The burned plot had a similar history until being burned by the Donner Ridge Fire in 1960. In 1965, the burned plot included a few scattered mature pines and firs that survived the fire, but otherwise it was dominated by bare ground, shrubs (primarily tobacco brush, *Ceanothus velutinus*, and greenleaf manzanita, *Arctostaphylos patula*), and standing fire-killed and regenerating conifers (Figure 2).

CLIMATE

Although our primary interest was in the effects of vegetation change over time, we included climate conditions in our study because Raphael et al. (1987) found climate to be correlated with bird populations in this area. In another study in the Sierra Nevada, DeSante (1990) likewise found that climate, in particular the time of melting of the snowpack, was a major correlate of bird-population changes. We summarized mean annual temperature (MAT), total snowpack depth for the months preceding each breeding season (PAS), and day of year on which the frost-free

FIGURE 2. Photographs of the burned study plot in 1966 (top) and 2012 (bottom).

period began (bFFP) for the years 1965 to 2013 by using ClimateWNA (version 5.21). This software application extracts and downscales PRISM data (Daly et al. 2002) and calculates seasonal and annual values for climate variables for a specific location on the basis of its latitude, longitude, and elevation (Wang et al. 2012). Weather data for this application include those from the same stations summarized by Raphael et al. (1987) but are generalized to be more broadly applicable to our Sagehen study area. The current version of ClimateWNA extends only to 2013, so we were not able to include data for 2014, the last year of our study. When reporting bFFP, we use the term "Julian day" to denote "ordinal day of year."

VEGETATION SAMPLING

For vegetation sampling, we repeated the methods described by Raphael et al. (1987) for the 2010–2014 period. Understory cover was previously sampled by a line-intercept technique in 1969, 1975, and 1983 on the burned plot, and in 1975 and 1983 on the unburned plot; overstory cover was estimated in 1975 on both plots. Density and basal area of trees on both plots had been estimated by the point-quarter method in 1975 and 1983. Density of standing dead trees was estimated in 1968, 1975, and 1983 on the burned plot, in 1975 and 1983 on the unburned plot.

To estimate vegetation attributes on both plots for the 2010–2014 study period, we repeated the same techniques and sampling design in 2011 and 2012. Specifically, we used the line–point-intercept method to estimate percent understory and overstory cover from a total of 1170 points located at 1-m intervals along three transects on each plot. We used a point-centered quarter method to estimate densities of canopy stems and basal areas of overstory trees from a sample of 192 grid points on each plot. Using the grid established on each plot, we tallied numbers of standing dead trees >1.5 m tall and >13 cm in diameter at breast height (dbh) within every other 30.5-m by 30.5-m quadrat along alternating lines (totaling about 23% of the area of each plot).

Bird Populations

We repeated the same bird-survey methods described by Raphael et al. (1987). We used the spot-mapping method, visiting each plot 11 times each year from early- to mid-June from 2010 to 2014. The number of visits per year approximated the mean numbers of visits during previous survey periods (Raphael et al. 1987). We visited plots on consecutive mornings, generally from 06:00 to 10:00; hence our study addresses populations of diurnal birds only. We sampled both plots on the same day, alternating which plot was visited first to reduce possible time-of-day bias. Most surveys (90%) were conducted by one of us (MGR), but on many dates others of us participated as second observers, sometimes allowing both plots to be surveyed simultaneously. Use of multiple observers reduced potential observer bias that might have resulted from differential knowledge of bird songs and hearing ability. All observers had many years of experience surveying or observing birds in the Sierra Nevada. To summarize results, we estimated numbers of territories within the boundary of each plot to the nearest quarter territory. We considered birds detected at least three times on a plot and known to nest within the Sagehen Creek Basin as breeders; if less than a quarter of a territory was within the plot in a given year, we assigned a value of 0.01 territory for that year, following Bock and Lynch (1970).

Following Raphael et al. (1987), we grouped species into one of five foraging groups (flycatching, foliage-searching, bark-gleaning, wood-excavating, and ground/brush-searching) and five nesting groups (brush, canopy, ground, primary cavity-nesting, and secondary cavity-nesting) and calculated total numbers of territories among all species in each category for each year. We then computed the mean and SE of number of territories per year in each foraging and nesting group, averaged over the years in each survey period (n = 3 in 1966–1968; n = 5 in all other periods).

We used Ruzicka's index to compute similarity of avifaunas between plots for a given year and within plots among years (Pielou 1984:44):

$$100 \times \frac{\sum_{s=1}^{n} \min(i,j)}{\sum_{s=1}^{n} \max(i,j)}$$

where i and j were the mean numbers of territories of each species s for any pair of plots or sampling periods, for the n species in that pair. The index varies from 0 (no similarity) to 100 (complete similarity).

Results

We documented bird-community and vegetation changes on burned and unburned plots over a period of about five decades after a large wildfire. In general, changes in vegetation structure and the avian community were most marked on the burned plot. While our study focused on bird community changes in relation to vegetation changes, we documented changes in climate conditions over the same period as well.

Climate

Temperatures in the study region increased over the 5 decades (r^2 = 0.71, Figure 3A). Most of the observed increase, however, occurred since 1980. Overall, the mean annual temperature increased by 3 °C over 50 years, by 2 °C since 1980 (Figure 3A). Mean temperature during the last sampling period (2010–2014) was higher than during each of the first three sampling periods, among which mean temperature did not differ substantially (Figure 4A). Mean annual snowpack was highly variable over this period and declined slightly over time (Figures 3B and 4B). Mean snowpack depth was greatest in the first period (485 mm) and lowest during the most recent sampling period (313 mm, Figure 4B). Day of year of the beginning of frost-free period varied from year to year and since the 1980s has occurred earlier in the year, from late June to early June (Figure 3C). The mean frost-free date was earliest during the most recent

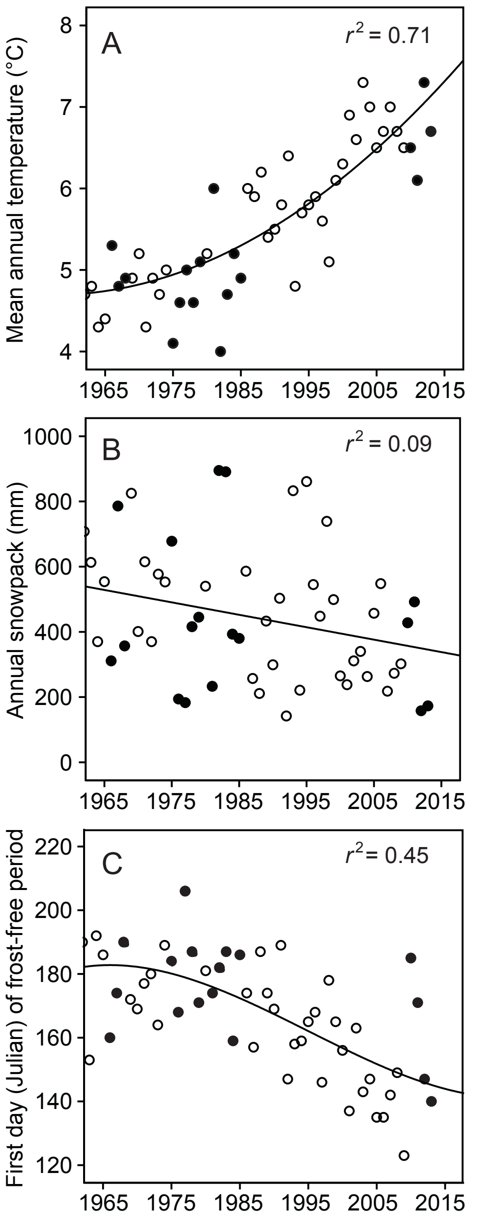

Figure 3. Yearly estimates of (A) mean annual temperature (°C), (B) total snowpack for months preceding each breeding season (mm), and (C) Julian day of beginning of frost-free period for years 1965–2013 at Sagehen Creek, California. Filled symbols denote years of surveys.

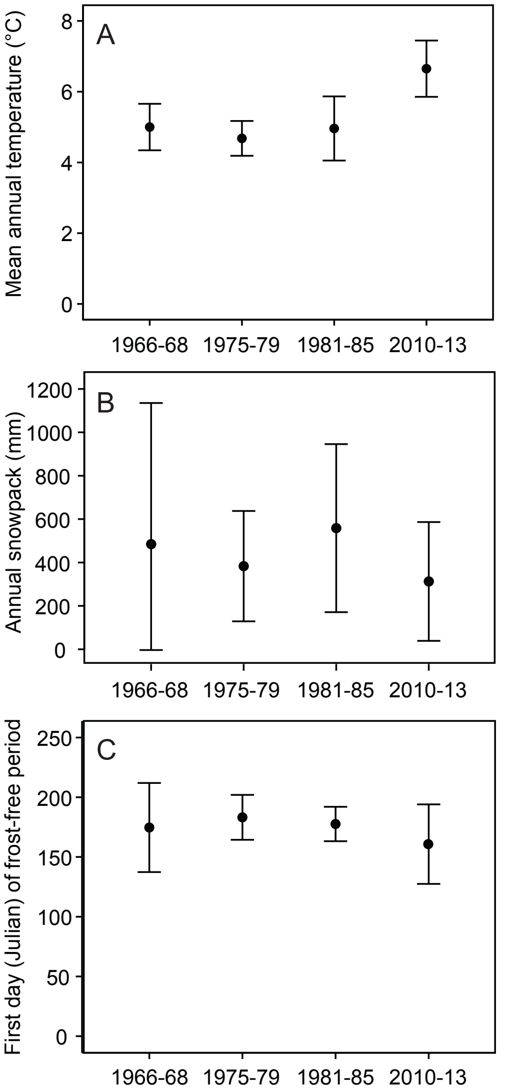

Figure 4. Mean estimates (bars denote 95% C.I.) of (A) mean annual temperature (°C), (B) total snowpack for months preceding each breeding season (mm), and (C) Julian day of beginning of frost-free period by the four periods of bird surveys.

sample period (Figure 4C). Overall, climatic conditions during the 2010–2014 period were warm and dry, with temperatures averaging 2 °C above the 30-year average and snowfall averaging 60% of the long-term average. This period coincided with a pronounced drought in California from 2011 to 2016, the driest period in California history (Griffin and Anchukaitis 2014).

Vegetation

On the burned plot, the most pronounced vegetation changes over the 43 years between 1969 and 2011 were increases of shrubs and trees (Table 1) and a decrease in standing dead trees (Figure 2). Predominant shrubs on the burned plot were tobacco brush and greenleaf manzanita, and absolute cover of shrubs overall increased from 22% to

Table 1. Percent of understory and overstory (tree) cover on the burned and unburned study plots, Sagehen Creek, California, 1969–2011. Cover estimated from line–intercept sampling with 1170 points per plot each year. Note that totals can sum to >100% because of layering of overstory and understory vegetation.

	Burned (%)				Unburned (%)		
Species	1969	1975	1983	2011	1975	1983	2011
Shrubs							
Tobacco brush (*Ceanothus velutinus*)	8.3	18.5	26.2	39.8	2.6	0.9	0
Greenleaf manzanita (*Arctostaphylos patula*)	0.8	3.8	6.0	8.5	0	0.3	0
Squaw carpet (*Ceanothus prostratus*)	9.4	17.4	7.5	19.1	11.8	10.9	6.7
Gooseberry (*Ribes cereum*)	1.2	1.5	3.3	1.7	0	0	0
Snowberry (*Symphoricarpos mollis*)	0.1	0	2.0	0.2	0	0.1	3.9
Rabbit brush (*Haplopappus bloomeri*)	1.9	1.8	0.8	1.3	0	0	0
Sagebrush (*Artemisia tridentata*)	0	0	2.0	0.2	0	0	0
Total	22.0	43.2	47.8	70.9	14.4	12.1	10.6
Herbs and grasses							
Mule ears (*Wyethia mollis*)	9.9	7.4	4.2	8.4	0	0	2.8
Other herbs	24.0	34.7	1.1	0.1	4.5	3.6	0.2
Grasses	23.2	20.0	8.5	1.7	0	0.2	0.3
Total	57.1	62.1	13.0	10.2	4.5	3.8	3.2
Non-vegetative ground cover							
Rock, bare ground	15.4	10.0	17.0	10.3	36.0	39.0	3.3
Litter	—[a]	10.3	20.2	8.5	37.4	39.3	58.6
Logs	3.3	23.3	4.9	0.4	6.2	3.7	13.6
Total	19.7	43.6	42.1	19.1	78.2	82.0	75.5
Trees							
Yellow pine (*Pinus jeffreyi and P. ponderosa washoensis*)	—	5.4	—	22.6	23.2	—	23.3
Lodgepole pine (*Pinus contorta*)	—	1.3	—	3.5	0.6	—	0
Sugar pine (*Pinus lambertiana*)	—	0	—	0	1.7	—	1.3
White fir (*Abies concolor*)	—	0.1	—	0.8	49.7	—	43.0
Incense-cedar (*Calocedrus decurrens*)	—	0	—	0	0	—	0.6
Bush chinquapin (*Chrysolepis sempervirens*)	—	0.2	—	0	1.5	—	0.7
Total	—	7.0	—	26.9	76.7	—	68.9

[a]—, no data collected.

71%. The basal area of trees on the burned plot increased from 5 m^2/ha in 1975 to 23 m^2/ha in 2011 (Table 2). By 2011, nearly all tree cover was composed of yellow pines. The density of white fir stems increased during this time, while basal area decreased, indicating that large-diameter firs decreased and small-diameter firs increased. Density of snags >38 cm dbh declined with each sampling period from about 26.0 snags/ha in 1968 to 1.5 snags/ha in 2012 (Figure 5). Ground cover of grasses and herbaceous plants first increased then decreased from about 62% in 1975 to 10% in 2011 (Table 1).

Vegetation changes were less dramatic on the unburned plot, with the exception of snag density, which tripled from about 9 stems >38 cm dbh per ha in 1975 to 31 in 2012 (Figure 5). Shrub and herbaceous cover did not change substantially, whereas conifer cover declined slightly from 77% in 1975 to 70% in 2001 (Table 1). From 1975

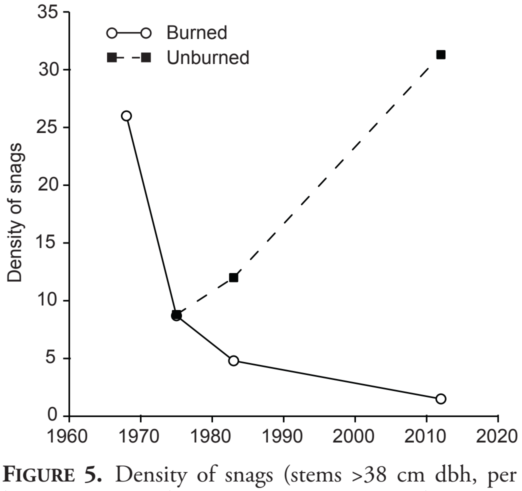

Figure 5. Density of snags (stems >38 cm dbh, per hectare) estimated in 1968, 1975, 1983, and 2012 on the burned and unburned study plots, Sagehen Creek, California. Snag density was not estimated on the unburned plot in 1968.

Table 2. Canopy-stem density (stems per ha) and basal area (m^2 per ha) on the burned and unburned plots at Sagehen Creek, California, in 1975, 1983, and 2011.

	Burned			Unburned		
Species and measure	1975	1983	2011	1975	1983	2011
Yellow pine						
Density	97.4	143.9	332.7	335.5	316.3	213.9
Basal area	3.1	4.4	21.5	24.2	30.1	29.2
Lodgepole pine						
Density	21.2	29.1	41.0	0	0	0
Basal area	0.1	0.2	1.4	0	0	0
Sugar pine						
Density	0	0	0	8.4	13.2	21.4
Basal area	0	0	0	0.3	1.0	2.2
Incense cedar						
Density	0	0	0	0	0	12.5
Basal area	0	0	0	0	0	0.7
White fir						
Density	4.0	9.2	12.4	415.2	381.3	344.4
Basal area	1.5	4.2	0.1	13.7	23.3	18.8
Red fir						
Density	0.6	0.9	0	33.6	19.7	3.0
Basal area	0.2	0.3	0	1.4	0.7	0.1
Totals						
Density	123.2	183.1	386.1	792.7	730.5	595.2
Basal area	4.9	9.1	23.0	39.6	55.1	51.0

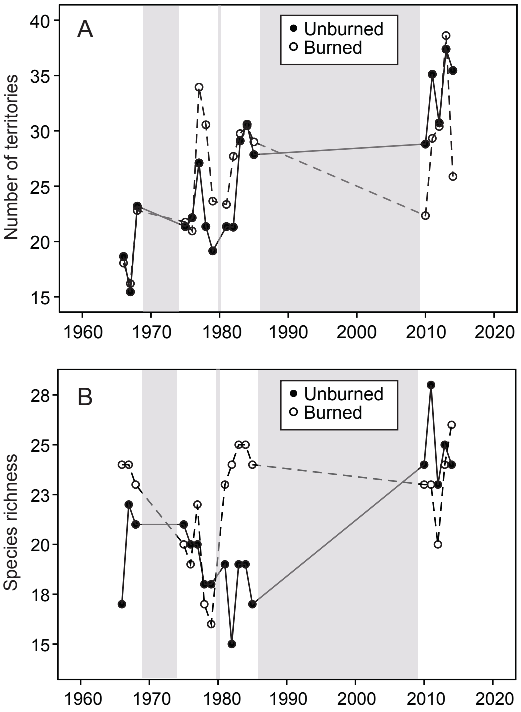

Figure 6. Yearly estimates of (A) total abundance (total number of territories) and (B) numbers of species of breeding birds on the burned and unburned study plots, Sagehen Creek, California, for four survey periods, 1966–2014. Shading denotes years with no bird surveys.

to 2011, the density of conifers declined by 25% on the unburned plot while the basal area of conifers increased by 29% (Table 2), indicating a transition to fewer but larger conifers as the stand continued to mature.

Tree canopy cover on the burned and unburned plots became more similar from 1975 to 2011, but on the burned plot it increased to only 39% of that on the unburned plot (Table 1). Shrub cover on the unburned plot remained low throughout the same period, while by 2011 it increased on the burned plot to seven times that on the unburned plot (Table 1). Overall, the burned plot developed over time into a more structurally and floristically diverse community of shrubs and trees, while the forest on the unburned plot remained relatively unchanged, except for the increase in snag density and a gradual increase in basal area.

Bird Populations

Total bird abundance (number of territories), although highly variable from year to year, increased over the five decades of monitoring in both the unburned ($r = 0.85$, $p < 0.001$) and burned plots ($r = 0.53$, $p = 0.02$; Figure 6A). Species richness (number of species) was also highly variable. On the burned plot it declined between 1966–1968 and 1975–1979 but then increased to early post-burn levels (Figure 6B). On the unburned plot, species richness was stable or declined slightly between 1966–1968 and 1975–1985, then by 2010–2014 it increased to or slightly above the initial 1966–1968 level. Species richness had a significant upward trend on the unburned plot ($r = 0.70$, $p < 0.001$) but had no trend on the burned plot ($r = 0.20$, $p = 0.42$). Note that for the 24-year-long gap in sampling between 1985 and 2010, we have no information on changes in bird species richness and abundance.

On the unburned plot, we found significant positive correlations of mean annual temperature with species richness ($r = 0.63$, $p = 0.01$) and total numbers of territories per year ($r = 0.61$, $p = 0.01$) for the years in which birds were surveyed; we found no significant correlations on the burned plot. We found no correlations of bird species richness or total abundance with snowpack or date of last freeze on either plot.

The abundance and composition of bird

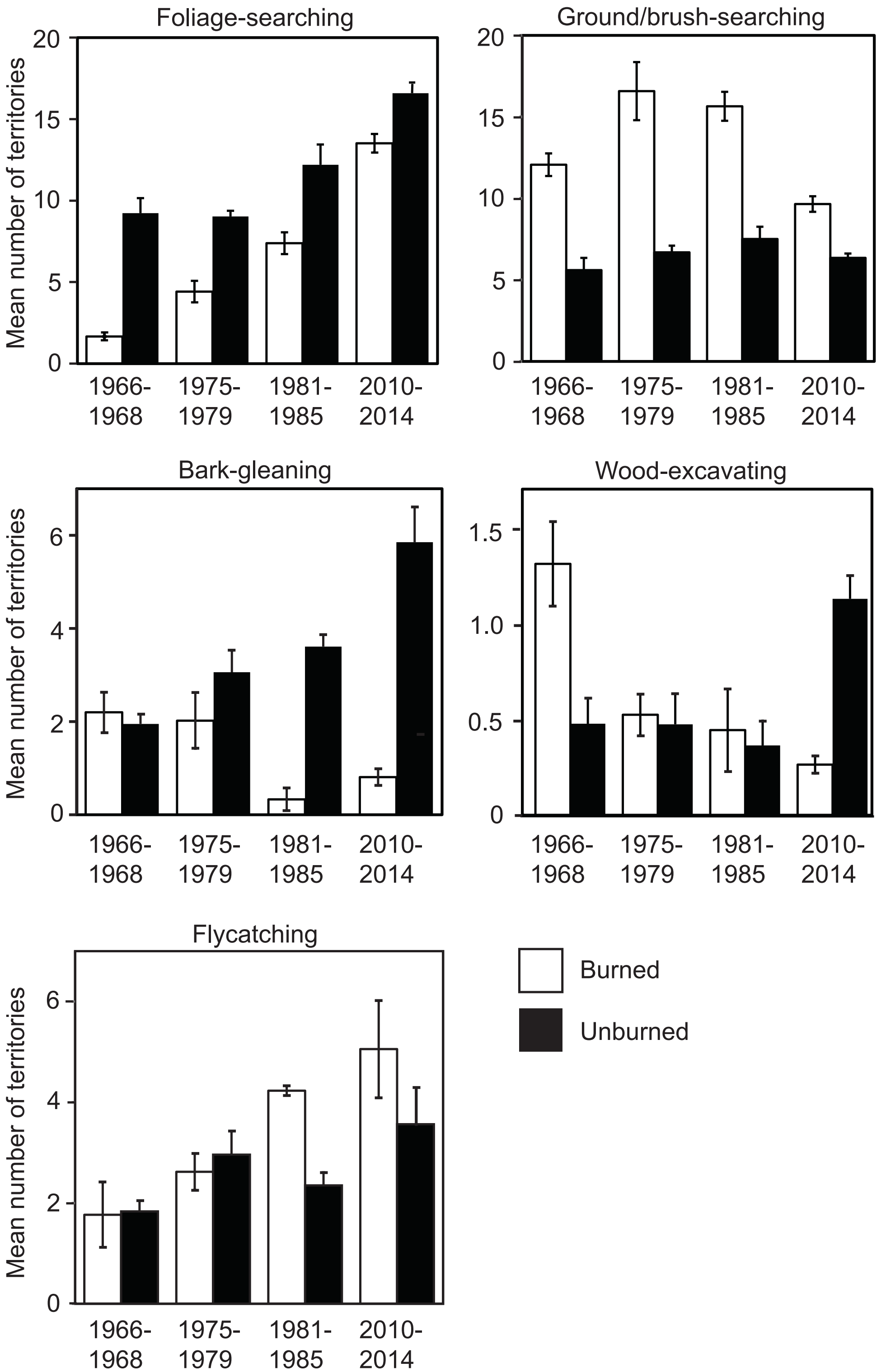

Figure 7. Mean abundance (bars denote SE) of breeding birds of five foraging groups on the burned and unburned study plots, Sagehen Creek, California, for four survey periods, 1966–2014. See Table 4 for the identity of species in each group.

TABLE 3. Numbers of territories on the burned and unburned study plots, Sagehen Creek, California, 2010–2014.[a]

	Burned						Unburned					
Species	2010	2011	2012	2013	2014	Mean	2010	2011	2012	2013	2014	Mean
Common Merganser *Mergus merganser*[b]	0	0	0	0	+	+	0	0	0	0	+	+
Mountain Quail *Oreortyx pictus*	0.8	1.0	0.5	0	0	0.5	0	0	0	0	0	0
Osprey *Pandion haliaetus*[b]	+	0	0	+	0	+	0	0	0	0	0	0
Northern Goshawk *Accipiter gentilis*	0	0	0	0	0	0	0	0	0	+	0	+
Band-tailed Pigeon *Patagioenas fasciata*	0	0	0	0	+	+	0	0	0	0	+	+
Mourning Dove *Zenaida macroura*	0	0	0	0	0	0	0	0	0	0	+	+
Common Nighthawk *Chordeiles minor*	0	0	0	+	0	+	0	0	0	0	0	0
Calliope Hummingbird *Selasphorus calliope*	0	+	0	0	0	+	0	0	0	0	0	0
Williamson's Sapsucker *Sphyrapicus thyroideus*	0.3	0.5	0.5	0	+	0.3	0.3	0.3	0.3	0.5	0.	0.3
Red-breasted Sapsucker *Sphyrapicus ruber*	0	0	0	0	0	0	0	0	0	0	+	+
Hairy Woodpecker *Picoides villosus*	0	0	0	0	0	0	0	0	0	0.3	0	0.1
White-headed Woodpecker *Picoides albolarvatus*	+	+	0.1	+	+	+	0.3	1.0	0.8	1.0	0.5	0.7
Black-backed Woodpecker *Picoides arcticus*	0	0	0	0	0	0	0	+	0	0	0	+
Northern Flicker *Colaptes auratus*	0.5	0	0.1	+	+	0.1	0	0.1	0.5	+	0	0.1
Pileated Woodpecker *Dryocopus pileatus*	0	0	0	0	0	0	0.5	0.1	0	+	0.1	0.1
Olive-sided Flycatcher *Contopus cooperi*	0	0	0	+	+	+	0	0	0	0	0	0
Western Wood-Pewee *Contopus sordidulus*	0	0	0	0	1.0	0.2	0	0	0.1	+	+	+
Dusky Flycatcher *Empidonax oberholseri*	3.0	7.0	3.3	7.0	4.0	4.9	2.8	4.5	3.0	4.0	3.5	3.6
Cassin's Vireo *Vireo cassinii*	0	0	0	+	0	+	1.5	0	+	0	0	0.3
Steller's Jay *Cyanocitta stelleri*	0.5	0.8	1.0	0.5	0.5	0.7	1.0	1.0	1.0	0.3	+	0.7
Clark's Nutcracker *Nucifraga columbiana*	0	0	0	0	0	0	0.1	0	0	+	+	+
Common Raven *Corvus corax*	0	0	0	+	0	+	0	0	0	+	+	+
Mountain Chickadee *Poecile gambeli*	3.8	2.0	3.3	3.8	2.5	3.1	3.3	4.0	3.5	4.0	3.3	3.6
Red-breasted Nuthatch *Sitta canadensis*	0.5	1.0	1.3	1.0	0.3	0.8	3.0	1.8	4.0	3.3	2.8	3.0
White-breasted Nuthatch *Sitta carolinensis*	+	0	0	+	+	+	0	0	+	0	0	+
Pygmy Nuthatch *Sitta pygmaea*	+	0	0	0	0	+	0	0	0	0	0	0
Brown Creeper *Certhia americana*	0	0	0	0	0	0	1.3	2.8	1.5	4.0	5.0	2.9
Golden-crowned Kinglet *Regulus satrapa*	+	0	0	0	+	+	1.5	3.8	2.5	3.8	4.3	3.2
Townsend's Solitaire *Myadestes townsendi*	0	0.8	1.0	1.0	1.0	0.8	1.0	2.0	2.0	2.0	2.3	1.9
Hermit Thrush *Catharus guttatus*	0	0.3	+	+	0	0.1	1.8	1.5	1.0	0.5	1.0	1.2
American Robin *Turdus migratorius*	+	+	+	0	0	+	0	0	0.1	+	0.3	0.1
Cassin's Finch *Haemorhous cassinii*	0	1.5	0	1.0	+	0.5	1.3	1.3	1.5	1.0	+	1.0
Red Crossbill *Loxia curvirostra*	0	+	+	+	+	+	0	0	0	0.1	+	+
Pine Siskin *Spinus pinus*	0	1.0	0	0	0	0.2	0	0	0	0	0	0
Evening Grosbeak *Coccothraustes vespertinus*	+	+	0	0	0	+	1.0	1.0	0.1	0	0	0.4
Nashville Warbler *Oreothlypis ruficapilla*	2.0	0	5.3	4.8	3.5	3.1	0	0	0	0	0	0
Yellow Warbler *Setophaga petechia*	0.8	1.0	3.3	6.0	1.0	2.4	0	0	0	0	0	0
Yellow-rumped Warbler *Setophaga coronata*	1.3	2.0	1.5	5.0	1.5	2.3	2.5	3.0	2.3	5.0	3.3	3.2
Black-throated Gray Warbler *Setophaga nigrescens*	0	0	0	0	1.0	0.2	0	0	0	0	0	0
Hermit Warbler *Setophaga occidentalis*	0	0	0	0	0	0	1.3	2.5	2.5	2.5	3.5	2.5
Green-tailed Towhee *Pipilo chlorurus*	+	+	+	+	0	+	0	0	0	0	0	0
Chipping Sparrow *Spizella passerina*	+	+	0.3	0	+	0.1	0	0	0.3	+	0	0.1
Fox Sparrow *Passerella iliaca*	5.0	4.3	5.5	5.5	5.0	5.1	0	0	0	0	0	0
Dark-eyed Junco *Junco hyemalis*	1.3	1.3	2.8	2.0	3.0	2.1	1.0	2.0	2.3	2.5	2.8	2.1
Western Tanager *Piranga ludoviciana*	1.8	3.0	1.0	1.0	1.5	1.7	3.8	2.8	1.8	2.8	3.0	2.8
Brown-headed Cowbird *Molothrus ater*	1.0	2.0	0	0	+	0.6	0	0	0.1	0	0	+
Totals	22.6	29.5	30.8	38.6	25.8	29.8	28.3	35.5	31.2	37.6	35.7	33.9

[a] +, <0.1 territory.

[b] Species recorded only as flying over the plot, so not included in analyses.

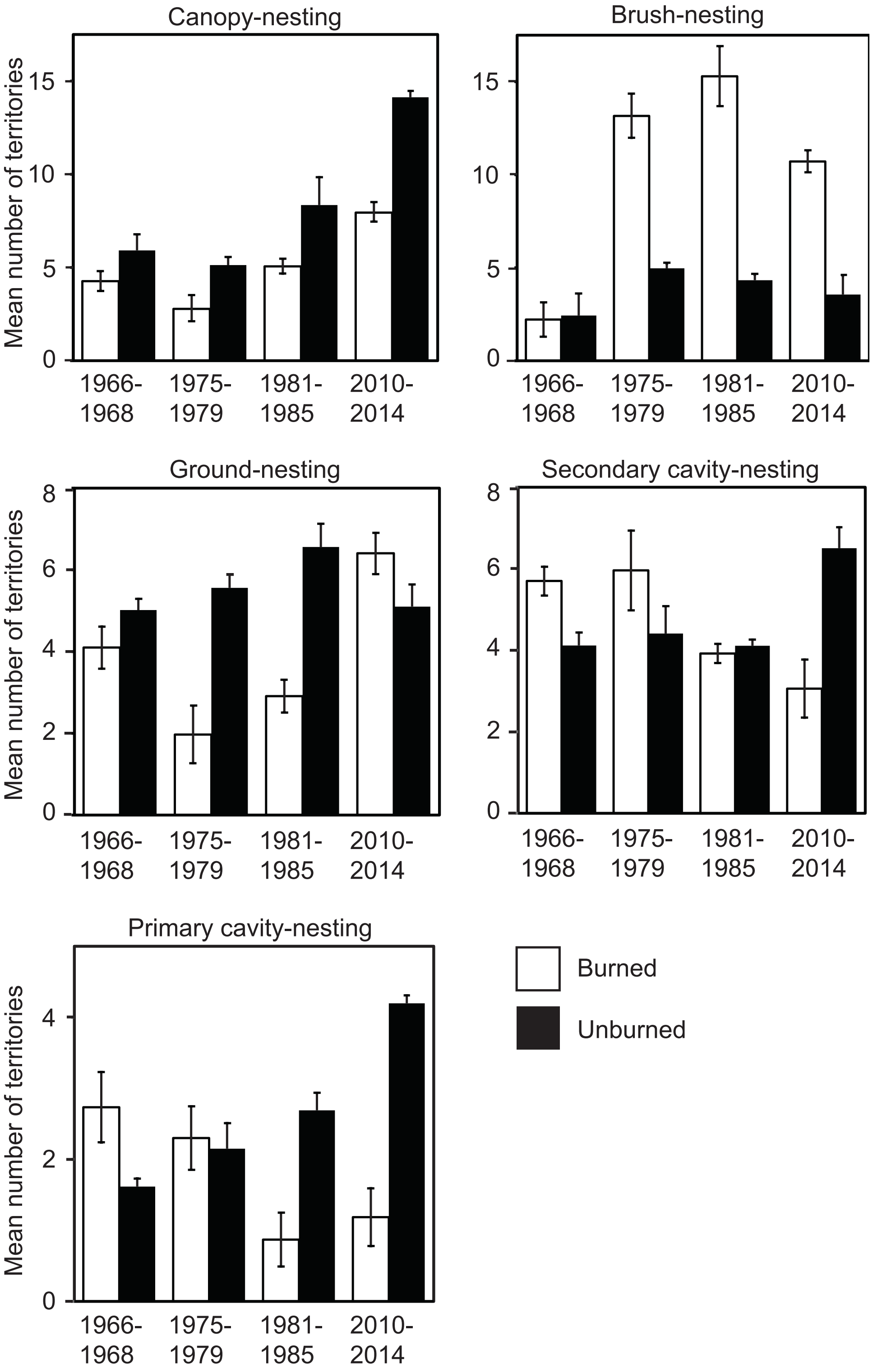

Figure 8. Mean abundance (bars denote SE) of breeding birds of five nesting groups on the burned and unburned study plots, Sagehen Creek, California, for four survey periods, 1966–2014. See Table 4 for the identity of species in each group.

Table 4. Mean numbers of territories per plot per year[a] of breeding bird species during four periods on the burned and unburned study plots, Sagehen Creek, California.

	Group		Burned[d]				Unburned[d]			
Species	Nesting[b]	Foraging[c]	1966–1968	1975–1979	1981–1985	2010–2014	1966–1968	1975–1979	1981–1985	2010–2014
Common Merganser[e]	SC	GB	0	0	0	+	0	0	0	+
Mountain Quail	GR	GB	0	0	0.4	0.5	0	0	0	0
Sooty Grouse	GR	GB	0	0	0	0	0	+	0	0
Band-tailed Pigeon	CA	GB	0	0	0	+	0	0	0	+
Mourning Dove	CA	GB	0	+	+	0	0	0	0	+
Common Nighthawk	GR	FL	0	0.1	0.7	+	0	0	0	0
Calliope Hummingbird	BR	GB	0	0.9	0.4	+	0	0.6	+	0
Osprey[e]	CA	GB	0	0	0	+	0	0	0	0
Cooper's Hawk	CA	GB	0	0	0	0	0	+	0	0
Northern Goshawk	CA	GB	0	0	0	0	0	0	0	+
Lewis' Woodpecker	PC	FL	0	+	+	0	0	0	0	0
Williamson's Sapsucker	PC	WE	0.2	0.1	0.1	0.3	0	0.3	0.3	0.3
Red-breasted Sapsucker	PC	WE	0.	0	0	0	0.3	0.1	0	+
Hairy Woodpecker	PC	WE	0.3	0.4	0.3	0	0.1	0.1	0.1	0.1
White-headed Woodpecker	PC	WE	0.1	0.1	+	+	+	+	0	0.7
Black-backed Woodpecker	PC	WE	0.7	0	0	0	0.1	+	+	+
Northern Flicker	PC	GB	0.7	0.7	0.2	0.1	0.1	+	0.2	0.1
Pileated Woodpecker	PC	WE	0	0	0	0	0	0	0	0.1
American Kestrel	SC	GB	0	0	+	0	0	0	0	0
Olive-sided Flycatcher	CA	FL	0.2	0.6	0.7	+	0	0	0	0
Western Wood-Pewee	CA	FL	0.6	+	0.4	0.2	0.1	+	0	+
Dusky Flycatcher	BR	FL	1.0	2.1	3.1	4.9	1.8	3.0	2.4	3.6
Cassin's Vireo	CA	FS	0	0	0	+	0.1	0	0	0.3
Steller's Jay	CA	FS	0	+	+	0.7	0.2	0.1	0.5	0.7
Clark's Nutcracker	CA	FS	0	0	0	0	0	0	0	+
Common Raven	CA	GB	0	0	0	+	0	0	0	+
Mountain Chickadee	SC	FS	1.1	3.2	2.9	3.1	3.3	3.0	2.6	3.6
Red-breasted Nuthatch	PC	BG	0	0	0	0.8	1.1	1.7	2.1	3.0
White-breasted Nuthatch	SC	BG	0.5	0.5	0.1	+	0.1	0.3	+	+
Pygmy Nuthatch	PC	BG	0.8	1.1	0.2	+	0	0	0	0

Continued

species on the burned and unburned plots became more similar over time, especially in the most recent sample period. Whereas Ruzicka's index of similarity between the burned and unburned plots was around 25–30% during the first three sampling periods, during the last period it was 56%. Comparing similarity within plots between the 1960s and the most recent sampling period, the avian community was more similar on the unburned plot (43% similarity) than on the burned plot (15%). The lower similarity on the burned plot indicates greater changes in bird abundance over time on that plot, consistent with a greater change in vegetation conditions there. But even on the unburned plot, avifaunal changes from 1966–1968 to 2010–2014 were substantial, resulting in a relatively low 43% similarity between those periods.

Patterns of change in bird abundance over the five decades varied among the five foraging and nesting groups (Figures 7 and 8, Tables 3 and 4). Among foraging groups, the abundance of wood-excavating species on the burned plot declined rapidly from 1966–1968 to 1975–1978, then continued to decline slowly thereafter, paralleling the pattern of decline in snags (Figures 5 and 7). Conversely, on the unburned plot wood-excavators remained at relatively low abundance through 1985, then increased markedly during the next sampling from 2010 to 2014, when excavators were several times more abundant on the unburned plot than on the burned plot (Figure 7). Bark-gleaning birds declined by two-thirds over time on the burned plot and increased nearly three-fold on the unburned plot (Figure 7). Flycatching species increased over time on both plots but more substantially and consistently on the burned plot (Figure 7), reflecting primarily

TABLE 4 (*continued*).

	Group		Burned[d]				Unburned[d]			
Species	Nesting[b]	Foraging[c]	1966–1968	1975–1979	1981–1985	2010–2014	1966–1968	1975–1979	1981–1985	2010–2014
Brown Creeper	SC	BG	0.4	0	0	0	0.8	1.2	1.5	2.9
House Wren	SC	GB	0.6	0.5	0	0	0	0	0	0
Golden-crowned Kinglet	CA	FS	0	0	0	+	3.7	2.7	2.6	3.2
Mountain Bluebird	SC	GB	3.2	1.8	1.0	0	0	0	0	0
Townsend's Solitaire	GR	GB	0.3	+	+	0.8	0.4	0.6	1.0	1.9
Hermit Thrush	GR	GB	0	0	0	0.1	0.5	1.9	1.6	1.2
American Robin	CA	GB	0.8	0.4	1.1	+	0.1	0.1	1.1	0.1
Cassin's Finch	CA	GB	0.9	1.1	0.9	0.5	0.7	0.6	0.6	1.0
Red Crossbill	CA	FS	0	0	+	+	0	0.1	0.5	+
Pine Siskin	CA	FS	0	+	0.7	0.2	0	0.3	0.7	0
Evening Grosbeak	CA	FS	0	0	0.1	+	0	0	0.8	0.4
Nashville Warbler	GR	FS	0	0	0.6	3.1	0.4	0.3	1.0	0
Yellow Warbler	CA	FS	0	0.9	2.5	2.4	0	0	0	0
Yellow-rumped Warbler	CA	FS	0.4	0.3	0.4	2.3	0.5	1.5	2.0	3.2
Black-throated Gray Warbler	BR	FS	0	0	0	0.2	0	0	0	0
Hermit Warbler	CA	FS	0	0	0	0	0	0	0	2.5
Green-tailed Towhee	BR	GB	0.2	1.8	2.1	+	0	0	0	0
Chipping Sparrow	CA	GB	1.2	0.4	0.5	0.1	0	0.2	0	0.1
Brewer's Sparrow	BR	GB	0.8	0.7	0	0	0	0	0	0
Fox Sparrow	BR	GB	0.3	6.8	6.4	5.1	0.2	+	0	0
Dark-eyed Junco	GR	GB	3.8	2.0	1.9	2.1	3.7	2.9	3.1	2.1
Western Tanager	CA	FS	0.2	0	0.2	1.7	1.2	1.3	1.7	2.8
Lazuli Bunting	BR	GB	+	0	+	0	0	0	0	0
Brown-headed Cowbird	BR	GB	0	0.2	0.9	0.6	0	0	0	+
Total territories (mean)			**19.1**	**22.2**	**26.0**	**33.5**	**19.0**	**26.2**	**28.1**	**29.3**
Sample size (years)			**3**	**5**	**5**	**5**	**3**	**5**	**5**	**5**
Standard error			**2.2**	**1.3**	**2.0**	**1.6**	**2.0**	**2.6**	**1.3**	**2.7**

[a] Data for periods through 1985 from Raphael et al. (1987); data for 2010–2014, this study.

[b] GR, ground; BR, brush; CA, canopy; PC, primary cavity-nesting (cavity excavators); SC, secondary cavity-nesting (users of existing cavities).

[c] GB, ground or brush; FS, foliage-searching; BG, bark-gleaning; WE, wood-excavating; FL, flycatching.

[d] +, <0.1 territory.

[e] Species recorded only flying over the plot, so not included in analyses.

the increased abundance of the Dusky Flycatcher (Table 4; scientific names of all birds detected on plots from 2010 to 2014 are in Table 3). Birds that search canopy foliage increased on both plots, but more substantially on the burned than the unburned plot, where densities were higher in all sample periods (Figure 7). Ground- and brush-searching birds increased initially on the burned plot but then declined (Figure 7) between the early 1980s and 2010–2014, despite brush cover having increased during this latter period.

Changes in abundance patterns within nesting groups were similar to those of foraging groups. Abundance of primary cavity-excavators decreased on the burned plot and increased on the unburned plot (Figure 8), in parallel with changes in snag abundance (Figure 5). Abundance of secondary cavity-nesters was greater on the burned than on the unburned plot during the first two sampling periods, but with the decline of snags on the burned plot that pattern reversed, so that in the most recent period, abundance of these birds was over two times greater on the unburned than on the burned plot (Figure 8). This pattern was driven largely by the loss from the burned plot of the Brown Creeper, House Wren (*Troglodytes aedon*), and Mountain Bluebird (*Sialia currucoides*), combined with an increase in the Brown Creeper on the unburned plot (Table 4). Notably, abundance of the Mountain Chickadee, also a secondary cavity-nester, changed little on either plot after an initial increase on the burned plot from 1966–1968 to 1975–1979. Abundance of canopy-nesting birds increased over time on both plots; abundance of brush-nesting birds (including the Dusky Flycatcher and Fox Sparrow) increased dramatically from 2.5 to 12.5 territories per ha on the burned plot following the first sampling period while remaining at 2 to 3 territories per ha on the unburned plot during all sampling periods.

Among individual species, the Hermit Warbler showed the most dramatic change in abundance over the 50-year study period. This species was not recorded on any surveys of either the burned or unburned plot during 13 years of survey between 1966 and 1985 (Table 4). From 2010 to 2014, it was among the most abundant species on the unburned plot (mean = 2.45 territories/year). Abundance of the Yellow-rumped Warbler increased over time on both plots, reaching its highest level from 2010 to 2014 (Table 4). The pattern shown by these species is not consistent with any apparent trend in habitat conditions.

Six species in addition to the Hermit Warbler were detected for the first time on at least one study plot during the 2010–2014 survey period: the Northern Goshawk, Band-tailed Pigeon, Pileated Woodpecker, Clark's Nutcracker, Common Raven, and Black-throated Gray Warbler (Table 4). The goshawk, pigeon, and warbler were seen during one year only, the other species in multiple years during this interval (Table 3).

Eight species detected in prior surveys were not detected from 2010 to 2014 (Table 4). Six that had occurred only on the burned plot were absent during the recent survey period: the American Kestrel (*Falco sparverius*), Lewis's Woodpecker (*Melanerpes lewis*), House Wren, Mountain Bluebird, Lazuli Bunting (*Passerina amoena*), and Brewer's Sparrow (*Spizella breweri*). All of these species except the wren and sparrow had been present up through the 1981–1985 survey period. Species that had been detected previously only on the unburned plot but were not found from 2010 to 2014 were the Cooper's Hawk (*Accipiter cooperii*) and Sooty Grouse (*Dendragapus fuliginosus*).

DISCUSSION

RESPONSES TO VEGETATION SUCCESSION

The most plausible explanation for many of the changes in abundances in various bird groups is that they are responses to changes in nesting or foraging habitat associated with natural succession following the fire. The wood-excavating guild is composed primarily of woodpeckers, which during the 1966–1968 sampling period fed in snags of trees killed in 1960 (Raphael and White 1984, Raphael et al. 1987) and were more abundant than in later periods. As snags age, their populations of wood-boring insects tend to decline (Laudenslayer 2005). During the most recent survey period there were many fewer snags in the burned plot, and most of these were older; excavators were likely using these snags for nesting, not feeding. Conversely, the rapid increase in excavators at the unburned plot matches the increase in snags over the 25 years since the previous survey, likely providing for both foraging and nesting.

Declines in bark-gleaning birds on the burned plot likely resulted from the decline in the surface area of bark, as the original snags left by the fire had fallen, and their bark surface had not been replaced by large live trees with well-developed bark structure. The continued increase in bark-foraging birds on the unburned plot likely represents a response to the large area of bark, increased surface area with deeper bark crevices on the larger trees (Jackson 1979), the large basal area of live conifers, and increased surface area of snags.

Increases in flycatchers on the burned plot may reflect increased insect production as the canopy volume increased, or increased opportunities for foraging as conifers increased in structural complexity, providing more perches for foraging flycatchers. In addition, the Dusky Flycatcher nests in taller shrubs that take time to mature, which could explain the increased abundance of that species. The relatively steady long-term abundance of flycatchers at the unburned plot likely reflects its retention of forest canopy structure over time.

Increases on the burned plot of birds that forage in the canopy are consistent with the increase in canopy volume due to regeneration of young conifers and the increase in shrub cover over the study period. The increase of this foraging group on the unburned plot, where canopy cover has declined slightly, suggests some other factor, possibly a milder climate, could also be contributing to increased populations. We found a positive correlation between overall abundance of birds and mean temperature on the unburned plot but not on the burned plot. Neotropical migrants made up a larger proportion of total abundance on the burned plot (81% in the 2010–2014 period) than on the unburned plot (53% in that same period), and it may be that a milder climate had a greater influence on the unburned plot because that plot had a higher proportion of residents that would have been affected by milder winters (see Response to Climatic Conditions below). Raphael and White (1984) previously demonstrated a correlation between greater abundance of resident songbirds and higher winter temperatures in the larger area that included the Sagehen basin.

The recent decline in ground- and brush-searching birds on the burned plot is not easily explained. On this plot, the coverage of brush and tree canopy increased over time while the percent cover of bare ground, litter, and logs declined. The decline in this foraging group may be in part an artifact of combining species that feed more on open ground with those that feed in brushy areas. Several species that tend to forage on open ground declined, including the American Kestrel, American Robin, Mountain Bluebird, Chipping Sparrow, and Dark-eyed Junco. Declines in four snag-nesting species in this guild, the American Kestrel, Northern Flicker, House Wren, and Mountain Bluebird, may also have been driven by the loss of snags. Disappearance of the Lazuli Bunting and Brewer's Sparrow may have been a response to increased tree and shrub canopy. The Lazuli Bunting is an edge species that favors open areas with some cover for nesting (Beedy and Pandolfino 2013). Its abundance in recently burned areas apparently results from the large increase in annual plants that provide abundant seed and insect resources after fires. The Brewer's Sparrow favors open low scrub for ground foraging (Beedy and Pandolfino 2013). As succession proceeded, the increase in the cover and height of shrubs and trees reduced the amount of this open habitat and of seed-bearing annuals, reducing the habitat's suitability for foraging Lazuli Buntings and Brewer's Sparrows. The relatively steady and low populations of most other ground- and brush-searching species on the unburned plot are not surprising, considering the unchanged ground and understory conditions there.

The decline in abundance of secondary cavity-nesters in the burned plot may reflect the natural history of the three species that largely drove this change. Mountain Bluebirds nest in forest–prairie ecotones, such as occur in recently burned areas (Power and Lombardo 1996). House Wrens tend to nest in cavities relatively near the ground and to avoid areas with poor visibility from the nest site, such as found near dense shrubs (Beedy and Pandolfino 2013, Johnson 2014). Brown Creepers nest almost always in cavities formed by loose bark (Poulin et al. 2013), which is most abundant in early-stage snags. In addition to the decrease in snags over time, for each of these species, conditions in the burned plot became less suitable for nesting: the loss of the ecotone between forest and open habitat for the bluebird as tree density and shrub cover increased, the increased shrub density (to 71% shrub cover by 2011) for the wren, and fewer total snags and fewer early-stage snags for the creeper. Conversely, in the unburned forest, the three-fold increase of snags between 1975 and 2012 likely contributed to the Brown Creeper's increase. As these three species declined on the burned plot, the Mountain Chickadee, another secondary cavity-nester, changed little on the burned plot after an initial increase from 1966–1968 to 1975–1979. This species differs from the other three in using a wide range of habitats and cavity types for nesting (McCallum et al. 1999, Beedy and Pandolfino 2013).

We can suggest likely causes for the appearance of one of the six species new to the plots from 2010 to 2014. The Common Raven's population has increased throughout the Sierra Nevada over the last few decades (Beedy and Pandolfino 2013), so its detection during multiple years from 2010 to 2014 may be a result of greater regional abundance. Reasons for the first appearance of the Northern Goshawk, Band-tailed Pigeon, Pileated Woodpecker, Clark's Nutcracker, and Black-throated Gray Warbler during the 2010–2014 period are not obvious. Although observed in very low numbers, the woodpecker and nutcracker occurred in more than one survey from 2010 to 2014 (Table 3), suggesting a range shift or change in regional abundance. It is also possible that the goshawk, woodpecker, and maybe the nutcracker occur in such low densities across a landscape of patchy suitability that their detection on the relatively small plots is largely a matter of chance.

During the initial sampling period of 1966–1968, the average number of total territories on both plots was similar (about 19 in 1966). By the most recent study period it had increased by 54% on the burned plot and 65% on the unburned, but the timing of the increase on the two plots differed (Table 4, Figure 6A). The total number of territories on the burned plot increased from the 1960s to the 1970s and was highly variable thereafter. In contrast, on the unburned plot the average number of territories increased with each successive period of sampling. Whereas vegetation growth and snag dynamics likely contributed to the initial post-fire increase on the burned plot, the increases in the number of territories and the rough parallel between numbers on the burned and unburned plots over the 50 years suggests that factors other than vegetation change may have contributed to the observed avifaunal changes. We discount observer variability, as MGR was present for most years of survey and the same observers sampled the burned and unburned plots each year. Because the intensity of sampling each year was also similar, and controlled for by day of survey and time of day, differences were likewise unlikely to have been due to sampling variation.

Responses to Climatic Conditions

Possibly contributing to the increased overall bird abundance we observed were the increased temperatures and reduced snowpack during the 2010–2014 survey period (Figure 4). In the Sagehen Creek region, Raphael and White (1984) showed that populations of resident species were higher after milder winters, and the winters during the 2010–2014 sampling period were exceptionally mild. As noted above, during our years of survey we found a positive correlation of total abundance and mean annual temperature on the unburned plot (but not the burned plot), possibly reflecting the higher proportion of resident birds on the unburned plot. Also in the Sierra Nevada, DeSante (1990) found a strong negative correlation between the number of territories in a year and the year's snow-free date (i.e., the number of territories increased when the habitat was free of snow earlier). In our study, however, we found no such correlation.

The colonization of the Hermit Warbler on the unburned plot is not simply explained by changes in habitat condition. Over the twenty-five years since the last sampling, however, aging of the forest had left fewer but larger conifers. Perhaps this change provided suitable conditions for this habitat specialist of generally older conifer forests with a high volume of canopy (Pearson 2014). Alternately, the colonization could represent an example of "niche tracking" with temperature increase (Tingley et al. 2009), in which a species' range changes in response to changes in the prevalent climate. This warbler, which is generally rare east of the Sierra Nevada crest (Beedy and Pandolfino 2013), appears to have expanded its geographic range to encompass the study plots concurrent with increases in mean annual (or spring–summer) temperature in the last two decades. We did not observe similar range expansions of other species. This may illustrate only that such niche tracking is difficult to detect with studies such as ours, which are not designed to evaluate larger-scale processes such as elevational or latitudinal changes in species' distributions. These subtler responses might include increases in the abundance of species whose ranges already included the study plots, such as the Yellow-rumped Warbler, which increased in abundance on the unburned plot.

The appearance and abundance of the Hermit Warbler on the unburned plot during the 2010–2014 period in the absence of a vegetation-based explanation is dramatic. Even so, the 25-year gap between the recent and previous surveys limits our ability to distinguish whether the change solely reflects the mild temperatures during our survey period or if it represents a longer-term trend. The temperature record for the Sierra Nevada (Figure 3) suggests that the warmer conditions during our latest survey period, and possibly the colonization by the Hermit Warbler, are part of the long-term trend, rather than a short-term anomaly.

Trends in climate represent a significant unknown for the distribution and abundance of birds in the Sierra Nevada and elsewhere (Wiens et al. 2009). Projections of continuing increases in temperature over the next 40–80 years suggest that 9–70% of current mixed montane forests will not remain within a suitable climate envelope (Elias et al. 2015). Large severe fires and other agents of ecosystem disturbance exacerbate this threat. Land managers will face increasing challenges in sustaining resilient ecosystems, including conifer forests, as they contend with changing climates and managing the array of disturbances that shape these systems. The long-term implications for bird communities are uncertain, but there are scientific principles and tools that will enable efforts to restore and maintain resilient landscapes and the biological communities they support (Scheffer 2009).

Management Implications

The large differences in vegetation and avifaunal communities between the burned and unburned plots, persisting over 50 years, indicate that both conditions promote landscape-level avian diversity. Notably, no active restoration of conifer forest was undertaken on the burned plot. By contrast, much of the surrounding area that burned during the Donner Ridge Fire was managed with site preparation, conifer planting, herbicide spraying to discourage shrubs from competing with conifers (Bock et al. 1978), and, more recently, even-spaced thinning to promote conifer growth and resistance to fire. As a result, much of the burned area outside the plot has changed through succession to dense monotypic conifer forest that is less diverse floristically and structurally, at both the stand and landscape level, than the range of conditions represented by the burned and unburned plots (MGR pers. obs). Therefore, our results, like those of Hutto (1995), suggest that leaving some burned areas in an unrestored condition may be important to regional avian diversity.

Changes in vegetation conditions and the bird community on the unburned plot also offer instructive guidance for management. While the unburned plot was originally conceived as a control for evaluating changes on the burned plot

(Bock and Lynch 1970), it nevertheless changed substantially despite the lack of active management. In particular, the density of snags in the unburned plot increased, as did cavity-nesting and bark-foraging birds. Maintaining areas of unmanaged, “overstocked” forest may be an alternative approach for conserving snag-dependent species, where management for snag retention in burned or harvested areas is not possible.

The unburned plot that survived the Donner Ridge Fire continued another 50+ years without the influence of fire. In mixed conifer forest in the Sierra Nevada fire-return intervals are typically between 10 and 20 years (Skinner and Chang 1996). Vaillant and Stephens (2009) concluded that the mean fire-return interval for the Sagehen basin was significantly shorter pre-settlement than since the inception of fire exclusion in 1924. This region, including the burned and unburned plots, has likely missed multiple fire cycles as a result of fire suppression, so the vegetation response observed in this >50-year period reflects conditions that land managers now seek to change by using managed burns. Presumably the reintroduction of fire to this system would remove some of the trees, snags, and downed material, particularly those of smaller diameter, resulting in an increase in the larger-diameter trees, particularly fire-resistant pines (Collins et al. 2007). Implications for bird populations are unclear.

The Sagehen plot study was originally conceived as a way to assess the effects of post–fire vegetation succession on bird populations. The long-term results, however, suggest that climatic changes (warmer temperatures and earlier snowmelt) may have also influenced the abundance and composition of the bird community during the last survey period. The study approach of dual-plot comparisons has faded from use because of its limited ability to both control for plot-specific effects and support statistical inference. Notwithstanding its limitations, our study has shown large effects of vegetation changes and less robust, but nonetheless suggestive, evidence for climate-induced changes to the avifauna. Future studies should be designed to better evaluate and distinguish between both effects.

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LITERATURE CITED

Bagne, K. E., and Purcell, K. L. 2011. Short-term responses of birds to prescribed fire in fire-suppressed forests of California. J. Wildl. Mgmt. 75:1051–1060; doi 10.1002/jwmg.128.

Beedy, E. C., and Pandolfino, E. R. 2013. Birds of the Sierra Nevada: Their Natural History, Status, and Distribution. Univ. of Calif. Press, Berkeley.

Bock, C. E., and Lynch, J. F. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

Bock, J. H., Raphael, M. G., and Bock, C. E. 1978. A comparison of planting and natural succession after a forest fire in the northern Sierra Nevada. J. Appl. Ecol. 15:597–602.

Collins, B. M., Moghaddas, J. J., and Stephens, S. L. 2007. Initial changes in forest structure and understory plant communities following fuel reduction activities in a Sierra Nevada mixed conifer forest. For. Ecol. Mgmt. 239:102–111; doi 10.1016/j.foreco.2006.11.013.

Daly, C., Gibson, W. P., Taylor, G. H., Johnson, G. L., and Pasteris, P. 2002. A knowledge–based approach to the statistical mapping of climate. Clim. Res. 22:99–113; doi 10.3354/cr022099.

DeSante, D. F. 1990. The role of recruitment in the dynamics of a Sierran subalpine bird community. Am. Nat. 136:429–445.

Elias, E., Steele, C., Havstad, K., Steenwerth, K., Chambers, J., Deswood, H., Kerr, A., Rango, A., et al. 2015. Southwest Regional Climate Hub and California Subsidiary Hub assessment of climate change vulnerability and adaptation and mitigation strategies (T. Anderson, ed.), U.S. Dept. Agric.; www.fs.usda.gov/treesearch/pubs/49341.

Engstrom, R. T., Crawford, R. L., and Baker, W. W. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: A 15-year study. Wilson Bull. 96:437–450.

Fontaine, J. B., and Kennedy, P. L. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecol. Appl. 22:1547–1561; doi 10.1890/12-0009.1.

Griffin, D., and Anchukaitis, K. J. 2014. How unusual is the 2012–2014 California drought? Geophys. Res. Lett. 41:9017–9023; doi 10.1002/2014GL062433.

Haney, A., Apfelbaum, S., and Burris, J. M. 2008. Thirty years of post-fire succession in a southern boreal forest bird community. Am. Midl. Nat. 159:421–433; doi 10.1674/0003-0031(2008)159[421:TYOPSI]2.0.CO;2.

Huff, M. H., Agee, J. K., and Manuwal, D. A. 1985. Postfire succession of avifauna in the Olympic Mountains, Washington, *in* Fire effects on wildlife habitat: Symposium proceedings (J. E. Lotan and J. K. Brown, compilers), pp. 8–15. Gen. Tech. Rep. INT–186, USDA For. Serv., Intermountain Res. Sta., Ogden, UT; www.treesearch.fs.fed.us/pubs/40119.

Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. Conserv. Biol. 9:1041–1058; doi 10.1046/j.1523-1739.1995.9051033.x-i1.

Jackson, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds, *in* The Role of Insectivorous Birds in Forest Ecosystems (J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, eds.), pp. 69–94. Academic Press, NY.

Johnson, L. S. 2014. House Wren (*Troglodytes aedon*), *in* The Birds of North America Online (A. Poole, ed.), no. 380. Cornell Lab. Ornithol., Ithaca, NY; doi 10.2173/bna.380.

Laudenslayer, W. J. 2005. Effects of site on the demographics of standing dead trees in eastside pine forests, *in* Proceedings of the symposium on Ponderosa Pine: Issues, trends, and management (M. W. Ritchie, D. A. Maguire, and A. Youngblood, tech. coord.), pp. 171–181. USDA For. Serv. Gen. Tech. Rep. PSW–GTR–198; www.fs.fed.us/psw/publications/documents/psw_gtr198/psw_gtr198.pdf.

Littell, J. S., Elsner, M. M., Whitely Binder, L. C., and Snover, A. K. (eds.). 2009. Executive summary, *in* The Washington Climate Change Impacts Assessment: Evaluating Washington's future in a changing climate, pp. 1–20. Climate Impacts Group, Univ. of Washington, Seattle; www.cses.washington.edu/db/pdf/wacciaexecsummary638.pdf.

Lowe, J., Pothier, D., Rompré, G., and Savard, J-P. L. 2012. Long-term changes in bird community in the unmanaged post-fire eastern Québec boreal forest. J. Ornithol. 153:1113–1125; doi 10.1007/s10336-012-0841-3.

McCallum, D. A., Grundel, R., and Dahlsten, D. L. 1999. Mountain Chickadee (*Poecile gambeli*), *in* The Birds of North America Online (A. Poole and F. B. Gill, eds.), no. 453. Cornell Lab. Ornithol., Ithaca, NY; doi 10.2173/bna.453.

Millar, C. [R.], Neilson, R. P., Bachelet, D., Drapek, R. J., and Lenihan, J. M. 2006. Climate change at multiple scales, *in* Forests, carbon and climate change: A synthesis of science findings, pp. 31–60, Oregon Forest Res. Inst., Oregon State Univ. College of Forestry, and Oregon Dept. of Forestry; www.fs.fed.us/psw/publications/millar/psw_2006_millar028.pdf.

Miller, J. D., Safford, H. D., Crimmins, M., and Thode, A. E. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12:16–32; doi 10.1007/s10021-008-9201-9.

Mote, P. W., Parson, E. A., Hamlet, A. F., Ideker, K. N., Keeton, W. S., Lettenmaier, D. P., Mantua, N. J., Miles, E. L., et al. 2003. Preparing for climate change: The water, salmon, and forests of the Pacific Northwest. Clim. Change 61:45–88; doi 10.1023/A:1026302914358.

Pearson, S. F. 2014. Hermit Warbler (*Setophaga occidentalis*), *in* The Birds of North America Online (A. Poole, ed.), no. 303. Cornell Lab. Ornithol., Ithaca, NY; doi 10.2173/bna.303.

Pielou, E. C. 1984. The Interpretation of Ecological Data. Wiley, New York.

Poulin, J-F., D'Astous, E., Villard, M-A., Hejl, S. J., Newlon, K. R., McFadzen, M. E., Young, J. S., and Ghalambor, C. K. 2013. Brown Creeper (*Certhia americana*), *in* The Birds of North America Online (A. Poole, ed.), no. 669. Cornell Lab. Ornithol., Ithaca, NY; doi 10.2173/bna.669.

Power, H. W., and Lombardo, M. P. 1996. Mountain Bluebird (*Sialia currucoides*), *in* The Birds of North America Online (A. Poole and F. B. Gill, eds.), no. 222. Cornell Lab. Ornithol., Ithaca, NY; doi 10.2173/bna.222.

Raphael, M. G., and White, M. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. 86:1–66.

Raphael, M. G., Morrison, M. L., and Yoder-Williams, M. P. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. Condor 89:614–626.

Russell, R. E., Royle, J. A., Saab, V. A., Lehmkuhl, J. F., Block, W. M., and Sauer, J. R. 2009. Modeling the effects of environmental disturbance on wildlife communities: Avian responses to prescribed fire. Ecol. Appl. 19:1253–1263; doi 10.1890/08-0910.1.

Saab, V. A., and Powell, H. D. W. (eds.). 2005. Fire and avian ecology in North America. Studies Avian Biol. 30:1–193.

Scheffer, M. 2009. Critical Transitions in Nature and Society. Princeton Univ. Press, Princeton, NJ.

Seavy, N. E., and Alexander, J. D. 2011. Interactive effects of vegetation structure and composition describe bird habitat associations in mixed broadleaf–conifer forest. J. Wildl. Mgmt. 75:344–352; doi 10.1002/jwmg.37.

Seavy, N. E., and Alexander, J. D. 2014. Songbird response to wildfire in mixed-conifer forest in southwestern Oregon. Int. J. Wildland Fire 23:246–258; doi 10.1071/WF12081.

Seavy, N. E., Humple, D. L., Cormier, R. L., Porzig, E. L., and Gardali, T. 2018. Evidence of the effects of climate change on landbirds in western North America: A review and recommendations for future research, *in* Trends and traditions: Avifaunal change in western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.), pp. 331–343. Studies of Western Birds 3. Western Field Ornithologists, Camarillo, CA; doi 10.21199/SWB3.18.

Skinner, C. N., and Chang, C-R. 1996. Fire regimes past and present, *in* Sierra Nevada Ecosystem Project: Final report to Congress. Volume II: Assessments and scientific basis for management options, pp. 1041–1070. Wildland Res. Center Rep. 37. Univ. of California, Davis; pubs.usgs.gov/dds/dds-43/VOL_II/VII_TOC.PDF.

Stephens, J. L., Ausprey, I. J., Seavy, N. E., and Alexander, J. D. 2015. Fire severity affects mixed broadleaf–conifer forest bird communities: Results for 9 years following fire. Condor 117:430–446; doi 10.1650/CONDOR-14-58.1.

Stephens, S. L., Moghaddas, J. J., Edminster, C., Fiedler, C. E., Hasse, S., Harrington, M., Keeley, J. E., Knapp, E. E., et al. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecol. Appl. 19:305–320; doi 10.1890/07-1755.1.

Tingley, M. W., Monahan, W. B., Beissinger S. R., and Moritz, C. 2009. Birds track their Grinnellian niche through a century of climate change. Proc. Natl. Acad. Sci. USA 106 (Suppl. 2): 19637–19643; doi 10.1073/pnas.0901562106.

Vaillant, N. M., and Stephens, S. L. 2009. Fire history of a lower elevation Jeffrey pine–mixed conifer forest in the eastern Sierra Nevada, California, USA. Fire Ecol. 5:4–19; doi 10.4996/fireecology:0503004.

Van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fule, P. Z., Harmon, M. E., Larson, A. J., et al. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524; doi 10.1126/science.1165000.

Venier, L. A., and Pearce, J. L. 2005. Boreal bird community response to jack pine forest succession. For. Ecol. Mgmt. 217:19–36; doi 10.1016/j.foreco.2005.05.058.

Wang, T., Hamann, A., Spittlehouse, D. L., and Murdock, T. Q. 2012. ClimateWNA—High-resolution spatial climate data for western North America. J. Appl. Meteorol. Climatol. 51:16–29; doi 10.1175/JAMC-D-11-043.1.

Watson, S. J., Taylor, R. S., Nimmo, D. G., Kelly, L. T., Haslem, A., Clarke, M. F., and Bennett, A. F. 2012. Effects of time since fire on birds: How informative are generalized fire response curves for conservation management? Ecol. Appl. 22:685–696; doi 10.1890/11-0850.1.

White, A. M., Manley, P. N., Tarbill, G. L., Richardson, T. W., Russell, R. E., Safford, H. D., and Dobrowski, S. Z. 2015. Avian community responses to post-fire forest structure: Implications for fire management in mixed conifer forests. Anim. Conserv. 19:256–264; doi 10.1111/acv.12237.

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., and Snyder, M. A. 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. Proc. Natl. Acad. Sci. USA 106 (Suppl. 2): 19729–19736; doi 10.1073/pnas.0901639106.