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Simulating avian species and foraging group responses to fuel reduction treatments in coniferous forests

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ABSTRACT

Over a century of fire suppression activities have altered the structure and composition of mixed conifer forests throughout the western United States. In the absence of fire, fuels have accumulated in these forests causing concerns over the potential for catastrophic wildfires. Fuel reduction treatments are being used on federal and state lands to reduce the threat of wildfire by mechanically removing biomass. Although these treatments result in a reduction in fire hazard, their impact on wildlife is less clear. We use a multi-species occupancy modeling approach to build habitat-suitability models for 46 upland forest birds found in the Lake Tahoe Basin in the Sierra Nevada based on forest structure and abiotic variables. Using a Bayesian hierarchical framework, we predict species-specific and community-level responses to changes in forest structure and make inferences about responses of important avian foraging guilds. Disparities within and among foraging group responses to canopy cover, tree size and shrub cover emphasized the complexities in managing forests to meet biodiversity goals. Based on our species-specific model results, we predicted changes in species richness and community similarity under forest prescriptions representing three management practices: no active management, a typical fuel reduction treatment that emphasizes spacing between trees, and a thinning prescription that creates structural heterogeneity. Simulated changes to structural components of the forest analogous to management practices to reduce fuel loads clearly affected foraging groups differentially despite variability in responses within guilds. Although species richness was predicted to decrease slightly under both simulated fuels reduction treatments, the prescription that incorporated structural heterogeneity retained marginally higher species richness. The composition of communities supported by different management alternatives was influenced by urbanization and management practice, emphasizing the importance of creating heterogeneity at the landscape scale.

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1. Introduction

The mixed-conifer forests of the Sierra Nevada have undergone substantial change in structure and composition due to over a century of fire suppression (Agee, 1993). Historically described as clusters of trees separated by large open-gap conditions, these fire-dependent systems have been replaced with dense, closed-canopy forests lacking the structural heterogeneity of their past (Barbour et al., 2002; Beaty and Taylor, 2007; North et al., 2007). The accumulation of fuels in these forests and their proximity to urban development has increased our awareness of the risks and costs associated with catastrophic wildfires (Dombeck et al., 2004), particularly in the face of climate change (Westerling et al., 2006). Surface fires that once would have burned at low to moderate severity now have the ability to spread rapidly and with high severity through the forest canopy. The consequence of this alteration to the fire regime has led to a more proactive approach to managing forests through fuel reduction treatments (e.g. Healthy Forest Restoration Act, 2003). Fuel reduction treatments are forest thinning efforts that aim to reduce fire hazard by decreasing surface fuels, removing mid- and understory vegetation (i.e. "ladder fuels") and opening the forest canopy (Agee and Skinner, 2005).

While fuel reduction treatments have been shown to reduce the risk of high-severity wildfires (Stephens and Moghaddas , 2005; Safford et al., 2009; Stephens et al., 2009), concerns about the incompatibility of fire hazard reduction and the needs of wildlife often lead to opposition in applying treatments in fire-suppressed

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forests (Stephens and Ruth, 2005; Collins et al., 2010; North et al., 2012). These concerns have made it challenging to assess the consequences of fuel reduction experimentally on wildlife as proposed treatments are often delayed, modified or not implemented. In attempts to balance potential trade-offs in these resource values, there has been increasing interest in designing silvicultural prescriptions that not only reduce fire hazard, but also increase forest resiliency and improve habitat conditions for wildlife (Carey, 2003; Verschuyl et al., 2008, 2011; North et al., 2009). Current silvicultural strategies that emphasize reducing ladder fuels and canopy closure result in homogenization of the forest stand (Dellasala et al., 2004; Westerling et al., 2006; North et al., 2009). For instance, forest thinning treatments failed to reconstruct historical forest composition, tree spacing, or past variation in tree size in a study conducted in a mixed-conifer forest of the Sierra (North et al., 2007). Consequently, fuel reduction prescriptions that include increasing forest structural heterogeneity are more likely to replicate historic forests and meet forest management goals targeted at conserving biological diversity (North et al., 2009). However, prescriptions that attempt to retain forest heterogeneity are only now starting to be implemented in Sierran mixed conifer forests. Whether these treatments improve wildlife habitat is untested and complicated by ill-defined biodiversity goals (North et al., 2012). For instance, an assessment of management actions that are intended to improve wildlife habitat could result in different conclusions depending on whether biodiversity targets are focused on a few ecologically important species, species richness, or species composition.

Many studies on the responses of wildlife to fuel reduction treatments thus far have focused on forest management in the wildlands, with less attention paid to treatments in more developed or urbanized areas (Noss et al., 2006; Kennedy and Fontaine, 2009). Urbanization may modify wildlife responses to forest treatments. As a stressor, urbanization may decrease habitat suitability for some species and the additive effects of fuel reduction treatments may further marginalize available habitat. Research has repeatedly demonstrated the impact that urbanization can have on ecological communities, with human activity, habitat loss and fragmentation, resulting in a reduction in species richness and changes in community composition (McKinney, 2002; Lepczyk et al., 2008; Schlesinger et al., 2008). Therefore, a species' response to urbanization may overshadow its response to fuel reduction treatments. Given that fuel reduction treatments are costly and may need to be repeated periodically to retain their fire-resistant properties (Collins et al., 2011; Stephens et al., 2012), the vast majority of fuel reductions will likely be targeted at the wildland–urban interface (Dombeck et al., 2004). When attempting to assess the impact of fuel treatments on biodiversity it is important to consider the level of urbanization and its combined impact on species responses.

Human impacts on avian diversity and abundance has led to a substantial loss in bird populations globally (Gaston et al., 2003; Jetz et al., 2007; Hoffmann et al., 2010). Birds are a primary conservation concern as they perform a diverse array of ecosystem services, including the control of invertebrate and vertebrate pest populations, pollination, seed dispersal, and nutrient cycling (Şekercioğlu et al., 2004; Şekercioğlu, 2006). Understanding how forest management practices may impact species occurrence, richness and community composition of forest-associated avian species is crucial to the effective management and conservation of these ecosystem services.

To predict the effects of fuel reduction treatments on avian biological diversity, we investigate how forest structure affects the probability of species occurrence in upland forested areas in the Sierra Nevada. Our objectives are to (1) determine if there is consistency in responses to structural components of the forest within

and among foraging guilds, (2) use estimates of species occurrence probabilities based on forest structure to predict and compare avian biodiversity under three simulated forest management scenarios: a fire-suppressed forest lacking management intervention, a standard fuel reduction prescription that removes ladder fuels and increases tree spacing, and a prescription where structural heterogeneity in the remaining forest is retained or increased while biomass is removed; and (3) determine if avian responses to these management practices are influenced by placement of the hypothetical treatment in an urbanized area, where fuel reduction treatments are often focused, and in areas without urbanization (i.e. wildlands).

2. Methods

2.1. Survey data and community occurrence model

The data used in this study were collected in the upland forests of the Lake Tahoe Basin, in the states of California and Nevada, USA. The elevation gradient within the basin (1900–3400 m) supports Jeffrey pine (*Pinus jeffreyi*), mixed-conifer, white fir (*Abies concolor*), red fir (*A. magnifica*), and lodgepole pine (*Pinus contorta*) forest types. Other common tree species include incense-cedar (*Calocedrus decurrens*) and sugar pine (*Pinus lambertiana*). Mean annual precipitation is 150 cm, falling primarily as snow between December and March and varying with elevation and latitude. Several distinctive institutional and ecological factors influence fuel reduction treatments within the Basin. The preservation of Lake Tahoe, an ultra-oligotrophic lake that is the centerpiece of the basin, complicates forest management practices as treatments to reduce fuel loads can mobilize sediment and nutrients and impact the clarity of the lake (Miller et al., 2010). Forest structure surrounding the lake has been dramatically altered by past practices including logging, grazing and suppression of natural fires. Approximately 67% of Basin forests were clear-cut during the last third of the 19th century with less intensive harvesting continuing into the 20th century for residential and recreational purposes (Lindström, 2000). Fuel reduction treatment costs are dramatically higher here than elsewhere in the Western US for a variety of reasons. Additionally, because the wildland–urban interface is extensive and concerns over the risks of fire damage to person and property are high, nearly 75% of the lower montane zone is planned for treatment (Marlow, 2007).

The avian data were collected at 742 point count stations in forested areas of the Lake Tahoe Basin during May–July 2002 through 2005 during which all birds detected (seen or heard) in a 10-min period within 100 m of the sample location were counted. Point count stations were located on a mixture of state, federal and private lands and were selected to represent a range of urbanization classes and elevation zones across the basin. All point counts were separated by a minimum of 200 m. Sample points were visited between two and three times during the course of the breeding season with visits separated by approximately 1 week. Within a season, stations were visited by multiple observers to limit observer bias across study sites. Although stations were visited repeatedly within a season, each station in the study was visited during a single year only.

As birds are likely to use a larger area than the area in which they were detected, we used a 150-m radius to characterize habitat around each sampling point. This area (17.5 acres) corresponds to the average size of a commercial thinning treatment in the Tahoe Basin. All forest structure parameters were derived from a GIS vegetation layer (30 m × 30 m raster cell) based on IKONOS satellite imagery collected in 2002 (Dobrowski et al., 2006) and the average and standard deviation in variables were calculated within the

150-m radius from the point count station. From these data, we included several parameters related to forest structure: the mean and standard deviation in tree size (diameter at breast height), the mean and standard deviation in percent canopy cover, and mean percent shrub cover (Table 1). These parameters were selected to represent forest structure because(1) their values are used as guidelines in fuel reduction prescriptions and in fire models (Franklin et al., 2002) and (2) they have been altered by fire suppression (Beaty and Taylor, 2007; North et al., 2009). Additionally, these covariates have low correlation and they are metrics that are known to shape avian distributions (Erdelen, 1984; Verschuyl et al., 2008; White et al., 2013). We also incorporated three abiotic variables from remotely sensed databases that affect the probability of species occurrence in the Tahoe basin: percentage of urban development (percent value based on land use and road density; Manley et al., 2009), elevation and mean annual precipitation (cm/year; Daly et al., 2002). Although we were not specifically interested in the effects of the abiotic covariates, their incorporation in the model was important because each is estimated to have significant effects on a number of species in the area (Schlesinger et al., 2008; White et al., 2013).

To assess how forest treatments may affect bird communities, we used the community modeling approach in White et al. (2013). Multi-species models combine single species occurrence and detection models by assuming that species parameter estimates come from a common community (or group level) normal distribution (Dorazio and Royle, 2005; Dorazio et al., 2006; Zipkin et al., 2009). White et al. (2013) modeled the avian point count data using a hierarchical multi-species model where the probability of occurrence, $\psi_{i,j}$, for each species i at location j, was estimated using the logit link function and the following location-specific covariates: percent development, elevation (linear and squared terms), average annual precipitation (linear and squared terms), average diameter at breast height (DBH) of trees (linear and squared terms), the standard deviation of DBH of trees at the survey location (linear term), percent canopy cover (linear and squared terms), the standard deviation of forest canopy cover, and percent shrub cover (linear and squared terms). The replicate surveys, conducted within a relatively short time frame (1–2 weeks) at each sampling point, were used to generate species-specific detection probabilities. The repeated sampling protocol serves two goals. First, it increases the likelihood that a species that is present will be detected at least once at a given location. Second, it allows for the explicit estimation of a detection probability, based on relevant covariates (MacKenzie et al., 2002). To account for any potential biases that may have occurred during sampling, we included covariates on the date (linear and square terms) and year of the sampling occasion into our species-specific detection models.

In their model, White et al. (2013) assumed that each of the species-specific covariate estimates was drawn from a common, community level distribution (Dorazio et al., 2006). Because we were interested in the differences at the level of foraging groups, we modified this assumption and categorized each species into one of six foraging guilds (Appendix A). Avian species can be placed into a variety of guilds based on their use of environmental resources (Root, 1967). In this case, we were interested in predicting the responses of foraging assemblages because they are likely to respond similarly to changes in habitat and they also provide essential ecosystem services through their trophic interactions (O'Connell et al., 2000; Mäntylä et al., 2011). We categorized 46 species observed during sampling that could be easily placed into one of the following foraging guilds based on their diet and foraging substrate: air foragers, bark foragers, bark gleaners, foliage invertivores, ground invertivores and seed eaters (Appendix B). Species-specific occurrence and detection parameters were estimated using a Bayesian approach that assumed parameter estimates for each guild had their own distribution (Ruiz-Gutierrez et al., 2010). For example, a species that was classified as a bark forager would have its own occurrence model but parameter estimates (e.g., effect of development) for all bark foragers would be drawn from the same normal distribution from which the parameter for species i would be drawn (e.g., effect of development for all bark foragers $\sim N(\mu_{development\_bark}, \sigma_{development\_bark})$).

We estimated the parameters using Markov chain Monte Carlo (MCMC) implemented in the programs R and WinBUGS (Lunn et al., 2000) with flat priors for each of the group-level parameters. We ran three chains for 50,000 iterations with a burn in of 30,000 and thinned by 20. Due to the hierarchical structure of the model, the results produced both species-specific estimates of each covariate (as well as an intercept term) in addition to "hyper-parameter" estimates for each of the foraging groups (Dorazio and Royle 2005). In a Bayesian analysis, parameter estimates are assumed to be random variables. We capitalized on this framework by using the full posterior distribution (in this case, 3000 values) to make predictions about the effects of different forest treatment and thus quantify uncertainty in our system (Zipkin et al., 2012).

2.2. Predicting species responses to forest prescriptions

Our interest lies in predicting species and foraging group responses to an assemblage of structural attributes that characterize different forest restoration prescriptions. In particular, we were interested in comparing probabilities of occurrence for avian species/groups between three management alternatives that forest practitioners commonly face: taking no management action (fire-suppressed forest – FSF), thinning from below to reduce fire hazard (fuel reduction prescription – FRP) and thinning to restore forest heterogeneity and fire resilience (structural heterogeneity prescription - SHP). To define the suite of variables that would characterize our hypothetical management actions, we relied on several recent publications that summarize forest variables in areas subjected to treatments and the change in these variables due to a typical fuel reduction treatment in mixed conifer forests of California (e.g. Stephens and Moghaddas, 2005; North et al., 2007; Bigelow et al., 2011). As little data exist on the structure of a forest following a heterogeneous thin, we used values that represented the in-

Table 1
Covariate values used in occurrence model and for predictions. The first three columns show the values used for simulated treatments of fire-suppressed forest (FSF), typical fuel reduction prescription (FRP), structural heterogeneity prescription (SHP). The last five columns show the range of each covariate observed within our data.

Parameter	FSF	FRP	SHP	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Development (%)	0.30	0.30	0.30	0.00	0.00	0.60	9.68	7.84	79.10
DBH (cm)	40	55	50	37.81	52.59	56.07	56.66	59.59	76.42
DBH variance	10	5	7.5	0.00	1.22	2.50	2.80	3.98	12.14
Canopy cover (%)	65	40	30	2.08	32.34	39.52	39.67	47.22	73.93
Canopy variance	10	5	25	0.00	5.44	9.88	9.92	13.83	27.35
Shrub cover (%)	10	20	25	9.08	24.10	30.23	30.58	36.28	65.92

tent of the prescription (i.e. increased variance in tree size and placement; North et al., 2009; North, 2012) and were partially informed by historic forest variables for the Tahoe Basin that have been interpolated in several studies (Manley et al., 2000; Barbour et al., 2002; Taylor, 2004). All values chosen to define our hypothetical management options were within the range of data used in our original analysis and are presented in Table 1. Each management option was considered under conditions in which there was no development and in which there was high development (30%), holding precipitation and elevation at their mean values for all combinations. We did this because urban development levels have been shown to have significant impacts on the occurrence probabilities of many species in the region (Schlesinger et al., 2008; White et al., 2013).

We used each value of the posterior distribution for species (and group level) covariates (3000 values for each parameter) to create a distribution of predicted occurrence probabilities for each species in all six forest structure combinations (three management options: FSF, FRP, SHP by two development categories: no development and development). We compared the occurrence probability for each species under both hypothetical management prescriptions (FRP and SHP) to the occurrence probabilities in a fire-suppressed forest in both developed and undeveloped areas. We report the number of species in which a treatment was predicted to result in a 30% change in mean occurrence relative to a FSF as

this is a threshold value often used as a guideline for indicating that a species may be vulnerable (IUCN, 2001).

We then used the species-specific occurrence probabilities to generate occurrences (0 if absent, 1 if present) with Bernoulli trials, which gave us a distribution of presence/absence values (3000 values consisting of 0 or 1 values) for each species in each forest structure. To estimate group richness, we summed the total number (or number within a specific foraging group) of individuals that were predicted to be present for each trial, which similarly produced 3000 estimates of richness for each management alternative. Species composition between alternatives was compared using the similarity index (which ranges from 0 to 1) described in Dorazio and Royle (2005) where a value of 0 indicates no overlap between treatment combinations and a value of 1 indicates complete overlap in species.

3. Results

Differences in the magnitude and direction of mean covariate values for each group included in our model emphasized the importance of Tahoe Basin habitat gradients in structuring avian communities. However, there was substantial variation in group-level responses to most modeled covariates (Appendix C) Parameter estimates for bark foragers and seed eaters suggested
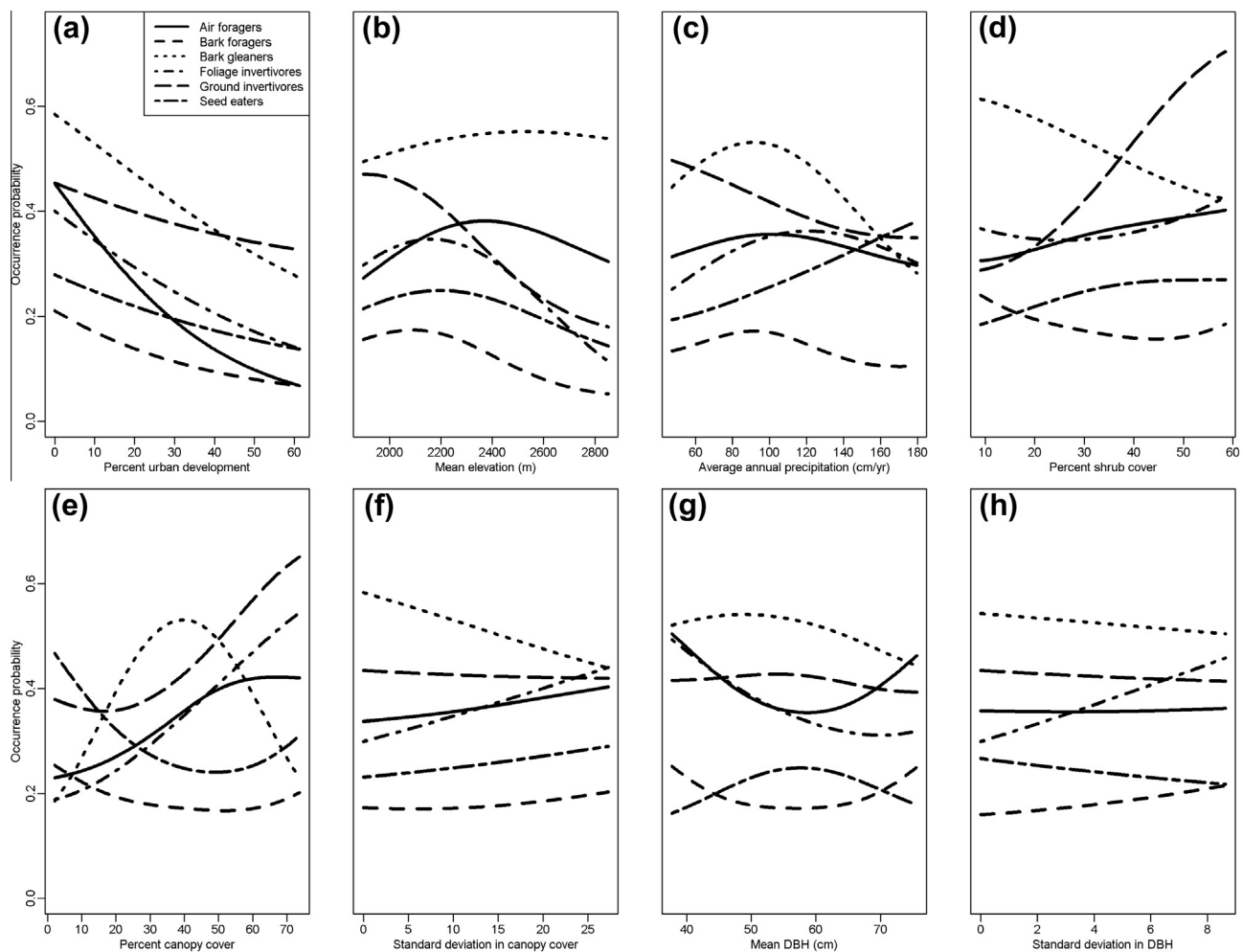

Fig. 1. Mean foraging group responses to modeled covariates: (a) percent urban development, (b) mean elevation, (c) average annual precipitation, (d) percent shrub cover, (e) percent canopy cover, (f) standard deviation in canopy cover, (g) mean DBH and (h) standard deviation in DBH on the group-level occurrence parameters for air foragers, bark foragers, bark gleaners, foliage invertivores, ground invertivores and seed eaters .

that the occurrence of these groups was more strongly associated with the range of variation in abiotic variables in the basin than the variables related to forest structure. The magnitude for the effect of percent urban development (one change in the standard deviation) on the occurrence probability was largest for all foraging groups with the exception of ground invertivores, underscoring the negative impact of urbanization on avifauna. The 95% posterior interval on the hyper-parameter estimate on the effect of development on air foragers and foliage invertivores did not overlap zero suggesting a consistently negative response by members of these groups to urbanization. (Appendix C).

The structural components of the forest had a substantial impact of the occurrence probabilities of the various foraging groups. In particular, increases in the percent of canopy cover tended to have large and opposing effects dependent on foraging group association (Fig. 1). For instance, increases across the range of canopy cover estimates observed in the basin were associated with at least a 20% increase in the occurrence probability of ground and foliage invertivores. Similarly, the occurrence probability for air foragers tended to increase with canopy cover, but this increase was only apparent at canopy cover values below 50%. In contrast, a strong quadratic response for bark gleaners indicated that this group preferred more moderate levels of canopy cover (30–50%), whereas the probability of seed eaters was positively associated with canopy cover values below 35%. The variation in canopy cover (as measured by the covariate SD cover) had a minimal impact on most groups, but was associated with a decreased probability of occurrence for bark gleaners. Increases in percent shrub cover tended to reduce the occurrence of bark gleaners, but had the opposite effect of forest invertivores. Variation in average tree size based on DBH measurements was less influential than canopy or shrub cover on the probability of occurrence of different foraging groups. However, changes in the occurrence probability of air and bark foragers suggest that members of these groups were associated with areas with forest stands containing either trees of small

average DBH or large average DBH. Foliage invertivores tended to be more likely to occur in areas with smaller average tree size, but also with greater variance in tree size.

3.1. Predicted responses to forest management alternatives

The number of species for which the occurrence probability was predicted to decline by ⩾30% following our simulated treatments was generally offset by a similar number of species that were predicted to benefit from the fuel reduction treatments (Fig. 2). The magnitude and direction of the change in the occurrence probability for individual species was modulated by both prescription type and urban development indicating that development was an important factor in predicting the impact of species responses to fuel reduction treatments (Appendix A). With the exception of *Pipilo maculatus* (Spotted towhee), all species whose predicted response was influenced by both development and treatment were predicted to have larger declines or smaller predicted increases in the probability of occurrence in developed areas. The occurrence probability for six species was not predicted to change by ⩾30% under any of the simulated forest treatments including *Myadestes townsendi* (Townsend's solitaire), *Picoides albolarvatus* (White-headed woodpecker), *Turdus migratorius* (American robin), *Junco hyemalis* (Dark-eyed junco), *Poecile gambeli* (Mountain chickadee) and *Dendroica coronata* (Yellow-rumped warbler), the latter four being some of the most commonly occurring species in the study area (Schlesinger et al., 2008; White et al., 2013).

Despite the indication that a number of species would benefit from a fuel reduction treatment in a fire-suppressed forest (Fig. 2), overall species richness (the number of species detected at a site) was predicted to decline slightly in areas where fuel reduction treatments were used to reduce fire hazard (Table 2). Although this change in species richness was minimal, even the loss of one native species would be undesirable from a socio-polit-

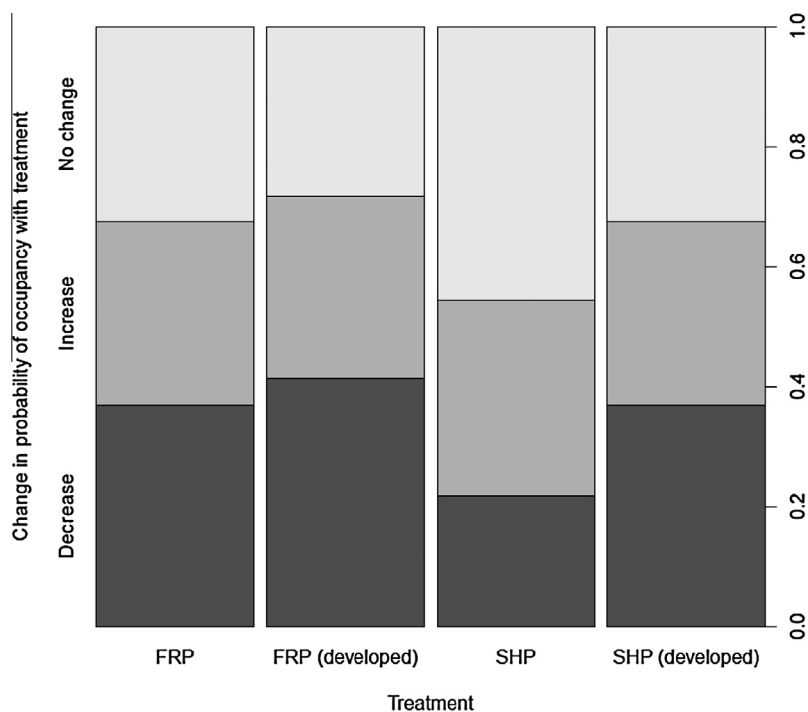**Fig. 2.** The proportion of species that are predicted to (1) decrease by >30% (dark gray), (2) increase by >30% (medium gray), and (3) remain the same (light gray) in occurrence probability under a typical fuel reduction prescription (FRP) and a structural heterogeneity prescription (SHP) relative to a fire suppressed forest in developed and undeveloped areas.

Table 2
Mean, standard deviation and posterior intervals in species richness for avian groups simulated under different forest management practices: fire-suppressed forest (FSF), typical fuel reduction prescription (FRP), structural heterogeneity prescription (SHP).

| Avian group	Undeveloped			Developed		
	FSF	FRP	SHP	FSF	FRP	SHP
All species (46)	21.11 ± 2.41 (16–26)	17.73 ± 2.62 (13–23)	19.18 ± 2.73 (14–25)	16.88 ± 2.47 (12–22)	13.47 ± 2.34 (9–18)	14.06 ± 2.60 (9–19)
Air foragers (5)	2.31 ± 0.98 (0–4)	2.31 ± 0.95 (1–4)	2.56 ± 0.91 (1–4)	1.04 ± 0.87 (0–3)	0.97 ± 0.84 (0–3)	1.26 ± 0.85 (0–3)
Bark foragers (5)	1.27 ± 0.90 (0–3)	1.29 ± 0.91 (0–3)	1.15 ± 0.88 (0–3)	0.93 ± 0.82 (0–3)	0.86 ± 0.80 (0–3)	0.82 ± 0.76 (0–2)
Bark gleaners (6)	2.35 ± 0.65 (1–4)	3.53 ± 0.94 (2–5)	2.92 ± 1.11 (1–5)	2.05 ± 0.63 (1–3)	2.80 ± 1.00 (1–5)	2.10 ± 1.07 (0–4)
Foliage Invertivores (15)	10.40 ± 1.33 (8–13)	5.84 ± 1.44 (3–9)	7.80 ± 1.60 (5–11)	8.90 ± 1.57 (6–12)	4.48 ± 1.23 (2–7)	5.85 ± 1.59 (3–9)
Ground Invertivores (5)	2.36 ± 0.76 (1–4)	2.25 ± 0.93 (0–4)	2.02 ± 0.84 (1–4)	2.03 ± 0.84 (1–4)	1.93 ± 0.82 (0–3)	1.82 ± 0.75 (1–3)
Seed eaters (10)	2.34 ± 1.09 (0–5)	2.54 ± 1.05 (1–5)	2.71 ± 1.16 (1–5)	1.99 ± 1.05 (0–4)	2.36 ± 0.98 (1–4)	2.24 ± 1.02 (1–4)
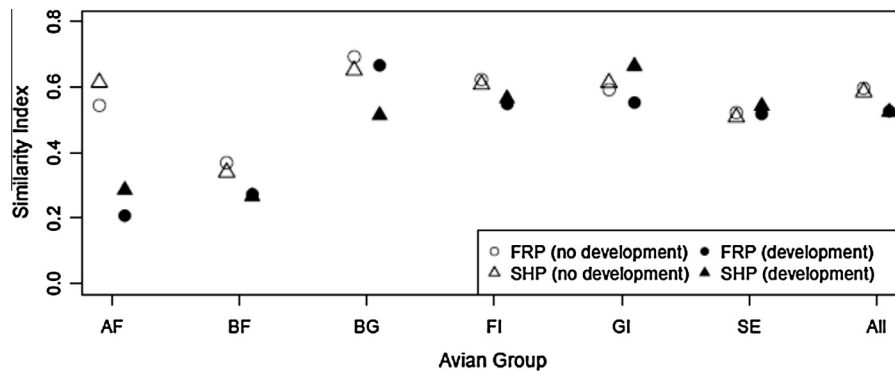
Fig. 3. Similarity in species composition (with 1 representing complete overlap and 0 indicating no overlap) for air foragers (AFs), bark foragers (BFs), bark gleaners (BGs), foliage invertivores (FIs), ground invertivores (GIs) and seed eaters (SEs) under a typical fuel reduction prescription (FRP) and a structural heterogeneity prescription (SHP) relative to a fire suppressed forest in developed and undeveloped areas.

ical and ecological perspective. A reduction in average species richness of foliage invertivores suggested this group, although the most species, would be impacted the greatest by fuel reduction treatments. These reductions in species richness were somewhat ameliorated in the treatment incorporating forest structural heterogeneity, particularly in undeveloped areas. Combined with the results predicted for individual species, this reduction in species richness indicates that although the cumulative effect of treatments tended to be negative, treatments including structural heterogeneity were predicted to lead to a >30% increase in the occurrence of several species. However, at larger spatial scales it is important to understand whether different habitat types support similar, or unique, communities. This is especially important to consider for depauperate communities, where loss of a species may not be ameliorated by the presence of others. Development appeared more important than forest treatment in predicting the similarity between avian communities (Fig. 3). However, for certain foraging groups the degree of community similarity depended on both treatment option and development.

4. Discussion

The use of fuel reduction treatments to address concerns regarding the unnaturally high fuel loads and altered conditions of many of the dry forests of the western US is ubiquitous (Brown et al., 2004). Recently, more emphasis has been placed on not only reducing fire hazard through forest thinning, but designing treatments to simulate a heterogeneous stand structure more characteristic of the past (Carey, 2003; North et al., 2009; Verschuyl et al., 2011). Our results on the impact of treatments on individual species support recent syntheses that suggest that forest thinning through the removal of small diameter trees typical of a fuel reduction prescription has a neutral to positive effect on many avian species (Hurteau et al., 2008; Gaines et al., 2010; Kalies et al., 2010; Verschuyl et al., 2011). Our results are therefore consistent with previous studies that suggest modest responses by avifauna to removal of small diameter trees, but our Bayesian hierarchical model provides further insight into how different treatments may affect the less commonly occurring species, species for which inferences are usually not possible under different statistical approaches due to small sample sizes. Our simulations suggest that although fuel reduction treatments may provide or improve suitable habitat for a number of species, treatments may cause an overall, albeit minimal, cumulative reduction in species richness. Our simulations also provide evidence that prescriptions resulting in a more complex stand structure will increase the occurrence probability by >30% for a larger number of avian species than typical fuel reduction methods and lead to smaller predicted reductions in species richness.

Conservation of biological diversity is one of the goals of multi-objective forest management. Maintaining the biological diversity of our forests is important as loss of native biodiversity can negatively affect ecosystem properties and the impacts of species loss

and compositional change of communities on ecosystem functioning have been the focus of much research (reviewed in Hooper et al., 2005). Because it is difficult to predict how the loss of a particular species would impact ecosystem functioning, many biodiversity targets focus on retaining or restoring the greatest number of species. Ecosystem functioning may not be affected by loss in species richness *per se*, if loss of a species is ameliorated by the presence of a functionally similar species (Walker, 1992; Naeem, 2002); therefore, maintaining redundancy in groups of species that fill similar ecological roles (i.e. guilds, functional groups) may improve ecosystem resiliency. Although the differences in species richness under the two management scenarios were small compared to a fire-suppressed forest, our models indicate that treatment would result in a loss in avian species richness. If maintaining the site richness and improving habitat for the greatest number of avian species is of concern in areas planned for fuel reduction treatments, our models suggest that a greater number of avian species would be retained by using a treatment that adds or retains forest structural heterogeneity. However, our models predict that the change in richness of different foraging groups and thus the services these groups provide will depend on the type of treatment used and some groups, such as the bark gleaners, would benefit more from a typical fuel reduction prescription.

The ability to predict whether there is consistency in functional group response to different stressors is of particular conservation concern as stressors affecting functionally important ecological groups are arguably of higher priority than stressors affecting a single species (Walker, 1995). Our model results suggest that variation in abiotic and biotic variables is associated with changes in the occurrence of different foraging groups. The occurrence probability of bark foragers and seed eaters was more closely associated with abiotic variables. As food resources (i.e. bark beetles and seed masts) for these two groups tend to be eruptive (Kelly, 1994; Raffa et al., 2008), annual variability or the composition of tree species may be more important than forest structure. Foliage invertivores, which glean invertebrates from foliage of trees and shrubs, were unsurprisingly associated with higher levels of cover for both these variables. An overall decrease in richness of foliage invertivores with fuel reduction treatments indicates that this association is more closely linked to changes in canopy cover. Species that glean invertebrates from bark (i.e. bark gleaners) responded differently than foliage invertivores, generally being associated with intermediate canopy cover and decreased shrub cover. Although these two groups use similar resources, substrate specialization may permit each group to occupy slightly different forest niches (see also Lesak et al., 2011).

Consistency in foraging group responses can be useful when making management decisions in cases where multi-species monitoring is not feasible. Due to the complexities of quantifying and measuring biodiversity response, surrogates or indicators are often used to measure the efficacy of management actions and several researchers have advocated using avian guilds as indicators for terrestrial ecosystems (Croonquist and Brooks, 1991; Canterbury et al., 2000; O'Connell et al., 2000; Niemi and McDonald, 2004). We found a high-level of variation among members of foraging guilds, suggesting that individual species would be inadequate indicators for predicting their guild's response to changes in forest structure. The lack of consistency of response within a guild may indicate a high level of resource partitioning, or suggest that other requirements, such as nesting habitat, are additionally important in predicting group-level responses to stand structure. Although this variability in functional group response makes inferences difficult, individual differences in response patterns will help ensure

that important functional groups are not lost entirely from a system due to a particular stressor.

Although species richness is often used synonymously with biodiversity, other aspects of biodiversity can be equally important for ecosystem functioning, including species composition and the presence of key species (Power et al., 1996; Hooper et al., 2005). Several studies have provided evidence that community composition is as important for ecosystem functioning as functional richness (Naeem et al., 1995; Hooper and Vitousek, 1997; Tilman et al., 1997) and researchers and managers should be cautious in assuming that species with similar ecological niches are ecologically equivalent (Cordeiro and Howe, 2003; Tylianakis et al., 2008). For instance, many species that require tree cavities for nesting are unable to excavate them and depend on woodpeckers for creating their nesting and roosting sites. Recent work has shown that white-headed woodpecker cavities are utilized by a greater diversity of secondary cavity nesters than are holes excavated by either black-backed or hairy woodpeckers (Tarbill, 2010), suggesting that species with similar roles may not be equivalent in the value of services provided. Species-specific differences in response to our hypothetical treatment options support the notion that the composition of important avian groups will be altered as forests move towards higher fuel loads. Additionally, choice of prescription and degree of urban development within treated areas will influence species composition.

Our results suggest that, on the landscape scale, the greatest avian diversity would be supported by an application of a variety of treatments (Benton et al., 2003; Tews et al., 2004; Warfe et al., 2008). For example, air and bark foraging communities in each treatment had higher beta diversity (differentiation among treatment/development combinations) than the other foraging communities and bark gleaners appeared to be the most sensitive to treatment type. Fuel reduction treatments in developed areas were predicted to exacerbate these differences in community composition and the choice of fuel reduction prescription had a larger impact on community similarity in developed areas. However, our results are only speculative since these treatments were not actually implemented in the Tahoe Basin. To evaluate the accuracy of our predictions, empirical forest thinning studies need to be implemented and the ensuing results rigorously compared to our model projections. Taken together our results suggest that although current forest management practices are often focused on the effects of biomass removal on biodiversity, the conservation and restoration of forest biodiversity will require fuel reduction treatments to have specific and clearly defined objectives for biodiversity outcomes.

Appendix A

Mean and standard deviation in the occurrence probability for each species simulated under each management alternative.

Common name	Scientific name	Foraging guild	Undeveloped			Developed		
			FSF	FRP	SHP	FSF	FRP	SHP
American robin	*Turdus migratorius*	Ground invertivore	0.89 ± 0.10	0.82 ± 0.06	0.93 ± 0.03	0.91 ± 0.10	0.85 ± 0.06	0.95 ± 0.03
Black-backed woodpecker	*Picoides arcticus*	Bark forager	0.05 ± 0.13	0.27 ± 0.15	0.10 ± 0.11	0.02 ± 0.07	0.09 ± 0.09	0.02 ± 0.04
Black-headed grosbeak	*Pheucticus melanocephalus*	Foliage invertivore	0.41 ± 0.23	0.18 ± 0.07	0.44 ± 0.13	0.40 ± 0.23	0.17 ± 0.06	0.42 ± 0.12
Brown creeper	*Certhia americana*	Bark gleaner	0.93 ± 0.06	0.89 ± 0.04	0.77 ± 0.08	0.82 ± 0.14	0.71 ± 0.08	0.51 ± 0.10
Band-tailed pigeon	*Patagioenas fasciata*	Seed eater	0.09 ± 0.08	0.23 ± 0.07	0.10 ± 0.05	0.20 ± 0.15	0.45 ± 0.10	0.23 ± 0.08
Cassin's finch	*Carpodacus cassinii*	Seed eater	0.44 ± 0.20	0.30 ± 0.09	0.30 ± 0.10	0.32 ± 0.19	0.19 ± 0.07	0.19 ± 0.07
Cassin's vireo	*Vireo cassinii*	Foliage invertivore	0.70 ± 0.18	0.15 ± 0.05	0.25 ± 0.09	0.42 ± 0.21	0.04 ± 0.02	0.08 ± 0.04
Chipping sparrow	*Spizella passerina*	Seed eater	0.02 ± 0.04	0.04 ± 0.02	0.33 ± 0.13	0.01 ± 0.02	0.02 ± 0.01	0.19 ± 0.09
Dark-eyed junco	*Junco hyemalis*	Seed eater	0.85 ± 0.15	0.96 ± 0.02	0.97 ± 0.02	0.77 ± 0.20	0.94 ± 0.04	0.94 ± 0.04
Downy woodpecker	*Picoides pubescens*	Bark forager	0.17 ± 0.17	0.14 ± 0.07	0.25 ± 0.12	0.12 ± 0.14	0.09 ± 0.05	0.17 ± 0.09
Dusky flycatcher	*Empidonax oberholseri*	Air forager	0.73 ± 0.17	0.44 ± 0.10	0.52 ± 0.11	0.31 ± 0.20	0.09 ± 0.04	0.12 ± 0.05
Evening grosbeak	*Coccothraustes vespertinus*	Seed eater	0.39 ± 0.18	0.52 ± 0.10	0.31 ± 0.09	0.43 ± 0.19	0.57 ± 0.09	0.35 ± 0.09
Fox sparrow	*Passerella iliaca*	Ground invertivore	0.38 ± 0.18	0.58 ± 0.09	0.49 ± 0.10	0.38 ± 0.18	0.58 ± 0.09	0.49 ± 0.10
Golden-crowned kinglet	*Regulus satrapa*	Foliage invertivore	0.88 ± 0.10	0.60 ± 0.09	0.56 ± 0.11	0.77 ± 0.16	0.39 ± 0.09	0.35 ± 0.10
Green-tailed towhee	*Pipilo chlorurus*	Seed eater	0.07 ± 0.09	0.04 ± 0.02	0.13 ± 0.07	0.05 ± 0.07	0.02 ± 0.01	0.09 ± 0.05
Hammond's flycatcher	*Empidonax hammondii*	Air forager	0.16 ± 0.25	0.00 ± 0.01	0.00 ± 0.02	0.09 ± 0.19	0.00 ± 0.00	0.00 ± 0.01
Hairy woodpecker	*Picoides villosus*	Bark forager	0.62 ± 0.19	0.59 ± 0.09	0.48 ± 0.11	0.37 ± 0.19	0.30 ± 0.08	0.22 ± 0.07
Hermit thrush	*Catharus guttatus*	Ground invertivore	0.92 ± 0.08	0.36 ± 0.09	0.26 ± 0.10	0.57 ± 0.27	0.05 ± 0.04	0.03 ± 0.03
Hermit warbler	*Dendroica occidentalis*	Foliage invertivore	0.96 ± 0.05	0.20 ± 0.08	0.27 ± 0.11	0.82 ± 0.18	0.05 ± 0.03	0.07 ± 0.05
House wren	*Troglodytes aedon*	Foliage invertivore	0.47 ± 0.24	0.08 ± 0.04	0.31 ± 0.12	0.35 ± 0.23	0.04 ± 0.02	0.19 ± 0.09
Macgillivray's warbler	*Oporornis tolmiei*	Foliage invertivore	0.88 ± 0.10	0.39 ± 0.09	0.78 ± 0.08	0.73 ± 0.17	0.18 ± 0.06	0.55 ± 0.11
Mountain chickadee	*Poecile gambeli*	Foliage invertivore	1.00 ± 0.01	0.98 ± 0.01	0.97 ± 0.03	1.00 ± 0.01	0.99 ± 0.01	0.98 ± 0.02
Mountain quail	*Oreortyx pictus*	Seed eater	0.37 ± 0.22	0.27 ± 0.09	0.30 ± 0.12	0.14 ± 0.14	0.07 ± 0.04	0.08 ± 0.05
Nashville warbler	*Oreothlypis ruficapilla*	Foliage invertivore	0.90 ± 0.08	0.41 ± 0.09	0.56 ± 0.11	0.83 ± 0.13	0.26 ± 0.08	0.39 ± 0.10
Northern flicker	*Colaptes auratus*	Ground invertivore	0.17 ± 0.12	0.47 ± 0.09	0.35 ± 0.09	0.16 ± 0.12	0.44 ± 0.08	0.32 ± 0.08
Olive-sided flycatcher	*Contopus cooperi*	Air forager	0.14 ± 0.11	0.55 ± 0.09	0.45 ± 0.10	0.07 ± 0.07	0.34 ± 0.08	0.25 ± 0.08
Pine grosbeak	*Pinicola enucleator*	Seed eater	0.08 ± 0.12	0.11 ± 0.06	0.19 ± 0.12	0.04 ± 0.09	0.05 ± 0.04	0.09 ± 0.08
Pine siskin	*Spinus pinus*	Foliage invertivore	0.53 ± 0.18	0.40 ± 0.08	0.48 ± 0.10	0.45 ± 0.19	0.31 ± 0.07	0.39 ± 0.09
Pileated woodpecker	*Dryocopus pileatus*	Bark forager	0.20 ± 0.21	0.07 ± 0.05	0.04 ± 0.04	0.08 ± 0.13	0.02 ± 0.02	0.01 ± 0.01
Purple finch	*Carpodacus purpureus*	Seed eater	0.00 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pygmy nuthatch	*Sitta pygmaea*	Bark gleaner	0.05 ± 0.05	0.28 ± 0.08	0.33 ± 0.10	0.07 ± 0.07	0.35 ± 0.09	0.41 ± 0.10
Red-breasted nuthatch	*Sitta canadensis*	Bark gleaner	1.00 ± 0.01	0.97 ± 0.01	0.71 ± 0.11	0.99 ± 0.01	0.96 ± 0.02	0.60 ± 0.11

Appendix A (*continued*)

Common name	Scientific name	Foraging guild	Undeveloped			Developed		
			FSF	FRP	SHP	FSF	FRP	SHP
Red-breasted sapsucker	*Sphyrapicus ruber*	Bark gleaner	0.09 ± 0.12	0.15 ± 0.07	0.25 ± 0.12	0.07 ± 0.10	0.11 ± 0.05	0.19 ± 0.09
Ruby-crowned kinglet	*Regulus calendula*	Foliage invertivore	0.03 ± 0.08	0.01 ± 0.01	0.05 ± 0.06	0.02 ± 0.05	0.00 ± 0.01	0.02 ± 0.03
Red crossbill	*Loxia curvirostra*	Seed eater	0.05 ± 0.07	0.08 ± 0.04	0.07 ± 0.05	0.04 ± 0.07	0.06 ± 0.03	0.06 ± 0.04
Spotted towhee	*Pipilo maculatus*	Ground invertivore	0.00 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.01 ± 0.02	0.01 ± 0.01	0.01 ± 0.00
Townsend's solitaire	*Myadestes townsendi*	Air forager	0.71 ± 0.18	0.78 ± 0.07	0.69 ± 0.10	0.31 ± 0.19	0.33 ± 0.10	0.24 ± 0.08
Warbling vireo	*Vireo gilvus*	Foliage invertivore	0.75 ± 0.15	0.39 ± 0.09	0.80 ± 0.07	0.50 ± 0.19	0.16 ± 0.05	0.55 ± 0.09
White-breasted nuthatch	*Sitta carolinensis*	Bark gleaner	0.25 ± 0.16	0.76 ± 0.07	0.61 ± 0.10	0.09 ± 0.08	0.46 ± 0.10	0.30 ± 0.09
Western tanager	*Piranga ludoviciana*	Foliage invertivore	0.94 ± 0.07	0.92 ± 0.03	0.72 ± 0.09	0.90 ± 0.10	0.85 ± 0.05	0.57 ± 0.10
Western wood-pewee	*Contopus sordidulus*	Air forager	0.56 ± 0.19	0.53 ± 0.09	0.89 ± 0.04	0.27 ± 0.16	0.22 ± 0.06	0.66 ± 0.09
White-headed woodpecker	*Picoides albolarvatus*	Bark forager	0.26 ± 0.16	0.25 ± 0.07	0.30 ± 0.09	0.34 ± 0.18	0.34 ± 0.09	0.40 ± 0.10
Williamson's sapsucker	*Sphyrapicus thyroideus*	Bark gleaner	0.03 ± 0.05	0.47 ± 0.11	0.26 ± 0.11	0.01 ± 0.02	0.20 ± 0.09	0.09 ± 0.05
Wilson's warbler	*Wilsonia pusilla*	Foliage invertivore	0.87 ± 0.11	0.16 ± 0.06	0.60 ± 0.12	0.74 ± 0.18	0.07 ± 0.04	0.38 ± 0.12
Yellow-rumped warbler	*Dendroica coronata*	Foliage invertivore	0.94 ± 0.06	0.94 ± 0.03	0.90 ± 0.05	0.92 ± 0.09	0.92 ± 0.04	0.86 ± 0.06
Yellow warbler	*Dendroica petechia*	Foliage invertivore	0.11 ± 0.16	0.04 ± 0.03	0.08 ± 0.07	0.07 ± 0.12	0.02 ± 0.02	0.04 ± 0.04

Appendix B

WinBUGS model code: For more details (including additional code and completed examples with data) on implementing multi-species occurrence models in R and WinBUGS, see: http://www.mbr-pwrc.usgs.gov/pubanalysis/communitymodeling.

```
model {

#Define the priors for the model

#Prior for the intercept term for the occurrence model (mean across species – also referred to as
the #hyper-parameter) that is uniform(0,1) -transform the prior to the logit scale
phi.mean ~ dunif(0,1)
mu.phi <- log(phi.mean) - log(1-phi.mean)

#Prior for the hyper-parameter intercept for the detection model
p.mean ~ dunif(0,1)
mu.p <- log(p.mean) - log(1-p.mean)

#Priors for the hyper-parameters for each of the covariate terms for the occurrence and detection
#models

#Hyper-parameter means
mua1 ~ dnorm(0, 0.01)
mua2 ~ dnorm(0, 0.01)
mua3 ~ dnorm(0, 0.01)
mua4 ~ dnorm(0, 0.01)
mua5 ~ dnorm(0, 0.01)
mua6 ~ dnorm(0, 0.01)
mua7 ~ dnorm(0, 0.01)
mua8 ~ dnorm(0, 0.01)
mua9 ~ dnorm(0, 0.01)
mua10 ~ dnorm(0, 0.01)
mua11 ~ dnorm(0, 0.01)
mua12 ~ dnorm(0, 0.01)
mua13 ~ dnorm(0, 0.01)

mub1 ~ dnorm(0, 0.01)
mub2 ~ dnorm(0, 0.01)


#Hyper-parameter variances
tau.a1 ~ dgamma(0.1,0.1)
tau.a2 ~ dgamma(0.1,0.1)
```

```
tau.a3 ~ dgamma(0.1,0.1)
tau.a4 ~ dgamma(0.1,0.1)
tau.a5 ~ dgamma(0.1,0.1)
tau.a6 ~ dgamma(0.1,0.1)
tau.a7 ~ dgamma(0.1,0.1)
tau.a8 ~ dgamma(0.1,0.1)
tau.a9 ~ dgamma(0.1,0.1)
tau.a10 ~ dgamma(0.1,0.1)
tau.a11 ~ dgamma(0.1,0.1)
tau.a12 ~ dgamma(0.1,0.1)
tau.a13 ~ dgamma(0.1,0.1)

tau.phi ~ dgamma(0.1,0.1)
tau.p ~ dgamma(0.1,0.1)
tau.b1 ~ dgamma(0.1,0.1)
tau.b2 ~ dgamma(0.1,0.1)

#Priors for the year effects on detection
b3 ~ dnorm(0,0.01)
b4 ~ dnorm(0,0.01)
b5 ~ dnorm(0,0.01)

#Loop across all n species that were observed during sampling
for (i in 1:n) {

  #Prior for each of the parameter estimates – drawn from the community-level hyper-priors

  #Occurrence parameters
  phi[i] ~ dnorm(mu.phi, tau.phi)
  a1[i] ~ dnorm(mua1, tau.a1)
  a2[i] ~ dnorm(mua2, tau.a2)
  a3[i] ~ dnorm(mua3, tau.a3)
  a4[i] ~ dnorm(mua4, tau.a4)
  a5[i] ~ dnorm(mua5, tau.a5)
  a6[i] ~ dnorm(mua6, tau.a6)
  a7[i] ~ dnorm(mua7, tau.a7)
  a8[i] ~ dnorm(mua8, tau.a8)
  a9[i] ~ dnorm(mua9, tau.a9)
  a10[i] ~ dnorm(mua10, tau.a10)
  a11[i] ~ dnorm(mua8, tau.a8)
  a12[i] ~ dnorm(mua9, tau.a9)
  a13[i] ~ dnorm(mua10, tau.a10)
```

```
   #Detection parameters
   p[i] ~ dnorm(mu.p, tau.p)
   b1[i] ~ dnorm(mub1, tau.b1)
   b2[i] ~ dnorm(mub2, tau.b2)

#Loop across all j sampling locations
    for (j in 1:J) {

    #Estimate occurrence psi, for species i at location j, for the latent Z matrix
       logit(psi[j,i])  <-  phi[i] + a1[i]*devel1[j] + a2[i]*elev1[j] + a3[i]*elev2[j] + a4[i]*prec1[j]
+
                        a5[i]*prec2[j] + a6[i]*DBH1[j] + a7[i]*DBH2[j]+ a8[i]*DBHSD1[j] +
a9[i]*cover1[j] +
                    a10[i]*cover2[j] + a11[i]*coverSD1[j] + a12[i]*scover1[j] +
a13[i]*scover2[j]
     Z[j,i] ~ dbin(psi[j,i], 1)

  #Estimate the species specific detection probability using the data X for every replicate k at
each point
   #where the  species occurs (Z=1)
    for (k in 1:K[j]) {
        logit(theta[j,i,k])  <-  p[i] + b1[i]*date1[j,k] + b2[i]*date2[j,k] + b3*year2003[j] +
b4*year2004[j] +
                             b5*year2005[j]
        mu.theta[j,i,k] <- theta[j,i,k]*Z[j,i]
        X[j,i,k] ~ dbin(mu.theta[j,i,k], 1)

        }
     }
}

}
```

Appendix C

Mean, standard deviation and posterior intervals for foraging group hyper-parameters for occurrence covariates.

Foraging group hyper-parameters	Air forager	Bark forager	Bark gleaner	Foliage invertivore	Ground invertivore	Seed eater
Intercept	−0.77 ± 1.12 (−3.02, 1.54)	−1.60 ± 0.76 (−3.00, 0.06)	0.13 ± 0.67 (−1.23, 1.40)	−0.80 ± 0.61 (−1.98, 0.40)	−0.33 ± 0.92 (−2.12, 1.55)	−1.24 ± 0.74 (−2.65, 0.25)
Development	**−0.91 ± 0.34** **(−1.58, −0.26)**	−0.52 ± 0.43 (−1.44, 0.25)	−0.44 ± 0.25 (−0.95, 0.06)	**−0.45 ± 0.13** **(−0.71, −0.20)**	−0.24 ± 0.48 (−1.30, 0.64)	−0.31 ± 0.21 (−0.76, 0.08)
Elevation	0.29 ± 0.59 (−0.86, 1.58)	−0.40 ± 0.49 (−1.35, 0.64)	0.11 ± 0.33 (−0.53, 0.80)	0.08 ± 0.15 (−0.20, 0.37)	−0.37 ± 0.64 (−1.71, 0.77)	0.04 ± 0.34 (−0.66, 0.67)
Elevation^2	−0.20 ± 0.21 (−0.62, 0.23)	−0.23 ± 0.28 (−0.85, 0.29)	−0.04 ± 0.15 (−0.33, 0.26)	**−0.23 ± 0.08** **(−0.40, −0.07)**	−0.20 ± 0.32 (−0.91, 0.34)	−0.16 ± 0.13 (−0.44, 0.11)
Precipitation	0.04 ± 0.33 (−0.59, 0.73)	−0.09 ± 0.24 (−0.59, 0.36)	−0.05 ± 0.37 (−0.77, 0.69)	0.16 ± 0.14 (−0.13, 0.44)	−0.22 ± 0.56 (−1.46, 0.88)	0.24 ± 0.31 (−0.41, 0.88)
Precipitation^2	−0.10 ± 0.20 (−0.48, 0.29)	−0.34 ± 0.50 (−1.47, 0.48)	−0.17 ± 0.17 (−0.52, 0.16)	−0.08 ± 0.07 (−0.23, 0.06)	−0.01 ± 0.20 (−0.40, 0.36)	−0.02 ± 0.11 (−0.24, 0.21)
Tree size (DBH)	−0.05 ± 0.26 (−0.57, 0.47)	0.13 ± 0.26 (−0.37, 0.70)	−0.07 ± 0.20 (−0.46, 0.35)	−0.18 ± 0.10 (−0.39, 0.03)	−0.04 ± 0.24 (−0.55, 0.41)	0.03 ± 0.14 (−0.25, 0.29)
Tree size (DBH^2)	0.06 ± 0.19 (−0.31, 0.43)	0.00 ± 0.19 (−0.39, 0.36)	−0.02 ± 0.14 (−0.30, 0.25)	0.03 ± 0.07 (−0.12, 0.17)	−0.04 ± 0.23 (−0.47, 0.37)	−0.08 ± 0.09 (−0.28, 0.09)
Tree size variance	0.00 ± 0.21 (−0.44, 0.41)	0.06 ± 0.22 (−0.39, 0.49)	−0.03 ± 0.15 (−0.33, 0.27)	0.17 ± 0.09 (−0.01, 0.35)	−0.02 ± 0.17 (−0.35, 0.32)	−0.07 ± 0.1 (−0.26, 0.12)
Canopy cover	0.32 ± 0.79 (−1.04, 2.05)	−0.19 ± 0.32 (−0.81, 0.38)	−0.01 ± 0.32 (−0.64, 0.65)	**0.34 ± 0.14** **(0.07, 0.62)**	0.31 ± 0.33 (−0.32, 0.96)	−0.11 ± 0.14 (−0.41, 0.16)
Canopy cover^2	−0.10 ± 0.19 (−0.49, 0.25)	−0.05 ± 0.18 (−0.40, 0.30)	−0.23 ± 0.14 (−0.50, 0.04)	0.00 ± 0.08 (−0.15, 0.16)	0.05 ± 0.19 (−0.33, 0.45)	0.06 ± 0.10 (−0.14, 0.26)
Canopy variance	0.07 ± 0.28 (−0.46, 0.65)	−0.11 ± 0.25 (−0.64, 0.39)	−0.14 ± 0.20 (−0.55, 0.26)	0.18 ± 0.10 (−0.02, 0.36)	−0.02 ± 0.20 (−0.42, 0.36)	0.07 ± 0.13 (−0.20, 0.34)
Shrub cover	0.11 ± 0.47 (−0.82, 0.97)	−0.23 ± 0.28 (−0.78, 0.24)	−0.18 ± 0.17 (−0.48, 0.14)	0.05 ± 0.10 (−0.14, 0.25)	0.46 ± 0.37 (−0.22, 1.22)	0.12 ± 0.18 (−0.26, 0.48)
Shrub cover^2	−0.04 ± 0.19 (−0.44, 0.32)	−0.03 ± 0.17 (−0.39, 0.29)	0.00 ± 0.14 (−0.27, 0.27)	0.04 ± 0.05 (−0.07, 0.14)	0.03 ± 0.15 (−0.27, 0.32)	−0.04 ± 0.08 (−0.21, 0.12)

Appendix D. Supplementary material Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.04.039.

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Appendix ABC. WinBUGS model code. For more details (including additional code and completed examples with data) on implementing multi-species occurrence models in R and WinBUGS, see: http://www.mbr-pwrc.usgs.gov/pubanalysis/communitymodeling

```
model {

#Define the priors for the model

#Prior for the intercept term for the occurrence model (mean across species – also referred to as the
#hyper-parameter) that is uniform(0,1) -transform the prior to the logit scale
phi.mean ~ dunif(0,1)
mu.phi <- log(phi.mean) - log(1-phi.mean)

#Prior for the hyper-parameter intercept for the detection model
p.mean ~ dunif(0,1)
mu.p <- log(p.mean) - log(1-p.mean)

#Priors for the hyper-parameters for each of the covariate terms for the occurrence and detection
#models

#Hyper-parameter means
mua1 ~ dnorm(0, 0.01)
mua2 ~ dnorm(0, 0.01)
mua3 ~ dnorm(0, 0.01)
mua4 ~ dnorm(0, 0.01)
mua5 ~ dnorm(0, 0.01)
mua6 ~ dnorm(0, 0.01)
mua7 ~ dnorm(0, 0.01)
mua8 ~ dnorm(0, 0.01)
mua9 ~ dnorm(0, 0.01)
mua10 ~ dnorm(0, 0.01)
mua11 ~ dnorm(0, 0.01)
mua12 ~ dnorm(0, 0.01)
mua13 ~ dnorm(0, 0.01)

mub1 ~ dnorm(0, 0.01)
mub2 ~ dnorm(0, 0.01)


#Hyper-parameter variances
tau.a1 ~ dgamma(0.1,0.1)
tau.a2 ~ dgamma(0.1,0.1)
tau.a3 ~ dgamma(0.1,0.1)
tau.a4 ~ dgamma(0.1,0.1)
tau.a5 ~ dgamma(0.1,0.1)
tau.a6 ~ dgamma(0.1,0.1)
tau.a7 ~ dgamma(0.1,0.1)
tau.a8 ~ dgamma(0.1,0.1)
```

```
tau.a9 ~ dgamma(0.1,0.1)
tau.a10 ~ dgamma(0.1,0.1)
tau.a11 ~ dgamma(0.1,0.1)
tau.a12 ~ dgamma(0.1,0.1)
tau.a13 ~ dgamma(0.1,0.1)

tau.phi ~ dgamma(0.1,0.1)
tau.p ~ dgamma(0.1,0.1)
tau.b1 ~ dgamma(0.1,0.1)
tau.b2 ~ dgamma(0.1,0.1)

#Priors for the year effects on detection
b3 ~ dnorm(0,0.01)
b4 ~ dnorm(0,0.01)
b5 ~ dnorm(0,0.01)

#Loop across all n species that were observed during sampling
for (i in 1:n) {

  #Prior for each of the parameter estimates – drawn from the community-level hyper-priors

  #Occurrence parameters
  phi[i] ~ dnorm(mu.phi, tau.phi)
  a1[i] ~ dnorm(mua1, tau.a1)
  a2[i] ~ dnorm(mua2, tau.a2)
  a3[i] ~ dnorm(mua3, tau.a3)
  a4[i] ~ dnorm(mua4, tau.a4)
  a5[i] ~ dnorm(mua5, tau.a5)
  a6[i] ~ dnorm(mua6, tau.a6)
  a7[i] ~ dnorm(mua7, tau.a7)
  a8[i] ~ dnorm(mua8, tau.a8)
  a9[i] ~ dnorm(mua9, tau.a9)
  a10[i] ~ dnorm(mua10, tau.a10)
  a11[i] ~ dnorm(mua8, tau.a8)
  a12[i] ~ dnorm(mua9, tau.a9)
  a13[i] ~ dnorm(mua10, tau.a10)

  #Detection parameters
  p[i] ~ dnorm(mu.p, tau.p)
  b1[i] ~ dnorm(mub1, tau.b1)
  b2[i] ~ dnorm(mub2, tau.b2)

#Loop across all j sampling locations
  for (j in 1:J) {

  #Estimate occurrence psi, for species i at location j, for the latent Z matrix
    logit(psi[j,i])  <-  phi[i] + a1[i]*devel1[j] + a2[i]*elev1[j] + a3[i]*elev2[j] + a4[i]*prec1[j] +
                  a5[i]*prec2[j] + a6[i]*DBH1[j] + a7[i]*DBH2[j]+ a8[i]*DBHSD1[j] + a9[i]*cover1[j] +
```

```
                    a10[i]*cover2[j] + a11[i]*coverSD1[j] + a12[i]*scover1[j] + a13[i]*scover2[j]
    Z[j,i] ~ dbin(psi[j,i], 1)


  #Estimate the species specific detection probability using the data X for every replicate k at each point
  #where the  species occurs (Z=1)
   for (k in 1:K[j]) {
         logit(theta[j,i,k])  <-  p[i] + b1[i]*date1[j,k] + b2[i]*date2[j,k] + b3*year2003[j] + b4*year2004[j] +
                         b5*year2005[j]
         mu.theta[j,i,k] <- theta[j,i,k]*Z[j,i]
         X[j,i,k] ~ dbin(mu.theta[j,i,k], 1)


         }
     }
}


}
```