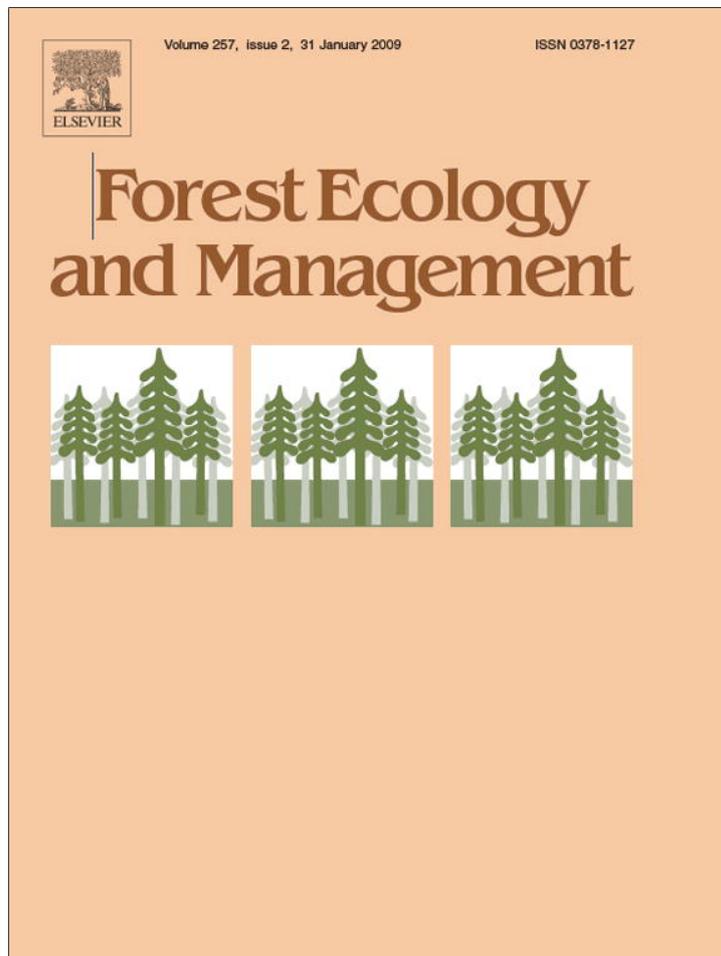


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Edge effects for songbirds vary with forest productivity

David B. McWethy^{a,*}, Andrew J. Hansen^a, Jacob P. Verschuy^b^a P.O. Box 173460, Ecology Department, Montana State University, Bozeman, MT, 59717, USA^b 3604 Seneca Dr., Mount Vernon, WA 98273, USA

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ABSTRACT

We hypothesized that edge density more strongly influences species abundances in more productive environments. To test this hypothesis we collected songbird point count data across broad biophysical gradients and gradients in forest patch edge density in the west and east slopes of the Cascade Mountains of Oregon and Washington, U.S.A., which differ in ecological productivity. We then analyzed bird response (75 species) at both the species and community level to gradients in edge density (m/ha) of open and closed-canopy forest within 1-km radius landscapes. We found that (1) differences in vegetation and structural conditions between open and closed-canopy stands were significantly greater at a highly productive landscape than a landscape with intermediate levels of productivity; (2) more bird species responded to changes in edge density in more productive west-slope Cascade forests than less productive east-side Cascade forests; (3) pooled abundance data from both sites showed that 25 of the 60 most abundant bird species responded significantly to the interaction between forest productivity and changes in landscape-level edge density; and, (4) at the community level, ordinations showed that bird community similarity in the productive west-slope Cascade forests differed across low and high levels of edge density whereas no such differentiation occurred in harsh, east-side Cascade forests. These results provide some of the first evidence supporting the hypothesis that edge effects are more pronounced in productive west-side forests where higher levels of edge density benefit generalist and open-canopy species while negatively influencing closed-canopy species. Consequently, forest management aimed at supporting species diversity will be most effective if tailored to ecosystem productivity.

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1. Introduction

A fundamental question in forestry is how to manage spatial patterns of timber harvest and other disturbances to best achieve biodiversity objectives (Perry, 1994). Current approaches in the northwestern United States recommend minimizing creation of forest edges to avoid loss of forest interior species (Lindenmayer and Franklin, 2002; Kohm and Franklin, 1997). It is poorly understood, however, whether species responses to forest edges vary across different types of ecosystems. Theory and initial empirical tests suggest that the response of biodiversity to edge effects may vary among ecosystems as a function of ecosystem productivity and accumulation of biomass (Verschuy^{et al.}, 2008; Hansen and DeFries, 2007; Gaston, 2000; Huston, 1979; Hansen *et al.*, in review). The Biomass Accumulation Hypothesis (Hansen and Rotella, 2000, Hansen *et al.*, in review) asserts that edge effects have the highest magnitude of influence in ecosystems that accumulate high levels of biomass.

Edge effects are one component of habitat fragmentation that have been widely studied by ecologists (Noss *et al.*, 2006; Harper *et al.*, 2005; Murcia, 1995), and are the result of the interaction between two adjacent ecosystems that are separated by an abrupt transition (Murcia, 1995). Three categories of edge effects have been identified: abiotic effects, direct biological effects, and indirect biological effects (Harper *et al.*, 2005). Abiotic effects include the alteration of microclimate and nutrients from patch exterior to interior. Change in species abundances is an example of a direct biological effect. Edge conditions might lead to indirect biological effects such as alterations of species interactions, including predation, herbivory, pollination, and seed dispersal. Efforts to develop general theory identifying situations where edge effects are most pronounced have focused largely on site-level factors (Harrison and Bruna, 1999). Harper *et al.* (2005) suggested particular ecosystem traits that influence edge effects including climate, disturbance, and community structure.

The Biomass Accumulation Hypothesis builds on the perspectives of Harper *et al.* (2005). The hypothesis asserts that edge effects have the highest magnitude of influence in ecosystems that accumulate high levels of biomass. In this paper, we test the hypothesis that bird response to the density of forest/non-forest

* Corresponding author. Tel.: +1 406 579 9995; fax: +1 406 994 6923.

E-mail address: dmcwethy@montana.edu (D.B. McWethy).

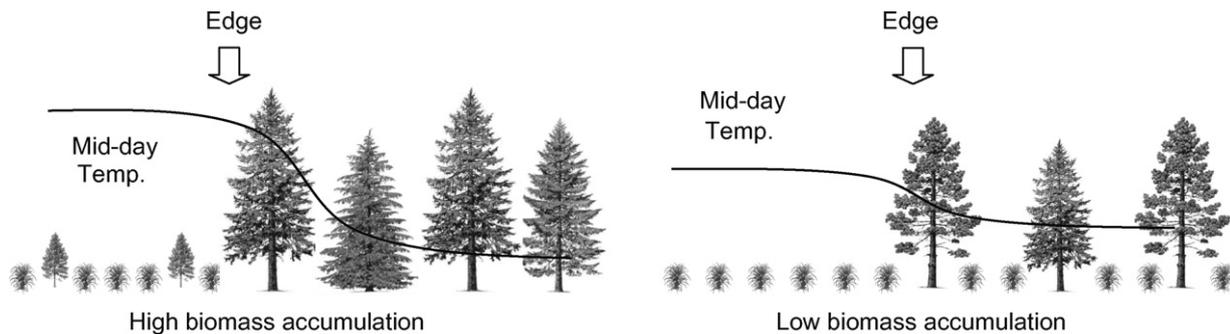


Fig. 1. Forest productivity and environmental gradients. Theoretical representation of environmental gradients between early-seral and later-seral habitats at a productive landscape and a less productive landscape (Hansen and Rotella, 2000).

edges varies across two landscapes differing in ecosystem productivity. If correct, this hypothesis offers a framework for effectively tailoring management of forest spatial patterns to local ecosystems.

The mechanism underlying the hypothesis involves the contrast in vegetation structure between disturbance patches and mid to late-seral forest (Fig. 1). Severe disturbance substantially reduces vegetation biomass. The gradient in vegetation density from disturbance patch to adjacent forest is predicted to be steepest in high biomass forests. Thus, in ecosystems with high biomass accumulation, gradients in microclimate, disturbance, and the resulting ecological processes should show high contrast between edge and interior habitats (Chen et al., 1995).

This steeper gradient in resources and conditions may be more finely partitioned by plants and animals, leading to a greater percentage of species specializing on forest interior, edge, or disturbance patch interior conditions. In contrast, we expect that less dense vegetation in ecosystems with low biomass accumulation result in gradients in microclimate and other processes that are less pronounced. In other words, environmental conditions will be relatively similar between disturbance patches and the more open forests that characterize these systems. Hence, more species will use forest without distinguishing between edge and interior or forest and disturbance patch.

The Biomass Accumulation Hypothesis was initially tested using published studies for forests ranging in biomass from low productivity boreal forests to high productivity tropical rainforests (Hansen et al., in review). Magnitude of edge effects for microclimate and proportion of mammal, bird, and beetle species specializing in forest interior were found to vary significantly with forest biomass. These results suggested that edge effects were pronounced in very high biomass forests but hardly discernable in very low biomass forests. Differences in edge effects between intermediate and high biomass forests were not resolvable in the study.

The Biomass Accumulation Hypothesis is important to management because it provides guidance for balancing habitat needs of species specializing on early-seral, edge, and late-seral habitats. Research and management on federal lands in the northwestern United States has emphasized the effects of fragmentation on late-seral species, especially those specializing on old growth forest interiors (USDA and BLM, 1994). The justification was that old-growth forests were being rapidly harvested, leading to the loss of some old-growth dependent species. However, early-seral and edge specialist species are also recognized as important components of biodiversity. In the U.S., the National Forest Management Act specifies retaining well distributed viable populations of all native vertebrates (National Forest Management Act of 1976). In the northwestern U.S., many early-seral species are considered at risk; Partners in Flight lists as sensitive a similar number of early-

seral bird species as late-seral species (Panjabi et al., 2005). Some early-seral species may be at risk in the region because of dramatic reductions in logging on federal lands, as specified in the Northwest Forest Plan (USDA and BLM, 1994). Thus, forest managers in the region will benefit from guidance on managing landscape pattern to maintain both early and late-seral species.

In this paper, we test the Biomass Accumulation Hypothesis by comparing edge effects between a west-side Cascade Mountains landscape with high productivity and an east-side Cascade Mountains landscape of intermediate productivity. We tested predictions involving vegetation structure and bird species and communities. Predictions were:

- (1) Vegetation and forest structure (canopy closure, understory herbaceous cover, volume of coarse woody debris and structural complexity) differs more between early and late-seral forest in the more productive landscape.
- (2) More bird species will specialize in either open-canopy, closed-canopy, or edge in productive systems; thus more species abundances will vary with edge density in productive systems. Specifically:
 - (2a) More bird species will respond to changes in edge density in the more productive landscape.
 - (2b) The interaction between landscape-level edge density and productivity is a significant predictor of relative species abundance.
 - (2c) In the more productive landscape, bird communities (composition and relative abundance) in stands surrounded by low edge density are significantly different from bird communities surrounded by high edge density, but less so in the intermediate productivity landscape.

We consider this comparative study a reasonable starting point for testing whether the effects of edge density vary across productivity levels in predictable ways. For this initial test, we use a correlational approach between two landscapes differing in productivity. These study areas are in relatively close proximity lying on the east and west side of the Cascade Range and overlap in dominant forest type. Hence, while correlational and involving only two study areas, this study is a strong initial test of the theory. If correct, this hypothesis offers a framework for effectively tailoring management of forest spatial patterns to local ecosystems.

2. Methods

2.1. Study areas

The study included two landscapes in the northwestern United States, Springfield, Oregon, a productive low-elevation landscape located in the foothills of the west-side Cascades surrounding the

Table 1
Characteristics of study sites. standard deviation (SD) shown in parentheses ().

	Springfield	Cle Elum
Elevation range (m)	300–1000	600–1800
Annual precipitation (cm)	120–200	50–200
Edge density (m/ha)		
Range	0.97–53.29	6.73–73.22
Mean	23.55	29.54
SD	10.87	13.67
Landscape pattern, mean (SD)		
Connectivity index	0.91 (0.15)	0.94 (0.03)
Total core area (ha)	158.98 (46.63)	127.46 (55.62)
Percent landscape forested	78.93 (12.27)	72.38 (14.50)
Productivity (g C m ⁻² day ⁻¹)		
Range	12.9–18.5	5.6–10.9
Mean	14.2	9.2
SD	1.1	1.2
Forest zone (Franklin and Dyrness, 1988)	<i>Tsuga heterophylla</i>	<i>Abies grandis</i> and <i>Pseudotsuga menziesii</i> , <i>Abies lasiocarpa</i> , <i>Pinus ponderosa</i>
Dominant tree species	Douglas fir (<i>Pseudotsuga menziesii</i>), western hemlock (<i>Tsuga heterophylla</i>), western redcedar (<i>Thuja plicata</i>), grand fir (<i>Abies grandis</i>)	Grand fir (<i>Abies grandis</i>), Douglas fir (<i>Pseudotsuga menziesii</i>), subalpine fir (<i>Abies lasiocarpa</i>), ponderosa pine (<i>Pinus ponderosa</i>)
Land ownership	Weyerhaeuser, BLM and USFS	Plum Creek Timber Co. and USFS
Basal area, mean (SD)		
Shrub-sapling (SS)	2.58 (0.61)	3.63 (1.76)
Small-tree (ST)	4.99 (1.57)	4.18 (1.39)
Mature-tree (MT)	7.86 (2.86)	6.57 (1.71)
Large-tree (LT)	11.57 (4.50)	7.20 (2.01)
Structural conditions	Mostly second and third growth, with a wide variety of structural conditions	Mostly second growth, increased structural retention on federal lands

Willamette Valley and Cle Elum, Washington, a less productive landscape east of the Cascade crest (Table 1, Fig. 2). Landscape selection emphasized forest sites that contained a similar pool of bird species across gradients in forest productivity. The Springfield site is dominated by Douglas-fir (*Pseudotsuga menziesii*) forests but western hemlock (*Tsuga heterophylla*), western red-cedar (*Thuja plicata*), and grand fir (*Abies grandis*) are important canopy dominants in some areas. The Cle Elum site spans a wider gradient in forest productivity with wetter hemlock/fir (*Tsuga heterophylla*/*Abies* spp.) forests on wetter sites, Douglas-fir forests and grand fir forests on intermediate sites, and ponderosa pine (*Pinus ponderosa*) forests on drier sites. Similar gradients in forest structural conditions and forest edge density are represented within each site (Table 1).

2.1.1. Springfield, OR

Weyerhaeuser's Springfield and Cottage Grove tree farms and surrounding BLM and USFS lands are located east of Eugene, Oregon, in the western foothills of the Oregon Cascades (Fig. 2). The study site ranges in elevation from 300 to 1000-m and precipitation averages 120–200-cm annually (Table 1). Mean monthly minimum temperatures range from 4 to 5 °C. Mean monthly maximum temperatures range from 16 to 17 °C. Productivity, represented by modeled values of gross primary productivity (GPP) (g C m⁻² day⁻¹) (Running et al., 2004) ranges from 12.9 to 18.5 with a mean of 14.2 and a standard deviation of 1.1. This area is within the *Tsuga heterophylla* Forest Zone (Franklin and Dyrness, 1988) and dominant species are Douglas-fir, western hemlock, western red cedar, and grand fir. However, hardwood species become more abundant on drier microsites at the southern end of the study landscape (e.g. oak [*Quercus* spp.], chinquapin [*Castanopsis chrysophylla*] and Pacific

madrone [*Arbutus menziesii*]). Land ownership is a checkerboard of Bureau of Land Management (BLM) and private lands bordered by the Willamette National Forest and the H.J. Andrews Experimental Forest. As a result of this ownership pattern, more than a third of the landscape contains older forests (>100 yrs.) on public lands, whereas the remaining private lands are short rotation (<60 yrs.) plantations of Douglas-fir (Ripple et al., 1991).

2.1.2. Cle Elum, WA

The Cle Elum landscape is located along the I-90 corridor between 600 and 1800-m in Washington's Central Cascades (Fig. 2). Plum Creek Timber Company's ownership totals roughly 57,000-ha distributed in a checkerboard pattern within Mount Baker-Snoqualmie and Wenatchee National Forest land. Precipitation varies from >200-cm per year near the crest of the Cascades to <50-cm per year in east-side forests at lower treeline (Table 1). Mean monthly minimum temperatures range from 0 °C near the Cascade crest to 2 °C further east. Mean monthly maximum temperatures range from 7 °C near the Cascade crest to 14 °C further east. This area is within the *Abies grandis* and *Pseudotsuga menziesii*, *Abies lasiocarpa*, and *Pinus ponderosa* Forest Zones (Franklin and Dyrness, 1988) and the dominant tree species are grand fir, Douglas fir, subalpine fir (*Abies lasiocarpa*), and ponderosa pine. Gross primary productivity estimates range from 5.6 to 10.9 (g C m⁻² day⁻¹) with a mean of 9.2 and a standard deviation of 1.2. Land ownership is a checkerboard of private (Plum Creek Timber Company) and National Forest land resulting in approximately a third of the landscape (mostly public lands) containing older forests (>100 yrs.) with increased structural retention and younger (<60 yrs.), mostly second growth forests on private lands.

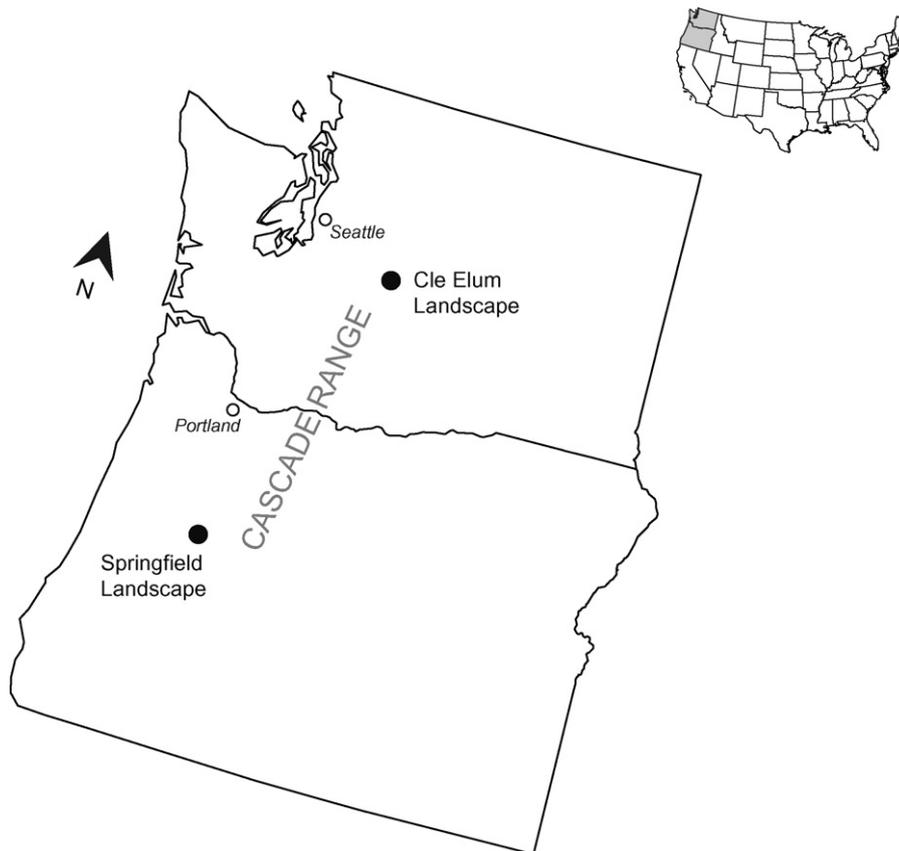


Fig. 2. Study area. Location of two study landscapes, Springfield, OR and Cle Elum, WA, USA.

2.2. Study design

We quantified how bird abundances in the sampled stands varied with density of forest edges within 1-km circular radii of the stands. Edges were defined as the linear edge between open canopy (mean canopy closure = 11%) and closed-canopy stands (mean canopy closure = 74%). Bird response was quantified as abundances of individual species and degree of overlap between open-canopy and closed-canopy bird communities. First, we compared the number of species of birds with abundances significantly related to edge density between the two landscapes and the degree of overlap between the open and closed canopy guilds. Next, we pooled abundance data for each bird species from both sites and tested whether site productivity modified the relationship between species abundance and edge density. Additionally, we examined how bird community organization differed between low and high levels of edge density at each landscape.

2.3. Bird data

We sampled birds at Springfield and Cle Elum during the breeding season in 2003, 2004, and 2005, with 2 years of sampling completed at each bird census point. Five bird census points were averaged to represent a forest stand and were positioned along a transect with 150-m separation between adjacent points. All census points were located greater than 150-m from any stand edge. During each survey year, each stand of five points was sampled three times during the breeding season (15 May–10 July). We sampled a total of 48 stands in Springfield and 64 stands in Cle Elum. Stands were typically several kilometers away from other stands and were greater than 20 ha in area. The ample number of

surveys used to represent each stand increased the likelihood that rare birds with low detectability would still be adequately sampled. The survey order and observer were varied throughout the season to avoid associated biases.

The manner in which data were recorded was consistent with the point count survey guidelines described by Ralph et al. (1995) within a 10-minute time interval. Every bird seen or heard was recorded with an associated first detection distance from the census point. Distances were measured using a laser rangefinder which estimates distance to objects with an accuracy of ± 2 -m. Analysis of detection probabilities using program DISTANCE (Thomas et al., 2002) revealed that the probability of detection did not change within 50-m for approximately 80% of species. For bird species where detectability was low, we examined if detectability varied between habitat types or seral stage or if they were disproportionately associated with any particular habitat type or seral stage. We found that detectability for these species was not biased by habitat type or seral stage. Therefore, there was no need to adjust species abundance for detectability. Analyses were done across all bird species and for a subset of species considered to be at risk. Partners in Flight (PIF) has identified bird species of regional concern for the Northern Pacific Rainforest Bird Conservation Region based on habitat requirements, threats to habitat, population trends, and other factors (Panjabi et al., 2005). Analyses were done on these species of regional concern to evaluate if species at risk responded to edges differently than the bird community at large and are identified in the results.

2.4. Vegetation and forest structure data

We sampled vegetation and forest structure at each point-count station once during the two years of survey work (Table 2). To capture characteristics of the entire survey stand we established

Table 2
Forest structure predictors (stand description measurements) and area of inventory.

Forest structure predictor	Definition	Area of inventory
Herbaceous cover	Percent understory cover that is herbaceous recorded as a decimal	20 0.25 m ² plots
Volume of coarse woody debris	Volume (m ³ /ha) $V = H \times (D^2 + d \times D + d^2) \times (\pi/12)$ per point	20 4-m radius plots
Horiz. var. in tree size diversity	Standard deviation of tree size diversity across 4 subplots	20 8-m radius plots
Structural complexity index	Tree size div. \times the horiz. var. in tree size div. among sub plots \times 100	20 8-m radius plots
Tree size diversity	Mean Shannon-Weiner tree size div. calculations (across 4 subplots): $-\sum(p_i \times \ln(p_i))$ where p_i = prop. of trees in size class i	20 8-m radius plots
Canopy closure	Percent canopy closure	Densimeter at 80 points

four sub-plots 20-m from each of the 5 survey stations in the four cardinal directions. Within each of the four sub-plots, attributes were measured within either a 0.25-m² sub-plot located 2-m north of the center of each plot, or within a 2-, 4-, or 8-m radius around the sub-plot center. Data collected during vegetation surveys resulted in a number of predictors representing the variation in size and horizontal distribution of trees, and shrubs, as well as canopy and understory measures (Table 2).

2.5. Landscape pattern mapping

To derive landscape-level predictor data to test our hypotheses, we used aerial photographs to map different patch types around each of the stands sampled for birds. We delineated two fundamental patch types, early-seral (open-canopy patch types) and mid/late-seral (closed-canopy patch types), based on the following criteria: (1) tree size class, stand age and understory conditions (i.e. relative dominance of shrubs, forbs and young seedlings vs. pole, saw-timber and dominant canopy trees); and, (2) the percent canopy cover of dominant canopy trees. Open-canopy stands consisted of very young forests (mean dbh = 8 cm) dominated by shrub communities and seedlings of small stature and low percentages of overstory canopy cover (mean canopy cover = 11%). Closed-canopy stands were dominated by canopy trees with larger mean size classes (mean dbh = 48 cm), few shrubs and higher mean percent forest canopy cover (mean percent canopy cover 74%).

Minimum patch size for mapping was 1-ha and >50-m wide in the narrowest dimension. We did not delineate patches smaller than 1-ha in size and those that were <50-m wide because of the resolution of the aerial photographs and the resolution of patch sizes assumed to be relevant to bird territory sizes [i.e. smallest estimated home range of bird species found in the study area (Brown, 1985)]. The minimum width was chosen to avoid delineating narrow patches that might skew quantification of landscape patch pattern with small narrow patches that are likely less important biologically to birds. We obtained forest patch attribute information from digital layers of stand age, canopy dominant, ownership and management history and validated information with field visits. Using Weyerhaeuser and U.S. Geological Survey (USGS) digital orthophotos, we digitized forest patches manually and used field information to validate forest patch attribute information. Digital polygon maps of forest patches within a 1-km circular radius surrounding survey stands were then imported into the landscape analysis program FRAGSTATS to derive landscape pattern predictor data (McGarigal and Marks, 1995).

2.6. Landscape predictor data

The density of edges between open and closed-canopy forest patches was quantified using FRAGSTATS software (McGarigal and Marks, 1995). Values representing the density of linear forest edge

across the landscape (edge density, m/ha) ranged from 1 to 53-m/ha at Springfield and from 7 to 73-m/ha at Cle Elum (Table 1). To obtain rates of biomass accumulation for our survey sites, we used remotely derived estimates of gross primary productivity (GPP: g C m⁻² day⁻¹) at a 1-km resolution by the MODIS satellite sensor (Running et al., 2004) (Table 1). Remotely derived estimates of GPP allowed us to derive predictor data at large scales and best represented productivity across our survey network. A comparison of net primary productivity (NPP) and GPP as predictors of regional and continental-scale bird richness showed that GPP was a much stronger predictor of bird richness than NPP (Phillips et al., 2008). Accuracy assessments of remotely sensed energy and productivity predictors are included in Heinsch et al. (2006, 2003). Productivity data were averaged over the years 2003–2005 to correspond with the bird sampling.

2.7. Data analysis

2.7.1. Forest structure across forest edges

Differences in mean values of key structural characteristics across seral stages and between open and closed-canopy stands were evaluated by fitting an analysis of variance model using the function aov in R-statistical program (Chambers et al., 1992). Forest structural variables included in analyses were: percent canopy closure, herbaceous cover, volume of coarse woody debris and an index of forest structural complexity. Where significant differences between factor level means were found we then used a Tukey's Honest Significant Difference test (Tukey HSD) to determine which factor level means were significantly different ($P < 0.05$) (Yandell, 1997). To test our prediction that mean structural values at the Springfield site were greater than at the Cle Elum site, we used bootstrap resampling of mean forest structural values for each canopy level to derive a sample of differences between mean forest structural values for each site. Sample sizes for the resampling were chosen based on the minimum number of samples collected for each canopy level. We then used a Kolmogorov–Smirnov test (Durbin, 1973) to determine whether the sample of differences from Springfield were significantly different than the sample of differences from Cle Elum in the direction we predicted: the difference between vegetation structural characteristics between open and closed-canopy stands would be greater in Springfield than Cle Elum.

2.7.2. Response to edge Density—bird species level

To test whether bird abundance was correlated to landscape-level edge density, we used linear regression. Examining diagnostic plots, we determined that a natural log transformation of bird species abundance data adequately met normality and constant variance assumptions necessary for linear regression analyses. However, because we were analyzing count data, we also considered Poisson and negative binomial distributions to assess the relationship between edge density and bird abundance. The

pattern of results was consistent regardless of the distribution chosen.

Linear regression model:

$$\log(y) = \beta_0 + \beta_1(X_1) \quad (1.1)$$

where:

$$\log(y) = \beta_0 + \beta_1(\text{edge_density}).$$

2.7.3. Ecosystem productivity effects—Bird species level

We tested for landscape effects across gradients in productivity both within and across sites. This allowed us to control for differences in site characteristics (other than productivity) that might confound bird response to landscape effects. We used a proportional Z-test to test the prediction that the difference between the overall proportion of significant responses to changes in edge density (m/ha) in Springfield would be greater than the overall proportion of significant responses to changes in edge density in Cle Elum. A Kolmogorov–Smirnov test was also used to determine whether the distributions of our response data for each site (*P*-values for each set of 60 birds by site) were significantly different ($P < 0.05$) (Durbin, 1973).

Using combined bird abundance data from both landscapes, we used linear regression with an interaction term to assess whether individual species responses to changes in edge density in the surrounding landscape were modified by site productivity. We used this approach to determine whether the interaction between edge density and productivity was significant both across and within sites.

We used MODIS derived estimates of GPP ($\text{g C m}^{-2} \text{ day}^{-1}$) to represent productivity. The following equation represents the general form of the interaction tested for species at each site. We quantified the number of species where the interaction between edge density and GPP was significant ($P < 0.05$). For species where the interaction term was significant, we then plotted fitted values at three different levels of productivity to examine changes in the slope of species response to changes in edge density.

$$y = \beta_0 + \beta_1(X_1) + \beta_2(X_2) + \beta_3(X_1 \times X_2) \quad (1.2)$$

where:

$$y = \beta_0 + \beta_1(\text{edge_density}_1) + \beta_2(\text{GPP}_2) + \beta_3(\text{edge_density}_1 \times \text{GPP}_2)$$

2.7.4. Ecosystem productivity effects—bird community level

To compare community-level response to edge effects we used dissimilarity matrices and Non-metric Multidimensional Scaling (NMDS) (Roberts, 2006; Venables and Ripley, 2002; Bray and Curtis, 1957) to plot ordinations of bird assemblages found within each forest stand at each landscape.

To evaluate bird community similarity in stands surrounded by low edge density and high edge density, we calculated a dissimilarity matrix (Bray–Curtis measure) based on species abundance within a survey stand (Bray and Curtis, 1957). We then used NMDS to plot an ordination based on the Bray–Curtis measure (R Development Core Team, 2006). After plotting NMDS ordinations of survey stands surrounded by low and high edge density, we calculated a within cluster (all bird assemblages within survey stands surrounded by low edge density and then by high edge density separately) to between cluster (bird assemblages within the low edge density stand cluster versus bird assemblages within the high edge density stand cluster) ratio to determine whether bird assemblages surrounded by low and high levels of

edge density were distinctly different from each other (functions *permtest* and *partana* developed by Roberts, 2006). We performed 1000 permutations of this calculation to derive a *P*-value associated with the test that the within-cluster to between-cluster ratio is >1 .

3. Results

3.1. Landscape structural and productivity characteristics

Measurements of edge density surrounding open and closed-canopy stands were similar between the two landscapes. Open-canopy stands were surrounded by landscapes with slightly higher edge densities than closed-canopy stands for both Springfield and Cle Elum. In Springfield, the mean edge density surrounding open-canopy stands (25 m/ha, SD = 8.7) was higher than closed-canopy stands (21 m/ha, SD = 12.3). Similarly, in Cle Elum, the mean edge density surrounding open-canopy stands (33 m/ha, SD = 10.6) was also higher than closed-canopy stands (25 m/ha, SD = 15.2). These results show that a small amount of covariation exists between canopy levels (open or closed) of the survey stand and edge density in the surrounding landscape at both sites.

The distributions of estimated GPP values for the Springfield and Cle Elum landscapes show little overlap and the sites together span more productive landscapes within North America (North American values: range = 0–28 $\text{g C m}^{-2} \text{ day}^{-1}$, mean = 8.2, SD = 1.9). At the Springfield landscape, GPP values ranged from 12.9 to 18.5 $\text{g C m}^{-2} \text{ day}^{-1}$ with a mean of 14.2 and a standard deviation of 1.1. At the Cle Elum landscape, GPP values ranged from 5.6 to 10.9 $\text{g C m}^{-2} \text{ day}^{-1}$ with a mean of 9.2 and a standard deviation of 1.2.

3.2. Prediction 1: Vegetation structure across edges

Mean differences between canopy closure, understory herbaceous cover, volume of coarse woody debris and structural complexity index were greater between open and closed-canopy stands in Springfield than in Cle Elum (Table 3, Figs. 3–4). A comparison of bootstrap resampling of these differences between canopy levels at each site was significant for all forest structural variables (Table 3).

3.3. Prediction 2: Ecosystem productivity effects

3.3.1. Individual species

Bird response to changes in edge density was more pronounced at the productive site, Springfield (Tables 4–5). A Z-test of proportional difference showed that the proportion of birds responding to changes in edge density at each site was significantly different ($P < 0.001$). A Kolmogorov–Smirnov test of the two samples of *P*-values also indicates that the responses from the two sites were significantly different ($P < 0.001$). At the Springfield site, 25 of 60 species (42%) responded significantly to changes in edge

Table 3

Mean differences between vegetation structural values for open and closed-canopy stands at each landscape.

Variable	Springfield	Cle Elum	<i>K</i>	<i>P</i>
% Canopy closure	0.55	0.48	0.57	<0.0001
Understory herbaceous cover	3.32	0.99	0.64	<0.0001
Volume of coarse woody debris (m^3/ha)	68.28	24.10	0.48	<0.0001
Structural complexity index	14.06	5.33	0.82	<0.0001

Mean differences between open and closed-canopy stands from bootstrap resampling are reported for each landscape along with the Kolmogorov–Smirnov test statistic (*K*) for a two-sided test and *P*-value.

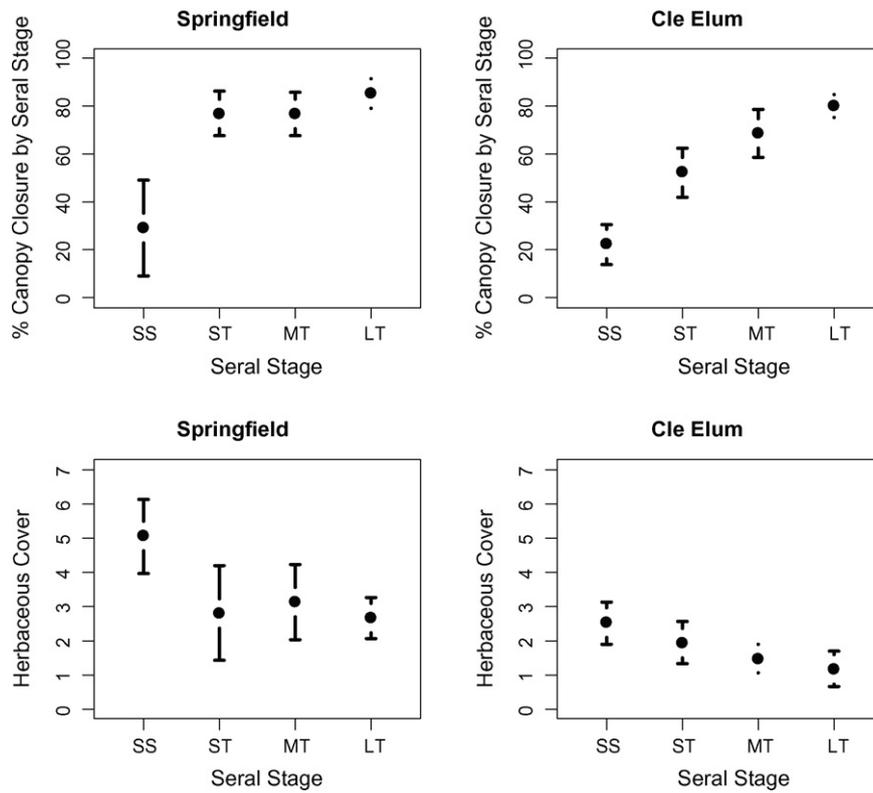


Fig. 3. Mean canopy closure and herbaceous cover for each landscape. Plot of mean values of percent canopy closure (top plot) and herbaceous cover (bottom plot) across seral stages for each landscape: shrub-sapling (SS), small-tree (ST), large-tree (LT), mature-tree (MT). Bars represent 95% confidence intervals around means.

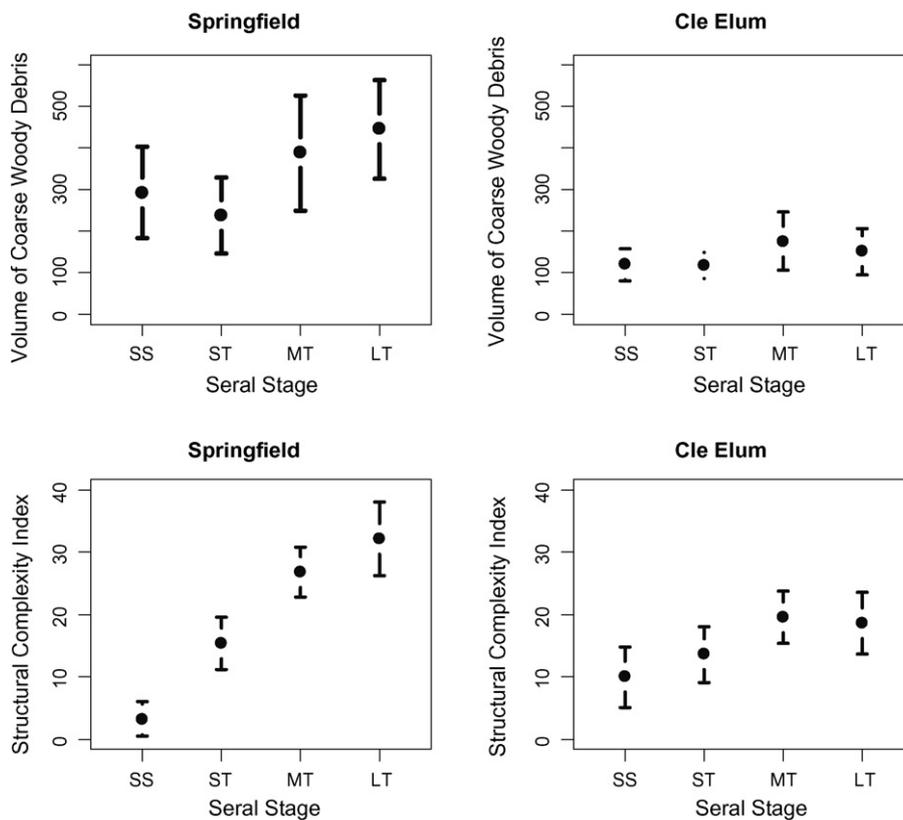


Fig. 4. Mean volume of coarse woody debris and structural complexity for each landscape. Plot of mean values of the volume of coarse woody debris m³/ha (top plot) and structural complexity index (bottom plot) across seral stages for each landscape: shrub-sapling (SS), small-tree (ST), large-tree (LT), mature-tree (MT). Bars represent 95% confidence intervals around means.

Table 4
Bird species responding significantly to changes in landscape-level (1-km radius) edge density (m/ha) at the Springfield landscape.

Species	Guild	Coefficient	P	R ²	RC	Species	Guild	Coefficient	P	R ²	RC
AUWA	Closed [†]	–	–	–	–	WISA	Generalist	–	–	–	–
BCCH	Closed [†] , OG	–	–	–	–	WIWA	Generalist	–	–	–	–
BRCSA	Closed [†]	Negative	0.008	0.281	–	AMGO	Open [*]	Positive	0.028	0.201	–
CBCB	Closed [†] , OG	Negative	0.001	0.375	PIF	AMRO	Open [*]	Positive	0.002	0.190	–
GCKI	Closed [†]	–	–	–	PIF	BEWR	Open [*]	–	–	–	–
GRJA	Closed [†]	–	–	–	–	CEDW	Open [*]	Positive	0.043	0.174	–
HAFL	Closed [†]	–	–	–	–	COYE	Open [*]	Positive	0.016	0.238	–
HEWA	Closed [†]	–	–	–	PIF	DEJU	Open [*]	Positive	0.027	0.102	–
PIWO	Closed [†]	Negative	0.010	0.266	–	DUFL	Open [*]	Negative	0.018	0.117	PIF
PSFL	Closed [†]	Negative	0.046	0.170	PIF	HOWR	Open [*]	–	–	–	–
RBNU	Closed [†]	Negative	0.008	0.278	–	LAZB	Open [*]	–	–	–	–
RBSA	Closed [†]	–	–	–	PIF	MGWA	Open [*]	Positive	0.037	0.183	PIF
TOWA	Closed [†]	–	–	–	PIF	MODO	Open [*]	Positive	0.000	0.254	–
VATH	Closed [†]	Negative	0.003	0.342	PIF	MOUQ	Open [*]	–	–	–	PIF
WBNU	Closed [†]	–	–	–	–	OCWA	Open [*]	–	–	–	PIF
WETA	Closed [†]	–	–	–	–	OSFL	Open [*]	–	–	–	PIF
WIWR	Closed [†]	Negative	0.036	0.185	–	RUHU	Open [*]	Positive	0.008	0.280	PIF
BTYW	Closed	–	–	–	PIF	SOSP	Open [*]	Positive	0.039	0.179	–
CORA	Closed	–	–	–	–	SPTO	Open [*]	Positive	0.000	0.264	PIF
HETH	Closed	–	–	–	–	WAVI	Open [*]	–	–	–	–
HETO	Closed	–	–	–	–	WCSP	Open [*]	Positive	0.045	0.170	–
STJA	Closed	–	–	–	PIF	WIFL	Open [*]	Positive	0.003	0.329	PIF
BHGR	Generalist	Positive	0.003	0.181	–	WREN	Open [*]	–	–	–	PIF
BTP1	Generalist	Negative	0.049	0.081	PIF	BHCO	Open	Positive	0.012	0.254	–
HAWO	Generalist	Negative	0.001	0.205	–	BUSH	Open	–	–	–	–
HUVI	Generalist	–	–	–	PIF	PUFI	Open	–	–	–	PIF
MOCH	Generalist	–	–	–	PIF	PUMA	Open	–	–	–	–
NAWA	Generalist	–	–	–	–	RSFL	Open	–	–	–	–
SWTH	Generalist	Positive	0.040	0.089	–	VGSW	Open	–	–	–	–
WEBL	Generalist	–	–	–	–	YWAR	Open	–	–	–	–

Guild designations based on literature review.

* Species with significant difference in abundance ($P < 0.05$) between open and closed canopy stands; OG = species with significantly higher abundance ($P < 0.05$) in old growth stands (mean dbh > 53 cm); PIF = Partners In Flight Birds of Regional Concern (RC) (Panjabi et al., 2005).

density (Table 4), compared to the less productive site, Cle Elum, where 4 of 60 species (7%) responded significantly to changes in edge density (Table 5). For models where edge density was a significant predictor of abundance ($P < 0.05$), R^2 values ranged from 0.08 to 0.38 in Springfield ($n = 25$, mean = 0.20, SD = 0.07) and from 0.13 to 0.40 in Cle Elum ($n = 4$, mean = 0.21, SD = 0.13).

The slope of response to changes in edge density followed predictable patterns for bird canopy guilds at both sites (Tables 4–5, Fig. 5). Open-canopy associated species and most generalist species responded positively to increases in edge density whereas closed-canopy associated species responded negatively to increases in edge density (Tables 4–5, Fig. 5). Of the 25 species that responded significantly ($P < 0.05$) to changes in edge density in Springfield, the relationship was positive for 15 species (13 open-canopy associates and 2 of 4 generalists) and negative for 10 species (7 closed-canopy associates and 2 generalists). All 4 species that responded significantly ($P < 0.05$) to changes in edge density in Cle Elum were closed-canopy associated species and responded negatively to increases in edge density.

More species identified by Partners in Flight as birds of regional concern responded significantly to changes in edge density in Springfield (9) than Cle Elum (1). Of those in Springfield, all but one of the five open-canopy associated species responded positively to increases in edge density, three closed-canopy species responded negatively to increases in edge density as well as one generalist. The one closed-canopy species of regional concern in Cle Elum responded negatively to increases in edge density.

3.3.2. Individual species–edge density/productivity interaction

With pooled data from both landscapes, individual bird species responded differently to edge density as a function of productivity (Tables 6–7, Fig. 6). The slope of the response to edge density

changed as a function of productivity (GPP) for 25 of 60 species. Examining individual species responses to changes in edge density at different levels of productivity, we found that the response to changes in edge density was most pronounced at high levels of productivity (Table 7, Fig. 6). Only a few species responded more acutely to changes in edge density at lower levels of productivity (Table 7). Generalist species and species associated with open-canopy forests responded positively to increases in edge density where productivity was moderate or high. Similarly, species associated with closed-canopy forests responded negatively to increases in edge density at moderate and high levels of productivity. With few exceptions, bird response to edge density (across all canopy guilds) was most pronounced at the highest levels of productivity (Table 7).

3.3.3. Community-level response

Paralleling species-level results, we found evidence that bird communities at the more productive site differentiate across a gradient in edge density whereas bird communities at a less productive site do not. In Springfield, bird community assemblages surrounded by low edge densities were significantly different than bird community assemblages surrounded by high edge densities (within to between cluster ratio $P = 0.003$) (Fig. 7). Bird communities in Cle Elum were not significantly different between low and high levels of edge density (within to between cluster ratio $P = 0.364$) (Fig. 7). In Springfield, edge density was a significant predictor at the community level, explaining 43% of the variation in bird composition and abundance (Goodness of Fit statistic from 1000 permutations of the maximum correlation between NMDS ordination scores and edge density). Conversely, in Cle Elum, edge density was not a significant predictor of bird community composition and abundance.

Table 5
Bird species responding significantly to changes in landscape-level (1-km radius) edge density (m/ha) at the Cle Elum landscape.

Species	Guild	Coefficient	P	R ²	RC	Species	Guild	Coefficient	P	R ²	RC
BRCR	Closed, OG	Negative	0.015	0.181	–	CAFI	Generalist	–	–	–	–
CAVI	Closed	Negative	0.043	0.130	PIF	CHSP	Generalist	–	–	–	–
CBCH	Closed, OG	–	–	–	PIF	MOCH	Generalist	–	–	–	PIF
CORA	Closed	–	–	–	–	REVI	Generalist	–	–	–	–
GCKI	Closed, OG	–	–	–	PIF	SOSP	Generalist	–	–	–	–
HAFL	Closed	–	–	–	–	SPTO	Generalist	–	–	–	PIF
HETO	Closed, OG	–	–	–	–	SWTH	Generalist	–	–	–	–
HEWA	Closed, OG	–	–	–	PIF	VEER	Generalist	–	–	–	–
RBNU	Closed, OG	–	–	–	–	BEWR	Open	–	–	–	–
TOWA	Closed, OG	–	–	–	PIF	DEJU	Open	–	–	–	–
WETA	Closed	Negative	0.005	0.123	–	DUFL	Open	–	–	–	PIF
WIWR	Closed, OG	–	–	–	–	FOSP	Open	–	–	–	–
BTYW	Closed	–	–	–	PIF	HOWR	Open	–	–	–	–
EVGR	Closed	Negative	0.000	0.403	–	LISP	Open	–	–	–	–
GRJA	Closed, OG	–	–	–	–	MOBL	Open	–	–	–	–
HAWO	Closed, OG	–	–	–	–	OSFL	Open	–	–	–	PIF
HETH	Closed	–	–	–	–	RSFL	Open	–	–	–	–
PISI	Closed	–	–	–	–	RUHU	Open	–	–	–	PIF
PIWO	Closed	–	–	–	–	STJA	Open	–	–	–	PIF
PSFL	Closed	–	–	–	PIF	WAVI	Open	–	–	–	–
RECR	Closed	–	–	–	PIF	WCSP	Open	–	–	–	–
TOSO	Closed	–	–	–	–	YWAR	Open	–	–	–	–
VATH	Closed	–	–	–	PIF	BHCO	Open	–	–	–	–
WEBL	Closed	–	–	–	–	LAZB	Open	–	–	–	–
WISA	Closed	–	–	–	–	MGWA	Open	–	–	–	PIF
WIWA	Closed	–	–	–	–	NAWA	Open	–	–	–	–
AMRO	Generalist	–	–	–	–	OCWA	Open	–	–	–	PIF
AUWA	Generalist	–	–	–	–	PUFI	Open	–	–	–	PIF
BHGR	Generalist	–	–	–	–	RNSA	Open	–	–	–	–
BLGR	Generalist	–	–	–	PIF	VVPE	Open	–	–	–	–

Guild designations based on literature review.

* Species with significant difference in abundance ($P < 0.05$) between open and closed canopy stands; OG = species with significantly higher abundance ($P < 0.05$) in old growth stands (mean dbh > 53 cm); PIF = Partners In Flight Birds of Regional Concern (RC) (Panjabi et al., 2005).

4. Discussion

4.1. Bird response to edge density as a function of productivity

The literature examining organism response to local and landscape effects is extensive (Noss et al., 2006; McElhinny et al., 2005;

Harper et al., 2005; Parker et al., 2005; Fahrig, 2003; Murcia, 1995; MacArthur and MacArthur, 1961), yet few studies compare these effects across ecosystems varying in productivity, especially for higher trophic levels (Sarr et al., 2005; Huston, 1994; Huston, 1979). The sensitivity of different organisms to landscape effects is poorly understood. Harper et al. (2005) outlined ecosystem traits

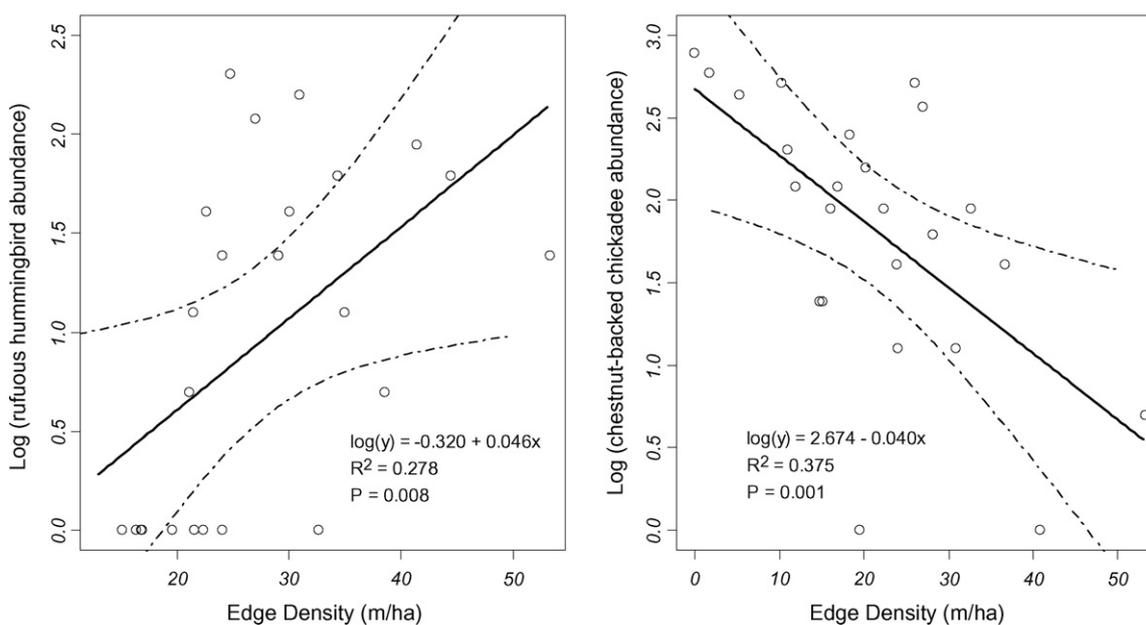


Fig. 5. Bird response to edge density. Example of relationship between species abundance and landscape-level edge density for two species: rufous hummingbird and chestnut-backed chickadee. Fitted regression with 95% confidence intervals shown. Data shown are from the Springfield landscape.

Table 6
Bird species responding significantly to changes in edge density (ED, m/ha) and the interaction between edge density and GPP (g C m⁻² day⁻¹) across both sites (bird species abundance data combined from both sites).

Species	Guild	ED–P	ED:GPP–P	R ²	RC	Species	Guild	ED–P	ED:GPP–P	R ²	RC
AUWA	Closed*	0.018	0.011	0.597	–	SWTH	Generalist	0.003	0.005	0.680	–
BCCH	Closed*, OG	0.053	0.020	0.469	–	AMGO	Open*	–	–	–	–
BRCR	Closed*, OG	0.029	0.007	0.363	–	AMRO	Open*	0.076	0.027	0.110	–
CBCH	Closed*, OG	0.001	<0.001	0.640	PIF	BEWR	Open*	–	–	–	–
CORA	Closed*	–	–	–	–	CEDW	Open*	–	–	–	–
GCKI	Closed*, OG	–	–	–	PIF	COYE	Open*	0.036	0.011	0.403	–
GRJA	Closed*, OG	–	–	–	–	DEJU	Open*	0.062	0.010	0.508	–
HAFL	Closed*	–	–	–	–	FOSP	Open*	–	–	–	–
HETO	Closed*, OG	0.075	0.027	0.368	–	HOWR	Open*	–	–	–	–
HEWA	Closed*, OG	0.035	0.026	0.702	PIF	LAZB	Open*	0.004	0.010	0.279	–
MOCH	Closed*	–	–	–	–	LISP	Open*	0.017	0.032	0.121	–
PIWO	Closed*, OG	0.027	0.005	0.473	–	MGWA	Open*	–	–	–	PIF
PSFL	Closed*, OG	0.002	0.001	0.550	PIF	MOUQ	Open*	–	–	–	PIF
RBNU	Closed*, OG	0.067	0.014	0.498	–	OCWA	Open*	–	–	–	PIF
RBSA	Closed*, OG	–	–	–	PIF	OSFL	Open*	–	–	–	PIF
TOWA	Closed*, OG	–	–	–	PIF	RSFL	Open*	0.038	0.050	0.304	–
VATH	Closed*, OG	0.019	0.003	0.343	PIF	RUHU	Open*	0.076	0.037	0.404	PIF
WETA	Closed*	–	–	–	–	SOSP	Open*	–	–	–	–
WIWR	Closed*, OG	0.019	0.009	0.542	–	SPTO	Open*	–	–	–	PIF
HETH	Closed*	–	–	–	–	WAVI	Open*	–	–	–	–
PISI	Closed	0.070	0.017	0.271	–	WCSP	Open*	–	–	–	–
RECR	Closed	–	–	–	PIF	WIFL	Open*	–	–	–	PIF
TOSO	Closed	–	–	–	–	WREN	Open*	–	–	–	PIF
WEBL	Closed	–	–	–	–	YWAR	Open*	–	–	–	–
WISA	Closed	0.004	0.006	0.486	–	BHCO	Open	<0.001	<0.001	0.472	–
WIWA	Closed	–	–	–	–	PUFI	Open	–	–	–	PIF
BHGR	Generalist	–	–	–	–	PUMA	Open	–	–	–	–
MOCH	Generalist	–	–	–	PIF	RNSA	Open	–	–	–	–
NAWA	Generalist	0.072	0.038	0.241	–	VGSW	Open	–	–	–	–
STJA	Generalist	0.022	0.015	0.547	PIF	WWPE	Open	0.074	0.030	0.195	–

* Species with significant difference in abundance ($P < 0.05$) between open and closed-canopy stands; OG = species with significantly higher abundance ($P < 0.05$) in old growth stands (mean dbh > 53 cm); PIF = Partners In Flight Birds of Regional Concern (RC) (Panjabi et al., 2005).

that are especially susceptible to edge effects. These include: climate (high mean air temperature and solar radiation, low cloud cover, frequent extreme winds); disturbance (infrequent stand replacing disturbances); community structure (many early-seral

and invasive species); and landscape patterns (low inherent habitat patchiness). Additionally, Hansen and Urban (1992) suggested that the life history attributes of species vary among ecosystems influencing their response to direct biotic edge effects.

Table 7
Bird species response (abundance) to changes in edge density (m/ha) at low, intermediate and high levels of productivity (GPP, (g C m⁻² day⁻¹).

Species code	Guild	Low productivity	Intermediate productivity	High productivity
AUWA	Closed*	---	+	+
BCCH	Closed*, OG	+	–	---
BRCR	Closed*, OG	+	–	---
CBCH	Closed*, OG	+	–	---
HETO	Closed*, OG	+	–	–
HEWA	Closed*, OG	+	–	---
PIWO	Closed*, OG	+	–	---
PSFL	Closed*, OG	+	–	---
RBNU	Closed*, OG	+	–	---
VATH	Closed*, OG	+	–	–
WIWR	Closed*, OG	+	–	---
PISI	Closed	–	+	++
WISA	Closed	---	–	+
AMRO	Open*	–	+	+++
COYE	Open*	–	+	+++
DEJU	Open*	–	++	++
LAZB	Open*	---	–	+
LISP	Open*	–	–	++
RSFL	Open*	---	–	+
RUHU	Open*	–	+	+++
BHCO	Open	–	+	+++
WWPE	Open	+	–	–
NAWA	Generalist	–	+	++
STJA	Generalist	+	–	---
SWTH	Generalist	+	+	---

Plus symbols indicate a positive relationship with increasing edge density and minus symbols represent a negative relationship with edge density. The number of symbols (plus or minus) represents the steepness of the slope of the relationship between abundance and increasing edge density.

* Species with significant difference in abundance ($P < 0.05$) between open and closed canopy stands; OG = species with significantly higher abundance ($P < 0.05$) in old growth stands (mean dbh > 53 cm).

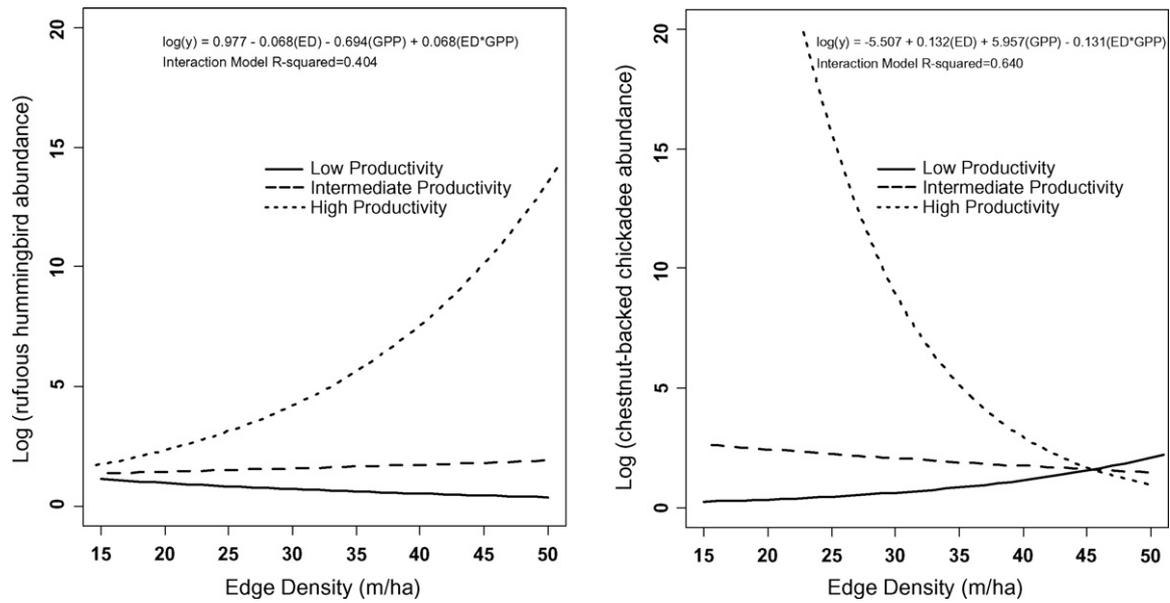


Fig. 6. Bird response to edge density at three levels of productivity. Fitted models represent the relationship between rufous hummingbird and chestnut-backed chickadee abundance (log transformed) and increasing edge density when low, intermediate and high values of productivity (GPP, $\text{g C m}^{-2} \text{ day}^{-1}$) are incorporated into a model with an edge density/productivity interaction. Values of productivity for each model represent the mean of the lower quartile (low), overall mean (intermediate), and mean of the upper quartile (high) values of GPP across the two landscapes.

The Biomass Accumulation Hypothesis integrates several of the ecosystem factors described by Harper et al. (2005) and Hansen and Urban (1992). Forests with high biomass accumulation tend to have warm temperatures, high solar radiation, periods of low clouds, infrequent stand replacing disturbance, and low natural patchiness in forest/non-forest conditions (Brown and Lugo, 1982). Moreover, species in high productivity and high biomass systems tend to have small home ranges, low dispersal, and habitat specialization. Hence, biomass accumulation appears to represent a syndrome of ecosystem characteristics that increases the magnitude of edge effects.

These predictions were tested by Hansen et al. (in review), who evaluated the results of 31 published studies from the major forest biomes of the world. They found that the magnitude of edge influence of microclimate was significantly related to ecosystem aboveground biomass for light levels, humidity, and for all microclimate samples, controlling for microclimate variable type. The percent of species that specialized on forest interiors was significantly related to biomass for mammals and birds, and nearly significantly for beetles. The results suggested that forest fragmentation is most likely to cause extinction of forest species in ecosystems in tropical and temperate rainforests, but may have

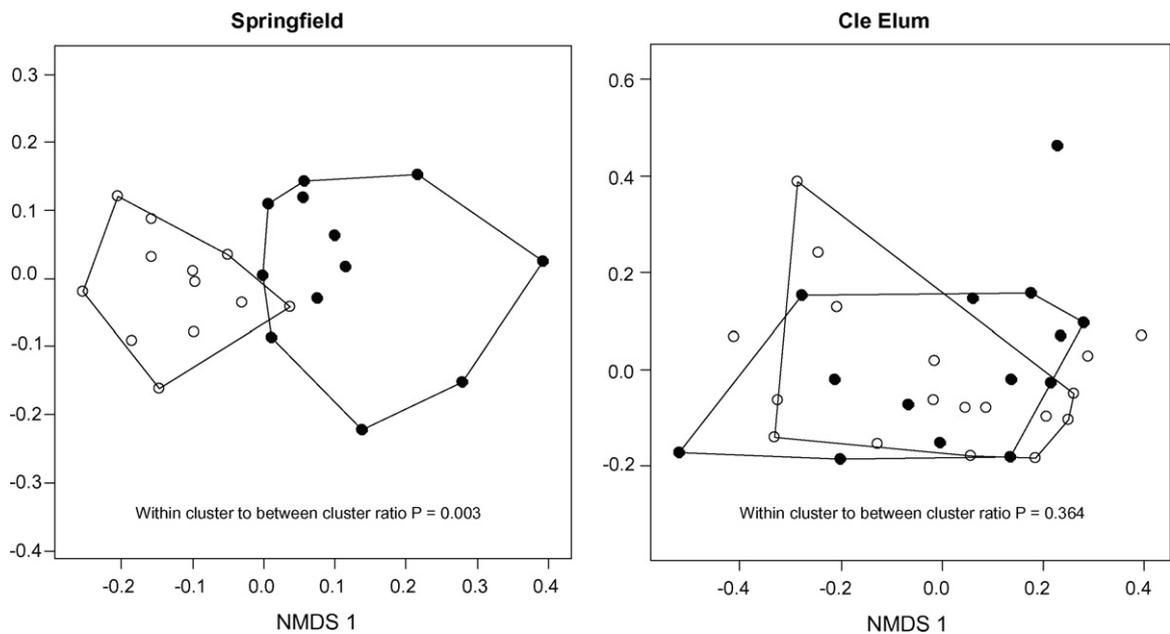


Fig. 7. Bird community response to edge density at each landscape. NMDS ordination of closed-canopy bird community similarity by site. Open circles represent forest survey stands surrounded by landscapes (1-km circular radii) with low edge density (m/ha). Closed circles represent survey stands surrounded by landscapes with high edge density.

little effect on forest species in low-biomass ecosystems such as boreal or subalpine forests.

The current study is the first to test the Biomass Accumulation Hypothesis in forests that are similar in forest physiogamy, in geographic region, and in bird communities, and differ moderately in forest biomass. In support of the hypothesis, we found that differences in vegetation and structural conditions between early-seral and late-seral stands were more pronounced in the more productive landscape. Canopy closure, understory herbaceous cover, the volume of coarse woody debris and structural complexity differed more between open and closed canopy stands in the productive Springfield landscape than the intermediate productivity Cle Elum site.

The results also indicated that bird response to edge effects was more pronounced in a more productive forest; nearly half of the 60 most abundant species at a more productive site responded to edge density, whereas only four species responded significantly at a less productive site, Cle Elum. Edge density explained a substantive amount of variation in abundance for several species at the more productive site, Springfield (>20% for 11 species). Bird community organization also responded significantly to the influence of spatial patterning where productivity was greater. Additionally, for a number of species the slope of response to edge density changed at different levels of productivity. Hence, bird response was consistently more pronounced where we found the contrast in environmental conditions between edge and interior environments to be most acute. Additionally, where landscape effects were significant, individual species responded predictably according to canopy guild association. All but one open-canopy associate and most generalists responded positively to increases in edge density, whereas closed-canopy associates responded negatively to increases in edge density.

One explanation for these results is the mechanism presented under the Biomass Accumulation Hypothesis. In high biomass forests, microhabitat conditions are predicted to differ substantially between forest edges and interiors allowing finer habitat partitioning among species and greater differences in species composition between edge and interior habitats. The strong response to edges by open-canopy species in the productive landscape suggests an additional mechanism. The rapid vegetative recovery following disturbance in productive ecosystems appears to create high-quality habitat and abundant foods for early-seral specialist species. This rapid recovery is thought to result because disturbance in highly productive late-seral forests breaks dominance of highly competitive tree species, releasing resources for other species (Huston, 1979). Support for interpretation comes from McWethy et al. (in review) who found that bird diversity increased with disturbance levels in the productive Springfield landscape but decreased with disturbance in the less productive Cle Elum site. Hence, both microhabitat differences between forest edge and interiors and more rapid recovery of early-seral habitats following disturbance are possible mechanisms explaining why more bird species respond to edge in the more productive landscape.

We are aware of no other studies that quantified bird response to edge across gradients in ecosystem productivity. In the forests of the northwestern United States, a few studies have quantified vertebrate response to forest edges. In the coastal redwood forests of Northern California, Brand and George (2001) found that 29% of the 14 bird species they sampled were associated with forest interiors. These forests have higher productivity and biomass than our Springfield landscape and the strong response to edge found by Brand and George are consistent our findings. However, other studies in the northwestern U.S. have mostly found fairly weak responses to edge. Rosenburg and Raphael (1986) and Lehmkuhl

et al. (1991) generally found weak relationships between species' abundance and forest configuration with most birds responding positively to increasing levels of forest fragmentation. In a study of bird response to the amount and configuration of later-seral forests in the Coast Range, McGarigal and McComb (1995) found few birds that responded significantly to changes in the configuration of later-seral forests. Of these, more species responded positively to increased fragmentation of later-seral forests than negatively. Only one species, the winter wren (*Troglodytes troglodytes*), was consistently shown to be more abundant in less fragmented later-seral forests. Also looking at bird response to habitat area and configuration in the Coast Range, Hansen et al. (1991) found 13% of bird species were associated with forest interior. These coast range forests have levels of productivity similar to the Springfield landscape (Verschuyl et al., 2008). We speculate that response to edge in the Coast Range is less than predicted given this high productivity due to forest structure. Fires were extensive in these Coast Range study areas in the late 1800s and current forests appear to be lower in forest structural complexity and canopy closure than the older, better developed forests in Springfield (Verschuyl et al., 2008).

4.2. Scope and limitations

Our results suggest that bird response to edge density varies across productivity levels based on the correlation between edge density and bird abundance. We attempted to control for factors unrelated to productivity that may influence bird response to edge density by looking at bird response both across and between sites and by incorporating an edge density/productivity interaction term in our models. Thus, while not causal, our results provide preliminary evidence supporting the hypothesis that bird response to landscape effects varies across productivity gradients. Experimental investigations of our hypotheses, while difficult to implement, would help clarify the relationship between landscape effects and bird abundance across productivity levels.

Studies examining the effects of different patterns of forest area and configuration on birds typically identify a small group of species associated with specific patterns in forest habitat area and configuration (McGarigal and McComb, 1995; Hansen and Urban, 1992; Lehmkuhl et al., 1991; Rosenburg and Raphael, 1986). Most birds responding to landscape-wide changes in pattern are found to be influenced more by changes in habitat area than configuration (Schmiegelow and Monkkonen, 2002; Villard et al., 1999; Trzcinski et al., 1999). In our study, changes in edge density were correlated with changes in habitat amount, number of patches, patch size and patch isolation yet correlations were typically low (<0.50). Based on the premise that the contrast between edge and interior environments is greater in more productive environments, we evaluated bird response to changes in edge density because it most directly tested our hypothesis that birds would respond differently to landscape effects across productivity levels. Hence, bird response to landscape effects in our study represents response to both changes in area and configuration of forest patches across the landscape.

Factors other than productivity may also explain how bird response to landscape effects varies across different landscapes. Differences in the composition of dominant canopy species and associated understory communities may influence bird response to the amount of edge present across the landscape. The vertical and horizontal configuration of vegetative structure and biomass is unique for each dominant canopy species. Productive Douglas-fir forests show more even distribution of vegetative layering from canopy to forest floor than occurs in ponderosa pine forests (Lefsky et al., 2002). The resulting gradient in environmental conditions

between edge and interior likely varies as a result of these differences in biomass distribution and layering. Hence, it is possible that bird response to the amount of edge across the landscape would vary across forests with different canopy dominants. We suggest, however, that abiotic conditions ultimately influence the distribution of these canopy dominants, and that birds are responding to both site productivity and the distribution of different canopy dominants influenced by site productivity. In our design, we test whether bird response to edge density interacts with productivity, both across and within each site. Our approach, therefore, incorporates a reasonable control for differences between sites, other than productivity, that might influence bird response to edge density.

4.3. Management implications

The primary implication of this study is that response of birds to forest edges varies with ecosystem productivity. Thus, management of forest landscape pattern should be tailored to local ecosystem conditions in order to best achieve biodiversity objectives. In the less productive Cle Elum landscape, where relatively few bird species responded to edge density, attention to forest edge configuration may not be a high priority for biodiversity managers. A higher priority for managers there may be judicious use of logging or other disturbances because recovery rates of vegetation are relatively slow in that landscape and total bird diversity decreases with increased disturbance (McWethy et al., in review).

In the relatively high productivity Springfield landscape, thirteen bird species associated with open-canopy stands responded positively to increases in edge density (Table 4), four of which are Partners In Flight species of regional concern exhibiting significant negative trends in abundance from 1966 to 2003 (Sauer et al., 2005). Hence, the maintenance of open-canopy patches within productive environments seems particularly important in supporting open-canopy associates, especially those experiencing population declines over the past four decades. Alternatively, a number of bird species associated with closed-canopy and old-growth forests responded negatively to higher edge density (Tables 4–5) and have been shown to depend on structural conditions only found in older forests (i.e. presence of abundant legacy snags, coarse woody debris, broken tops, and large mature trees) (Franklin et al., 2002).

In order to balance the needs of these differing groups of birds in productive landscapes, it may be most effective to focus on creation of relatively large late-seral patches with low edge density in parts of the landscape to favor closed-canopy species. In other parts of the landscape, creation of more forest edge and smaller patch sizes would allow larger populations of open-canopy specialists. More detailed studies are needed to determine the thresholds in landscape configuration that are needed to maintain viable populations of various open and closed-canopy species.

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