BIODIVERSITY POTENTIAL IN THE PACIFIC AND INLAND NORTHWEST: THE RELATIVE IMPORTANCE OF FOREST STRUCTURE AND AVAILABLE ENERGY IN DRIVING SPECIES DIVERSITY

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Ecology and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2007

APPROVAL

of a dissertation submitted by

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This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

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April, 2007

ACKNOWLEDGEMENTS

I thank the National Council for Air and Stream Improvement (NCASI) and the National Fish and Wildlife Foundation for their support of this research, and data contributors Kevin McGarigal, William McComb and Rex Sallabanks. I am grateful to my advisor, Andrew Hansen, for his assistance and guidance throughout the project, and to my graduate committee: Lorin Hicks, Jim Robison-Cox, and Jay Rotella for their contributions. My peers in the Landscape Biodiversity Lab and the Department of Ecology deserve thanks for their advice and camaraderie, specifically Dave McWethy who worked with me on nearly every aspect of this research. A very special thank you also goes out to the field assistants who made this project possible: Andy Arens, Jose Blanco, Caanan Cowles, Jessica Eselius, Julia Esposito, Valerie Eurs, Louise Gava, Lurah Klaas, Carolyn Matkovich, and Karen Weber. Finally, I would like to thank my wife, Jen Verschuyl, for her support both in and out of the field.

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ABSTRACT

Currently, the most common strategy of forest biodiversity managers in the Pacific and Inland Northwest (PINW) is to maintain structural complexity within forest stands and create the full range of seral stages across the landscape. Recent advances in ecological theory reveal that biodiversity at regional to continental scales is strongly influenced by available energy (i.e. factors influencing vegetative growth such as precipitation, temperature, radiation, soil fertility). We hypothesized bird species richness (BSR) exhibits a positive or unimodal relationship with energy across landscapes and the relationship between energy and BSR within a landscape is positive in energy limited landscapes and flat or decreasing in energy rich landscapes. Additionally, we hypothesized that structural complexity explains a lower percentage of the variation in BSR in energy limited environments and higher percentage in energy rich environments and that the slope of the relationship between structural complexity and BSR is greatest in energy rich environments. Ours is the first study to test the relative influence of energy and vegetation structure on BSR at local scales, and to offer predictive theory on how these influences differ across energy gradients. We sampled bird communities and vegetation across a matrix of seral stages and biophysical settings at each of 5 landscapes. We analyzed the response of BSR to structural complexity and energy covariates at each landscape. We found that (1) BSR had a unimodal relationship with available energy across the PINW region, (2) the landscape-scale relationships between energy and BSR were positive or unimodal in energy limited locations and were flat or negative in energy rich locations, (3) forest structural complexity explained more of the variation in bird species richness in energy rich landscapes, and (4) the slope of the relationship between forest structural complexity and BSR was steepest in energy limited locations and negative in energy rich locations. In energy rich locations, forest managers will likely increase landscape-scale diversity by providing all seral-stages and a range of forest structural complexity. In low-energy environments, biodiversity will likely be maximized by managing local high-energy hotspots judiciously and adjusting harvest intensities in other locations to compensate for slower regeneration rates.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

Managing forest lands for biodiversity is a common goal in the public and private forests of the Pacific and Inland Northwest (PINW) (Hunter 1999, Loehle et al. 2002). Managers of private timberlands and other forests currently assume that the causative factors of biodiversity do not vary geographically. This may be due in part to the unbalanced focus of past research toward stand level effects of forest harvest and within stand structural retention rather than the interaction of structural complexity and the spatial distribution of harvest units across gradients in climate and forest productivity.

This is the first body of research to test the relative influence of energy and vegetation structure on bird species richness (BSR) at local scales, and to offer predictive theory on how these influences differ across energy gradients. The conclusions from the research presented in this dissertation suggest that forest management strategies in the Pacific and Inland Northwest should be tailored to the strong gradients in forest productivity that exist across the region.

Organization of the Dissertation

After this brief introduction, Chapter two covers the core of the research and tests the relative influence of forest structure and available energy in driving species diversity across the Pacific and Inland Northwest (PINW). We hypothesized BSR exhibits a positive or unimodal relationship with energy across landscapes and the relationship between available energy and BSR within a landscape is positive in energy limited landscapes and flat or decreasing in energy rich landscapes. Additionally, we hypothesized that structural complexity explains a lower percentage of the variation in BSR in energy limited environments and higher percentage in energy rich environments and that the slope of the relationship between forest structural complexity and BSR is greatest in energy rich environments.

Conservationists and land managers do not have the funding to conserve all species under threat. One way to prioritize conservation efforts is to identify biodiversity hotspots where large concentrations of species can be preserved in a relatively small spatial extent (Meyers et al. 2000). Chapter three examines the resulting spatial patterns of biodiversity hotspots across landscapes with different controls on biodiversity. We developed best models for predicting bird species richness across two landscapes and examined the spatial configuration of biodiversity hotspots. We expected hotspots to be diffuse and predictive models to be weak in energy rich sites. In energy-limited sites, we expected hotspots to be concentrated in comparatively high-energy locations and the predictive model to have a higher R^2.

Chapter four is a synthesis of the management implications from chapters two and three and from collaborative research led by Dave McWethy (Appendices A & B) investigating the effects of edge density and patch size in different biophysical settings (Appendix A) and testing whether bird diversity increases with increasing disturbance intensity in high productivity sites (Appendix B). Management implications relevant to several aspects of forest biodiversity management are defined for low, intermediate and high productivity forests in the PINW. The final chapter includes direction for future research and conclusions.

This dissertation presents a comprehensive assessment of how the influences on biodiversity differ across the energy gradients of a large and complex region. Previous research on the subject has focused on stand level management and the influence of forest structure alone. The application of structure-focused research and legislation has resulted in similar management strategies being applied across forests with different levels of productivity. I expect that this research will guide biodiversity managers across the PINW to apply unique strategies for forest management in each biophysical setting. We have also provided the framework for this type of research being conducted in other regions where similar management issues may have been overlooked.

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CHAPTER 2

PRODUCTIVITY AND FOREST STRUCTURE INTERACT TO DRIVE BIRD DIVERSITY IN THE PACIFIC NORTHWEST

Abstract

Currently, the most common strategy of forest biodiversity managers in the Pacific and Inland Northwest (PINW) is to maintain structural complexity within forest stands and create the full range of seral stages across the landscape. Recent advances in ecological theory reveal that biodiversity at regional to continental scales is strongly influenced by available energy (i.e. factors influencing vegetative growth such as precipitation, temperature, radiation, soil fertility among others).

We hypothesized bird species richness (BSR) exhibits a positive or unimodal relationship with energy across landscapes and the relationship between available energy and BSR within a landscape is positive in energy limited landscapes and flat or decreasing in energy rich landscapes. Additionally, we hypothesized that structural complexity explains a lower percentage of the variation in BSR in energy limited environments and higher percentage in energy rich environments and that the slope of the relationship between forest structural complexity and BSR is greatest in energy rich environments. Ours is the first study to test the relative influence of energy and vegetation structure on BSR at local scales, and to offer predictive theory on how these influences differ across energy gradients.

We sampled bird communities and vegetation across a matrix of seral stages and biophysical settings at each of the five landscapes. We analyzed the response of BSR to structural complexity and available energy covariates at each landscape. We found that (1) BSR had a unimodal or threshold relationship with available energy across the PINW region, (2) the landscape-scale relationships between available energy and BSR were positive or unimodal in energy limited locations and were flat or negative in energy rich locations, (3) forest structural complexity explained more of the variation in bird species richness in energy rich landscapes, and (4) the slope of the relationship between forest structural complexity and BSR was steepest in energy limited locations and negative in energy rich locations. In energy rich locations, forest managers will likely increase landscape-scale diversity by providing all seral stages and a range of forest structural complexity. In low energy environments, biodiversity will likely be maximized by managing local high-energy hotspots judiciously and harvesting other locations at intensities adjusted for the slower recovery rates resulting from energy limitation.

Introduction

Managing for biodiversity is widely considered to be important for the preservation of ecosystem services such as clean air, clean water, soil fertility, and human disease prevention (Noss 1983, Tillman et al. 1997, McCann 2000). Thus, maintenance of biodiversity is a common goal of the managers of public and private forests of the Pacific and Inland Northwest (PINW) (Hunter 1999, Loehle et al. 2002). Managers of private timberlands and other forests currently assume that the causative factors of biodiversity do not vary geographically. New information suggests that biodiversity varies with energy levels (i.e. factors influencing vegetative growth such as precipitation, temperature, radiation, soil fertility among others) (Currie 1991, Hurlbert 2004), and that the effect of forest structure on biodiversity may vary with the level of available energy (Hansen et al. 2003). Research efforts have not evaluated the changing role of forest structure in driving biodiversity in the energetically diverse forested lands of the PINW (Ishii 2004, Sallabanks and Arnett 2005). In this paper we test the effects of energy in driving bird species richness within and across landscapes in the PINW, and examine how the effect of forest structure in driving BSR changes with energy level.

Vegetation structure refers generally to the horizontal and vertical distribution of vegetation. MacArthur and MacArthur (1961) refined the broad concept of vegetation structure by defining Foliage Height Diversity (FHD) as a measure of canopy layering, and suggesting its use as an indicator of biodiversity. FHD recognizes the importance of the number and evenness of canopy layers (MacArthur and MacArthur, 1961). Variations on the foliage height diversity concept have led to the development of several indices of forest structural complexity incorporating vertical and horizontal variation in tree size, canopy cover, shrub size, shrub cover, coarse woody debris and snags (McElhinny et al. 2005). Vertical and horizontal structural complexity drives biodiversity by creating a greater variety of microclimates and microhabitats, which in turn produce more diverse food and cover for a more diverse group of species (MacArthur and Mac Arthur 1961, Carey et al. 1999, Hunter 1999).

Seral stages are defined, in part, by their associated levels of forest structural complexity (Oliver and Larson 1990, Spies and Franklin 1991, Spies 1998). Temperate coniferous forests experience intermediate levels of structural complexity in early seral forests before canopy closure occurs. Canopy closure reduces the number of canopy layers in the understory, and decomposition reduces the abundance of standing and fallen dead trees, hence structural complexity decreases in intermediate successional stages (Spies and Franklin 1991, Spies 1998) (Figure 2.1). Structural complexity then rebuilds in mature and old-growth stages due to gap formation processes and the death of large trees (Figure 2.1). Bird species specialize on particular seral stages due to the unique characteristics of forest structure that exist within each stage (Sallabanks et al. 2002, 2006). Therefore, managing for the representation of a variety of seral stages can provide higher levels of landscape scale diversity.

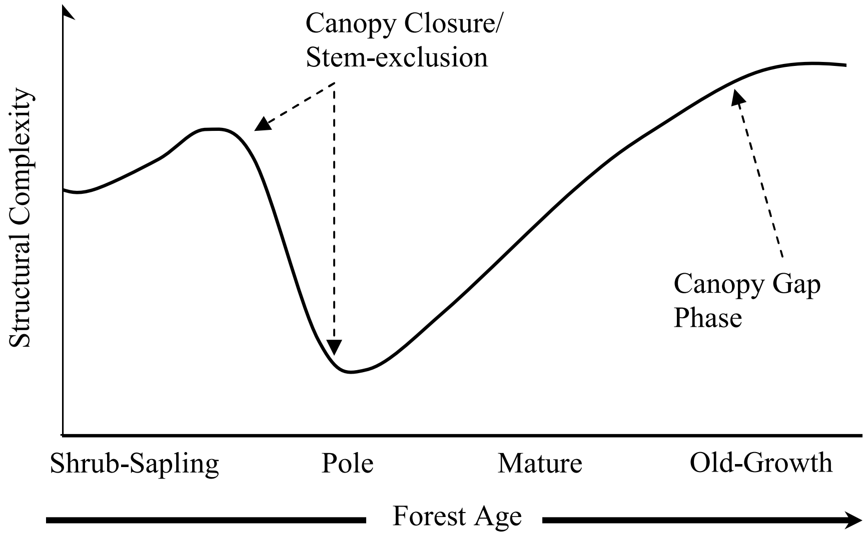

Figure 2.1. Structural complexity by seral stage in temperate coniferous forests.

An increasing understanding of the importance of forest structure in natural systems is being used to guide forest management. In temperate coniferous forests under a natural disturbance regime, structural complexity is relatively high in early seral and late seral stages and lower in intermediate stages (Hansen et al. 1991). This is because natural disturbance often leaves high levels of biological legacy, including live plants of many sizes and high levels of dead trees. Species richness in natural forests is thought to mirror the patterns of structural complexity, being highest in early and late seral forests and lowest in mid seral stages (Franklin and Spies 1991, Halpern and Spies 1995).

Traditional forestry practices such as clear-cutting tend to reduce structural complexity across all seral stages; hence these forests are often lower in structural and biological diversity when compared to naturally disturbed forests (Hansen et al. 1991). Thus within forest stands, biodiversity managers now focus on maintaining variation in tree size, multiple canopy layers, presence of coarse woody debris, and other elements of forest structural complexity, in balance with wood production needs (Hunter 1999, Rapp 2004). In addition, forest managers with biodiversity objectives typically attempt to retain a variety of seral stages across the landscape, most commonly done using a shifting mosaic approach (Loehle et al. 2002).

A different perspective on biodiversity emerged in the 1990's — the "species-energy" hypothesis. This perspective focuses on the role of available energy in driving species and communities (for reviews see Irwin 1998, Hansen and Rotella 1999, Waide et al. 1999, Mittelbach et al. 2001). Available energy can be defined as the energy accessible to a community, which can be turned into biomass (Storch et al. 2005). In this paper we use measures of productivity (net primary productivity (NPP: $gm^{C}m^{-2}day^{-1}$), gross primary productivity (GPP: $gm^{C}m^{-2}day^{-1}$), normalized difference vegetation index (NDVI: correlated with the fraction of photosynthetically active radiation (fPar), leaf area index, and total green biomass)), and potential productivity (represented by climate variables such as: precipitation, temperature, solar radiation, etc.) to represent energy available to bird species. The primary mechanism by which available energy leads to higher levels of species diversity is labeled the “More Individuals Hypothesis” (Hurlbert, 2004, Monkkonen et al. 2006). This hypothesis suggests that higher levels of productivity lead to more food resources, which leads to more individuals, and communities with more individuals contain more species. Others have suggested an alternative mechanism where higher productivity leads to more species by increasing the probability of occurrence of critical resources that enable the persistence of viable populations without necessarily increasing local population densities (Bonn et al 2004).

Available energy, which sets fundamental limits on ecosystem properties such as energy flow, nutrient cycling, and disturbance regimes, also influences the composition of native species and communities. At both regional and continental scales, community diversity has been found to be strongly associated with available energy such as potential evapotranspiration, temperature, precipitation, and elevation (Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002, Hawkins et al. 2003, Bailey et al. 2004). Much debate exists over the nature of the energy-diversity relationship and the effects of spatial scale, species life-history traits, and the specific measures of energy used in analysis (Waide et al. 1999, Chase and Leibold 2002, Mittelbach et al. 2002). Most studies have incorporated regional, continental, or global extents, and have found positive or hump-shaped relationships between diversity measures (most commonly species richness) and available energy (Mittelbach et al. 2002). The downturn in richness at the highest levels of available energy has been shown at both regional and continental scales, and is thought to be due to interspecific competition (Waide et al. 1999). Often in highly productive systems with lengthy inter-disturbance periods, a few species come to dominate the community, leading to reduced species richness (Huston, 2004). Previous research conducted across the PINW provides evidence of a hump-shaped energy-diversity relationship at the regional scale (Hansen et al. 2003). Energy-diversity relationships have not been widely examined at stand and landscape scales, and the importance of energy in driving the structural complexity-diversity relationship is not known.

Previous studies have emphasized the need for structure-focused management to retain high levels of species diversity across all forest types in the PINW (Harris 1984, Kohm and Franklin 1997). We suggest that species diversity reflects an interaction between vegetation structure and available energy, and that the specific factors that limit species diversity likely vary across biophysical gradients. In productive environments, where energy is not limiting, we predict that structural complexity is primary in limiting species diversity. In low energy environments, we predict that structural complexity is secondary to energy in limiting species diversity. In cold or dry systems, energy limitations may constrain diversity such that even the most structurally complex habitats have few species. Thus, the proportion of the total variation in species diversity explained by structural complexity may decrease where energy is the primary limiting factor. Similarly, the slope of the relationship between species diversity and structural complexity may be less steep in energy poor environments. Patterns of diversity among seral stages may also vary with available energy. Forest recovery rates after disturbance are slower in cold, dry, energy limited systems, leading to a longer delay for the production of critical resources. Thus, species diversity is likely to be lowest in early seral stages in energy limited systems.

If this hypothesis is correct, there are important implications for management. Maintenance of forest structure within a shifting mosaic harvest scheme is likely to be effective in high energy environments. In low energy environments, species diversity is often concentrated in localized areas of relatively high energy (Hansen & Rotella 2002, Bailey et al. 2004). Identifying and managing these hot spots judiciously will be critical for maintaining species diversity in these landscapes.

The goal of this paper is to examine the relative and interactive effects of energy and forest structural complexity on bird species richness (BSR) in the forests of the PINW. This region has strong gradients in climate, topography, and soils. Thus, forest productivity ranges from among the highest in North America west of the Cascade Crest, to very low in the cold continental setting on the east slopes of the Rocky Mountains. In this study we use BSR to test our predictions about biodiversity. Birds are a suitable taxonomic group for this study for several reasons. Birds are well understood ecologically and taxonomically, and represent a range of feeding guilds and habitat niches (Erdelen 1984, O'Connell et al. 2000). Furthermore, birds represent the only taxonomic group that has been sampled sufficiently across the study landscapes to allow for these fine-scale analyses. Species richness is a simple way to represent regional diversity (Magurran 1988), and bird species richness has proven to be a valuable indicator of overall biodiversity (Furness and Greenwood 1993). We used a combination of satellite data representing available energy, and field data representing forest structure and BSR from five study landscapes distributed across the climatic gradient of the PINW to test the following hypotheses:

1. Energy as a regional and landscape-scale driver of species diversity
    - 1a. BSR exhibits a unimodal relationship with energy across all landscapes in the study region.
    - 1b. The relationship between available energy and BSR at the landscape-scale is positive in energy limited environments and flat or decreasing within energy rich environments.
2. The interaction of forest structural complexity and available energy drives species diversity.
    - 2a. Forest structural complexity explains a lower percentage of the variation in BSR in energy limited environments and a higher percentage in energy rich environments.
    - 2b. The slope of the relationship between forest structural complexity and BSR is greatest in energy rich environments.

Methods

Study Areas

We selected five study landscapes to span the gradient of available energy that exists in managed forest lands of the PINW (Figures 2.2 & 2.3). Landscape selection emphasized ownerships where land managers had biodiversity management objectives, and locations where existing data might supplement our sampling efforts. Three of the five study landscapes center on forest industry planning areas, including some surrounding portions of the ecoregion for which bird data were available. These landscapes include: Springfield and Cottage Grove Tree Farms (here after referred to as Springfield) on the west slope of the Oregon Cascades (Weyerhaeuser Co.); the Central Cascades Habitat Conservation Area (here after referred to as Cle Elum) on the eastern slope of the Washington Cascades (Plum Creek Timber Co.); and the Goldfork watershed in the southern Idaho Batholith. The Coast Range and Yellowstone landscapes were selected to represent the extremes of the biophysical gradient in the region (Figure 2.3). Existing biodiversity data was used to complete analyses for the Coast Range and Yellowstone landscapes (McGarigal and McComb 1995, and Hansen et al. 2000).

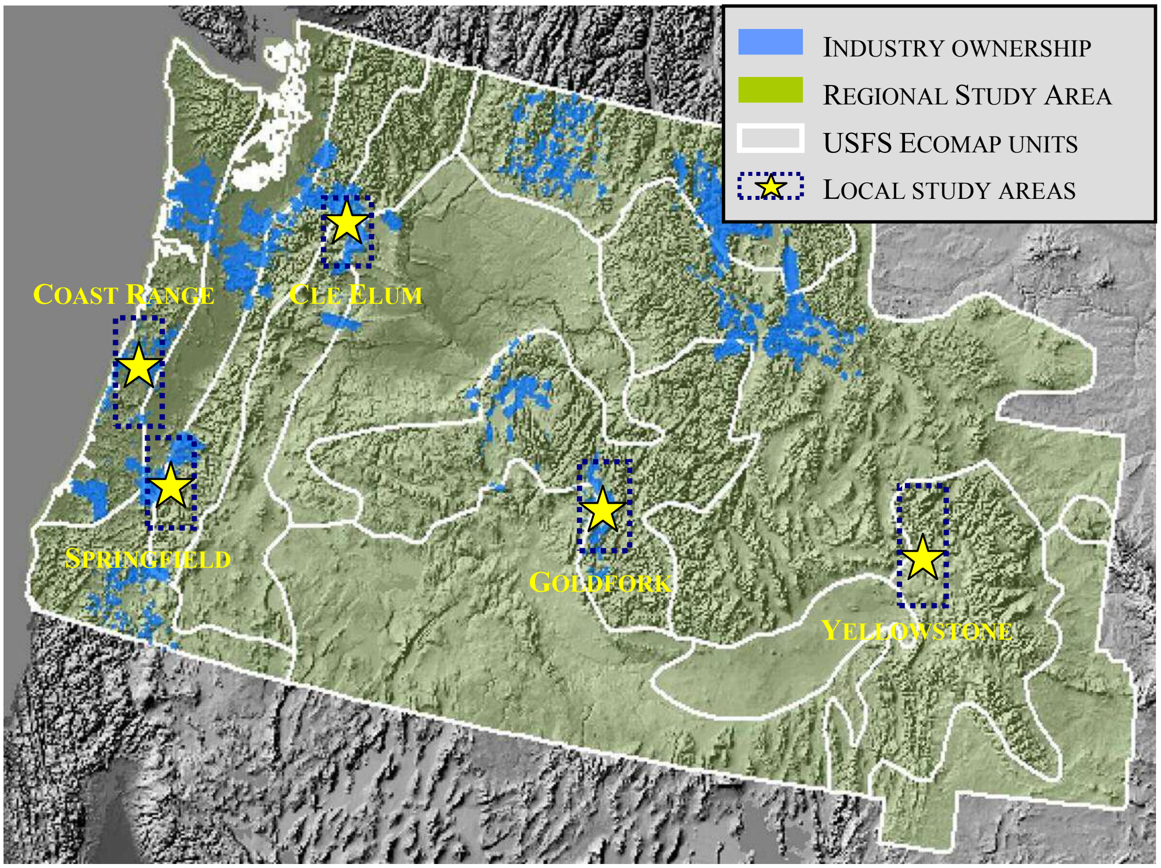

Figure 2.2. Location of study landscapes.

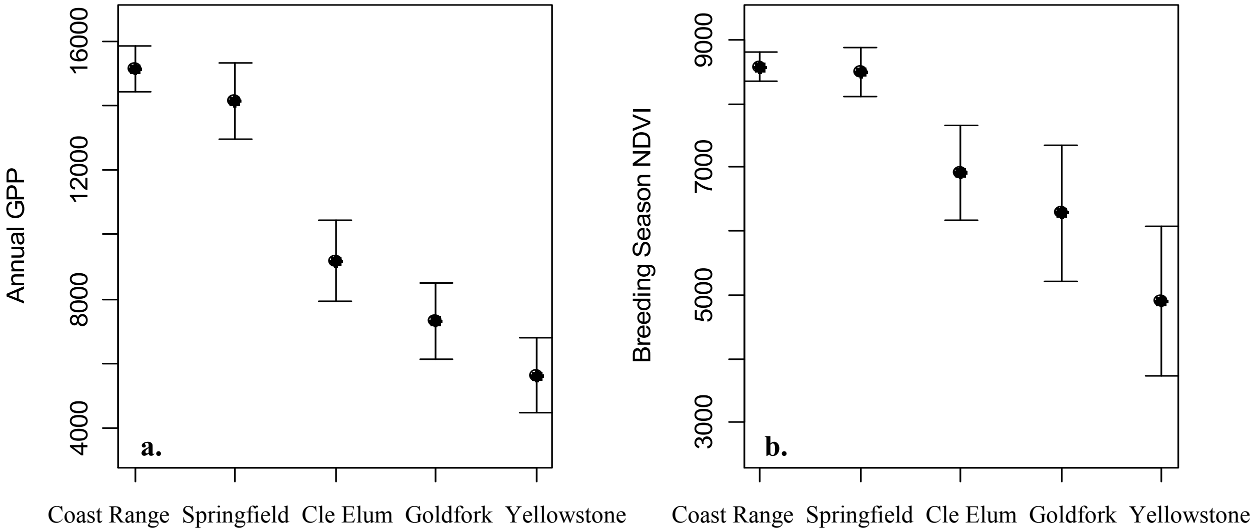

Figure 2.3. Gradient of annual gross primary productivity (GPP: $\mathrm{gm}^{C}\mathrm{m}^{-2}\mathrm{day}^{-1}*10^{3}$) (a), and breeding season average normalized difference vegetation index (NDVI: 0-1 index $*10^{4}$) (b) across landscapes from west to east (mean +/-1 sd).

Coast Range, OR: The Oregon Coast Range data resulted from a study by McGarigal and McComb (1995) on the effects of landscape pattern on breeding birds. The data were collected in the Drift Creek, Lobster Creek, and Nestucca River basins in the central Oregon Coast Range. The study area ranges in elevation from sea level to 968-m and precipitation averages 150- to 300-cm annually. The land is characterized by steeply cut drainages that lie almost exclusively in the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1973). Forests on federal land (the majority of the study area) have a bimodal age distribution with a mix of 0-40 yr old forests and > 140 yr old forests (McGarigal and McComb 1995). The private land in the Oregon Coast range is intensively harvested with primarily second- and third-growth trees (< 50 yrs old) remaining. A wide variety of structural conditions exist in the area. A more detailed description of the study area is included in McGarigal and McComb (1995).

Springfield, OR: Weyerhaeuser's Springfield and Cottage Grove tree farms and surrounding BLM and USFS lands are located just east of Eugene, Oregon in the western toe slopes of the Oregon Cascades. The study landscape ranges in elevation from 300-1000-m and precipitation averages 120- to 200-cm annually. Due to little variation in mean temperature and precipitation across the study area, Douglas-fir (*Pseudotsuga menziesii*) is the dominant forest type across the region. However, upland hardwood species become more abundant in the southern end of the study landscape. Forests in this region have been highly fragmented due to a dominance of short rotation plantations on private lands (Ripple et al. 1991).

Cle Elum, WA: The Cle Elum landscape is located along the I-90 corridor between 600m and 1800m in Washington's Central Cascades. Plum Creek Timber Company's ownership totals roughly 57,000-ha distributed in a checkerboard pattern with Mount Baker-Snoqualmie and Wenatchee National Forest land. The dominant forest types found in this study area vary greatly from wet hemlock/fir forests averaging over 200-cm of precipitation per year near the crest of the Cascades, to dry open ponderosa pine (*Pinus ponderosa*) forests averaging 50-cm of precipitation per year on the east slopes. Landscape pattern also varies greatly with large wilderness and roadless areas bordering more intensively managed plantations at the north and south end of the study area.

Goldfork, ID: The Goldfork study area is situated in the Southern Idaho Batholith section of the Northern Rocky Mountain Province in west-central Idaho. Existing data was collected across the entire area encompassing about 200,000-ha of forested land managed by Forest Capital Partners (formerly Boise Cascade Corporation), and the Boise and Payette National Forests. Forested habitats in this area range from dry ponderosa pine at 1200-m, to mid-slope grand fir (*Abies grandis*) and Douglas-fir, to subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) at 2800-m. Annual precipitation ranges from 50-150-cm, with most of the precipitation falling as snow at higher elevations.

Yellowstone, WY, MT, ID: The 950,000-ha study area includes parts of the upper Gallatin, Madison and Henry's Fork Watersheds (Hansen et al. 2000). Each of these rivers originates in Yellowstone National Park and then passes through the Gallatin or Targhee National Forest on their way to large privately owned agricultural valleys (Gallatin and Upper Snake). The variation in temperature and precipitation between upper and lower elevations is extreme. Vegetation in the area is a mosaic of forests, shrublands, and grasslands. Forest harvest has occurred primarily in the middle and lower elevations consisting of lodgepole pine (*Pinus contorta*) and Douglas-fir forests. Clearcuts are slow to regenerate, and structural complexity is low in all seral stages when compared with dense productive forests west of the Cascade Crest. A more detailed description of the study area is included in Hansen et al. (2000). In order to have a balanced design across the structural complexity/seral stage gradient, we only used data from lodgepole pine dominated stands.

Sampling Methods

Bird diversity data for each landscape were collected/compiled within a stratified matrix of stand age/structure class and stand vegetation/habitat class/site index (representing available energy) (Table 2.1). The objective of sample stratification was to have biodiversity samples across the full gradients of forest structural complexity and available energy, allowing meaningful tests of our hypotheses. Bird diversity data were generated from bird point-count data collected at four to six points (depending on the landscape) within each stand.

Table 2.1. Generic matrix of sampling categories. Matrix values (x) correspond to the number of stands (four to six points each) needed to sample at least 20 points in each category.

GRADIENT OF AVAILABLE ENERGY (DOMINANT VEGETATION TYPE, HABITAT CLASS, OR SITE INDEX)	FOREST STRUCTURE/SERAL STAGE GRADIENT			
	SHRUB SAPLING/ "CLEARCUT" (0-2in. QMD east and west)	SMALL TREE/ "POLE" (2-9in. QMD east 2-10in. QMD west)	MEDIUM TREE/ "MATURE" (9-16in. QMD east 10-21in. QMD west)	LARGE TREE/ "OLD-GROWTH" (>16in. QMD east >21in. QMD west)
LOW	x	x	x	x
MEDIUM-LOW	x	x	x	x
MEDIUM-HIGH	x	x	x	x
HIGH	x	x	x	x

Samples for each landscape were obtained and organized under a stratified random design (e.g., Table 2.1). Data from four or more stands were obtained within each of four forest growth stages (structural/seral stage gradient) and three to five vegetation type, habitat class, or site index classes (energy gradient). Due to the range of conditions sampled at the Yellowstone landscape, only two seral stages were sampled. With the exception of the Yellowstone landscape, sampling at each landscape occurred across the full range of seral stages. However, the range of various indicators of structural complexity within seral stages varied significantly among landscapes due to the different management practices of land owners. Consequently, we could more fully test the effect of structure across, rather than within, seral stages.

The stratification of samples based on seral-stage categories were separated by quadratic mean tree diameter (QMD) cutoff values adapted from Oliver et al. (1995). The QMD cutoff values differed for landscapes west or east of the Cascade crest based on structural classifications provided in Brown (1985) for west-side habitats, and Thomas (1979) for east-side habitats. To represent the energy gradient, we initially selected samples based on site index, habitat type or vegetation class, which integrates climate, topography and soils and are highly correlated with productivity. Once census point locations were acquired, we confirmed that they represented the full gradient of available energy by plotting the values of primary productivity (an annual measure of available energy) for each sample point and comparing the distribution with the full range of the local energy gradient. The energy stratification classes varied among landscapes as determined by local habitat types. The methods included below pertaining to the collection of bird and forest structure data are relevant only to the Springfield, Cle Elum and upper elevations of the Goldfork landscape. For specific information on the data collection methods of data contributors please see McGarigal and McComb (1995), Hansen et al. (2000) and Sallabanks et al. (2006).

Bird Data: The Springfield, Cle Elum and upper elevations of the Goldfork landscapes were sampled during the breeding season in 2003, 2004, and 2005, with two years of sampling completed at each bird census point. Four to six bird census points were located along a transect with 150-200-m separation between adjacent points. During each survey year, points were sampled three times during the breeding season (15 May-10 July). Given the redundancy of effort per stand, we 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 variation in transect length and point spacing depended on the conditions of the landscape being surveyed and the protocol of any existing data sets that we were matching. The manner in which data were recorded was consistent with the point count survey guidelines described by Ralph et al (1995) within a 10-min time interval. Every bird seen or heard was recorded with an associated first detection distance from the census point. Distance sampling (Thomas et al. 2002) confirmed that not all species were fully detectable at all landscapes within a 50-m radius. However, individual species detectability did not vary between habitat types or seral stage in our results. Species richness values were not biased by habitat type based on differential species detectability. Therefore, to simplify analyses, we used a 50-m fixed radius, and did not adjust species abundance for detectability. Species richness was calculated as the total number of bird species detected at each survey point over the three breeding season visits. A stand-level species richness response variable was then created by averaging the four to six point richness values and then averaging the stand totals over the two years of survey work.

Forest Structure Data: We sampled vegetation at each point-count station once during the two years of survey work. To capture characteristics of the entire survey stand we established four sub-plots 20-m from each survey station in the four cardinal directions. Within each of the four sub-plots, attributes were measured within either a 0.25-m^2 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 (Table 2.2).

Table 2.2. Forest stand description measurements and area of inventory.

AREA OF INVENTORY	MEASUREMENT	DESCRIPTORS
Bird census point	Aspect, slope, distance to nearest road, slope position.	Aspect and slope (deg.); dist. to road (m); slope position (creek, mid-slope, or ridge)
8-m radius plot	Tree and snag density	Species, size class (8 dbh classes), decay class (5 decay classes), and height (m)
4-m radius plot	Seedling-sapling density, coarse woody debris volume	Species, height class (3 height classes for saplings), and decay class (5 decay classes for CWD)
2-m radius plot	Shrub density	Species and basal diameter class (8 basal diameter classes)
0.25-m square	Understory cover	% shrub, % conifer, % herbaceous and % total understory cover

Energy Data: To test the hypothesis of the energy based controls on biodiversity, 1-km-scale remotely sensed predictor data were used at all sites. Elevation data were gathered from a 10-m resolution digital elevation model, and information on slope, aspect, and slope position were gathered during the vegetation surveys. Remotely sensed predictor variables were categorized as shown in Table 2.3.

Data Analysis

Available Energy: Remotely sensed energy data resulted in 31 predictors describing many aspects of potential available energy and productivity. We compared the mean and standard deviation of available energy predictors for each of the five landscapes to investigate how much variation there is in available energy within each landscape, and how much overlap there was between landscapes. AIC values from linear, quadratic (unimodal), cubic (non-symmetric unimodal), and threshold (breakpoint) linear models were compared to explain the relationship between BSR and both breeding season and annual measures of available energy across the entire region (all five landscapes). The third order relationships were used because they would allow the relationship between BSR and energy to exhibit a non-symmetric unimodal relationship. The relationship between breeding season and annual measures of energy and BSR within each landscape was examined by creating simple linear models. The R^2 values of the univariate energy models, as well as the significance and direction of the relationships were reported to provide evidence about the relationship between energy and diversity at each landscape.

Table 2.3. Remotely sensed predictor data required in the study listed by category, variable, source and the methods of data collection.

CATEGORY	PREDICTOR VARIABLE	RESOLUTION / SCALE	SOURCE AND YEARS SAMPLED	TIME PERIOD REPRESENTED
Topography	Elevation	10m	USGS source: 1 km digital elevation model	N.A.
Climate	Precipitation, temperature, vapor pressure deficit, solar radiation, frost and growing days	1km	DAYMET source: (remodeled) 18 years averaged (1982-2000)	Annual, April through September, and May/June measurements for all predictors
Vegetation productivity	NDVI (Normalized Difference Vegetation Index), GPP (Gross Primary Productivity), NPP (Net Primary Productivity), Growing Season Index	1km	MODIS source: NDVI = 3 year avg. (2003, 2004 & 2005) GPP and NPP = 5 year avg. (2000-2004)	NDVI = 3 single day measurements and a breeding season average; GPP and NPP = average annual measures

Interaction of Forest Structure and Available Energy. Data collected during vegetation surveys resulted in 28 predictors representing the variation in size and horizontal distribution of trees, shrubs, and snags, as well as canopy and understory measures. We first compared the strength and direction of simple relationships between forest structural complexity and BSR at different landscapes by identifying the three strongest (low P-value, high R^2) measures of structural complexity across all landscapes. These include Shannon diversity index of tree size classes (here after referred to as tree size diversity), percent shrub cover, and a structural complexity index of horizontal vertical variation in tree size and density (here after referred to as SCI and computed as: tree size diversity * standard deviation of tree density between 20 subplots * 100) (Zenner and Hibbs 2000, McElhinney et al. 2005).

Structural complexity co-varies with energy to some extent at all landscapes. We found that covariates describing shrubs and understory cover were the only predictors that had consistently moderate correlations with measures of energy (45-60% correlation) at most landscapes. To more cleanly separate the effect of structure and energy in driving species diversity at each landscape we removed the correlated shrub and understory covariates from the interaction analysis, leaving each landscape with 18 predictors of forest structure representing variation in the size and density of trees, snags, saplings, coarse woody debris, and canopy cover.

Eighteen of the 28 structural complexity predictors and the entire suite of available energy (31) predictors were used to test the relative strength of available energy and forest structural complexity in driving species diversity at each landscape. However, many of the predictors of forest structure and especially available energy were variations of the same measurement (e.g., annual precipitation vs. breeding season precipitation). To reduce the number of redundant predictors for the interaction analysis, single predictors of forest structure and available energy were selected to represent each of ten meaningful categories (Table 2.4). In this way, we also helped to insure that the suite of forest structure covariates used in the models for each landscape would have similar potential for explaining the variation in BSR. Collinearity between variables in different predictive categories of the same gradient was not considered to be a problem because the relationships between individual predictors and BSR were not evaluated while testing this hypothesis. The predictor categories for forest structure and available energy remained the same for each landscape, but the predictor representing the category was allowed to differ. In addition, predictors were allowed quadratic or cubic functional relationships when the resulting relationship with BSR was determined to be ecologically meaningful. This method allowed for a more complete explanation of the relationship between forest structural complexity, available energy, and BSR at each landscape.

Table 2.4. Descriptive categories of forest structure and available energy.

FOREST STRUCTURE	**AVAILABLE ENERGY**
Canopy cover	Vapor pressure deficit
Horizontal variation in canopy cover	Solar radiation
Density of trees	Frost days or Growing days
Horizontal variation in tree density	Precipitation
Size of trees	Temperature
Horizontal variation in tree size	Normalized difference vegetation index
Density of snags	Primary productivity
Size of snags	Elevation
Density of saplings	Growing season index
Coarse woody debris	Aspect and slope

Energy explains the variation in BSR with varying strength at all landscapes. To control for the effect of energy when assessing the strength of the relationship between structural complexity and BSR we calculated the additional explanatory power of forest structural complexity covariates when added to a five predictor energy model at each landscape. We used five predictors to provide a balance between adequate representation of the energy and structure gradients and model parsimony. To create the five predictor energy model we selected the most significant univariate energy predictors ($P < 0.05$) from each of the ten descriptive categories and included them in a stepwise model selection procedure (forward, backward and exhaustive methods of variable selection) using the "regsubsets" function in the R statistical package. Regsubsets uses R^2 as the criterion for best model selection, thus ensuring that the resulting energy model explained the highest level of variation possible using five predictors. The best energy models were used as the base condition for each landscape.

To test the interaction of structural complexity with available energy in driving diversity at each landscape we used the same automated model selection procedure to select the best ten predictor model (five structure and five energy) while forcing the selected five predictor energy model to be the base condition. Again, this process used R^2 as the criterion for model selection which ensured that the five structural complexity covariates added the most additional explanatory power possible, given the five energy predictors already in the model. We then compared the R^2 values of the five predictor energy model to the ten predictor structure and energy model to identify the additional explanatory power added by the structural complexity covariates. We tested for the potential effects of spatial autocorrelation of stands within each landscape and found that spatial autocorrelation terms were not significant in any of the models. The percent of the model R^2 corresponding with the addition of structural complexity covariates were compared descriptively to weight the evidence for a trend in the explanatory power of forest structure across the regional energy gradient. In addition, the model selection procedure was run in reverse, adding forest structure predictors to the model first and then comparing the percent increases in model R^2 after adding five available energy covariates.

To test our prediction that the slopes of forest structural complexity covariates would be steeper in high energy environments we investigated the slopes of significant linear relationships between BSR and SCI. The comparison of slopes required the stand structure data to have been collected with identical protocols (dbh class definitions, plot sizes, etc.). Therefore, we restricted the comparison to include only the Springfield, Cle Elum and Yellowstone landscapes. We conducted a test of slopes using the formula: $t = (b_1 - b_2) /\sqrt{(SEb_1^2 + SEb_2^2)}$, where $df_1 = n_1-1$ and $df_2 = n_2-1$, for all possible combinations.

Results

Variation in Bird Diversity

Average BSR was highest in Springfield, intermediate in Coast Range and Cle Elum, lower in Goldfork, and lowest in Yellowstone (Figure 2.4). All landscapes had similar levels of variation in BSR. All landscapes had significantly different ranges of BSR values ($P < 0.05$) except the Coast Range and Cle Elum which had similar ranges of BSR.

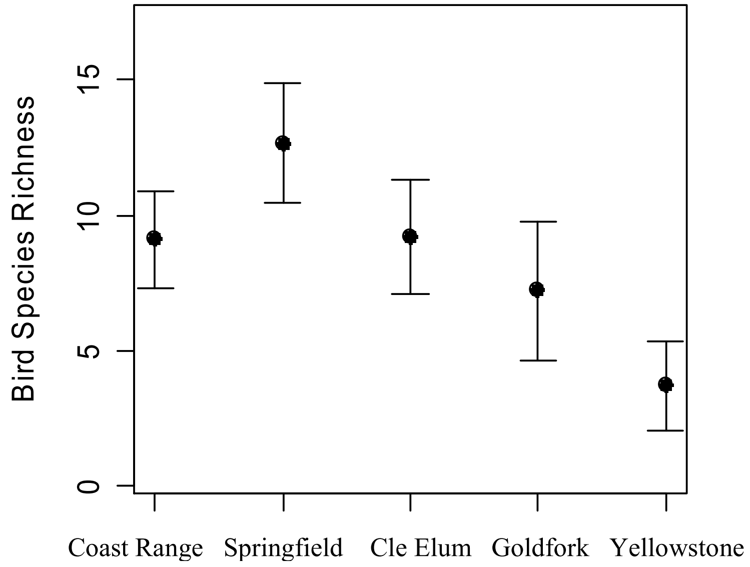

Figure 2.4. Bird species richness by landscape. Mean +/- 1 SD of the number of bird species detected within 50-m; cumulative over three 10-min. visits and averaged by year.

Hypothesis 1. Energy as a Regional and Landscape Scale Driver of Species Diversity

Measures of energy were highest in the Springfield and Coast Range landscapes, and decreased to the east, with Yellowstone being lowest (Table 2.5). There was more variation in energy covariates in the Cle Elum, Goldfork and Yellowstone landscapes, and less in the Coast Range and Springfield landscapes (Table 2.5, Figure 2.3b). The variation in energy predictors can be viewed as a measure of the width of the energy gradient at each landscape. The widths of the gradient of available energy differ between the various managed forest lands of the PINW. However, the width of the energy gradient for a particular managed forest region will play a significant role in its management. Therefore, comparison between landscapes without standardizing for the width of the energy gradient was preferable.

Table 2.5. Mean and standard deviation (SD) of available energy covariates.

	Coast Range		Springfield		Cle Elum		Goldfork		Yellowstone	
ENERGY MEASURE	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Gross Primary Productivity ($gm^{C}m^{-2}day^{-1}*10^{3}$)	15133	719	14152	1184	9176	1241	7321	1176	5620	1152
Breeding Season NDVI (avg. highest 0-1 index values from 4 periods (May 6 – June 26))*10^{4})	8576	231	8502	388	6911	739	6281	1067	4899	1169
Growing Degree Days (annual sum)	361.8	25.3	371.6	22.3	228.5	29.7	212.1	42.4	184.2	29.5
Temperature (monthly average of annual temp in (degrees Celsius))	9.4	0.7	9.5	0.7	4.6	1.2	3.2	1.8	1.4	1.3
Annual Precipitation (monthly average of annual precipitation (cm))	19.2	1.3	13.4	2	11.8	4.5	7.9	1.7	7	1.5

BSR exhibited a threshold (breakpoint regression) relationship with the annual measure of available energy (GPP) and a cubic relationship with the breeding season measure of available energy (NDVI) across all five landscapes (Table 2.6, Figure 2.5). The ΔAIC value between the best (linear with a breakpoint at GPP = 12266) and second best (quadratic GPP) model was 8.71 for the relationship between BSR and the annual measure of available energy (Table 2.6). The threshold occurred between the Cle Elum (east slope Cascades) and Springfield (west slope Cascades) landscapes, and the slope after the breakpoint was negative (P = 0.082), showing a downturn in BSR for the two energy rich sites west of the Cascade crest. The relationship between breeding season energy and BSR was asymmetric unimodal. The ΔAIC value between the best (cubic NDVI) and second best (linear with a breakpoint at NDVI = 8007) model was 3.25 (Table 2.6). All breeding season energy models had lower AIC scores than the best annual energy model.

Table 2.6. Best regional univariate models of BSR using annual and breeding season measures of available energy (all landscapes).

Breeding Season Energy Models	**AIC**	**Δ AIC**	**R-squared**	**P-values**
Breeding season NDVI cubic	*1258.37*	*0*	*0.49*	*0.003 & <0 .001 & <0 .001*
Breakpoint Breeding Season NDVI = 8007	1261.62	3.25	0.48	< 0.001 for values < 8007 0.586 for values > 8007
Breeding season NDVI linear	1269.81	11.44	0.46	< 0.001
Breeding season NDVI quadratic	1269.94	11.57	0.46	< 0.001 & 0.174
Annual Energy Models	**AIC**	**Δ AIC**	**R-squared**	**P-values**
Breakpoint Annual GPP = 12266	*1270.2*	*0*	*0.46*	< 0.001 for values < 12266 0.098 for values > 12266
Annual GPP quadratic	1278.91	8.71	0.44	< 0.001 & < 0.001
Annual GPP cubic	1280.62	10.42	0.44	0.152 & 0.909 & 0.594
Annual GPP linear	1301.77	31.57	0.39	< 0.001

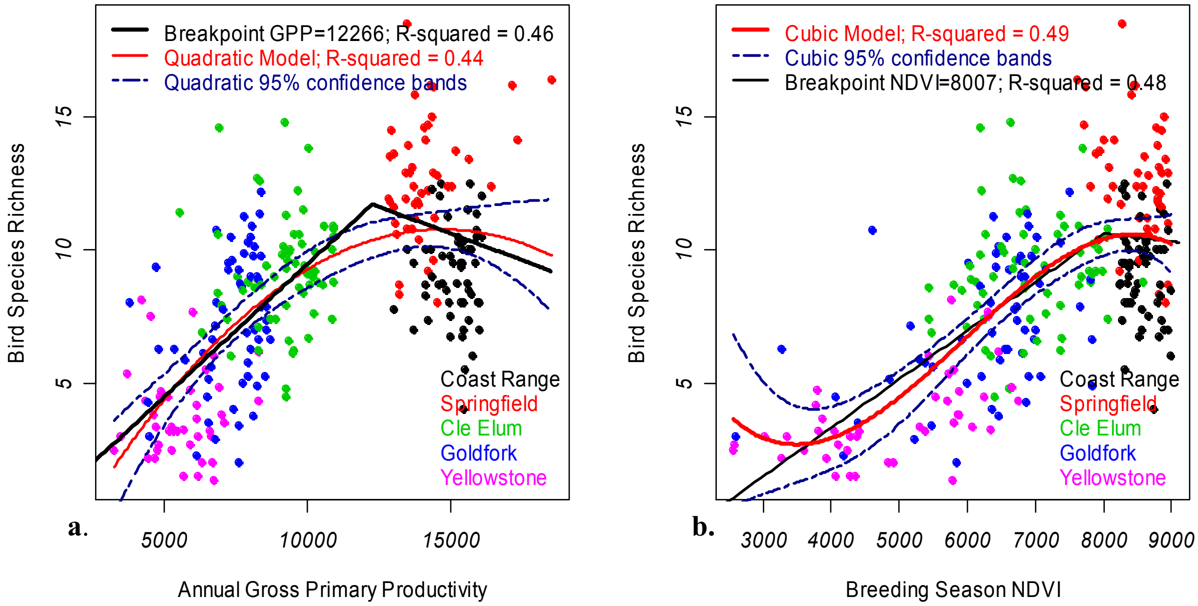

Figure 2.5. BSR across the PINW by annual energy (GPP) (a), and breeding season energy (NDVI) (b).

BSR had negative relationships with breeding season NDVI at the Coast Range and Springfield Landscapes (Table 2.7). The remaining available energy predictors had non-significant relationships with BSR at the Coast Range and Springfield landscapes. Positive or unimodal relationships existed between BSR and available energy covariates at the Cle Elum, Goldfork and Yellowstone landscapes. At the Cle Elum, Goldfork and Yellowstone landscapes, precipitation was negatively correlated with BSR. Where precipitation was negatively correlated with BSR it was positively correlated with elevation ($P < 0.001$), and in the Goldfork and Yellowstone landscapes, precipitation was negatively correlated with primary productivity ($P < 0.001$). The available energy hypothesis was supported at all landscapes. The significance and direction of the relationship between BSR and available energy for a given landscape corresponded to where that landscape is positioned on the regional gradient of available energy.

Table 2.7. Direction and significance of relationships between available energy and BSR. See Table 2.5 for units of measure.

	Coast Range		Springfield		Cle Elum		Goldfork		Yellowstone	
ENERGY MEASURE	Sig.	Dir.	Sig.	Dir.	Sig.	Dir.	Sig.	Dir.	Sig.	Dir.
Gross Primary Productivity	-		-		***	pos. (cubic)	***	pos. (quad.)	***	pos.
Breeding Season NDVI	*	neg.	**	neg.	**	pos.	***	pos.	***	pos.
Annual Growing Degree Days	-		-		*	pos. (cubic)	***	pos. (quad.)	***	pos.
Annual Temperature	-		-		*	pos. (cubic)	***	pos. (quad.)	***	pos.
Annual Precipitation	-		-		**	neg.	*	neg.	***	neg.

- = not significant   * = $P < 0.05$ ** = $P < 0.01$ *** = $P < 0.001$

Hypothesis 2. Interaction of Structure and Energy

Structural Complexity Across Landscapes and Seral Stages: The range and mean values of covariates representing forest structural complexity within each seral stage varied widely among landscapes (Table 2.8). The variation in covariates representing forest structural complexity was significantly higher across landscapes in the early seral stages (Shrub-sapling (SS), Small Tree (ST)) than in the later seral stages (Medium Tree (MT), Large Tree (LT)) ($P < 0.001$). More specifically, the Shrub-sapling seral stage CV was significantly higher than CV's in all other seral stages (ST: $P = 0.01$; MT: $P < 0.001$; LT: $P < 0.001$) across landscapes.

Table 2.8. Mean and coefficient of variation (CV) of covariates representing structural complexity by landscape and seral stage.

		Coast Range		Springfield		Cle Elum		Goldfork		Yellowstone	
STRUCTURAL COMPLEXITY PREDICTOR	SERAL STAGE	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Tree size diversity: Shannon diversity index of tree abund. in 8 dbh classes	SS	0.5	0.5	0.2	1.3	0.4	0.9	0.7	0.6	0.0	1.5
	ST	0.2	0.8	0.9	0.2	0.7	0.5	1.1	0.2		
	MT	0.8	0.4	1.0	0.2	1.0	0.2	1.0	0.1	0.8	0.2
	LT	1.6	0.1	1.2	0.2	0.9	0.5	1.3	0.1		
	AVG	0.9	0.5	0.8	0.5	0.8	0.5	1.0	0.3	0.4	0.9
Structural Complexity Index (SCI: vertical and horizontal variation in tree size)	SS	1.8	1.1	3.3	1.3	10.0	0.9	18.8	0.6	2.4	1.5
	ST	1.0	1.1	15.4	0.4	13.6	0.6	41.0	0.4		
	MT	26.9	1.0	32.1	0.2	18.6	0.4	46.1	0.4	8.1	0.8
	LT	13.4	0.5	26.9	0.3	19.5	0.5	36.5	0.3		
	AVG.	10.7	0.9	19.4	0.6	15.4	0.6	35.6	0.4	5.2	1.2
Percent Shrub Cover	SS	37.9	6.5	22.3	7.8	23.9	5.6	44.8	4.9	11.9	1.8
	ST	64.8	3.0	22.7	5.1	30.4	5.7	31.5	6.1		
	MT	44.2	3.8	19.3	7.2	29.1	6.4	28.5	5.2	19.4	3.1
	LT	50.6	2.5	21.7	7.1	20.0	7.1	38.4	5.3		
	AVG.	48.2	4.1	21.5	6.7	25.8	6.3	36.1	5.5	15.4	2.5

BSR exhibited positive or unimodal relationships with structural complexity predictors across seral stages at all landscapes, except Springfield (Table 2.9). In the Coast Range landscape, BSR had a positive relationship with SCI and a unimodal relationship with shrub cover. In the Springfield landscape, measures of overstory complexity (tree size diversity, SCI) were negatively related to BSR, but shrub cover was positively related to BSR (Table 2.9). The mean and standard deviation of shrub cover was similar across all seral stages in Springfield, but the highest mean density of large shrubs was in the Shrub-sapling seral stage stands. SCI was positively related to BSR in the Cle Elum and Yellowstone landscapes. In the Goldfork landscape BSR had a unimodal relationship with shrub cover and no correlation with either measure of overstory complexity.

Table 2.9. Direction and significance of relationships between covariates representing structural complexity and BSR. See Table 2.8 for units of measure.

	Coast Range		Springfield		Cle Elum		Goldfork		Yellowstone	
STRUCTURAL COMPLEXITY MEASURE	Sig.	Dir.	Sig.	Dir.	Sig.	Dir.	Sig.	Dir.	Sig.	Dir.
Tree size diversity	-		**	Cubic	-		-		-	
SCI	*	Pos.	**	Neg.	***	Pos.	-		**	Pos.
Shrub cover	*	Quad.	*	Pos.	-		*	Quad.	-	

- = not significant * = P < 0.05 ** = P < 0.01 *** = P < 0.001

The data collected at each site within each seral stage did not offer enough power to complete a broad-scale test of the relationship of forest structural complexity and BSR within each site/seral-stage combination. However, some notable relationships between BSR and forest structural complexity within seral stages emerged at the Springfield site.

Tree size diversity, which exhibits a cubic relationship with BSR across all seral stages (Table 2.9), had no significant relationship with BSR in the Shrub-sapling, Medium Tree, or Large Tree seral stages. However, in the Small Tree seral-stage, where canopy closure typically occurs, there was a significant decrease in BSR with increasing tree size diversity (Figure 2.6a). In addition, the range of BSR in the Small Tree seral stage was much larger than the ranges contained by all other seral stages, and BSR decreased with increasing canopy closure in Small Tree seral stage forests (Figure 2.6b). The same decrease in BSR occurred with increasing tree size diversity in the Small Tree stands in the Coast Range, although it was not significant. In Cle Elum, Goldfork, and Yellowstone, all seral stages exhibited weak positive relationships between BSR and Tree Size Diversity.

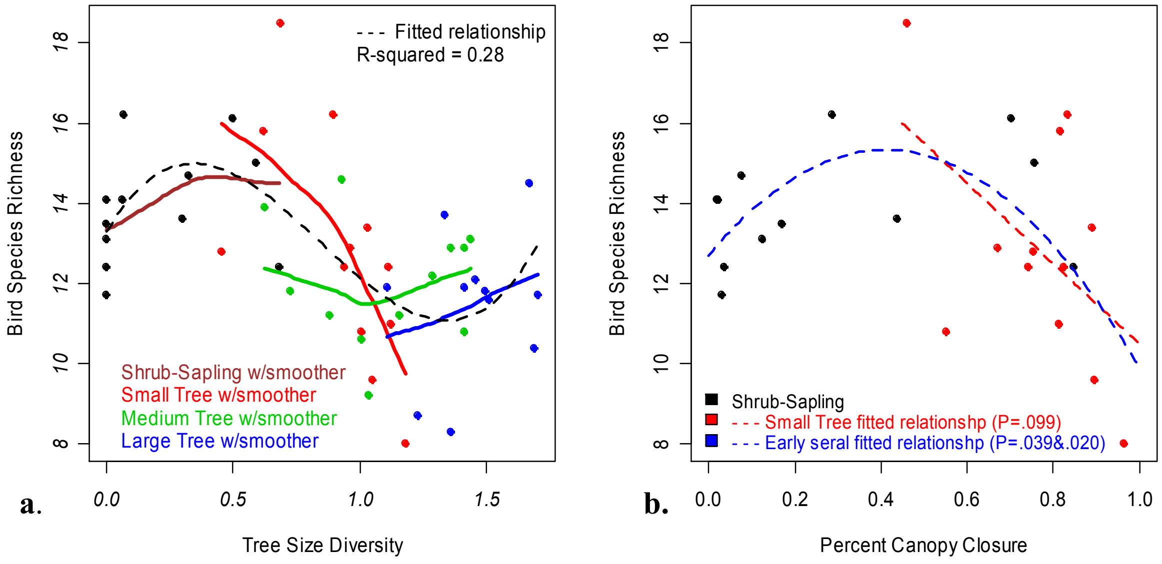

Figure 2.6. Tree size diversity vs. BSR separated by seral stage in Springfield (a). canopy closure vs. BSR in the Shrub-sapling and Small Tree seral stages in Springfield (b).

Explanatory Power of Structure and Energy: The R^2 values for available energy models used to predict BSR ranged from 0.30 in the Springfield landscape to 0.67 in the Yellowstone landscape (Table 2.10, Figure 2.7). The available energy only models explained more of the variation in BSR in the three landscapes east of the Cascade crest. A larger portion of the ten predictor model R^2 values corresponded with the addition of five forest structure covariates in the two landscapes west of the Cascade crest than in the energy limited landscapes to the east. When the analysis was reversed and the structural predictors were added to the model first, the energy limited landscapes east of the Cascade crest had a larger percentage of the total model R^2 associated with the addition of five available energy covariates (Table 2.11, Figure 2.8).

Table 2.10. Predictors from best ten predictor energy first models by landscape. See Appendix C for all predictor definitions.

LANDSCAPE	MODEL	PREDICTORS				
Coast Range	*energy*	ndvi145	frosummj	frosummj^2	tempavgas	radavgas
	structure	stdev.treecov	stdev.treecov^2	per.con	per.con^2	per.con^3
Springfield	*energy*	ndvi129	nppmodis	vpdavgjja	gsi05	preavgas
	structure	trdiv	trdiv^2	trdiv^3	qmd	st.complex
Cle Elum	*energy*	radavgas	preavgan	preavgan^2	preavgan^3	vpdavgann
	structure	num.mtree	num.mtree^2	stdev.trdiv	stdev.trdiv^2	st.complex
Goldfork	*energy*	tempavgmj	ndviavgan	ndviavg	frosummj	frosummj^2
	structure	num.sap	shade.sap	canopy	canopy^2	lsnag
Yellowstone	*energy*	tempavgan	ndvi129	ndviavg	ndviavgan	frosuman
	structure	qmd	avg.dbh	snpp	trdiv	num.58tree

Table 2.11. Predictors from best ten predictor structure first models by landscape. See Appendix C for all predictor definitions.

LANDSCAPE	MODEL	PREDICTORS				
Coast Range	*structure*	stdev.canopy	stdev.canopy^2	per.dec	per.dec^2	per.dec^3
	energy	radavgas	ndvi145	ndvi145^2	ndvi145^3	grosuman
Springfield	*structure*	trdiv	trdiv^2	trdiv^3	qmd	stdev.canopy
	energy	ndvi145	nppmodis	vpdavgjja	gsi05	preavgas
Cle Elum	*structure*	num.mtree	num.mtree^2	stdev.trdiv	stdev.trdiv^2	st.complex
	energy	radavgas	preavgan	preavgan^2	temavgmj	tempavgmj^2
Goldfork	*structure*	num.sap	lsnag	canopy	canopy^2	shade.sap
	energy	tempavgmj	tempavgmj^2	ndviavg	frosuman	frosuman^2
Yellowstone	*structure*	canopy	canopy	qmd	stdev.trdiv	snpp
	energy	gsi05	tempavgan	ndviavg	frosuman	ndviavgan

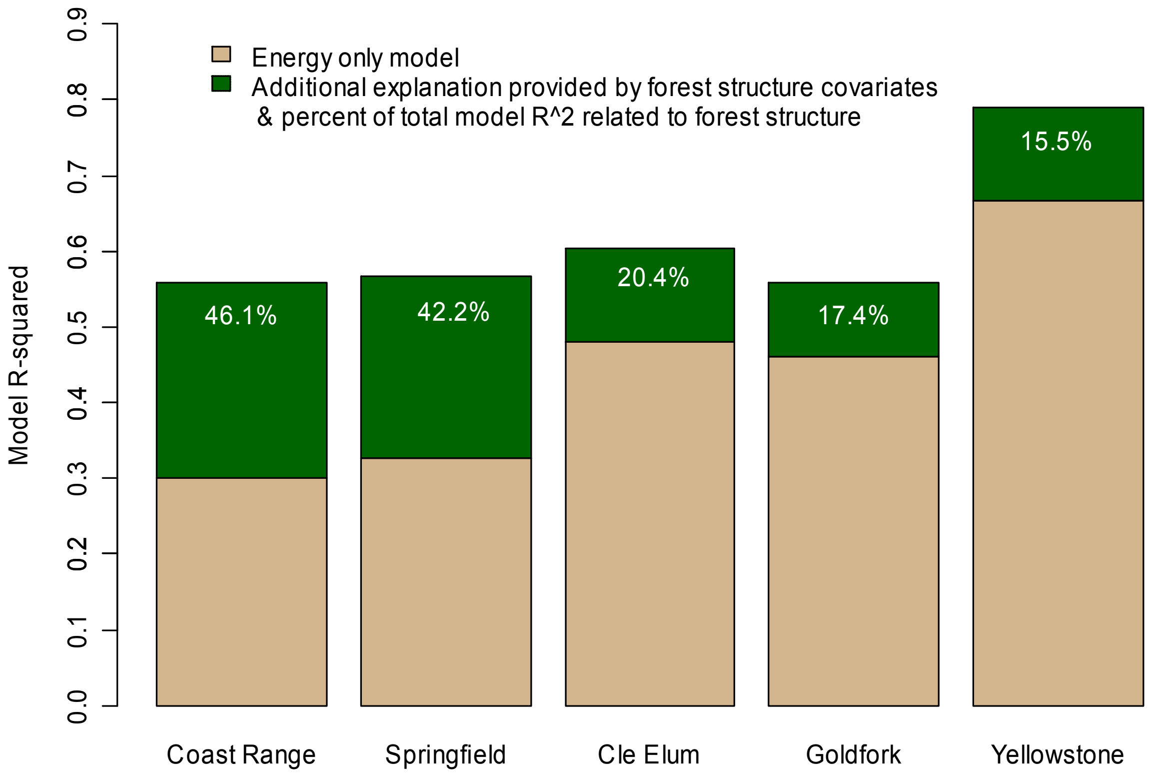

Figure 2.7. Percent of the total model R^2 resulting from the addition of five predictors of forest structure to a five predictor energy model at each landscape.

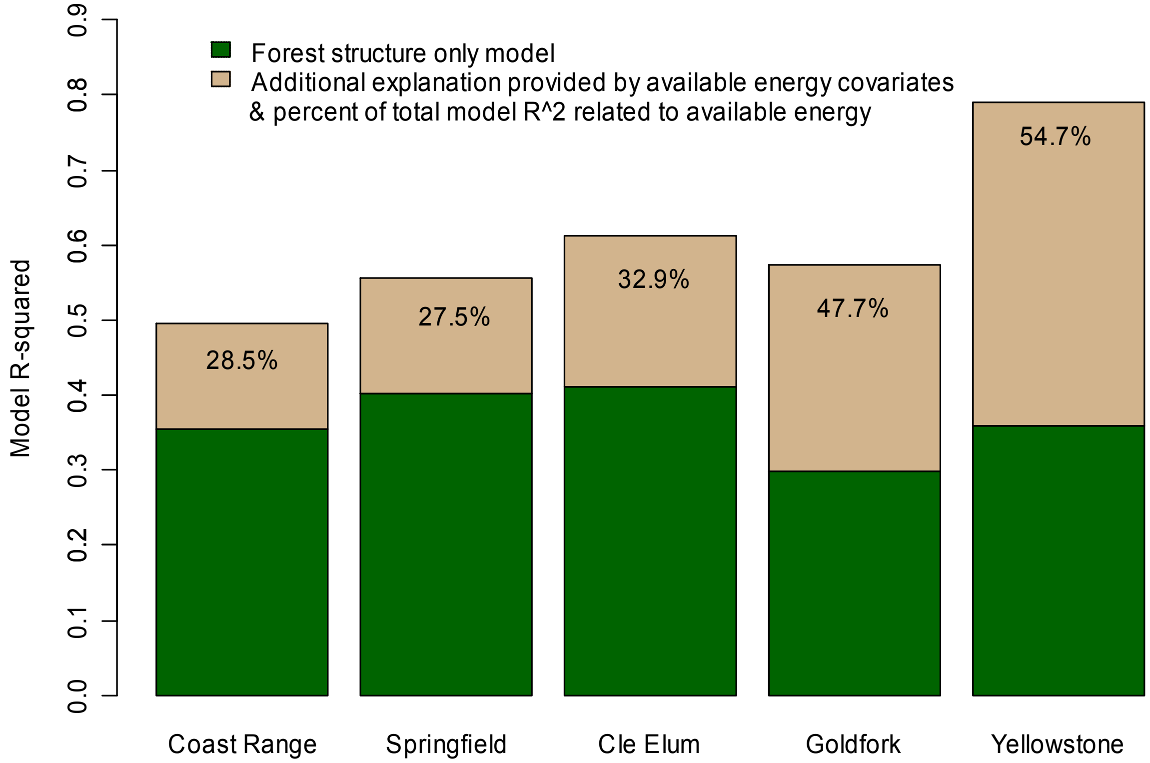

Figure 2.8. Percent of the total model R^2 resulting from the addition of five predictors of available energy to a five predictor forest structure model at each landscape.

Forest Structural Complexity Test of Slopes: The slope of the relationship between BSR and SCI varied in direction and strength between the three landscapes (Figure 2.8). The Springfield landscape had a significant negative relationship between BSR and SCI. The Cle Elum and Yellowstone landscapes both had significantly positive relationships between BSR and the structural complexity index. The slopes of the relationship at Springfield differed significantly from the slopes at the Cle Elum and Yellowstone landscapes ($P < 0.001$, and $P < 0.001$, respectively). The Cle Elum and Yellowstone slopes did not differ ($P = 0.82$). The slope of the relationship between BSR and SCI was steeper in both Cle Elum and Yellowstone than it was in Springfield.

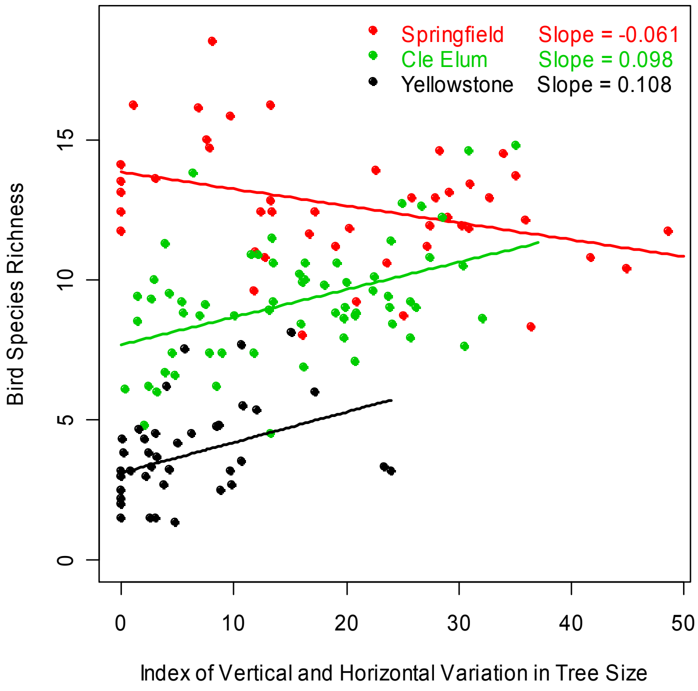

Figure 2.9. Comparison of slopes between BSR and an index of vertical and horizontal variation in tree size (SCI) at the Springfield, Cle Elum and Yellowstone landscapes.

Discussion

Hypothesis 1. Energy as a Regional and Landscape Scale Driver of Species Diversity

The results supported our predictions that BSR is significantly related to available energy at both the landscape and regional level across the PINW. At the regional level, the relationship between annual GPP and BSR exhibited a threshold, having a positive slope in the Yellowstone, Gold Fork and Cle Elum site and a negative slope across the Springfield and Coast Range landscapes. The threshold occurred between the Cle Elum and Springfield landscapes, which suggests a notable difference in the way that BSR responds to additional energy between forested landscapes west and east of the Cascades.

The cubic relationship between breeding season NDVI and BSR was generally positive but showed some leveling at the highest end of the regional energy gradient, suggesting a potential plateau in the beneficial effects of additional energy (Figure 2.5). Further support for the leveling or downturn in BSR at the highest end of the regional energy gradient was found at the landscape level, where negative relationships between BSR and breeding season NDVI occurred at the two most energy rich landscapes.

The strength and direction of the landscape level relationship between BSR and available energy correspond with the relationships that could be inferred by the landscape's location along the regional energy gradient (Figure 2.5). In landscapes east of the Cascade crest (Cle Elum, Gold Fork, and Yellowstone), where the availability of resources may limit population processes, BSR was strongly and positively related to measures of available energy. In energy rich landscapes west of the Cascade crest (Coast Range, Springfield) there were insignificant or negative relationships between measures of available energy and BSR.

Hypothesis 2. Interaction of Structure and Energy

Primary Drivers of Diversity: The increasing variation in BSR explained by forest structure in energy rich landscapes, and the increasing variation in BSR explained by available energy in energy limited landscapes provides evidence of the shifting drivers of diversity across the PINW. Forest structure contributed little to the R^2 of the BSR ten predictor (energy first) model in energy limited landscapes, suggesting that energy at least partially overrides the impact of forest structural complexity in driving BSR in energy limited landscapes. In addition, available energy contributed little to the R^2 of the

BSR ten predictor (structure first) model in energy rich landscapes. Recently published work from west-central Idaho, including the Gold Fork landscape included in our study, indicated that forest structure variables explained only 19% of the variation in BSR (Sallabanks et al. 2006). Such studies from energy limited landscapes suggest that considerable variation in BSR is explained by factors other than forest structure, such as energy and/or larger scale, landscape-level features.

There are many other potential drivers of diversity that we could not consider in this analysis (e.g. competition, home-range size, food availability, or larger scale landscape-level features). In addition, we didn't expect to be able to explain all of the variation in BSR using forest structure and energy covariates. Although we found forest structure to be a stronger driver of BSR in energy rich sites, we found that the variation of BSR explained by structure was less than we expected at all sites. Therefore, the total variation of BSR explained by structure and energy covariates in energy rich sites was also low.

Slope of the BSR - Forest Structural Complexity Relationship: We found that the slope of the relationship between BSR and structural complexity was steepest in the Yellowstone landscape. This is in contrast to our prediction that slopes would be less steep in energy poor locations. Most of the landscapes showed positive relationships between BSR and covariates representing forest structural complexity. However, in the Springfield landscape we found that diversity did not increase with increasing overstory complexity. Unlike the other landscapes, BSR was higher in the Shrub-sapling seral stage than older seral stages, which led to negative relationship between BSR and many measures of forest structural complexity. We speculate higher levels of BSR in early seral stages at the Springfield landscape may be due to the high level of available energy and favorable conditions for rapid shrub and tree growth following timber harvest. More specifically, the energy rich environment may help to produce the well developed and diverse shrub layer in the Shrub-sapling seral stage in Springfield that is not present in other locations.

In high energy locations, disturbance, in this case forest harvest, can act to break competitive dominance of certain plant species and free resources, making homogeneous forests more diverse (Huston 1994, 2004). In support of this hypothesis, McWethy et al. (Appendix B) found that BSR was positively correlated with amount of disturbance in the surrounding landscape in Springfield; the opposite was true in Cle Elum. These findings point to the importance of early-seral habitats in energy rich environments, where disturbance leads to reduced competitive plant dominance which appears to outweigh the benefit of increased structural complexity to bird diversity. The influence of forest structural complexity on BSR is not evenly distributed across all seral stages in Springfield (Figure 2.6). The overall relationship between BSR and SCI was negative, but the impact of structural complexity covariates such as tree size diversity and canopy cover on BSR were found to be significant only in the Small Tree seral stage. In addition, the greatest range of BSR values occurred in the Small Tree seral stage, suggesting that the structural complexity covariates have the potential for more influence on BSR in this seral stage than in others. Although the slope of the relationship between SCI and BSR was less steep in Springfield, more structural complexity covariates were found to be significant univariate predictors of BSR in the Coast Range and Springfield landscapes than in the other three energy limited landscapes. The overall strength of explanation from forest structural complexity covariates in the two energy rich landscapes is likely due to the influence of several orthogonal aspects of forest structure, and may not be adequately represented by the slope of the relationship between BSR and SCI.

Related Research

Many studies have focused on the effects of energy in driving species diversity at local, continental, and global scales (Hansen and Rotella 1999, Irwin 1999, Waide et al. 1999, Mittelbach et al. 2001). Additionally, a large number of studies have investigated patterns of diversity at a local scale based on forest structural complexity or seral stage (Kohm and Franklin 1997, Carey 1998, Ishii et. al. 2004, Sallabanks et al. 2006). The effects of energy and habitat on diversity differ among studies. In the region of Lake Constance in Europe, Bohning-Gaese (1997) found that diversity of habitat types explained 30.7% of the variation in bird species richness, while climate factors explained less than 3.3%. Across South Africa, climate and productivity explained 52% and habitat variety and evenness explained 32% of the variation in bird species richness (van Rensburg et al. 2002). In the Buenos Aires Province, Argentina, the R^2 was 0.65 for climate variables and 0.65 for numbers of vegetation strata (Cueto and de Casenave 1999). One factor that likely contributes to these differences is the magnitude of the gradient of energy and habitat within these study areas. Energy varied little relative to habitat diversity in the Lake Constance area where energy was a weak predictor. Strong climate and productivity gradients existed across South Africa, where energy was a strong predictor. In the South Africa study site, NPP ranged from near 0 to 1100 $gm^{C}cm^{-2}yr^{-1}$, a range similar to the PINW and North America as a whole. A second factor affecting the relative influences of habitat and energy on diversity is the resolution of the analyses. The three studies above and Fraser (1998), Rahbek and Graves (2001), and Hurlbert and Haskell (2003) all found that habitat variety was an increasingly strong predictor when analyses were done in increasingly large sample units. Van Rensburg et al. (2002) suggested that this is due to the increase in the range of heterogeneity in habitat diversity at coarser resolutions. Thus, both factors above indicate variation in a predictor variable (whether actual or statistical) is an important determinant of strength of association in these biodiversity analyses (see also Wright et al. 1993). Our results suggest that forest structure and available energy drive species diversity with varying strengths throughout the PINW, and that management will be most effective when accounting for the strength of energy limitations.

Management Implications

Biodiversity management will be most effective if it is tailored to the local setting especially in energy limited landscapes. Hansen et al. (2003) found that in low-energy landscapes in the PINW, biodiversity was concentrated in small localized hotspots with high energy. These hotspots not only contain many species, and high population densities, they are also sometimes population source areas that maintain viable populations across the larger landscape (Hansen and Rotella 2002). In low-energy locations, it is important to identify and judiciously manage these hotspots. Forest managers in the past have often harvested intensively in such hotspots, sometimes leading to a change in dominant cover type, a loss of structural complexity, and reduced duration of later seral stages (Hansen et al. 2003). Given that disturbance is a natural component of low energy locations, it is likely that some level of disturbance will best maintain diversity in these hotspots, but the type, rate, and intensity needs be carefully matched to local conditions.

Across the remainder of low-energy regions, management will best maintain biodiversity if it takes into account the longer rotation periods required to maintain ecological productivity. McWethy et al. (Appendix B) found that disturbance reduced diversity in low-productivity landscapes possibly because disturbance reduces resources and recovery rates of organisms. Harvest rates and intensities may be based on the goals of promoting rapid re-colonization of disturbed landscapes and maintaining populations of species dependent on late-seral forests. In addition, when harvesting smaller forest tracts in energy limited regions comprised primarily of lodgepole pine, management that promotes increased shrub density and size will likely benefit local scale biodiversity. However, when managing the entire biophysical gradient that exists at Yellowstone, management attentions would be better focused in comparatively high energy valley fringe and river bottom locations.

In energy rich environments, growing conditions are often good over most of the landscape. Thus, most places across the landscape have high potential to support biodiversity. Here, diversity may be limited by competitive dominance of a few plant species leading to specialized bird communities. In such high energy locations, disturbance can act to break competitive dominance of plants and free resources, dividing homogeneous forests into a variety of habitat types that support a greater diversity of bird species (Huston 1999, Huston 2004, McWethy et al. (Appendix B)). The downturn in diversity in the Small Tree seral stage (Figure 2.6a) may be preventable with management techniques (e.g. pre-commercial thinning practices, wider spacing of planted saplings, etc.) applied before canopy closure and competitive exclusion occurs. Many species in energy rich environments specialize in forest interior, edge, or early seral conditions. Hence, creation of the full suite of seral stages and attention to patch size and edge relationships is especially important. Therefore, a shifting-mosaic of patches of different seral stages across the landscape may increase diversity at the landscape scale (McWethy et al. (Appendix B)).

The unimodal relationship between diversity and structural complexity in early seral stages at the Springfield landscape has revealed potentially critical habitat that reaches a diversity peak just before canopy closure occurs. At the remaining four landscapes where higher levels of species richness correspond with older seral stages and higher levels of structural complexity, the older forests may be of greater value to species diversity.

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CHAPTER 3

SPATIAL PATTERNS OF BIODIVERSITY ACROSS MANAGED FOREST LANDSCAPES

Introduction

Conservation strategies in the forests of the Pacific and Inland Northwest (PINW) commonly focus on promoting diverse habitat structure (often characterized as "old-growth" forests). In addition, the primary approach for managing for biodiversity in PINW forests is currently to maintain structural complexity within forest stands and to harvest in a shifting pattern across the landscape (Loehle et al., 2002), maintaining a variety of seral stages. Recent advances in ecological theory suggest that biodiversity at regional to continental scales is strongly influenced by available energy (e.g., heat, primary productivity) (Hurlbert 2004, Currie 1991), and that the effect of forest structure on biodiversity may vary with the level of available energy (Hansen et al. 2003). However, the implications of applying species energy theory to the development of regional conservation strategies are not yet defined (Hansen et al. 2003).

Conservationists and land managers often find it difficult to support and maintain diversity on all lands because of conflicting conservation strategies or a lack of funding. This dilemma suggests that prioritizing conservation efforts is necessary. One way to prioritize conservation efforts is to identify biodiversity hotspots where large concentrations of species can be maintained in a relatively small spatial extent (Meyers et al. 2000). Biodiversity hotspots can be defined as areas with higher concentrations of species compared with surrounding areas (Reid 1998). Promoting the diversity of habitats and species is one way that land managers of industrial forests, parks, and nature preserves attempt to preserve viable populations of as many species as possible (Thomas et al. 1979). Locations that have more individuals and higher levels of diversity are of interest to managers of working landscapes, because these hotspots can be managed to favor maintenance of biodiversity while management of the remainder of the landscape can be managed more intensively for wood production or other objectives. The strength of energy limitation at a given landscape is likely to cause different spatial configurations of biodiversity hotspot locations. Therefore, shifting mosaic style forestry may not benefit biodiversity in all landscapes.

Previous studies have mapped species richness as a function of forest structure (Hansen et al. 1991, and several gap analysis studies) or energy/productivity (Hansen et al 2003) or by overlapping species range maps over a large scale (Meyers et al. 2000). We used our knowledge of the primary drivers of diversity across the PINW (Chapter 2) to map species richness based on forest structure and energy for two sites with different gradients in available energy. We used the maps resulting from the modeling effort to investigate the spatial configuration of predicted richness hotspot locations (highest 20 percent of predicted bird species richness, by area) at each landscape, and across both landscapes.

We predict bird species richness (BSR) across two landscapes with different levels of energy limitation, as a function of remotely sensed satellite data representing available energy and digitized stand data representing coarse forest structure measurements. Birds are a suitable taxonomic group for this study for several reasons.

Birds are well understood ecologically and taxonomically, and represent a range of feeding guilds and habitat niches (O'Connell et al. 2000, Erdelen 1984). Species richness is a simple way to represent regional diversity (Magurran 1988), and bird species richness has proven to be a valuable indicator of overall biodiversity (Furness and Greenwood, 1993).

In our previous work considering the relative influence of stand level forest structural characteristics vs. available energy in driving biodiversity (Chapter 2), we found that energy explained more of the variation in BSR in energy limited landscapes, and that forest structural complexity explained more of the variation in bird species richness in energy rich landscapes. Here, we contrast the spatial maps of predicted BSR hotspots from a productive landscape with narrow range of available energy, with predicted richness maps from a less productive landscape with a broader range of available energy.

We expect the model at the more productive landscape to predict little variation in BSR and have weak predictive capability (coefficient of determination (R^2)) due to generally high levels of richness across the landscape and little energy limitation (Chapter 2). In addition, we expect the more productive landscape model will be composed primarily of predictors representing the forest structural characteristics. At the less productive landscape with the wider gradient of available energy, we expect the best model will predict more variation in BSR, have a higher R^2, and rely primarily on measures of energy and productivity due to the higher level of energy limitation across the landscape. In addition, we expect the highest values of predicted BSR (here after referred to as hotspots) in the less productive landscape to be concentrated because of the stronger energy limitation. We expect that the landscape scale pattern of hotspots in the more productive landscape will be more diffuse where changes in within stand forest structure drive more of the variation in BSR. When investigating the pattern of hotspots regionally, we expect that predicted BSR values will be higher across much of the more productive landscape resulting in few "regional" biodiversity hotspots in the less productive site.

Methods

Study Areas

Springfield, OR: Weyerhaeuser's Springfield and Cottage Grove tree farms and surrounding BLM and USFS lands are located just east of Eugene, Oregon, in the western toe slopes of the Oregon Cascades and represent the productive site with a narrow range of available energy (Figures 3.1 & 3.2). The study landscape ranges in elevation from 300-1000-m and precipitation averages 120 to 200-cm annually. Mean monthly minimum temperatures range from 4-5° C. Mean monthly maximum temperatures range from 16-17° C. Due to little variation in mean temperature and precipitation across the study area, Douglas-fir (*Pseudotsuga menziesii*) is the dominant forest type across the region. However, hardwood species become more abundant in the southern end of the study landscape.

Land ownership is a checkerboard of federal (primarily Bureau of Land Management) and private lands bordered by the Willamette National Forest and the H.J. Andrews Experimental Forest. Private forests in this region are dominated by short rotation (40-60 yrs.) plantations and patch sizes of 15-50-ha. (Ripple et al. 1991). The young stand regeneration strategy often includes planting genetically selected conifer seedlings and applying broad-leaf herbicide treatments to suppress competing deciduous vegetation. Regeneration is typically followed with a pre-commercial or commercial thin before final harvest (Emmingham 1998, Curtis et al. 1998). Federal lands are dominated by late successional (old-growth) stands of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) with high levels of vertical structural complexity.

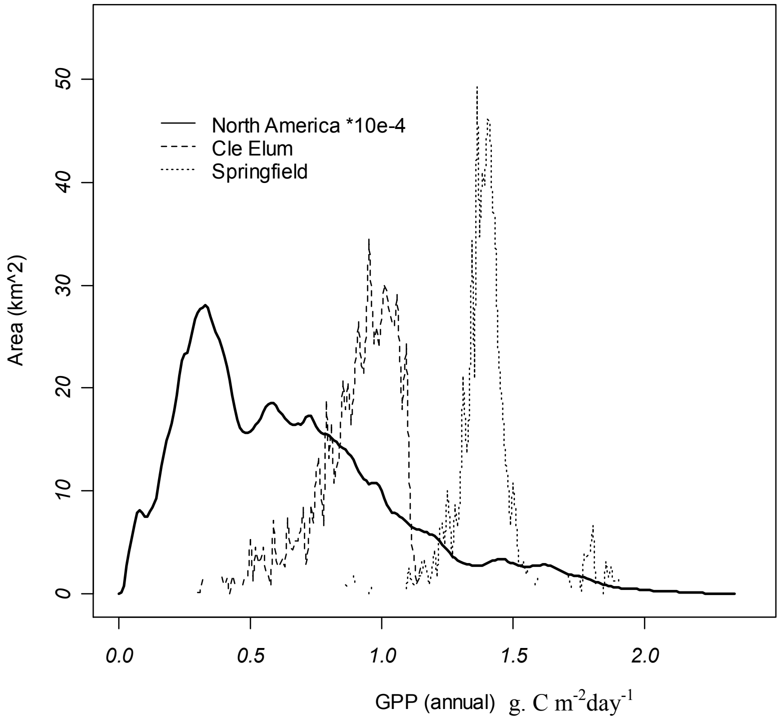


Figure 3.1. Area (km^2) of land representing GPP gradient for North America (*10^{-4}), and 3 km radius landscapes surrounding the Cle Elum and Springfield survey sites.

<u>Cle Elum, WA</u>: The Cle Elum landscape is located along the I-90 corridor between 600-m and 1800-m in Washington's Central Cascades and represents a less productive site with a broad gradient of available energy (Figures 3.1 & 3.2). Plum Creek Timber Company's ownership totals roughly 57,000-ha distributed in a

checkerboard pattern with Mount Baker-Snoqualmie and Wenatchee National Forest land. The dominant forest types found in this study area vary from wet hemlock/fir forests averaging over 200-cm of precipitation per year near the crest of the Cascades, to dry open ponderosa pine (*Pinus ponderosa*) forests averaging 50-cm of precipitation per year on the east slopes. Mean monthly minimum temperatures range from 0° C near the Cascade crest and 2° C further east. Mean monthly maximum temperatures range from 7° C near the Cascade crest and 14° C further east.

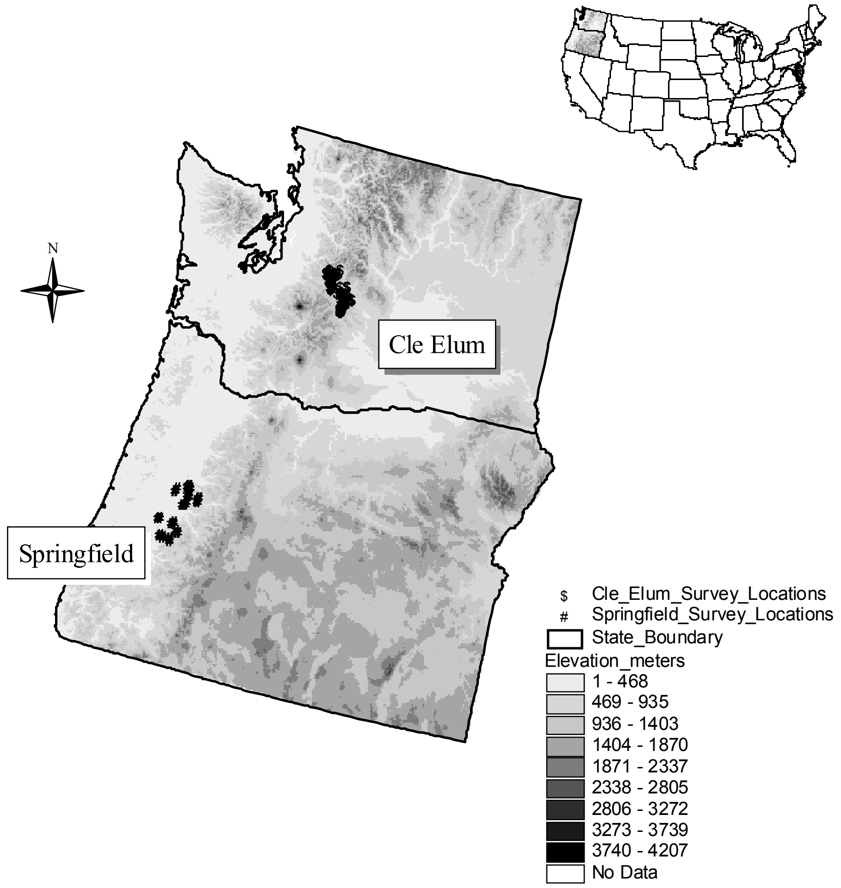


Figure 3.2. Location of 2 study sites, Springfield, Oregon and Cle Elum, Washington.

In addition to the diversity of dominant forest types, forest structure is also widely variable throughout the Cle Elum landscape. Dense stands of true fir and western hemlock near the crest of the Cascades offer high levels of vertical structural complexity but little variation horizontally. Eastern forest types such as ponderosa pine have more variable levels of forest structural complexity with many canopy openings. Landscape pattern also varies greatly with large wilderness and roadless areas bordering more intensively managed plantations at the north and south end of the study area.

Spatial Coverage Digitizing

To derive the database layers used for predicted BSR mapping we used aerial photographs to map different patch types within a 3-km radius around each of the stands sampled for birds. The patch types were delineated based unique combinations of the following characteristics: 1) seral stage (clear-cut, sapling, pole and mature) 2) percent canopy cover (0-33%, 34-66%, 67-100%), and 3) dominant habitat type (Douglas-fir, western hemlock, Subalpine (includes noble (*Abies procera*) silver (*Abies amabilis*) and subalpine fir (*Abies lasiocarpa*)), grand fir (*Abies grandis*), ponderosa pine and riparian deciduous (including black cottonwood (*Populous balsamifera*) and several species of willow (*Salix spp.*)).

We defined a 1-ha minimum patch size for mapping and patches were > 50-m wide in their narrowest dimension. This area corresponds to roughly the smallest estimated home range size of bird species found in the study area (Brown 1985). The minimum width was determined to avoid delineating narrow patches that are likely less important biologically to birds. We used Weyerhaeuser and USGS digital orthophotos to digitize forest patches manually using field visits and industry coverages of stand age, dominant canopy species, and management history to validate forest patch attribute information. Digital polygon coverages of the different attributes forest patches were then converted to raster grids with a 15-m resolution. The polygon attributes were paired with the BSR data from the survey points to be used for modeling.

Model Building and Extrapolation

We used average temperature (annual and breeding season), elevation, precipitation (annual and breeding season), NDVI (annual and breeding season), GPP (annual), seral stage, percent canopy cover, and dominant habitat type to predict BSR values from each survey point in our automated best model selection process. We selected best models for the Springfield and Cle Elum landscapes that were within 2 AIC units of the model with the highest likelihood, had most variation explained, and contained only predictors with significant explanation of the response. We found spatial autocorrelation terms in each model to be insignificant. We recorded the predictor coefficients for spatial extrapolation at each landscape. Although we use a "best" modeling approach to derive the predictive maps, we did not interpret model coefficients in this paper (See Chapter 2 for more detail on univariate BSR/predictor relationships). The model R^2 values were expected to be lower than those shown in Chapter 2 due to the limited number of digitized predictors of forest structure.

Once the best model was derived, each of the digitized 15-m grids (from covariates used in the best model) were used to extrapolate the best model within the 3-km digitized radius around each surveyed stand using the "map calculator" function in ArcView. We extrapolated diversity only for areas where all predictors were within the sampled range of the data (i.e. bird species richness was not predicted for un-surveyed habitat types, temperatures or productivity ranges). To emphasize the pattern of biodiversity hotspots we selected the highest 20 percent (by area) of predicted bird species richness and highlighted those areas at both landscapes for comparison.

Results

The resulting grids of predicted bird species richness covered 738.7 km^2 at the Springfield landscape and 818.6 km^2 at the Cle Elum landscape. The best model at the Springfield landscape had a coefficient of determination (R^2) of 0.279 and included seral stage and the normalized difference vegetation index (NDVI) measured in May as predictors of BSR (Figure 3.3, Table 3.1). The best model at the Cle Elum landscape had a coefficient of determination (R^2) of 0.651 and included percent canopy cover, dominant cover type and average daily temperature from April through September as predictors of BSR (Figure 3.4, Table 3.1).

Table 3.1. BSR prediction model results for the Springfield and Cle Elum landscapes (red = positive relationship with BSR; blue = negative relationship with BSR; black = categorical variable with a non-linear relationship with BSR)

Site	**Response**	**Predictors**			**AIC**	**Comparison P-Value**	**R^2**
		1	2	3			
Springfield	BSR	Seral Stage			72.84	0.025	0.189
	BSR	Seral Stage	NDVI May		69.17	-	0.279
Cle Elum	BSR	% Canopy Cover			111.1	< 0.001	0.244
	BSR	% Canopy Cover	Dominant Cover		72.33	0.047	0.627
	BSR	% Canopy Cover	Dominant Cover	Temp. (Apr. - Sept.)	69.78	-	0.651

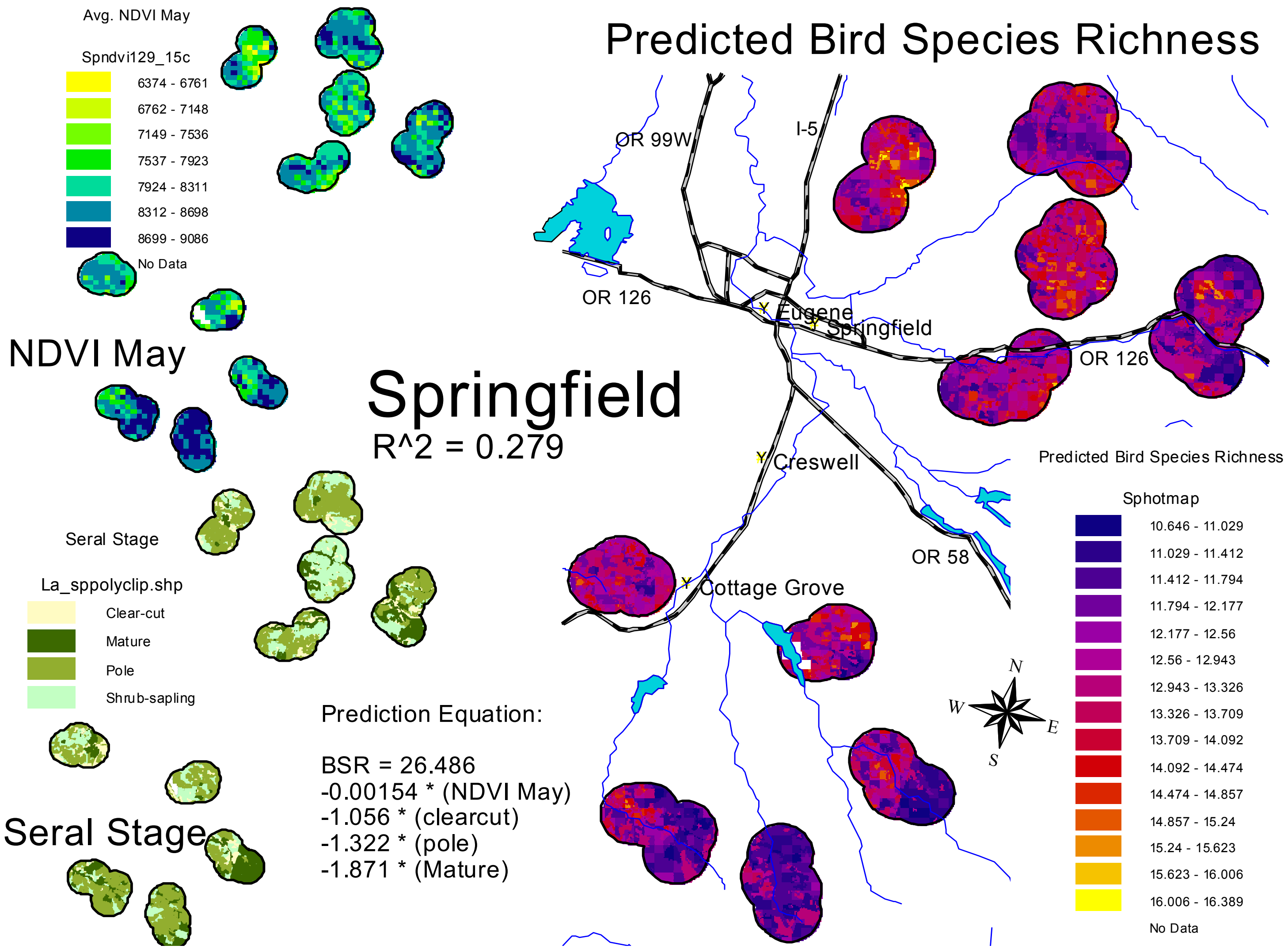
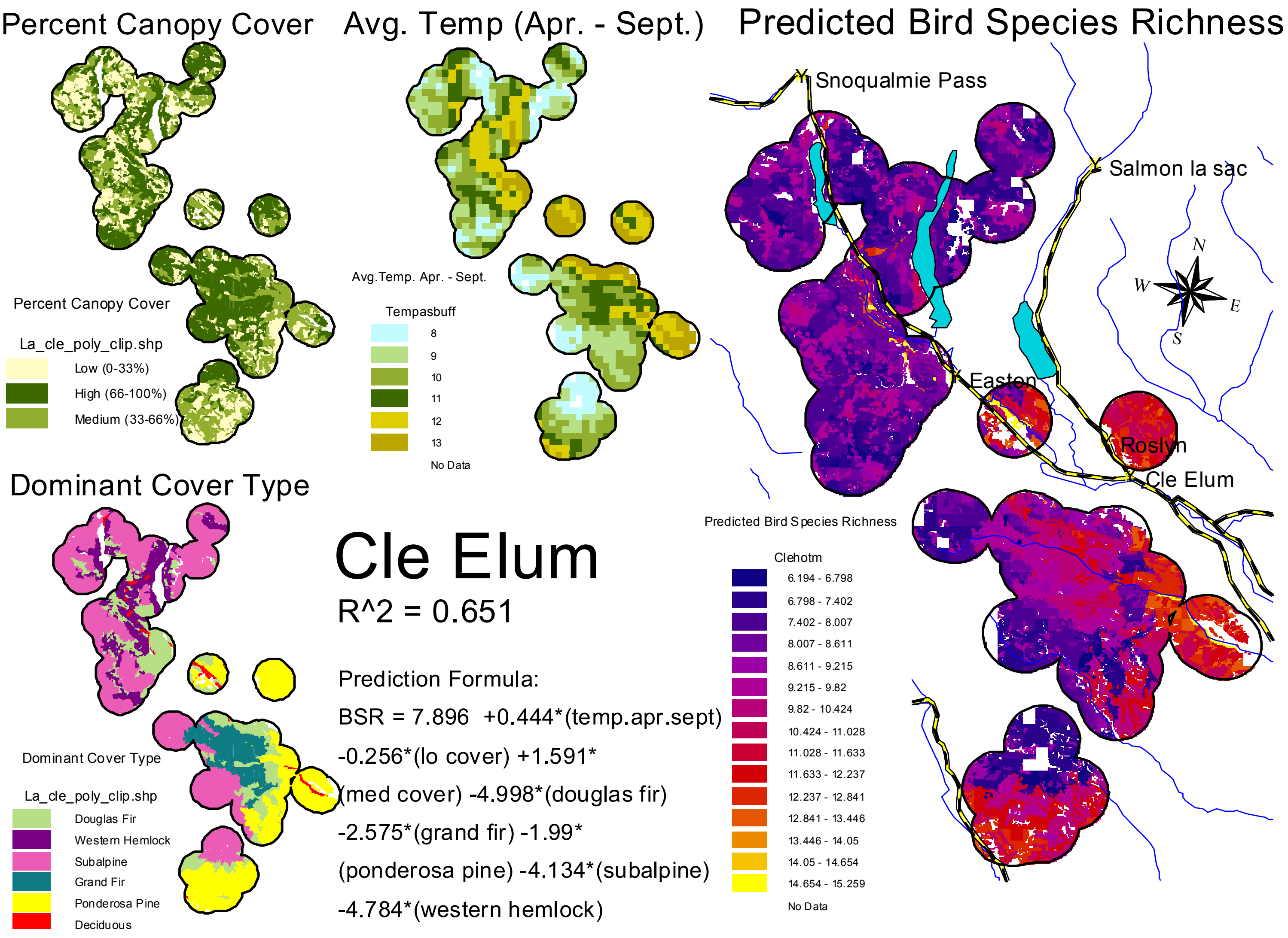


Figure 3.3. Predicted bird species richness at the Springfield landscape including the predictors used in the map calculation effort, the best model equation and model R^2.



R^2 = 0.651

Prediction Formula:

BSR = 7.896 +0.444*(temp.apr.sept) -0.256*(lo cover) +1.591*(med cover) -4.998*(douglas fir) -2.575*(grand fir) -1.99*(ponderosa pine) -4.134*(subalpine) -4.784*(western hemlock)

Figure 3.4. Predicted bird species richness at the Cle Elum landscape including the predictors used in the map calculation effort, the best model equation and model R^2.

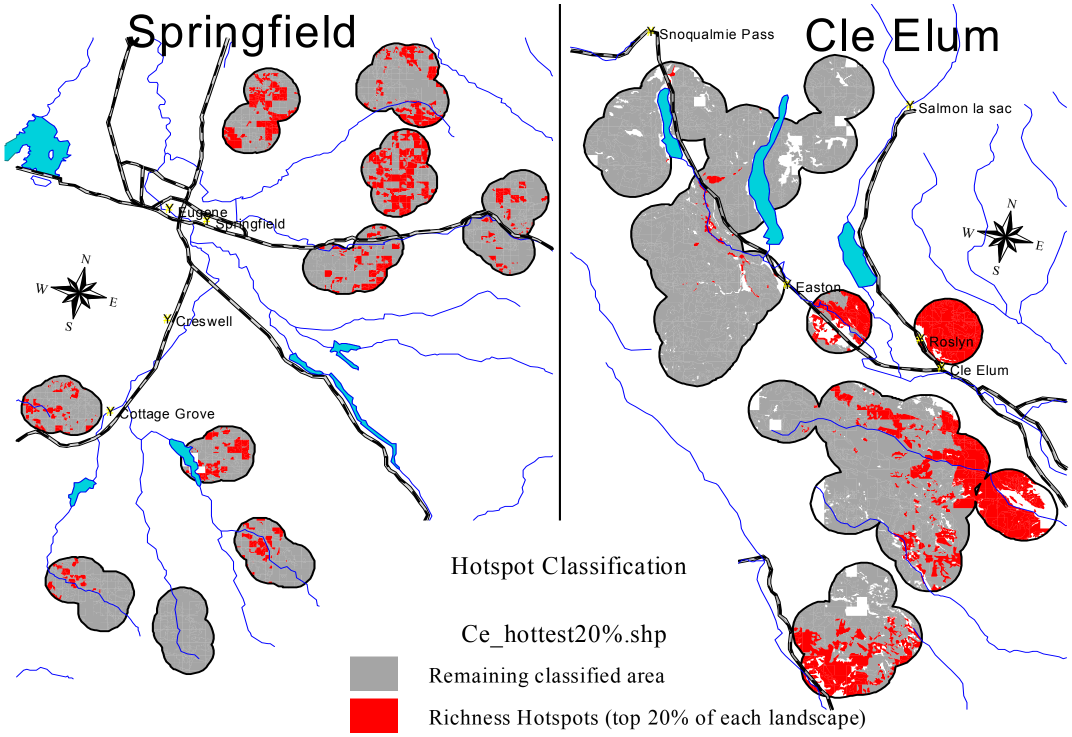


Figure 3.5. Highest 20 percent (by area) of predicted bird species richness displayed for the Springfield and Cle Elum landscapes

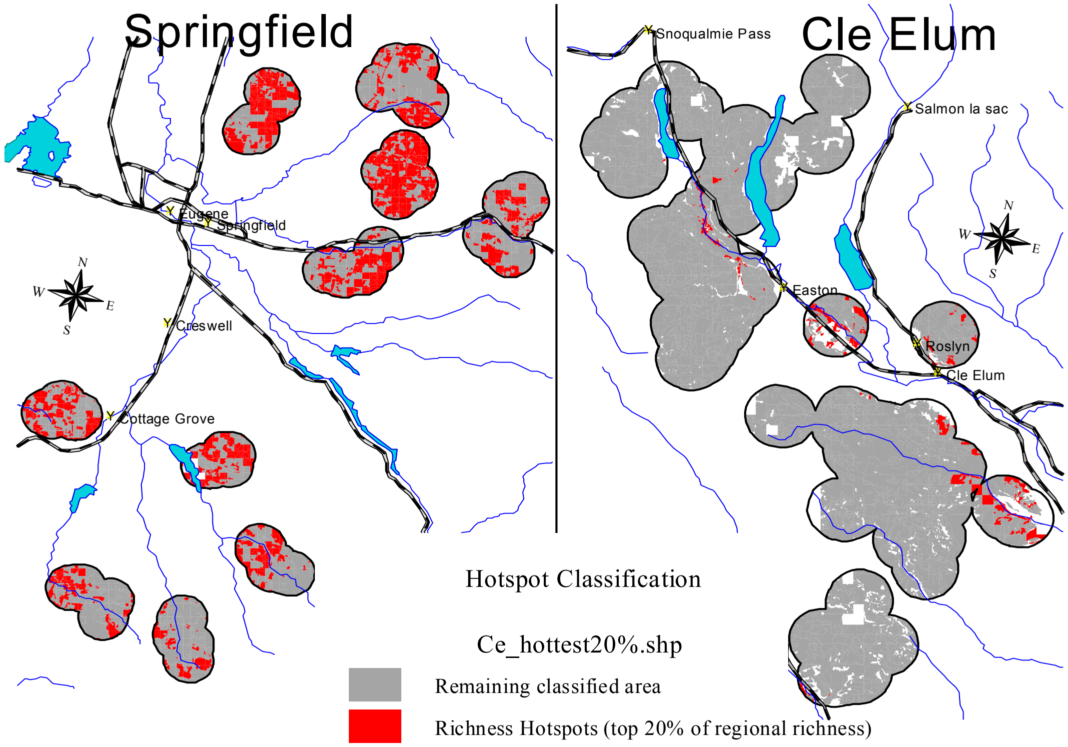


Figure 3.6. Highest 20 percent of regional (both sites) predicted bird species richness displayed for the Springfield and Cle Elum landscapes

Displaying the highest 20 percent of predicted BSR at each landscape resulted in a diffuse pattern of hotspots in the Springfield landscape, although the northern portion of the landscape, which had lower values of May NDVI and a higher percentage of clear-cut and Shrub-sapling seral-stage stands, also had a higher percentage of predicted hotspot locations (Figure 3.5). The highest 20 percent of predicted BSR in Cle Elum was clumped in the eastern half of the study area and in the valley bottoms primarily in ponderosa pine and riparian deciduous habitats that had higher average temperature (Apr. – Sept.) values (Figure 3.5). When looking at the highest 20 percent of predicted richness regionally, it becomes quite clear that the forests of the more productive site (Springfield) support more species than those of the less productive site (Cle Elum) (Figure 3.6). The more productive valley bottom locations are the only places in the Cle Elum landscape that are highlighted as regional biodiversity hotspots (Figure 3.6).

Discussion & Management Implications

The best model and hotspot map at the Springfield landscape supported our expectations of little variation in predicted BSR, diffuse hotspot locations, and low model R^2 values for a productive landscape with a narrow energy gradient. The predicted hotspot locations were diffuse, but were slightly more prevalent in the northern half of the study area, which is likely due to a higher percentage of the digitized landscape being composed of clear-cut and Shrub-sapling aged stands. The best model for the Springfield landscape included NDVI, a measure of available energy which did not follow our expectation. However, breeding season NDVI is a significant (negative) univariate predictor of BSR at the Springfield landscape (Table 2.7). We expected the model at the

Springfield landscape to have weak predictive capability (low R^2) due to generally high levels of richness across the landscape and little energy limitation (Chapter 2).

The best model and hotspot map for the Cle Elum landscape supported our expectations of more variation in predicted BSR, concentrated hotspot locations and higher model R^2 values. The predicted hotspot locations were clumped primarily in ponderosa pine and riparian deciduous habitat types that are situated in the eastern half of the study landscape and in the upper Yakima Valley along I-90.

The pattern of biodiversity hotspots closely matches the pattern of cutting resulting from a shifting mosaic style of forestry at the Springfield landscape. Continuing this style of forestry in productive landscapes will likely move the hotspots around the landscape following the distribution of early seral-stage forests. In the Cle Elum landscape, using the low-mid elevation zones at the western end of the landscape to achieve wood production goals (western hemlock/Douglas-fir zone) will likely benefit landscape scale biodiversity because productivity is higher, and the diversity of habitat types may increase as a result of shifting-mosaic forest harvest patterns (McWethy et al. (Appendix B)). The eastern (drier) half of the study area, where the majority of diversity hotspots are located is dominated by ponderosa pine. In these regions, timber resource extraction potential over the long term is lower due to harsh conditions caused in part by long dry summers and colder winters. Selective harvest may be preferred in these locations to lessen the extreme effects of soil moisture loss caused by clear-cutting. In addition, the drier habitat is more heterogeneous and patchy, and the organisms depending on these forests will likely respond better to a selective type of harvest, where residual live and dead trees are left in abundance in the cutting units (Hansen and Rotella 2000).

Conclusions

Our results support the premise that biodiversity management will be most effective if it is tailored to the local setting, especially in energy limited landscapes. Forest managers already consider the landscape context when managing timber resources. However, forest managers often apply the same approach for managing species diversity across landscapes that differ in their biophysical setting. Defining the spatial configuration of hotspot locations across a landscape allows managers to focus conservation to smaller more diverse areas while less-diverse locations can remain in rotation for resource extraction. By contrasting the hotspot maps from 2 landscapes with different levels and ranges of available energy, we have provided a visual example of how important it is to consider all factors influencing the distribution of species across the landscape. A successful strategy for planning patterns of forest harvest or managing species diversity will likely be determined by the factors controlling landscape scale patterns of biodiversity.

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CHAPTER 4

TAILORING FOREST MANAGEMENT TO SUPPORT SPECIES DIVERSITY ACROSS PRODUCTIVITY GRADIENTS

Introduction

Current management of forest lands aimed at maintaining biodiversity is largely prefaced on the idea that providing gradients in structural complexity within stands and across landscapes will best support species diversity. This approach is often applied similarly across many different ecosystem types. Our results show that the effects of structure within stands and across landscapes are modified by energy level. In this chapter, we draw out implications for management of our research findings. Before considering how management might differ across landscapes with different productivity we briefly review the conceptual framework supporting a landscape specific management approach, then revisit the historical context within which private forest lands have previously been managed for timber and to maintain species diversity. We then summarize evidence from our work that suggests that energy levels modify species response to local and landscape scale structural conditions. Lastly, within the context of historical management approaches and our results, we outline implications for management in landscapes with different levels of productivity by developing both broad conceptual approaches and specific management guidelines for managing for diversity in these landscapes.

It is well known that in forested environments, species diversity is linked to aspects of vertical and horizontal structural diversity. MacArthur and MacArthur (1961) demonstrated this link with the finding that foliage height diversity is an important characteristic of forest structure influencing bird diversity. Based on an extensive body of literature supporting the correlation between local structural diversity and species diversity (Carey et al. 1999, Hunter 1999), management of timber lands for biodiversity typically focuses on maintaining gradients in horizontal and vertical forest structural diversity (Franklin and Spies 1991, Halpern and Spies 1995). However, recent research suggests that the magnitude of the influence of structural conditions on species diversity varies among different biophysical settings (Chaper 2, McWethy et al. (Appendix A)). We hypothesized that gradients in available energy (i.e. factors influencing vegetative growth such as precipitation, temperature, radiation, soil fertility among others) help explain why species diversity responds differently to the same (or similar) structural conditions in different settings. In support, we found that bird diversity is influenced more by changes in available energy than structural conditions where available energy likely limits species diversity (e.g. Yellowstone). Alternatively, in more productive settings, local and landscape-level structural conditions influence species diversity more so than gradients in available energy (e. g. west-side Cascade forests). Other examples from Europe, South Africa and Argentina suggest that the influence of climate and structure vary across gradients in productivity (Bohning-Gaese 1997, Cueto and de Casenave 1999, van Rensburg et al. 2002).

At a landscape scale, structural conditions related to spatial patterning of habitat patches have also been shown to influence bird abundance and diversity (McGarigal and McComb 1995, Fahrig 2003, Ferraz et al. 2007). Yet little research examines how landscape effects might vary in different settings. We found that landscape effects were more pronounced in a more productive landscape and that species diversity responded in opposite directions to disturbance intensity in two landscapes representing a more and less productive setting (McWethy et al. (Appendix A), McWethy et al. (Appendix B)). While forest structural conditions are known to influence species diversity at both local and landscape scales, our results suggest that this influence varies across gradients in productivity. This is important because management prescriptions aimed at supporting species diversity are oftentimes applied similarly across landscapes with different ecosystem types that vary in productivity, likely influencing species diversity in unexpected ways. Therefore, a consideration of landscape setting will be necessary if forest management practices are to be effective in maintaining species diversity across different landscapes.

Following several years of research examining the influence of stand and landscape structural characteristics on bird diversity within landscapes varying in productivity (Hansen et al. 2003, Chapter 2, McWethy et al. (Appendix A), McWethy et al. (Appendix B)), we found evidence supporting the idea that the influence of local and landscape level forest structure on biodiversity does vary across biophysical settings. This chapter builds on the results from this study to develop a framework for tailoring current biodiversity management practices to landscapes with low, intermediate and high levels of productivity (gross primary productivity (GPP)). Specifically, we set out to: 1) review historical and current approaches for managing forests for timber and biodiversity in the Pacific Northwest, 2) outline the primary results of our research efforts, 3) consider the implications of our results for modifying current practices to more effectively support species diversity, and, 4) summarize specific management treatments for three landscapes varying in productivity.

Management of Private Industrial Forests for Timber and Biodiversity: An Historical Context

Early Logging in West-side and East-side Forests (1880's-1950's)

In the late 1800's and early 1900's forest management of both east and west-sides of the Cascades focused on removing the most merchantable trees (Curtis and Carey 1996, Curtis 1998, Curtis et al. 1998, Emmingham 1998). Given the limitations of accessing, cutting and transporting timber, the highest-value timber was extracted using the most economical means, (Curtis et al. 1998). This resulted in "high-grading" of west-side forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) as well as east-side forests dominated by ponderosa-pine (*Pinus ponderosa*), Grand fir and mixed conifer (ponderosa pine and Douglas-fir). During this early period, harvests were primarily driven by the desire to remove large volumes of timber. Consequently, in the removal of timber there was little regard for regeneration, future stand condition or maintaining species diversity. Soon after this initial period of liquidation, foresters strived to employ silvicultural techniques to promote regeneration, rapid growth and to minimize insect and disease outbreaks. Knowing little about how forests would respond to different harvest techniques, foresters experimented with a variety of harvest methods including even-aged management techniques (i.e. shelterwood, seed tree, clearcutting) as well as uneven-aged management through various forms of individual tree selection (Oliver et al. 1994, Curtis and Carey 1996). Improved timber harvest and extraction technology, including the advent of the chainsaw, facilitated easier access and harvest of forest stands, resulting in increases in the volume of timber extracted (Oliver et al. 1994). In the mid 1900's, managers began to experiment with seed-tree or selective cutting to promote regeneration (Mason 1929, Munger 1933, Kirkland and Brandstrom 1936). While referred to as selective cutting, harvests under this approach represented a wide variety of harvest methods, from single trees to patch-cuts of various sizes (typically < 15-ha) and would not generally be compared to today's selective cutting methods (Curtis 1998). Early forms of selective cutting often took the form of "high-grading". Early seed-tree and selective harvest or partial cutting methods (highly variable in practice and not comparable to today's systems) resulted in poor regeneration and were perceived to have led to stand deterioration (Isaac 1943, 1956). As a result of several studies documenting these outcomes, selective logging was largely abandoned by the 1950's (Curtis et al. 1998).

The "Shifting Mosaic" Period (1950-1990's)

From 1950 to the 1990's, forest managers scattered even-aged management harvest units (size of harvest units generally increased to >15-ha) across the landscape, placing them adjacent to older stands as a way of reducing the number of roads required for harvests. This approach was thought to better promote regeneration, foster rapid growth of forests and prevent weak, diseased and injured trees from remaining in stands. In west-side landscapes, this approach was generally regarded as the best method for harvesting Douglas-fir on productive sites. In east-side forests, regeneration of other dominant canopy species was often less successful than Douglas fir, yet regeneration following even-aged management was often considered adequate. In both east and west-side forests, shelterwood harvests were used to a limited extent on severe sites where erosion or regeneration was a major concern.

The "staggered setting" approach to harvesting stands led to a mosaic of even-aged clearcut stands and later-seral closed canopy stands across the landscape, what is now commonly referred to as a "shifting mosaic" pattern of harvest (Loehle et al. 2002). Accompanying this even-aged shifting mosaic approach was the introduction of artificial regeneration and, eventually, intensive planting of genetically selected seedlings as the primary method for regenerating stands. Initially, commercial thinning was commonly used and thought to be the best silvicultural technique for promoting rapid growth of intermediate age stands. As shorter rotations were adopted, commercial thinning was replaced with pre-commercial thinning to promote rapid growth in younger stands approaching stem-exclusion. Later in this period it became common for managers to promote the regeneration of intermediate sized (~15-50-ha) clearcut harvests of 40-60 yr old stands with a post-harvest burn and planting of genetically selected Douglas-fir and ponderosa pine seedlings (and occasionally western white pine, larch and lodgepole pine in east-side forests). In some cases, various forms of uneven-aged management were applied to east-side harvests, especially where conditions were warmer and dryer and/or soil fertility was poor. At the same time, managers of east-side Cascade forests began to recognize that the application of various forms of uneven-aged management combined with fire suppression led to a change in the composition of understory seedlings and saplings from shade intolerant and fire adapted species to more shade tolerant and fire intolerant species. Consequently, thinning was used to reduce stocking densities resulting from uneven-aged harvests and in stands where years of fire exclusion led to densely stocked stands. Thinning was also more widely used to reduce the risk of widespread mortality from natural disturbances such as fire, disease and insect outbreaks.

Recent Approaches (1990-2007)

The implementation of the Northwest Forest Plan in 1994 marked a significant shift in the management of both east and west-side forests. Following litigation which temporarily halted all logging of forest habitat deemed suitable for the northern spotted owl (*Strix occidentalis caurina*) on public lands, a cascade of events re-shaped the way in which both public and private lands were managed in the Pacific Northwest. Public land managers shifted management focus within the range of the northern spotted owl to promote the development of characteristics associated with late successional and old growth forests of the Pacific Northwest (USDA Forest Service and USDI Bureau of Land Management 1994). Management emphasis on USFS and BLM lands shifted to selective logging and silvicultural treatments aimed at promoting late-successional and old-growth characteristics such as larger tree diameters, large snags and coarse woody debris among other characteristics. While the impetus for this change in management approach came from an analysis of habitat suitable for northern spotted owl, the Northwest Forest Plan was thought to manage forests to support species diversity more generally:

> "We have tried to protect old growth forests while providing a sustainable timber harvest. The administration's forest plan is comprehensive and broad based. It moves beyond the issue of owls and provides a plan to wisely manage an entire ecosystem for the benefit of people, their jobs, the environment, and all the species that depend on old growth forest -- of which the spotted owl is just one."
>
> Attorney General Lois Schiffer
> (USDA Forest Service and USDI Bureau of Land Management 1994)

At the same time, the northern spotted owl was listed as an endangered species under the Endangered Species Act in 1990. As a result, private industrial forests were required to identify northern spotted owl nest locations and manage a percentage of habitat surrounding owl nests to maintain and promote late-successional and old growth characteristics. Concomitant with this new legal landscape, changes in public opinion and consumer demand led many private timber entities to voluntarily participate in forest certification programs such as the Sustainable Forest Initiative (SFI) and the Forest Stewardship Council (FSC). These programs often encourage alternatives to even-aged management (i.e. shelterwood harvest, green-tree retention, riparian and wildlife buffers). Similarly, public and private timberlands have shown increasing interest in alternative management approaches to support multiple resource objectives. Under various names such as “restoration forestry” (Maser 1986) “new forestry” (Franklin 1989), or “ecological forestry” (Minckler 1989), these approaches are characterized by increased structural retention, longer rotations and the creation of greater structural complexity through spatial heterogeneity of harvests and retention of snags and coarse woody debris (Franklin et al. 2002). Hence, several factors influenced changes to management of industrial forests, primarily to encourage, and sometimes require, the use of alternative management approaches that involve longer rotations, retained structure, and treatments facilitating structural conditions intended to represent older natural forests in the Pacific Northwest.

Despite the influence of these factors, changes to management of private industrial timberlands have been relatively modest. Even-aged management is still considered the most effective approach for providing large volumes of merchantable timber while promoting rapid regeneration and growth of forests. Consequently, within legal constraints and forest certification program requirements, most private industrial forests continue to manage forests to maintain timber volume and maintain biodiversity through short rotation, even-aged management. In west-side forests, managers currently rely on short rotation (40-60 yrs.) even-aged harvests of forest stands between 15-50-ha. This is followed by planting of genetically selected conifer seedlings, the application of broad-leaf herbicides to limit competition of deciduous shrubs and trees, and a pre-commercial or commercial thin before final harvest (Oliver 1995, Curtis et al. 1998, Emmingham 1998). In some cases, green trees and snags are retained in upland and riparian leave tree zones to enhance structural diversity for wildlife.

In east-side forests, even-aged management of similar sized stands with slightly longer rotation lengths (50-70 yrs) is also still used to manage large tracts of private industrial lands to provide wood products and maintain species diversity. However, managers of east-side forests have recently begun to experiment with a much more diverse set of silvicultural techniques to address conditions unique to east-side forests (eg. more frequent yet highly variable fire regimes, soil moisture loss) including supporting habitats that are historically well adapted to fire. Alternative forms of even-aged management, oftentimes combined with selective harvests and prescribed fire are intended to mimic natural disturbance, promote better stand conditions following regeneration and to support fire adapted species in these landscapes. Additionally, combinations of shelterwood, seedtree, partial cuts and individual tree selection are now more commonly used to create more multi-layered mixed species forests (Oliver et al.

1995). These experiments are typically implemented on lands aimed at supporting multiple resource objectives, where timber output is not the primary management objective.

Managing Private Forests in the Future

While even-aged management of short-rotation stands of Douglas-fir continues in west-side forests and more varied management of east-side forests develops, changes in the ownership and business structure of private industrial lands is already becoming an important factor changing the way forests are managed. These changes have led to a decrease in the acreage of land owned by the timber products industry (operations that were typically involved in harvest, mill and wood product operations) and increases in land ownership by investment entities such as Timber Investment Management Organizations (TIMOs), Real Estate Investment Trusts (REITs) and Master Limited Partnerships (MLPs). Market forces, influenced by tax structures and changes in profit margins and liabilities associated with owning large timberland operations are largely responsible for this shift (Lacy 2004). These changes will likely result in greater variability in the management of forests (i.e. shorter rotations when timber values are high and a shift to other forest values such as real estate when market values for timber are low). These developments will affect species diversity within these forests, yet in ways that are difficult to predict.

Linking Historical Management of Private Timberlands to our Research

Managers of private industrial forests are increasingly compelled to manage forests to address multiple objectives. While maintaining a steady flow of timber volume and wood products will likely continue to be a primary management objective for most private forests, managing forests to support species diversity is increasingly becoming an important objective (Oliver et al. 1994). Changes in public attitudes towards management of both public and private forests resulting from the development of the Northwest Forest Plan and the listing of the northern spotted owl coupled with new legal requirements are largely responsible for this shift in emphasis. Importantly, while some species have likely benefited from changes in forest management, the widespread application of the approach outlined in the Northwest Forest Plan as a panacea to maintain overall species diversity may be misguided. Our results suggest that forest management aimed at supporting species diversity is most effective when tailored to landscape setting and site productivity. Forest managers currently tailor management of forests to site conditions in an effort to promote rapid regeneration of marketable wood products. However, forest managers rarely consider how species respond to different harvest approaches across landscapes varying in productivity. Our results provide information useful for developing a framework for doing this. Next, we review key findings from research investigating species response to forest structural conditions across productivity gradients and then develop a framework for managing species diversity in the context of landscape setting.

Key Findings From Biodiversity in PINW Forests Research

Background: Building on a well supported premise that horizontal and vertical forest structural diversity are related to ecological diversity, our research considered how the influence of stand and landscape structural characteristics on biodiversity may vary across biophysical settings. A previous phase of this research found that climatic conditions and measures of primary productivity better explain variation in bird diversity in harsh settings such as Yellowstone than in more productive settings such as west-side Cascade and Coast Range forests (Hansen et al. 2003). With the collection of extensive stand and landscape-level forest structural data as well as the compilation and collection of bird species richness (BSR) data designed to answer our questions, we expanded on these results by investigating the relative influence of forest structure vs. available energy (including climate and productivity) in driving diversity at several landscapes across the Pacific and Inland Northwest (PINW) (Chapter 2).

We also examined the degree to which landscape effects influence bird abundance and diversity within stands where they were sampled. First, we tested the assumption that sampling birds within relatively large forest stands minimizes the influence of landscape effects such as the spatial pattering of open and closed canopy forest patches. (McWethy et al. (Appendix A)). Second, if landscape effects were present, we hypothesized that they would more pronounced in more productive settings where steep gradients in environmental conditions between edge and interior forest likely influence important processes driving bird abundance and diversity within sampled stands (McWethy et al. (Appendix A)). Lastly, we considered how bird species diversity may respond differently to timber harvest across landscapes varying in productivity (McWethy et al. (Appendix B)). Our results have several implications for managing biodiversity in PINW forests.

Summary of Results: Considering the relative influence of stand level forest structural characteristics vs. available energy in driving biodiversity, we found that (1) BSR exhibited a unimodal relationship with available energy across the PINW region, (2) the landscape scale relationships between available energy and BSR were positive or unimodal in energy limited locations and were flat or negative in energy rich locations, (3) forest structural complexity explained more of the variation in bird species richness in energy rich landscapes (4) The slope of the relationship between forest structural complexity and BSR was steepest in energy limited locations and negative in energy rich locations.

Testing for the influence of landscape effects we found that (1) a number of individual bird species respond significantly to landscape effects (landscape level edge density between open and closed canopy forests) (2) while highly species specific, the slope of response to changes in edge density followed predictable patterns for bird canopy guilds at both sites (3) many more species responded to landscape effects at a more productive setting and (4) landscape effects appear to be more pronounced at the community level in more productive settings (5) BSR and diversity responded oppositely to increases in the amount of the landscape recently disturbed by timber harvest.

Relevance to management

As a result of the changing effect of energy on diversity, the management implications of this work are necessarily specific to the energy setting of a given landscape. To adequately address the management for a variety of landscape settings we have divided the following discussion into management implications for low, intermediate and high energy settings (Table 4.1 and 4.2). We chose to classify management implications into three energy settings because the slope of the relationship between bird diversity and available energy across the PINW exhibits a unimodal relationship. BSR increases sharply with increasing energy in harsh landscapes, increases moderately with increasing energy in intermediate energy landscapes, and is flat or decreases with increasing energy in highly productive landscapes (Table 2.7, Figure 2.5). The strength and direction of the relationship between BSR and energy across a landscape provides a foundation for addressing several biodiversity conservation strategies (Table 4.2). Our results do not lead to specific guidelines for stand level management, but do support more general biodiversity management strategies for the three broadly defined energy settings. This is especially true when considering landscape effects and disturbance intensity. For landscape analyses we examined bird response to gradients in disturbance extent in landscapes surrounding surveyed stands based on a mean harvest size of ~25-ha and a rotation lengths ranging from 40-100 yrs. Therefore, how BSR responds to gradients in the extent of edge density (m/ha) and recent disturbance (harvest) must be interpreted in the context of the characteristics of current management (i.e. the average size of harvest and rotation length). This is important because our findings suggest that birds respond differently to landscape effects and landscape level disturbance in different settings, but the results do not allow for specific recommendations on how large or frequent disturbances should be.

Table 4.1 Categorical definitions of three energy settings in the PINW.

	Low Energy	**Intermediate Energy**	**High Energy**
Dominant Cover Types	lodgepole pine, whitebark pine, subalpine fir, mountain hemlock and Engelmann spruce	ponderosa pine, dry grand fir, dry Douglas fir and western larch	western hemlock and wet Douglas fir
Range of MODIS GPP	0.3 – 0.8	0.8 – 1.25	1.25 – 1.9
PINW Locations	W. Cascades >1000m N. and >1300m S. E. Cascades > 1400m West Central Idaho > 1900m N. Idaho & NW Montana > 1500m All forest zones of the Greater Yellowstone Area	East Slope Cascades < 1400 m. West Central Idaho 1200 - 1900 m. N. Idaho & NW Montana < 1500 m. Blue and Wallowa Mountains < 2000 m.	Coast Range & W. Cascades < 1000 m. N. and < 1300 m. S. (may include some low elevations east of the crest near Snoqualmie Pass and in the Columbia River Gorge)
Seasonal Limitations to Vegetation Growth	Temperature limited in the spring and fall. Regenerating stands in mountain hemlock and subalpine fir stands in the Cascades may be snow pack limited in the spring.	Temperature limited in spring, and moisture limited in late summer and fall	Some light limitation in the middle of winter, otherwise no energy based growth limitations

<u>High Energy Settings</u>: In energy rich environments, growing conditions are often favorable over most of the landscape. In these settings, a rapid flush of vegetative growth resulting from disturbance appears to benefit species diversity, suggesting that bird species richness will be maximized through relatively more frequent disturbance in highly productive systems. As a result, the rotation age for forest stands can be rather short due to quick biomass regeneration. In support, Huston (1999, 2004) and

Table 4.2 Management implications by conservation category and energy setting

CONSERVATION CATEGORIES	ENERGY GRADIENT		
	HIGH ENERGY	INTERMEDIATE ENERGY	LOW ENERGY
Harvest Treatments	• Small patch size • Harvest units spread across the landscape • Disturbance reduces competition for resources (Huston 1999, 2004 and Sarr et al. 2005) • Keep matrix habitat suitable for the dispersal of many species • Variable Density thinning practices may help young forests to be structurally complex earlier	• Selective harvest may lessen the effects of soil moisture loss • Organisms depending on naturally patchy forests are likely better adapted to a selective type of harvest	• Harvest treatments should follow the natural disturbance patterns of the specific habitat type • Promote quick stand regeneration to avoid soil loss due to wind or erosion • The comparatively high energy areas across the landscape are crucial for sustaining biodiversity and should be managed cautiously
Landscape Pattern (Spatial Distribution of Harvest)	• Maintain structural complexity to ensure high niche diversity • An existing checkerboard pattern of ownership may provide a good balance of habitat types • Shift harvest units across the landscape. (McWethy et. al. (Appendix A)) • Provide for species with specific patch size and edge requirements	• Less harsh environments mean less seasonal movement of individuals • However, ensure that seasonal movement to low elevation habitats is possible • Consider the effect of edge and patch size especially in more productive parts of the landscape	• Maintain habitat connectivity due to seasonal migrations of large mammals following ephemeral food resources. • Design landscape pattern to preserve movement corridors
Rotation Age	• Forests may be kept in short harvest rotations due to quick biomass regeneration (50-70 yrs.)	• Intermediate rotation to allow for slower biomass regeneration. (70-120 yrs.)	• Longer rotation to more closely match natural disturbance and allow for very slow biomass regeneration (> 120 yrs.)
Special Management or Protected Areas	• Small protected areas should focus on preserving specific habitat characteristics associated with specialist species	• Rural residential development is a major concern (Gude et al. 2006) • Large protected areas may not be feasible due to the amount of land development. • Consolidate ownerships to allow for larger protected areas	• Protect large areas to ensure protection for species with large home ranges and long distance seasonal migration patterns

Table 4.2 continued

CONSERVATION CATEGORIES	ENERGY GRADIENT		
	HIGH ENERGY	INTERMEDIATE ENERGY	LOW ENERGY
Conservation Zones	• Most locations contain high levels of biodiversity • The highest energy locations are not the most diverse (Chase and Leibold, 2002) • Conservation zone locations in "lower energy" locations may hold more rare species (Huston 1999)	• Few conservation zones are in mid-energy locations • Biodiversity hotspot mapping or risk analysis may determine which habitat types contain the highest levels of diversity or at at greatest risk • Protect more area with selection of locations based on conservation priority	• The species-energy relationship is strongly. • Protect areas that are comparatively higher in available energy than the surrounding landscape. • Conservation zone locations should follow a simple determination of small scale local (high energy) hotspots.
Renewable Resource Extraction Potential	• High potential for large volume resource extraction due to high levels of productivity	• Shorter growing seasons, less water availability, or heavy snow loads may reduce timber output	• May not be suited for multiple rotation timber harvest due to the low volume of marketable timber produced

Sarr et al. (2005) suggest that increasing levels of disturbance in highly productive sites may reduce competitive exclusion, facilitate rapid growth and colonization of recently disturbed sites by early seral plant communities and increase vegetative diversity and landscape heterogeneity. Therefore, disturbance can act to free resources creating a variety of habitat types and supporting a greater diversity of vegetation and bird species (Huston 1999, Huston 2004, McWethy et al. (Appendix B)).

In these settings, maintaining parts of the landscape in short rotations can provide a high volume of marketable timber while still supporting high levels of diversity associated with early seral stages. This approach stands in contrast to the management focus of the Northwest Forest Plan and the increasing attention paid to promoting late-seral forests following the listing of the northern spotted owl as an endangered species.

Early successional forests in productive landscapes dominated by shrubs and sapling conifers often support higher numbers of bird species than any other seral stage (Harris 1984, Chapter 2). We are not suggesting that managing for high levels of forest structural complexity is not important. In fact, management strategies for young forest types that lead to dense conifer sapling stands with an absent shrub component support the fewest number of bird species of any stage of forest development (Meslow and Wight 1975). Our results show that diversity is typically low in young densely stocked pole forests approaching complete canopy closure and stem exclusion (Chapter 2). Tree stem density in young forest stands has a large influence on the resulting mature forest characteristics such as tree size, and understory development (Harrington and Tappeiner 2007). Consequently, management techniques (e.g. pre-commercial thinning practices, wider spacing of planted saplings, etc.) applied before canopy closure may help to support higher diversity in these forests. The concept of thinning is widely used by industrial forest managers. However, in many industrial forests thinning of young stands is used primarily to maximize growth of the best young trees and consequently increase timber volume during harvest. The resulting stands (overstory and understory) are often more homogenous in structure and species composition than natural stands following stem exclusion (Carey 2003)

Variable density thinning (Carey and Wilson 2001) is an alternative thinning process that uses more biologically meaningful criteria than simply spacing marketable trees evenly across a harvest unit. Variable density thinning in young stands focuses on creating canopy openings large enough to promote the development of diverse understory and mid-story vegetation, and to retain a representative mixture of tree and shrub species, both of which are important components for biodiversity in productive young forests (Carey and Wilson 2001, Chapter 2).

Many species in energy rich environments specialize in forest interior, edge, or early seral conditions. Therefore, creation of the full suite of seral stages with attention to species that have specific patch size and edge relationships is especially important. Where mid/late seral forests dominate the landscape, harvesting to produce a shifting-mosaic of patches of different seral stages across the landscape will likely increase diversity at the landscape scale (Zavala and Oria 1995, McWethy et al. (Appendix A)). This process is similar to existing management strategies; however, many specialist species require unique structural attributes to succeed that may not be adequately provided for with the traditional shifting pattern of harvest alone. For example, many specialist birds (i.e. woodpeckers) depend on cavities which are only found in abundance in stands managed specifically to retain green trees and snags of various sizes and states of decay. In productive landscapes, some long distance dispersers, such as the spotted owl, need suitable quality dispersal habitat with canopy layer trees and an open understory. In addition, several rare species depend on unique structural attributes such as abundant shrubs, legacy snags, abundant coarse woody debris, broken tops, and large or mature trees. Structural retention or green forestry in harvest units may still further promote biodiversity. In addition, managing stands under short rotations presumes that soil fertility will be maintained throughout many rotations, making the sustainability of soil nutrients an important consideration for managers. Management practices that promote the development of structural features typical of old forests may help regenerating forests provide the important structural attributes required by these species more rapidly than would occur naturally. In contrast, the maintenance of open canopy patches within productive environments seems particularly important to support sustainable populations of open canopy associates. Across some landscapes an existing pattern of ownership (e.g. checkerboard) between federal and private lands may provide the balance of habitat types needed for species associated with both early and later seral stages, resulting in high landscape scale diversity.

In high energy regions, we found high levels of bird diversity across the entire landscape with a few species keying in on particular structural features or habitat types. Consequently, providing gradients in seral stage and addressing the needs of rare species and structural features associated with these species is important. A hump-shaped energy diversity gradient (Chase and Leibold 2002) exists across the forests of the PINW, pointing to the fact that the very highest energy locations are not the most diverse. In some landscapes the negative relationship between energy and diversity will be strong enough to deserve consideration when prioritizing conservation efforts. Under these circumstances, targeting conservation zones in comparatively "low energy" locations may support the highest levels of diversity (Huston 1999).

Intermediate Energy Settings: A large portion of the forested lands of the PINW are neither highly productive nor representative of low productivity areas. Because these environments may have some abiotic conditions favorable for vegetative growth yet are limited by one or two important conditions (precipitation, temperature, available solar radiation), they are considered intermediate in productivity. For example, many landscapes in the PINW with intermediate levels of available energy experience a combination of temperature limitations in the spring and significant moisture limitations in late summer and fall. These landscapes support moderate rates of vegetative growth and biomass. Thus, longer rotations will allow for full stand structural development despite slower biomass regeneration. This rotation length encompasses the Moderate winter climates mean less seasonal movement of vertebrates than occur in the lowest energy settings such as the Greater Yellowstone Ecosystem. However, wildlife often migrates to lower elevations due to high winter snow pack in the upper elevations. As a result, it is important to maintain habitat connectivity that supports these migrations. The effect of edge and patch size is less pronounced in this habitat than in high energy sites, but may still important where canopy closure results in edge and interior environments that are distinct.

Shorter growing seasons and less available water result in reduced timber output. Dry, intermediate productivity forests under a natural disturbance regime experience frequent low intensity fires that leave behind residual snags and mature live trees and increase forest structural complexity in regenerating stands (Hessburg et al. 2005, Schoennagel 2004). Selective harvest may be preferred in these locations to mimic patterns of natural disturbance, and to lessen the effects of soil moisture loss caused by clear-cutting. In addition, the habitat in the drier portions of intermediate energy landscapes often becomes patchy, and the organisms depending on these patchy forests are likely better adapted to a selective type of harvest where residual live and dead trees are left in abundance in the cutting units (Hansen and Rotella 2000).

A major concern in mid-energy environments is the risk of habitat conversion to residential and rural residential development (Gude et al. 2006). Consequently, protecting large contiguous landscapes in these settings may be difficult due to existing and planned private development. Spatial mapping of biodiversity hotspots or risk analysis may play a particularly important role here to highlight both hotspots of diversity and areas most at risk for development (Noss et al. 2002).

Low Energy Settings: Past land management has included setting aside high elevation reserves (Hansen and Rotella 2002), developing low elevation habitat (Gude et al. 2006), and harvesting across the entire forested portion of the energy gradient. Our results show that available energy is a stronger driver of biodiversity than forest structure in low productivity landscapes (Chapter 2). In low energy settings, species diversity is typically concentrated in small localized “higher” energy hotspots (Hansen et al. 2003). In addition to containing many species and high population densities, biodiversity hotspots can serve as population source areas that may help to maintain viable populations across the larger landscape (Hansen and Rotella 2002). In contrast to the location of protected areas, these hotspots are often located in lower elevation valley bottoms and along riparian areas, which are commonly in private ownership and have high potential for development (Gude et al. 2006). Therefore, in low energy locations, it is important to identify, retain and judiciously manage these hotspots. Across the remainder of low energy regions, management will best maintain biodiversity when considering the longer rotation periods required to maintain all structural stages and levels of biomass that support resources (i.e. food, nesting structure etc.) necessary for bird diversity.

Natural disturbance is a strong driver of landscape pattern in low energy locations. Unlike highly productive settings, in low productivity landscapes, intense disturbance typically reduces species diversity, at least temporarily (Osem et al. 2002, Bakker et al. 2006, McWethy et al. (Appendix B)). One possible explanation is that disturbance in harsh settings reduces resources and recovery rates of organisms. In many low energy environments, fire plays an important role in supporting habitat types and the many species associated with these fire adapted habitats resulting in canopy dominants and understory vegetation that are adapted to fires of various frequencies and intensities. Consequently, while increasing disturbance intensity may result in a decrease in species diversity immediately following disturbance, disturbance plays an important role in supporting the diversity of species associated with these environments. Therefore, some level of disturbance will best maintain diversity in the hotspot locations, but the type, rate, and intensity needs be carefully matched to local conditions. In these settings, timber harvest may better support species diversity when focused on promoting rapid re-colonization of disturbed landscapes and maintaining populations of species dependent on later-seral forests.

In low energy settings, birds appear to respond less acutely to landscape effects than in highly productive landscapes, possibly because birds are already adapted to landscapes that are more open and fragmented as a result of abiotic constraints (Hansen and Rotella 1999). Although landscape pattern effects, such as edge density and patch size, are not as pronounced as they are in higher energy settings, some aspects of landscape pattern are still important to consider. Due the occurrence of large energy gradients and ephemeral resources in most energy limited landscapes in the PINW, seasonal migrations of vertebrate populations are common. As a result, some large protected areas (spanning summer and winter habitats) may be necessary to contain species with large home ranges that follow seasonal resources.

Forest management that recognizes the processes limiting resource availability can be tailored to reduce the loss of vegetative biomass and promote more rapid re-colonization of disturbed sites and even maintain populations dependent on later seral forests. Temperature limitations are likely the limiting factors for the growth of lodgepole pine, whitebark pine, and Engelmann spruce in the Rockies. The mountain hemlock and subalpine fir stands in the high elevations of the Cascades have more moderate temperatures year round but instead contend with heavy snow-loads which can have a large impact on regenerating stands. It may be beneficial in these regions to leave patches of mature forest that will provide overstory and understory structure and shelter for regenerating saplings until the saplings and shrubs have time to grow above the average spring snow depth.

Lodgepole pine differs from some other low energy forest types in that high intensity stand replacing fire (leaving little usable structural legacy) is the most common form of natural disturbance (Schoennagel 2004). Clear-cutting matches this form of disturbance most closely, although timber harvests rarely leave residual timber at rates approaching those following natural stand-replacing fire. Additionally, when harvesting lodgepole pine forests in energy limited regions, biodiversity management should focus on promoting increased shrub density and size (Chapter 2).

We suggest that at less favorable sites, factors other than competitive exclusion act to limit to species diversity (McWethy et al. (Appendix B)). In these less favorable landscapes, the significant removal of forest biomass likely removes resources and further limits plant growth. Therefore, slow plant growth rates and recovery following disturbance may decrease even further with intense harvest resulting in less landscape heterogeneity and associated bird diversity. Selective harvests, longer rotations and modest expectations for timber volume output should help minimize these effects and help to maintain habitat heterogeneity and biomass levels that support diverse plant and animal assemblages.

Conclusions

Management of private industrial forests has focused on providing a steady supply of timber volume and wood products. More recently, changes in public opinion and federal and state regulatory environments have shifted management of private lands to also help support species diversity. Within this historical context, forest management aimed at supporting species diversity has traditionally relied on the premise that maintaining gradients in seral stages will provide structural diversity and adequately support species diversity. Additionally, in the mid-1990's the Northwest Forest Plan shifted the focus of federal land managers towards providing a larger proportion of late-seral or old-growth habitat. That shift, in combination with federal requirements to preserve habitat for the northern spotted owl, has had influenced private land managers to also focus on maintaining and promoting later-seral forests reserves, and retention of residual structure in cutting units that resemble older natural forests. The intent of the Northwest Forest Plan was to "wisely manage an entire ecosystem" to support northern spotted owls as well as species diversity more generally. Our results suggest species respond to these management approaches differently depending on the landscape in which they occur. Species diversity does not benefit from the application of this approach in all settings. Consequently, the widespread adoption of ideas generally thought to support species diversity in the Pacific Northwest may be misguided. We have provided evidence suggesting that productivity is a strong driver of species diversity, especially in energy limited systems. Therefore, efforts to maintain and promote species diversity will be most effective if they are tailored to landscapes varying in productivity. Based on our findings, management of both public and private forests in the Pacific Northwest aimed at supporting species diversity will be most successful when accounting for landscape setting.

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CHAPTER 5

CONCLUSIONS AND FUTURE RESEARCH

Direction for Future Research

In productive forests, we suggest the shifting mosaic pattern of timber harvest, already in place in many locations, may increase landscape-scale species diversity, when applied with attention to the retained structure, patch size, and edge density requirements of specialist species. In these environments, young seral forests with well developed shrub layers and open canopies are the highest in diversity. However, diversity can also reach its lowest levels in closed canopy forests young forests. The high variation in biodiversity potential in this age class points to a need for more research on the factors driving diversity in young productive forests. Research testing different strategies for harvest or regeneration that may reduce the negative effect of canopy closure on habitat and species diversity may be especially useful.

In less productive forests, we suggest that biodiversity conservation should more deliberately focus on higher energy settings in the landscape. These concentrated higher energy zones typically have the highest variation in biodiversity potential. The management strategies or disturbance regimes that will maximize diversity in these hotspot areas needs to be carefully studied, with an emphasis on balancing short and long term risks to these habitats.

Conclusions

Our results support the premise that biodiversity management will be most effective if it is tailored to the local setting. Forest managers may already consider the landscape context and biophysical setting when it concerns the regeneration rates or growth patterns of timber resources. However, forest managers often apply the same approach for managing species diversity across landscapes that differ in the amount of energy limitation. We have found that the primary drivers of diversity differ based on the energy setting of the landscape (Chapter 2), the role of forest structural complexity at the local and landscape scale in driving species diversity is dependent on the energy setting (Chapter 2 and Appendix A), the resulting spatial pattern of biodiversity hotspot locations are dependent on how strongly energy controls the landscape scale patterns of species diversity (Chapter 3), and finally that species response to disturbance is also contingent on energy setting (Appendix B). A successful strategy for planning patterns of forest harvest or managing species diversity will likely be determined by the factors controlling landscape scale patterns of biodiversity (Chapter 4).

This dissertation presents a comprehensive assessment of how the influences on biodiversity differ across the energy gradients of a large and complex region. We have identified the need for unique forest management strategies to be applied in each biophysical setting. Some of the management implications of this research stand in contrast to the widespread application of structure based management, and the suggestion that old-growth conservation zones function as biodiversity reserves. This research has the potential for widespread application in industrial forests of the PINW. In addition, the framework provided will allow this type of research to be conducted wherever gradients in energy play a role in driving species diversity.

APPENDICES

APPENDIX A

EDGE DENSITY AND FOREST PRODUCTIVITY INTERACT TO INFLUENCE BIRD DIVERSITY IN THE PACIFIC NORTHWEST

Abstract

Wildlife habitat suitability for forest passerines is typically determined by examining the relationship between bird abundance and habitat attributes measured within a stand where birds are surveyed. However, populations of organisms are known to sometimes be influenced by habitat fragmentation and measures of spatial patterning in the surrounding landscape. First, we assessed the extent to which relative bird abundance is affected by spatial patterning of habitat in landscapes surrounding stands where birds occur. Second, we hypothesized that the influence of landscape effects on population processes would be more pronounced in highly productive environments. According to this hypothesis, species will more finely partition resources from forest edge to forest interior where steep gradients in environmental conditions between forest edge and interior occur. Therefore, in areas where biomass accumulation is high (i.e. high productivity) bird response to changes in the density of edge environments across the landscape would be more pronounced. To address our questions we collected songbird point count data across broad biophysical gradients and gradients in forest patch area and configuration in the west and east slopes of the Cascade Mountains of Oregon and Washington, U.S.A, which differ in ecological productivity. We 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 at two different scales (1 kilometer and 3 kilometer radius landscapes). We found that (1) at both the community and species level, birds responded significantly to patterning in the surrounding landscape, (2) bird response was more pronounced at a 1-km radius landscape than at a 3-km radius landscape, (3) more birds responded to changes in edge density in more productive west-slope Cascade forests than less productive east-side Cascade forests, (4) approximately a third of the birds considered in our analysis responded conditionally to changes in landscape level edge density based on different levels of productivity, that is, bird response to edge density was modified by levels of productivity (5) 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 at a harsh, east-side Cascades site. These results suggest population processes are partially influenced by patterning in landscapes and that organism response to spatial patterning is contingent on the productivity of the site. Consequently, changes in forest patch pattern likely matter more to forest passerines where steep energy gradients occur. Conservation and management of forest passerines should consider how patterns of timber harvest might influence bird communities differently across gradients in productivity.

Introduction

Wildlife habitat suitability is often quantified by measuring the attributes of the habitat in which the organism is found. In the case of forest birds, the habitat is typically defined as the stand within which bird observations are collected. There is often the assumption that bird diversity within the stand is not influenced by the characteristics of the surrounding landscape, especially within landscapes where the matrix is forested. However, population processes are known to sometimes be mediated by the spatial configuration of habitats across the landscape (Ferraz et al. 2007, Fahrig 2003, McGarigal and McComb 1995, Hansen and Urban 1992, Rosenburg and Raphael 1986). Ecological theory suggests that the responses of organisms to surrounding landscape pattern should be greatest in highly productive ecosystems. In order to tailor conservation and management of forest birds it is important to know whether landscape-level spatial processes influence organism abundance within a stand. This study is designed to evaluate the extent to which relative bird abundance and diversity within forest stands are influenced by spatial patterning of habitat in the surrounding landscape and to compare potential effects between landscapes differing in ecosystem productivity.

It has long been known that forest bird abundance and diversity are strongly related to the characteristics of the local forest (MacArthur and MacArthur 1961, Grant et al. 2000, Hansen et al. 1995, Verner et al. 1986, Cody 1985). Forest structure and composition influence resources and conditions that limit birds within the forest (Sallabanks et al. 2005, Ishii et al. 2004, Spies 1998). This approach assumes that bird species and communities are determined by characteristics of the sampled stand. The advent of landscape ecology over the last few decades has focused on the influence of spatial patterns of habitats across landscapes on population processes of organisms (Forman and Godron 1986, Turner et al. 2001). Organisms within one habitat may sometimes be influenced by conditions in the surrounding landscape. Such effects are known to be most pronounced if the target habitat is small in size or isolated from similar habitats relative to the scaling of the organisms (Ferraz et al. 2007, Gehring and Swihart 2003). Accordingly, birds in large forest patches are thought to be less influenced by the surrounding landscape than those in smaller stands, especially within forested landscapes

(Donovan et al. 1995, Robinson et al. 2005). Hence, a typical approach in forest management has been to sample birds and habitat within the core of relatively large forest stands to quantify bird habitat relationships in the absence of landscape effects (Sallabanks and Arnett 2000, Vega 1993, Cody 1985). Efforts to maintain bird diversity also typically assume landscape effects are minimal. Thus, it is important to test this assumption to know whether conservation efforts might be tailored to be more effective.

The spatial scaling of population processes is not well known for many organisms. There are several mechanisms by which habitat pattern in the surrounding landscape could influence birds within forest stands. First, if there is abundant suitable habitat at the landscape scale supporting larger populations of a species there is a greater chance of settlement of breeders in a patch. Hence, bird populations within a stand may reflect immigration and emigration from suitable habitat in the surrounding landscape and breeding success related to demographic processes (Bowman et al. 2002, Hames et al. 2001, Lawton 1995, Fahrig and Paloheimo 1988, Pulliam 1988). Second, resources and conditions within a stand may reflect edge effects from neighboring stands (Harper et al. 2005, Parker et al. 2005, Murcia 1995). Some birds are attracted to the amount of forest edge, and are facilitated by increasing amounts of edge across a landscape (Rich et al. 1994) while other species are “sensitive” to edge, requiring forest stands large enough to buffer them from the influence of edges such as brood parasitism and predation (Batary and Baldi 2004, Stephens et al. 2003, Chalfoun et al. 2002, Rolstad 1991). Third, abundant suitable habitat at the landscape scale may provide more food resources for birds foraging beyond a forest stand in which they are surveyed. Hence, previous research suggests that landscape level spatial processes sometimes mediate organism abundance and diversity across landscapes, yet little is known about how spatial processes mediate organism abundance at local scales.

The effects of landscape pattern on organisms may be influenced by the productivity of the surrounding ecosystem. The rationale for the effects of ecosystem productivity is found in the Biomass Accumulation Hypothesis (Hansen and Rotella 2000). This hypothesis purports that species will more finely partition resources from forest edge to forest interior when there is high contrast in biomass accumulation. High primary productivity allows late seral stage forests to accumulate very high levels of vegetative biomass relative to early seral stage forests. Vegetation biomass strongly influences microclimate, structure, and ecological processes such as decomposition and the distribution and abundance of organisms (Vasconcelos et al. 2005, Franklin and Forman 1987). Consequently, environmental conditions between edge and interior forest habitats contrast more in highly productive environments than less productive habitats (Figure 1) (Kapos et al. 1997, Chen et al. 1995, Williams-Linera 1990).

Microclimate gradients along stand edges influence structure and composition of understory vegetation as well as biotic interactions such as competition and predation. In highly productive environments, the result is steep environmental gradients between forest edge and interior, a mechanism likely facilitating niche specialization (Figure 1).

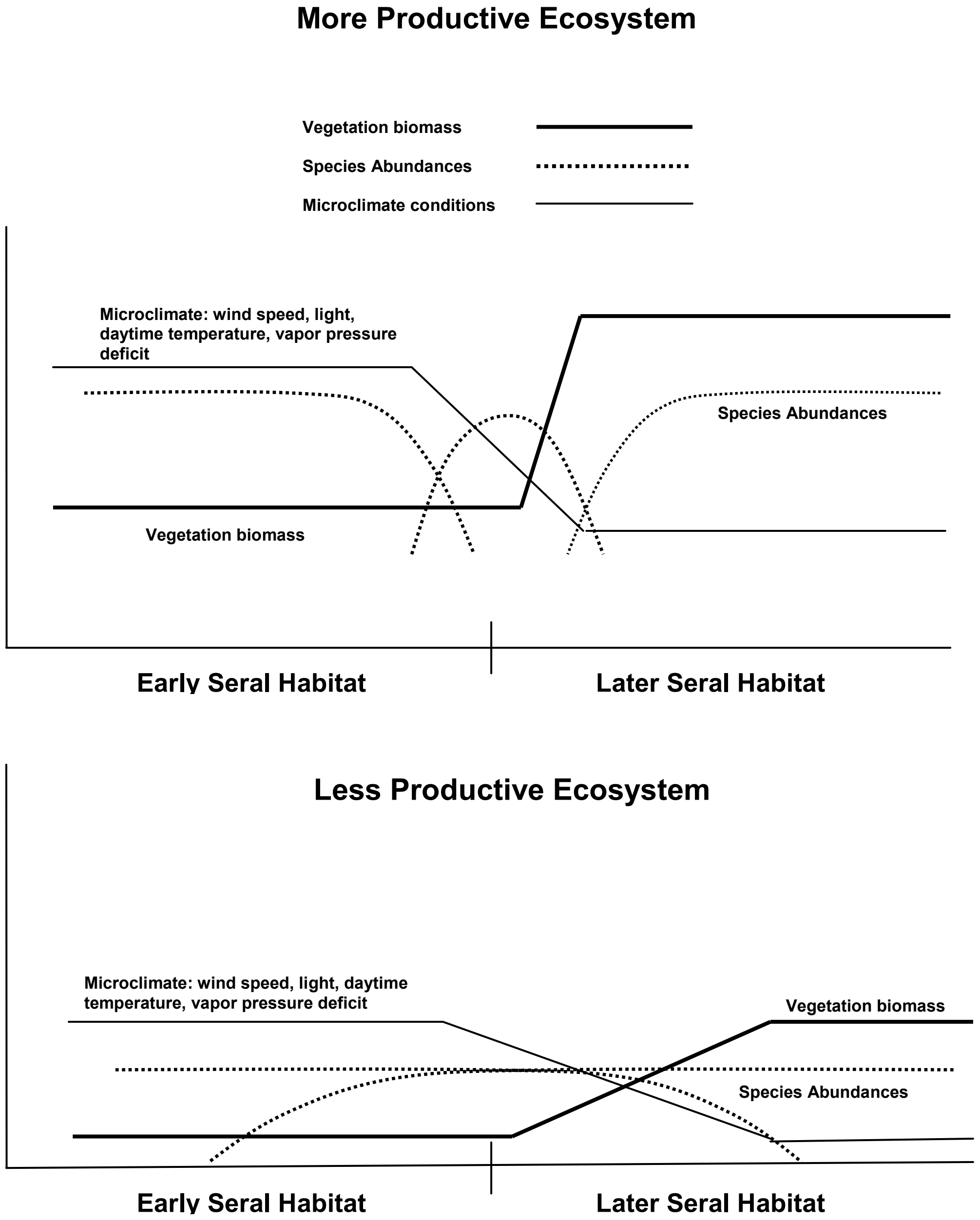

Figure 1. Theoretical representation of environmental gradients between early seral and later seral habitats and changes in vegetation biomass and species abundances across these gradients at a highly productive site and a less productive site.

In support of this reasoning, studies in high biomass ecosystems such as tropical rain forests show strong effects of edges and patch sizes on biodiversity (Ferraz et al.

2007, Carvalho and Vasconcelos 1999, Kapos et al. 1997). In a fragmented landscape in Amazonia, Stouffer and Bierregaard (1995) found that edge effects significantly altered insect communities in remnant forest patches resulting in declines and local extinctions of insectivorous birds. In contrast, studies in lower biomass ecosystems have found that organism response to edge effects is weak or less predictable (Hansen and Rotella 2000, Kremsater and Bunnell 1999, Tewksbury et al. 1998).

We expect that by determining the severity of the gradient in microclimate conditions between early and late seral stages, site productivity mediates organism response to the amount of edge or interior habitats across the landscape. Thus, forest edge and interior specialists should respond more acutely to changes in the amount of forest edge and interior across the landscape in highly productive environments (Figure 1). Alternatively, where available energy and biomass accumulation is low, forest edge and interior specialists should respond less definitively to changes in forest edge and interior at landscape scales. Hence, if spatial patterning of forest patches at a landscape scale influences birds within relatively large forest stands, we propose that these effects may vary across productivity levels.

In this paper we first set out to assess the extent to which landscape effects influence relative bird abundance and species diversity, and second, test whether bird response to landscape effects varies across productivity levels. Our objectives include:

1. Quantify the number of bird species within a forest stand that respond to gradients in edge density (m/ha) in landscapes surrounding forest stands (1-km and 3-km radius).

2. Test the hypothesis that landscape effects would be more pronounced in more productive environments. More specifically, test whether:
    - 2a. More bird species respond to changes in edge density in a more productive landscape than a less productive landscape.
    - 2b. The interaction between landscape level edge density and productivity is a significant predictor of relative species abundance.
    - 2c. In a productive landscape, bird communities (composition and relative abundance) in stands surrounded by low edge density are significantly different than bird communities surrounded by high edge density. In a less productive landscape, bird communities do not differentiate across low and high levels of edge density.

We consider this comparative study a reasonable starting point for testing whether landscape effects, if present, vary across productivity levels in predictable ways. We test for landscape effects across gradients in productivity both within and across sites. This allows us to control for differences in site characteristics (other than productivity) that might confound bird response to landscape effects.

Methods

Study Area

Springfield, OR: Weyerhaeuser's Springfield and Cottage Grove tree farms and surrounding BLM and USFS lands are located just east of Eugene, Oregon, in the western toe slopes of the Oregon Cascades (Figure 2). The Study site ranges in elevation from

300-1000-m and precipitation averages 120-200-cm annually. Mean monthly minimum temperatures range from 4-5° C. Mean monthly maximum temperatures range from 16-17° C. Due to little variation in mean temperature and precipitation across the study area, Douglas fir (*Pseudotsuga menziesii*) is the dominant forest type across the region. However, hardwood species become more abundant in the southern end of the study site. 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. Private forests in this region are dominated by short rotation plantations (Ripple et. al. 1991).

Cle Elum, WA: The Cle Elum site is located along the I-90 corridor between 600 and 1800-m in Washington's Central Cascades (Figure 2). Plum Creek Timber Company's ownership totals roughly 57,000-ha distributed in a checkerboard pattern with Mount Baker-Snoqualmie and Wenatchee National Forest land. The dominant forest types found in this study area vary from wet hemlock/fir (*Tsuga heterophylla/Abies spp.*) forests averaging over 200 cm of precipitation per year near the crest of the Cascades, to dry open ponderosa pine (*Pinus ponderosa*) forests averaging 50-cm of precipitation per year on the east slopes. Mean monthly minimum temperatures range from 0° C near the Cascade crest and 2° C further east. Mean monthly maximum temperatures range from 7° C near the Cascade crest and 14° C further east. Landscape pattern also varies greatly with large wilderness and roadless areas bordering more intensively managed plantations at the north and south end of the study area.

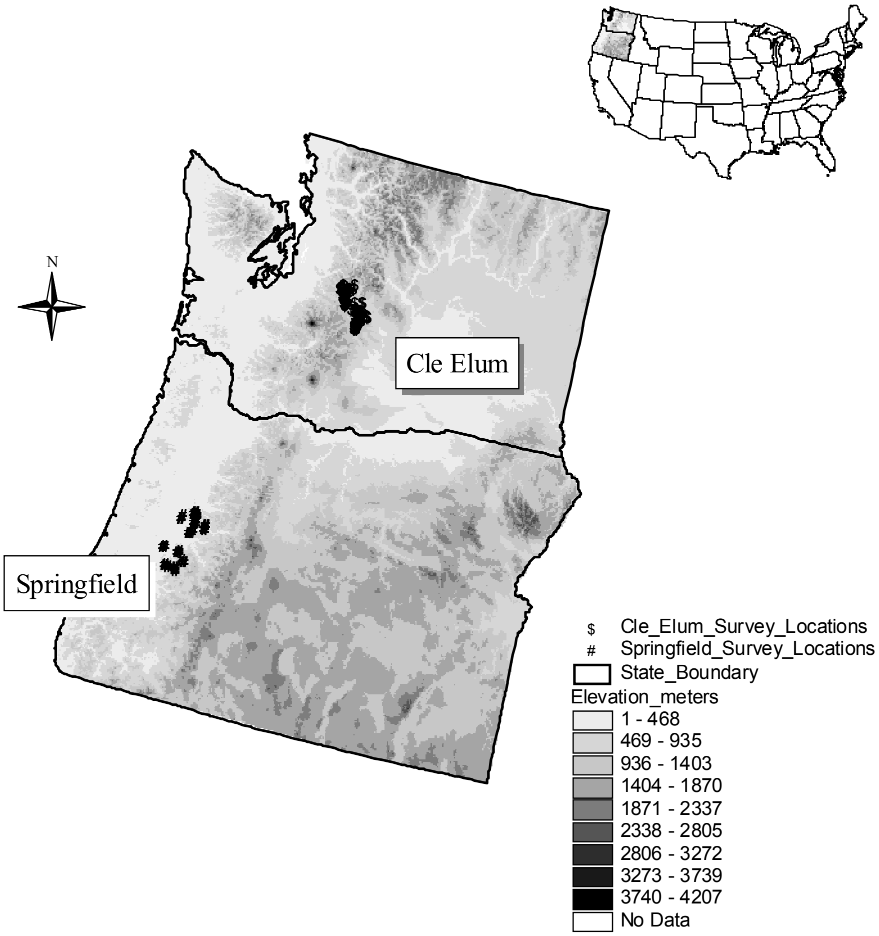

Figure 2. Location of two study landscapes, Springfield, Oregon and Cle Elum, Washington.

Study Design

Relative bird abundance was collected in each landscape within a stratified matrix of stand age/structure class and site productivity to allow for a meaningful evaluation of landscape effects across productivity levels. We chose to sample birds to represent biological diversity because birds are well understood ecologically and taxonomically, and represent a range of feeding guilds and habitat niches (O'Connell et. al. 2000, Erdelen 1984). Furthermore, birds represent the only taxonomic group that has been sampled sufficiently across the study sites to allow for these fine-scale analyses. The stratification of samples based on seral stage categories were separated by quadratic mean tree diameter (QMD) cutoff values adapted from Oliver et al. (1995). The QMD cutoff values differed for landscapes west or east of the Cascade crest based on structural classifications provided in Brown (1985) for west-side habitats, and Thomas (1979) for east-side habitats. To represent a productivity gradient, we initially selected samples based on site index (King 1966, McArdle et al. 1961), habitat type or vegetation class, which integrates climate, topography and soils and are highly correlated with productivity (Gross primary productivity, GPP). Once census point locations were acquired, we confirmed that they represented the full gradient of productivity by plotting the values of GPP for each sample point and comparing the distribution with the full range of the local productivity gradient. The productivity stratification classes varied among sites as determined by local habitat types.

Bird Sampling

Relative bird abundance (hereafter referred to as bird abundance) was sampled at five point count locations within each stand. Study sites were sampled during the breeding season in 2004 and 2005. During each survey year, points were sampled three times during the breeding season (May 15th - July 10th). Given the redundancy of effort per stand, we assumed that rare birds with low detectability were adequately sampled. We rotated survey order and observer to minimize observer affect and bias. The five census points were located along a transect with 150-200-m separation and 150-m distance from any habitat edge to control for edge effects and double sampling. Data were recorded consistent with 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. Distance sampling (Thomas et al. 2002) suggested that not all species were fully detectable at all sites within the 50-m fixed radius. However, individual species detectability did not vary between habitat types or seral stage in our results. Additionally, because modifying count data for species with lower detectability would only alter the magnitude of abundance in stands where birds were present, we included species with lower rates of detectability in our analyses.

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. Based on structural conditions characteristic of patch types that serve two distinct functional roles, we delineated two fundamental patch types, early seral (open canopy patch types) and mid/late seral (closed canopy patch types). The two patch types were delineated 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. The open canopy patch type represents very young forest stands (mean dbh = 8-cm) dominated by shrub communities and seedlings of small stature and low percentages of canopy cover (mean canopy cover = 11%). The closed canopy forest patches represent patches 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%).

We defined minimum patch size for mapping as 1 hectare and > 50 m wide in the narrowest dimension. This area corresponds to roughly the smallest estimated home range size of bird species found in the study area (Brown 1985). The minimum width was determined 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, management history and validated with field visits. Using Weyerhaeuser and U.S. Geological Survey (USGS) digital orthophotos we digitized forest patches manually using field visits to validate forest patch attribute information. Digital polygon coverages of forest patches at both scales were then converted to raster grids and imported into the landscape analysis program FRAGSTATS to derive landscape pattern predictor data (McGarigal and Marks 1995).

Because landscape effects have been shown to be scale dependent (Mitchell et al. 2001, McGarigal et al. 2001, Lloyd et al. 2005), we derived landscape predictor data at two scales, a 1-km and 3-km radius surrounding survey stands. Previous studies have found effects at comparable scales (McGarigal et al. 2001, McGarigal and McComb 1995) and areas much smaller than a 1=km radius approach large stands of forest which we consider to represent more local effects.

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 Index, m/ha) ranged from 5 to 55-m/ha at Springfield and 5 to 70-m/ha at Cle Elum. At the stand scale we quantified the size of the patch and the amount of core area within a patch where a survey took place. We used remotely derived measurements (MODIS satellite) of annual gross primary productivity ($gm^C/m^2/day$) to represent productivity. A number of abiotic conditions influence site productivity and vegetative growth (i.e. number of growing season days or frost free days, precipitation, available solar radiation, soil fertility among others). Annual measurements of GPP adequately represent site productivity for our purposes by integrating important abiotic conditions into one value. We assessed the extent to which each landscape represented gradients in productivity by plotting the range of GPP values associated with each site.

Statistical Analysis

Landscape effects; 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 with the influence of zero data we also considered Poisson and negative binomial distributions to assess the relationship between edge density and bird abundance. With slightly different assumptions, each of these distributions has attributes better suited to data that take different forms. The pattern of results was consistent regardless of the distribution chosen. Because many species occurred only in either closed or open canopy forest stands we quantified the relationship between abundance and edge density only in stands where a species occurred. In this way we controlled for seral stage and minimized the influence of zero data in models. For generalist species that occurred in early, mid and later seral stands equally, we used data from all stands.

Linear Regression Model:

Equation 1 $y = \beta_0 + \beta_1(X_1)$

Where: $y = \beta_0 + \beta_1(edge\_density)$

Generalized Linear Model:

Equation 2 $y = \beta_0 + \beta_1(X_1)$ $family = Poisson$

Where: $y = \beta_0 + \beta_1(edge\_density)$ $family = Poisson$

Landscape effects; Community level: To compare community-level response to landscape patterning at different scales we used Non-metric Multidimensional Scaling (NMDS) (Venables and Ripley 2002, Roberts 2005) to plot ordinations of bird assemblages found within each forest stand at each site. We then used the *envfit* function (Oksanen 2006) in R-statistical program and computing language for calculating vectors with maximum correlation between ordination scores and closed canopy forest edge density (R Development Core Team 2006). The *envfit* function fits environmental vectors or factors to ordination scores, which in this case, represent bird assemblages for each forest survey stand. Vectors were derived at a 1-km and 3-km scale. Additionally, a vector for one patch-level metric, (patch core area) was derived to compare the relative difference in strength of explanation of bird community organization at the patch scale versus the two landscape scales (R Development Core Team 2006). Vectors of each landscape metric were then plotted over NMDS ordinations of bird community organization at each site and the goodness of fit statistic (R^2) values were derived from 1,000 permutations of the maximum correlations with ordination scores (Oksanen 2006). The significance of fitted vectors or factors was assessed using permutation of environmental variables.

Ecosystem productivity effects; Species level: To test the prediction that the difference between the overall proportion of significant responses to changes in landscape indices in Springfield would be greater than the overall proportion of significant responses to changes in landscape indices in Cle Elum we used a proportional Z-test.

$$H_0 = (proportion\_significant\_responses\_Springfield) - (proportion\_significant\_response\_Cle\_Elum) = 0$$

$$H_a = (proportion\_significant\_responses\_Springfield) - (proportion\_significant\_response\_Cle\_Elum) > 0$$

We also used a Kolmogorov-Smirnov test to determine whether our response data (P-values for each set of 60 birds by site) originate from different distributions (Durbin 1973). The Kolmogorov-Smirnov test allows us to determine whether the sample of resulting P-values for each landscape are significantly different from each other.

Using combined bird abundance data from both landscapes and within the Cle Elum landscape alone, we used linear regression with an interaction term to assess whether individual species responses to changes in edge density in the surrounding landscape varied across levels of productivity. The combined bird data allowed us to test whether bird response to changes in edge density varies across two landscapes with different productivity levels. To control for the possibility that factors other than productivity (characteristics specific to each landscape such as dominant canopy species) would influence bird response to landscape effects. We also tested whether bird response to changes in edge density varied across productivity levels within the Cle Elum landscape only. We chose the remotely derived (MODIS satellite) measurements of GPP (annual) to represent productivity. The following equation represents the general form of the interaction tested for species at each site.

Equation 3 $y = \beta_0 + \beta_1(X_1) + \beta_2(X_2) + \beta_3(X_1 * X_2)$

Where: $y = \beta_0 + \beta_1(edge\_density_1) + \beta_2(NDVI_2) + \beta_3(edge\_density_1 * NDVI_2)$

We quantified the number of species where the main effects, edge density and GPP (annual), and the interaction term were significant at an alpha < 0.05. For species where these coefficients were 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.

Ecosystem productivity effects; Community level: To evaluate bird community similarity at sites surrounded by low edge density and high edge density we calculated a similarity matrix (Bray-Curtis distance 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 distance measure. 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 for 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 where distinctly different from each other (functions *permtest* and *partana* developed by Roberts 2006). We performed 999 permutations of this calculation to derive a P-value associated with the test that the within cluster to between cluster ratio is greater than 1. This ordination method allowed us to test our hypothesis that, at the community level, bird assemblages in highly productive environments are regulated by changes in landscape level edge density more acutely than bird assemblages in less favorable environments.

Results

Landscape Structural and Energy Characteristics

Open canopy stands were surrounded by landscapes with slightly higher edge densities than closed canopy stands for both Springfield and Cle Elum (Figure 3). In Springfield, the mean edge density surrounding open-canopy stands (25 m/ha) was higher than closed-canopy stands (21.0 m/ha), however, this difference was not statistically significant and the gradient in edge density is similar for both categories of stands (Figure

3). Similarly, in Cle Elum, the mean edge density surrounding open-canopy stands (33 m/ha) was also higher than closed-canopy stands (25 m/ha), but not statistically significant and the gradient in edge density was also similar for both categories of stands (Figure 3).

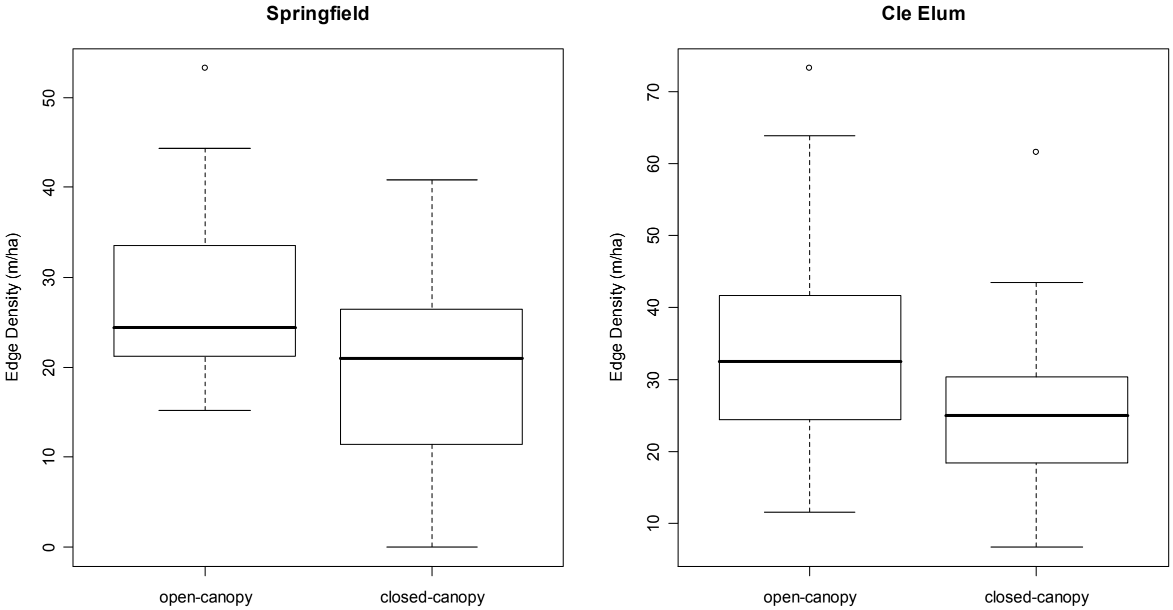

Figure 3. Boxplots of landscape-level edge density (m/ha) data for open and closed canopy stands for Springfield and Cle Elum (1-km radius).

The range of GPP (annual) values for each landscape represent two distinct distributions and represent more productive landscapes within North America (Figure 4). At the Springfield landscape, GPP values ($gm^C/m^2/day$) range from 1.29 to 1.85 with a mean of 1.42 and a standard deviation of 0.11. At the Cle Elum landscape, GPP values range from 0.56 to 1.09 with a mean of 0.92 and a standard deviation of 0.12. The combined range of values for each site represent a significant portion of the gradient of possible values of GPP for all of North America (Figure 4), and encompasses almost the entire range of GPP values that represent forested ecosystems in North America (GPP values > 0.2).

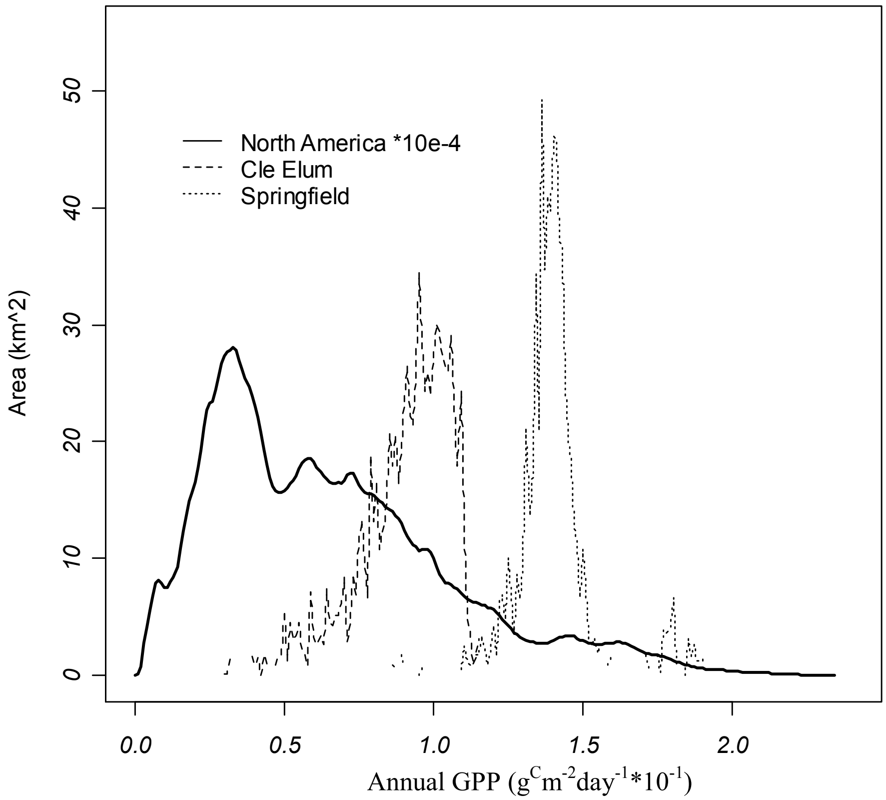

Figure 4. Area (km^2) of land representing GPP gradient for North America (*10^4), and 3-km radius landscapes surrounding the Cle Elum and Springfield survey sites.

Landscape pattern effects

Individual species: At the 1-km landscape scale we found evidence that a number of birds species respond to landscape effects. At the more productive site, Springfield, 25 of 60 species (42%) responded significantly to changes in edge density (Table 1), compared to the less productive site, Cle Elum, where four of 60 species (7%) responded significantly to changes in edge density (Table 2). For models where edge density was a significant predictor of abundance ($P < 0.05$), R-squared values ranged from 0.08 to 0.38

in Springfield (n = 25, mean 0.20, SD 0.07) and 0.13 to 0.40 in Cle Elum (n = 3, mean 0.21, SD 0.13).

While highly individualistic, the slope of response to changes in edge density followed predictable patterns for bird canopy guilds at both sites (Tables 1 & 2). Open canopy associated species and most generalist species responded positively to higher levels of landscape level edge density whereas closed canopy associated species responded negatively to increases in edge density (Tables 1 & 2, Figure 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 (all nine open canopy associates and six of nine generalists) and negative for 10 species (six closed canopy associates and three generalists). Of the four species that responded significantly ($P < 0.05$) to changes in edge density in Cle Elum all three closed canopy associated species responded negatively to increases in edge density as well as one generalist species. Edge density was a stronger predictor at the 1-km scale than the 3-km scale for all analyses (data not shown).

Community-level response*:* In Springfield we found that edge density was a significant predictor at the community level, explaining 43% of the variation in bird composition and abundance within survey stands at the 1-km scale compared to 21% at the 3-km scale. Conversely, in Cle Elum, edge density was not a significant predictor of bird community composition and abundance. At the patch level, the amount of core area within each survey stand (area within a 100 m buffer from edge) explained 23% of the variation in bird community organization in Springfield and 12% in Cle Elum and was a significant predictor at both sites.

Table 1. Species responding significantly to edge density (m/ha) at the Springfield site (1 km scale). See Appendix D for bird code definitions

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

Table 2. Species responding significantly to edge density (m/ha) at the Cle Elum site (1-km scale). See Appendix D for bird code definitions.

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

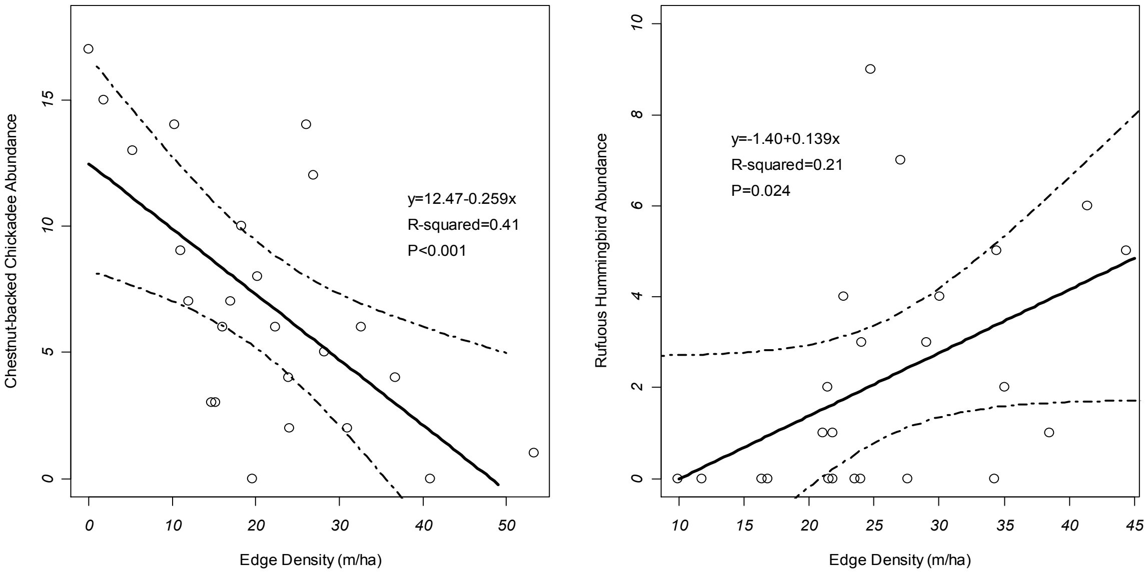

Figure 5. Chestnut-backed chickadee and rufuous hummingbird abundance as a function of landscape level edge density (1-km radius). Fitted regression with 95% confidence intervals shown (data from the Springfield site).

Ecosystem productivity effects

Individual species: We found evidence that bird response to changes in edge density was more pronounced at a more productive site than a less productive site. More birds responded to changes in edge density in Springfield than Cle Elum (Tables 1 & 2, Figure 6). A Z-test of proportional difference suggests that the proportion of birds responding significantly to changes in edge density at each site is 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 are significantly different ($P< 0.001$) (Figure 6).

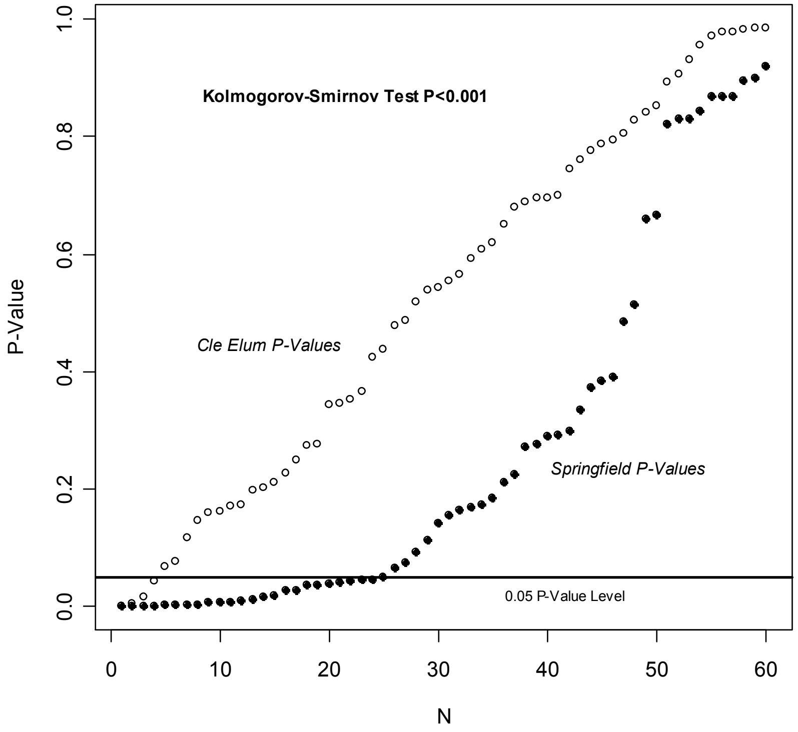

Figure 6. Plot of sorted P-values from models examining the relationship between changes in edge density and bird abundance for the 60 most abundant species at each site. Closed circles represent P-values for Springfield bird species and open circles represent P-values for Cle Elum bird species. A Kolmogorov-Smirnov test indicates that the two samples of response data are significantly different. Solid black horizontal line indicates an alpha level of 0.05.

<u>Individual species; edge density-productivity interaction:</u> With pooled data from both landscapes, individual bird species responded differently to edge density as a function of productivity (Tables 3 & 4, Figure 7). The slope of the response to edge density changed as a function of productivity (annual GPP) for 25 of 60 species. We found similar results when we tested for this interaction with Cle Elum data only (data not shown). Examining individual species responses to changes in edge density at different levels of productivity we found that the response to changes in edge density is most pronounced at high levels of productivity (Table 4, Figure 7). Only a few species

responded more acutely to changes in edge density at lower levels of productivity (Table 4). 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, birds within each canopy guild responded to increases in edge density most acutely at the highest levels of productivity (Table 4).

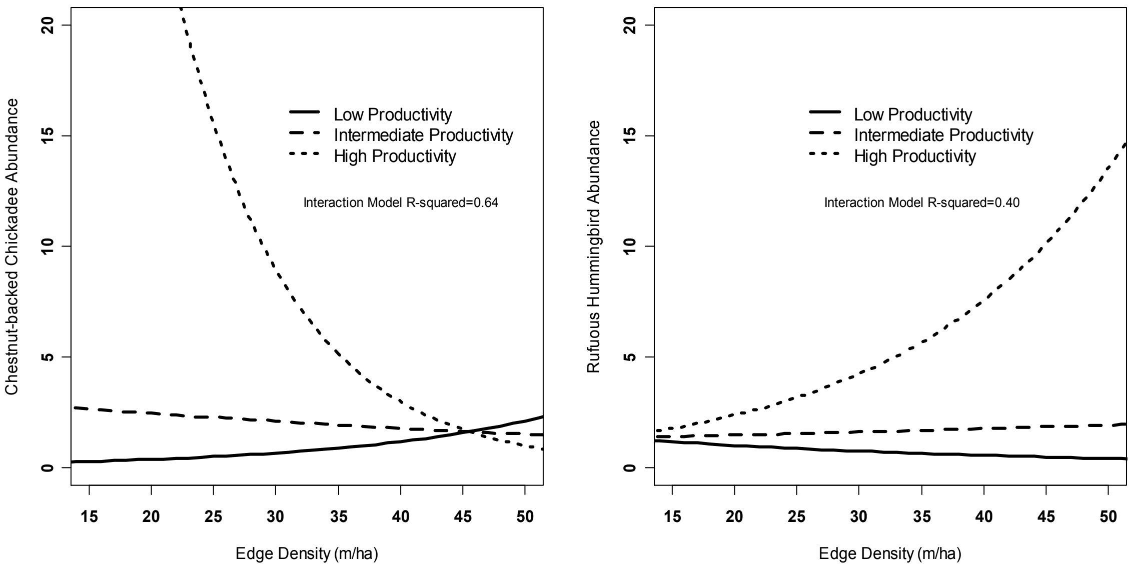

Figure 7. Fitted models representing the relationship between chestnut-backed chickadee (left plot) and rufuous hummingbird (right plot) abundance and increasing edge density (m/ha) at low, intermediate and high levels of productivity (GPP annual).

Table 3. Species responding significantly to edge density (ED, m/ha) and the interaction between landscape level edge density (m/ha) and GPP (annual). Data is combined for both sites. See Appendix D for bird code definitions.

Species Code	**Guild**	**ED P**	**ED:GPP P**	**R-squared**	**Species Code**	**Guild**	**ED P**	**ED:GPP P**	**R-squared**
BCCH	Closed	0.053	0.020	0.469	FOSP	Open	-	-	-
BRCR	Closed	0.029	0.007	0.363	HOWR	Open	-	-	-
CBCH	Closed	0.001	0.000	0.640	LAZB	Open	0.004	0.010	0.279
CORA	Closed	-	-	-	LISP	Open	0.017	0.032	0.121
GCKI	Closed	-	-	-	MGWA	Open	-	-	-
GRJA	Closed	-	-	-	MOUQ	Open	-	-	-
HAFL	Closed	-	-	-	NAWA	Open	-	-	-
HETH	Closed	-	-	-	OCWA	Open	-	-	-
HETO	Closed	0.075	0.027	0.368	OSFL	Open	-	-	-
HEWA	Closed	0.035	0.026	0.702	PUFI	Open	-	-	-
PISI	Closed	0.070	0.017	0.271	PUMA	Open	-	-	-
PIWO	Closed	0.027	0.005	0.473	RNSA	Open	-	-	-
PSFL	Closed	0.002	0.001	0.550	RSFL	Open	0.038	0.050	0.304
RBNU	Closed	0.067	0.014	0.498	RUHU	Open	0.076	0.037	0.404
RBSA	Closed	-	-	-	SOSP	Open	-	-	-
RECR	Closed	-	-	-	VGSW	Open	-	-	-
STJA	Closed	0.022	0.015	0.547	WAVI	Open	-	-	-
TOSO	Closed	-	-	-	WCSP	Open	-	-	-
TOWA	Closed	-	-	-	WIFL	Open	-	-	-
VATH	Closed	0.019	0.003	0.343	WREN	Open	-	-	-
WEBL	Closed	-	-	-	WWPE	Open	0.074	0.030	0.195
WETA	Closed	-	-	-	YWAR	Open	-	-	-
WISA	Closed	0.004	0.006	0.486	AMRO	generalist	0.076	0.027	0.110
WIWA	Closed	-	-	-	AUWA	generalist	0.018	0.011	0.597
WIWR	Closed	0.019	0.009	0.542	BHGR	generalist	-	-	-
AMGO	Open	-	-	-	DEJU	generalist	0.062	0.010	0.508
BEWR	Open	-	-	-	NAWA	generalist	0.072	0.038	0.241
BHCO	Open	0.000	0.000	0.472	SWTH	generalist	0.003	0.005	0.680
CEDW	Open	-	-	-	MOCH	generalist	-	-	-
COYE	Open	0.036	0.011	0.403	SPTO	generalist	-	-	-

Table 4. Species response (abundance) to edge density (m/ha) at low, intermediate and high levels of productivity (GPP annual). 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. See Appendix E for bird code definitions.

Species Code	Guild	Low Productivity	Intermediate Productivity	High Productivity
BCCH	Closed	+	-	---
BRCR	Closed	+	-	---
CBCH	Closed	+	-	---
HETO	Closed	+	-	--
HEWA	Closed	+	-	---
PISI	Closed	-	+	++
PIWO	Closed	+	-	---
PSFL	Closed	+	-	---
RBNU	Closed	+	-	---
STJA	Closed	+	-	---
VATH	Closed	+	-	--
WISA	Closed	---	-	+
WIWR	Closed	+	-	---
BHCO	Open	-	+	+++
COYE	Open	-	+	+++
LAZB	Open	---	-	+
LISP	Open	--	-	++
RSFL	Open	---	-	+
RUHU	Open	-	+	+++
WWPE	Open	+	-	--
AMRO	generalist	-	+	+++
AUWA	generalist	---	+	+
DEJU	generalist	--	++	++
NAWA	generalist	--	+	++
SWTH	generalist	+	+	---

Community level response: Paralleling species-level results, we found evidence that bird communities at a more productive site differentiate across a gradient in edge density whereas bird communities at a less productive site do not. In Springfield, bird communities surrounded by low edge densities were significantly different than bird communities surrounded by high edge densities (within to between cluster ratio P = 0.003) (Figure 8). Bird communities in Cle Elum were not significantly different between low and high levels of edge density (m/ha) (within to between cluster ratio P = 0.364) (Figure 8).

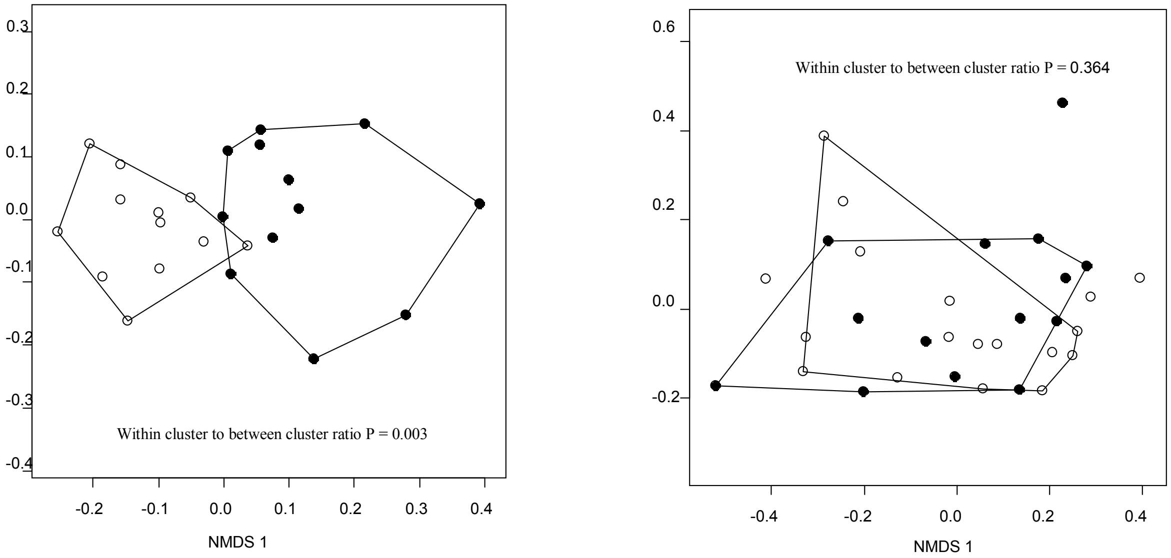

Figure 8. NMDS ordination of closed canopy bird community similarity by site. Open circles represent forest survey stands surrounded by landscapes (1 km radius) with low edge density (m/ha). Closed circles represent forest survey stands surrounded by landscapes with high edge density.

Discussion

Landscape Effects

The literature examining organism response to landscape effects is extensive (Fahrig 2003), yet few studies have attempted to test the extent to which spatial patterning of habitat influences organism population processes within a habitat or stand in which they are sampled (Rosenburg and Raphael 1986, Hagan and Meehan 2002). Challenging the assumption that landscape effects are absent within relatively large forest stands where bird habitat relationships are often tested, we found that nearly half of the 60 most abundant species at a productive site responded to landscape effects. Bird community organization also responded significantly to the influence of spatial patterning at a productive site. Supporting our hypothesis that the effects of spatial patterning may vary at different levels of productivity, bird response to landscape effects were more pronounced at a more productive site and minimal at a less productive site. Edge density alone, explained a substantive amount of variation in abundance for several species in Springfield (> 20% for 11 species).

Where landscape effects were significant, individual species responded predictably according to canopy guild association. All open canopy associates and most generalists responded positively to increases in edge density, whereas closed canopy associates responded negatively to increases in edge density. In addition, the size of stands where birds are surveyed influences birds at both the community and species level. Consequently, while our results suggest that one cannot assume that surveying birds within large forest stands mediates landscape effects, choosing larger forest stands likely reduces this influence.

We expect that many of the mechanisms driving bird response to changes in landscape-wide gradients in pattern also influence bird species and communities within a stand (Donovan et al. 1997). Nest predation, brood parasitism, population affects such as crowding have all been shown to influence bird communities with changes in the area and configuration of habitats across the landscape. In a landscape where a stand is isolated from other stands of suitable habitat, isolation may constrain immigration and emigration (Debinski and Holt 2000, Bierregaard et al. 1992, Lovejoy et al. 1986). For example, a mid/late seral stand surrounded by a landscape of early seral stands may have lower rates of immigration than if it was surrounded by landscapes of contiguous habitat of older forest. This process also likely influences the probability that a potential breeder will find a mate (Burke and Nol 1998, 2000). Predation rates that affect bird abundance and reproductive success within a stand are often influenced by landscape attributes of habitats surrounding a stand (Lloyd et al. 2005, Stephens et al. 2003, Chalfoun et al. 2002, Tewskbury et al. 1998). Hence, predation and brood parasitism might also explain bird response to landscape effects for closed-canopy or interior associates that responded negatively to increased edge density. Increases in suitable habitat at the landscape scale likely support higher population numbers as well as more food availability contributing to the abundance of individuals within a forest stand. A species typically foraging on insects, thriving in forest edge habitat, would likely benefit from high densities of forest edge at landscape scales. In support, studies of bird foraging ecology note that birds often forage outside of breeding territories (Zanette et al. 2000, Donovan et al. 1995).

Landscape effects as a function of productivity

We found consistent evidence suggesting that species response to spatial patterning is contingent on productivity levels. Almost half of the most abundance bird species in Springfield responded significantly to changes in landscape level edge density whereas only four species responded significantly in Cle Elum. Therefore, bird response was more pronounced where we would expect the contrast in environmental conditions between edge and interior environments to be most acute (Chen et al. 1995). Additionally, for a number of species the slope of response to edge density changed at different levels of productivity. These results suggest that gradients in environmental conditions between edge and interior environments drive processes that influence bird abundance within a stand, as well as bird diversity more generally. We think that steep gradients between edge and interior and open and closed-canopy forest patches influence important population processes in a more productive environment than a less productive environment where landscape effects are less distinct.

Scale effects

We found that for all analyses, birds respond more acutely to landscape effects at a 1-km radius scale than larger landscapes. While the influence of landscape affects has been shown to occur at scales larger than 1-km (Mitchell et al. 2006, Lloyd et al. 2005, Trzcinski et al. 1999), we would expect that local scale effects would influence breeding birds with territories typically extending much less than a kilometer radius surrounding nest sites (Poole 2007). Resource availability, density of viable mates, habitat structure necessary for a number of activities (foraging, building nests, perching) are factors influencing breeding site selection. It is likely that birds respond to these factors at scales related to their territory sizes, therefore, we might expect that bird response to patterning in the surrounding landscape might be more acute at moderate to small scales (Gehring and Swihart 2003).

Scope and Limitations

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 (Cushman and McGarigal 2003, McGarigal and McComb 1995, Hansen et al. 1993, 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, we chose to examine the bird response to landscape scale changes in edge density between open and closed-canopy forests because of the processes associated with the contrast between edge and interior environments as well as open and closed-canopy forests. While not highly correlated (< 0.70), edge density is correlated with changes in the area of open and closed canopy forest. Consequently, bird response to landscape effects in our study represents response to both changes in area and configuration of forest patches across the landscape. We chose not to separate these effects so that we might more easily interpret the relationship between individual species and changes in a metric that integrates the effects of both the density of edge and the amount of closed and open canopy forest in the landscape surrounding a forest stand.

Factors other than productivity may also explain how bird response to landscape effects varies across different landscapes. 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. In productive west-side Douglas fir forests, tree morphology and profiles of canopy layering show more even distribution of vegetative layering from canopy to forest floor than what would be expected for ponderosa pine forests (Lefsky et al. 2002). The resulting gradient in environmental conditions between edge and interior likely vary as a result of these differences in biomass distribution and layering. For example, the effects of wind are likely to be more pronounced at the edges of open vs. closed canopy patches of productive Douglas fir forests where the contrast between edge and interior habitat is high versus a ponderosa pine forest where the contrast between edge and interior habitat is more moderate. The effects of wind between edge and interior ponderosa pine stands would likely be more diffuse but would penetrate further into the stand. These differences might explain the degree to which landscape effects such as edge density influence forest passerines. Hence, it is possible that bird response to the amount of edge across the landscape would vary across forests with different canopy dominants. Even so, we think that birds are responding to compositional characteristics that are ultimately driven by gradients in abiotic conditions.

Additionally, while our results generally support the hypothesis that population processes within a stand are influenced by landscape effects, some of the characteristics unique to these sites limit broad application until further research is replicated across broad gradients in productivity and landscape pattern at additional sites. The west-side foothills of the Cascades are one of the most productive locales in the United States. Rates of colonization of disturbed forests by early seral vegetation are unique to these low-elevation sites. Consequently, the widespread application of management prescriptions appropriate for this site could be devastating to organism diversity at higher elevations and where climatic conditions are less favorable.

Management Implications

As a comparative study of how birds respond to landscape effects at two sites differing in productivity, our results suggest that bird response to higher levels of edge density and forest patches is more pronounced at a more productive site. These results support the premise that management of forest lands for bird diversity will be more effective if tailored to site conditions such as productivity. Previous research demonstrates the importance of vertical and horizontal structural diversity in maintaining bird diversity (McElhinny et al. 2005, MacArthur and MacArthur 1961, Chapter 2). At the landscape scale, it follows that management providing gradients in both the amount of closed and open canopy forest and the extent to which open and closed canopy patches create edges across the landscape would also benefit bird diversity. Management in highly productive sites might strive to maintain gradients in forest structural complexity, successional stage and landscape forest patch pattern that provide habitat for species associated with different forest characteristics. The maintenance of open canopy patches within productive environments seems particularly important in supporting open canopy associates. An important caveat being that the viability of several more rare species depend on unique structural features such as the presence of abundant shrubs, legacy snags, coarse woody debris, broken tops, and large mature trees among other features (Franklin et al. 2002). Therefore, maintaining complete gradients in forest successional age, forest patch pattern and forest vertical and structural complexity at the microhabitat scale (stand scale) will likely benefit bird diversity. Species diversity in less favorable environments may benefit from management that protects the most productive enclaves across these landscapes, limits harvest intensity to maintain biomass where harvests do occur and maintains structural complexity whenever possible.

Conclusions

Our results reinforce the claim that landscape effects surrounding a forest stand act to regulate population dynamics within a stand. We believe the mechanisms driving this differential response to landscape patterning may relate to the influence of productivity on population demographics, food availability and predation in landscapes surrounding forest stands that we surveyed. We expect that high rate of biomass accumulation occurring in the productive forests west of the Cascade Crest influences these processes more acutely, as the contrast between edge and interior environments is high compared to less productive east-side Cascade forests. Conversely, where biomass accumulation is low, birds respond less acutely to edge density as the contrast between edge and interior less defined. Future efforts could robustly test these questions with several replicates that span both gradients in landscape pattern and productivity. Importantly, forest management aimed at supporting bird diversity may be more effective if tailored to the processes regulating species response to landscape effects resulting from management.

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APPENDIX B

BIRD RESPONSE TO DISTURBANCE VARIES WITH FOREST PRODUCTIVITY IN THE PACIFIC NORTHWEST

Abstract

Management of vertebrate diversity in forests of the Pacific Northwest is often achieved by planning harvests that provide gradients in seral stage and structural complexity. The Intermediate Disturbance Hypothesis leads forest managers to schedule harvests across the landscape to achieve a full suite of seral stages to favor diversity. The assumption is made that species respond to disturbance similarly across gradients in climate, soils, and ecosystem productivity. Huston's Dynamic Equilibrium Model (DEM) suggests that response to disturbance varies with productivity. If correct, there are important implications for supporting diversity through activities such as timber harvest across landscapes varying in productivity. The DEM predicts that competitive exclusion is an important driver of species diversity at local scales, and increasingly so when productivity is high. Thus, species would respond differently to disturbance at sites with different levels of productivity. In highly productive environments, disturbance and mortality temporarily weaken intense plant competition, resulting in opportunities for rapid colonization by diverse plant species and abundant resources for birds. Conversely, where harsh climatic conditions limit plant growth and resources for birds in all seral stages, increasing disturbance intensity further reduces resources and increases physiological stress on plants in early seral stages and decreases bird species richness. We hypothesized that bird diversity would increase with increasing disturbance intensity where favorable climatic conditions result in high levels of competitive exclusion in the forest overstory and more homogeneous forest habitats. We tested our hypothesis with songbird point count data from productive west-side Cascade forests of Oregon and less productive east-side Cascade forests of Washington U.S.A. Using linear regression we found that bird richness and diversity increased with increasing levels of disturbance intensity within highly productive west-side Cascade forests ($R^2 = 0.16$, $P = 0.005$) whereas bird richness and diversity decreased with increasing disturbance intensity (quadratic relationship) within highly productive east-side Cascade forests ($R^2 = 0.30$, $P = 0.036$). Partners In Flight birds of regional concern for the Pacific Northwest responded similarly to overall bird richness. These results provide initial evidence supporting the hypothesis that bird response to disturbance varies across levels of productivity and suggests that bird species richness will be maximized through relatively more frequent disturbance regimes in highly productive systems.

Introduction

Managing forest lands for biodiversity is a common goal in the public and private forests of the Pacific and Inland Northwest (Hunter 1999, Loehle et. al. 2002) and is typically achieved through harvests that result in an array of vegetation structural conditions that provide suitable habitat for a number of species. The rationale for managing forest diversity through harvest is based on sound theoretical and empirical evidence suggesting that forest community diversity is primarily driven by gradients in seral stage and structural complexity (Kohm and Franklin 1997, Harris 1984, McElhinny et al. 2005). The intermediate disturbance hypothesis suggests that species diversity is often highest at intermediate levels of disturbance (Grime 1973, Huston 1979). Consequently, forest managers often plan timber harvests to provide a range of seral stage conditions to support diversity. The assumption is made that the causative factors of biodiversity do not vary geographically and that silviculture, as a tool for managing factors important for biological diversity, can be applied similarly across different biophysical locales. While supporting evidence shows that managing for forest structural gradients addresses habitat needs for some species, recent research suggests that organism response to disturbance varies across gradients in available energy which influence species growth rates and recovery following disturbance (Bakker et al. 2006, Osem et al. 2002, Sarr et al. 2005, Huston 1994). Understanding how vertebrate diversity might respond differently to disturbance across productivity levels is important for developing effective management strategies for maintaining diversity in different biophysical settings. The primary purpose of this paper is to investigate how organism response to timber harvest varies across productivity levels. We analyzed songbird response to forest harvest across broad gradients in available energy and consider how species diversity, community composition, and individual species targeted for conservation respond to different levels of landscape level disturbance.

Timber harvest as a form of disturbance influences resource availability in a number of ways. First, it can free resources from living organisms through mortality and decomposition, allowing more resources for surviving organisms. Second, harvest removes canopy dominant tree species, reducing competition on other plants, allowing increased plant species diversity. Third, resources can be lost from the site via erosion, runoff, combustion, volatilization and other mechanisms, making them no longer available for local organisms. Huston (1979, 1994) developed a model to predict community response to disturbance across gradients in disturbance rate and growth rate. Huston's Dynamic Equilibrium Model (DEM) suggests that organism recovery following disturbance is fundamentally related to the characteristics of the disturbance events (frequency and intensity) and the growth rate of individuals determined by the productivity of the environment (Huston 1979, 1994). In productive environments, where competitive exclusion is generally high, disturbance events, depending on their frequency and intensity, reduce competitive exclusion through mortality, increase the availability of resources and are generally followed by rapid species recovery (Figure 1). Alternatively, organism recovery following disturbance events occurring in harsh environments is predicted to be slow and more variable as available energy and resources limit species growth rates. Disturbance events in these environments typically result in more physiological stress for organisms and decreased species richness (Huston 2004). Consequently, timber harvest as a form of disturbance in forests is predicted to affect species diversity and individual species recovery differently in highly productive environments than less productive environments.

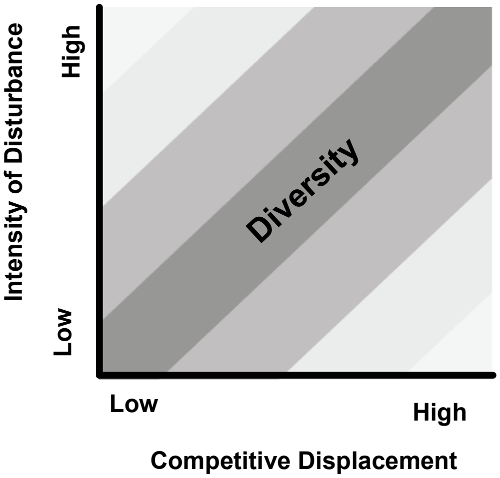

Figure 1. Theoretical representation of the predictions of the Dynamic Equilibrium Model for species diversity in relation to productivity (and associated competitive displacement) and mortality-causing disturbance. High diversity is represented by darker shading with the highest diversity along the diagonal. Figure adapted from Huston (1994).

Previous research supports the idea that disturbance may act to reduce competitive exclusion, facilitating high local diversity (Petraitis et al. 1989, Davis et al. 1988, Connell 1978, Sousa 1979). Likewise, numerous studies corroborate conceptual models suggesting that available energy drives species richness at certain scales (Mittlebach et al. 2001, Currie and Paquin 1987, Whittaker 1960). A number of theoretical models lend support for Huston's prediction that species response to disturbance varies across productivity levels (Dynamic Equilibrium Hypothesis). However, few studies test the hypothesis with empirical data. Rashit and Bazin (1987) found that in less productive environments where growth rates were low, microbial diversity decreased with fluctuations in resources caused by disturbance, whereas the opposite was true in more productive environments where growth rates were high. Huston (1980) found empirical support from plant communities responding to disturbance (mowing) within plots receiving varying levels of fertilizer. More recently, the Dynamic Equilibrium Hypothesis (DEH) has been supported for plants (Bakker et al. 2006, Osem et al. 2002, Sarr et al. 2005), primary producers in stream communities (Cardinale et al. 2006) and marine benthic infaunal systems (Widdicombe 2001). We know of no studies testing Huston's DEH for organisms at higher trophic levels such as birds.

While Huston initially developed the DEM considering plant response to disturbance under different levels of productivity and consequent competitive exclusion, he suggested that factors driving these responses would be true for other organisms as well (Huston 1999). Bird diversity is expected to follow this model, because at highly productive sites, increased disturbance would reduce competitive exclusion by dominant plants, increasing plant diversity and food and habitat resources for birds (Figure 2). In landscapes with harsh biophysical conditions, recovery from disturbance is slow and, consequently, we expect diversity to decrease with increasing levels of disturbance.

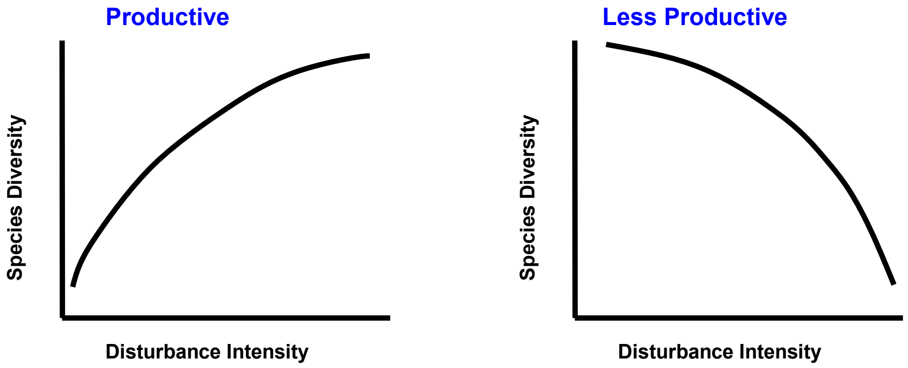

Figure 2. Predicted relationship between disturbance intensity and species diversity at a productive and less productive site. Figure adapted from Huston (1994).

In this study we tested the DEH for bird diversity across two forested landscapes varying in productivity. Our design is unlike previous ones in that we sampled birds within forest stands and analyzed the effects of the proportion of the surrounding landscape that was in closed canopy forest, an indication of the amount of recent disturbance in the surrounding landscape. One landscape was on the west side of the Cascade range in the Pacific Northwest, an area with a wet temperate rainforest climate and some of the highest levels of forest productivity in North America. The other landscape was east of the Cascade crest and graded from wet montane at the crest to dry continental to the east. We asked: Does bird richness and diversity within a stand respond differently to disturbance intensity in the surrounding landscape within landscapes varying in productivity? The specific predictions we examined were:

1. Bird richness and diversity will increase within a stand surrounded by increasing levels of timber harvest within a productive landscape.
2. Bird richness and diversity will decrease within a stand surrounded by increasing levels of timber harvest within a productive landscape.

The results are important because current efforts to manage forests for diversity assume that vertebrate response to disturbance does not vary in different biophysical settings. If correct, our hypotheses would suggest that effective management of bird diversity through timber harvest should be tailored to local settings varying in productivity. We test our hypotheses using bird diversity because it adequately represents regional diversity (O'Connell et. al. 2000, Erdelen 1984), it is feasible to sample across different landscapes and we know of no empirical data testing Huston's DEH for higher trophic levels. Likewise, because forest managers often focus on managing for threatened and sensitive species, we were interested in testing whether our predictions hold for Partners In Flight bird species of regional concern.

Methods

Study Area:

Springfield, OR: Weyerhaeuser's Springfield and Cottage Grove tree farms and surrounding BLM and USFS lands are located just east of Eugene, Oregon, in the western toe slopes of the Oregon Cascades (Figure 3). The Study site ranges in elevation from 300-1000-m and precipitation averages 120-200-cm annually. Mean monthly minimum temperatures range from 4-5° C. Mean monthly maximum temperatures range from 16-

17° C. Due to little variation in mean temperature and precipitation across the study area, Douglas fir (*Pseudotsuga menziesii*) is the dominant forest type across the region. However, upslope hardwood species become more abundant in the southern end of the study site. Land ownership is a checkerboard of BLM and private lands bordered by the Willamette National Forest and the H.J. Andrews Experimental Forest. Private forests in this region are dominated by short rotation plantations (Ripple et. al. 1991).

<u>Cle Elum, WA:</u> The Cle Elum site is located along the I-90 corridor between 600 and 1800-m in Washington's Central Cascades (Figure 3). Plum Creek Timber Company's ownership totals roughly 57,000-ha distributed in a checkerboard pattern with Mount Baker-Snoqualmie and Wenatchee National Forest land. The dominant forest types found in this study area vary from wet hemlock/fir (*Tsuga heterophylla/Abies spp.*) forests averaging over 200-cm of precipitation per year near the crest of the Cascades, to dry open ponderosa pine (*Pinus ponderosa*) forests averaging 50-cm of precipitation per year on the east slopes. Mean monthly minimum temperatures range from 0° C near the Cascade crest and 2° C further east. Mean monthly maximum temperatures range from 7° C near the Cascade crest and 14° C further east. Landscape pattern also varies greatly with large wilderness and roadless areas bordering more intensively managed plantations at the north and south end of the study area.

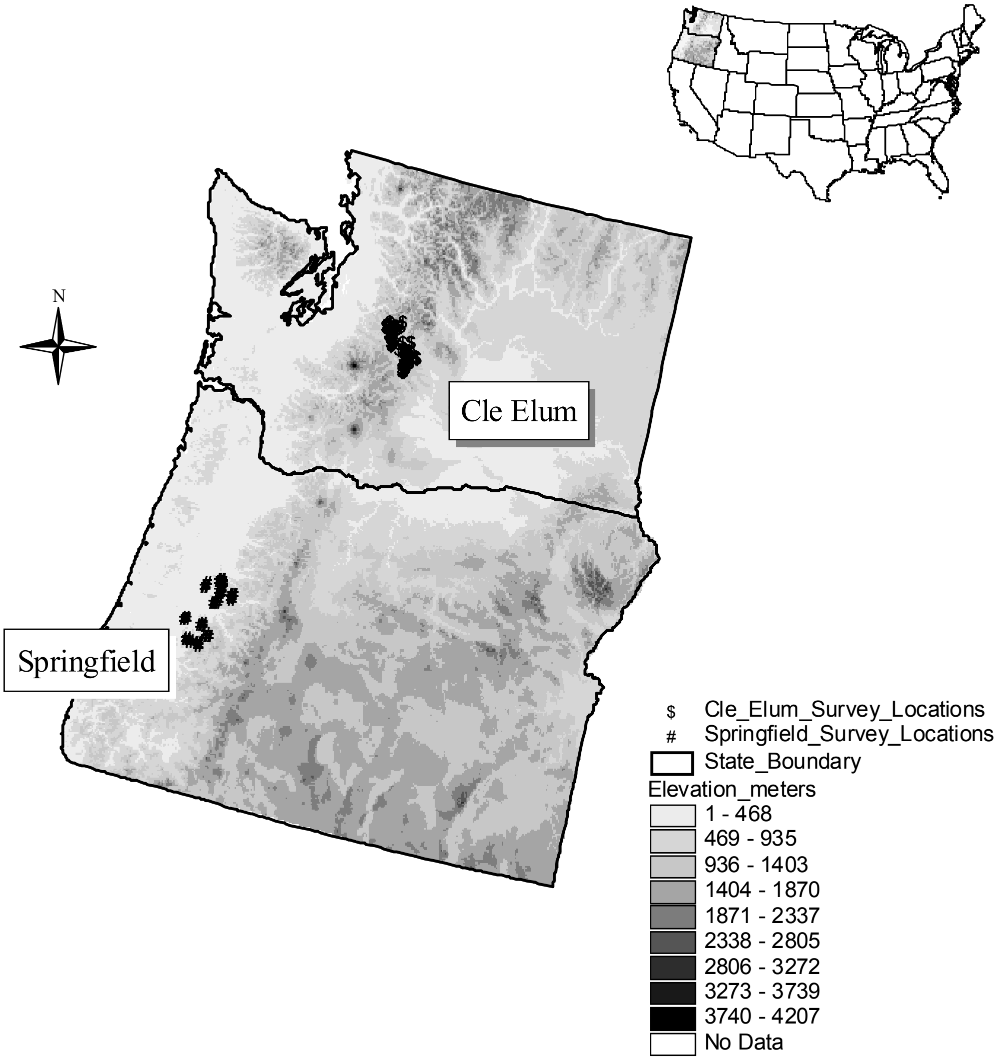

Figure 3. Location of two study sites, Springfield, Oregon and Cle Elum, Washington.

Study Design

Our overall approach was to first quantify bird community composition and individual species abundances across two landscapes varying in productivity. We then mapped the spatial patterning of recently disturbed and recently undisturbed forest patches within a 1-km radius area surrounding each stand. Bird diversity within stands was quantified as a function of the proportion of the surrounding landscape that was in a recently disturbed, early seral forest. We then compared the slopes of these relationships between the high and lower energy areas within the context of Huston's DEM. We use a data set here that was derived from a study of how diversity in large stands is influenced by surrounding landscape pattern. In that study (McWethy et al. (Appendix A)), we found that bird species abundances and community richness were influenced by the pattern of seral stages in the surrounding landscape. These landscape effects explained an average of 21% (range 8-40%) of the variation in the abundance of individual species and up to 30% of the variation in bird richness at a given site. We use this data set to test the DEH because richness in a stand partially reflects spatial patterning of suitable habitat in the surrounding landscape and the intensity of disturbance within landscapes varying in productivity.

Landscape Pattern Mapping: Our goal was to map the proportion of the landscape that had been subjected to timber harvest within the past decade. Thus, we used aerial photographs to delineate two patch types, recently disturbed and recently undisturbed. The two patch types were delineated 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. Recently disturbed patches represent very young forest stands (mean dbh = 8-cm) dominated by shrub communities and seedlings of small stature and low percentages of canopy cover (mean canopy cover = 11%). Recently undisturbed patches represent forests dominated by canopy trees with larger mean size classes (mean dbh = 48-cm) and higher mean percent forest canopy cover (mean percent canopy cover 74%).

We defined minimum patch size for mapping as > 50-m wide in the narrowest dimension, and > 1-ha in area. This area roughly corresponds to the smallest estimated home range size of bird species found in the study area (Brown 1985). The minimum width was determined 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, management history and validated with field visits. Using Weyerhaeuser and USGS digital orthophotos we digitized forest patches manually using field visits to validate forest patch attribute information.

<u>Bird Sampling:</u> Study sites were sampled during the breeding season in 2004 and 2005. During each survey year, points were sampled three times during the breeding season (May 15th – July 10th). Given the redundancy of effort per stand, we assumed that rare birds with low detectability were still be adequately sampled. We rotated survey order and observer to minimize observer affect and bias. Five census points were located along a transect with 150-200-m separation and 150-m distance from any habitat edge to control for edge effects and double sampling. Data were recorded 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. Distance sampling (Thomas et al. 2002) suggested that not all species were fully detectable at all sites within the 50-m fixed radius. However

individual species detectability did not vary between habitat types or seral stage in our results. Additionally, because modifying count data for species with lower detectability would only alter the magnitude of abundance in stands where birds were present, we included species with lower rates of detectability in our analyses. Species richness was first calculated as the cumulative number of birds seen at each survey point over the two breeding season visits. A stand level species richness response variable was then created by averaging the five point richness values and then averaging the stand totals over the two years of surveys. To evaluate species of regional concern we calculated species richness and diversity values for the subset of species we sampled that were listed as Partners in Flight species of regional concern for the Northern Pacific Rainforest Bird Conservation Region (Panjabi et al. 2005).

Landscape Predictor Data: The area of the landscape surrounding each survey stand undisturbed by harvest (in recent years) was calculated using FRAGSTATS software (McGarigal and Marks 1995). The percent of landscape occupied by recently undisturbed forest was chosen as the primary metric to represent a gradient in disturbance across the landscape. Values of the percentage of recently undisturbed forest were calculated within a 1-km radius surrounding survey stands. The range of the gradient for percent of the landscape occupied by recently undisturbed forest ranged from 55% to 100% at Springfield and between 35% to 100% in Cle Elum. Because we were interested in assessing the relationship between bird diversity and changes in the extent of landscape disturbed by harvest within landscapes representative of industry lands in the

Pacific Northwest we did not seek to locate landscapes where the range of percent cover closed canopy forested included the entire gradient between 0% and 100% forest cover.

Site Productivity: We used remotely derived measurements of annual Gross primary productivity (GPP) to represent productivity. A number of abiotic conditions influence site productivity and vegetative growth (i.e. number of growing season days or frost free days, precipitation, available solar radiation, soil fertility among others). Annual measurements of GPP adequately represent site productivity for our purposes by integrating important abiotic conditions into one value. We assessed the extent to which each landscape represented gradients in productivity by plotting the range of GPP (annual) values associated with each site (Figure 4). The range of GPP values for each landscape represent two distinct distributions and represent more productive landscapes within North America generally (Figure 4). At the Springfield landscape, GPP values ($gm^C/m^2/day$) range from 1.29 to 1.85 with a mean of 1.42 and a standard deviation of 0.11. At the Cle Elum landscape, GPP values range from 0.56 to 1.09 with a mean of 0.92 and a standard deviation of 0.12. The combined range of values for each site represent a significant portion of the gradient of possible values of GPP for all of North America (Figure 4), and encompasses almost the entire range of GPP values that represent forested ecosystems in North America (GPP values > 0.2).

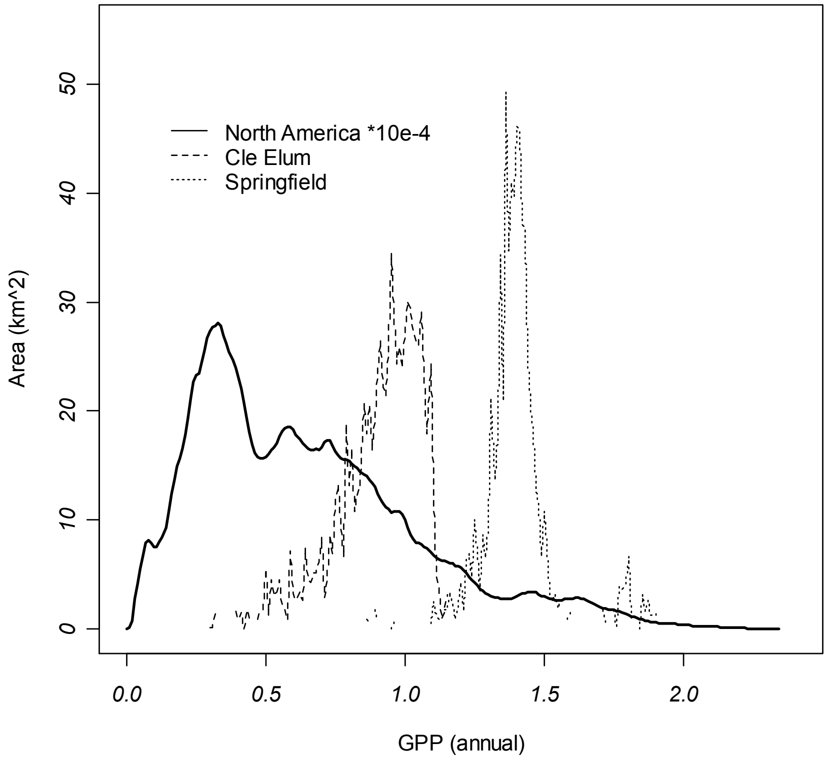

Figure 4. Area (km^2) of land representing GPP gradient for North America (*10^4), and 3 km radius landscapes surrounding the Cle Elum and Springfield survey sites.

Statistical Analysis

Bird richness values were calculated as the cumulative number of species observed at each point within one survey season. These values were then averaged across the five points within a stand and across sampling years to obtain a mean value of bird richness for each survey stand. Therefore, bird richness was calculated as the mean of bird richness of each stand across sampling years. Simpson's Diversity Index values were calculated with the following formula: $\widetilde{D} = 1 - D = 1 - \sum_{i=1}^{S} P_i^2$ where the Simpson's Index (D) equals 1- the proportional abundance (P) of species i squared and S equals the total number of species in each stand. This index integrates consideration of species richness and species evenness (the relative abundances of species). The value of this index ranges between 0 and 1, the greater the value, the greater the sample diversity. The index represents the probability that two individuals randomly selected from a sample will belong to different species.

We compared bird response to disturbance intensity within the context of Huston's DEM using linear regression. We fit both linear and quadratic models to determine the best functional relationship between species richness, diversity and landscape disturbance intensity. Regression techniques assume that residuals (error terms) are independent, normally distributed, and with constant variance. We found the Normal Q-Q plots provided support for normality for species richness and Simpson's Diversity Index. Homogeneity of variance was confirmed with spread-location plots, which showed no trend in the absolute residuals over the fitted values.

Results

We found evidence suggesting that the response in bird diversity to disturbance (harvest) was opposite at sites with high and low productivity. In Springfield, a highly productive site, bird richness decreased linearly as the percent of recently undisturbed forest increased across a 1-km radius landscape surrounding surveyed stands (Figure 5). In Cle Elum, where productivity is generally low, bird richness exhibited a slightly "hump-shaped" unimodel relationship with increasing recently undisturbed forest cover. Both models were statistically significant (Springfield P = 0.005, Cle Elum P = 0.036), explaining 16% percent of the variance in bird richness in Springfield and 30% of the variance in bird richness in Cle Elum The response in bird diversity (Simpson's Diversity Index) was similar to that of bird richness (Figure 6).

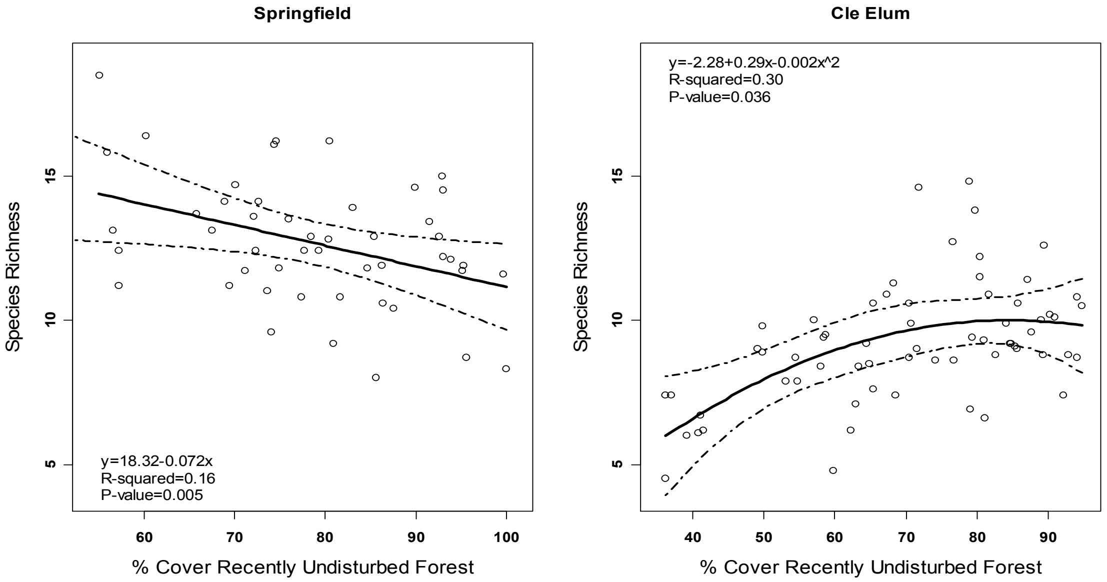

Figure 5. Bird richness within a sampled stand as a function of percentage of the landscape (1-km radius surrounding survey stands) occupied by recently undisturbed forest. Fitted regression and 95% confidence intervals shown.

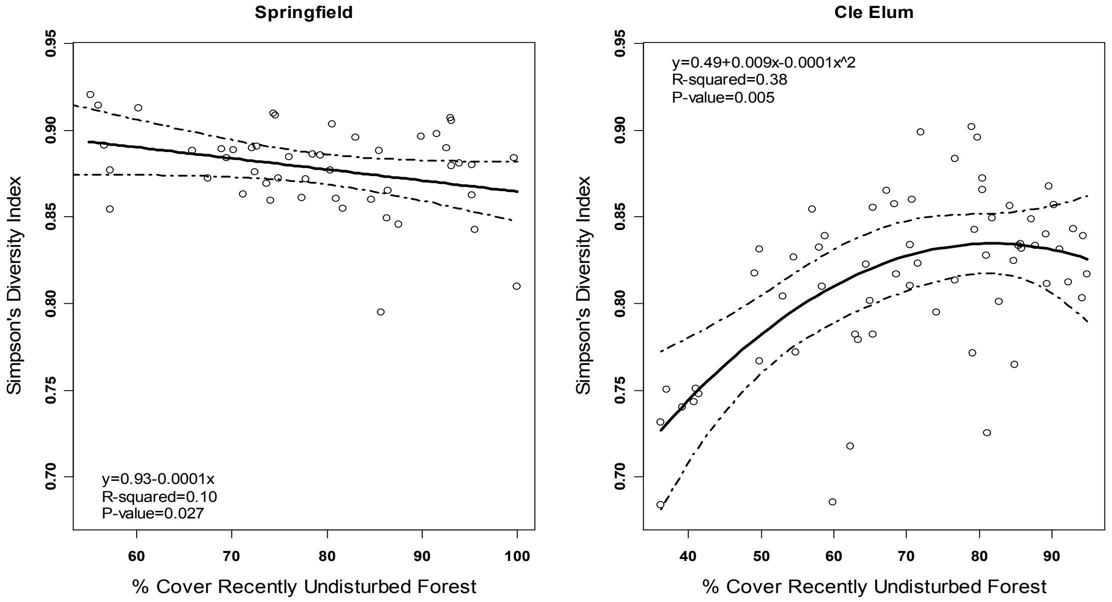

Figure 6. Bird diversity (Simpson's Diversity Index) within a sampled stand related to increasing percentage of the landscape (1-km radius) occupied by recently undisturbed forest. Fitted regression and 95% confidence intervals shown.

Bird richness for PIF birds of regional concern also decreased linearly as the percent of recently undisturbed forest increased (Figure 7). At the Cle Elum site, birds of regional concern species richness exhibited a slightly “hump-shaped” unimodel increase with increasing undisturbed forest. Both models were significant (Springfield P = 0.008, Cle Elum P < 0.001) but the amount of variance explained was much higher at the Cle Elum site (Springfield R-squared = 0.063, Cle Elum R-squared = 0.231)

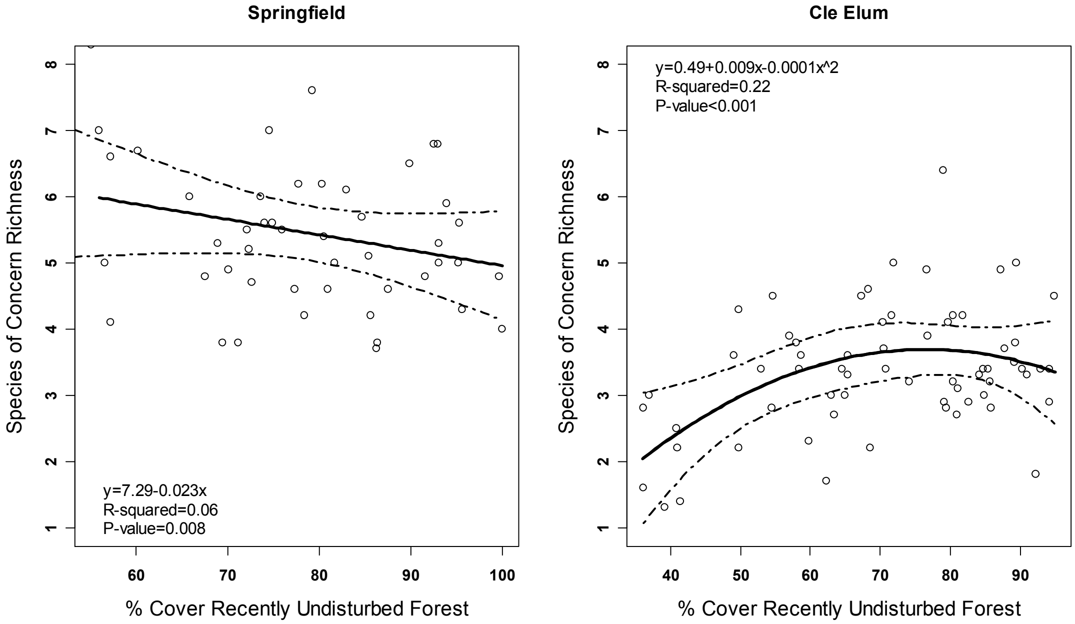

Figure 7. Sensitive species richness within a stand related to increasing percentage of the landscape (1 km radius) occupied by recently undisturbed forest. Fitted regression and 95% confidence intervals shown.

Discussion

Huston (1979, 1999) suggested that the relationship between disturbance and species diversity at local scales (0.01 to 10,000 km^2) is contingent on site productivity because competitive exclusion is influenced by both disturbance regimes and the processes regulating the rate at which dominance develops. We found that both species richness and diversity (Simpson's Diversity Index) increase with increasing disturbance in a highly productive environment whereas species richness and diversity decrease with increasing disturbance in a less productive landscape. Hence, the response of bird richness and diversity to disturbance at a highly productive site was opposite of the response found for a less productive site. This comparison supports the idea that bird response to disturbance varies across gradients in productivity. The same result also held true for Partners In Flight species of regional concern richness, but was slightly weaker. As previous research demonstrates for plants, microbes, marine microorganisms and primary producers in streams (Bakker et al. 2006, Osem et al. 2002, Sarr et al. 2005, Huston 1994) our results lend empirical support for Huston's DEH, and, adding to previous studies, suggests the DEM model applies to organisms at higher trophic levels.

We interpret our results to suggest that the relationship between competitive exclusion and productivity acts as a mechanism influencing species response to varying levels of disturbance. During the breeding season favorable soils, moderate temperatures, ample sunlight and adequate precipitation facilitate high rates of vegetative growth and associated food resources for birds such as fruits, seeds, and insects within productive west-side Cascade forests. Vegetative growth may be most rapid at recently disturbed forested areas where mortality makes light readily available for a rapid pulse of new vegetative growth. Early seral forests also experience rapid and intense colonization by forest passerines where an abundance of new and diverse shrub, grass and forb growth is apparent following disturbance. As a result, increasing levels of disturbance and consequent mortality in these highly productive sites likely reduces strong competition for resources, promoting rapid growth of colonizing species and increases in species diversity and early seral associated species abundances (Huston 1994, 1999).

Previous research testing Huston's hypothesis typically involved experimental tests subjecting communities to different levels of disturbance. Our design is unlike previous ones in that we sampled birds within forest stands and analyzed the effects of the proportion of the surrounding landscape that was in closed canopy forest, an indication of the amount of recent disturbance in the surrounding landscape. This approach assumes that diversity within a stand is influenced by the patterning of the surrounding landscape. In support, McWethy et al. (Appendix A) found when controlling for seral stage, significant variation in relative bird abundance and species richness was explained by the patterning of the landscape within 1-km radius of the sampled stand. We consider this a more conservative test than previous studies because the disturbance occurs in the surrounding landscape and only influences our sampled community indirectly via landscape scale demographic processes. Thus, our results provide a reasonable strong case study with which to consider Huston's DEH. The hypothesis also assumes that more productive sites have more rapid vegetative recovery following disturbance than less productive sites. This was the case in our study areas. Verschuyl et al. (Chapter 2) found that shrub and tree density and cover were higher in early seral stands in the Springfield site than the Cle Elum site. It is also important to emphasize that our study only examined landscapes with greater than 40% of the landscape occupied by recently undisturbed forests. It is likely that diversity will drop even in productive sites when mid/late seral forests fall below some threshold level in the surrounding landscape (Flather and Bevers 2002, Fahrig 2002). Further study is needed to determine at what level such thresholds may exist. Finally, our study included areas representing two levels of productivity. A more robust test of the hypothesis would consider several levels of productivity and attempt to find thresholds in productivity where the relationship between disturbance and diversity changes slopes.

Management Implications

Our results suggest a framework for considering how forest management may influence vertebrate diversity across different productivity settings. At highly productive sites where competitive exclusion likely limits species diversity, we expect that well planned harvesting activities would free resources for rapid colonization and growth resulting in benefits to plant and animal diversity. Hence, where mid/late seral forests dominate the landscape, the maintenance of early seral forests at highly productive sites will likely benefit vertebrate diversity. Under these conditions, harvesting as a form of disturbance could be tailored to reduce strong competition for resources, facilitating rapid growth and colonization of recently disturbed sites by early seral plant communities and generalist and early seral associated bird species. In highly productive settings, the rapid flush of vegetative growth resulting from disturbance appears to benefit species diversity, suggesting that bird species richness will be maximized through relatively more frequent disturbance regimes in highly productive systems.

An important caveat for productive settings where disturbance may play an important role in maintaining diversity is that a number of mid/late seral forest obligates rely on characteristics of older forests and sometimes require contiguous patches of mid/late seral forests to persist and succeed. Where large contiguous mid/late seral forests and complex old-growth structural attributes are already well represented across the landscape, the shifting mosaic pattern of harvest will likely foster diverse plant communities and increase habitat heterogeneity and associated vertebrate diversity (Loehle et al. 2002). In this sense, a shifting mosaic pattern of harvest is most appropriate where productivity and biomass accumulation is high, resulting in rapid pulses in re-vegetation following disturbance. It is important to recognize that beyond providing a number of ecological goods and services, mid/late seral forests and accompanying structural characteristics (coarse-woody debris, large legacy snags, forest tree species and size class diversity) are essential for the persistence and success of mid/late seral associated species (Franklin et al. 2002, Franklin and Spies 1991).

We suggest that at less favorable sites, competitive exclusion is no longer a primary constraint on species diversity. At less favorable sites where resources are already limited, the significant removal of forest biomass likely depresses plant growth rates and overall diversity, resulting in less landscape heterogeneity and associated bird diversity. Consequently, forest management in these environments should focus on protecting the most productive environments where diversity has been shown to be high. Across the remainder of the landscape, where available resources are low, the goal should be to reduce management intensity and retain biomass at levels that will reduce the negative effects of loss of resources important for plant and vertebrate colonization and growth. Within these environments, selective harvests, longer rotations and modest expectations for timber volume output should help to maintain habitat heterogeneity and biomass levels that support diverse plant and animal assemblages. Forest management that recognizes the processes limiting resource availability can be tailored to reduce the loss of vegetative biomass and promote more rapid re-colonization of disturbed sites and even maintain populations dependent on later seral forests.

Conclusions

Disturbance, as a process of mortality, regulates population processes that influence species diversity. While research investigating the effects of disturbance on organism diversity is extensive, few studies provide empirical data that test the assumption that species response to disturbance is uniform across sites with varying levels of productivity and we know of none that test this hypothesis for vertebrate species. Using a comparative approach to test this assumption, we found that bird response to disturbance intensity varies as a function of site productivity. Consequently, within highly productive landscapes where mid/late seral forests are already well distributed across the landscape, community diversity can benefit from relatively high levels of disturbance. In less productive settings, it appears that high levels of disturbance influence conditions limiting species diversity.

Because forest management is typically applied across broad gradients in productivity, the finding that species respond differently to disturbance across productivity levels is important. Forest management of vertebrate diversity would likely be more effective if tailored to abiotic conditions that regulate population processes influenced by landscape level management. Therefore, in highly productive landscapes, maintaining gradients in forest structural complexity, successional stage and disturbance intensity will likely benefit species diversity. Alternatively, management in less favorable environments might better support species diversity by modifying harvest intensity to maintain biomass where harvests do occur and maintain structural complexity whenever possible. Within the context of Huston's theoretical framework, we stress the need for further investigation of the relationship between species diversity, disturbance and productivity at different scales and for taxa at different trophic levels. While we expect that these relationships hold outside of our study area, more research is needed to consider these relationships across larger gradients in a number of landscapes.

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APPENDIX C

PREDICTOR CODE DEFINITIONS

Table 1. Forest Structure Predictor Code Definitions

PREDICTORS	DEFINITION
avg.dbh	Average Tree DBH (in.) based on midline values in each of 8 DBH categories
avg.sap	Average number of sapling trees across 4 subplots
avg.sh.bd	Average shrub basal diameter based on midline values in each of 8 basal diameter categories
canopy	Percent Canopy Closure
cwd.m3.pt	Coarse Woody Debris volume (m3/ha) V = H x (D^2 + d x D + d^2) x (PI / 12) per point
dbh.cat	Number of DBH categories of trees at a given point.
lshrub	Number of shrubs larger than 2 cm basal diameter
lsnag	Snags >20 cm dbh per point (4-201.062 m^2 (8m radius) subplots: 804.248 m^2 total)
num.58tree	Number of trees >50cm dbh (dbh classes 5-8)
num.mtree	Number of canopy layer trees in all 4 subplots (canopy layer = dbh class>2 or >20cm)
per.dec	Percent of canopy trees that are deciduous
qmd	Quadratic mean tree diameter in inches sqrt(($\sum_i^n$(dbh$_i$^2))/n))
shade.sap	Total number of shade tolerant saplings at all 4 suplots
shpp	Number of Shrubs per point
shr.cat	Number of basal diameter categories of shrubs at a given point.
snpp	Snags per point (4-201.062 m^2 (8m radius) subplots: 804.248 m^2 total)
st.complex	Structural complexity measured by multiplying trdiv by stdev.trdiv and then by 100 to make the coeffiecients easier to interpret
stdev.canopy	Standard deviation of the % canopy cover measured at 4 subplots
stdev.lshrub	Standard deviation of the number of large shrubs (large shrubs >2cm bd) measured at 4 subplots
stdev.mtree	Standard deviation of the number of canopy layer trees (canopy layer = dbh class>2 or >20cm) measured at 4 subplots
stdev.shrub	Standard deviation of the number of shrubs measured at 4 subplots
stdev.trdiv	Standard deviation of trdiv across 4 subplots
tpp	Trees per point (4-201.062 m^2 (8m radius) subplots: 804.248 m^2 total)
trdiv	Mean Shannon-Weiner tree size diversity calculations (across 4 subplots): -sum(pi*ln(pi)) where pi = proportion of trees in size class i
undercon	Percent understory cover that is conifer recorded as a decimal
underdecid	Percent understory cover that is deciduous recorded as a decimal
underherb	Percent understory cover that is herbaceous recorded as a decimal
undertot	Percent understory cover total recorded as a decimal

Table 2. Energy Predictors Code Definitions

PREDICTORS	DEFINITION
av	Aspect Value = ((1+cos(x-30))/2) where x = aspect in degrees
elev	Elevation (GPS derived)
frosuman	Frosty days annually
frosumas	Frosty days from April through September
frosummj	Frosty days in May and June
gpp	Gross Primary Productivity (5 year average 2000-2004)
grosuman	Growing days in annually
grosumas	Growing days in April through September
grosummj	Growing days in May and June
gsi05	Growing season index May
gsi06	Growing season index June
ndvi129	Normalized Difference Vegetation Index (16 day period starting May 8)
ndvi145	Normalized Difference Vegetation Index (16 day period starting May 24)
ndvi161	Normalized Difference Vegetation Index (16 day period starting June 9)
ndvi177	Normalized Difference Vegetation Index (16 day period starting June 25)
ndviavg	Normalized Difference Vegetation Index (breeding season average)
ndviavgan	Normalized Difference Vegetation Index (Annual average)
npp	Net Primary Productivity (5 year average 2000-2004)
preavgan	Average precipitation annually
preavgas	Average precipitation April - September
preavgmj	Average precipitation in May and June
radavgan	Average solar radiation annually
radavgas	Average solar radiation April- September
radavgmj	Average solar radiation in May and June
slope	Slope in degrees
tempavgan	Average temperature annually
tempavgas	Average temperature from April through September
tempavgmj	Average temperature in May and June
vpdavgan	Vapor pressure deficit annually
vpdjuly	Vapor pressure deficit July
vpdjuly	Vapor pressure deficit in June, July, and August

APPENDIX D

BIRD CODES, COMMON NAMES, SCIENTIFIC NAMES AND SITE WHERE BIRDS OCCURRED FOR LANDSCAPE EFFECTS ANALYSIS

Table 1. Banding code, common name, scientific name and site where bird occurred for birds included in landscape effects analysis. Site where bird occurred: s=Springfield, c=Cle Elum, *=both sites.

Banding Code	**Common Name**	**Scientific Name**	**Site**
AMGO	American Goldfinch	*Carduelis tristis*	s
AMRO	American Robin	*Turdus migratorius*	*
AUWA	Audubon's Warbler	*Dendroica coronata*	*
BCCH	Black-capped Chickadee	*Poecile atricapillus*	s
BEWR	Bewick's Wren	*Thryomanes bewickii*	*
BHCO	Brown-headed Cowbird	*Molothrus ater*	*
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*	*
BLGR	Blue Grouse	*Dendragapus obscurus*	c
BRCR	Brown Creeper	*Certhia americana*	*
BTPI	Band-tailed Pigeon	*Patagioenas fasciata*	s
BTYW	Black-throated Gray Warbler	*Dendroica nigrescens*	*
CAFI	Cassin's Finch	*Carpodacus cassinii*	c
CAVI	Cassin's Vireo	*Vireo cassinii*	c
CBCH	Chestnut-backed Chickadee	*Poecile rufescens*	*
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	s
CHSP	Chipping Sparrow	*Spizella passerina*	c
BUSH	Bushtit	*Psaltriparus minimus*	s
CORA	Common Raven	*Corvus corax*	*
COYE	Common Yellowthroat	*Geothlypis trichas*	s
DEJU	Dark-eyed Junco	*Junco hyemalis*	*
DUFL	Dusky Flycatcher	*Empidonax oberholseri*	*
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	c
FOSP	Fox Sparrow	*Passerella iliaca*	c
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	*
GRJA	Gray Jay	*Perisoreus canadensis*	c
HAFL	Hammond's Flycatcher	*Empidonax hammondii*	*
HAWO	Hairy Woodpecker	*Picoides villosus*	*
HETH	Hermit Thrush	*Catharus guttatus*	*
HETO	Hermit-Townsend's Warbler	*Dendroica spp.*	*
HEWA	Hermit Warbler	*Dendroica occidentalis*	*
HOWR	House Wren	*Troglodytes aedon*	*
HUVI	Hutton's Vireo	*Vireo huttoni*	s
LAZB	Lazuli Bunting	*Passerina amoena*	*
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	c
MGWA	MaGillivray's Warbler	*Oporornis tolmiei*	*
MOBL	Mountain Bluebird	*Sialia currucoides*	c
MOCH	Mountain Chickadee	*Poecile gambeli*	*

Table 1 (continued).

Banding Code	**Common Name**	**Scientific Name**	**Site**
MODO	Mourning Dove	*Zenaida macroura*	s
MOQU	Mountain Quail	*Oreortyx pictus*	s
NAWA	Nashville Warbler	*Vermivora ruficapilla*	*
OCWA	Orange-crowned Warbler	*Vermivora celata*	*
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	*
PISI	Pine Siskin	*Carduelis pinus*	*
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	*
PSFL	Pacific Slope Flycatcher	*Empidonax difficilis*	*
PUFI	Purple Finch	*Carpodacus purpureus*	*
PUMA	Purple Martin	*Progne subis*	s
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	*
RECR	Red Crossbill	*Loxia curvirostra*	c
REVI	Red-eyed Vireo	*Vireo olivaceus*	c
RNSA	Red-naped Sapsucker	*Sphyrapicus nuchalis*	c
RBSA	Red-breasted Sapsucker	*Sphyrapicus ruber*	s
RUHU	Rufus Hummingbird	*Selasphorus rufus*	*
SOSP	Song Sparrow	*Melospiza melodia*	*
SPTO	Spotted Towhee	*Pipilo maculatus*	*
STJA	Stellar's Jay	*Cyanocitta stelleri*	*
SWTH	Swainson's Thrush	*Catharus ustulatus*	*
TOSO	Townsend's Solitaire	*Myadestes townsendi*	c
TOWA	Townsend's Warbler	*Dendroica townsendi*	*
RSFL	Red-shafted Flicker	*Colaptes auratus cafer*	*
VATH	Varied Thrush	*Ixoreus naevius*	*
VEER	Veery	*Catharus fuscescens*	c
VGSW	Violet-green Swallow	*Tachycineta thalassina*	s
WAVI	Warbling Vireo	*Vireo gilvus*	*
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	*
WBNU	White-breasted nuthatch	*Sitta carolinensis*	s
WEBL	Western Bluebird	*Sialia mexicana*	*
WETA	Western Tanager	*Piranga ludoviciana*	*
WIFL	Willow Flycatcher	*Empidonax traillii*	s
WISA	Williamson's Sapsucker	*Sphyrapicus thyroideus*	*
WIWA	Willson's Warbler	*Wilsonia pusilla*	*
WIWR	Winter Wren	*Troglodytes troglodytes*	*
WREN	Wrentit	*Chamaea fasciata*	s
WWPE	Western Wood Peewee	*Contopus sordidulus*	c
YWAR	Yellow Warbler	*Dendroica petechia*	*

APPENDIX E

BIRD CODES, COMMON NAMES, SCIENTIFIC NAMES AND SITE WHERE BIRDS OCCURRED FOR PARTNERS IN FLIGHT SPECIES OF REGIONAL CONCERN (PACIFIC NORTHWEST RAINFOREST)

Table 1. Banding code, common name, scientific name and site where bird occurred for Partners In Flight species of regional concern (Northern Pacific Rainforest Bird Conservation Region). Site where bird occurred: s=Springfield, c=Cle Elum, *=both sites.

Banding Code	**Common Name**	**Scientific Name**	**Site**
BLGR	Blue Grouse	*Dendragapus obscurus*	*
BTPI	Band-tailed Pigeon	*Patagioenas fasciata*	s
BTYW	Black-throated Gray Warbler	*Dendroica nigrescens*	*
BUOR	Bullock's Oriole	*Icterus bullockii*	*
CAQU	California Quail	*Callipepla californica*	c
CAVI	Cassin's Vireo	*Vireo cassinii*	*
CBCH	Chestnut-backed Chickadee	*Poecile rufescens*	*
DUFL	Dusky Flycatcher	*Empidonax oberholseri*	*
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	*
HEWA	Hermit Warber	*Catharus guttatus*	*
HUVI	Hutton's Vireo	*Vireo huttoni*	s
MGWA	MaGillivray's Warbler	*Oporornis tolmiei*	*
MOCH	Mountain Chickadee	*Poecile gambeli*	c
MOUQ	Mountain Quail	*Oreortyx pictus*	s
NOPO	Northern Pygmy Owl	*Glaucidium gnoma*	s
OCWA	Orange-crowned Warbler	*Vermivora celata*	*
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	*
PSFL	Pacific Slope Flycatcher	*Empidonax difficilis*	*
PUFI	Purple Finch	*Carpodacus purpureus*	*
RBSA	Red-breasted Sapsucker	*Sphyrapicus ruber*	*
RECR	Red Crossbill	*Loxia curvirostra*	*
RUGR	Ruffed Grouse	*Bonasa umbellus*	*
RUHU	Rufus Hummingbird	*Selasphorus rufus*	*
SPTO	Spotted Towhee	*Pipilo maculatus*	*
STJA	Stellar's Jay	*Cyanocitta stelleri*	*
TOWA	Townsend's Warbler	*Dendroica townsendi*	*
VASW	Vaux's Swift	*Chaetura vauxi*	*
VATH	Varied Thrush	*Ixoreus naevius*	*
WIFL	Willow Flycatcher	*Empidonax traillii*	*
WREN	Wrentit	*Chamaea fasciata*	s