

# Avian community responses to post-fire forest structure: implications for fire management in mixed conifer forests

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## Keywords

avian community; forest fires; salvage logging; fire severity; post-fire management; hierarchical modeling; biodiversity; forest management.

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## Abstract

Fire is a natural process and the dominant disturbance shaping plant and animal communities in many coniferous forests of the western US. Given that fire size and severity are predicted to increase in the future, it has become increasingly important to understand how wildlife responds to fire and post-fire management. The Angora Fire burned 1243 hectares of mixed conifer forest in South Lake Tahoe, California. We conducted avian point counts for the first 3 years following the fire in burned and unburned areas to investigate which habitat characteristics are most important for re-establishing or maintaining the native avian community in post-fire landscapes. We used a multi-species occurrence model to estimate how avian species are influenced by the density of live and dead trees and shrub cover. While accounting for variations in the detectability of species, our approach estimated the occurrence probabilities of all species detected including those that were rare or observed infrequently. Although all species encountered in this study were detected in burned areas, species-specific modeling results predicted that some species were strongly associated with specific post-fire conditions, such as a high density of dead trees, open-canopy conditions or high levels of shrub cover that occur at particular burn severities or at a particular time following fire. These results indicate that prescribed fire or managed wildfire which burns at low to moderate severity without at least some high-severity effects is both unlikely to result in the species assemblages that are unique to post-fire areas or to provide habitat for burn specialists. Additionally, the probability of occurrence for many species was associated with high levels of standing dead trees indicating that intensive post-fire harvest of these structures could negatively impact habitat of a considerable proportion of the avian community.

## Introduction

Fire is a natural disturbance in the dry coniferous forests of the western US where variability in fire severity and frequency creates heterogeneous habitat across the landscape (Agee, 1993). Low-severity fires reduce understory vegetation and only kill the most susceptible trees, while high-severity fires (i.e. stand-replacing fires) result in high tree mortality and remove most of the vegetation in the mid- and understory, thus drastically modifying the existing habitat. These modifications to forest structure and composition consequently affect wildlife communities (Brown & Smith, 2000). While some species may respond favorably to vegeta-

tion conditions resulting from low-severity fire, other species may rely on conditions created only by high-severity fires (Hutto, 1995; Smucker, Hutto & Steele, 2005). However, generalizations of species responses to fire and fire severity, even within fire-adapted ecosystems, can be challenging because of past forest management practices, vegetation responses to fire caused by climatic conditions and adaptations (e.g. resprouting, serotiny), species community composition and natural disturbance regimes (Rost *et al.*, 2012).

In fire-suppressed forests in the western US, changes in climate and forest structure have resulted in an increase in the size and frequency of high-severity stand-replacing fires (Miller *et al.*, 2009; Collins *et al.*, 2010). These fires leave

large areas of standing dead trees (snags), which may contribute fuel to future fires and pose a risk to human life or property when they fall (Brown, Reinhardt & Kramer, 2003; Metz *et al.*, 2011). In many areas, removal of dead and dying trees (salvage logging) is conducted to reduce these risks and to realize economic benefits. However, snags and coarse woody debris are valuable for many wildlife species, as they provide critical and often limited post-fire habitat for breeding, foraging and denning (Kotliar *et al.*, 2002; Morissette *et al.*, 2002). The treatment of dead and dying trees is one of the most immediate and controversial issues surrounding post-fire forest management (Beschta *et al.*, 2004; Donato *et al.*, 2006; Hutto, 2006).

The value of dead and dying trees to cavity-nesting birds in recently burned forests is well-documented (Raphael & White, 1984; Saab & Powell, 2005; Saab, Russell & Dudley, 2007). Concerns over the dependence on burned forests of one of these species, the black-backed woodpecker (*Picoides arcticus*), has fueled much of the debate surrounding salvage logging (Saab & Dudley, 1998; Saab *et al.*, 2007). The black-backed woodpecker tends to nest in areas with dense stands of snags in recently burned forests and nest densities decrease significantly in salvage logged areas (Saab & Dudley, 1998). However, other species that prefer open-habitat conditions indicative of early successional forest may actually benefit from the removal of standing dead trees (Rost *et al.*, 2012). Therefore, not only understanding the impact of salvage logging, but also the densities of live and dead trees needed to support a range of species is important in the management of post-fire landscapes, particularly with the increased frequency, size and intensity of fires predicted in western dry forests.

We used a multi-species occurrence model to understand how differences in live and dead tree densities and shrub cover influence the occurrence probability of bird species in the Angora wildfire that burned approximately 1243 hectares near South Lake Tahoe, California in June and July 2007. Although many studies have been conducted on the impacts of fire on wildlife species and habitat, particularly on birds in frequent-fire forests (Kalies, Chambers & Covington, 2010; Fontaine & Kennedy, 2012; Pastro, Dickman & Letnic, 2014), this study builds on previous work by directly modeling species responses to post-fire habitat structure, while accounting for variability in the probability of detecting different species. In addition, by using a hierarchical Bayesian approach, we were able to make inferences about responses by a broad spectrum of species, including those that were rare or less frequently detected (Russell *et al.*, 2009; Zipkin, Dewan & Royle, 2009; White *et al.*, 2013). The objective of this study was to elucidate the complex relationship between fire severity, forest conditions and individual species to inform post-fire management decisions in support of wildlife. Additionally, because these models were based on covariates related to post-fire forest structure, implications about the impact of salvage logging were indirectly inferred and the uncertainty in these relationships quantified. Largely due to public concerns related to wildlife habitat, logging of dead and dying

trees was limited to urban lots and along roads and trails until a record of decision could be reached in July 2010 (after completion of this study). Although salvage logging causes an additional disturbance that we are unable to incorporate in our model, we present data on the range of dead tree densities needed to support the avian community within the fire area.

## Materials and methods

### Data collection

The 2007 Angora Fire occurred within the southern portion of Lake Tahoe basin located in the central Sierra Nevada (38°53'8"N, 120°2'24"W). Much of the basin is dominated by dense, even-aged coniferous forest as a result of intensive logging during the late 19th and early 20th centuries and subsequent fire suppression. Common tree species in the Angora Fire were Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*) and lodgepole pine (*P. contorta*). Whitethorn ceanothus (*Ceanothus cordulatus*), a shrub; and spreading groundsmoke (*Gayophytum diffusum*), a forb, were the most common post-fire ground cover. For a full description of the study site and details of the fire, see Safford *et al.*, 2009.

Sample sites were selected to represent a range of post-fire conditions. A systematic grid of points spaced 400 m apart within the fire perimeter was established as part of a companion study to monitor post-fire vegetation response (Safford *et al.*, 2009). From this grid, a selection of sampling points ( $n = 70$ ) was chosen across fire severity classes based on satellite-derived measures of fire severity [Relative differenced Normalized Burn Ratio (RdNBR) calibrated to canopy cover mortality; Miller *et al.* 2009]. Because the majority of the fire burned at high severity (i.e. high tree mortality), we established additional points ( $n = 26$ ) outside and within the fire perimeter to provide a wider range of ecological conditions, including unburned areas.

Avian point counts surveys were conducted at 40 core sites in all sample years (2008–2010). An additional 26 sites were surveyed in 2009 only and an additional 29 sites in 2010 only. Birds were surveyed at a single point count station located at each site center. Counts were 10 min in duration, recording all individuals seen or heard within 100 m. Surveys were conducted during the first 4 h of daylight on days with suitable weather conditions. Three counts were conducted at each site in the month of June with a minimum of 3 days separating each visit. Observers were rotated through the sites to ensure that each site was visited by at least two different observers over the three visits per year to reduce observer bias. By conducting multiple surveys at each site, we could use modeling techniques that formally differentiate between the detection of an individual species at a survey site and the probability of occurrence of the species at the site.

We measured woody vegetation structure at each site during the year(s) in which bird surveys were conducted; for sites where surveys were conducted across years, we used the average site-specific values in our analysis (Table 1). Density

**Table 1** Mean and standard deviation in the number of live trees and snags per hectare and the percent cover of shrub in different burn severity classes (low severity: 1–20%; moderate severity: 21–70%; high severity: > 70% tree mortality)

Burn severity	Sites	Trees/HA	Snags/HA	% Shrub cover
Unburned	24	232.5 ± 151.7	26.4 ± 54.21	3.8 ± 9.4
Low	7	129.1 ± 55.0	42.7 ± 60.9	2.6 ± 3.0
Moderate	28	111.7 ± 77.6	49.8 ± 57.7	2.1 ± 6.0
High	37	10.6 ± 28.4	138.5 ± 125.4	1.2 ± 2.2
All	96	104.2 ± 124.1	77.6 ± 101.4	2.2 ± 6.0

Burn severity was based on the relative differenced normalized burn ratio (RdNBR).

of live trees and snags and ocular estimates of the percent cover of shrubs were characterized in 0.08-ha plots. All trees were identified to species and measured at diameter at breast height (DBH). However, there was little variation in DBH, thus we only used live tree and snag densities in our models. The fire burned at the intersection of urban development and public and private forest; therefore, we classified sites as located in either an urbanized area or in undeveloped forest. Based on (Manley *et al.*, 2009), areas were considered urban if > 20% of the area within a 100-m radius of the survey station consisted of impervious surfaces. Although landscape attributes such as patch size, configuration and proximity to unburned habitat are undoubtedly important variables in predicting responses to fire (Halofsky *et al.*, 2011), the relatively small size and linear configuration of the Angora Fire resulted in low variability in these metrics and thus they were not considered here (see also Tarbill, Manley & White, 2015).

## Data analysis

Species-specific occurrence probabilities and responses to post-fire vegetation were estimated using a multi-species modeling framework (Dorazio & Royle, 2005; Dorazio *et al.*, 2006). This approach combines individual species occurrence models in a single hierarchical model by assuming that species covariate effects come from a single distribution. This assumption provides more precise estimates for the less commonly occurring species in the community that are not feasible using single-species methods (Zipkin *et al.*, 2009; White *et al.*, 2013).

Site-specific occurrence for species *i* at site *j* denoted  $z_{ij}$  was 1 if the species occurred at the site, and 0 otherwise. This occupancy state was modeled as a Bernoulli process, whereby  $z_{ij} \sim \text{Bernoulli}(\psi_{ij})$  and  $\psi_{ij}$  was the probability that site *j* was occupied by species *i*. At sites where a species was not detected during a visit, the true value of  $z_{ij}$  is not known with certainty. Repeated sampling at a site allowed us to account for imperfect species detection by estimating  $\psi_{ij}$  with the observation data  $y_{i,j,k}$ . The observation process was characterized as  $y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} * z_{ij})$  where  $p_{i,j,k}$  was the detection probability of species *i* at site *j* during sampling period *k*.

We modeled the occurrence probability for each species *i* at location *j* as a function of the covariates we predicted would influence species occurrence using the logit link function such that  $\text{logit}(\psi_{i,j,t}) = \alpha 0_{i,t} + \alpha 1_i \text{snag density}_j + \alpha 2_i \text{live tree density}_j + \alpha 3_i \text{shrub cover}_j + \alpha 4_i \text{urbanization}_j$ . Although a species' response to the effects of fire may be intensified or mediated by time (Smucker *et al.*, 2005; Fontaine *et al.*, 2009), we treated sampling year as categorical covariate (i.e. allowing for independent intercepts in occupancy across years) in our model because of the relatively short post-fire timeframe considered. In our model, sampling year *t* was specified as a categorical effect on the species-specific intercept.  $\alpha 1_i - \alpha 4_i$  were the species-specific logit-linear coefficients for the model covariates. We allowed detection probability to vary by species and year by modeling the detection probability as  $\text{logit}(p_{i,j,t}) = b 0_{i,t}$ . Although habitat covariates (i.e. live tree density or shrub cover) may also influence the probability of detection, we were primarily interested in how these variables influenced occurrence. Our model consisted of 10 parameters for each species including year-specific intercepts on occurrence and detection and four habitat covariate effects. All covariates were standardized so that the means of all covariates were equal to zero.

For several species, the number of detections was low and species-specific parameters could not be estimated using an individual species approach. To make inferences about the effects of covariates on all species in the community, we included an additional hierarchical component in the model that treats species-level parameters as random effects, each governed by community-level hyper-parameters. We assumed that each species-specific coefficient came from a normal distribution with a common mean and precision (the reciprocal of the variance) across all species (i.e. the hyper-parameter). Therefore, for each covariate:

$$\alpha_{li} \sim \text{Normal}(\mu_l, \tau_l); \text{ where } \tau_l \text{ is equal to } 1/\sigma_l^2$$

This model was implemented using a Bayesian analysis with Markov chain Monte Carlo (MCMC) in programs R version 2.15.2 (Team, 2014) and JAGS (Plummer, 2003). We specified vague priors (i.e. a prior distribution with a similar probability over a large range of possible parameter values) for each hyper-parameter to estimate individual model parameters and community-level summaries. We ran three parallel chains for 10 000 iterations after a burn-in of 2000 iterations and saved every 10th iteration to reduce correlation between values. To assess chain convergence, we calculated the R-hat statistic (Gelman & Hill, 2007), which evaluates within and between chain variance. R-hat values were less than 1.1 for all parameters indicating model convergence (Gelman & Hill, 2007). We considered an effect of a covariate to be significant if the Bayesian credible interval of the coefficient (BCI; defined as the 2.5% and 97.5% quantiles of the posterior distribution) did not overlap zero. We used occurrence probabilities for each species to generate occurrences ( $z_{ij}$ ) with Bernoulli trials (0 = absent, 1 = present). We then summed across these trials (in this

case 3000 values of 0 or 1) to generate species richness at each site and under specific habitat covariate combinations.

## Results

Sixty-four species were observed across the 3-year study period. In 2008, 807 detections of 54 bird species were recorded across 40 sites. In 2009, 1518 detections of 64 species were recorded across 66 survey locations. In 2010, 1453 detections of 56 species were recorded across the 69 sites surveyed. Of the species observed in more than 5% ( $\geq 9$  detections) of the surveys, all were observed in burned areas, although Cassin's vireo (scientific names for all detected species are listed in Supporting Information Appendix S1) was not recorded at any of the survey sites classified as high severity. In contrast, western bluebirds and lazuli buntings were not observed at any unburned survey sites.

The density of snags, live trees and shrubs not only varied across the survey plots, but varied substantially within satellite-derived fire severity classes (Table 1) commonly used to predict wildlife response (e.g. Smucker *et al.*, 2005; Kotliar, Kennedy & Ferree, 2007; Dickson *et al.*, 2009). Despite the variability within and among severity classes, post-fire conditions indicated that the number of live trees and the percent shrub cover initially decreased with fire severity, whereas the number of snags increased with fire severity.

Snag and live tree densities had the greatest influence on the bird community and the probability of occurrence for most species was more strongly linked to the change in the densities of live trees and snags than to the observed variability in percent shrub cover (Supporting Information Appendix S1). Snag density was positively associated with the probability of occurrence of 39 species (Supporting Information Appendix S1). Of these 39 species, estimates for black-backed woodpecker, brown creeper, hairy woodpecker, hermit thrush, house wren, mountain bluebird, olive-sided flycatcher and Townsend's solitaire were significant (i.e. the 95% credible interval for the estimate did not overlap zero). Of the 25 species negatively associated with snag density, the probability of occurrence for Brewer's blackbird, European starling, mourning dove, red-winged blackbird and Steller's jay was significant. Forty-one species were positively associated with live tree density, of which estimates for 14 species were significant (Supporting Information Appendix S1). The probability of occurrence for 23 species was negatively associated with tree density, of which seven species were significant. Parameter estimates for seven species were significantly associated with shrub cover (five positively, two negatively). The fox sparrow was the only of these seven species in which occurrence was more strongly associated with shrub cover than either live tree or snag densities.

Covariate estimates for individual bird species in relation to live tree and snag densities showed strong affiliations for a large number of species (Fig. 1). Covariate estimates for eight bird species were strongly associated with sites with high snag density and few live trees, conditions typical of

high-severity fire. Most of the species associated with high snag densities were cavity nesters that utilize snags as nesting sites. We also found several species that were associated with both low live tree density and low snag density. At the extreme end of this gradient were Brewer's blackbird, European starling, lesser goldfinch and white-crowned sparrow, typically non-forest associates that are likely to be responding to the ephemeral open-habitat conditions created by fire. At the other end of the spectrum, there were six bird species that were strongly associated with high tree density and low snag density, representing primarily low-severity burned or unburned forest conditions.

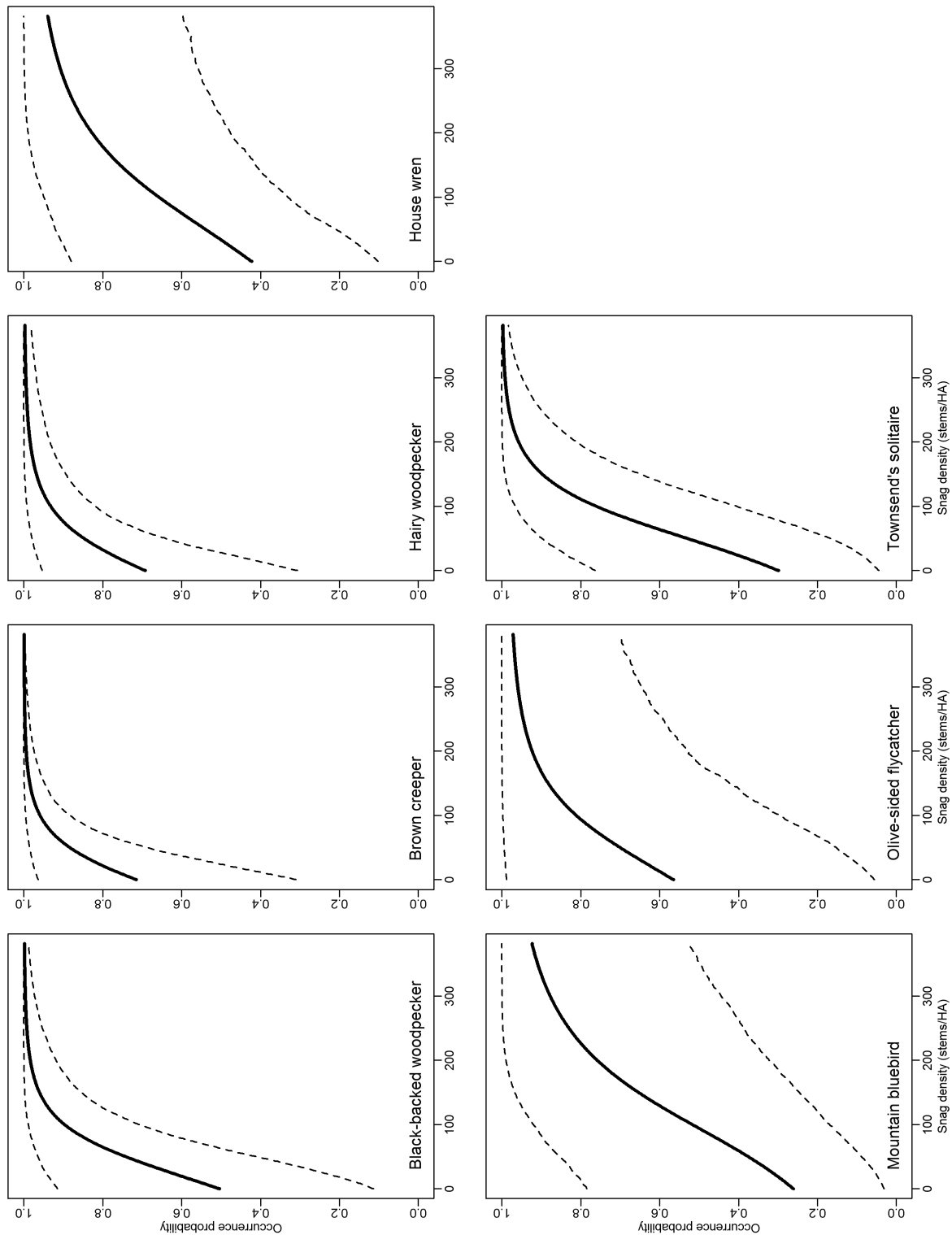
To make inferences about the potential impact of snag removal on species evaluated in our model, we investigated the influence of decreasing snag densities on the probability of occurrence for species for which this variable was predicted to have a significant positive effect. Confidence in our estimates varied, but the probability of occurrence for several species including the black-backed woodpecker and brown creeper, decreased markedly at particular levels of snag densities (Fig. 2). Of the species whose occurrence was positively associated with snag density, the house wren, mountain bluebird and Townsend's solitaire were also identified as species that were found in a narrower range of post-fire habitat conditions (Fig. 1).

Year since fire did not markedly influence the probability of individual species' occurrences (Supporting Information Appendix S1). Based on Bernoulli trials, only three species varied with time since fire: dusky flycatchers were significantly more widely distributed in year 2 than year 1; whereas European starlings and evening grosbeaks were more widely distributed in year 3 than year 1 (grosbeaks) or year 2 (starlings). In contrast, species richness appeared to be affected by both habitat components and time since fire (Fig. 3). Individual species' responses to snag and live tree densities influenced the number of species predicted, with highest species richness in areas with high tree densities and also in areas with low live tree and low snag densities. Variation in species richness in response to different densities of snags and live trees appeared to be greatest in the first year after the fire and decreased in subsequent years (Fig. 3).

Although we were not specifically interested in the response of species to urbanization, we included it as a covariate in the model as it is associated with a decreased probability of occurrence for many species (Schlesinger, Manley & Holyoak, 2008; White *et al.*, 2013). Of all the response variables in the model, urbanization had the most consistent effect and was negatively associated with the occurrence of 84% of species (Supporting Information Appendix S1). This response was significantly negative for the black-backed woodpecker, mountain bluebird and mountain chickadee.

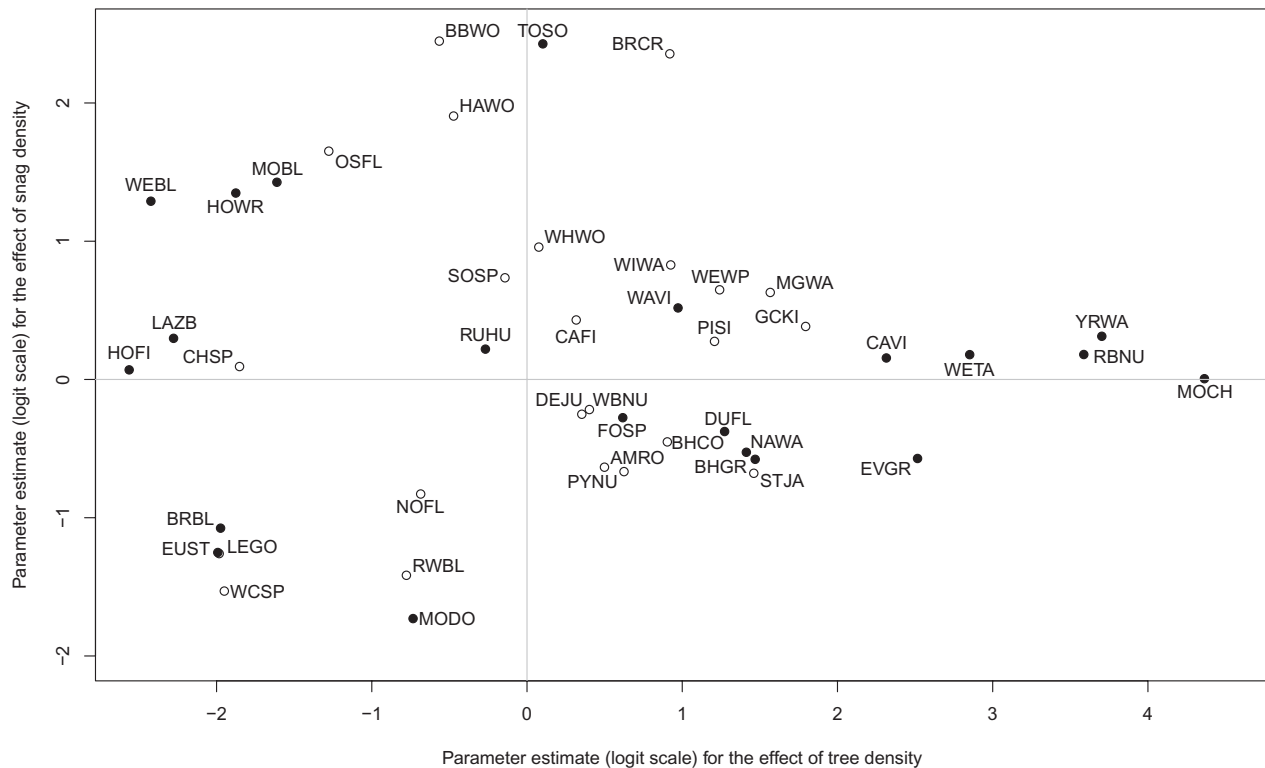
## Discussion

Fire can greatly modify forest structure and resource availability, particularly at high burn severities. Over time, fires

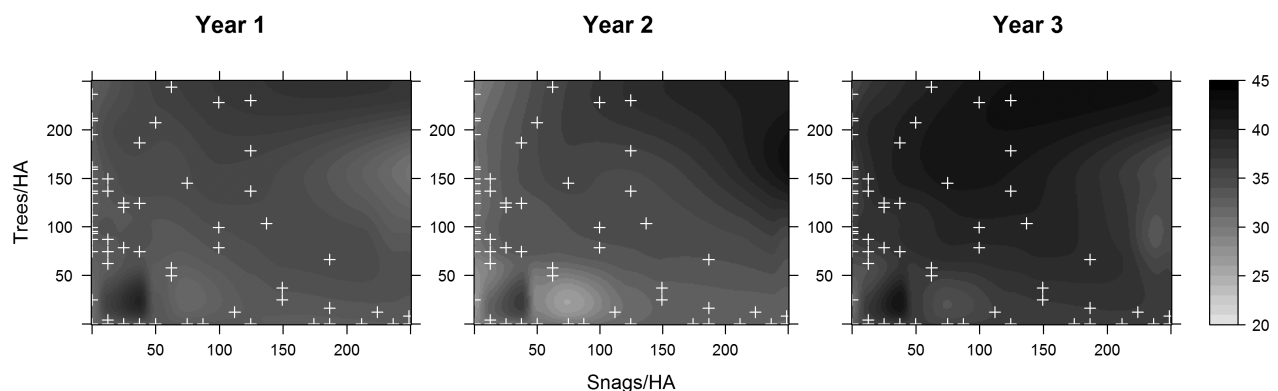


**Figure 1** The predicted mean change in a species' probability of occurrence as a function of snag density. Species with a significant positive relationship with snag densities are shown. Posterior credible intervals are indicated with dashed lines.





**Figure 2** Parameter estimates of tree and snag densities for each avian species in our study. We used these parameter estimates to predict the probability of occurrence for each species based on mean covariate values calculated for each fire severity category (Table 1). Filled circles denote species with changes in probability of occurrence of  $\geq 30\%$  across fire severity categories (see Appendix S1 for AOU codes).



**Figure 3** Predicted species richness as a function of live tree and snag densities in each year of the study. Species richness (gray-black gradient) at each site (white cross) was calculated using species-specific occurrence probabilities to generate presence/absence data from Bernoulli trials (see Methods). Species richness between sites was extrapolated using local polynomial regression fitting.

create areas with high densities of snags, an open canopy, and high shrub and herbaceous ground cover that provide important nesting and foraging habitat for many bird species. Many avian species respond positively to fire (Smucker *et al.*, 2005; Dickson *et al.*, 2009; Russell *et al.*, 2009; Bagne & Purcell, 2011) and some species even appear to be largely restricted to severely burned areas (Hutto, 1995; Kotliar *et al.*, 2002). In general, our results are

consistent with previous research however, by directly modeling species' occurrences based on structural components of the forest that are impacted by fire, we were able to make stronger inferences on how the effects of fire influence avian communities. Our results indicate that many species may be responding neutrally to fire because they are less restricted in their use of forest structural elements and are flexible in their preferences for live tree and snag densities

and ground cover. In contrast, species whose occurrences are more strongly associated with snag and live tree density are predicted to respond more strongly to specific post-fire habitat conditions. This issue is not only pertinent to managers tasked with decisions regarding post-fire management options such as the removal of snags, but improves our understanding of how fire-induced heterogeneity maintains biodiversity.

Wildfires can create habitat heterogeneity, resulting in unique assemblages and high species diversity (Smucker *et al.*, 2005; Saab *et al.*, 2007). Although all species encountered in this study utilized burned areas, several species such as Cassin's vireo, evening grosbeak, red-breasted nuthatch, western tanager and yellow-rumped warbler, were more likely to occur in areas with high densities of live trees. Previous studies have found that these species may respond positively, neutrally or negatively to fire (see Bagne & Purcell, 2011). Based on these studies and our analysis, we suggest that these species can tolerate, and possibly benefit from surface fires provided that the resulting habitat retains a high density of live trees. The probability of occurrence for other species, such as brown creeper and dusky flycatcher were associated with both higher shrub cover and density of live trees, indicating that these species may benefit from mixed/moderate severity fire, particularly in fire-suppressed forests that lack shrubs. In contrast, several species were strongly associated with higher densities of snags and may only benefit from fire when it results in high tree mortality (i.e. stand-replacing fires). The probability of occurrence for the majority of these snag-associated species was also negatively associated with live tree densities, with the exception of the brown creeper, which was positively associated with live trees and may therefore be observed in smaller patches or on edges of stand-replacing fires.

Within the post-fire habitat in our study area, the predicted probability of occurrence of several species rapidly declined when snag densities decreased below 100–150 stems/ha. This included several species that are considered burn specialists, such as black-backed woodpecker and mountain bluebird, as well as other species that exploit the ephemeral increase in prey and nest habitat, such as olive-sided flycatcher and Townsend's solitaire. Post-fire management often includes the removal of snags and other biomass from burned areas (Lindenmayer & Noss, 2006) with approximately 10–15 large snags per hectare retained for wildlife use in the Sierra Nevada. Prescriptions that remove most snags and coarse woody debris result in homogenized habitat with reduced foraging and nesting substrates, thereby degrading the features that make burned habitat unique (Hutto, 1995, 2006; Saab & Dudley, 1998; Russell, Saab & Dudley, 2007; Saab *et al.*, 2007; Saab, Russell & Dudley, 2009). At the landscape scale, prescriptions that leave some high-density stands of dead trees may better serve strongly snag-associated species such as black-backed woodpecker, mountain bluebird and olive-sided flycatcher than prescriptions that reduce snag density by evenly thinning all stands. Our data suggest that these residual stands in Sierra mixed conifer should contain at least 100–150 dead

or dying trees/ha; however, we have provided a possible methodology for managers in other forest types wishing to conserve snag-dependent species. The ideal extent and configuration of these patches needs to be addressed in further research.

By modeling species associations to snag densities, we were able to identify species that would be negatively impacted by the removal of dead or dying trees, an effect that may be compounded by other disturbance-related impacts. Our study did not address disturbance-related effects of salvage logging on the avian community. In addition to the removal of biomass, logging operations may also create immediate and long-term disturbance through the erosion and compaction of soils, noise and air pollution, and the creation of roads that may increase habitat fragmentation or nest predation or parasitism (Lindenmayer & Noss, 2006). These impacts of snag removal in the urban interface may be reduced given that avian communities in urban areas are likely to be less speciose and many snag-dependent species, such as the black-backed woodpecker and mountain bluebird, tend to avoid urbanized areas. In addition, operations in the urban interface will remove trees that present the greatest risk to human life and property and represent the lowest cost to remove.

Post-fire habitats are dynamic and change over time as shade-intolerant shrubs and herbs respond to the open-canopy conditions, live trees succumb to fire-related injury, and snags break and fall (Raphael, Morrison & Yoder-Williams, 1987; Sugihara *et al.*, 2006; Fontaine *et al.*, 2009; Angers *et al.*, 2011). While species that are flexible in their use of forest structures will likely remain fairly constant over time in the burned area, we expect species that are strongly associated with particular post-fire features to blink in and out as forest succession results in dramatically different habitat over time. Our study suggests that species that are more closely associated with these habitat features were more likely to be affected by these successional changes. In the short term, we may observe black-backed and hairy woodpeckers moving to lower fire severity areas as highly burned areas suffer from higher snag attrition and new snags are recruited to low-severity burns via fire-related injury. In contrast, fox sparrows and other shrub-associated species may move into highly burned areas as shrub cover increases.

An integrated fire management strategy directed at creating patchy and variable fire severity will be important for maintaining avian communities and populations of fire-adapted bird species. Ideally, fire management plans would recognize the benefits of fire and early-seral conditions and allow some wildland fires to burn to obtain the resource benefits of dead wood, open canopy and shrub habitats (Swanson *et al.*, 2011). Further, prescribed fire is a valuable, if not essential, tool for landscape-scale forest management for long-term resilience. Creating and maintaining post-fire habitat heterogeneity is challenging under current forest conditions and policies (Beschta *et al.*, 2004; Stephens & Ruth, 2005; Stephens *et al.*, 2013). Although costly, the Angora Fire was relatively small compared with more recent

forest fires and those predicted under future climates (Westerling *et al.*, 2006). As fire perimeters become larger and burn at higher severities, we may find that species that can utilize, or benefit from, smaller scale high-severity burns are unable to persist within larger areas of severe burns.

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## Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Parameter estimates for the probability of occurrence for each species included in our model. Significant estimates in which the 95% posterior confidence interval does not overlap zero are in bold.