Conserving avian richness through structure retention in managed forests of the Pacific Northwest, USA

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Conserving avian richness through structure retention in managed forests of the Pacific Northwest, USA

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ABSTRACT

Structure retention is a practice used in managed forests to assist the conservation of biological diversity, whereby green trees, dead trees (i.e. snags), and downed wood are retained during timber harvest. This activity is recognized as beneficial. However, there is little scientific support to guide the management prescriptions (e.g. patch sizes, distribution pattern). We quantified the short-term response of birds to structure retention in timber harvest areas located in the Pacific Northwest. We used a hierarchical community model to examine how attributes of retention sites (number of trees and snags, distance to forest edge) were associated with the species richness of birds using the sites. The modeling framework integrated multiple species-specific occupancy models that accounted for imperfect detection to produce estimates of species richness. We sampled a biogeoclimatic gradient by selecting harvest units within four separate regions (two in Washington, one each in Oregon and California) that support different forest types. Observations were conducted at a random selection of retention sites (e.g. patches, individual trees) within harvest units to record bird use during the breeding seasons of 2008 and 2009. Estimated occupancy and detection probabilities differed by species and region. Retained tree count was associated with an increased occupancy probability for all observed species. The community response to tree count was consistent across all study regions and years – species richness estimates increased with tree count and approximated a species–area curve. Snag count and edge distance did not significantly affect occupancy probability for any observed species, and therefore, had no relationship with species richness. These results suggest that the diversity of birds using structure retention in harvest units can be maximized at patches of >10–15 rotation-age trees. Forest managers are encouraged to group green-trees around high-quality snags and other unique wildlife trees where possible, and to vary prescriptions across stands to provide habitat heterogeneity at the landscape scale.

1. Introduction

Conservation of biological diversity has become a common consideration during forest management (Lindenmayer and Franklin, 2002). One approach to conservation efforts within intensively managed forests is structure retention, a management practice whereby green trees, dead trees (i.e. snags), or downed wood are retained at some density during timber harvest. Structure retention provides residual habitat elements of mature forests that might otherwise be lost during timber harvesting and forest regeneration activities (Franklin et al., 1997); these habitat elements are critical resources for numerous forest-dwelling wildlife (Thomas et al., 1979; Swanson and Franklin, 1992; Bull et al., 1997; Hunter and Bond, 2001; Rosenvald and Lõhmus, 2008). While the practice is generally recognized as beneficial (Lindenmayer and Franklin, 2002), the effectiveness of structure retention as a means to conserve biological diversity is poorly understood (NCASI, 2008). The impact of structure retention on biological diversity will depend on whether patterns of habitat complexity and the amounts of critical resources (like snags) meet the requirements of individual species at relevant scales (Tews et al., 2004).

Structure retention is currently regulated at the stand-scale on state and private lands in the Pacific Northwest, USA (Washington, Oregon, and California). In this region, state forest practices rules include criteria for retaining minimum densities and diameters of green trees, snags and downed wood during forest management activities (Washington Forest Practices Board, 2002; Oregon Department of Forestry, 2005; California Department of Forestry and Fire Protection, 2007). The rules were developed to balance timber management objectives with the broader conservation needs of the forested landscape. Structure retention rules were

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intended to mitigate the impacts of even-aged forest management on snag availability and snag-dependent wildlife species by providing a sufficient density of large-diameter snags within new harvest units (NCASI, 2008). Green-tree retention is intended to serve as the source of future snags, but it may also influence stand-level occurrence of some wildlife species depending on the density and pattern of green trees in the harvest unit (Chambers et al., 1999; Schieck and Hobson, 2000; Bunnell et al., 2002; Walter and Maguire, 2005; Preston and Harestad, 2007). Little empirical evidence exists to support decisions regarding the pattern (i.e. aggregated or dispersed) and location of retained green trees and snags during harvest. Aggregated retention may serve as refugia for some organisms, acting as a temporary "lifeboat" within the harvest unit, while dispersed retention can more evenly distribute critical resources (Franklin et al., 1997). Forest managers could maximize the utility of retained structures as a habitat resource by implementing retention patterns that address the needs of a diverse wildlife community.

Evaluation of management actions requires that a biologically relevant quantity of interest (i.e. state variable) be properly defined for monitoring. Species richness is a common choice for state variable when monitoring biological diversity (Yoccoz et al., 2001) and evaluating forest management practices (Bunnell and Huggard, 1999), despite potential issues with estimation and interpretation. Heterogeneity in species detectability can invalidate naïve estimates of richness that do not account for detection probability (Boulinier et al., 1998). Additionally, species do not have the same relative value toward meeting conservation and management goals due to differences in their functional traits and subsequent importance to ecosystem processes (Chapin et al., 2000; Hooper et al., 2005) and differences in local or regional conservation status (e.g. rare or declining vs. common). Hence, the evaluation of species richness without some consideration of species detectability and identity can be misleading. A hierarchical modeling approach that incorporates imperfect species detection during sampling and generates species-specific occupancy probabilities can be used to produce valid estimates of species richness (Dorazio et al., 2006; Kéry and Royle, 2008; Royle and Dorazio, 2008). One strength to this approach is that data on rarely detected species can be incorporated due to the hierarchical model structure, which uses information from all species to inform parameter estimates for individual species (Dorazio et al., 2010). This type of multi-species occupancy model has been used to evaluate the impacts of management actions and landscape changes on species richness for entire communities and subsets of functionally similar species (or habitat guilds) that may have different responses to specific habitat alterations (e.g. Ruiz-Gutierrez et al., 2010; Zipkin et al., 2010).

We evaluated how attributes of structure retention sites in timber harvest units were associated with avian species occurrence and richness within industrial forests of the Pacific Northwest using a hierarchical multi-species occupancy model. Hereafter, we use the term retention sites as a descriptor for single trees or patches of multiple trees that were left standing during harvesting operations to meet or exceed the requirements mandated by state forest practices rules (Fig. 1). Retention sites were essentially microhabitats (relative to birds) found throughout a harvest unit where vegetation structure was different from that in the surrounding plantation. Our objective was to examine community-level bird responses to retention site attributes, at the scale of a retention site. The model incorporated three retention site attributes that could be directly manipulated during harvesting operations and were likely to influence occupancy: (1) number of trees retained (i.e. tree count, equivalent to patch size); (2) number of snags retained (snag count); and (3) location within the harvest unit (i.e. distance to edge). Tree count served as a general index to the amount of potential resources available at the retention site, whether through the surface area of bark, the amount of foliage, or any other habitat conditions associated with large trees. Relationships between bird communities and habitat physiognomy have long been established (MacArthur and MacArthur, 1961; Rotenberry, 1985), and we felt the number of large standing trees best captured the dominant features of vegetation structure provided by a retention site. Similarly, snag count represented the amount of standing dead wood available at a retention site. Edge distance was a potential obstacle for species using adjacent mature forests that typically avoid young forests due to a lack of canopy cover and vertical vegetation structure.

Fig. 1. Retention site with multiple green trees on a private industrial forest in northern California.

We calculated community-level metrics at each retention site including richness of all avian species and richness of several species groups that were defined by habitat preferences (i.e. foraging guilds; De Graaf et al., 1985) and regional conservation status (Rich et al., 2004). Species that typically forage in large trees and snags would presumably be absent from recently harvested forests that lack structure retention. The response by species that are typically negatively affected by timber harvest should be a priority for evaluating the effectiveness of structure retention practices. Furthermore, species occurring within managed forests with low or declining populations that represent a conservation concern would also be useful to examine within the context of structure retention practices.

2. Methods

2.1. Study regions

Our study was conducted in four separate locations in the Pacific Northwest (Washington, Oregon, and California) that spanned multiple biogeoclimatic regions (i.e. sections, sensu Bailey, 1988), including the Northern Cascades, Oregon and Washington Coast Ranges, and the Southern Cascades (Fig. 2.). We refer to each study region by the general location in the state within which it occurred: central Washington (CWA), southwest Washington (SWA), southwest Oregon (SOR), and northern California (NCA). All study regions were located within forested watersheds on private industrial ownership with a long history of management (2nd and 3rd rotation stands). Watersheds contained a heterogeneous matrix of stand age classes and some had mixed ownership (e.g. the NCA region was juxtaposed with the Shasta-Trinity National Forest). We identified all harvest units that had been logged 3–12 years prior using a geographic information system (GIS). For each study region, we calculated summary statistics on stand area and elevation and randomly selected ~20 harvest units that represented typical conditions on the landscape (i.e. area and elevation values were <1 standard deviation from the region mean). In total, we selected 84 harvest units that fell into two general area classes, small (4–12 ha) and large (22–61 ha), and ranged from 20 to 1830 m in elevation and 41.1–47.7° latitude (Table 1).

2.2. Retention site selection and measurement

We examined the harvest units in each study region to identify retention sites (Fig. 1) that could be selected for sampling using 1 m resolution aerial photography collected from the National Agriculture Imagery Program (NAIP; http://www.apfo.usda.gov/) during 2005–2006. We field-verified all photo-identified retention sites during reconnaissance surveys in 2006. Reconnaissance surveys included a thorough census of each harvest unit to identify

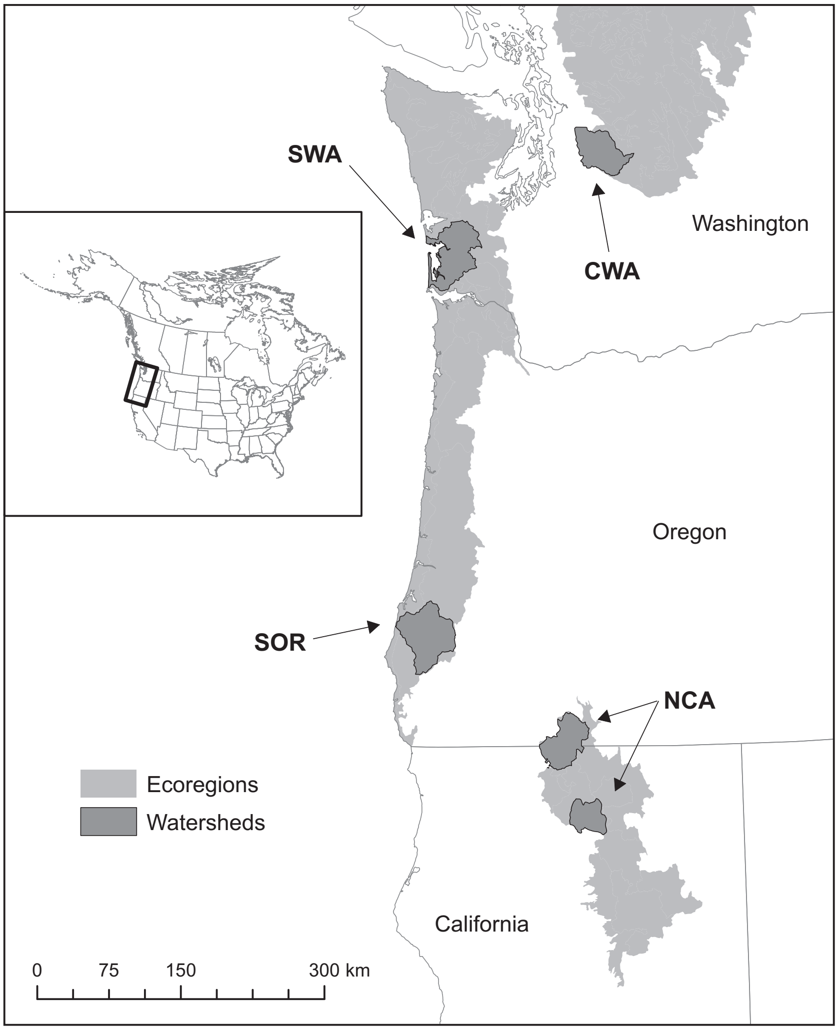

Fig. 2. Map of structure retention locations within ecoregions and watersheds in the Pacific Northwest, USA. Region codes represent the following locations: CWA = central Washington; SWA = southwest Washington; SOR = southwest Oregon; NCA = northern California.

Table 1
Attributes of harvest units selected for observing bird use at structure retention sites in managed forests of the Pacific Northwest.

Region[a]	n	Area (ha)			Elevation (m)			Dominant tree species[b]
		Mean	Min	Max	Mean	Min	Max	
CWA	22	8	4	12	350	200	470	WH, DF, RC, Ald
SWA	20	37	24	57	170	20	330	WH, DF, RC, Ald, SS
SOR	20	40	22	61	610	300	800	DF, WH
NCA	23	9	4	11	1500	1250	1830	WF, PP, DF, RF, IC

[a] Regions are ordered by latitude, from north to south. Region codes represent the following locations in the Pacific Northwest: CWA = central Washington; SWA = southwest Washington; SOR = southwest Oregon; NCA = northern California.

[b] Dominant tree species codes represent the following: Ald = Red alder (*Alnus rubra*); DF = Douglas-fir (*Pseudotsuga menziesii*); IC = California incense-cedar (*Calocedrus decurrens*); PP = ponderosa pine (*Pinus ponderosa*); RC = western redcedar (*Thuja plicata*); RF = red fir (*Abies magnifica*); SS = Sitka spruce (*Picea sitchensis*); WF = white fir (*Abies concolor*); WH = western hemlock (*Tsuga heterophylla*).

additional retention sites not visible from the imagery (e.g. individual snags). We delineated retention sites in the field based on the felling distance of trees at and around the site. For example, an individual tree was considered a distinct retention site only if the distance to the nearest adjacent tree was greater than the height of either tree. GPS coordinates were recorded at the center of each retention site and edge distance was calculated in a GIS to the nearest mature forest (>40 years old) as determined by interpretation of the NAIP imagery. We used a stratified random selection to identify retention sites for further sampling in each study region. Stratification was necessary to ensure that retention sites with a range of tree counts were selected given the prevalence of retention sites with tree count = 1. The strata were defined by the tree count at each retention site and consisted of four groups: 1 tree, 2–5 trees, 6–15 trees, and >16 trees. Selected retention sites located within the same harvest unit were required to be >150 m apart to decrease spatial dependence, resulting in 1–6 sites per harvest unit depending on the area and shape of the unit. For each selected retention site, we used variable-radius plot sampling to tally and measure trees >12.7 cm diameter at breast height (dbh) with a wedge prism (basal area factor = 10).

2.3. Bird surveys

We observed birds using retention sites during the breeding season (May–July) at 226 sites in 2008 and 195 sites in 2009. Given that 94 sites were surveyed in both years, we had 327 unique retention sites over the duration of the study. Each survey consisted of two observers recording all birds that interacted with a retention site (e.g. perched on a branch, foraged on a trunk) for a duration of 30 min starting at a randomly selected time between sunrise and 5 h later. The long duration of the survey (compared to a typical 5 or 10 min point count; Ralph et al., 1995) was necessary to increase our probability of detecting birds using trees at the retention site. Observers were located >25 m to the east of the retention site to avoid disturbance and obtain the best lighting for visual detection; surveys began after a 2 min settling period upon arrival. Observers recorded the species of all individuals detected at a retention site, in addition to the times (recorded to the nearest second) at which the individual arrived and departed. Both observers made an effort to detect birds visually and aurally, though one observer was primarily responsible for recording while the other focused solely on viewing the retention site; these duties were alternated. Although the use of a double-observer method would have enabled us to estimate observer bias in detection probability, we chose to allow observers to work together to improve data quality. Surveys were conducted during adequate wind (<12 km h^{-1}) and weather (no rain or fog) conditions (Ralph et al., 1995). We trained observers for 2 weeks prior to sampling with portable media players (http://www.birdjam.com) to improve their abilities in identifying bird species by sight and sound in the field.

2.4. Modeling framework

We used the hierarchical modeling framework as described in Royle and Dorazio (2008) and applied in other studies (e.g. Dorazio et al., 2006, 2010; Kéry and Royle, 2008; Ruiz-Gutierrez et al., 2010; Zipkin et al., 2010). The multi-species occupancy model treats species-specific model parameters as random effects governed by a common community-level distribution, resulting in a more parsimonious model with greater precision for parameter estimates, especially for rare species (Royle and Dorazio, 2008). Estimates for each individual species are informed by the data across all species (Dorazio et al., 2010). The approach is more efficient than estimating fixed parameters separately for each species in a large multi-species dataset, which would be limited to those species having an adequate number of detections for analysis (Royle and Dorazio, 2008).

To create the repeated measures design necessary for estimating occupancy and detection probabilities (MacKenzie et al., 2002), we divided each 30 min bird survey into three 10 min intervals. Following MacKenzie and Royle (2005), we interpreted occupancy as "use" given that the closure assumption was not valid – we assumed most bird species had territories that were larger than retention sites and, therefore, would be periodically unavailable for detection during surveys. We also assumed that detection was primarily a function of that availability (i.e. the probability that a species is available for detection, given that it uses the site) and not a function of imperfect detection by the observers. We were confident that two observers could adequately detect all species that were present at a retention site during a survey. To account for the potential lack of independence between observation intervals, we estimated detection probabilities for intervals with previous detections separately from intervals with no previous detections (Mordecai et al., 2011).

We constructed a detection history for each species i at retention site j which indicated for each survey interval k in year t whether a species was detected ($y = 1$) or undetected ($y = 0$). Our model notation follows the typical state-space formulation for modeling occupancy and detection probabilities (e.g. Royle and Kéry, 2007). For a species to be detected during a survey interval, the species had to be periodically present at the retention site during a given year; therefore, the detections y_{ijkt} were conditional on the unobserved occupancy state z_{ijt} such that $y_{ijkt} \sim \text{Bernoulli}(z_{ijt}\cdot p_{ijkt})$ where p_{ijkt} is the probability that species i is detected, given that it uses a site. We modeled the unobserved occupancy state z_{ijt} such that $z_{ijt} \sim \text{Bernoulli}(\psi_{ijt})$ where ψ_{ijt} represents the occupancy probability.

We used logit-linear models for the probabilities of detection (p_{ijkt}) and occupancy (ψ_{ijt}) to incorporate the effects of covariates for each process. We assumed that species-specific detection and occupancy probabilities were also specific to an individual study region h, and likely varied across years. In the model for detection, we included survey date as a potential covariate with both linear and quadratic terms to accommodate peaks of availability that may occur during the season (Royle and Dorazio, 2008). We also included a binary variable to indicate whether a species had been detected in a previous survey interval (Mordecai et al., 2011). We defined the model of detection as:

$$logit(p_{ijkt}) = \alpha_{0iht} + \alpha_{i1} date_{jt} + \alpha_{2i} date_{jt}^2 + \alpha_{3i} Prev_{ijkt} + \eta_{ihs}^{[p]} \quad (1)$$

where α_{0iht} is the mean logit-scale detection probability for species i in region h during year t; α_{1i} and α_{2i} are the regression parameters for the linear and quadratic effects of survey date; α_{3i} is the regression parameter estimating the effect of a previous detection, $Prev_{ijkt}$; and $\eta_{ihs}^{[p]}$ is the zero-mean random effect of stand s.

We modeled occupancy across the two years using the dynamic model structure (Royle and Kéry, 2007) with an initial occupancy probability in year 1 (ψ_{ij1}) followed by a subsequent occupancy probability in year 2 (ψ_{ij2}) that is specified to have a Markovian dependence on the unobserved occupancy state in year 1 (z_{ij1}). In this manner, year 2 occupancy probability is a function of either survival (when $z_{ij1} = 1$) or colonization (when $z_{ij1} = 0$) depending on the occupancy state estimated for the previous year. The models of occupancy for each year incorporated the three site covariates of management interest (tree count, snag count, and edge distance), with both linear and quadratic terms. We restricted tree count to stems >25 cm diameter given that this was the minimum diameter resulting in compliance with the state forest practices rules (NCASI, 2008). We were not interested in modeling occupancy dynamics per se (i.e. effects of covariates on colonization and survival), thus, covariates were assumed to have the same additive effect on occupancy probability for both years. We defined the occupancy model in year 1 as:

$$\begin{aligned} logit(\psi_{ij1}) = {} & \beta_{0ih} + \beta_{1i} trees_j + \beta_{2i} trees_j^2 + \beta_{3i} snags_j + \beta_{4i} snags_{j4i}^2 \\ & + \beta_{5i} dist_j + \beta_{6i} dist_j^2 + \eta_{ihs}^{[\psi]} \end{aligned} \quad (2)$$

where β_{oih} is the mean logit-scale occupancy probability for species i in region h at mean values for the covariates; the remaining regression coefficients represent the linear and quadratic effects of tree count (β_{1i}, β_{2i}), snag count (β_{3i}, β_{4i}), and edge distance (β_{5i}, β_{6i}) at retention site j; and $\eta_{ihs}^{[\psi]}$ is the zero-mean random effect of stand s. Accordingly, the occupancy model for year 2 was:

$$\begin{aligned} logit(\psi_{ij2}) = {} & \phi_{ih} z_{ij1} + \gamma_{ih}(1 - z_{ij1}) + \beta_{1i} trees_j + \beta_{2i} trees_j^2 \\ & + \beta_{3i} snags_j + \beta_{4i} snags_j^2 + \beta_{5i} dist_j + \beta_{6i} dist_j^2 + \eta_{ihs}^{[\psi]} \end{aligned} \quad (3)$$

where ϕ_{ih} and γ_{ih} are the mean logit-scale probabilities of survival (continued presence at a site) and colonization (new presence at a site), respectively, for species i in region h at mean values for the covariates. Occupancy probability in year 2 is defined by survival ϕ_{ih} when $z_{ij1} = 1$ and by colonization γ_{ih} when $z_{ij1} = 0$. The remaining regression parameters are specified the same as in year 1.

As described above, we treated the parameters for occupancy and detection models as random effects with each species param-

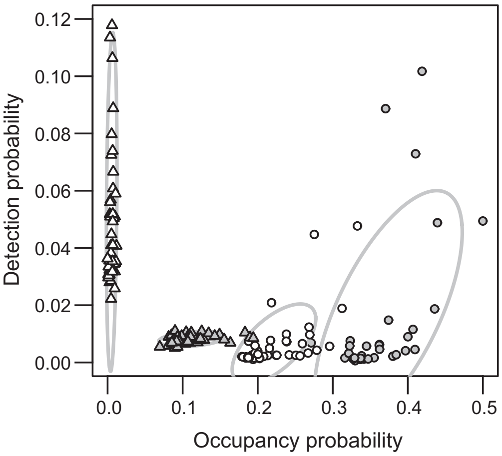

Fig. 3. Mean probabilities of occupancy and detection for all avian species detected using retention sites during 2008–2009 within the four study regions: central Washington (gray triangle); southwest Washington (white circle); southwest Oregon (white triangle); and northern California (gray circle). Each species-specific probability is defined by the mean of the posterior distribution for the intercept in the logit-linear models, averaged across the two years. Standard deviation ellipses (shown in gray) characterize the dispersion of values for each region.

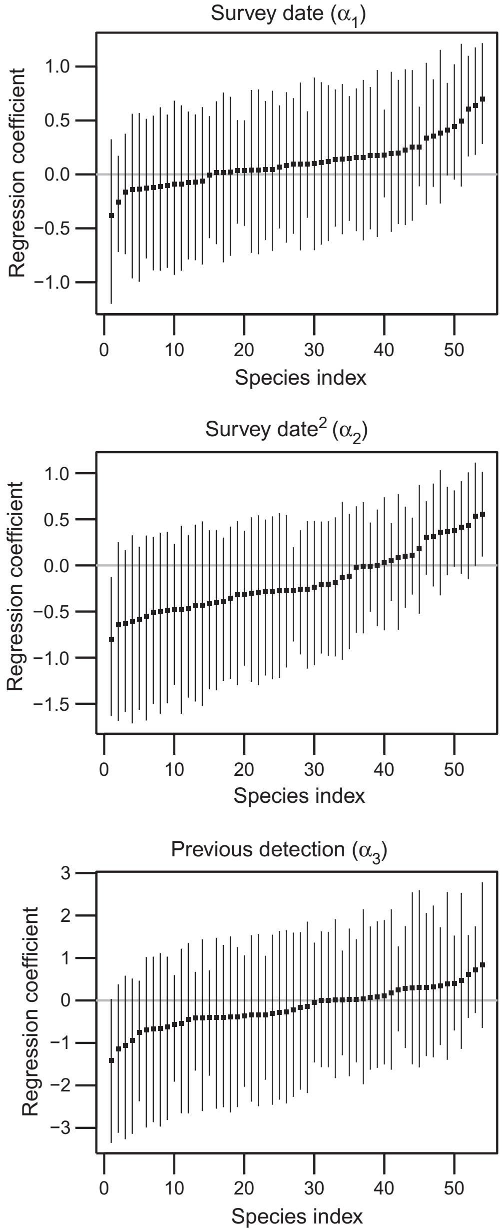

Fig. 4. Posterior estimates (mean with 95% credible interval) of the species-specific regression coefficients from the logit-linear model of detection. Species are ordered by increasing mean estimate of the coefficient. Covariate values were standardized to have a zero mean and unit variance prior to model estimation (previous detection was a binary indicator).

eter being drawn from a common distribution specified by a mean and variance. The mean and variance quantified the community-level responses across species, assuming that the heterogeneity across species could be described by a normal distribution (Kéry and Royle, 2008). As an example, we defined the parameter representing the linear effect of tree count on occupancy probability such that $\beta_{1i} \sim N(\mu_{\beta_1}, \sigma_{\beta_1})$ where μ_{β_1} is the mean response across all species and σ_{β_1} is the standard deviation. Each parameter in the models for occupancy and detection was assigned its own hyperparameters (i.e. μ and σ), and the species-specific parameter estimate was drawn from the distribution specified by the hyperparameters.

We calculated site-level richness in each year, N_{jt}, by summing the unobserved occupancy states across species such that $N_{jt} = \sum_{i=1}^{n[h]} z_{ijt}$ for the $i = 1, \ldots n[h]$ species that were observed in region h. We also calculated the site-level richness for each of our species groups. We examined relationships between site-level richness and the covariates associated with occupancy (tree count, snag count, and edge distance) using graphical representations. Given that site-level richness is a derived quantity estimated by the model, we could not formally quantify these relationships.

We used a Bayesian analysis to estimate the parameters and calculate community-level summaries in WinBUGS (Spiegelhalter et al., 2003) through the R2WinBUGS package (Sturtz et al., 2005) in program R. WinBUGS code for model specification is presented in Appendix A1. We chose non-informative prior distributions for all hyperparameters. All continuous covariates were standardized to have a mean of 0 and a unit variance of 1; covariates in the logit-linear model for occupancy were log-transformed prior to standardizing. We examined model results based on 3 chains of 25,000 iterations after discarding the first 5000 iterations and thinning by 20; this process resulted in 3000 values forming the posterior distribution for each parameter. Markov chain convergence was determined by trace plots of the posterior distributions for each chain and by assessing the $\hat{R}$ statistic, or scale reduction factor, which should be <1.1 for all parameters (Gelman et al., 2003). We also used a posterior predictive check to compare model fit of the actual data with that of simulated data (based on the model parameters) by calculating a Bayesian p-value; values near 0.50 suggest adequate fit (Gelman et al., 2003). Our diagnostics were indicative of model convergence and model fit (Bayesian p-value = 0.37).

3. Results

We observed 54 songbird and woodpecker species (Apodiformes, Columbiformes, Piciformes, Passeriformes) using retention

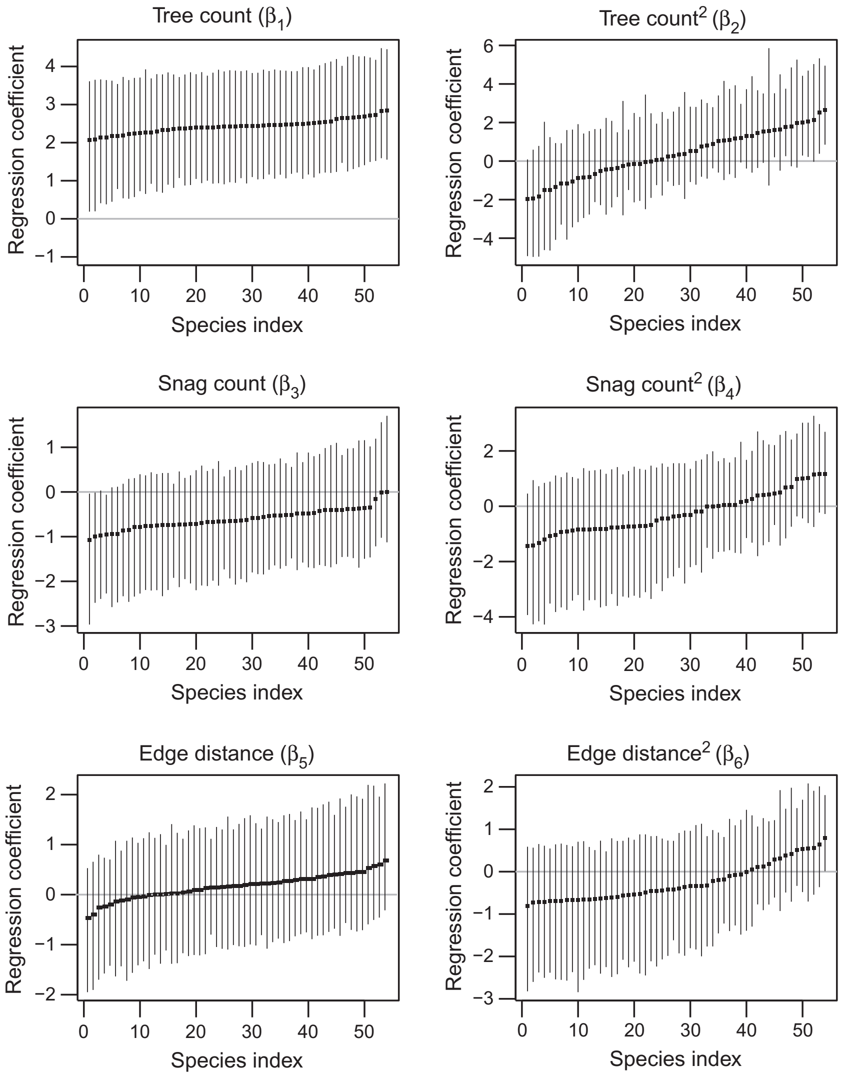

Fig. 5. Posterior estimates (mean with 95% credible interval) of the species-specific regression coefficients from the logit-linear model of occupancy. Species are ordered by increasing mean estimate of the coefficient. Covariate values were log-transformed and standardized to have a zero mean and unit variance prior to model estimation.

sites across both years. We observed 7 species known to forage in the upper canopy, 6 species known to forage on bark, and 8 species listed as a regional concern by Partner's in Flight (Rich et al., 2004). Total detections were relatively low for every species, indicating that birds were rarely observed using retention sites during the surveys (Appendix A2). Average species-specific detection probabilities reflected the rarity of observations and, along with occupancy probabilities, were variable within and across study regions (Fig. 3). Birds were most likely to use retention sites in the northern California stands ($\hat{\psi} = 0.37$; $\mu_{\beta_{0h}} = -0.53$) and least likely to use retention sites in the southern Oregon stands ($\hat{\psi} = 0.01$; $\mu_{\beta_{0h}} = -4.58$), though the average probability of a bird being available for detection was highest in southern Oregon ($\hat{p} = 0.05$; $\mu_{\alpha_{0h}} = -2.94$; Fig. 3).

Covariates affecting occupancy and detection probabilities in the logit-linear models differed by species in effect size and strength of evidence indicated by their regression coefficients (Figs. 4 and 5); evidence for a relationship is indicated when the 95% credible interval [CRI] of the posterior distribution does not overlap zero. Given the low detection probabilities there was considerable uncertainty in the parameter estimates (most CRIs were relatively wide), necessitating caution during interpretation. Detection probabilities were shown to increase with survey date for two species, American Robin and Dark-eyed Junco. There was evidence for a negative quadratic relationship between detection probability and survey date for Hairy Woodpecker, and a positive quadratic relationship for Band-tailed Pigeon. We did not find evidence for a difference in detection probability during a given time interval after a detection had occurred in a previous time interval for any species (Fig. 4).

Occupancy probability for all observed species exhibited strong evidence for a positive linear relationship with tree count (Fig. 5). Six species (American Robin, Northern Flicker, Pacific-slope Flycatcher, Steller's Jay, Swainson's Thrush, and White-crowned Sparrow) displayed evidence for a positive quadratic relationship, suggesting that occupancy probability was greatest for retention sites with either few trees or many trees. We did not find evidence for a relationship between snag count and occupancy probability for any species, though mean parameter estimates were overwhelmingly negative for the linear effect. Likewise, edge distance did not display evidence for a relationship with occupancy probability as parameter estimates overlapped zero for each species.

Mean estimates of site richness were variable within and across study areas for all species (range: 1–32), upper canopy foragers/gleaners (range: 0–4), bark foragers/gleaners (range: 0–4) and species of regional concern (range: 0–5) during both years (Figs. 6–8). Observed site richness was considerably lower than model-predicted site richness for most retention sites (Fig. 6), reflecting the low detection probabilities estimated for the bird community. Mean estimates of site richness increased with tree count in both years for the entire bird community and each species group (Figs. 6 and 7), an expected result given the relatively large effect sizes across all species for tree count in the occupancy model (Fig. 5). The forms of the relationships between tree count and site richness were similar to power functions with maximum richness estimates generally occurring at retention sites having >10–15 trees, though there was some variation between study regions (Figs. 6 and 7). The lack of evidence for relationships between species-specific occupancy and the other covariates, snag count and edge distance (Fig. 5), resulted in no apparent relationships between those covariates and site richness (Fig. 8). Lower site richness was generally estimated for retention sites at the largest distances (e.g. >300 m; Fig. 8), but those sites also tended to have few trees.

4. Discussion

The effectiveness of structure retention at meeting wildlife conservation objectives may be enhanced by using specific strategies that influence species use of the resources provided by the management actions. Our modeling results suggested that tree count had a positive association with the predicted species richness of birds using retention sites in managed forests of the Pacific Northwest. This positive association was observed for all species and for each species group, as defined by foraging guilds and regional conservation status. The relationships between species richness and tree count were similar to a power function, which has often been used to describe species–area relationships (Connor and McCoy 1979). The richness curves were a result of the regression coefficients from the multi-species occupancy model, which suggested that all observed species had higher probabilities of occupancy for retention sites containing more large trees, regardless of habitat associations (Fig. 5). One interpretation of these results is that larger patches of retained trees offered a greater amount and diversity of resources (e.g. food, cover) that were beneficial to numerous species (MacArthur and MacArthur, 1961). Lower canopy and shrub-associated species were already present in the harvest units due to the understory vegetation cover provided by the young plantation trees and may have been opportunistically using retention sites with an increasing probability as the contrast in resources between retention and plantation increased. Conversely, species that forage in the upper canopy or the bark of large trees might be more likely to visit a retention site within a harvest unit

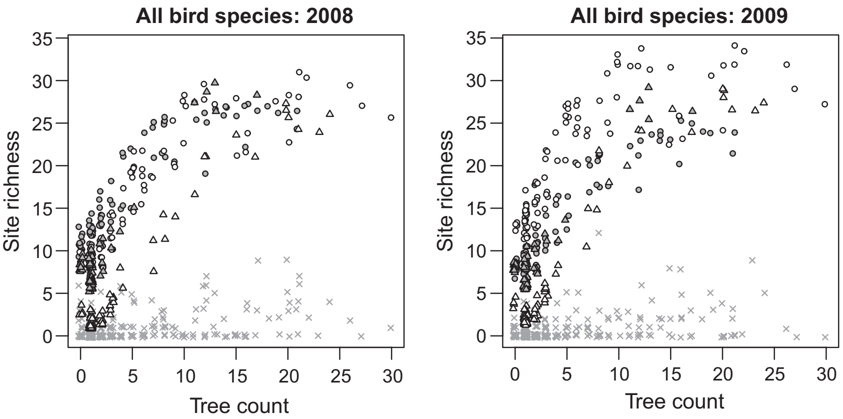

Fig. 6. Mean estimated site richness for all bird species in 2008 (left) and 2009 (right) in relation to tree count at the retention site. Study regions include central Washington (gray triangle), southwest Washington (white circle), southwest Oregon (white triangle), and northern California (gray circle). Observed site richness shown by gray × symbols.

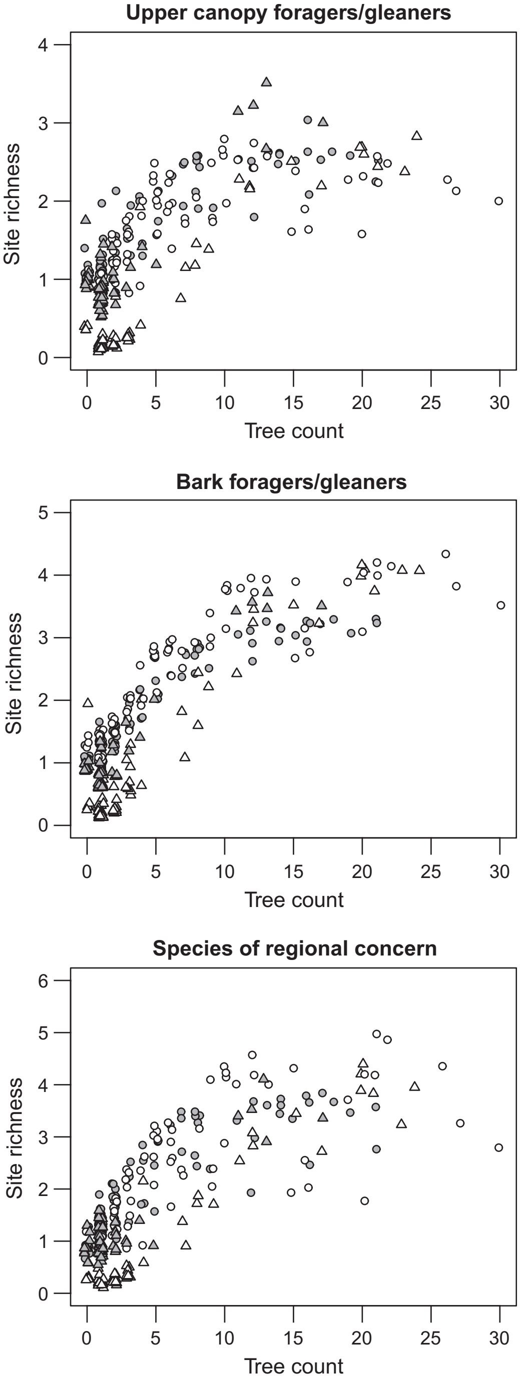

Fig. 7. Mean estimated site richness for upper canopy foragers/gleaners (top), bark foragers/gleaners (middle) and species of regional concern (bottom) in relation to tree count at the retention site during 2008–2009. Species of regional concern were designated by Partner's in flight (Rich et al., 2004). Study regions include central Washington (gray triangle), southwest Washington (white circle), southwest Oregon (white triangle), and northern California (gray circle).

once the amount of resources (e.g. number of large trees) reaches some threshold. In either case, the mechanism driving the response is the quantity and quality of habitat resources provided by the retention sites.

Another interpretation could be related to a sampling effect caused by the change in area of retention sites as the number of large trees increases. We used tree count as a quantitative measure of habitat resources provided by a retention site, from the perspective of bird species using large trees to fulfill various life history requisites (e.g. food), though patch size could be used to serve as a similar proxy. We chose tree count over patch size because we felt that birds would perceive retention sites based on the number of trees serving as substrate for resources as opposed to "habitat islands" with different areas; the two measures (tree count and area) were highly correlated. As the area or patch size of a retention site increases, the probability that a retention site overlaps an individual's territory also increases. Thus, it is possible that larger retention sites were spatially interacting with more individual territories, both within and across species, resulting in a higher probability of species detection due to increased availability of individuals (i.e. the detection/abundance relationship; Royle and Nichols, 2003). We explored this problem in previous iterations of our multi-species occupancy model by incorporating tree count as a covariate in the logit-linear model for detection; we did not find evidence for a relationship between tree count and detection probability, nor were the relationships with occupancy and species richness changed. Given the sparse detection data, the power of the model to detect relationships between covariates and detection probability was low. Our results should therefore be interpreted with some caution.

Most previous studies of green-tree retention effects on the avian community in the Pacific Northwest have focused on stand-level responses of species richness and abundance to varying intensities of harvest, with some combination of unharvested control forests, total-harvest clearcuts, and partial-harvest or variable-retention stands serving as treatment units (Beese and Bryant, 1999; Chambers et al., 1999; Preston and Harestad, 2007). These studies have shown that moderate-intensity harvests typically result in stands with an avian species composition more similar to unharvested forests than to clearcuts and can actually increase avian species richness as a response to greater habitat complexity, though forest-dependent birds often exhibit a decreased abundance. Preston and Harestad (2007) suggested that forest-dependent birds increased their use of green-tree retention with increasing patch size ranging from 0.25 to 2 ha, though their design did not allow for formal inferences regarding patch size. In boreal forests of Alberta, large residual patches (>100 trees) supported bird communities that were more similar to old contiguous forests than small patches ($\leqslant$10 trees) immediately following stand-replacing disturbances (i.e. fire or harvest) and those differences gradually decreased with time (15, 30 and 60 years post-disturbance) as regenerating trees formed a closed canopy (Schieck and Hobson, 2000). These studies highlight the importance of green-tree retention to the forest bird community but their results are useful for informing management decisions at the scale of forest stands, not at the scale of retention sites within stands.

The other attributes of retention sites that we examined, snag count and edge distance, were not strong predictors of occupancy probability for any observed species and, thus, appeared to have no influence on species richness at retention sites (Fig. 8). Snag count appeared to have a weak negative effect on occupancy for most species. Snags provide a different set of resources than live trees and these differences can positively or negatively impact habitat use by a species depending on life history requirements (Thomas et al., 1979; Bull et al., 1997); the same is true for snags with differences in decay state, tree species, or size (Bull, 2002). It is possible that the ubiquity of snags in many of the harvest units and surrounding landscapes could have dampened the relative probability of use for any individual snag or snag patch selected for observation (Kroll et al., 2012). We rarely detected birds on individual snags during surveys, though evidence of use by excavating species was frequently observed, in addition to active cavity nests in snags that were not selected for observation (D.W. Linden, unpublished data). Richness estimates were generally low at edge distances >300 m, but the small sample size at those distances

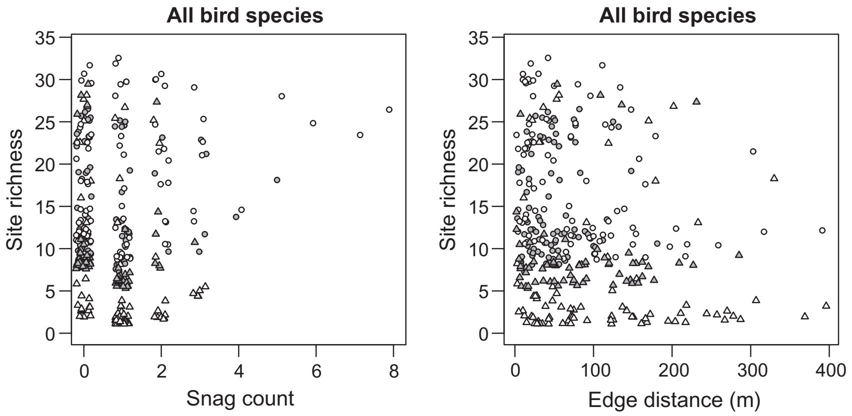

Fig. 8. Mean estimated site richness for all bird species in relation to snag count (left) and edge distance (right) at the retention site during 2008–2009. Study regions include central Washington (gray triangle), southwest Washington (white circle), southwest Oregon (white triangle), and northern California (gray circle).

($n = 7$) precludes robust conclusions. While it is possible that bird species responding negatively to edge distance were never observed using retention sites, the lack of evidence for an effect may also be attributed to the limited range of distances observed: distance to adjacent forest was <50 m for 50% and <200 m for 92% of observed retention sites. The distances we observed may have been too small to limit movement by most bird species, especially given that the edge contrast induced by structural differences in the vegetation between the regenerating harvest unit and the surrounding mature forest could be perceived as relatively benign by most of the observed species (Ries et al., 2004). Additionally, the calculation of edge distance did not take into account the presence of additional nearby retention sites which may have diluted real effects. Several examples in the literature have assisted our understanding of territory-scale movements by birds in search of resources outside the preferred habitat type. Desrochers and Fortin (2000) observed Black-capped Chickadee flocks regularly foraging along forest boundaries at distances up to 100 m from the edge in a matrix of forest and agriculture. Fraser and Stutchbury (2004) found that an area-sensitive forest bird was willing to move >1 km across extensive areas of non-forest in search of a mate, with no indication that movement was restricted to forest corridors. Given the high dispersal capability of birds, the distances to adjacent forest for retention sites observed in our study may have been too small to affect site use. The absence of large distances to adjacent forest are an artifact of existing forest practices rules which contain restrictions on the size and juxtaposition of harvest units to prevent large contiguous areas of young forest.

Our sampling methodology had several limitations in the context of understanding the benefits of structure retention to avifauna. We interpreted occupancy as use because retention sites were typically smaller than the expected territory sizes of the bird species observed in the harvest units and, thus, availability of birds with territories that overlap retention sites determined our observed differences in detection. It is for this reason that detection probabilities were estimated to be so low (Fig. 3) – the probability of an individual being available for detection decreases as the size of a sample site decreases, relative to the home range size. A more appropriate sampling methodology for understanding bird use of microhabitats might involve spot mapping or radio-telemetry, yet neither approach is typically feasible for multiple species within the context of biodiversity monitoring. Importantly, we defined use as the detection of a species at a retention site despite variation in the ecological values of different detections: an individual perching for a short time on the branch of a retained green tree is qualitatively different than an individual foraging on a trunk or using a retained snag for a cavity nest. While we observed the full spectrum of use during the study, the small sample size of detections prevented distinctions from being made for this analysis. The small sample sizes also bring into question the importance of these retention sites to birds on the landscape, given the low frequency with which birds were detected using the sites. Without a frame of reference regarding how often a forest bird uses trees within its territory, this question is difficult to answer. Species adapted to disturbance regimes that create open forests with scattered trees may benefit from retention sites more so than forest birds that occupy the adjacent forest. Finally, the covariates included in our analysis, tree count (for stems >25 cm), snag count, and edge distance, represented three attributes that were hypothesized to affect probability of use and were attributes directly linked to operational management decisions and the forest practices rules. However, these variables may not have captured the range of biologically relevant characteristics that influence retention site use. Evaluations of woody stem composition did not find significant differences between retention sites and random locations within the harvest unit (D.W. Linden, unpublished data), suggesting that the number of large trees (live or dead) was the primary attribute describing vegetation at a retention site.

5. Conclusion

Our multi-season, multi-species hierarchical model enabled an estimation of species-specific habitat use across multiple years while accounting for imperfect detection. Our approach followed a modeling framework that has proven effective for estimating multi-species responses to environmental changes resulting from management practices (Russell et al., 2009; Zipkin et al., 2010) and landscape-scale forest fragmentation (Zipkin et al., 2009; Ruiz-Gutierrez et al., 2010). The major benefit to this approach stems from the specification of species as a random effect governed by a community-level distribution which allows rarely detected species to be incorporated into estimates of species richness and represents a parsimonious approach to modeling multi-species datasets (Royle and Dorazio, 2008). While the parameter estimates exhibited much uncertainty given the sparse detection data, our approach made the most of the information available.

Our model suggested that bird use of retention sites in harvest units of the Pacific Northwest was positively related to the number of large trees at the site and, therefore, forest managers may increase the short-term utility of structure retention to avifauna by strategically grouping trees to maximize the richness of birds using the sites. Whether maximizing richness is an appropriate or relevant target will vary by region and specific management objectives. Our data support a minimum group size for retention sites of >10–15 green trees (with diameters >25 cm). Retention sites with 10–15 large trees will typically range in area from approximately 100–200 m^2 depending on the target planting density (e.g. 900 trees ha^{-1} for units in Snoqualmie, WA; T. McBride, Hancock Forest Management, personal communication). Our observations suggested that single green trees were rarely used compared to larger patches and given the risk of blowdown, may not be useful for meeting tree and snag retention objectives. Given that snag retention is often opportunistic, centering green-tree retention groups around high-quality snags (Bull, 2002) could serve to guide the placement of retention sites during harvest.

Regardless of the plans for green trees, retention should not be abandoned for single snags or unique wildlife trees that cannot be grouped for operational reasons – these resources should always be left in the harvest unit where operational and safety concerns allow. Snag retention is one of the most difficult management objectives for intensively managed forests given that snags have limited lifespans (i.e. amount of time standing) and that snag creation is naturally a highly stochastic process. While the current study did not assess stand-level differences in structure retention, it is understood that forest management prescriptions which are applied similarly at local scales (i.e. stands) can reduce habitat heterogeneity at larger scales as landscapes develop homogenous patterns (Lindenmayer and Franklin, 2002). Therefore, the management target should not be viewed as an unvarying prescription. Rather, varying the group sizes of green-tree retention across harvest units (e.g. many small groups vs. few large groups) will help create habitat diversity at the landscape scale.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.08.002.

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