BIRD RESPONSE TO LANDSCAPE PATTERN AND DISTURBANCE ACROSS

PRODUCTIVITY GRADIENTS IN FORESTS OF THE PACIFIC NORTHWEST

by

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APPROVAL

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This dissertation has been read by each member of the thesis 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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ABSTRACT

Managing forest lands for biodiversity is a common goal in the public and private forests of the Pacific Northwest 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 assumption is made that the causative factors of biodiversity do not vary geographically and that silviculture, as a management tool, can be applied similarly across different biophysical locales. The primary aim of this research is to better understand how species respond to both local and landscape-scale forest structural conditions in landscapes with different levels of productivity (e.g. gross primary productivity). We hypothesized that the influence of landscape effects on bird richness, abundance and community organization would be more pronounced in highly productive environments. We also hypothesized that species response to disturbance would differ across gradients in ecosystem productivity. We predicted that bird diversity would increase with increasing disturbance extent where favorable climatic conditions result in high levels of competitive exclusion. Alternatively, we predicted that bird diversity would decrease with increasing disturbance extent when factors other than competition limit or regulate bird species diversity. We found that (1) a number of individual bird species respond significantly to landscape effects; (2) the slope of response to changes in edge density followed predictable patterns for bird canopy guilds; (3) many more species responded to landscape effects in a more productive setting; (4) landscape effects appear to be more pronounced at the community level in more productive settings; and, (5) bird species richness responded differently to increases in the amount of the landscape recently disturbed by timber harvest. 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. In productive landscapes, forest managers will likely increase landscape-scale diversity by providing all seral-stages and a range of forest structural complexity. In less productive settings, biodiversity will likely be maximized by managing local productive hotspots judiciously and adjusting harvest intensities in other locations to compensate for slower recovery and growth rates of vegetation following timber harvest.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

Forests cover approximately 30% of all land area in the world, yet estimates

suggest that forest habitat supports over two-thirds of the world's ecological diversity

(Mathews et al. 2000). In North America, almost 75% of Canada's forests and over half

of U.S. forests are managed to provide wood products and other goods and services

(USDA Forest Service 2001, Natural Resources Canada 2000). Additionally, estimates

suggest that more than 90% of threatened and endangered species occur on private lands

(Scott et al. 2001). Hence, management of forest habitats occurring on private lands is

important for supporting ecological diversity. While management of forest lands for

biodiversity is a common goal in the public and private forests of the U.S., managers of

private timberlands and other forests currently assume that the causative factors of

biodiversity do not vary geographically (Hunter 1999, Loehle et al. 2002). This may be

due in part to the unbalanced focus of past research toward the effects of stand-level

forest harvest and within-stand structural retention rather than the interaction of structural

complexity and distribution of harvest units across landscapes and regions.

The primary aim of this research is to better understand how species respond to

both local and landscape-scale forest structural conditions in landscapes with different

levels of productivity (e.g. gross primary productivity). We suspect that species respond

differently to local and landscape-scale structural conditions as a result of variations in productivity. Following this premise, we examined bird response to local and landscape-level forest structural conditions across two landscapes, one highly productive landscape in the west-side Cascades of Oregon and one less productive landscape on the east-side Cascades, Washington. Results from this research suggest that management of forest habitats to support ecological diversity will be more effective if tailored to broad gradients in productivity that occur in the Pacific Northwest. Additionally, our results lead to predictive theory on how species may respond to forest structural conditions across productivity gradients more generally.

The purpose of this dissertation is to consider how fundamental abiotic conditions such as climate and soils play an important role in influencing species response to local and landscape-level forest structural conditions in the Pacific Northwest. The general theme linking our efforts is based on the hypothesis that species respond very differently to similar structural conditions across landscapes varying in productivity. If this is correct, there are important implications for supporting diversity through activities such as timber harvest across gradients in productivity.

<u>Organization of the Dissertation</u>

In Chapter 2 we assessed the extent to which relative bird abundance is affected by spatial patterning of habitat in landscapes surrounding stands where birds occurred. We hypothesized that the influence of landscape effects on bird abundance, richness and community organization is more pronounced in highly productive environments. According to this hypothesis, species will more finely partition resources from forest

edge to forest interior where environmental gradients are steep. 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.

In Chapter 3, using a comparative analysis of species response to landscape-level timber harvest, we tested the assumption that species respond to disturbance similarly across gradients in climate, soils, and ecosystem productivity. We employ Huston's Dynamic Equilibrium Model (DEM) as a conceptual framework for predicting how species might respond to disturbance in highly productive and less productive environments (Huston 1979, 1994). Based on the DEM, we predicted that bird diversity would increase with increasing disturbance extent where favorable climatic conditions result in high levels of competitive exclusion in the forest overstory and more homogeneous forest habitats. Alternatively, we predicted that bird diversity would decrease with increasing disturbance extent when factors other than competition (i.e. food resources, metabolic constraints) limit or regulate bird species diversity.

Chapter 4 synthesizes the implications of our results for managing forests to support species diversity within an historical context. This synthesis draws on collaborative research led by Jake Verschuyl (Appendices A & B) investigating the relative influence of structure vs. productivity on productivity (Appendix A) and spatial mapping of biodiversity levels across the Pacific Northwest based on model selection of the best predictive models of bird diversity (Appendix B). Management implications relevant to several aspects of forest biodiversity management are described for low, intermediate and high productivity forests in the Pacific Northwest (PNW). The final chapter provides a summary of important conclusions and directions for future research.

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CHAPTER 2

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 gradients in edge density (m/ha) (density of edge between early
and later-seral forest patches) and productivity in the west and east slopes of the Cascade
Mountains of Oregon and Washington, U.S.A. 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 and 3 km 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 forests than less productive east-

side 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 forest

productivity; and (5) at the community level, ordinations showed that bird community

similarity in the productive west-slope 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 songbirds where steep productivity 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 when the matrix is forested. However, population processes are sometimes known to 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). 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 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 assumes that bird species and communities are determined by characteristics of the sampled stand. More recent research efforts have focused on better understanding 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 or body size of the organism (Ferraz et al. 2007, Gehring and Swihart 2003). Accordingly, birds in large forest stands are thought to be less influenced by the surrounding landscape than those in smaller stands, especially within forested regions

(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-scale effects are minimal, although this assumption is not

well tested.

The spatial scaling of population processes is not well known for many

organisms. Habitat pattern in the surrounding landscape could influence birds within

forest stands in several ways. First, if there is abundant suitable habitat at the landscape

scale (supporting larger populations of a species) there is a greater chance that breeders

can settle in a patch. Bird populations within a stand may reflect immigration and

emigration from adjacent 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 facilitated by

increasing amounts of edge across a landscape (Rich et al. 1994), whereas 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 food resources for birds foraging beyond a

forest stand in which they are surveyed. Hence, previous research suggests that spatial

processes influence organism abundance and diversity at the landscape scale, yet little is

known about how large-scale 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, as described in the Biomass Accumulation Hypothesis (Hansen and Rotella 2000). This hypothesis purports that species will more finely partition resources when there is high contrast in biomass accumulation between edge and interior forest patches. We define productivity to be the rate at which vegetative biomass accumulates at a given site representing the amount of food resources available to birds and the steepness of environmental gradients between early and later-seral forested environments. High primary productivity allows late-seral forests to accumulate very high levels of vegetative biomass relative to early-seral 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 2.1) (Kapos et al. 1997, Chen et al. 1995, Williams-Linera 1990).

Microclimate gradients across edges influence the 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 2.1).

Edge

⇩

Mid-day
Temp.

Edge

⇩

Mid-day
Temp.

High Biomass Accumulation

Low Biomass Accumulation
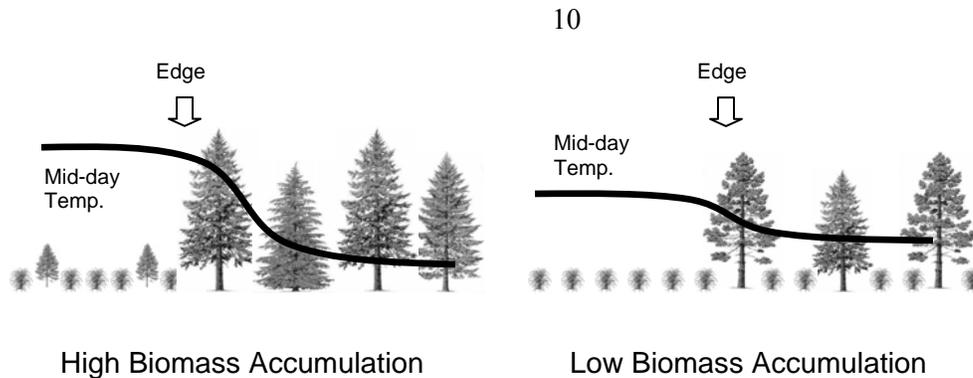
Figure 2.1 Theoretical representation of environmental gradients between early-seral and later-seral habitats at a productive site and a less productive site. Figure adapted from Hansen and Rotella (2000).

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).

The sharpness or steepness of the microclimate's gradient between early and late-seral forests should accentuate organism response to the amount of edge or interior habitats across the landscape. Forest edge and interior specialists should be more influenced by changes in the amount of forest edge and interior in highly productive environments. In contrast, where productivity and biomass accumulation are low, the influence of forest edge should be less strong. Thus, we propose that the influence of landscape effects such as the density of forest edge will vary across regions varying in

productivity. In this paper we assess the extent to which edge density (m/ha) influence bird abundance and species diversity at the stand level, and, test whether bird response to landscape effects is determined by productivity levels of different habitats and the nature of environmental gradients between them. 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 and 3 km radius).

2. Test the hypothesis that landscape effects are 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 from 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 east of Eugene, Oregon, in the western foothills of the Oregon Cascades (Figure 2.2). 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. Productivity, represented by modeled values of gross primary productivity (GPP) ($gCm^{-2}day^{-1}$) range from 1.29 to 1.85 with a mean of 1.42 and a standard deviation of 0.11. Douglas-fir (*Pseudotsuga menziesii*) is the dominant conifer across the region. However, hardwood species become more abundant at the southern end of the study site (e.g. oak (*Quercus spp.*), chinquapin (*Castanopsis chrysophylla*) and Pacific madrone (*Arbutus menziesii*)). Land ownership is a checkerboard of Bureau of Land Management (BLM) and private lands bordered by the Willamette National Forest and the H.J. Andrews Experimental Forest. As a result of this ownership pattern, more than a third of the landscape is composed of older forests (>100 yrs) on public lands, whereas the remaining private lands are short rotation (<60 yrs) plantations of Douglas-fir (Ripple et. al. 1991).

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 2.2). 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 in areas receiving > 200 cm of precipitation per year near the crest of the Cascades, to open ponderosa pine (*Pinus ponderosa*) forests in areas receiving 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. Gross primary productivity ($gCm^{-2}day^{-1}$) estimates range from 0.56 to 1.09 with a mean of 0.92 and a standard deviation of 0.12. Landscape pattern varies greatly with large wilderness and roadless areas bordering more intensively managed forests at the north and south end of the study area. Similar to the Springfield landscape, public lands comprise approximately a third of forested lands and are primarily occupied by older forests (>100 yrs), while the remaining private lands are mostly composed of younger (<60 yrs), managed forests.
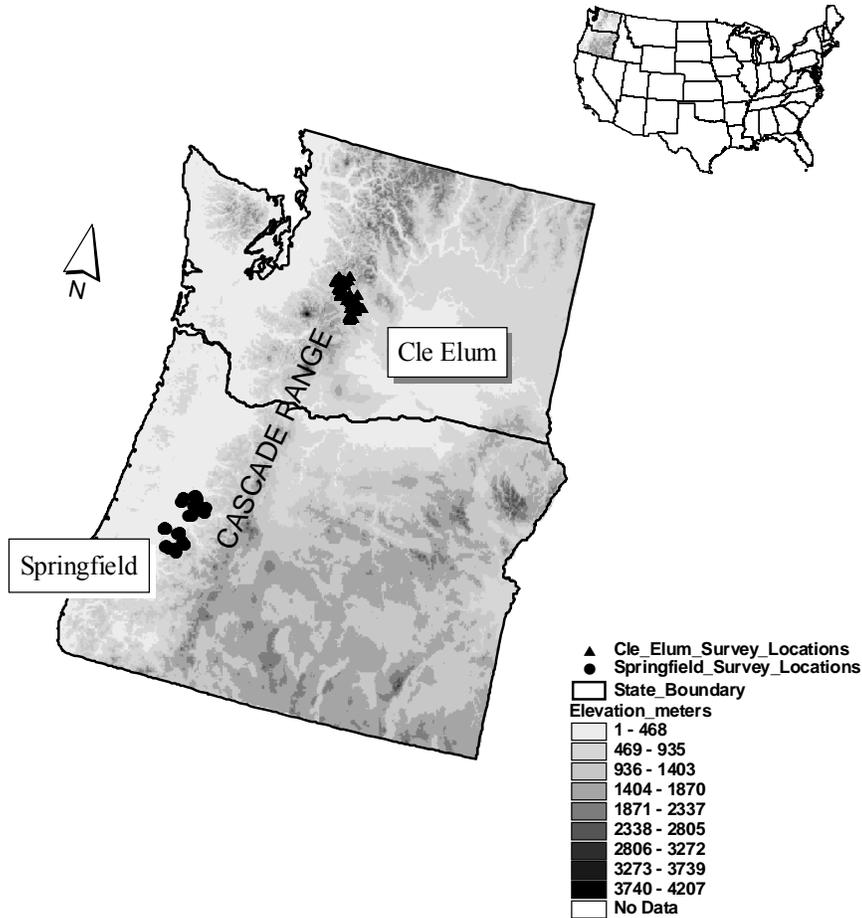
Figure 2.2 Location of two study landscapes, Springfield, Oregon and Cle Elum, Washington.

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 as a metric of

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 fine-scale analyses. The stratification of samples based on seral-stage categories was 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. This stratification led to four seral-stage categories that were equally represented across the two landscapes: scrub-shrub, small-tree, large-tree and old-growth. To represent a gradient of gross primary productivity, 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 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.

<u>Bird Sampling</u>

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). 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. 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. 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. Partners in Flight (PIF) bird species of regional concern for the

Northern Pacific Rainforest Bird Conservation Region are identified in the results

(Panjabi et al. 2005).

Landscape Pattern Mapping

To derive landscape-level predictor data to test our hypotheses, we used aerial

photographs to map different patch types around each of the stands sampled for birds.

We delineated two fundamental patch types, early-seral (open-canopy patch types) and

mid/late-seral (closed-canopy patch types), based on the following criteria: 1) tree size

class, stand age and understory conditions (i.e. relative dominance of shrubs, forbs and

young seedlings vs. pole, saw-timber and dominant canopy trees); and, 2) the percent

canopy cover of dominant canopy trees. The open-canopy patch type consisted of very

young forest stands (mean dbh = 8 cm) dominated by shrub communities and seedlings

of small stature and low percentages of overstory canopy cover (mean canopy cover =

11%). The closed-canopy forest patches consisted of 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%).

Minimum patch size for mapping was 1 ha and > 50 m wide in the narrowest

dimension. This area corresponds to roughly the smallest estimated home range of bird

species found in the study area (Brown 1985). The minimum width was chosen to avoid

delineating narrow patches that might skew quantification of landscape patch pattern with

small narrow patches that are likely less important biologically to birds. We obtained

forest patch attribute information from digital layers of stand age, canopy dominant,

ownership and management history and validated information with field visits. Using

Weyerhaeuser and U.S. Geological Survey (USGS) digital orthophotos, we digitized

forest patches manually and used field information to validate forest patch attribute

information. Digital polygon maps of forest patches at two scales (1 km and 3 km radius

surrounding survey stands) were then 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 1km and 3km radius surrounding survey stands. Previous studies have

found effects at comparable scales (McGarigal et al. 2001, McGarigal and McComb

1995). Areas much smaller than a 1 km radius approach the size of forest stands that we

consider to represent more local effects.

<u>Landscape Predictor Data</u>

The density of edges between open and closed-canopy forest patches was quantified using FRAGSTATS software (McGarigal and Marks 1995). Values representing the density of linear forest edge across the landscape (edge density, m/ha) ranged from 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 (the area of the stand within 100m of any edge) within a patch where a survey took place.

To obtain rates of biomass accumulation for our survey sites, we used remotely derived estimates (MODIS satellite) of gross primary productivity ($gCm^{-2}day^{-1}$). Remotely derived estimates of GPP allowed us to derive predictor data at large scales and best represented productivity across our survey network for several reasons. A comparison of net primary productivity (NPP) and GPP as predictors of regional and continental-scale bird richness showed that GPP was a much stronger predictor of bird richness than NPP (Phillips et al. 2007). NPP more directly represents the amount of carbon (i.e. vegetative biomass) available for organism use by accounting for carbon lost through respiration yet requires many more parameter estimates in its calculation (Heinsch et al. 2003). MODIS GPP was shown to have an accuracy of 74% in predicting flux tower measurements of GPP in the PNW (Heinsch et al. 2006), whereas there is no comparable validation data available with which to assess the predictive accuracy of NPP for our study area. Because GPP shows a strong correlation with regional-scale bird richness, requires few parameter estimates, and performs well in predicting flux tower

measurements of GPP, we used MODIS derived estimates of GPP to represent

productivity.

<u>Statistical Analysis</u>

  <u>Response to Edge Density--Species Level:</u> To test whether bird abundance was

correlated to landscape-level edge density, we used linear regression. Examining

diagnostic plots, we determined that a natural log transformation of bird species

abundance data adequately met normality and constant variance assumptions necessary

for linear regression analyses. However, because we were analyzing count data, we also

considered Poisson and negative binomial distributions to assess the relationship between

edge density and bird abundance. 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 closed or open-canopy forest stands we quantified the relationship

between abundance and edge density only in stands where a species occurred. For

generalist species that occurred in early, mid and later-seral stands equally, we used data

from all stands.

Linear Regression Model:

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

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

Generalized Linear Model:

Equation 1.2 $y = \beta_0 + \beta_1(X_1)$ *family = Poisson*

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

Response to Edge Density--Community Level: To compare community-level

response to landscape patterning at different scales we used dissimilarity matrices and

Non-metric Multidimensional Scaling (NMDS) (Bray and Curtis 1957, 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 1 km and 3

km landscape scales (R Development Core Team 2006). A goodness-of-fit (GOF)

statistic ranging from 0-1 was derived for each metric by calculating 1,000 permutations

of the maximum correlation between NMDS ordination scores and edge density

(Oksanen 2006).

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 allowed us to determine whether the samples of resulting P-values for each landscape was 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 varied across two landscapes with different productivity levels. Data from the Cle Elum site only was used 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 used this approach to determine whether the interaction between edge density and productivity was significant both across and within sites.

We used MODIS derived estimates of GPP ($gCm^{-2}day^{-1}$) to represent productivity. The following equation represents the general form of the interaction tested for species at each site.

Equation 1.5 $\quad y = \beta_0 + \beta_1(X_1) + \beta_2(X_2) + \beta_3(X_1 * X_2)$

Where: $y = \beta_0 + \beta_1(edge\_density_1) + \beta_2(GPP_2) + \beta_3(edge\_density_1 * GPP_2)$

We quantified the number of species where the interaction between edge density and GPP was significant ($P<0.05$). For species where the interaction term was significant, we then plotted fitted values at three different levels of productivity to examine changes in the slope of species response to changes in edge density.

Ecosystem Productivity Effects--Community Level: To evaluate bird community similarity at sites surrounded by low edge density and high edge density, we calculated a dissimilarity matrix (Bray-Curtis measure) based on species abundance within a survey stand (Bray and Curtis 1957). We then used NMDS to plot an ordination based on the Bray-Curtis measure. After plotting NMDS ordinations of survey stands surrounded by low and high edge density, we calculated a within cluster (all bird assemblages within survey stands surrounded by low edge density and then by high edge density separately) to between cluster (bird assemblages within the low edge density stand cluster versus bird assemblages within the high edge density stand cluster) ratio to determine whether bird assemblages surrounded by low and high levels of edge density were distinctly different from each other (functions *permtest* and *partana* developed by Roberts 2006). We performed 1,000 permutations of this calculation to derive a P-value associated with the test that the within-cluster to between-cluster ratio is > 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 Productivity Characteristics

Open-canopy stands were surrounded by landscapes with slightly higher edge

densities than closed-canopy stands for both Springfield and Cle Elum (Figure 2.3). In

Springfield, the mean edge density surrounding open-canopy stands (25 m/ha) was higher

than closed-canopy stands (21 m/ha) (Figure 2.3). 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) (Figure 2.3). These results show that some covariation occurred

between the canopy category (open or closed) of the survey stand and edge density in the

surrounding landscape at both sites.
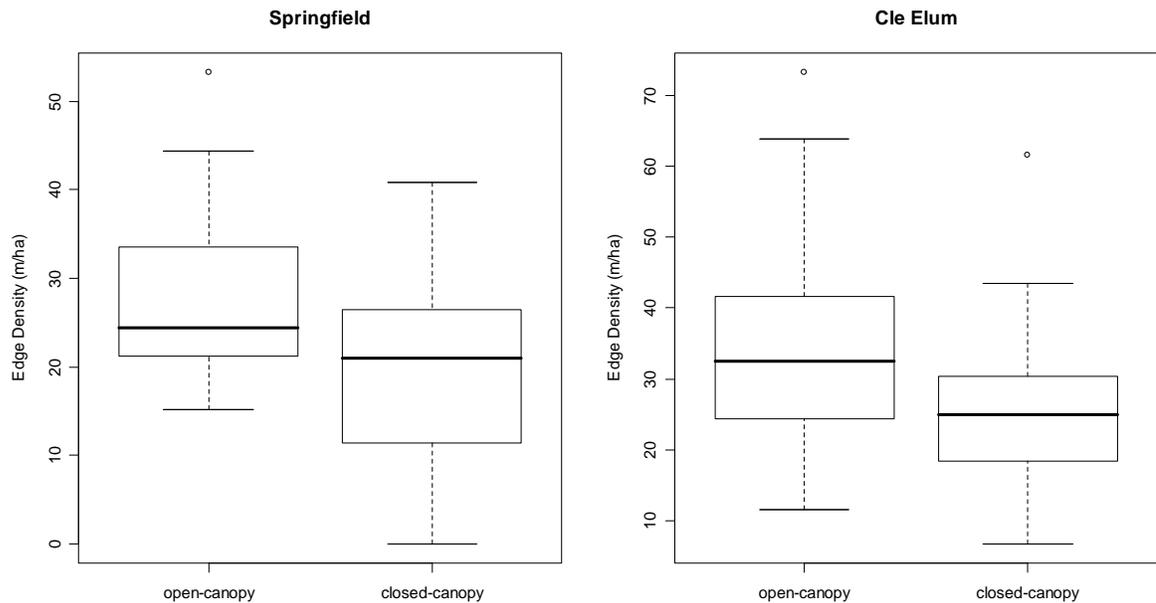
Figure 2.3 Boxplots of landscape-level edge density (m/ha) data for open and closed-canopy stands for Springfield and Cle Elum (1 km radius).

The range of estimated GPP values for the Springfield and Cle Elum landscapes shows little overlap and span more productive landscapes within North America (Figure 2.4). At the Springfield landscape, GPP values ($gCm^{-2}day^{-1}$) ranged 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 ranged 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 represented a significant portion of the gradient of possible values of GPP for all of North America (Figure 3.4), and encompassed almost the entire range of GPP values in forested ecosystems in North America (GPP values > 0.2).
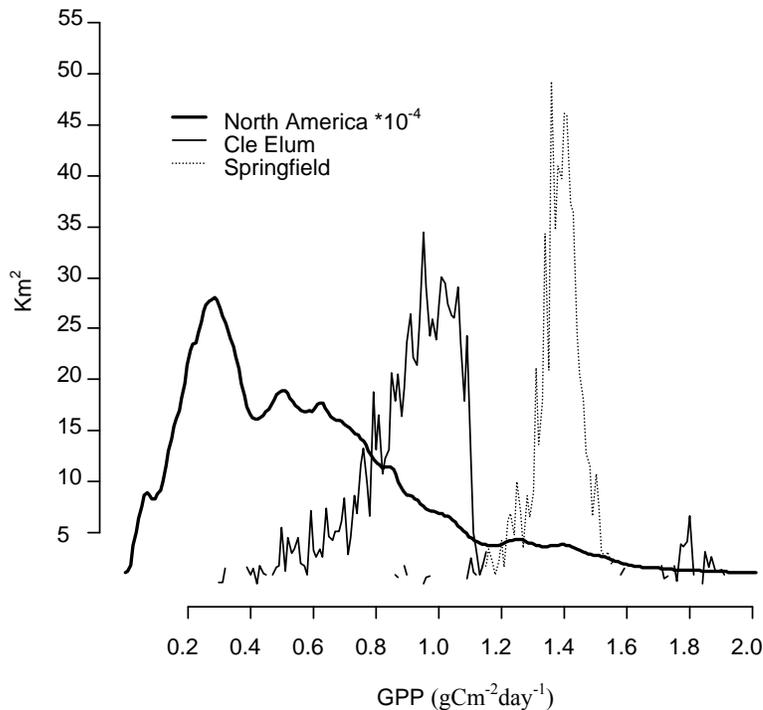
Figure 2.4 Area (km^2) of land representing GPP values for North America, and 3 km radius landscapes surrounding the Springfield and Cle Elum survey sites.

Bird Response to Gradients in Edge Density

Individual Species: We found evidence that a number of birds species respond to edge density at a 1 km scale. At the more productive site, Springfield, 25 of 60 species (42%) responded significantly to changes in edge density (Table 2.1), compared to the less productive site, Cle Elum, where 4 of 60 species (7%) responded significantly to changes in edge density (Table 2.2). 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 = 4, mean 0.21, SD 0.13).

The slope of response to changes in edge density followed predictable patterns for bird canopy guilds at both sites (Tables 2.1-2.2). Open-canopy associated species and most generalist species responded positively to increases in edge density whereas closed-canopy associated species responded negatively to increases in edge density (Tables 2.1-2.2, Figure 2.5). Of the 25 species that responded significantly (P<0.05) to changes in edge density in Springfield, the relationship was positive for 15 species (13 open-canopy associates and 2 of 4 generalists) and negative for 10 species (7 closed-canopy associates and 2 generalists). All 4 species that responded significantly (P<0.05) to changes in edge density in Cle Elum were closed-canopy associated species and responded negatively to increases in edge density. Edge density was a stronger predictor at the 1 km scale than at the 3 km scale for all analyses (data not shown).
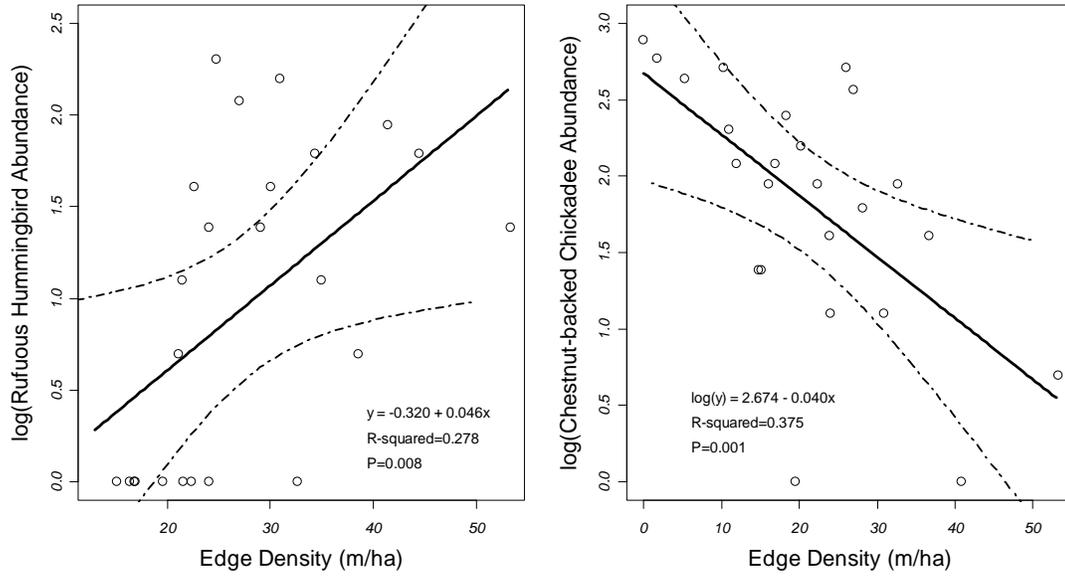
Figure 2.5 Rufuous hummingbird and chestnut-backed chickadee abundance (log transformed) as a function of landscape-level edge density (1 km scale). Fitted regression with 95% confidence intervals shown. Data shown is from the Springfield landscape.

Table 2.1 Species responding significantly to edge density (m/ha) at the Springfield site (1 km scale). Guild designations based on literature review.
* = species with significant difference in abundance (P<0.05) between open and closed canopy stands; OG = species with significantly higher abundance (P<0.05) in old growth stands (average d.b.h.> 53 cm); PIF = Partners In Flight Birds of Regional Concern (Panjabi et al. 2005).

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

Table 2.2 Species responding significantly to edge density (m/ha) at the Cle Elum site (1 km scale). Guild designations based on literature review.
* = species with significant difference in abundance (P<0.05) between open and closed canopy stands; OG = species with significantly higher abundance (P<0.05) in old growth stands (average d.b.h.> 53 cm); PIF = Partners In Flight Birds of Regional Concern (Panjabi et al. 2005).

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

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 stands at the 1 km scale compared to 21% at the 3 km scale (GOF from 1,000 permutations of the maximum correlation between NMDS ordination scores and edge density). Conversely, in Cle Elum, edge density was not a significant predictor of bird community composition and abundance at either the 1 km or 3 km scale. The amount of core area within each 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.

Ecosystem Productivity Effects

Individual Species: We found evidence that bird response to changes in edge density was more pronounced at the productive site, Springfield (Tables 2.1-2.2, Figure 2.6). A Z-test of proportional difference suggests that the proportion of birds responding 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 2.6).
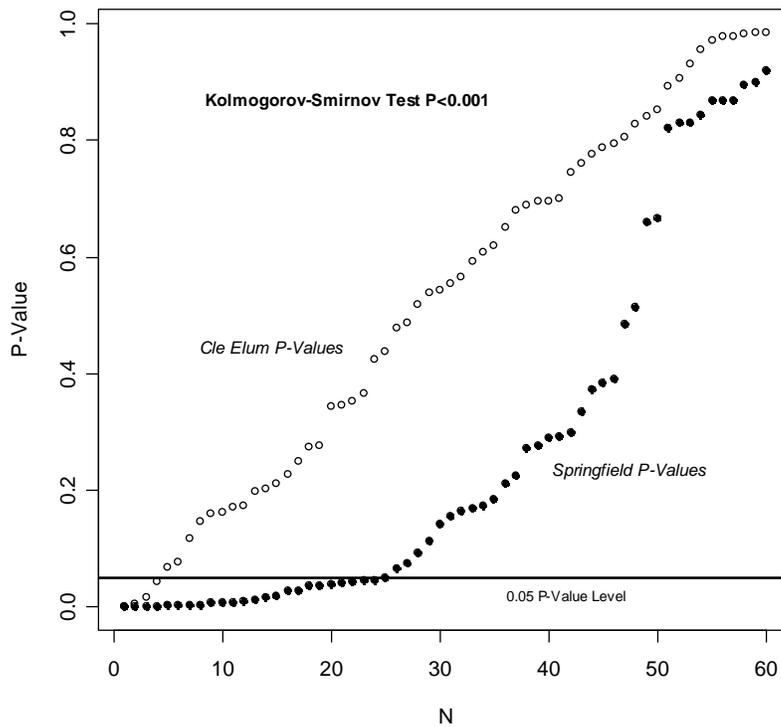
Figure 2.6 Plot of sorted P-values from models examining the relationship between changes in edge density and bird abundance for the 60 most abundant species at each site. Closed circles represent P-values for Springfield bird species and open circles represent P-values for Cle Elum bird species. A Kolmogorov-Smirnov test indicates that the two samples are significantly different. Solid black horizontal line indicates an alpha level of 0.05.

Individual Species--Edge Density/Productivity Interaction: With pooled data from

both landscapes, individual bird species responded differently to edge density as a

function of productivity (Tables 2.3-2.4, Figure 2.7). The slope of the response to edge

density changed as a function of productivity (GPP) for 25 of 60 species. To determine

whether site level factors might confound the interaction between landscape-level edge

density and productivity, we also tested for an interaction with Cle Elum data only and

found similar results (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 was most pronounced at high levels of productivity (Table 2.4, Figure 2.7). Only a few species responded more acutely to changes in edge density at lower levels of productivity (Table 2.4). 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 2.4).
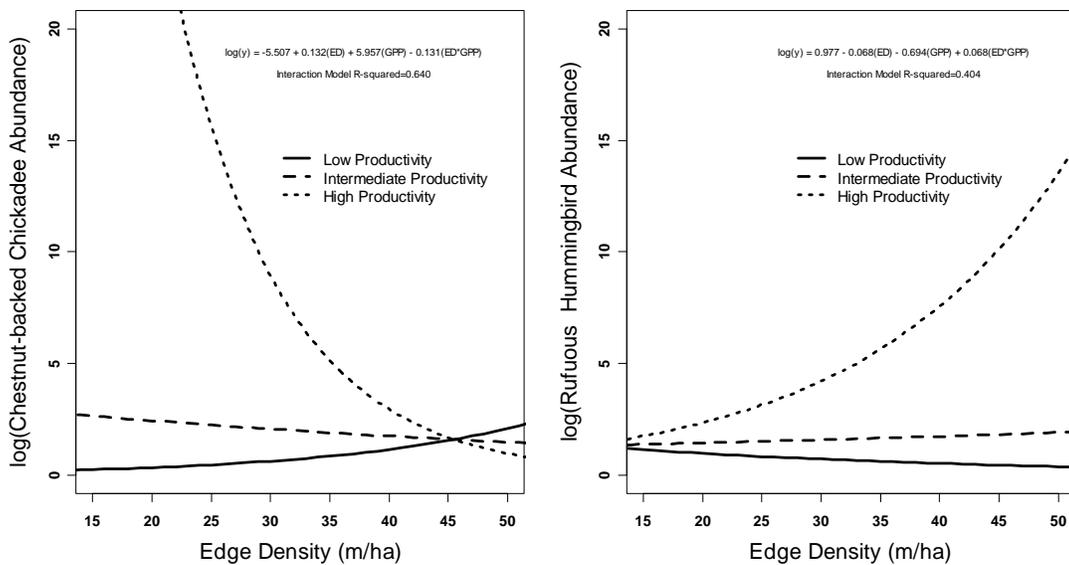
Figure 2.7 Fitted models representing the relationship between chestnut-backed chickadee and rufuous hummingbird abundance (log transformed) and increasing edge density (m/ha) at low, intermediate and high levels of productivity (GPP, $gCm^{-2}day^{-1}$).

Table 2.3 Species responding significantly to edge density (ED, m/ha) and the interaction between edge density and GPP ($gCm^{-2}day^{-1}$). Data is combined for both landscapes. * = species with significant difference in abundance ($P<0.05$) between open and closed canopy stands; OG = species with significantly higher abundance ($P<0.05$) in old growth stands (average d.b.h.> 53 cm); PIF = Partners In Flight Birds of Regional Concern (Panjabi et al. 2005).

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

Table 2.4 Species response (abundance) to edge density (m/ha) at low, intermediate and high levels of productivity (GPP, $(gCm^{-2}day^{-1})$. Plus symbols indicate a positive relationship with increasing edge density and minus symbols represent a negative relationship with edge density. The number of symbols (plus or minus) represents the steepness of the slope of the relationship between abundance and increasing edge density. * = species with significant difference in abundance ($P<0.05$) between open and closed canopy stands; OG = species with significantly higher abundance ($P<0.05$) in old growth stands (average d.b.h.> 53 cm).

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

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 2.8.). 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 2.8).

Springfield   **Cle Elum**
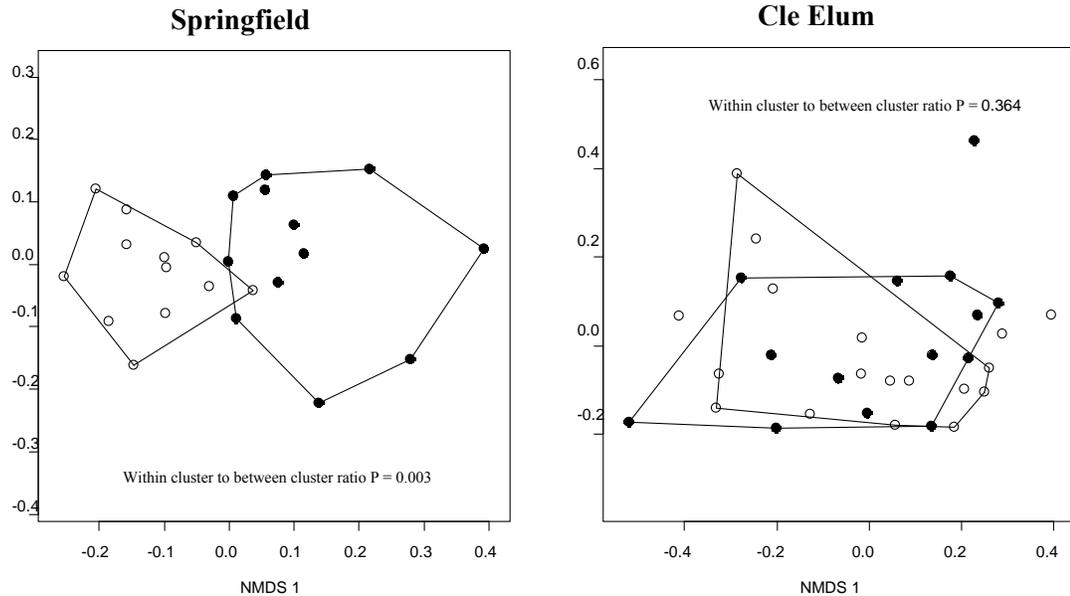
Figure 2.8 NMDS ordination of closed-canopy bird community similarity by site. Open circles represent forest survey stands surrounded by landscapes (1 km radius) with low edge density (m/ha). Closed circles represent survey stands surrounded by landscapes with high edge density.

Discussion

Bird Response to Gradients in Edge Density

The literature examining organism response to landscape effects is extensive

(Fahrig 2003, Parker et al. 2005, Murcia 1995, Harper et al. 2005, Noss et al. 2005), yet

few studies have attempted to test the extent to which spatial patterning of habitat

influences organism diversity and abundance within the 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 edge density. 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 was more pronounced at a 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 but one open-canopy associate and most generalists responded positively to increases in edge density, whereas closed-canopy associates responded negatively to increases in edge density. In addition, the size of stands where birds were surveyed influenced 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 the influence of population processes operating at these larger scales.

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). Changes in the area and configuration of forested habitats across the landscape have been shown to influence rates of nest predation, brood parasitism, and immigration and emigration all factors which may influence bird abundance and diversity. 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, Tewksbury 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 and 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).

Bird Response to Edge Density 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.

Scale Effects

We found that for all analyses, birds respond more acutely to landscape effects at

a 1 km radius scale than at larger scales. While the influence of landscape affects has

been shown to occur at scales > 1 km (Mitchell et al. 2006, Lloyd et al. 2005, Trzcinski et

al. 1999), we would expect that more local-scale effects would have a greater influence

on breeding birds with territories typically extending much less than a kilometer radius

surrounding nest sites (Poole 2007). Resource availability, density of viable mates and

habitat structure influence 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 and Urban 1992, 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.

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. Productive west-side Douglas-fir forests show more even distribution of vegetative layering from canopy to forest floor than occurs in ponderosa pine forests (Lefsky et al. 2002). The resulting gradient in environmental conditions between edge and interior likely varies as a result of these differences in biomass distribution and layering. 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 as compared with 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, because abiotic conditions influence the distribution of these canopy dominants, birds are responding to conditions associated with both site productivity and the distribution of different canopy dominants associated with site productivity.

Additionally, while our results generally support the hypothesis that bird diversity and abundance within a stand are influenced by landscape effects, some of the characteristics unique to these sites limit broad application without further research 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 North America. Rapid 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

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). 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 a range of forest characteristics. Thirteen bird species associated with open-canopy stands responded positively to increases in edge density (Table 2.1), four of which are Partners In Flight species of regional concern exhibiting significant negative trends in abundance from 1966-2003 (Sauer et al. 2005). Hence, the maintenance of open-canopy patches within productive environments seems particularly important in supporting open-canopy associates, especially those experiencing population declines over the past four decades.

Alternatively, a number of bird species associated with closed-canopy and old-growth forests respond negatively to higher edge density (Table 2.1) and have been shown to depend on structural conditions only found in older forests (i.e. presence of abundant legacy snags, coarse woody debris, broken tops, and large mature trees) (Franklin et al. 2002). 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 in productive settings. 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 harvest occurs and maintains structural complexity whenever possible.

Conclusions

Our results reinforce the idea 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. We expect that the high rate of biomass accumulation occurring in the productive forests west of the Cascade crest influences these processes more acutely, because the contrast between edge and interior environments is high compared to that of less productive east-side Cascade forests. Conversely, bird response to changes in edge density is less pronounced where biomass accumulation is low and the contrast between edge and interior environments is less acute. 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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CHAPTER 3

BIRD RESPONSE TO DISTURBANCE VARIES WITH FOREST PRODUCTIVITY

IN THE PACIFIC NORTHWEST

Abstract

Management of vertebrate diversity in forests of the Pacific Northwest (PNW) 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 this is 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 extent 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. Using linear regression, we found that bird richness increased with increasing levels of disturbance extent within highly productive west-side Cascade forests ($R^2 = 0.16$, $P = 0.005$), whereas bird richness decreased with increasing disturbance extent (quadratic relationship) within less 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 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 (Connell 1978, 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 management tool, can be applied similarly across different biophysical locales. Although 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 productivity that influence species growth rates and recovery following disturbance (Bakker et al. 2006, Osem et al. 2002, Sarr et al. 2005, Huston 1994). The premise of this idea is that competitive exclusion is greater in productive environments, leading to increased dominance and decreased diversity. We define productivity as the rate at which vegetative biomass accumulates at a given site and use remotely derived estimates of gross primary productivity (MODIS satellite) to represent vegetative biomass accumulation (Heinsch et al. 2003).

Understanding how vertebrate diversity might respond differently to disturbance across productivity levels is important for developing effective management strategies to maintain diversity in different biophysical settings. The primary purpose of this paper is to investigate how bird community response to timber harvest varies across productivity levels. We analyzed songbird response to forest harvest across broad gradients in productivity and consider how species diversity, community composition, and individual species targeted for conservation respond to different levels of landscape-level disturbance.

A number of different hypotheses offer to explain why productive conditions lead to increased competition and decreased species diversity. Most support the idea that competitive exclusion increases in productive environments, whether it is because of a total increase in competition for all resources, (Grime 1977), competition for light based on the scaling of the organism (Tilman and Pacala 1993, Newman 1973), or a change in population dynamics that lead to more rapid competitive exclusion (Huston 1979). Timber harvest influences resource availability in a number of ways that can break competitive dominance that is often observed in productive forests (Rajaniemi 2003, Wohlgemuth et al. 2002). First, it can free resources from living organisms through mortality and decomposition, allowing more resources for surviving organisms. Second, harvest removes dominant canopy tree species, reducing competition on other plants, allowing increased understory 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 Huston (1979) argues 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 (Wohlgemuth et al. 2002, Figure 3.1).

Alternatively, recovery following disturbance events occurring in harsh environments is predicted to be slow and more variable as productivity 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.
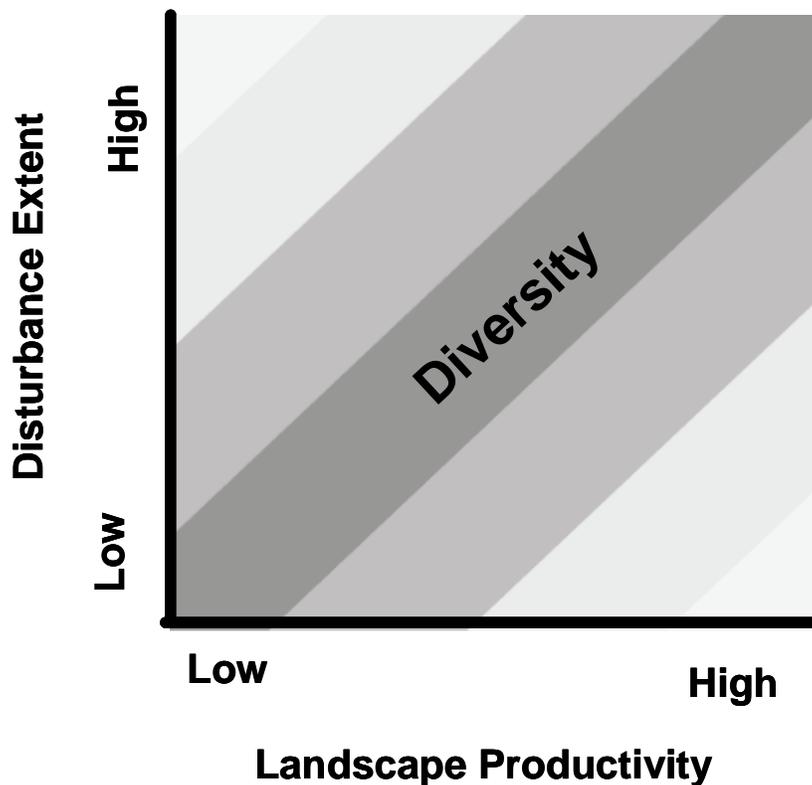
Figure 3.1 Theoretical representation of the predictions of the Dynamic Equilibrium Model (Huston 1979, 1994) for species diversity in relation to productivity and mortality-causing disturbance. High diversity is represented by darker shading with the highest diversity along the diagonal. Figure adapted from Huston (1994).

Previous research supports the idea that disturbance may act to reduce competitive exclusion, increasing high local diversity (Prouxl and Mazumder 1998, Petraitis et al. 1989, Davis et al. 1988, Connell 1978, Sousa 1979). Likewise, numerous studies corroborate conceptual models suggesting that productivity 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 (1979, 1994) prediction that species response to disturbance varies across productivity levels. However, few studies test the DEM 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 that plant communities responded to disturbance (mowing) differently within plots receiving varying levels of fertilizer. More recently, the DEM has been supported for plants (Bakker et al. 2006, Osem et al. 2002, Sarr et al. 2005, Prouxl and Mazumder 1998), marine microalgal communities (Worm et al. 2002), primary producers in stream communities (Cardinale et al. 2006), and marine benthic infaunal systems (Widdicombe 2001). We know of no studies testing Huston's DEM for organisms at higher trophic levels such as birds.

Bird diversity is expected to follow this model, because at highly productive sites, increased disturbance would reduce competitive exclusion by dominant plants, increasing habitat heterogeneity and food and habitat resources for birds (Figure 3.2). This would be especially true in west-side Cascade forests where canopy closure limits light

availability in undisturbed forests and where light availability in recently disturbed

forests results in rapid and diverse understory growth (Verschuyl et al. 2007). In

landscapes with harsh biophysical conditions, recovery from disturbance is slow, and,

consequently, we expect habitat heterogeneity, plant diversity and associated bird

diversity to decrease with increasing levels of disturbance.
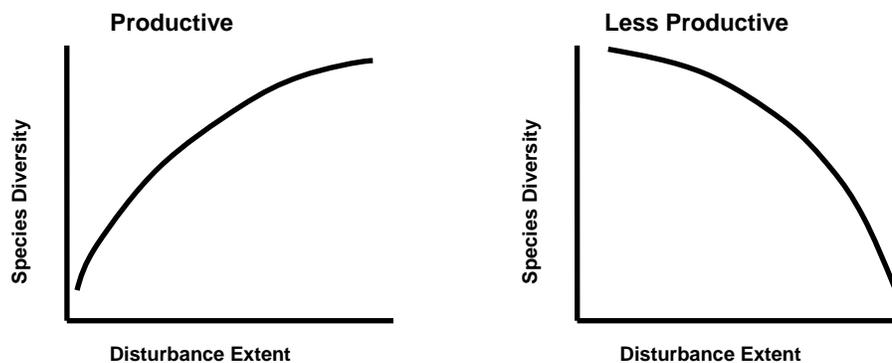
Figure 3.2 Predicted relationship between disturbance extent and species diversity at a
productive and less productive site. Figure adapted from Huston (1994).

In this study we tested the DEH for bird diversity in two forested landscapes with

different levels of 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 open-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 PNW, an area with a wet temperate rainforest climate and some of

the highest levels of forest productivity in North America (Heinsch et al. 2003). 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 extent in the surrounding landscape within landscapes varying in productivity? The specific predictions we examined were:

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

The ideas 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 in managed ecosystems. 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 (Panjabi et al. 2005).

Methods

<u>Study Area:</u>

    <u>Springfield, OR</u>*:* Weyerhaeuser's Springfield and Cottage Grove tree farms and surrounding BLM and USFS lands are located east of Eugene, Oregon, in the western foothills of the Oregon Cascades (Figure 3.3). 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. Productivity, represented by modeled values of gross primary productivity (GPP) (gCm^2day^{-1}) range from 1.29 to 1.85 with a mean of 1.42 and a standard deviation of 0.11. Due to little variation in mean temperature and precipitation across the study area, Douglas-fir (*Pseudotsuga menziesii*) is the dominant conifer across the region. However, hardwood species become more abundant at the southern end of the study site (e.g. oak (*Quercus spp.*), chinquapin (*Castanopsis chrysophylla*) and Pacific madrone (*Arbutus menziesii*)). Land ownership is a checkerboard of Bureau of Land Management (BLM) and private lands bordered by the Willamette National Forest and the H.J. Andrews Experimental Forest. As a result of this ownership pattern, more than a third of the landscape is composed of older forests (>100 yrs) on public lands, whereas the remaining private lands are short rotation (<60 yrs) plantations of Douglas-fir (Ripple et. al. 1991).

    <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 3.3). 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 in areas receiving > 200 cm of precipitation per year near the crest of the

Cascades, to open ponderosa pine (*Pinus ponderosa*) forests in areas receiving 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. Gross

primary productivity estimates (gCm^2day^{-1}) range from 0.56 to 1.09 with a mean of 0.92

and a standard deviation of 0.12. Landscape pattern varies greatly with large wilderness

and roadless areas bordering more intensively managed forests at the north and south end

of the study area. Similar to the Springfield landscape, public lands comprise

approximately a third of forested lands and are primarily occupied by older forests (>100

yrs), while the remaining private lands are mostly composed of younger (<60 yrs),

managed forests.
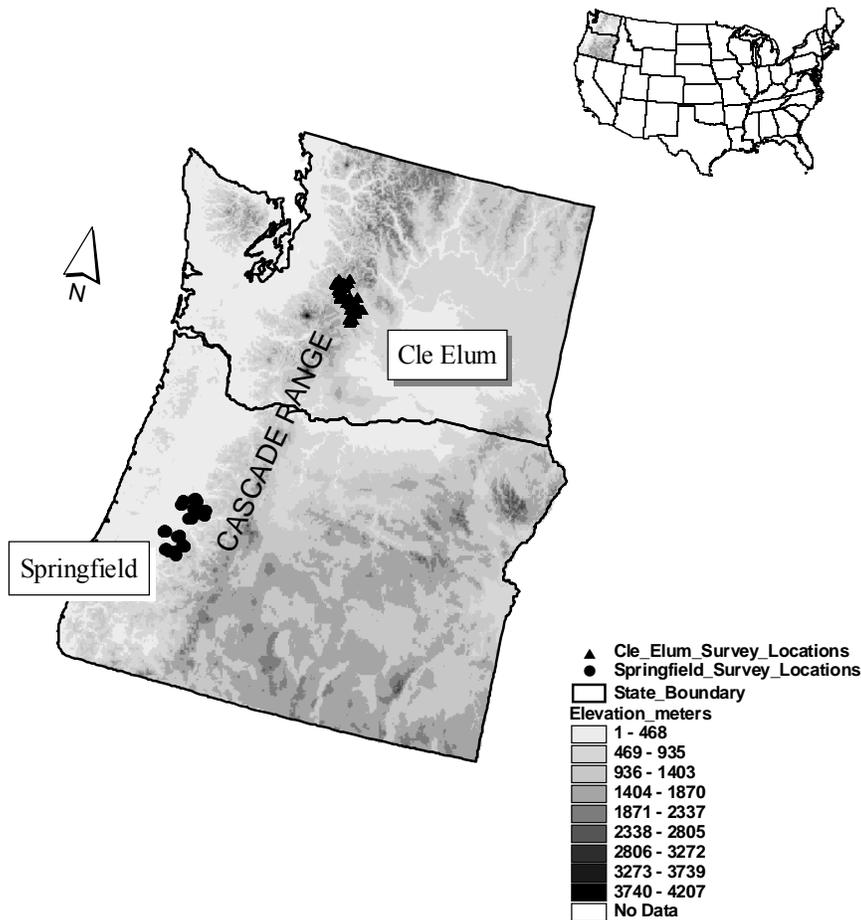
Figure 3.3 Location of two study sites, Springfield, Oregon and Cle Elum, Washington.

<u>Study Design</u>

Our approach was to first quantify bird community composition and individual

species abundances in the two study areas. 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 regressed against the proportion

of the surrounding landscape recently disturbed by even-aged timber harvest. We then

compared the slopes of these relationships between the high and lower productivity areas

within the context of Huston's DEM. Our data were derived from a study of how bird

diversity in large stands is influenced by surrounding landscape pattern (Chapter 2). In

that study we found that bird species abundances and community richness were

influenced by the amount of edge between early and later-seral forest stands in the

surrounding landscape. These landscape affects 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 predictions of the

DEM because stand richness partially reflects spatial patterning of suitable habitat in the

surrounding landscape and partially the affect of disturbance extent within landscapes

varying in productivity.

     Landscape Pattern Mapping: Our goal was to map the proportion of the landscape

in the early stages of recovering from even-aged timber harvest. 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 consist of 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 consist of 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%).

Minimum patch size for mapping was > 50 m wide in the narrowest dimension, and > 1 ha in area. This area roughly corresponds to the smallest estimated home range 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 to birds. We obtained forest patch attribute information from digital layers of stand age, canopy dominant, ownership, and management history and validated the information with field visits. Using Weyerhaeuser and USGS digital orthophotos, we digitized forest patches manually and used field information to validate forest patch attribute information.

Bird Sampling: Survey stands 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. 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 estimated 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. Species richness was first calculated as the cumulative number of birds seen at each survey point

over the 2 breeding season visits. A stand-level species richness response variable was then created by averaging the 5 point richness values and 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 listed as Partners in Flight (PIF) 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 disturbed by harvest (in recent years) was calculated using FRAGSTATS software (McGarigal and Marks 1995). Harvests consisted of even-aged cuts (mean harvest size = 27 ha) with small numbers of trees retained for riparian buffers and wildlife purposes. The proportion of recently disturbed forest was calculated within a 1 km radius surrounding survey stands. The percent of the landscape occupied by recently disturbed forest ranged from 0 to 45% in Springfield and 0 to 65% in Cle Elum.

Site Productivity: To obtain rates of biomass accumulation for our survey sites, we used remotely derived estimates (MODIS satellite) of gross primary productivity ($gCm^{-2}day^{-1}$). Remotely derived estimates of GPP allowed us to derive predictor data at large scales and best represented productivity across our survey network for several reasons. A comparison of net primary productivity (NPP) and GPP as predictors of regional and continental-scale bird richness showed that GPP was a much stronger predictor of bird richness than NPP (Phillips et al. 2007). NPP more directly represents the amount of carbon (i.e. vegetative biomass) available for organism use by accounting

for carbon lost through respiration yet requires many more parameter estimates in its

calculation (Heinsch et al. 2003). MODIS GPP was shown to have an accuracy of 74%

in predicting flux tower measurements of GPP in the PNW (Heinsch et al. 2006), whereas

there is no comparable validation data available with which to assess the predictive

accuracy of NPP for our study area. Because GPP shows a strong correlation with

regional-scale bird richness, requires few parameter estimates, and performs well in

predicting flux tower measurements of GPP, we used MODIS derived estimates of GPP

to represent productivity.

We assessed the extent to which each landscape represented gradients in

productivity by plotting the range of GPP values associated with each site (Figure 3.4).

There is little overlap in the range of estimated GPP values for each study site and both

study areas fell within the range of more productive landscapes within North America

generally (Figure 3.4). At the Springfield landscape, GPP estimates ($gCm^{-2}day^{-1}$) ranged

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 estimates ranged 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 3.4),

and encompassed almost the entire range of GPP values in forested ecosystems in North

America (GPP values > 0.2).
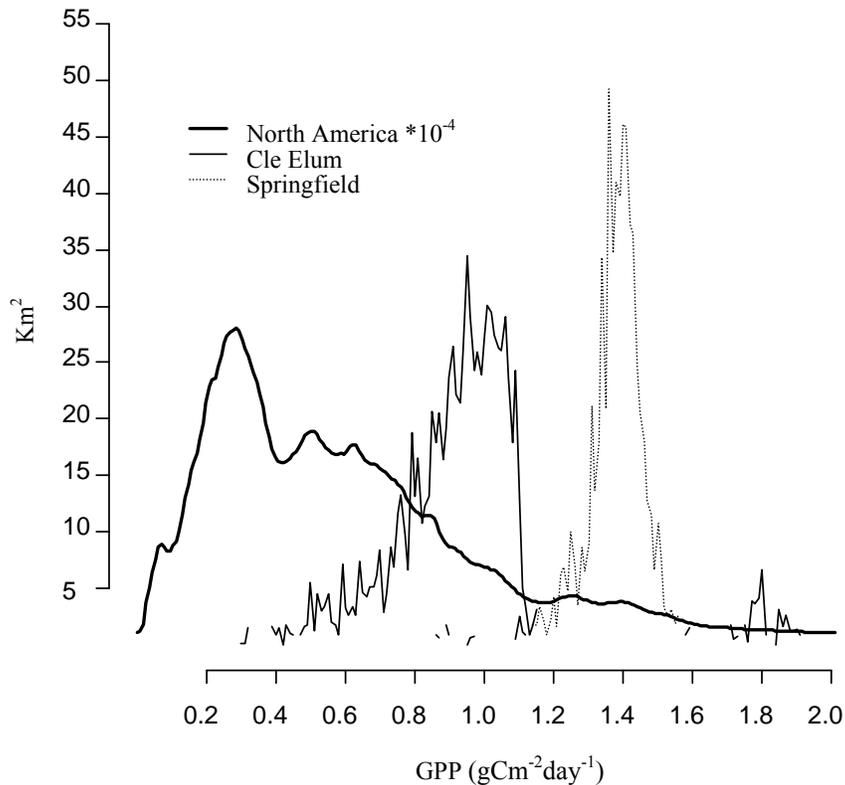
Figure 3.4 Area (km^2) of land representing GPP gradient (gCm^{-2}day^{-1}) for North America (*10^4), and 3 km radius landscapes surrounding the Cle Elum and Springfield survey sites.

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 5 points within a stand and across sampling years to obtain a cumulative value of bird richness for each survey season by stand. Therefore, bird richness was calculated as the mean of bird richness of each stand across sampling years.

We compared bird response to disturbance extent using linear regression. In separate analyses, we regressed bird richness and Partners In Flight (PIF) bird species of

regional concern richness on the proportion of recently disturbed forests at both sites. We fit both linear and quadratic models to determine the best functional relationship between species richness and diversity and landscape disturbance extent. 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 (timber harvest) was different at sites with high and low productivity. In Springfield, a productive site, bird richness decreased linearly as the percent of recently disturbed forest increased across a 1 km radius landscape surrounding surveyed stands (Figure 3.5). In Cle Elum, where productivity is generally low, bird richness exhibited a slightly "hump-shaped" unimodel relationship with increasing recently disturbed forest cover. Both models were statistically significant (Springfield $P = 0.005$, R-squared $= 0.159$, Cle Elum $P = 0.037$, R-squared $= 0.299$), explaining 16% percent of the variance in bird richness in Springfield and 30% of the variance in bird richness in Cle Elum.

Springfield

y = 11.160 + 0.072x
R-squared=0.159
P=0.005

Cle Elum

y = 9.588 + 0.054x - 0.002x^2
R-squared=0.299
P=0.037

Species Richness

% of Landscape in Recently Disturbed Forest
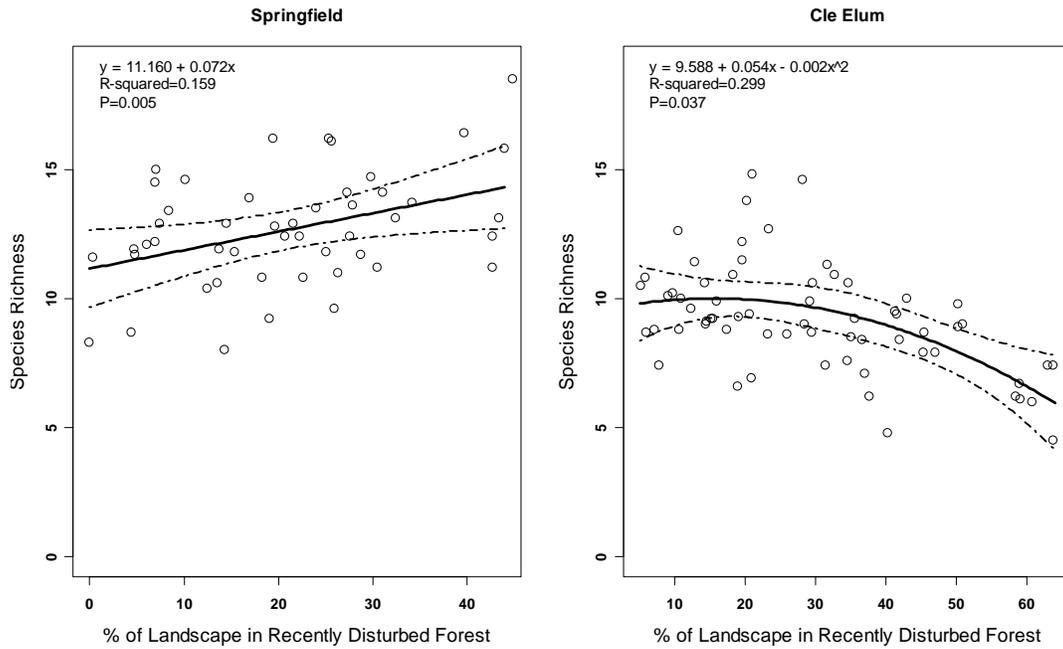
Figure 3.5 Bird richness within a sampled stand as a function of the percentage of the landscape (1 km radius surrounding survey stands) occupied by recently disturbed forest. Fitted regression and 95% confidence intervals shown.

Bird richness for Partners In Flight (PIF) birds of regional concern also decreased linearly as the percent of recently disturbed forest increased in Springfield (P = 0.087, R-squared = 0.062, Figure 3.6). At the Cle Elum site, birds of regional concern species richness exhibited a slightly "hump-shaped" unimodel increase with increasing disturbed forest (P = 0.011, R-squared = 0.216, Figure 3.6).

Springfield

y = 4.961 + 0.023x
R-squared=0.062
P=0.087

Cle Elum

y = 3.138 + 0.047x - 0.001x^2
R-squared=0.216
P=0.011
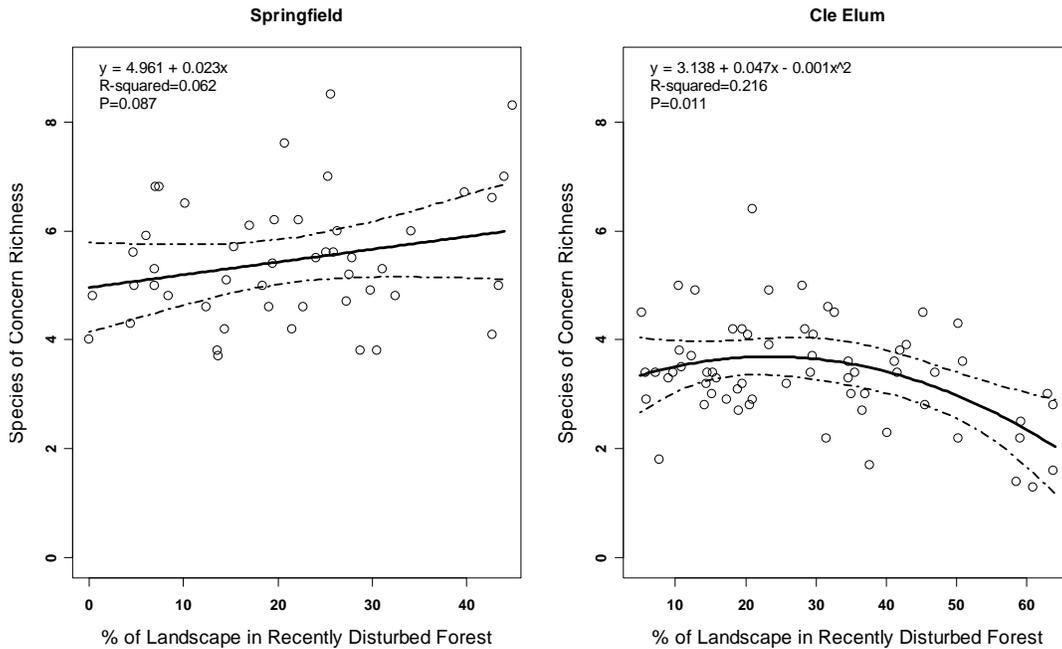
Figure 3.6 Sensitive species richness within a sampled stand as a function of increasing percentage of the landscape (1 km radius) occupied by recently disturbed forest. Fitted regression and 95% confidence intervals shown.

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 species richness increased as the extent of disturbance increased in a highly productive environment whereas species richness decreased with increasing disturbance extent in a less productive landscape. This comparison supports the idea that bird response to disturbance is moderated by 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 (1994) DEM, and suggests the model applies to organisms at higher trophic levels, which in the case of birds is expected to be strongly correlated with plant diversity.

We interpret our results to suggest that the relationship between competitive exclusion and productivity influences 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, 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 or removal of canopy trees makes light readily available for a rapid pulse of new vegetative growth (Wohlgemuth et al. 2002). Early-seral forests also experience rapid and intense colonization by forest songbirds where diverse shrub, grass and forb growth is apparent following disturbance.

A number of theories attempt to explain the decrease in species diversity in highly productive settings: decreased habitat heterogeneity (Tilman and Pacala 1993), limited light availability (Newman 1973), the amount of variation in the availability of resources over time and space (Rosenzweig 1995), competitive intensity and the rate at which competitive exclusion develops (Grime 1977, Huston 1979) are thought to explain why plant diversity decreases at the high levels of productivity. We think Huston (1979, 1994) provides the most likely explanation; the rate of growth within all populations

increases with increasing productivity, poor competitors are excluded faster in highly

productive environments. Hence, increasing levels of disturbance and subsequent

mortality in highly productive forested sites reduces strong competition for resources,

promoting rapid growth of colonizing species and increases in plant species diversity,

habitat heterogeneity and early-seral associated species abundances (Huston 1994). It

follows that this increase in plant diversity and habitat heterogeneity in younger forests

would lead to higher bird species diversity and abundances for those birds associated

with open-canopy forests.

Previous research testing Huston's hypothesis typically involved experimental

tests subjecting communities to different levels of disturbance. Our design samples birds

within forest stands and analyzes the effects of the proportion of the surrounding

landscape that was in open-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, associated

analyses (Chapter 2) found when controlling for seral stage, significant variation in

relative bird abundance and species richness was explained by the patterning of the

landscape within a 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 reasonably strong case for testing

predictions related to Huston's DEM. 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 where we found that shrub and tree diversity,

density and cover were higher in early-seral stands in the Springfield site than the Cle

Elum site (Appendix A). It is also important to emphasize that our study only examined

landscapes with < 65% of the landscape occupied by recently disturbed 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 between positive and negative slopes.

Management Implications

Our results suggest a framework for predicting how forest management will

influence bird diversity across different productivity settings. At highly productive sites

where competitive exclusion likely limits plant species diversity, we expect that, at

certain levels, 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 bird diversity and seems particularly important in

supporting open-canopy associates. Under these conditions, harvesting as a form of

disturbance could be used 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 more frequent disturbance regimes in highly productive systems.

This paper fundamentally deals with how bird diversity within forest stands is influenced by the extent of timber harvest in landscapes surrounding these stands. Species diversity is a useful metric for guiding conservation efforts, but alone, does not address objectives that are an important component of any conservation strategy (Groom et al. 2005). In addition to supporting overall species diversity, conservation efforts should also support less common species that occur in less diverse habitats and recognize the importance of maintaining ecosystem function (e.g. patterns of disturbance, nutrient flow). While bird diversity was higher in recently disturbed forest stands in a productive landscape, a number of bird species were significantly more abundant in later-seral forest stands (Table 3.1), some of which appear to rely on larger contiguous patches of later-seral forests.

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). Hence, an important caveat for productive settings where disturbance may play an important role in maintaining diversity is that a number of bird species associated with mid/late-seral forests rely on characteristics of older forests and sometimes require contiguous patches of undisturbed forests to persist and succeed.

Table 3.1 Bird guild associations and population trends during the period 1966-2005. Guild designations based on literature review. * = species with significant difference in abundance (P<0.05) between open and closed canopy stands; OG = species with significantly higher abundance (P<0.05) in old growth stands (average d.b.h.> 53 cm); PIF = Partners In Flight Birds of Regional Concern (Panjabi et al. 2005); BBS Trend = coefficient for trend in abundance models for the period 1966-2005, trends with P<0.01 highlighted in bold (Sauer et al. 2005).

Species Code	Guild	PIF	BBS Trend	P	Species Code	Guild	PIF	BBS Trend	P
AUWA	Closed*	-	**1.128**	**0.009**	WISA	Generalist	-	-1.761	0.224
BCCH	Closed*, OG	-	-0.811	0.380	WIWA	Generalist	-	**-0.984**	**0.005**
BRCR	Closed*	-	-1.118	0.155	AMGO	Open*	-	**-1.430**	**0.043**
CBCH	Closed*, OG	PIF	**-1.569**	**0.027**	AMRO	Open*	-	**-0.389**	**0.075**
GCKI	Closed*	PIF	**-2.795**	**<0.001**	BEWR	Open*	-	0.013	0.991
GRJA	Closed*	-	0.701	0.525	CEDW	Open*	-	0.897	0.215
HAFL	Closed*	-	**1.741**	**0.035**	COYE	Open*	-	**3.399**	**<0.001**
HEWA	Closed*	PIF	0.048	0.963	DEJU	Open*	-	**-0.961**	**0.021**
PIWO	Closed*		0.601	0.599	DUFL	Open*	PIF	**1.526**	**0.087**
PSFL	Closed*	PIF	**-1.210**	**0.018**	HOWR	Open*	-	-0.456	0.523
RBNU	Closed*		-0.038	0.925	LAZB	Open*	-	-0.427	0.629
RBSA	Closed*	PIF	-0.333	0.802	MGWA	Open*	PIF	-0.742	0.213
TOWA	Closed*	PIF	0.518	0.451	MODO	Open*	-	**-1.114**	**0.002**
VATH	Closed*	PIF	-0.880	0.203	MOUQ	Open*	PIF	1.004	0.199
WBNU	Closed*	-	**1.876**	**0.075**	OCWA	Open*	PIF	**-1.443**	**0.057**
WETA	Closed*	-	**0.948**	**0.066**	OSFL	Open*	PIF	**-3.604**	**<0.001**
WIWR	Closed*		**0.731**	**0.038**	RUHU	Open*	PIF	**-2.240**	**0.003**
BTYW	Closed	PIF	0.282	0.762	SOSP	Open*	-	-0.318	0.332
CORA	Closed	-	**2.344**	**0.005**	SPTO	Open*	PIF	-0.200	0.614
HETH	Closed	-	-0.639	0.219	WAVI	Open*	-	0.319	0.479
HETO	Closed	-	na	na	WCSP	Open*	-	**-2.316**	**0.002**
STJA	Closed	PIF	0.387	0.235	WIFL	Open*	PIF	**-2.210**	**0.008**
BHGR	Generalist	-	0.495	0.416	WREN	Open*	PIF	-1.074	0.186
BTPI	Generalist	PIF	-1.064	0.254	BHCO	Open	-	**-0.874**	**0.047**
HAWO	Generalist	-	-0.194	0.649	BUSH	Open	-	**-2.194**	**0.089**
HUVI	Generalist	PIF	0.612	0.412	PUFI	Open	PIF	**-1.417**	**0.007**
MOCH	Generalist	PIF	**-1.371**	**<0.001**	PUMA	Open	-	1.500	0.600
NAWA	Generalist	-	**-1.356**	**0.011**	RSFL	Open	-	**-0.838**	**0.004**
SWTH	Generalist	-	**-0.849**	**0.024**	VGSW	Open	-	-0.286	0.689
WEBL	Generalist	-	-0.363	0.563	YWAR	Open	-	**-1.153**	**0.014**

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.

Our results do not, however, provide guidance for specifying the amount of a landscape that should be maintained in early-seral forests to support bird species dependent on younger forests in productive landscapes. Research suggests that the percentage of open-canopy forest resulting from disturbance in west-side Cascade forests varied dramatically during the last several thousand years (Whitlock et al. 2003, Wimberly et al. 2004) with some large disturbance events affecting >90% of some landscapes while more frequent disturbances affecting small percentages of the landscape (<1%). Prior to European settlement, approximately 10-20% of forests in west-side Cascade landscapes were composed of young (<30 yrs), open-canopy forests as a result of disturbances; primarily fire, insect outbreaks and windthrow (Nonaka and Spies 2005, Wimberly et al. 2004, Wimberly 2002, Wallin et al. 1996, Teensma et al. 1991). This suggests that there was likely enough open-canopy forest to maintain species associated with these younger forests. Our results come from landscapes where between 0 and 65% of the landscapes were recently disturbed by timber harvest. Because some open-canopy bird species exhibit declining trends in abundance (Table 3.1), it seems particularly important to maintain some percentage of early-seral forests for both maximizing diversity and supporting species associated with these forests.

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, at least initially, resulting in decreased bird diversity and abundance. 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 loss of resources important for plant and bird colonization and growth. Within these environments, selective harvests, longer rotations and modest expectations for timber volume output should help 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 abundances and 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 different 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 extent varied with 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 affect bird diversity adversely.

Because forest management is typically applied across broad gradients in productivity, the finding that species respond differently to disturbance at different productivity levels is important. Forest management of bird diversity will be more effective if tailored to productivity levels because productivity influences vegetative recovery and associated resources important for birds following disturbance. Therefore, in highly productive landscapes, maintaining gradients in forest structural complexity, successional stage and disturbance will likely benefit species diversity. Alternatively, management in less favorable environments may 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. Although 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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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 productivity level. In this chapter,

we describe the implications of our research findings for management. Before

considering how management approaches might differ across landscapes with different

productivity, we briefly review the conceptual framework supporting landscape-specific

management approaches, 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 species response to local and

landscape scale structural conditions will vary depending on site productivity. 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

supporting species 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 in different biophysical settings (Chapters 2-3, Appendix A). We hypothesized that gradients in productivity (e.g. gross primary productivity) help explain why species diversity responds differently to local and landscape-scale structural conditions in different settings. In support, we found that bird diversity is influenced more by changes in productivity than structural conditions where productivity likely limits species diversity (e.g. Yellowstone region). Alternatively, in more productive settings, local and landscape-level structural conditions influence species diversity more so than gradients in productivity (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 (Chapter 2) but that species diversity responded more to disturbance extent in a less productive setting (Chapter 3). 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, consideration of landscape setting is necessary if forest management practices aimed at maintaining species diversity are to be effective.

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, Chapters 2-3, Appendix A-B), supports the idea that the influence of local and landscape-level forest structure on biodiversity varies with productivity. This chapter draws on the results from Chapter 2 and 3 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: 1) review historical and current approaches for managing forests for timber and biodiversity in the PNW; 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 (1880s-1950s)

In the late 1800s and early 1900s 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 by 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 (*Abies grandis*) 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, and there was little regard for regeneration, future stand
condition or maintaining species diversity. By the 1930s, foresters began to employ
silvicultural techniques to promote regeneration and rapid growth and 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 1900s, 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 focused on removing the most merchantable trees, where highly variable in practice, resulted in poor regeneration and led to stand deterioration (Isaac 1943, 1956). As a result of several studies documenting these outcomes, selective logging was largely abandoned by the 1950s (Curtis et al. 1998).

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

From 1950 to the 1990s, 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 (e.g. *Abies grandis, Abies procera, Abies lasiocarpa Tsuga heterophylla*) 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 year old stands with a post-harvest burn, an herbicide application to eliminate broad-leaf shrubs and deciduous trees such as the bigleaf maple (*Acer macrophyllum*), 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, drier 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 that 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 that 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 PNW (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), that encouraged alternatives to even-aged management (i.e. shelterwood harvest, green-tree retention, riparian and wildlife buffers). Similarly, managers of public and private timberlands showed 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 in the management of industrial forests, primarily to encourage, and sometimes require, longer rotations, retention of late-seral forest, and treatments to facilitate structural conditions representative of older PNW forests.

Despite the influence of the Northwest Forest Plan and shifts in public opinion, changes in the 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 biodiversity through short-rotation, even-aged management. In west-side forests, managers currently rely on short rotation (40-60 yrs) even-aged harvests of between 15-50 hectares. 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 involve slightly longer rotation periods (50-70 years) applied to 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 more diverse set of silvicultural techniques to address the more frequent variable fire regimes and low soil moisture characterizing a majority of east-side forests. 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 support fire-adapted species. Additionally, combinations of shelterwood, seed-tree, partial cuts and individual tree selection are now more commonly used to create multi-layered mixed-species forests (Oliver et al. 1995). These experiments are commonly implemented on lands aimed at supporting multiple resource objectives, where timber output is not the primary management objective.

Managing Private Forests in the Future

Although 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 are already becoming important in management. 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 values are low), and affect forest species diversity 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 becoming an increasingly 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. Industrial forest managers currently tailor

management of forests to site conditions in an effort to promote rapid regeneration of

marketable wood products, but they 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 PNW Forests Research

Background: Building on a well-supported premise that horizontal and vertical

forest structural diversity is 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 the Yellowstone region, 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.

productivity in driving diversity at several landscapes across the PNW (Appendix A).

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 edge density (m/ha) (Chapter 2). Second, if landscape effects

were present, we hypothesized that they would be more pronounced in 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 (Chapter 2). Lastly, we considered how bird species diversity would

respond to timber harvest across landscapes varying in productivity (Chapter 3). Our

results have several implications for managing biodiversity in PNW forests.

Summary of Results: Considering the relative influence of stand-level forest

structural characteristics vs. productivity in driving biodiversity, we found that (1) BSR

exhibited a unimodal relationship with productivity across the PNW region; (2) the

landscape-scale relationships between productivity and BSR were positive or unimodal in

less productive locations and were flat or negative in productive locations; (3) forest

structural complexity explained more of the variation in bird species richness in

productive landscapes; and (4) the slope of the relationship between forest structural

complexity and BSR was steepest in less productive locations and negative in productive locations (Appendix A).

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 in a more productive setting; (4) landscape effects appear to be more pronounced at the community level in more productive settings; and, (5) BSR and diversity responded differently to increases in the amount of the landscape recently disturbed by timber harvest (Chapters 2-3).

Relevance to Management

As a result of the changing effect of productivity on diversity, the management implications of this work are necessarily specific to the productivity setting of a given landscape. To adequately address the management of a variety of landscape settings, we divide the discussion into management implications for low, intermediate and high productivity levels (Table 4.1 and 4.2). We classify management implications into three productivity settings because the slope of the relationship between bird diversity and productivity across the PNW exhibits a unimodal relationship. BSR increases sharply with increasing productivity in harsh landscapes, increases moderately with increasing productivity in intermediate-productivity landscapes, and is flat or decreases with increasing productivity in highly productive landscapes (Appendix A). The strength and

direction of the relationship between BSR and productivity 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 support more
general biodiversity management strategies for the three broadly defined productivity
settings. This is especially true when considering landscape effects and disturbance
extent. 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 rotation lengths ranging from 40-100 years. Therefore, how BSR responds to
gradients in the extent of edge density (m/ha) and recent disturbance (timber 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, although our results do not allow for specific
recommendations on how large or frequent disturbances should be.

High-Productivity Settings: In productive 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
BSR will be maximized through 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 Sarr et al. (2005) suggest that
increasing levels of disturbance in 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, Chapter 3)

Table 4.1 Categorical definitions of three productivity levels in the PNW.

	Low Productivity	Intermediate Productivity	High Productivity
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 $(gCm^{-2}day^{-1})$	0.3 – 0.8	0.8 – 1.25	1.25 – 1.9
PNW Locations	W. Cascades >1000m elevation, N. and S. Cascades >1300m, 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 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 minimal productivity based growth limitations

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, Appendix A).

Table 4.2 Management implications by conservation category and productivity setting

CONSERVATION CATEGORIES	PRODUCTIVITY GRADIENT		
	HIGH PRODUCTIVITY	INTERMEDIATE PRODUCTIVITY	LOW PRODUCTIVITY
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 productivity 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 conditions • Shift harvest units across the landscape. (Chapters 2-3) • Provide for species with specific patch size and edge requirements	• Less harsh environments mean less seasonal movement of individuals • 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 allow for slow biomass accumulation (> 120 yrs.)

Table 4.2-Continued

CONSERVATION CATEGORIES	PRODUCTIVITY GRADIENT		
	HIGH PRODUCTIVITY	INTERMEDIATE PRODUCTIVITY	HIGH PRODUCTIVITY
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
Conservation Zones	• Most locations contain high levels of biodiversity • The highest productivity locations are not the most diverse (Chase and Leibold, 2002) • Conservation zone locations in "lower productivity" locations may hold more rare species (Huston 1999)	• Few conservation zones are in mid-productivity locations • Biodiversity hotspot mapping or risk analysis may determine which habitat types contain the highest levels of diversity or at greatest risk • Protect more area with selection of locations based on conservation priority	• The species-productivity relationship is strongly. • Protect areas that are comparatively higher in productivity than the surrounding landscape. • Conservation zone locations should follow a simple determination of small scale local (high productivity) 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

Therefore, emphasizing management that promotes high levels of forest structural

complexity in older forests is only misguided because it ignores the importance of young

forests and the role of high structural complexity in young forests for supporting high

BSR and the viability of bird species associated with these forests. While young forests with more open canopies support the highest levels of BSR of any seral stage (Appendix A), young forests with high densities of conifer saplings, almost complete canopy closure and little understory support the fewest number of bird species of any stage of forest development (Meslow and Wight 1975, Appendix A). Our results show that diversity is typically low in young densely stocked pole forests approaching complete canopy closure and stem exclusion (Appendix A). 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) 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 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, Appendix A).

Many species in productive environments specialize in forest interior, edge, or early-seral conditions (Chapter 2-3). 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, Chapter 3). This process is similar to existing management strategies.

Many specialist species require unique structural attributes to succeed that may not be adequately provided for by the traditional shifting pattern of harvest alone. For example, many specialist birds (e.g. woodpeckers, purple martins) depend on cavities that 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 northern spotted owl, need suitable dispersal habitat with canopy layer trees and an open understory. In addition, several rare species depend on specific 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 through many rotations, making the sustainability of soil nutrients an important consideration for managers. Management practices that promote 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 conditions needed for species associated with both early and later-seral stages, resulting in high landscape-scale diversity.

In productive 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 are important. A hump-shaped productivity diversity gradient (Chase and Leibold 2002, Appendix A) exists across the forests of the PNW, pointing to the fact that the highest productivity locations are not the most diverse. In some landscapes a negative relationship between productivity and diversity will be strong enough to deserve consideration when prioritizing conservation efforts. Under these circumstances, targeting conservation zones in comparatively "low productivity" locations may support the highest levels of diversity (Huston 1999).

Intermediate-Productivity Settings: A large portion of the forested lands of the PNW is 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 PNW 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. In these settings, longer rotations would allow for

full stand structural development despite slower biomass regeneration. Additionally, moderate winter climates mean less seasonal movement of vertebrates than occur in the lowest productivity 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 facilitates movement. The effect of edge and patch size is less pronounced in these settings than in productive sites but still may be important for species highly associated with edge environments.

In intermediate productivity settings, shorter growing seasons and less available water result in reduced timber output. With natural disturbance, these forests often 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 et al. 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, habitat in the drier portions of intermediate productivity landscapes often becomes patchy, and birds 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).

Low-Productivity 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 productivity gradient. Our results show that productivity is a stronger driver of biodiversity than forest structure

in low-productivity landscapes (Appendix A). In these settings, species diversity is typically concentrated in small localized "higher" productivity 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 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-productivity locations, it is important to identify, retain and judiciously manage these hotspots. Across the remainder of low-productivity regions, management will best maintain biodiversity where longer rotation periods that maintain all structural stages and levels of biomass necessary for bird diversity are maintained.

Natural disturbance is a strong driver of landscape pattern in low productivity locations. Unlike highly productive settings, intense disturbance typically reduces species diversity, at least temporarily (Osem et al. 2002, Bakker et al. 2006, Chapter 3). One possible explanation is that disturbance in harsh settings reduces resources and recovery rates of organisms. In many low-productivity environments, many species are adapted to fire. Consequently, increasing disturbance intensity may result in a decrease in species diversity immediately following disturbance, but 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 hotspot locations, but the extent, frequency and intensity need 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-productivity 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, 2000). Although landscape pattern effects, such as edge density and patch size, are not as pronounced as they are in higher-productivity settings, some aspects of landscape pattern are still important to consider. Due to the occurrence of large productivity gradients and ephemeral resources in most less productive landscapes in the PNW, 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 extremes during key growth stages are likely a primary factor limiting the growth of lodgepole pine, whitebark pine, and Engelmann spruce in the PNW. 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 other low-productivity forest types in that high-intensity stand-replacing fire (leaving little usable structural legacy) is the most common form of natural disturbance (Schoennagel et al. 2004). Clear-cutting may match 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 less productive regions, biodiversity management should focus on promoting increased shrub density and size (Appendix A).

We suggest that at less favorable sites, factors other than competition act to limit to species diversity (Chapter 3). In these less favorable landscapes, 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-1990s 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 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. Thus, 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 not be effective in all settings. Our evidence suggests that productivity is a strong driver of species diversity, especially in less productive 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 productivity.

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CHAPTER 5

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Conclusions

Our results suggest that species respond differently to similar forest structural conditions in landscapes varying in productivity. The relative influence of local and landscape-level structural conditions in driving species diversity is stronger in highly productive settings whereas climatic conditions and soil fertility play an important role in driving species diversity in less productive settings (Chapter 2, Appendix A).

These findings are important because forest managers, while already tailoring management to provide a continuous supply of timber and wood products, often apply the same approach for managing species diversity across landscapes that differ in forest productivity. Management of forests to support species diversity will likely be more effective when tailored to landscape setting and associated productivity. Management guidelines aimed at supporting species diversity where climate is known to be a strong driver of species diversity will be quite different than guidelines designed for a setting where structural conditions influences species diversity less more than climate.

A striking example illustrating how species respond differently to structural conditions in landscapes with different levels of productivity is how species diversity responds to harvest in young forests in highly productive settings compared to less productive settings. Bird diversity increases with increasing disturbance extent in a

highly productive environment, whereas bird diversity decreases with increasing

disturbance in a less productive landscape. Consequently, a "shifting mosaic" harvest

approach may benefit species diversity by maintaining younger forests across productive

landscapes. Likewise, maintaining more continuous, older forests in less productive

settings and retaining forest structure and biomass in harvested stands will likely benefit

species diversity in harsh settings. In both productive and less productive landscapes,

both rare and specialist species often rely on unique structural conditions, such as large

contiguous forest blocks, legacy trees and snags, coarse woody debris, broken tops and

other characteristics associated with mid/ later-seral forests. Therefore, to support both

overall species diversity and the viability of less common species and specialists, it is

important to combine management aimed at addressing landscape productivity with

management that provides the entire suite of forest conditions that rare and specialist

species require.

Directions for Future Research

We see three primary directions for future research. First, research aimed at

better understanding the mechanisms driving high species diversity in young forests in

productive settings will be important in managing these forests to benefit both species

diversity and species that key in on structural features unique to these settings. Research

focusing on young forests that include sites spanning productivity gradients in several

landscapes in different types of environments will help clarify the important factors

supporting diversity at these sites, and determine whether thresholds exist where the

relationship between species diversity and disturbance changes. Currently, very little is

known about how young forests influence overall species diversity and rare and specialist species.

Second, in less productive environments we found that "hotspots" in species diversity exist not only in areas with high habitat heterogeneity (e.g. riparian areas with a diverse mixture of deciduous and coniferous forest canopy dominants) but also in some intermediate productive forests dominated by one or two overstory species. In these forests it will be important to better understand the factors that lead to higher species diversity and how management may more effectively promote conditions that support higher species diversity. For example, many of the most diverse stands east of the Cascades were found in ponderosa pine and mixed ponderosa pine and Douglas-fir forests. While fire frequency and intensity vary dramatically depending on microclimate and other conditions, these forests are typically more influenced by fire, supporting many species adapted to fire as a disturbance. Managing these forests to maintain high species diversity will, first, require a better understanding of how highly site specific and variable patterns of natural disturbance influence species diversity as well as less common species keying in on these forests. In order to manage these forests in the context of patterns of natural disturbance, it will then be necessary to determine management approaches that best support high species diversity in these sites. Thus, there is much work to be done to link an understanding of how natural disturbance influence structural conditions that support high species diversity in these settings to timber management that best emulates these conditions.

Lastly, the structure of ownership and consequent management of industrial timberlands and smaller private forests is changing rapidly. Changes in market forces

and tax structures are already dramatically influencing the way in which vast acreages of forest are managed in the United States. The dynamic nature of new entities such as Timber Investment Management Organizations, Real Estate Investment Trusts and Master Limited Partnerships is resulting in the dissolution of the forest-to-mill ownership structure of timberland companies and the creation of new constraints on how forests are managed. Patterns of exurban growth and land ownership transfers in the PNW suggest that the conversion of vast acreages of managed forest lands to residential development will continue, resulting in dramatic changes to vegetation structure at local and landscape-scales (Gude et al. 2006). It will be important to consider how these changes in ownership and management structure will influence species diversity and link this new dynamic to our understanding of biological factors driving species diversity in the PNW.

This dissertation outlines important principles for managing forests to support species diversity across gradients in forest productivity. We think this is reasonable first attempt to highlight how site productivity influences important processes regulating species populations. With further research, we expect that our results will prove to apply to other forests and to non-forested ecosystems more generally. Our hope is that future research will lead to a better understanding of how productivity and structure interact to drive species diversity in different ecosystems worldwide.

APPENDICES

APPENDIX A

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 1). Structural complexity then rebuilds in mature and old-growth stages due to gap formation processes and the death of large trees

(Figure 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.
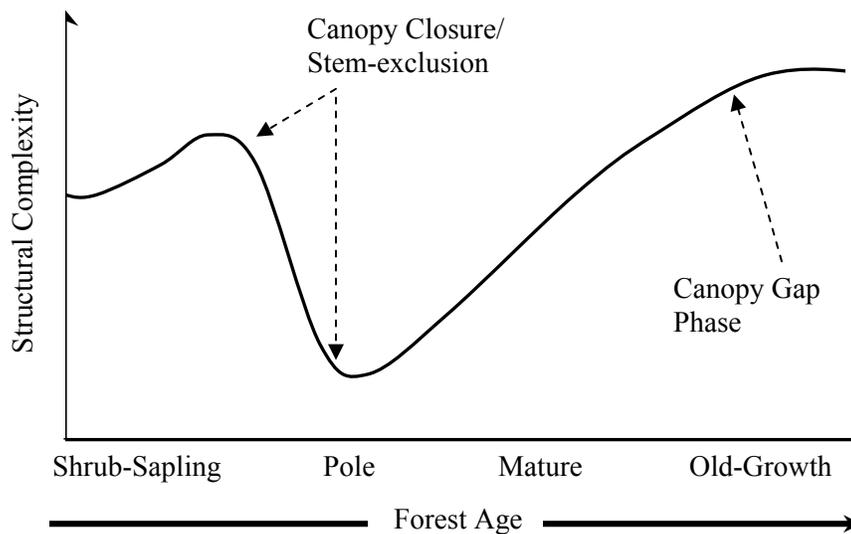
Figure 1. Structural complexity by seral stage in temperate coniferous forests.

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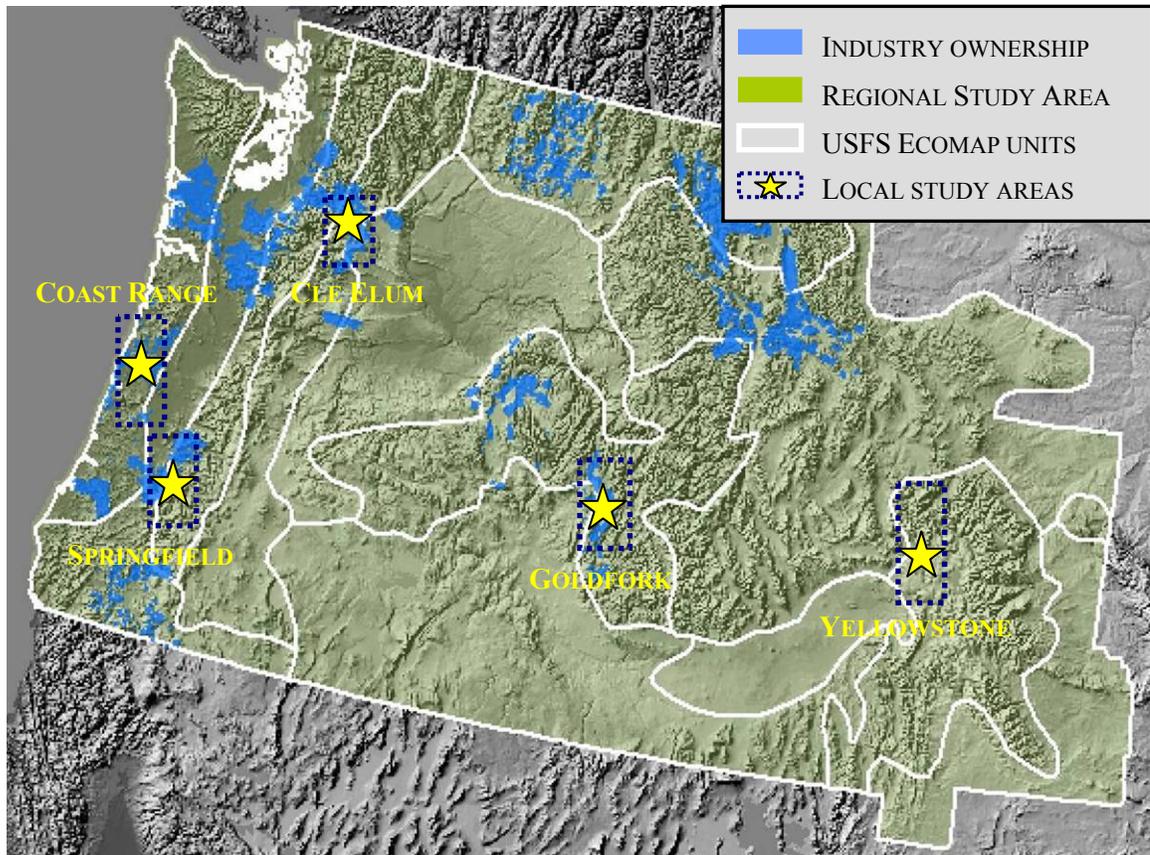
Figure 2. Location of study landscapes.
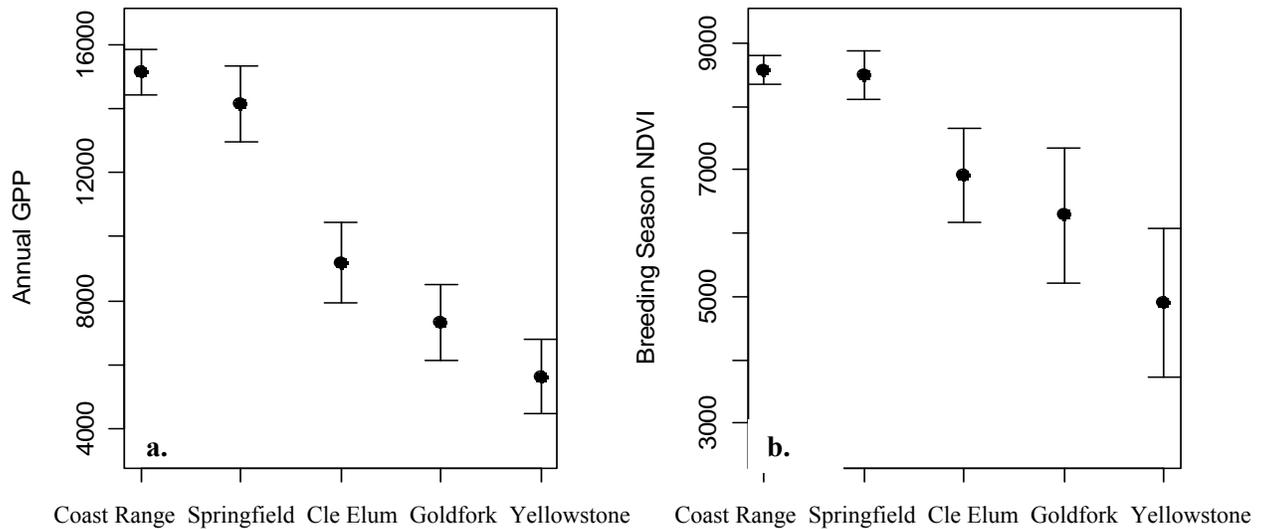
Figure 3. Gradient of annual gross primary productivity (GPP: $gm^C m^{-2} day^{-1} *10^3$) (a), and breeding season average normalized difference vegetation index (NDVI: 0-1 index $*10^4$) (b) across landscapes from west to east (mean +/-1 sd).

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 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 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 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).

Table 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 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 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

<u>Interaction of Forest Structure and Available Energy</u>. 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 4a).   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 4a. 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

Table 4b. 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) $V = H \times (D^2 + d \times D + d^2) \times (PI / 12)$ 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 $\mathrm{sqrt}((\sum_i^n (dbh_i^2))/n))$
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 coefficients 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 4c. 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

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 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.
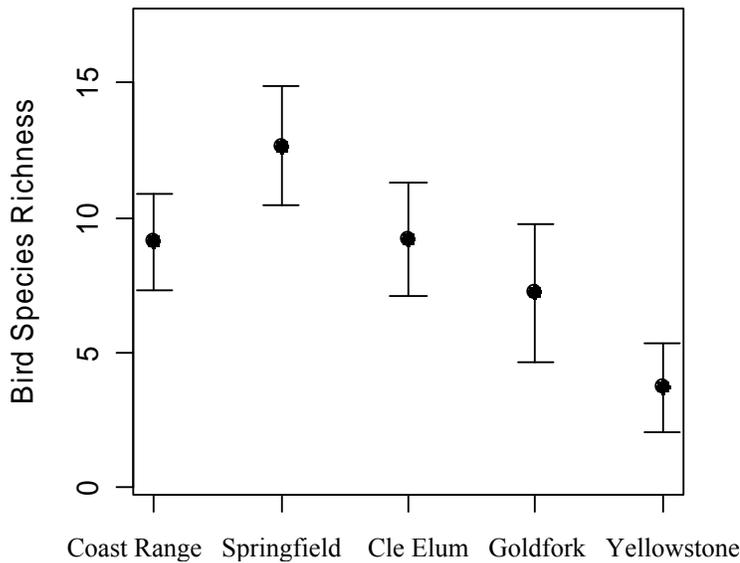
Figure 4. Bird species richness by landscape. Mean +/- 1 SD of the number of bird species detected within 50-m; cumulative over three 10-min. visits and averaged by year.

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 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 5, Figure 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 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 ($gm^Cm^{-2}day^{-1}*10^3$)	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 6, Figure 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 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 6). All breeding season energy models had lower AIC scores than the best annual energy model.

Table 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
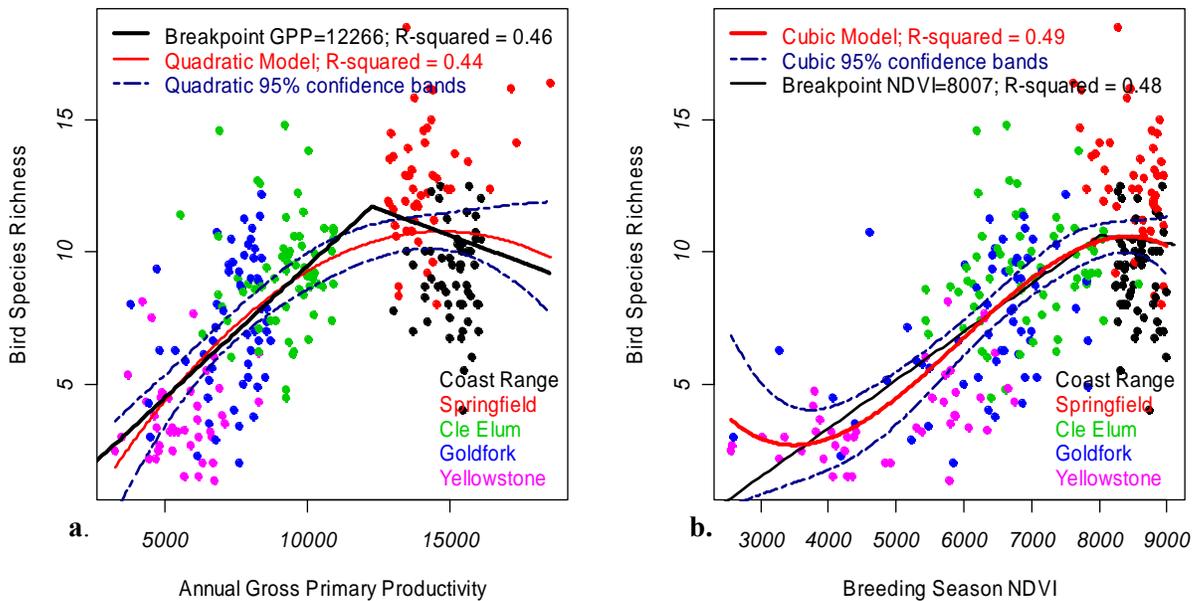
Figure 5. BSR across the PINW by annual energy (GPP) (a), and breeding season energy (NDVI) (b).

BSR had negative relationships with breeding season NDVI at the Coast Range and Springfield Landscapes (Table 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 7. Direction and significance of relationships between available energy and BSR. See Table 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 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 8. Mean and coefficient of variation (CV) of covariates representing structural
complexity by landscape and seral stage.

STRUCTURAL COMPLEXITY PREDICTOR	SERAL STAGE	Coast Range		Springfield		Cle Elum		Goldfork		Yellowstone	
		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 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 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 9. Direction and significance of relationships between covariates representing
structural complexity and BSR. See Table 8 for units of measure.

STRUCTURAL COMPLEXITY MEASURE	Coast Range		Springfield		Cle Elum		Goldfork		Yellowstone	
	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 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 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 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.
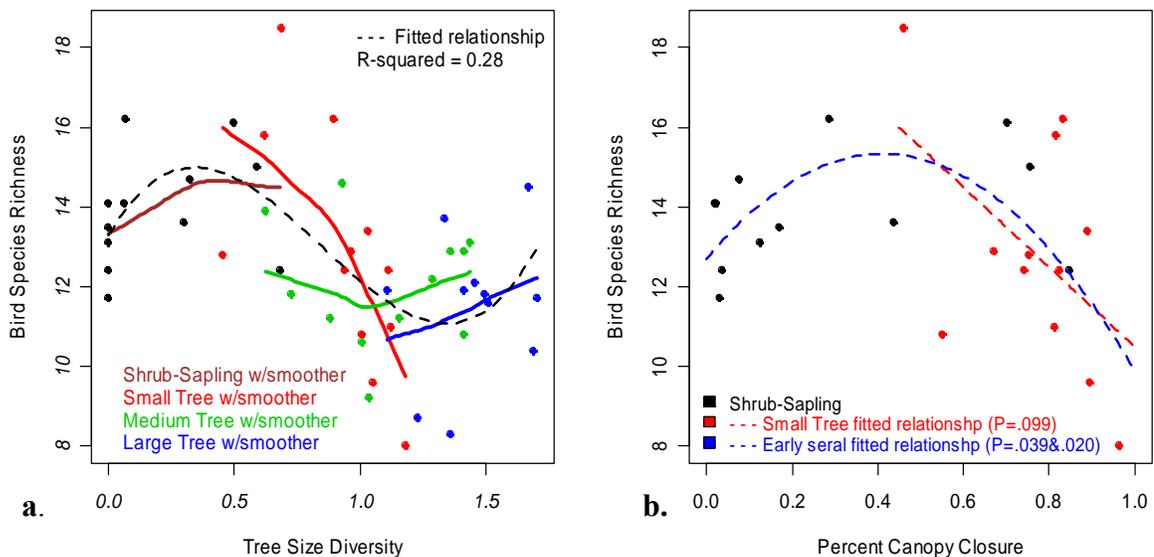

Figure 6. Tree size diversity vs. BSR separated by seral stage in Springfield (a). canopy closure vs. BSR in the Shrub-sapling and Small Tree seral stages in Springfield (b).

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 10, Figure 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 11, Figure 8).

Table 10. Predictors from best ten predictor energy first models by landscape. See Tables
4b-4c 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 11. Predictors from best ten predictor structure first models by landscape. See Appendix 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
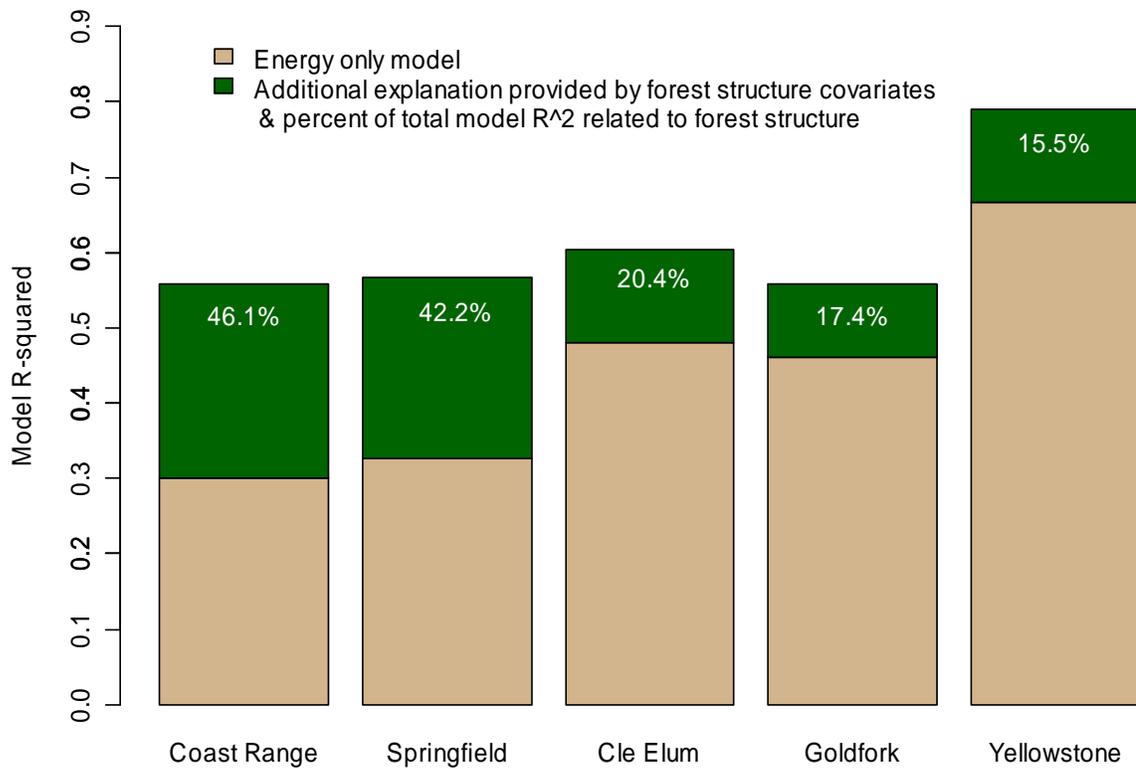
Figure 7. Percent of the total model R^2 resulting from the addition of five predictors of forest structure to a five predictor energy model at each landscape.
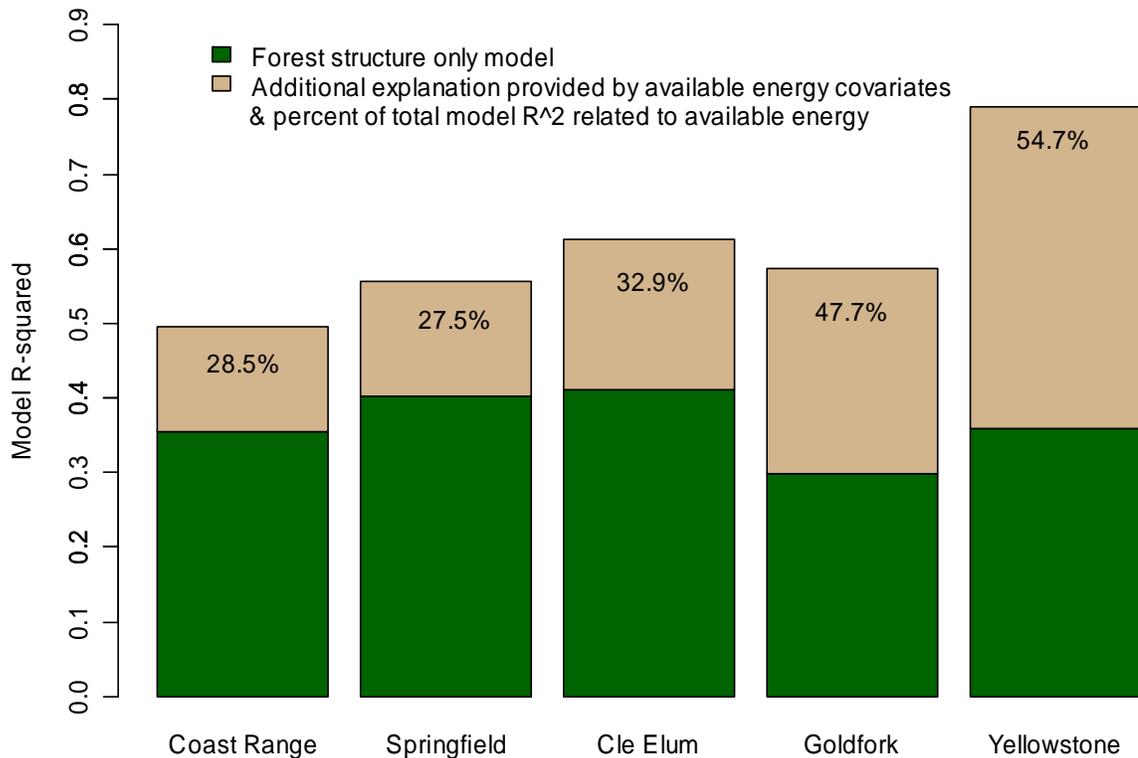
Figure 8. Percent of the total model R^2 resulting from the addition of five predictors of available energy to a five predictor forest structure model at each landscape.

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 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.
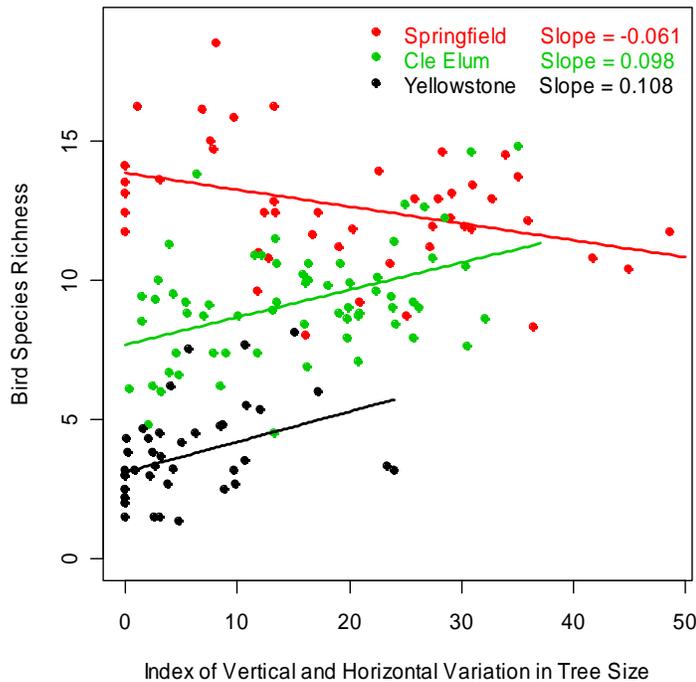
Figure 9. Comparison of slopes between BSR and an index of vertical and horizontal variation in tree size (SCI) at the Springfield, Cle Elum and Yellowstone landscapes.

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 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 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 (Chapter 3) 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 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 $gm^Ccm^{-2}yr^{-1}$, 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 (Chapter 3) 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 (Chapter 3)). The downturn in diversity in the Small Tree seral stage (Figure 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 (Chapter 3)).

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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APPENDIX B

SPATIAL PATTERNS OF BIODIVERSITY ACROSS MANAGED FOREST
LANDSCAPES

<u>Introduction</u>

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 (Appendix A) 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 (Appendix A), 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 (Appendix A). 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.
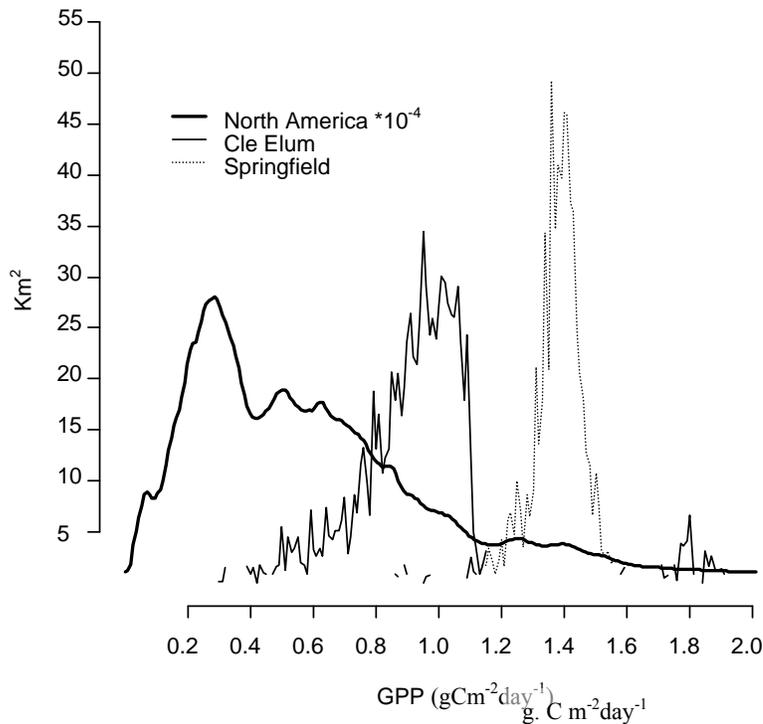
Figure 1. Area (km^2) of land representing GPP gradient for North America (*10^{-4}), and 3 km radius landscapes surrounding the Cle Elum and Springfield survey sites.

Cle Elum, WA: 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 1 & 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.

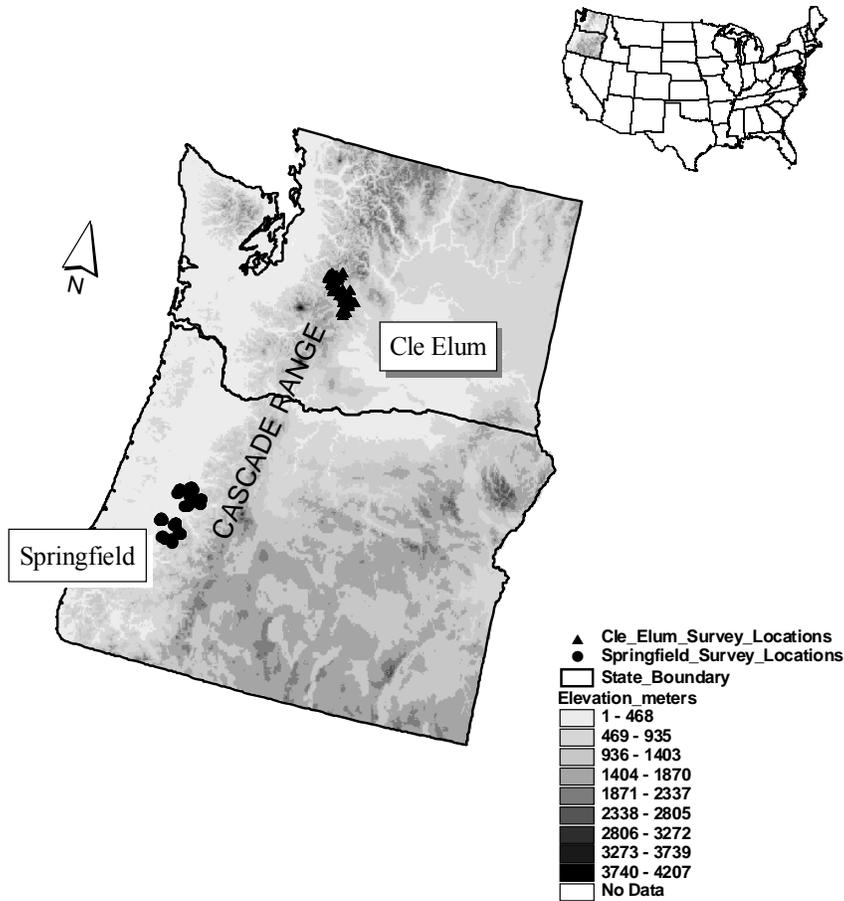Figure 2. Location of 2 study sites, Springfield, Oregon and Cle Elum, Washington.

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 Appendix A for more detail on univariate BSR/predictor relationships).

The model R^2 values were expected to be lower than those shown in Appendix A 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.

<u>Results</u>

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, Table 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 4, Table 1).

Table 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)

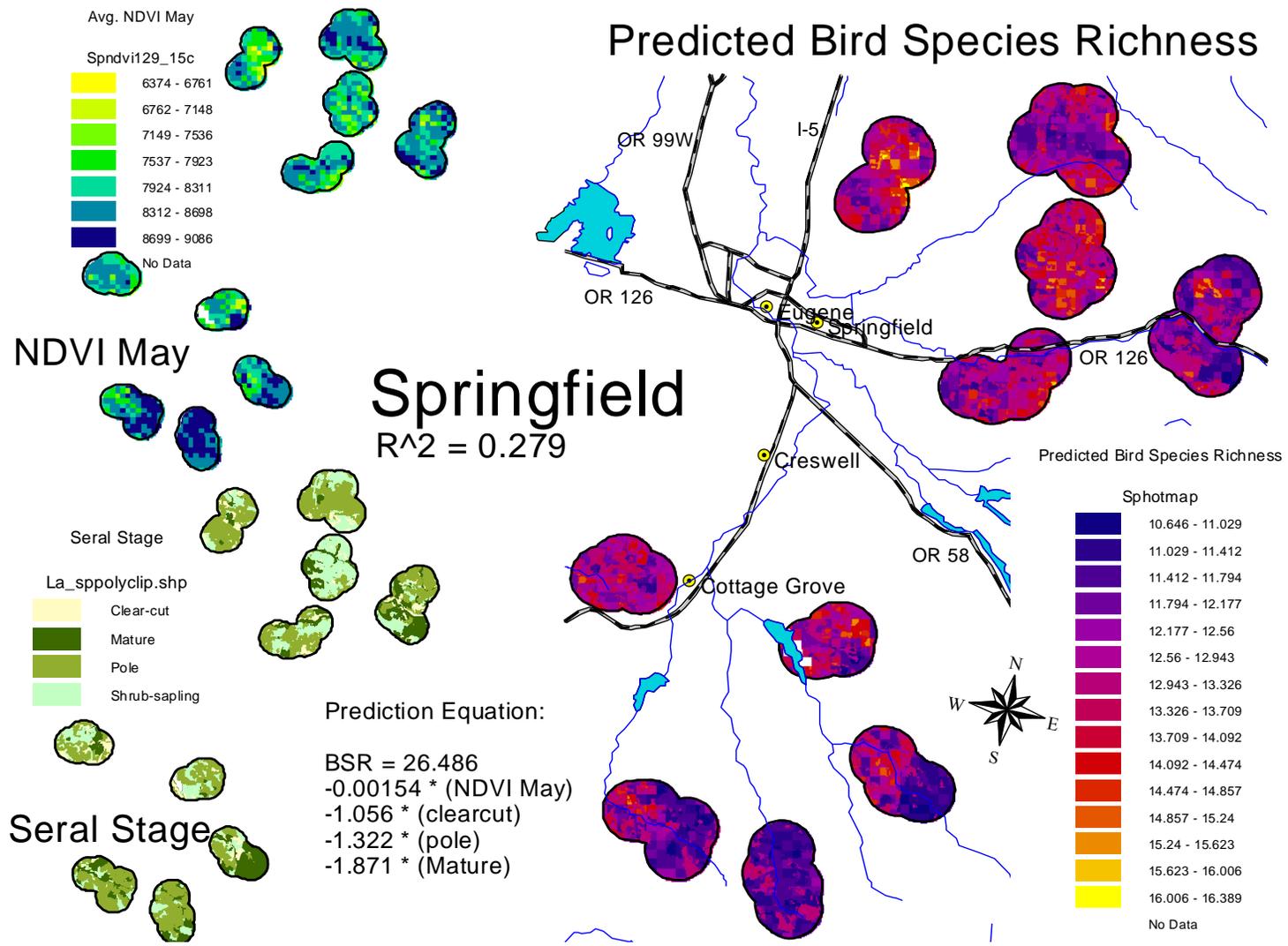| Site	Response	Predictors			AIC	Comparison P-Value	R^2
		1	2	3			
Springfield	BSR	Seral Stage			72.84	0.025	0.189
	BSR	Seral Stage	NDVI May		69.17	-	0.279
Cle Elum	BSR	% Canopy Cover			111.1	< 0.001	0.244
	BSR	% Canopy Cover	Dominant Cover		72.33	0.047	0.627
	BSR	% Canopy Cover	Dominant Cover	Temp.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

Figure 3. 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.

Percent Canopy Cover

Percent Canopy Cover

La_cle_poly_clip.shp
- Low (0-33%)
- High (66-100%)
- Medium (33-66%)

Avg. Temp (Apr. - Sept.)

Avg.Temp. Apr. - Sept.

Tempasbuff
- 8
- 9
- 10
- 11
- 12
- 13
- No Data

Predicted Bird Species Richness

Snoqualmie Pass

Salmon la sac

Easton

Roslyn

Cle Elum

Predicted Bird Species Richness

Clehotm
- 6.194 - 6.798
- 6.798 - 7.402
- 7.402 - 8.007
- 8.007 - 8.611
- 8.611 - 9.215
- 9.215 - 9.82
- 9.82 - 10.424
- 10.424 - 11.028
- 11.028 - 11.633
- 11.633 - 12.237
- 12.237 - 12.841
- 12.841 - 13.446
- 13.446 - 14.05
- 14.05 - 14.654
- 14.654 - 15.259
- No Data

Dominant Cover Type

Dominant Cover Type

La_cle_poly_clip.shp
- Douglas Fir
- Western Hemlock
- Subalpine
- Grand Fir
- Ponderosa Pine
- Deciduous

Cle Elum

$R^2 = 0.651$

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*

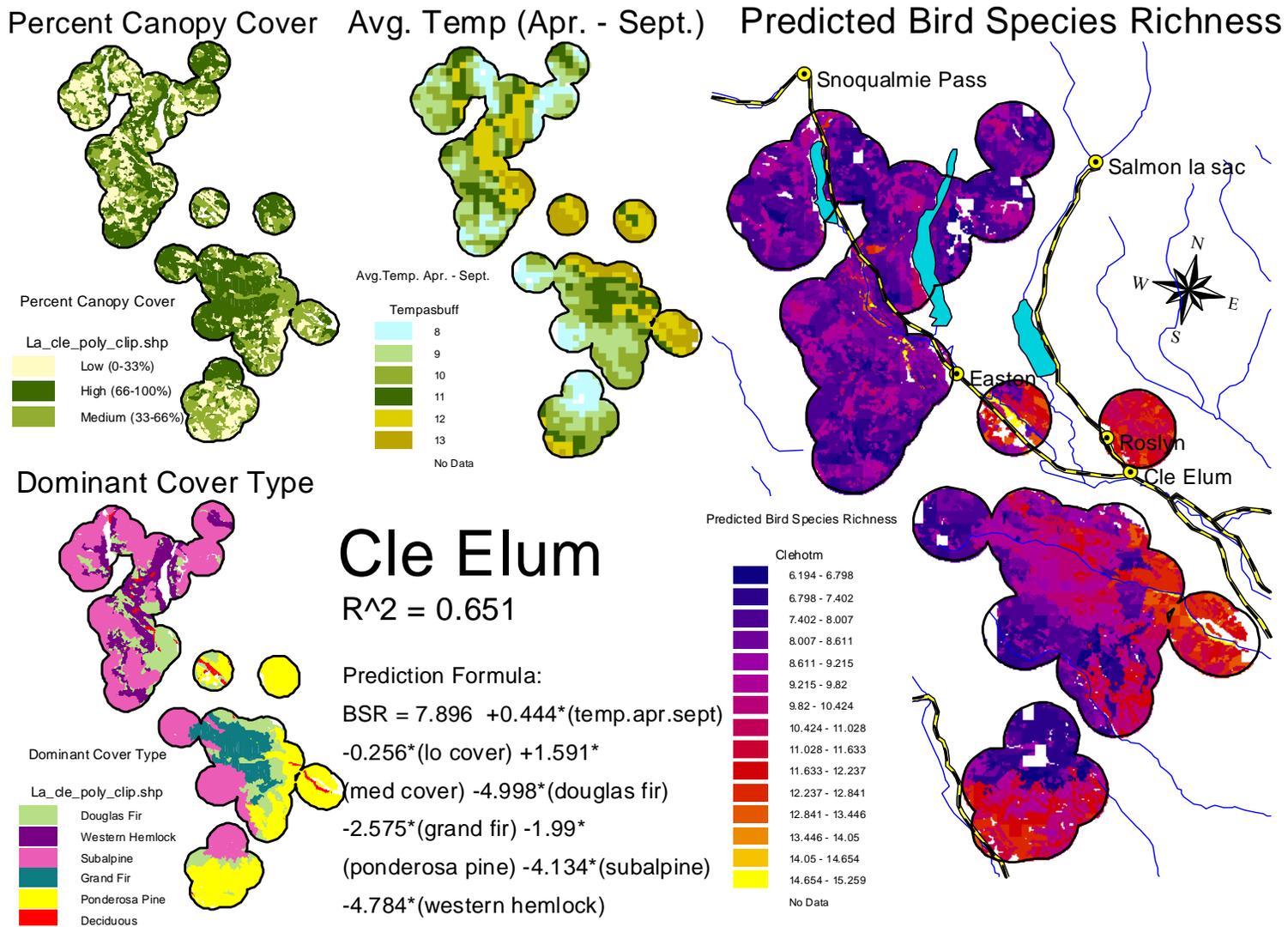(ponderosa pine) -4.134*(subalpine)

-4.784*(western hemlock)

Figure 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.
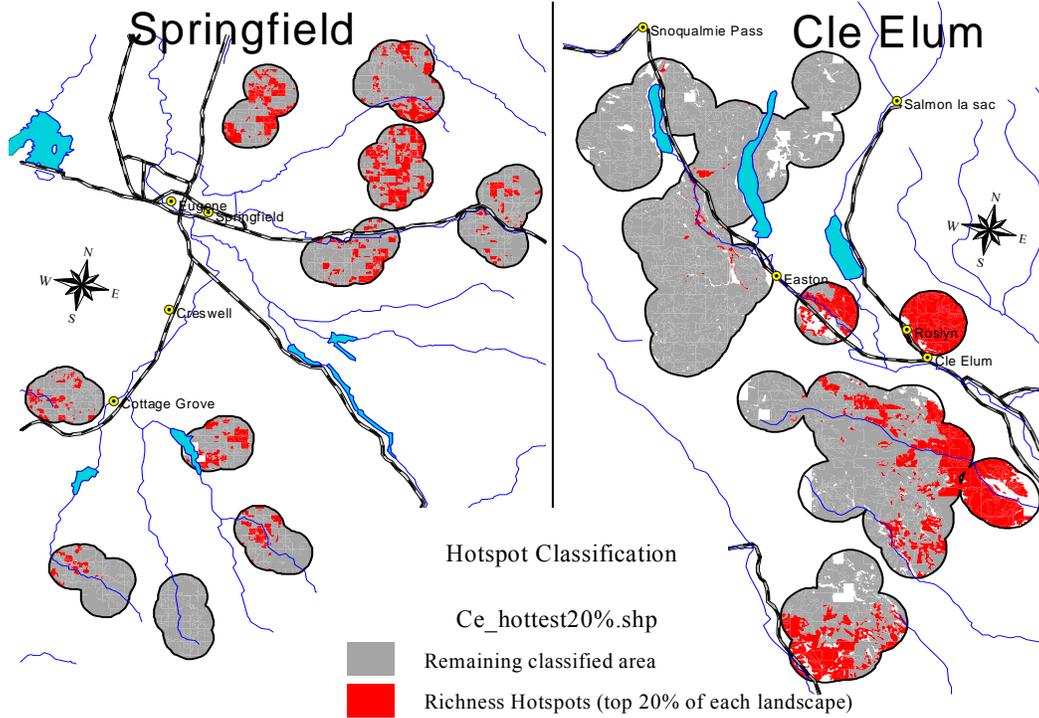
Figure 5. Highest 20 percent (by area) of predicted bird species richness displayed for the Springfield and Cle Elum landscapes
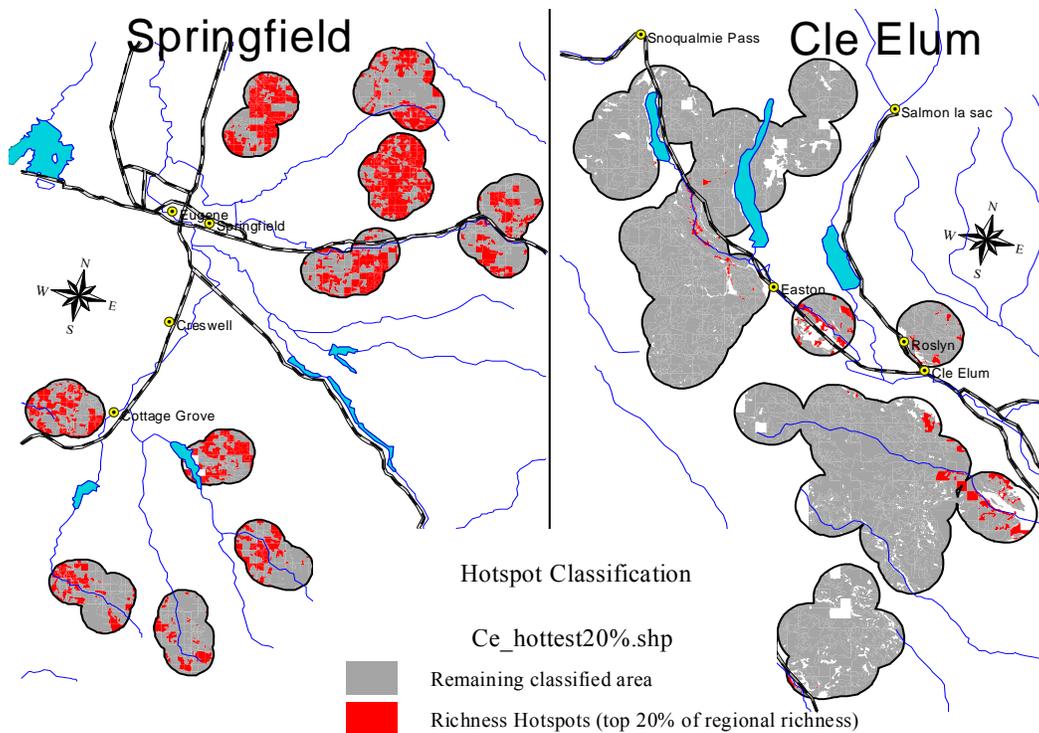

Figure 6. Highest 20 percent of regional (both sites) predicted bird species richness displayed for the Springfield and Cle Elum landscapes

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 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 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 6). The more

productive valley bottom locations are the only places in the Cle Elum landscape that are

highlighted as regional biodiversity hotspots (Figure 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 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 (Appendix A).

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 (Chapter 3)). 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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APPENDIX C

BANDING CODE, COMMON NAME, SCIENTIFIC NAME
AND SITE WHERE BIRD OCCURRED FOR BIRDS INCLUDED IN
LANDSCAPE EFFECTS ANALYSIS

Appendix C. Bird species banding code, common name, scientific name and site where bird occurred; * = both landscapes, s = Springfield, c = Cle Elum.

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*	*

Appendix C.—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 D

BANDING CODE, COMMON NAME, SCIENTIFIC NAME
AND SITE WHERE BIRD OCCURRED FOR PARTNERS IN FLIGHT
SPECIES OF REGIONAL CONCERN

Appendix D. Partners In Flight species of regional concern for the Northern Pacific Rainforest Bird Conservation Region (Panjabi et al. 2005). Bird species banding code, common name, scientific name and site where bird occurred; * = both landscapes, s = Springfield, c = Cle Elum.

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

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