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Bird communities following high-severity fire: response to single and repeat fires in a mixed-evergreen forest, Oregon, USA

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ABSTRACT

Fire is a widespread natural disturbance agent in most conifer-dominated forests. In light of climate change and the effects of fire exclusion, single and repeated high-severity (stand-replacement) fires have become prominent land management issues. We studied bird communities using point counting in the Klamath-Siskiyou ecoregion of Oregon, USA at various points in time after one or two high-severity fires. Time points included 2-3 years after a single fire, 17-18 years after a single fire, 2-3 years after a repeat fire (15 year interval between fires), and >100 years since stand-replacement fire (mature/old-growth forest). Avian species richness did not differ significantly among habitats. Bird density was highest 17-18-years after fire, lowest two years after fire, and intermediate in repeat burns and unburned forest. Bird community composition varied significantly with habitat type (A=0.24, p <0.0001) with two distinct gradients in species composition relating to tree structure (live to dead) and shrub stature. Using indicator species analysis, repeat burns were characterized by shrub-nesting and ground-foraging bird species while unburned mature forests were characterized by conifer-nesting and foliage-gleaning species. Bird density was not related to snag basal area but was positively related to shrub height. Contrary to expectations, repeated high-severity fire did not reduce species richness, and bird densities were greater in repeat burns than in once-burned habitats. Broad-leaved hardwoods and shrubs appear to play a major role in structuring avian communities in the Klamath-Siskiyou region. In light of these results, extended periods of early seral broadleaf dominance and short-interval high-severity fires may be important to the conservation of avian biodiversity.

INTRODUCTION

In most coniferous forests, fire is a dominant ecological process promoting and maintaining ecosystem structure, function, and biodiversity at multiple spatial scales (Pickett and White, 1985; Agee, 1993; Attiwill, 1994; Pyne *et al.*, 1996; Lindenmayer *et al.*, 2004; Vandvik *et al.*, 2005). Over time, the frequency and intensity of repeated fires may act to retain or exclude particular species and regulate forest structure and seral stage (Agee, 1993; Pyne *et al.*, 1996). Recurrent disturbance by low-severity fire is well known from fire history studies, particularly in drier forest types (Pyne *et al.*, 1996; Swetnam *et al.*, 1999). However, high-severity fires recurring over short time scales have received little attention despite their known occurrence in several vegetation types, notably chaparral and mixed conifer forests (Zedler *et al.*, 1983; Agee, 1993; Delitti *et al.*, 2005). Recent increases in the frequency and extent of large wildfires in western North America (Westerling *et al.*, 2006) raises the probability of recurrent (short-interval) high-severity fires via greater probability of fire overlap. Thus, managers and policy makers have an increased need to better understand the ecological consequences of short-interval high-severity fire on ecosystems, particularly in light of the stated goal of most postfire rehabilitation to reduce the risk of recurrent fires (McIver and Starr, 2001; Brown *et al.*, 2003).

A second fire may simply reset a successional clock, creating communities indistinguishable from those occurring after just one fire; or repeat fires may provide a novel set of ecological conditions, such as altered species composition, vegetation structure, and nutrient cycling. Limited evidence suggests that repeated short-interval fires may be unique (Zedler *et al.*, 1983; Delitti *et al.*, 2005; Johnstone, 2006; Donato *et al.*, in press-b), although the influence of inter-fire interval, vegetation type, and environmental conditions remain poorly understood. Additionally, it is unknown whether repeat burn communities and single-fire communities will

converge into similar communities over time. Rate of change in postfire communities and the timescale over which they retain early successional characteristics are not well understood.

Many species of birds are adapted to, or dependent upon, disturbances such as fire or insect outbreaks in all or portions of their distribution (MacArthur, 1958; Brennan *et al.*, 1998; Saab and Powell, 2005). Fire heavily influences vertical and horizontal heterogeneity of vegetation; characteristics well known to structure avian communities in terms of abundance and species richness (MacArthur and MacArthur, 1961; Holmes *et al.*, 1979). Recognition of the importance of postfire early seral habitats for birds and the uniqueness of postfire bird communities has been documented across many ecosystem types ranging from boreal regions to Mediterranean systems to pine forests of the southwestern and southeastern U.S. (Brennan *et al.*, 1998; Herrando *et al.*, 2003; Bock and Block, 2005; Hannon and Drapeau, 2005; Noss *et al.*, 2006). Research has largely been focused on short-term (<5 years) responses of birds to single high-severity fire events in boreal (Morissette *et al.*, 2002) and mixed conifer forests (Smucker *et al.*, 2005) and single prescribed fires in pine-dominated forests (Bock and Block, 2005; Engstrom *et al.*, 2005; Hurteau *et al.*, 2008). Studies of repeated fire and fire interval on birds are limited to repeated prescribed surface fire in longleaf pine forests (Provencher *et al.*, 2002; Whiting *et al.*, 2007) and grasslands (Reinking, 2005). Thus avian response to short-interval high-severity fires in forested ecosystems remains poorly understood. This is key information for forest managers tasked with conserving disturbance-dependent bird species as well as landscape-scale avian biodiversity.

We conducted our study in the Klamath-Siskiyou region in northwestern North America that is characterized by a wet Mediterranean climate and a mixed severity fire regime in which fires burn every 5-75 years (Agee, 1993; Taylor and Skinner, 1998). The mixed severity fire

regime is among the most complex and least understood of ecological disturbance regimes; the combination of surface and stand-replacement fire over varying spatial and temporal scales results in a complex mosaic of plant communities and successional stages on the landscape (Agee, 1993). In stand-replacement patches, rapid vegetation recovery and resulting fuel continuity create the potential for recurrent high-severity fires over short (~decadal, <50 yrs) time scales (Thompson *et al.*, 2007). A related study (Donato *et al.*, in press-b) found that nearly all plant species found in mature/old-growth stands were present at similar relative abundance in both long-interval and short-interval burns, indicating high community persistence through multiple high-severity fires. The short-interval burn had the highest species richness and total plant cover with additions of disturbance-associated forbs and low shrubs, likely due to a propagule bank of early seral species that developed between fires.

Our objectives were to compare bird communities at different times since stand-replacement fire and use the unique opportunity afforded by the 200,000 ha Biscuit Fire--which reburned a pre-existing 15-year old fire--to assess the effect of short-interval repeated high-severity fire on bird communities. We used community-level (species richness, total density, ordination) and species-level (indicator species) metrics to identify bird communities and species associated with fire-based disturbance as well as the predominant environmental gradients associated with those communities. Identification of bird community response patterns and environmental gradients contributes to a broader understanding of postfire bird community dynamics and how they may interact with postfire management or subsequent high-severity fire.

METHODS

Study Area

In July 2002, at least two separate lightning strikes ignited fires in southwestern Oregon which became the 200,000 ha Biscuit Fire. The Biscuit Fire completely reburned the 38,000 ha 1987 Silver Fire while the nearby 8,000 ha 1987 Galice Fire remained outside the Biscuit Fire perimeter (Fig 1). All three fires burned for extended periods (weeks to months), generating a complex mosaic pattern of fire severities. Within the Biscuit Fire, relative proportions of low, mixed, and high-severity (as assessed by remotely sensed vegetation change) were ~30%, 27%, and 43%, respectively (USDA 2004). Precise estimates of the Silver and Galice Fires are not available but relative proportions of each severity class were fairly similar to the Biscuit Fire (see Thompson *et al.*, 2007). Sampled high-severity areas were consistent with effects of active crown fire (>95% overstory mortality with complete needle and leaf consumption as well as 100% litter consumption and understory mortality).

Forest types in the study area are typical of the upper mixed evergreen zone, trending into the white fir zone (Franklin and Dyrness, 1973), dominated by conifer species such as Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*). Typical evergreen hardwoods include Pacific madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflorus*), and canyon live-oak (*Quercus chrysolepis*) and shrubs such as manzanita (*Arctostaphylos sp.*) and ceanothus (*Ceanothus sp.*). Elevations spanned 400-1400m on a full range of aspects, primarily on slopes >20°. Areas with ultramafic soils were excluded from sampling due to differences in forest structure, plant species composition, and fire behavior.

Study Design

Substituting space for time, we took advantage of the landscape configuration of the two 1987 fires and one 2002 fire to establish geographically proximate study sites with distinct

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disturbance histories (Table 1, Fig. 1). A burn patch, the experimental unit of this study, was defined as a relatively discrete, homogeneous area of similar stand condition (basal area, species composition) that experienced high-severity fire severity, ranging in size from ~10-50 ha (i.e.. patches of stand-replacement with >95% overstory mortality). All patches were mature to old-growth conifer-dominated forests prior to recent fire(s). Each patch was subsampled with vegetation and avian point count plots. Patches sampled experienced a combination of zero, one, or two high-severity fire events (in cases of the latter, burns were separated by 15 years). Patches with differing disturbance histories were located as close to one another as possible and in similar plant associations to maximize similarity prior to fire. Because burned patches were preexisting and not selected randomly, inference from our results may be limited to our study area. Groups of patches with similar disturbance histories are referred to as treatments for brevity in the remainder of the paper.

Fire and salvage logging (harvest of fire-killed trees) occurred on all three sampled fires. Salvage logging is a widespread postfire management practice in most coniferous forest types across North America (McIver and Starr, 2001). In this study, we focus on broad changes in forest successional stage driven by high-severity fire, with potential minor influences of salvage logging. Salvage logging removed >50% of standing basal area from high-severity patches of all three fires and tended to be more intense in the two older fires (3-29 snags ha^{-1} retained in Biscuit Fire, 7-18 snags ha^{-1} in the two 1987 fires). The intensity (snag retention) and extent (proportion of high-severity burn affected) of salvage logging examined here, particularly for the Biscuit and Silver Fires, is below that reported from other regions (interior mixed conifer: Hutto and Gallo, 2006; boreal mixedwood: Koivula and Schmiegelow, 2007). Salvage logging may affect bird species in burned landscapes (e.g. Saab *et al.*, 2007), but the magnitude of change in

community composition and abundance associated with high-severity fire likely is much greater than that due to salvage logging. High-severity fire resets plant succession and vastly alters live and dead biomass pools, while salvage logging modifies existing vegetation structure at finer spatial scales than wildfire. For example, we found the effect of high-severity fire (mature forest vs recent burn) on bird community composition and abundance to be 18 times larger than that of salvage logging within the Biscuit Fire; comparison of groups using a multi-response permutation procedure (MRPP; McCune and Grace 2002) yielded A-statistics of 0.18 for mature forest vs. recent burn and 0.01 for salvage vs. no salvage within the Biscuit Fire (A-statistics >0.10 are considered biologically relevant; see McCune and and Grace (2002)). We examine avian response to salvage logging of the Biscuit Fire elsewhere (Fontaine, 2007).

Bird Data.

Avian point counts were conducted during days with no precipitation and light to no wind from mid-May to early July. Point counts were conducted from just after dawn until 10:00 am, using standard point counting techniques for five minutes (Ralph *et al.*, 1993); observers recorded all birds seen and heard and their distance with an unlimited radius. To maximize accuracy of distance estimation and proper bird identification, observers were trained extensively prior to beginning point counts, used range finders in the field, and performed double observer counts for a subset of points. To reduce spatial dependence and edge effects, individual point counts were spaced at 225-250-m intervals and were >75-m from patch edges. Point counts were visited 1-2 times each year from 2004-2005 with lower rates of resampling in 2005; sampling intensity was similar across treatments (Table 1). Number of point counts per patch and per treatment varied based on the size of each patch and number of patches in each treatment, respectively (Table 1). Sampling effort was proportional to the size of each of the three wildfires

and the consequent availability of patches of high-severity fire. In the two smaller wildfires

(Galice and Silver), we sampled nearly 100% of all accessible high-severity patches.

Vegetation and Environmental Data.

Vegetation and environmental data were collected at each point count station using a

circular plot with a 10-meter radius centered on the point with the goal of characterizing

vegetation strata present (ground, shrub, canopy). These data allowed us to assess plant species

composition of plots as well as structural composition at differing heights from the ground,

which have been shown to affect bird community composition and abundance (MacArthur and

MacArthur, 1961). Data included topographic characteristics (elevation, slope, aspect), ground

cover (visual estimates of percent cover of forbs and grass, litter, bare soil, rock, wood,

moss/lichen), and tree composition (live/dead, species, dbh, height, decay class (Cline *et al.*,

1980)). Hardwood and shrub species were divided into two categories based on life history and

growth form; species capable of re-sprouting and obtaining large stature and biomass

(hardwoods and shrubs: 26 species) were measured separately from low-stature species generally

less than 0.5-m in height and having little secondary growth (low shrubs: 39 species). Large re-

sprouting shrubs were tallied by individual, percent cover estimated by species, and the diameter

and height of live and dead stems were estimated. For hardwoods, we used a 10-cm dbh cutoff

between tree and shrub categories. Low shrubs were identified to species and percent cover

estimated visually.

Data Analysis

We used community level metrics of abundance and species richness together with

ordination and indicator species analysis to quantify bird response to high-severity fires(s) and

time since fire. We tested for overall differences in community composition using a

multiresponse permutation procedure (MRPP). Vegetation structure and the association of avian

traits with each treatment were used to understand likely mechanisms associated with observed

changes in bird communities. We compared means and parameter estimates and their 95%

confidence intervals; lack of overlap of the mean with adjacent confidence intervals was

interpreted as evidence for a statistical difference between groups while asymmetrical overlap of

means (intervals overlap one mean but not the other) was interpreted as suggestive evidence of a

statistical difference between groups (Ramsey and Schafer, 2002).

Vegetation and Environmental Data. Vegetation data from plots were averaged to

generate patch-level estimates of cover classes, total shrub volume, live and dead shrub heights,

and basal area of trees >2-m tall and >10-cm diameter at breast height (live conifers, live

hardwoods, sound snags, and soft snags). For comparison of treatments, patches were averaged

and 95% confidence intervals estimated.

Bird Species Richness. Comparisons of communities with varying abundance structures

must be corrected by the number of individuals in order to compare unbiased estimates of

species richness (Gotelli and Colwell, 2001).   To correct for this, we used EstimateS (Colwell,

2006) to estimate species richness by treatment and year. Data were first truncated at 100m to

control for variation in detectability between treatments (see Appendix A for further discussion

of this topic). Next, for each of the eight treatment by year combinations, a matrix of abundance

values organized by point counts (rows) and species (columns) were entered into EstimateS.

Using 10,000 Monte Carlo simulations, species accumulation (rarefaction) curves were

generated by treatment. Estimated species richness per point (alpha diversity) and total richness

per treatment (gamma diversity) were recorded at the same number of individuals across all

treatment by year combinations. Total richness was the estimated asymptote of the species accumulation curve using a Michealis Menton equation. Ninety-five percent confidence intervals were estimated by EstimateS via resampling using 2000 Monte Carlo randomizations. We present estimated species richness for each plot (alpha diversity) and total estimated species richness for each of the treatments in both years.

Avian Density. Density of birds per hectare was estimated for each patch using program DISTANCE 5.0 (Thomas, 2006). Application of distance sampling and program DISTANCE allows for estimation of bird densities unbiased by differences in detectability between habitats (Buckland *et al.*, 2001; Pacifici *et al.*, 2008). Following methods outlined in Buckland et al (2001), aural detections were truncated at probability of detection ~0.10 and detection functions were modeled using a hazard rate or half normal key function with a simple polynomial expansion. Data for each of the eight treatment-by-year combinations were modeled separately. Top models were selected on the basis of ΔAICc and overall fit (Buckland *et al.*, 2001; Burnham and Anderson, 2002). Patch level bird density estimates were averaged within treatment and their 95% confidence intervals estimated. Further details of this analysis are given in Appendix A.

Community Analysis. To assess differences in overall species composition among treatments we used MRPP and community ordination using Sørensen (Bray-Curtis) distance. MRPP is a non-parametric procedure for testing the hypothesis of no difference between pre-defined groups relative to random and the A-statistic from MRPP provides a useful estimate of effect size and within-group homogeneity of groups (McCune and Grace, 2002). Nonmetric Multidimensional Scaling (NMS, Kruskal, 1964) was used for ordination of bird community data. NMS is an iterative multivariate ordination technique based on ranked distances among

sample units (McCune and Grace, 2002). Ordinations were implemented using PC-ORD 5.04 (McCune and Mefford, 2006) and standard procedures outlined in McCune and Grace (2002).

Ordinations were evaluated as patches in species space. Each value within the species by patch matrix represented the abundance of a bird species at a patch in each year. Data were limited to detections within 100-m to control for differences in detectability among habitats (appendix A). Patch-level values were obtained by averaging visits within each point count and then averaging point counts within each patch. Rare species occurring at less than 5% of patches were removed. Overlays of environmental variables with Pearson correlations of >0.50 with at least one axis were used to evaluate vegetation and environmental correlates of bird community gradients.

Indicator Species Analysis. Indicator species analysis (ISA, Dufrene and Legendre, 1997) was conducted on bird species patch-level data (McCune and Mefford, 2006) to assess the strength of bird species associations with particular treatments and to aid interpretation of ordinations. As with ordination analyses, data were limited to detections within 100-m to control for detectability differences (appendix A). ISA identifies species associated with groups (i.e. treatments) by calculating an indicator value (ranging from 0-100) that is a composite of both frequency and abundance of species in defined groups. High indicator values reflect both high abundance and prevalence within a group. The application of ISA allows for examination of all species, both common and rare, within a community rather than focusing solely on common species for which adequate data exist to estimate detection probabilities (see appendix A for further details). Significance of indicator values was assessed using Monte Carlo simulations with 2000 randomizations; *P*-values represent the probability of a similar observation relative to randomized data.

Postfire habitat relationships. Finally, to focus on the effects of recent and repeated fire, we examined the relationship between avian density and the two principal elements of postfire habitats: snags and regenerating shrubs and hardwoods. For both years of the study (2-3 years after fire), we performed simple linear regression to estimate the relationship of avian density with the basal area of snags and shrub height 2-3 years after fire in both single and repeat burn treatments.

RESULTS

Vegetation Response

Vegetation structure among treatments strongly reflected effects of high-severity fire and postfire succession (Fig. 2). The short-term effect of high-severity fire was to transition mature forest from high basal area of live conifers to a high basal area in sound snags (Fig. 2a). The older burn was characterized by low amounts of tree basal area, most of which was composed of regenerating conifers and hardwoods (Fig. 2a). The repeat burn also had low tree basal area but was composed largely of snags (Fig. 2a). Postfire shrub growth (canopy volume accumulation) was significantly greater in repeat burn stands at 7200 m^3ha^{-1} by three years postfire, than in recent once-burned stands (3027 m^3ha^{-1}) (Fig. 2b). Additional effects of the Biscuit Fire included a reduction in litter cover and an increase in bare ground (Table B1); repeat burn stands had higher forb cover than any other treatment type (Table B1). Dominant hardwoods and shrubs such as tanoak, madrone, snowbrush, and chinquapin (see Table B1 for scientific names) were present in all treatments while repeat burn stands had reduced amounts of Sadler oak and old burn stands had the highest cover of madrone (Table B1).

Avian Species Richness and Density

Estimates of species richness per point count had overlapping confidence intervals for all treatments and years, showing no statistical difference (Fig. 3a). At the treatment scale, species richness patterns were similar. Total estimated species richness was 38 species for mature forest in 2004 and 2005, 36 species for recent burns in 2004 and 2005, 43 and 42 in 2004 and 2005 respectively for old burns, and 40 and 42 for repeat burns in 2004 and 2005 respectively. In contrast to species richness, avian density was significantly different among treatments based on lack of confidence interval overlap (Fig. 3b); recent burn stands had the lowest densities of birds in both years while mature forest and old burn stands had higher bird density. Avian density in repeat burn stands was intermediate between recent burn and old burn, and showed a significant increase in density from 2004 to 2005 (2 and 3 years after fire), paralleling the increase in shrub volume over the same period (Fig. 2b). Recently burned areas 2-3 years postfire, therefore, had lower overall bird densities but comparable species richness relative to the other three treatments sampled.

Community Analysis.

The MRPP test using treatments as *a priori* groups yielded a large A-statistic (A=0.24, *P*<0.00001), reflecting the distinct qualities of species assemblages in each treatment and high within-group homogeneity. Ordination of the patch-level dataset using mean abundance yielded a 2-dimensional solution (Fig. 4, final stress = 16.5, instability = 0.0002) and total R^2=0.82. The R^2 represents the proportion of variance in the original distance matrix represented by the Euclidean ordination space (straight line distance between two points in a Cartesian coordinate system). Correlations (Pearson r > 0.5) of environmental variables associated with the first axis (R^2=0.41) included shrub volume in one direction and the basal area of sound snags in the opposite direction. Mature forest and recent burn treatments were at opposite ends of axis 1

suggesting that axis 1 represented a gradient of vegetation complexity with multi-layered treatments (mature forest, old burn) at one end and simplified treatments at the other (recent burn and, to a lesser degree, repeat burn). Axis 2 (R^2=0.41) separated the mature forest and repeat burn treatments with a strong correlation with number of times burned and basal area of live conifers (Fig 4). This gradient also separated repeat burn and recent burn treatments from one another.

Indicator Species Analysis

Species with statistically significant indicator values were identified for all treatments (Table 3). Mature forest and repeat burn treatments had the largest numbers of species with indicator values >40, reflecting their more unique species composition. Single burn treatments (recent and old) had smaller numbers of indicator species (Table 2). Several rare species with significant associations but low indicator values were identified (e.g. green-tailed towhee, golden-crowned kinglet, winter wren; see Appendix C for scientific names and relative frequency of each species within treatments) while species with high indicator values reflected both abundance and restricted occurrence in one treatment (e.g. lazuli bunting, hermit warbler, hairy woodpecker, Table 2).

Habitat relationships.

In both years, the basal area of snags was a poor predictor of avian density with correlation coefficients of -0.26 and -0.25 in 2004 and 2005 respectively and slope estimates not different from zero (2005 values: slope = -0.01, SE=0.01, t= -1.3, p=0.22). In contrast, shrub height was positively correlated with avian density with correlation coefficients of 0.67 and 0.75 in 2004 and 2005, respectively, and positive slope estimates significantly different from zero (2005 values: slope=2.76, SE=0.50, t=5.5, p<0.0001).

DISCUSSION

Single burn response

Short-term (<5 years) bird community response to fire has been well characterized from a number of forest types (interior west: Kotliar *et al.*, 2002; longleaf pine: Engstrom *et al.*, 2005; boreal: Schieck and Song, 2006). Distinct knowledge gaps exist with respect to mixed severity fire regimes and longer term responses (e.g. >5 years) of bird communities within drier forest types of western North America (but see Raphael *et al.*, 1987; Saab *et al.*, 2004). Furthermore, a central challenge to understanding the relationship between fire and birds are the impacts of multiple disturbances (e.g. repeated fires, fire + logging, etc) on birds.

Bird community composition shortly after high-severity fire in our study was similar to those reported from other forest types (Bock and Lynch, 1970; Morissette *et al.*, 2002; Smucker *et al.*, 2005; Kotliar *et al.*, 2007). Species associated with dead wood (hairy woodpecker), bare ground (dark-eyed junco) and aerial foraging (Townsend's solitaire) were prevalent whereas fire obligate species typical of stand-replacement fire regime forests such as black-backed (*Picoides arcticus*) and American three-toed woodpeckers (*P. dorsalis*) did not occur in our study area (Hutto, 1995; Koivula and Schmiegelow, 2007). The observation of decreased avian densities is consistent with the decrease in vegetation complexity following high-severity fire. However, the lack of decrease in species richness following high-severity fire may be due to the mosaic of mixed severity fire with complex patch shapes and arrangement which create increased fine-scale heterogeneity.

Longer-term (17-18 year) response of birds was consistent with Raphael et al. (1987) who characterized bird communities following high-severity fire in the Sierra Nevada of California. Important structural elements in older postfire stands are dense broad-leaved shrubs

and scattered snags in advanced stages of decay. Shrub-associated species such as wrentit and weak excavators such as acorn woodpecker were prevalent in old burn stands we studied. Old burn stands also possessed the highest estimate of species richness and bird densities similar to unburned forest despite possessing much simpler vegetation complexity. This likely results from the intermediate nature of these stands possessing some bird species characteristic of both recent burns (dark-eyed junco, hairy woodpecker) and mature forest (Swainson's thrush, hermit warbler). Similar to the review of boreal bird and fire studies by Schieck and Song (2006), our ordination results placed old fire patches between mature forest and recent burns. This suggests that, as expected, avian community succession is following a trajectory of recovery from recent burn to old burn to mature forest. In the absence of further disturbance, rates of succession are likely tied to major factors separating forest types such as shrub recovery rates, conifer establishment, and snag longevity.   In particular, our results suggest that bird densities are strongly related to the rate of vegetation recovery following fire.

Repeat burn response

The effect of a repeat burn on bird communities was not to simply 'reset' the successional clock; rather, it resulted in a species assemblage (defined in terms of composition and abundance) unique from both recent and old burns. This result likely stemmed from legacy effects of the initial fire disturbance, which created an early seral plant community characterized by snags and regenerating shrubs and hardwoods. Propagule banks for both seeding and sprouting early seral vegetation were likely larger prior to the second fire, leading in part to the rapid recovery of shrubs and hardwoods following the repeat burn (Donato *et al.*, in press-b).

Ordination results were consistent with the expectation that, over time, twice burned and once burned avian communities may converge. Convergence of bird community composition could occur after once-burned stands possess a more developed shrub component, small snags fall resulting in more open stands, and large snags advance in decay stage, losing their bark and fine branches. Schieck and Song (2006) reviewed bird community succession in boreal forests, noting that logged and burned communities within the same forest type converged once snags fell and communities became dominated by shrub-associated birds after ~25 years. Rates of snag-fall, shrub development, and conifer regeneration vary by forest type and strongly influence stand structure at intermediate time scales following fire or logging. These rates of plant succession are important predictors of the rate at which bird communities converge following different types and combinations of disturbance. In our study, shrub stature was an important predictor of both avian abundance and composition while snag abundance was associated with compositional differences but not abundance. Strengthening understanding of the linkages between stand structure, rates of change, and bird community composition will aid in predicting the responses of communities and species to wildfire and prescribed fire, as well as fire surrogates such as thinning and shrub mastication.

The prevalence of shrub-associated species in the repeat burn reflects the unique nature of the resulting habitat and is a novel result for a dry forest type. Previous studies (Jehle *et al.*, 2006) have shown and reviews (e.g. Saab and Powell, 2005) have hypothesized a negative response of shrub nesting birds to fire. However, these observations and hypotheses come from less productive systems where postfire shrub response is slower and with higher rates of ungulate herbivory (Verts and Carraway, 1998). Previous studies from longer time periods following fire and similar climate (Raphael *et al.*, 1987) have reported a positive relationship between shrub-

associated species and shrub-dominated postfire plant communities. Research from boreal

forests with similar shrub response rates (mostly resprouting aspen) have found results similar to

ours over comparable time scales (e.g. Morissette *et al.*, 2002). The Mediterranean climate and

prevalent resprouting shrubs of our study area are distinct from forest types in interior western

North America dominated by a continental climatic regime, in which shrubs may have slower or

less vigorous postfire responses.

Study Limitations

The results presented in this paper are from patches that experienced stand replacement

fire and postfire salvage logging 1-3 years after the initial fire event. High-severity fire in this

study constituted >95% overstory mortality while postfire salvage logging represented partial

removal of fire-killed trees. Salvage logging intensities were somewhat higher in the two 1987

fires than the 2002 Biscuit Fire due to changes in management practices. In 1987 fires, snag

retention ranged from 7-18 snags ha^{-1} while Biscuit Fire snag retention levels were 3-29 large

(>41 cm) snags per hectare, and variable retention of smaller (<41 cm) snags depending on

merchantability (USDA, 2004, see results). In a separate study of avian response to salvage

logging of the Biscuit Fire, Fontaine (2007) found non-significant responses of most species to

salvage logging and, most importantly, very little change in overall community composition (see

also Methods, above). The few published studies examining the effects of postfire salvage

logging from the western United States, where logging prescriptions are similar, have shown

some negative responses of cavity-nesting species (e.g. Saab *et al.*, 2007) but no extirpations of

the species detected in this study or broad changes in community composition (Hutto and Gallo,

2006; Cahall, 2007). Despite the confounding of fire and postfire salvage in our study, we

believe that the amplitude of short-term ecological change resulting from high-severity fire is much greater than that of postfire salvage logging and that the results presented are correctly attributed to gross changes in seral stage due to fire. Nevertheless, studies comparing effects of fire-only and fire-plus-salvage in mixed-evergreen forest will further refine our understanding of avian response to natural and anthropogenic disturbances.

This study is retrospective without any pre-fire data and utilizes a common approach of substituting space for time. Thus, effects of fire are confounded with pre-existing spatial variation in environmental conditions and size of high-severity burn patches. Burn patch size may influence the prevalence of edge-associated bird species and residual surviving trees. Although patch size distributions overlapped among the fires we studied, the recent fire included larger patches than did the older fires. Even in that fire, however, a parallel study (Donato *et al.*, in press-a), found that ~80% of high-severity portions were <400m from an edge, suggesting that all patches we studied were likely influenced by habitat edges associated with the burn mosaic. This level of fine-scale heterogeneity is consistent with expectations from a mixed-severity fire regime but may differ from patterns in high severity portions of fires in other ecosystems (interior ponderosa pine, boreal spruce-fir forest, etc).

To minimize confounding variation, we strove to closely match edaphic conditions (elevation, slope, soil, etc) and vegetation composition (plant association group) between treatments as well as maximize proximity. While the lack of spatial interspersion of treatments cannot be fully addressed, the strong pattern in the bird data, obvious effects due to fire (i.e. tree mortality, changes in shrub stature, litter consumption), and identical plant associations suggest that this confounding of source of variation is not exerting a large influence on our dataset.

Management Implications

Following wildfire, management on public lands often is focused on achieving conifer dominated forests as rapidly as possible (USDA Forest Service, 2004). Such a focus, particularly in the Pacific Northwest, is widely accepted given the high economic value of timber and the visibility of threatened late-seral/old growth associated species such as the Northern Spotted Owl (*Strix occidentalis caurina*) and Marbled Murrelet (*Brachyramphus marmoratus*). In our study of high-severity wildfire, many species were significantly associated with mature forests but a greater number were associated with early seral postfire habitats. The high number of indicator species, and similar species richness suggest that early seral conditions created by wildfire are integral to maintaining landscape-scale biodiversity.

Repeated high-severity fire ('reburn') has been characterized as detrimental to both forest productivity and biodiversity (USDA, 1988, 2004) with postfire management frequently aimed at minimizing the likelihood of future repeat burns (USDA, 2004). In our study, the repeat burn (15 year interval) possessed a unique bird community characterized by both shrub-associated and open-habitat associated bird species with species richness and density comparable to unburned forest. Given the historic regime of frequent mixed severity fire, this habitat type has likely occurred on the landscape in the past. Recognition of the importance of a variety of early seral habitats as well as late-seral forests will likely bolster the maintenance of regional avian biodiversity.

Taken together –the lack of a negative impact of repeated high-severity fire on bird species richness, the unique composition of early seral bird communities, and the association of broad-leaved vegetation with bird abundance and traits—our study suggests that land managers faced with competing goals and limited resources could consider allowing naturally generated

early seral conditions to persist for a period in some places, rather than focusing on rapid establishment of conifers and/or closed forest. Extended periods of early successional conditions in the Klamath-Siskiyou ecoregion likely would benefit a broad suite of species and complement regional biodiversity within a landscape mosaic.

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APPENDICES

Appendix A. Avian detectability and estimation of avian densities.

Detectability considerations

      Comparisons of habitat types using point count data can be confounded by potential differences in detectability (Buckland *et al.*, 2001). Community-level analysis of birds requires the inclusion of rare species which then presents a problem with respect to estimating detection probabilities of species for which few data are available. To account for differences in detection rates between habitats in our community-level analyses, we truncated point counts a posteriori by habitat at distances corresponding to similar declines in detection probability. We chose this approach over estimating species-specific detection probabilities because of our focus on community level differences between treatments. Estimating detection probabilities for rare species with <50 detections can be problematic (Buckland *et al.*, 2001) and would have removed a substantial portion of the species from our analyses. Ideally, detectability could be estimated for each species using approaches like those outlined by Alldredge et al (2007). However, as Alldredge et al (2007) show, the application of a detection guild covariate to single observer distance sampling data often is not the best model. Rather species-level detection functions often outperform those with multispecies pooled data. However, when species composition is grossly similar across habitat types, accounting for observer and habitat differences in detectability may reduce this problem substantially (Pacifici *et al.*, 2008). Given the assumption of a common detection process that varies primarily by sound attenuation rate (Pacifici *et al.*, 2008), we identified cut points corresponding to similar levels of detectability among habitats, pooling across all species. Cut points were determined based on visual inspection of histograms of all

detections; distances at which the cumulative percentage of detections leveled out corresponded

to the distance at which probability of detection declined markedly. All four habitats sampled

showed similar declines in detections around 100-m, thus all data were truncated at 100-

m. Given the broadly similar species lists occurring in treatments and fairly even distribution of

observer effort, this approach likely accounts for a large portion, but not all, of the bias due to

differing detection probabilities among habitats.

Avian densities

Using program DISTANCE, we first constructed appropriate cut points and confronted

the data with the two key functions and three levels of stratification. Stratification included three

levels of increasing complexity: a global detection function, a detection function with a patch

covariate allowing for patch-level changes in the scale but not the shape of the function, or a

separate detection function estimated for each patch (e.g. post-stratification by patch).

Generally, the hazard rate key function with varying degrees of stratification was supported over

the half normal key function (see Buckland *et al.*, 2001 for function definitions). Summaries of

detection function, truncation distances, and detection probabilities are summarized below (table

A1).

Table A1. Summary of models used to estimate bird density.

Trtmt	Year	N obs	# int	w	Model Form	Detect Func	Detect Prob (95% CI)	EDR	# param	GOF Chi-p	ΔAICc	w_i
Mature Forest	2004	853	8	106	Haz-Simple	cov.Patch	0.47 (0.45-0.50)	73	15	0.92†	0	0.80
	2005	607	9	121	Haz-Simple	cov.Patch	0.49 (0.46-0.52)	85	10	0.002 †	0	0.96
Recent Burn	2004	946	9	123	Haz-Simple	cov.Patch	0.56 (0.54-0.59)	92	14	0.21†	0	0.99
	2005	1474	9	146	Haz-Simple	cov.Patch	0.52 (0.50-0.54)	105	21	0.82†	0	0.99
Old Burn	2004	374	8	126	Haz-Simple	Patch	0.51 (0.41-0.61)‡	89‡	15	6/7 ns‡	0	0.99
	2005	194	8	121	Haz-Simple	cov.Patch	0.38 (0.33-0.44)	75	7	0.87†	0	0.77
Repeat Burn	2004	806	9	131	Haz-Simple	cov.Patch	0.54 (0.52-0.57)	97	8	0.15†	0	0.81
	2005	649	8	126	Half Norm-Simple	Gbl	0.45 (0.41-0.50)	85	1	0.83	0	0.51
					Haz-Simple	Gbl	0.55 (0.49-0.62)	94	2	0.95	0.31	0.44

Note: N obs: number of bird observations; # intervals: number of distance intervals; w: truncation distance (m); Detect Func: detection function calculated globally (Gbl), globally using patch as a covariate (cov.Patch), or estimated per patch (Patch); Detect Prob: probability of detection; EDR: effective detection radius (m); # param: number of parameters in model; GOF Chi-p: p-value from a chi-square goodness of fit test; w_i: Akaike weight of model, only models with ΔAICc < 2 are reported.

†Goodness of fit tests were not possible with models using patch as a covariate; p-values reported are from the Haz-Simple model with a global detection function.

‡Values represent averages of each of the seven individually estimated detection functions. Six of seven goodness of fit tests were not significant at the 95% level.

Appendix B. Cover of dominant shrub species in the Klamath-Siskiyou Mountains 2004-2005.

Table B1. Percent cover of dominant shrubs and surface classes across treatments 2004-2005.

Common Name	Species	Mature Forest‡	Recent Burn (2-3 yrs postfire)		Old Burn (17 yrs postfire) ‡	Repeat Burn	
		2004	2004	2005	2004	2004	2005
Pacific madrone	*Arbutus menziesii*	0.3 (0.2)	0.9 (0.3)	1.2 (0.4)	4.6 (1.5)	2.5 (0.9)	4.9 (1.5)
manzanita sp.	*Arctostaphylos sp.*	1.8 (1.2)	0.1 (0.03)	2.1 (0.9)	3.1 (1.9)	0.9 (0.7)	2.3 (1.6)
chinquapin	*Castonopsis chrysophylla*	0.6 (0.4)	1.5 (0.6)	2.2 (0.8)	6.9 (2.2)	0.8 (0.4)	1.1 (0.7)
deer brush	*Ceanothus integerrimus*	0 (0)	0 (0)	0.7 (0.3)	1.8 (1.7)	3.4 (2.4)	5.7 (2.8)
snowbrush	*Ceanothus velutinus*	0 (0)	0.3 (0.1)	1.4 (0.6)	9.6 (5.4)	9.4 (3.1)	16.8 (6.2)
yerba santa	*Eriodictyon californicum*	0 (0)	0 (0)	0.6 (0.6)	1.3 (1.3)	0 (0)	1 (1.0)
tanoak	*Lithocarpus densiflorus*	14 (3.2)	9.4 (2.0)	11.4 (2.4)	13.7 (4.6)	10.6 (1.8)	20.1 (2.4)
Sadler oak	*Quercus sadleriana*	2 (0.9)	2.2 (1.0)	4.9 (2.0)	6.4 (5.6)	0.2 (0.2)	0 (0)
oak sp (Canyon live oak, huckleberry oak)	*Quercus sp.*	12.9 (3.7)	4.6 (1.4)	7.2 (1.8)	4.8 (1.5)	3.2 (0.9)	4.4 (1.0)
myrtlewood	*Umbellularia californica*	1.4 (1.4)	0.6 (0.6)	0.6 (0.4)	0 (0)	0 (0.02)	0.1 (0.1)
Vaccinium sp.	*Vaccinium sp.*	7.2 (5.1)	1.8 (1.3)	2 (0.8)	0.6 (0.4)	0.1 (0.03)	0.5 (0.2)
low-stature shrubs	*Gaultheria shallon*, *Berberis* sp., *Rubus* sp., *Ribes* sp.	6.6 (2.8)	9.1 (3.3)	10.9 (1.9)	9.3 (1.0)	6.6 (1.5)	12.2 (3.1)
rock		4.9 (2.3)	45.0 (3.7)	24.3 (4.6)	10.3 (3.7)	29.7 (4.4)	22.8 (4.8)
soil		2.7 (0.9)	18.9 (2.2)	17.5 (2.3)	13.7 (5.2)	11.6 (1.2)	9.4 (2.1)
litter		63.4 (4.0)	18.2 (2.9)	16.1 (3.0)	48.1 (7.8)	9.4 (3.9)	11.6 (2.3)
wood		10.8 (1.7)	4.9 (0.9)	17.7 (2.9)	17.2 (3.2)	5.7 (1.1)	17.1 (4.0)
moss-lichen		9.1 (3.0)	2.6 (1.6)	2.4 (1.0)	2.0 (1.0)	1.3 (1.1)	4.5 (1.1)
herb		9.5 (4.3)	10.6 (3.6)	21.2 (4.5)	9.2 (3.5)	42.6 (6.7)	34.1 (7.6)

Notes: Numbers represent means (standard error) of percent cover values across patches within each treatment by year (see Table 1 for number of patches per treatment).
‡Mature Forest and Old Burn treatments were not remeasured for vegetation in 2005.

Appendix C. List of bird species and their scientific names

Table C1. Bird species detected and their frequency of occurrence within each sampled treatment in the Klamath-Siskiyou mountains, 2004-2005.

Common Name	Scientific Name	Unburned	Recent Burn	Old Burn	Repeat Burn
ruffed grouse	*Bonasa umbellus*	0.009	0.000	0.000	0.000
sooty grouse	*Dendragapus fuliginosus*	0.068	0.030	0.000	0.047
mountain quail	*Oreortyx pictus*	0.026	0.100	0.026	0.208
mourning dove	*Zenaida macroura*	0.000	0.000	0.026	0.028
rufous hummingbird	*Selasphorus rufus*	0.111	0.139	0.237	0.434
acorn woodpecker	*Melanerpes formicivorus*	0.026	0.013	0.447	0.226
red-breasted sapsucker	*Sphyrapicus ruber*	0.051	0.013	0.105	0.019
downy woodpecker	*Picoides pubescens*	0.009	0.039	0.000	0.019
hairy woodpecker	*Picoides villosus*	0.094	0.613	0.026	0.132
northern flicker	*Colaptes auratus*	0.111	0.157	0.368	0.302
pileated woodpecker	*Dryocopus pileatus*	0.034	0.035	0.026	0.028
olive-sided flycatcher	*Contopus cooperi*	0.120	0.457	0.526	0.509
western wood-pewee	*Contopus sordidulus*	0.009	0.374	0.421	0.264
willow flycatcher	*Empidonax traillii*	0.000	0.004	0.000	0.000
Hammond's flycatcher	*Empidonax hammondii*	0.188	0.274	0.289	0.189
dusky flycatcher	*Empidonax oberholseri*	0.000	0.009	0.105	0.047
Pacific-slope flycatcher	*Empidonax difficilis*	0.530	0.061	0.053	0.019
Cassin's Vireo	*Vireo cassinii*	0.137	0.030	0.237	0.085
Hutton's Vireo	*Vireo huttoni*	0.094	0.000	0.053	0.000
warbling vireo	*Vireo gilvus*	0.128	0.022	0.237	0.057
Steller's Jay	*Cyanocitta stelleri*	0.470	0.283	0.605	0.443
common raven	*Corvus corax*	0.051	0.004	0.000	0.000
Tachycineta sp†	*Tachycineta sp.*	0.000	0.009	0.053	0.038
black-capped chickadee	*Poecile atricapillus*	0.017	0.004	0.000	0.000
mountain chickadee	*Poecile gambeli*	0.017	0.004	0.000	0.000
chestnut-backed chickadee	*Poecile rufescens*	0.308	0.022	0.105	0.028
Bushtit	*Psaltriparus minimus*	0.034	0.004	0.053	0.028
red-breasted nuthatch	*Sitta canadensis*	0.718	0.304	0.421	0.292
white-breasted nuthatch	*Sitta carolinensis*	0.000	0.009	0.026	0.000
brown creeper	*Certhia americana*	0.282	0.230	0.026	0.019
rock wren	*Salpinctes obsoletus*	0.000	0.013	0.000	0.019
Bewick's wren	*Thryomanes bewickii*	0.000	0.013	0.053	0.075
house wren	*Troglodytes aedon*	0.009	0.330	0.158	0.396
winter wren	*Troglodytes troglodytes*	0.111	0.000	0.000	0.000
golden-crowned kinglet	*Regulus satrapa*	0.171	0.004	0.000	0.000
western bluebird	*Sialia mexicana*	0.000	0.143	0.026	0.104
Townsend's solitaire	*Myadestes townsendi*	0.026	0.378	0.053	0.094
hermit thrush	*Catharus guttatus*	0.581	0.043	0.263	0.038
American robin	*Turdus migratorius*	0.017	0.109	0.105	0.019
varied thrush	*Ixoreus naevius*	0.068	0.000	0.000	0.000
Wrentit	*Chamaea fasciata*	0.145	0.004	0.658	0.047
orange-crowned warbler	*Vermivora celata*	0.009	0.004	0.526	0.396
Nashville warbler	*Vermivora ruficapilla*	0.291	0.126	0.632	0.604

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yellow-rumped warbler	*Dendroica coronata*	0.282	0.470	0.316	0.085
black-throated gray warbler	*Dendroica nigrescens*	0.274	0.009	0.211	0.066
hermit warbler	*Dendroica occidentalis*	0.846	0.091	0.447	0.057
Macgillivray's warbler	*Oporornis tolmiei*	0.145	0.226	0.553	0.396
Wilson's warbler	*Wilsonia pusilla*	0.034	0.000	0.000	0.000
Western tanager	*Piranga ludoviciana*	0.393	0.217	0.447	0.142
green-tailed towhee	*Pipilo chlorurus*	0.000	0.009	0.000	0.057
spotted towhee	*Pipilo maculatus*	0.077	0.048	0.526	0.575
fox sparrow	*Passerella iliaca*	0.000	0.017	0.053	0.179
song sparrow	*Melospiza melodia*	0.000	0.017	0.026	0.085
white-crowned sparrow	*Zonotrichia leucophrys*	0.000	0.057	0.026	0.217
dark-eyed junco	*Junco hyemalis*	0.333	0.739	0.237	0.321
black-headed grosbeak	*Pheucticus melanocephalus*	0.402	0.265	0.789	0.736
lazuli bunting	*Passerina amoena*	0.009	0.296	0.105	0.925
purple finch	*Carpodacus purpureus*	0.034	0.130	0.158	0.208
red crossbill	*Loxia curvirostra*	0.026	0.061	0.079	0.038
pine siskin	*Carduelis pinus*	0.043	0.078	0.053	0.179

†Swallow species (tree swallow: *Tachycineta bicolor* and violet-green swallow: *Tachycineta thalassin*a) were pooled for all analyses.

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Table 1. Disturbance history and sampling intensity of four treatments 2004-2005 in the Klamath-Siskiyou Mountains, USA.

Treatment	year sampled	years since fire	# patches†	visits per point
mature forest	2004	100+	12	1.6
	2005	100+	9	1.3
recent burn (Biscuit Fire)	2004	2	13	1.7
	2005	3	19	1.5
old burn (Galice Fire)	2004	17	7	1.7
	2005	18	6	1.0
repeat burn (Silver Fire)	2004	2	7	1.7
	2005	3	7	1.0

† Point counts per patch ranged from 2-14 (mean 6.1). Across both years and all treatments, a total of 727 point counts were conducted with 7620 detections of birds.

Table 2. Indicator species analysis of common bird species organized by four treatments (indicator values >40 in bold, range 0-100 based on species prevalence and abundance).

Treatment of maximum association	Species‡	% Indicator Value				†P-Value
		Mature Forest	Recent Burn	Old Burn	Repeat Burn	
Mature Forest	Pacific-slope flycatcher	**68**	2	0	0	0.0002
	hermit warbler	**68**	1	19	0	0.0002
	hermit thrush	**61**	1	6	1	0.0002
	red-breasted nuthatch	**51**	10	17	10	0.0002
	brown creeper	**47**	27	0	0	0.0002
	chestnut-backed chickadee	**45**	1	7	1	0.0002
	black-throated gray warbler	**44**	0	5	2	0.0014
	golden-crowned kinglet	**42**	0	0	0	0.0004
	winter wren	33	0	0	0	0.0006
	Hutton's vireo	32	0	4	0	0.0014
	western tanager	30	12	24	3	0.1076
	Steller's Jay	29	10	26	21	0.2178
	Wilson's warbler	19	0	0	0	0.017
	common raven	16	0	0	0	0.0384
	sooty grouse	8	4	0	7	0.6789
Recent Burn	hairy woodpecker	2	**71**	0	5	0.0002
	Townsend's solitaire	1	**51**	1	4	0.0002
	dark-eyed junco	15	**51**	7	14	0.0002
	yellow-rumped warbler	15	34	14	1	0.0182
	western bluebird	0	21	1	18	0.125
	downy woodpecker	1	9	0	2	0.3775
	pileated woodpecker	4	4	2	4	0.9988
Old Burn	wrentit	4	0	**69**	0	0.0002
	orange-crowned warbler	0	0	**52**	36	0.0002
	black-headed grosbeak	11	6	**41**	34	0.0004
	MacGillivray's warbler	4	10	**40**	30	0.0052
	olive-sided flycatcher	3	19	33	26	0.0348
	acorn woodpecker	0	0	33	13	0.0036
	western wood-pewee	0	25	27	17	0.1046
	warbling vireo	6	1	23	3	0.0456
	dusky flycatcher	0	0	20	4	0.0326
	Hammond's flycatcher	6	16	19	13	0.6863
	Cassin's vireo	11	0	17	5	0.1668
	red-breasted sapsucker	10	0	14	1	0.2446
	American robin	1	10	12	1	0.4377
	red crossbill	3	8	12	2	0.6541
	bushtit	4	0	6	3	0.6811
Repeat Burn	lazuli bunting	0	14	1	**76**	0.0002
	rufous hummingbird	3	6	10	**56**	0.0002
	spotted towhee	1	0	31	**56**	0.0002
	fox sparrow	0	0	4	**52**	0.0002
	white-crowned sparrow	0	5	0	**43**	0.0004

Nashville warbler	9	2	40	**41**	0.0046
house wren	0	29	5	38	0.0056
green-tailed towhee	0	0	0	35	0.0004
northern flicker	2	5	24	34	0.0184
purple finch	1	12	15	31	0.0258
mountain quail	1	6	1	28	0.0154
song sparrow	0	1	1	27	0.004
Bewick's wren	0	0	6	25	0.0086
pine siskin	4	7	2	20	0.1422
mourning dove	0	0	2	15	0.0308
Tachycineta sp.╫	0	0	5	11	0.184

‡See Appendix C for a complete list of bird species and their scientific names.

†P-values are presented to aid in intrepetation of analysis but should be interpreted with caution given the large number of significance tests; a bonferonni correction to an alpha level of 0.05 suggests a critical P-value of ~ 0.001. P-values were calculated from 2000 Monte Carlo randomizations of the species abundance by patch matrix. Bolded indicator values correspond to this level of confidence.

╫Tree and violet-green swallows were pooled for this analysis.

FIGURE LEGENDS:

Fig 1. Study area located in the Klamath-Siskiyou Mountains of southwestern Oregon, USA. The Silver and Galice Fires burned in 1987 and the Biscuit Fire burned in 2002, completely reburning the Silver Fire.

Fig 2. Above-ground structural characteristics of treatments sampled: (a) Basal area (m^2/ha) of live conifers, live hardwood, sound snags, soft snags, and hardwood snags as measured in 2004; (b) shrub volume (m^3/ha) from 2004-2005, NM: treatments without recent fire were not remeasured in 2005. High-severity fire killed and consumed much of the aboveground vegetation which was followed by a rapid recovery of the shrub layer.

Fig 3. (a) Species richness (estimated species point^{-1}, 95% CIs) and (b) mean (birds ha^{-1}, 95% CIs) bird densities by treatment 2004-2005. Species richness was not significantly impacted by high-severity fire while total avian density showed an initial postfire decrease followed by recovery.

Fig 4. (a) Ordination of patches (2004-2005) in species space using nonmetric multidimensional scaling (NMS). The disturbance histories are associated with distinct bird communities (MRPP, A=0.24, $P<0.0001$). Vectors along axes are correlations of environmental variables with the indicated ordination axes: shrub volume (m^3 ha^{-1}) -0.64; live conifer basal area (m^2 ha^{-1}) 0.78; sound snag basal area (m^2 ha^{-1}) 0.64. Arrows indicate the change in bird community composition following single and repeat fire events.

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Fig. 1
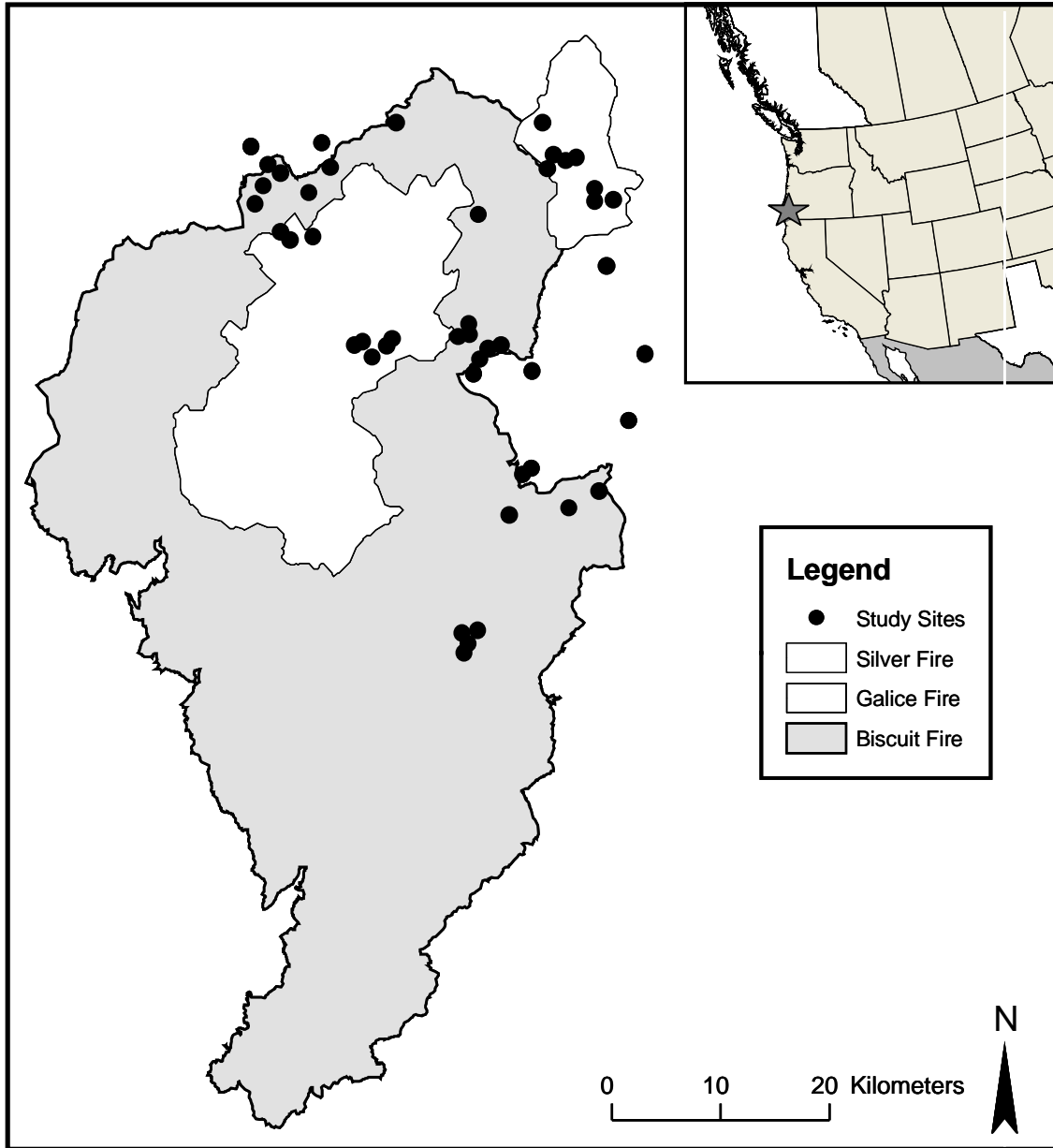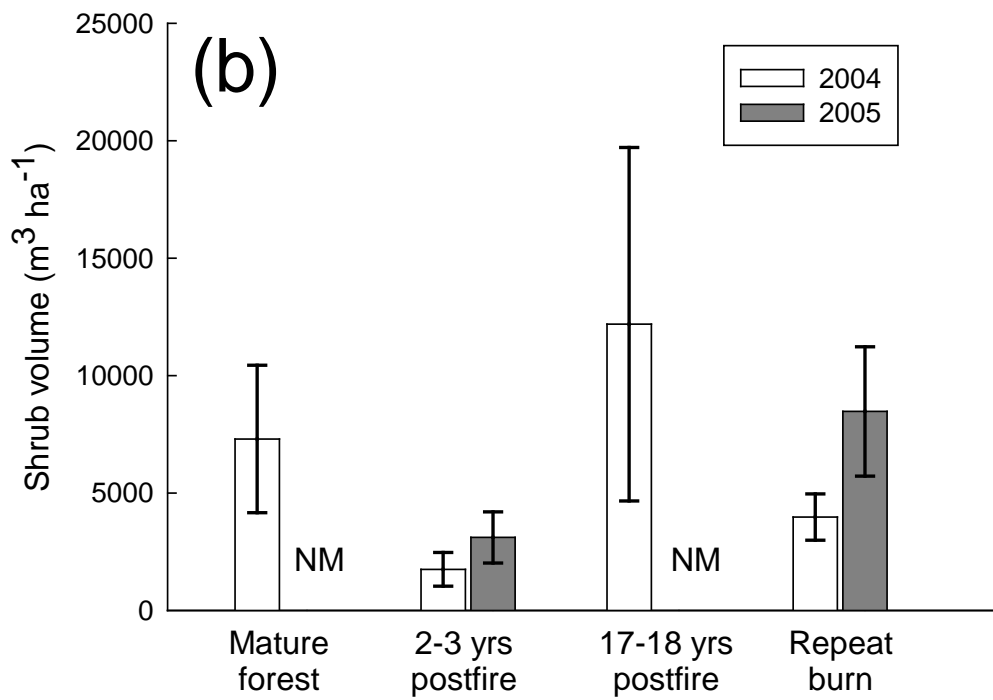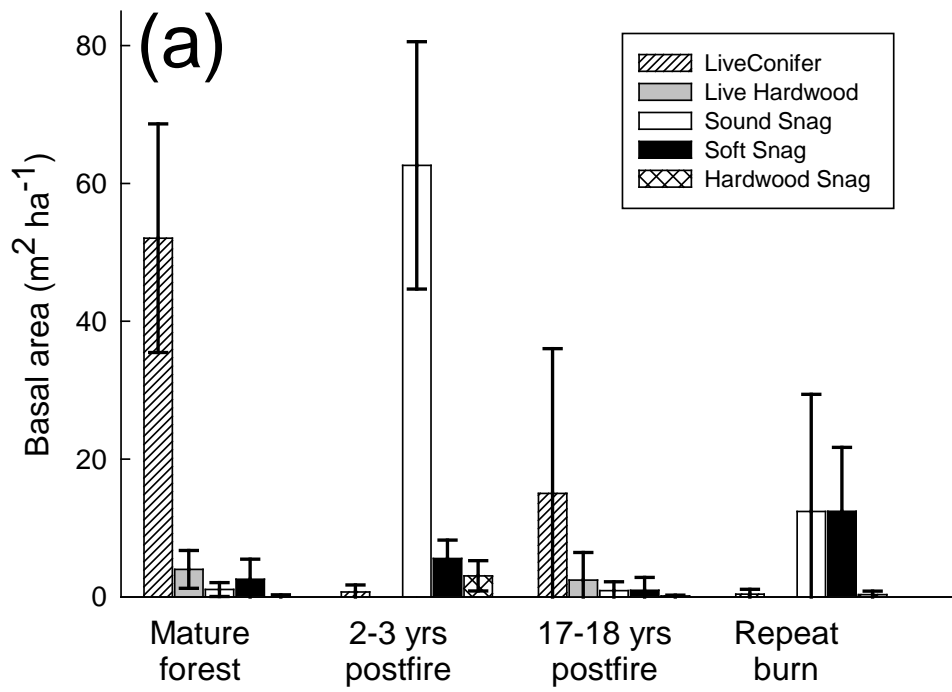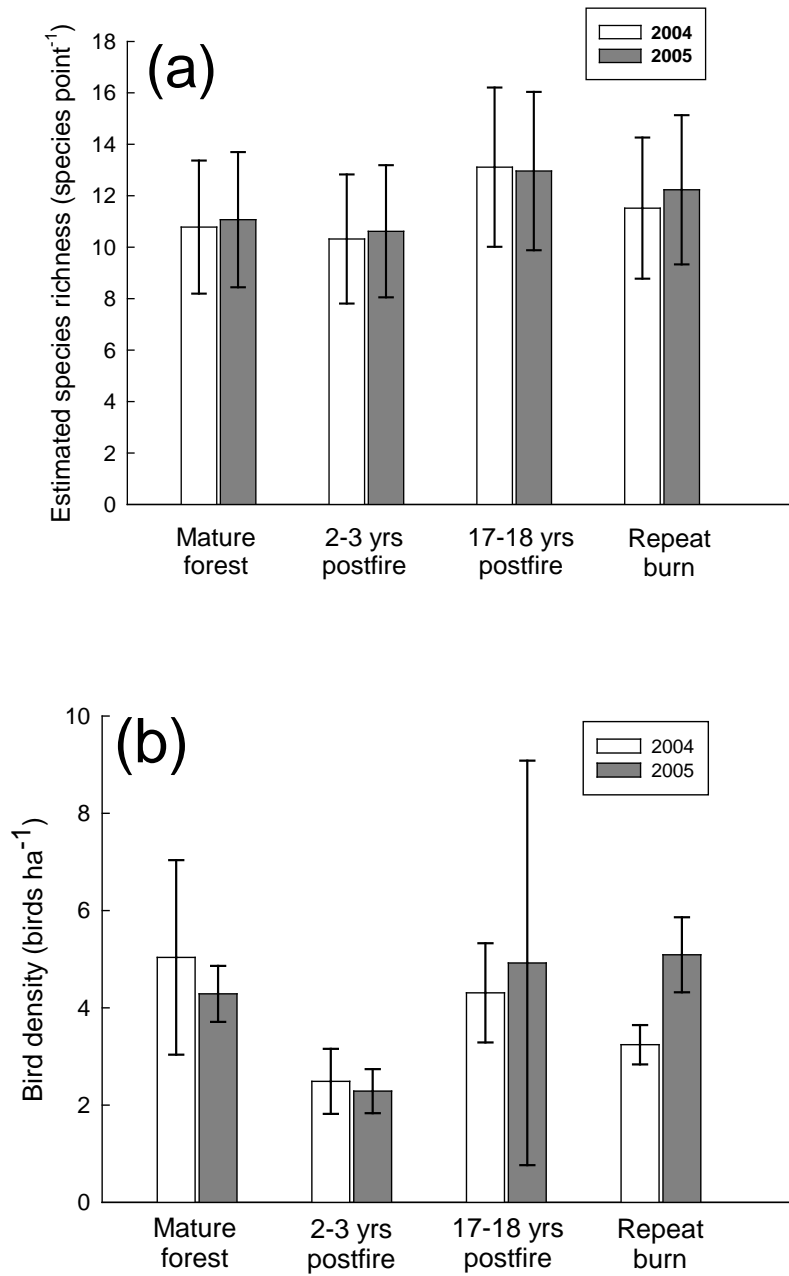
Fig. 2.

Fig. 3.

Fig. 4.