Biological Conservation 152 (2012) 145–151

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Landscape composition influences avian colonization of experimentally created snags

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ARTICLE INFO

Article history:
Received 30 November 2011
Received in revised form 21 March 2012
Accepted 27 March 2012
Available online 23 June 2012

Keywords:
Cavity nester
Colonization
Created snags
Forest management
General estimating equations
Landscape composition
Nest-site
Spatial dispersion

ABSTRACT

Landscape composition may have a substantial influence on species use of habitat at local scales and effectiveness of structural enrichment practices (e.g., augmenting existing amounts of snags or downed logs). If sufficient mature (i.e., cavity containing) habitat exists at the landscape scale, cavity nester demand for nest sites could be reduced due to the surplus of existing sites (*habitat surplus hypothesis*). Alternatively, if mature forest acts as source habitat for cavity nesters, increased amounts of mature forest in the landscape will inflate the demand for snags in clearcuts (*habitat source hypothesis*). In Oregon, USA, we evaluated cavity nesting bird colonization of experimentally created snags distributed across a gradient in amount of mature forest at the landscape scale. We sampled 28 plots, each of which represented one of six combinations of created snag density (~0.5, 1, and 2 snags/ha) and spatial dispersion (clumps of 5–7 snags or dispersed individual snags). We tested whether early successional and mature forest species groups responded differently to plot-level treatments and if the percentage of mature forest (>40 years old) within a 1000 m radius surrounding each experimental plot influenced this response. Mature forest species more readily colonized created snags as the percentage of mature forest declined in the landscape, supporting the *habitat surplus hypothesis*. Estimated use by mature forest species increased from 7% to 17% as percent mature forest in the landscape declined from 58% to 13% (estimated for average levels of created snag density, 0.4 snags/ha, and a spatial distribution of 45 m). Colonization of snags by early seral species also increased with decreasing mature forest (from 3% to 9%), which may support the *habitat source hypothesis*. Our study suggests that creating snags in commercial harvest units is an effective practice for increasing structural complexity and maintaining nesting communities of cavity-dependent birds. At the local level, created snags should be spaced as widely as possible within individual harvest units. However, our results indicate that effectiveness of snag creation will be highest in the most intensively managed landscapes where the amount of structurally diverse habitat is limited.

1. Introduction

The rising global demand for commodities and increased rates of resource consumption have necessitated the intensive management of landscapes (Berlik et al., 2002). Intensive management has potentially dire consequences for the maintenance of biological diversity and ecosystem functions, and managers require information to allocate resources to promote positive ecological outcomes and ameliorate deleterious practices where and when they occur (Bunnell et al., 2002; Brockerhoff et al., 2008; Armsworth et al., 2010). However, ecological responses are often influenced by factors that operate at multiple spatial scales, potentially reducing the effectiveness of specific practices (Kotliar and Wiens, 1990; Bunnell and Huggard, 1999). Evaluating associations between local and landscape conditions may provide a more accurate description of the effectiveness of different management prescriptions.

Intensive forest management intends to maximize biomass of favored commercial species and can reduce the number and distribution of structural features such as snags and downed logs, thereby reducing habitat quality for forest wildlife (Bailey and Tappeiner, 1998; Hayes et al., 2005). In these situations, alternative silvicultural prescriptions may create new, or modify existing, habitat structures (e.g., standing and fallen dead wood) to increase

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http://dx.doi.org/10.1016/j.biocon.2012.03.029

retention of native wildlife populations (Chambers et al., 1997; Walter and Maguire, 2005). So-called “structural enrichment” (Rosenvald and Lõhmus, 2008) is generally thought to yield positive conservation outcomes and, in some areas, to be critical for maintaining local populations where intensive management has reduced the amount of natural habitat structures (Franklin et al., 2002; McKenny et al., 2006; Lindenmayer et al., 2010). However, relatively few structural enrichment prescriptions are directed to yield specific ecological outcomes (e.g., increased productivity or survival of a target species), or monitored over long time frames, thereby limiting confidence in their effectiveness (Rosenvald and Lõhmus, 2008; Kroll et al., 2012).

In addition, research on the interaction between structural enrichment and landscape pattern is an important information need. Management programs only rarely consider landscape pattern (Boutin and Hebert, 2002; Rosenvald and Lõhmus, 2008). Landscape pattern is not a directed outcome, but rather a cumulative outcome of numerous decisions made at the stand scale by multiple landowners with varying objectives and management regimes (Foster et al., 2003; Spies et al., 2007). However, information about population responses to structural enrichment in landscapes that vary in the amount and configuration of habitat that they contain could encourage more efficient implementation of these practices. Landscape composition is known to influence bird species occurrence (Andrén, 1994; Betts et al., 2006). We expected that this information could provide clear direction about how, where, and, potentially, when structural enrichment will be most effective.

We used an experimental approach to examine response of cavity nesting avian species to structural enrichment at local scales and landscape composition in intensively-managed forest landscapes, Oregon, USA. Specifically, we evaluated whether early seral (ES) and mature forest species (MF) use of created snags is (1) lower in landscapes with large amounts of mature forest because natural snags are not a limiting resource (*habitat surplus hypothesis*) or (2) higher in landscapes with large amounts of mature forest, as mature forest serves as a source habitat that produces a surplus of individuals to use created snags (*habitat source hypothesis*) (Fig. 1). We expected that MF species would be more sensitive to landscape composition than ES species due to their increased reliance on mature, multi-canopied forest (Zarnowitz and Manuwal, 1985; Lundquist and Mariani, 1991). Also, we evaluated whether ES and MF species groups responded differently to snag treatments that varied by density (created snags/ha) and spatial distribution (clumped or dispersed) within harvest stands. At this finer scale, we expected that, at a given snag density, dispersed snags would experience a higher level of use as intra-specific territorial dynamics would limit use of closely-spaced snags.

2. Methods

2.1. Study area

We conducted our study on Weyerhaeuser Company’s Calapooya Tree Farm, located on the west slope of the Cascade Mountain Range in Lane and Douglas Counties, Oregon, USA. The study area occurred at the junction of the Western Cascades and Coast Range Physiographic Provinces and was characterized by a maritime climate with wet, mild winters and cool, dry summers (Franklin and Dyrness, 1988). Elevations ranged from 180 m to 1375 m. The study area was dominated by natural and planted stands of Douglas-fir (*Pseudotsuga menziesii*) but other conifers were present including western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Red alder (*Alnus rubra*) was abundant in riparian areas. Understory vegetation was typically dominated by salmonberry (*Rubus spectabilis*), thimbleberry (*Rubus parviflorus*), salal (*Gaultheria shallon*), huckleberry (*Vaccinium* spp.), and swordfern (*Polystichum munitum*). Since the mid 1960s, planted stands have been managed primarily for wood production using intensive high-yield timber practices, including planting of nursery-grown seedlings, fertilization, control of competing deciduous vegetation, precommercial and commercial thinning, and clearcutting on 45–60 year rotations. However, management intensity is not consistent (i.e., practices do not occur on all stands). At the landscape level, conifer forests were interspersed with primary growth and mature 2nd growth stands (aged 40–330 years old), riparian reserves and other inoperable areas, recent clearcuts, and small gaps associated with streams, topography, and roads.

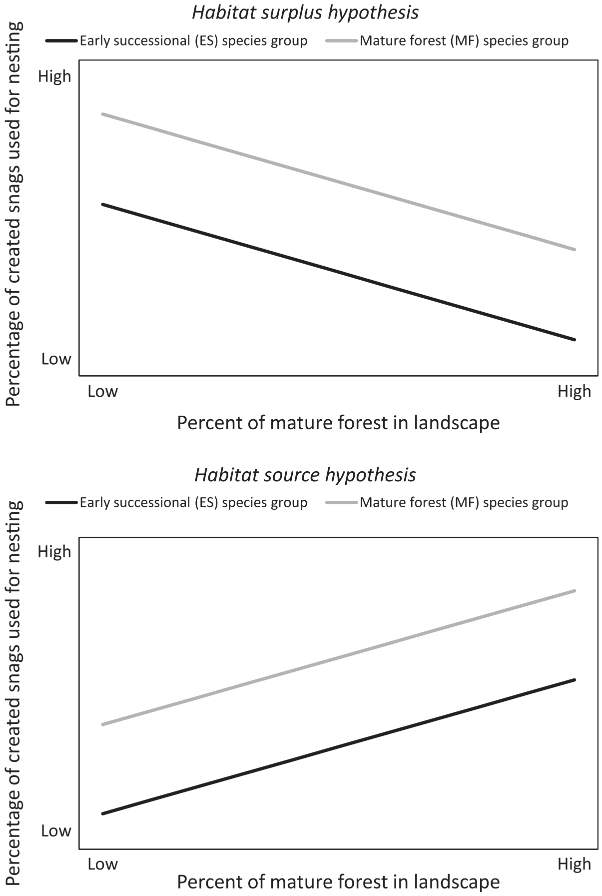

Fig. 1. Hypothesized use of created snags by mature forest (gray lines) and early successional (black lines) species groups as a function of percentage of mature forest in the landscape (landscape composition) under the *habitat surplus* (top) and *habitat source* (bottom) hypotheses. In general, mature forest species are expected to be more sensitive to landscape composition.

2.2. Experimental design and treatments

We used a completely randomized design with repeated measures (Milliken and Johnson, 1992) with harvest unit as the experimental unit. The year evaluated was a repeated factor, because snags were evaluated for nesting use in 2008, 2009, and 2010. All scheduled 1997–1999 clearcut harvest units >20 ha and with >50% of the unit available for harvesting with ground-based equipment were considered available for inclusion in the study. Treatments were defined by snag density [expressed as trees per ha (TPH)] and distribution pattern (dispersed versus clumped) (Fig. 2). We subjectively defined three different density levels

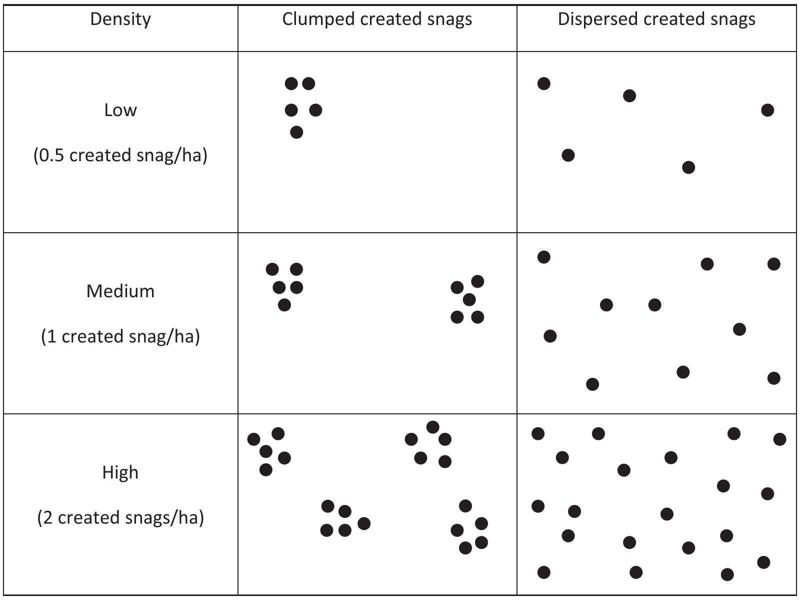

Fig. 2. Density and spatial arrangement of created snags in each of six treatment types, Cottage Grove, Oregon, USA, 2008–2010.

(low, 0.5 TPH; medium, 1 TPH; and high, 2 TPH) based on coordination with operations foresters and compromises based on logistical, safety, and financial considerations. These densities were multiplied by the area of each unit to derive a target number of trees for topping. Clumps constituted 5–7 trees/clump with trees no greater than 10 m apart from one another. For example, a 40 ha unit assigned the high density/dispersed treatment would have 80 individual trees dispersed across the unit; the high density/clumped treatment would have ~13 clumps created in the unit. We randomly assigned the 6 treatment combinations to harvest units.

We consulted with harvest managers and equipment operators regarding specific treatment prescriptions and size and distribution of created snags desired for each experimental unit, and operators had flexibility to choose trees to top based on value and location relative to safety and logistical constraints. Operators used a feller-buncher to create snags by raising the saw and topping a tree as high as the machine could safely extend (generally 5–10 m high). We instructed operators to target trees with minimum dimensions of >30.5 cm diameter at the top of the tree and >6 m high. Operators created 1111 snags on 28 experimental harvest settings in the study area from February 1997 to April 1999 (1012 snags were standing in 2008; Table 1). Harvest units ranged in size from 21 to 50 ha. Randomization resulted in the interspersion of treatments across the full range of landscape conditions that we observed in the study. We note that forest practice regulations in Oregon require retention of either five green trees (live, merchantable trees) or five snags (>10 m in height and 27 cm in diameter) per ha (Oregon Department of Forestry, 2007). Finally, the majority of the trees (>80%) used to make created snags were green, merchantable conifers. These trees do not generally have cavities or defects. As a result, most of the cavities that we monitored in our study resulting from avian foraging and nesting activities that occurred after snags were created.

2.3. Data collection

We monitored each created snag from April to August, 2008–2010, to determine nesting use by cavity nesting birds. Daily monitoring began at dawn and continued throughout the day. On occasion, monitoring was conducted for several hours prior to dusk if nearby harvest operations created safety concerns or excessive noise. Each stand was visited at least once per week throughout the monitoring season. We used audio and visual clues to locate nesting attempts in created snags. An average of 5 min was spent watching each snag to identify active nests. During each visit, field technicians recorded the number of active cavity nests in each created snag. We wanted to test whether ES species were less likely to respond to landscape composition than MF species. To calculate an accurate estimate of this relationship, we counted an individual created snag as having been used for nesting once per year by species group, even if multiple nests were constructed during that year. In contrast, a created snag could be counted as having been used by both an ES and a MF species in the same year.

We used ArcGIS (v. 9.3) and stand inventory data to calculate the amount of forest >40 years old in a 1000 m buffer around each experimental unit (following Warren et al., 2005 and Betts et al., 2006). In addition, our original treatment structure treated both density and dispersion as categorical covariates (following Arnett et al., 2010). However, enough additional variation had developed in snag density and dispersion since the time of snag creation (because some snags had fallen) that we decided to treat these measures as continuous covariates. To this end, we used ArcGIS to estimate the median nearest neighbor distance (Ripley, 1981) among created snags within a harvest unit and to calculate snag density (number/ha) in each of the 28 experimental units. Large nearest neighbor values indicate the snags are well-dispersed and small values suggest clumping (Table 1).

Finally, we estimated snag densities in mature forest stands (>40 years of age) in order to evaluate our assumption that mature stands contained adequate numbers and sizes of snags to support cavity-nesting birds. In 2009, we randomly selected nine harvest units for sampling from all harvest units 40–65 years of age in our study area. We randomly placed belt transects in each stand so that 20% of each stand would be sampled (Thompson, 2002). Each belt transect was 6.1 m wide. The length of each transect varied because transects began and ended at harvest unit boundaries, which are irregular in shape. We placed transects parallel to one another and constrained the nearest distance so that double-sampling of snags did not occur. Our population totals only included snags >8 cm in diameter. Mature stands contained an average of 3.4 snags/ha (95% CL: 1.2, 5.5) >36 cm in diameter and 14.2 snags/ha (95% CL: 6, 22.5) <36 cm in diameter.

Table 1
Original treatment factors (distribution and categorical density, as measured in 2002) and continuous covariates (as measured in 2008–2010) used to describe snag density and snag dispersion (as measured by median nearest neighbor distance) used in the present analysis, Cottage Grove, Oregon, USA, 2008–2010.

Original treatment distribution	Original treatment density	Number of stands	Number of created snags in treatment	Mean snag density (snags/ha)	Mean snag dispersion (m)
Clumped	Low	4	43	0.35 (0.20–0.50)	5 (3–7)
Clumped	Medium	4	173	0.89 (0.62–1.17)	7 (4–9)
Clumped	High	4	306	1.69 (1.14–2.23)	5 (4–6)
Dispersed	Low	6	62	0.32 (0.12–0.55)	113 (49–190)
Dispersed	Medium	5	195	0.99 (0.89–1.07)	49 (32–67)
Dispersed	High	5	233	1.54 (1.22–2.06)	42 (23–60)

2.4. Statistical analysis

We treated harvest units as the experimental units and individual snags as subsamples. In order to evaluate our main hypotheses, two additional covariates were evaluated: (1) the percent of mature (>age 40) forest in the landscape within 1000 m of the stand and (2) and whether a nesting attempt was made by an early successional (ES) or mature forest (MF) species. The binary responses assessed over time were individual nesting attempts. We used generalized estimating equations (GEEs) to model treatment (density and dispersion), year, and the covariates for cavity nester responses using the GENMOD procedure in SAS Institute (2004). The GEE method is an extension of generalized linear models that provides for correlated discrete data (Stokes et al., 2000; Fieberg et al., 2009) and is commonly used for repeated measures or longitudinal data (Diggle et al., 2002). The method requires specifying a working correlation structure, but the resulting standard errors are consistent even if the assumed structure is not correct (Stokes et al., 2000; Meyers et al., 2002). Our generalized linear model used a logit link and binomial errors with an autoregressive order one (AR1) correlation structure. AR1 implies that the correlation between measurements depends on time between measurements and decreases as time between measurements increases, which seems to be reasonable based on the biology of our study system. We verified this to be a reasonable working correlation structure by comparing the model-based standard error estimates with the final robust estimates (Meyers et al., 2002).

The main model (Table 2) included terms implied by the structure of the experiment (year, density, dispersion, and density $*$ dispersion), the covariates (species group [i.e., ES or MF] and percent of mature forest in landscape), and cross-product terms we thought could be biologically important (species group $*$ density, species group $*$ dispersion, and species group $*$ percent of mature forest). We standardized the continuous factors to minimize the potential for problems with multicollinearity. We examined Type III chi-square tests to determine the statistical significance of the factors. We computed estimated values (e.g., Fig. 3) using a more parsimonious model from which non-significant cross-product terms had been removed. Estimated values were computed on the logit scale and back-transformed to the percent scale.

3. Results

We recorded nesting use of created snags by 6 ES species (house wren *Troglodytes aedon*, northern flicker *Colaptes auratus*, purple martin *Progne subis*, red-breasted sapsucker *Sphyrapicus ruber*, violet-green swallow *Tachycineta thalassina*, and western bluebird *Sialia mexicana*) and 4 MF species (chestnut-backed chickadee *Poecile rufescens*, hairy woodpecker *Picoides villosus*, northern saw-whet owl *Aegolius acadicus*, and red-breasted nuthatch *Sitta canadensis*). Cavity nesting birds built 59, 64, and 43 ES nests and 70, 98,105 MF nests in 2008, 2009, and 2010, respectively. Four hundred and eleven (93%) of the nests were constructed by chestnut-backed chickadees, house wrens, and northern flickers.

One thousand twelve, 980, and 950 created snags remained standing in 2008, 2009, and 2010, respectively. Mean diameter at breast height of all 1012 created snags was 49.7 cm (SE = 1.7, range = 17.8–101.1) and mean height was 6.5 m (SE = 0.1, range = 3.7–10.1). Diameter at breast height ($n = 28$, $F_{5,22} = 0.79$, $P = 0.57$) and snag height ($n = 28$, $F_{5,22} = 1.12$, $P = 0.38$) did not differ among treatments. We did not find evidence of a correlation between diameter at breast height and snag height (Pearson's correlation coefficient = 0.01; 95% CL: −0.06, 0.07). The average (1 SE; range) amount of mature forest in the landscape was 0.38 (0.02; 0.13–0.58), 0.33 (0.02; 0.14–0.57), and 0.33 (0.02; 0.15–0.57) in 2008, 2009, and 2010, respectively.

We found a significant interaction between spatial dispersion of created snags and bird species group ($\chi^2 = 5.81$, $P = 0.016$; Table 2) on avian use of created snags. Use of created snags was positively associated with spatial dispersion of snags, with MF species displaying greater sensitivity to spatial dispersion than ES species (Fig. 3).

We found a significant effect of landscape composition on created snag use ($\chi^2 = 8.84$, $P = 0.003$; Table 2). Both ES and MF species groups were less likely to use created snags for nesting as the percentage of mature forest in the landscape increased (Fig. 3), a result that provided support for the *habitat surplus hypothesis*. However, this relationship was more pronounced for MF species, as the percentage of created snags used by ES species varied only from 3% to 10% across the range of values of mature forest in the landscape that we sampled (13–58%), while percent use by MF varied from 4% to 35% (Fig. 3). We did not find support for an interaction between species group and landscape composition ($\chi^2 = 1.5$, $P = 0.221$; Table 2).

4. Discussion

Large-scale field experiments can provide strong inference about operational practices that balance commercial extraction of resources and conservation of wildlife communities. For example, intensive management of forest stands can reduce the number and distribution of structural features such as snags and downed logs, thereby reducing habitat quality for organisms that rely on these features (Hayes et al., 2005). Alternative practices can retain or provide supplemental structures that will increase habitat quality at the local level (Bunnell et al., 2002; Vuidot et al., 2011), yet information is not available about population responses to local structural enrichment in landscapes that vary in the amount and configuration of habitat that they contain. Given that the acreage of intensively managed forest is increasing to meet the growing global demand for wood products and other ecological services (Binkley et al., 2005; Carnus et al., 2006), managers require information about efficient operational practices and how to implement them to increase ecological benefits (Nájera and Simonetti, 2010).

We found a significant effect of landscape composition on created snag use by cavity-dependent birds. Both ES and MF species groups were less likely to use created snags for nesting as the percentage of mature forest in the landscape increased, although the

Table 2
Type III tests for treatment and covariate effects on percent of created snags used for nesting by early successional (ES) or mature forest (MF) associated species, Cottage Grove, Oregon, USA, 2008–2010.

Contrast	Degrees of freedom	χ^2	Pr > χ^2
Year	2	3.57	0.167
Snag density (snags/ha)	1	0.15	0.702
Dispersion of snags (m)	1	3.51	0.061
Snag density (snags/ha) ⁎ dispersion of snags (m)	1	0.25	0.616
Species group (ES or MF)	1	9.07	0.003
Species group ⁎ snag density (snags/ha)	1	0.46	0.496
Species group ⁎ median nearest neighbor distance (m)	1	5.81	0.016
Percent of mature forest (>40 years old) in landscape	1	8.84	0.003
Species group ⁎ percent of mature forest (>40 years old) in landscape	1	1.50	0.221

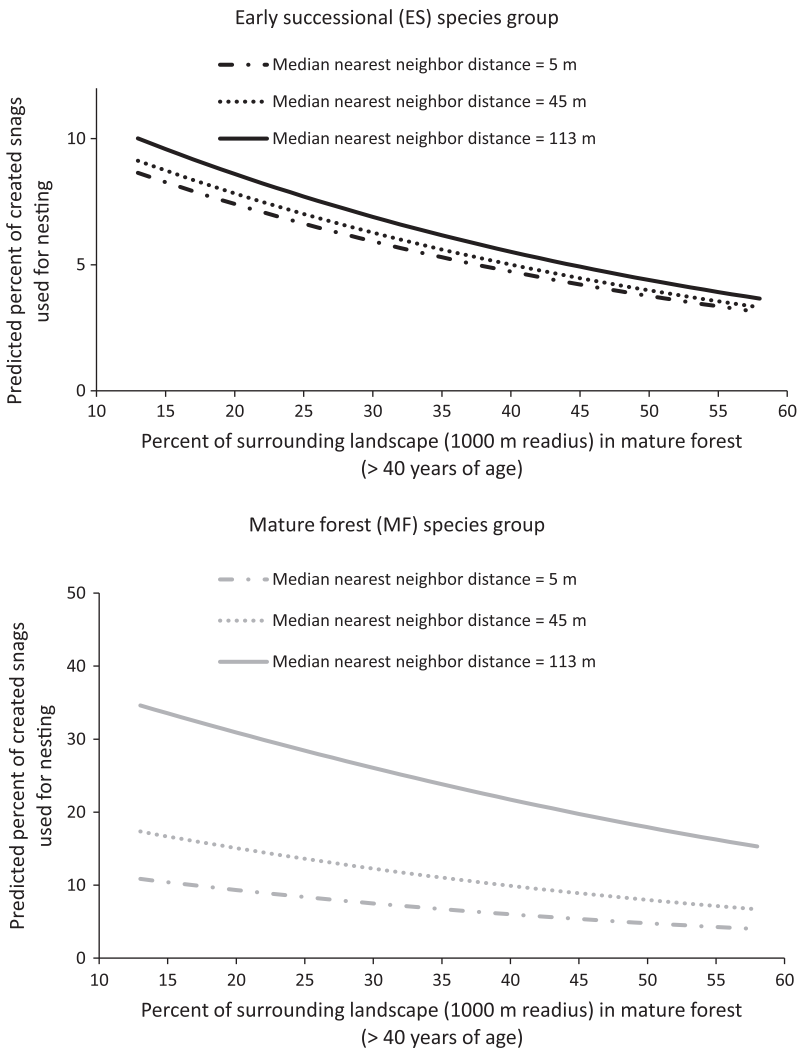

Fig. 3. Predicted percent of snags used for nesting as a function of the percent of mature forest (>40 years old) in the landscape (surrounding 1000 m buffer) and median nearest neighbor distance of created snags (5, 45, and 113 m). The panels show the relationship for early successional (ES; top) and mature forest (MF; bottom) species groups. Snag density was set to the mean value (0.4 snags/ha) and the results were averaged across years (2008–2010).

relationship was more pronounced for MF species. These results support the *habitat surplus hypothesis* although we note that the mechanisms driving these responses appear to differ by seral-stage association. In landscapes dominated by mature forest, sufficient amounts of early successional habitat might not exist to supply ES colonists to use created snags in harvest units (*the habitat source hypothesis*). In contrast, MF species may be less likely to use created snags in landscapes dominated by mature forests because snags are not a limiting factor (*the habitat surplus hypothesis*) and the subsidy provided by created snags is not required. Although Lawler and Edwards (2002) determined that landscape composition was a strong predictor of nesting habitat for three of four cavity nesting birds that they studied, our results contrast with those reported by Warren et al. (2005), who did not find strong effects of landscape composition on the occurrence of cavity nesting birds. Warren et al. (2005) posited that landscape composition cannot influence bird distributions if local habitat attributes are lacking. Our results extend this supposition, and indicate that suitable habitat at the local scale has a greater chance of remaining unoccupied if habitat is relatively abundant at the landscape scale. We presume that the effect of increasing rates of created snag colonization with mature forest loss likely has a limit; at extremely low amounts of mature forest, few, or no, dispersers should be available to settle in created snags. However, we did not observe such thresholds, despite the fact that the amount of mature forest cover ranged from 13% to 58% in our landscapes.

Raphael and Morrison (1987) recommended leaving snags in clumps to meet nesting and foraging requirements, in part because natural snags are typically found in clumps (Bull et al., 1997 although see Harmon et al., 2004). In addition, clumping snags may be more practical given factors such as efficiency of creation, equipment operation, and logistics of monitoring (Chambers et al., 1997). However, in situations where cavities are limited or clustered, agonistic or territorial interactions can be more evident (Bull et al., 1997; Walter and Maguire, 2005). Indeed, our results indicate that clumping may lead to reduced levels of nesting use. We suggest that a conservative approach to addressing this problem is to distribute created snags in both clusters and individually within individual harvest units.

In a review of deadwood distribution, Bunnell et al. (2002) suggested leaving up to 23 snags/ha in managed conifer forests. Our data suggest that stands 40 years or older will contain large snags (>36 cm dbh) at densities ~150% higher than what we evaluated in our highest density treatment, largely as a result of mortality from self-thinning (Oliver and Larson, 1996). Other researchers in our study region have reported variable snag densities required for maintaining cavity nesting bird communities, ranging from 0.3 snags/ha (Neitro et al., 1985) to 14 snags/ha (Schreiber and deCalesta, 1992). We evaluated created snags at densities on the lower end of this range and did not find an effect of snag density on nesting use. However, those species that used the created snags for nesting most frequently may not be sensitive to snag density. For example, nest survival for the three primary species utilizing created snags was generally similar to or higher than survival rates reported for these species, suggesting that created snags may be equivalent substitutes for natural snags (Kroll, unpub. data). Additional research is needed to determine what densities of created snags are required to support nesting populations of cavity-dependent birds that occur in our study area but which we observed in very low numbers (although regenerating harvest stands may lack other structural features that are required by these species, e.g., well-developed canopies).

5. Management implications

Structural enrichment is often proposed as a management tool to promote species retention on intensively managed landscapes. However, information is limited about ecological effectiveness of different structural types and how to distribute structures at local and landscape levels. Our results suggest that created snags will receive the highest levels of nesting use by cavity-dependent birds when they are widely spaced within individual harvest units. Clumping of created snags within harvest units is operationally more efficient, and may be preferred when worker safety regulations are taken into account, but our results suggest that this decision will lead to reduced levels of nesting use. In addition, we found that use of created snags was highest when the proportion of mature landscape (>40 years old) in the landscape was relatively low (<30%). That is, local structural enrichment will be most effective when snags are limited in availability at the landscape scale. Managers should consider preferentially targeting intensively managed landscapes for placement of created snags, rather than mixed-ownership landscapes where multiple values are targeted in management programs (e.g., biological reserves as well as commodity production) and snags are less likely to be a limiting factor for populations of cavity-dependent organisms.

Acknowledgments

Matthew Etterson and two anonymous reviewers provided useful comments that improved the manuscript. We thank Weyerhaeuser Company and Oregon Forest Industry Council for financial support for the study. We are grateful to F. Williams, R. Wininger, J. Christianson, H. McIntyre, K. Bachelder, and D. VanWinkle for their assistance.

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.biocon.2012.03.029.

References

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71, 355–366.

Armsworth, P.R., Armsworth, A.N., Compton, N., Cottle, P., Davies, I., Emmett, B.A., Fandrich, V., Foote, M., Gaston, K.J., Gardiner, P., Hess, T., Hopkins, J., Horsley, N., Leaver, N., Maynard, T., Shannon, D., 2010. The ecological research needs of business. J. Appl. Ecol. 47, 235–243.

Arnett, E.B., Kroll, A.J., Duke, S.D., 2010. Avian foraging and nesting use of created snags in intensively-managed forests of western Oregon, USA. Forest Ecol. Manage. 260, 1773–1779.

Bailey, J.D., Tappeiner, J., 1998. Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. Forest Ecol. Manage. 108, 99–113.

Berlik, M.M., Kittredge, D.B., Foster, D.R., 2002. The illusion of preservation: a global environmental argument for the local production of natural resources. J. Biogeogr. 29, 1557–1568.

Betts, M.G., Forbes, G.J., Diamond, A.W., Taylor, P.D., 2006. Independent effects of fragmentation on forest songbirds: an organism-based approach. Ecol. Appl. 16, 1076–1089.

Binkley, C.S., Aronow, M.E., Washburn, C.L., New, D., 2005. Global perspectives on intensively managed plantations: implications for the Pacific Northwest. J. Forest. 103, 61–64.

Boutin, S., Hebert, D., 2002. Landscape ecology and forest management: developing an effective partnership. Ecol. Appl. 12, 390–397.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951.

Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and Logs Important to Wildlife in the Interior Columbia River Basin. US Department of Agriculture, Forest Service, Portland, OR, p. 55.

Bunnell, F.L., Huggard, D.J., 1999. Biodiversity across spatial and temporal scales: problems and opportunities. Forest Ecol. Manage. 115, 113–126.

Bunnell, F.L., Boyland, M., Wind, E., 2002. How should we spatially distribute dead and dying wood? In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.F., Weatherspoon, C.P., Lisle, T.E. (Eds.), Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests. Gen. Tech. Rep. PSW-GTR-181, Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Albany, CA, USA, pp. 739–752.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. J. Forest. 104, 65–77.

Chambers, C.L., Carrigan, T., Sabin, T.E., Tappeiner, J., McComb, W.C., 1997. Use of artificially created Douglas-fir snags by cavity-nesting birds. Western J. Appl. Forest. 12, 93–97.

Diggle, P.J., Heagerty, P.J., Liang, K.Y., Zeger, S.L., 2002. Analysis of Longitudinal Data. Oxford University Press, Oxford, England.

Fieberg, J., Rieger, R.H., Zicus, M.C., Schildcrout, J.S., 2009. Regression modelling of correlated data in ecology: subject-specific and population averaged response patterns. J. Appl. Ecol. 46, 1018–1025.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. Bioscience 53, 77–88.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecol. Manage. 155, 399–423.

Harmon, M.E., Franklin, J.F., Swanson, F., Sollins, P., Gregory, S.V., Lattin, P.D., Andersen, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Leinkaemper, G.W., Cromack Jr., K., Cummins, K.W., 2004. Ecology of coarse woody debris in temperate ecosystems. In: Caswell, H. (Ed.), Advances in Ecological Research, vol. 34. Elsevier, Oxford, UK, pp. 59–234.

Hayes, J.P., Schoenholtz, S.H., Hartley, M.J., Murphy, G., Powers, R.F., Berg, D., Radosevich, S.R., 2005. Environmental consequences of intensively managed forest plantations in the Pacific Northwest. J. Forest. 103, 83–87.

Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59, 253–260.

Kroll, A.J., Lacki, M.J., Arnett, E.B., 2012. Research needs to support management and conservation of cavity-dependent birds and bats on forested landscapes in the Pacific Northwest, USA. Western J. Appl. Forest., http://dx.doi.org/10.5849/wjaf.10-021.

Lawler, J.J., Edwards Jr., T.C., 2002. Landscape patterns as habitat predictors: building and testing models for cavity-nesting birds in the Uinta Mountains of Utah, USA. Landscape Ecol. 17, 233–245.

Lindenmayer, D.B., Knight, E., McBurney, L., Michael, D., Banks, S.C., 2010. Small mammals and retention islands: an experimental study of animal response to alternative logging practices. Forest Ecol. Manage. 260, 2070–2078.

Lundquist, R.W., Mariani, J.M., 1991. Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. Pacific Northwest Research Station, Forest Service, US Department of Agriculture, Portland, OR, USA, pp. 221–240.

McKenny, H.C., Keeton, W.S., Donovan, T.M., 2006. Effects of structural complexity enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood forests. Forest Ecol. Manage. 230, 186–196.

Meyers, R.H., Montgomery, D.C., Vining, G.G., 2002. Generalized Linear Models with Applications in Engineering and Other Sciences. John Wiley and Sons, New York, NY, USA.

Milliken, G.A., Johnson, D.E., 1992. Analysis of Messy Data: Designed Experiments, vol. 1. Chapman & Hall, London, UK.

Nájera, A., Simonetti, J.A., 2010. Enhancing avifauna in commercial plantations. Conserv. Biol. 24, 319–324.

Neitro, W., Mannan, R.W., Taylor, D., Binkley, V.W., Marcot, B.G., Wagner, F.F., Cline, S.P., 1985. Snags (wildlife trees). In: Brown, E.R. (Ed.), Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. US Department of Agriculture, Forest Service, Publication Number R6-F&WL-192-1985, Portland, OR, pp. 129–169.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. John Wiley and Sons, New York, New York, USA.

Oregon Department of Forestry, 2007. Forest Practice Administrative Rules and Forest Practices Act. Oregon Department of Forestry.

Raphael, M.G., Morrison, M., 1987. Decay and dynamics of snags in the Sierra Nevada, California. Forest Sci. 33, 774–783.

Ripley, B.D., 1981. Spatial Statistics. John Wiley & Sons, New York, NY, USA.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. Forest Ecol. Manage. 255, 1–15.

SAS Institute, 2004. The SAS System for Windows, Version 9.1. SAS Institute, Inc., Cary, North Carolina, USA.

Schreiber, B., deCalesta, D.S., 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. Forest Ecol. Manage. 50, 299–316.

Spies, T.A., McComb, B.C., Kennedy, R.S.H., McGrath, M.T., Olsen, K., Pabst, R.J., 2007. Potential effects of forest policies on terrestrial biodiversity in a multi-ownership province. Ecol. Appl. 17, 48–65.

Stokes, M.E., Davis, C.S., Koch, G.G., 2000. Categorical Data Analysis Using the SAS System. SAS Institute Inc., Cary, NC, USA.

Thompson, S.L., 2002. Sampling, second ed. John Wiley and Sons, Inc., New York, NY, USA.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, G., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. 144, 441–450.

Walter, S.T., Maguire, C.C., 2005. Snags, cavity-nesting birds, and silvicultural treatments in western Oregon. J. Wildlife Manage. 69, 1578–1591.

Warren, T.L., Betts, M.G., Diamond, A.W., Forbes, G.J., 2005. The influence of local habitat and landscape composition on cavity-nesting birds in a forested mosaic. Forest Ecol. Manage. 214, 331–343.

Zarnowitz, J.E., Manuwal, D.A., 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. J. Wildlife Manage. 49, 255–263.