

CONSERVING AVIAN BIODIVERSITY ON MANAGED FOREST LANDSCAPES: THE
IMPORTANCE OF PATTERN AND SCALE

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degrees of

Fisheries and Wildlife – Doctor of Philosophy
Ecology, Evolutionary Biology, and Behavior – Dual Major

2017

ABSTRACT

CONSERVING AVIAN BIODIVERSITY ON MANAGED FOREST LANDSCAPES: THE IMPORTANCE OF PATTERN AND SCALE

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The shift in forest management goals over the last several decades to meet societal demands for more non-timber benefits has led to a move towards ecosystem-based approaches to management, with biodiversity conservation being a major objective. Within this context, maintaining the richness and diversity of bird species on working forest landscapes has continued to be a priority in sustainable forest management. Ecosystems are heterogeneous in space and time, and regional species diversity is maintained by spatial patterns of heterogeneity at multiple scales. Understanding how patterns of heterogeneity in forest composition and structure influence species diversity is crucial to sustainable forest management. However, despite a great deal of research on habitat relationships of forest bird species, there is little understanding of how patterns of heterogeneity across scales influence regional bird species diversity. Therefore, my research goal was to investigate the relationship of bird species diversity to patterns of forest composition and structure across multiple spatial scales on a managed forest landscape. The first chapter investigates how patterns of heterogeneity in stand-level attributes impact patterns of bird community diversity across multiple spatial scales. Chapter 2 demonstrates a novel application of the conservation filters strategy to maintaining avian diversity on managed forests by working at 2 different operational scales. The third chapter looks at monitoring beta diversity in bird communities at multiple spatial scales as an alternative paradigm to species-level strategies for tracking changes in regional biodiversity.

The research in these chapters draws several conclusions that are fundamental to the problem of maintaining regional biodiversity on managed forest landscapes. The first is that the relationship of environmental heterogeneity to bird community diversity changes across spatial scales. The second conclusion is that uncommon vegetation community types have a greater relative contribution to regional diversity, and the importance of specific compositional and structural attributes changes among types. Third, quantifying beta diversity of bird communities (differences among spatial units within a region) across multiple scales, using a hierarchical cluster sampling design, reflects environmental heterogeneity and offers an efficient and effective system for monitoring changes in regional biodiversity.

The research presented in this dissertation offers an expanded and integrated view of the problem of maintaining biodiversity on managed forests. I have demonstrated that large-scale management systems must explicitly address how forest planning will impact patterns at multiple scales simultaneously, and maintain both homogenous and heterogeneous landscapes at the appropriate scales. My work offers an integrated set of guidelines for biodiversity conservation on managed forests that explicitly accounts for the multiple scales at which biodiversity is generated and maintained. I believe that this research provides ecologists, land managers, and planners with an improved framework for managing forests under the ecosystem management paradigm.

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This dissertation is dedicated to the memory of my father, Donald Charles Crosby, who loved nature and cared deeply about protecting it throughout his life. Thank you Dad for setting me on my path and giving me the skills and passion I needed to walk it.

ACKNOWLEDGEMENTS

This work was made possible through funding provided from the Boone and Crockett Club through the Boone and Crockett Quantitative Wildlife Center at Michigan State University. Additional support was provided by the Michigan State University Graduate School through the University Distinguished Fellows program and by Frontier Renewable Resources LLC.

I would like to thank my major advisor, Dr. William F. Porter, for help and guidance throughout the research process and for providing a first-class working environment. I would also like to thank the members of my graduate committee, Drs. Gary Roloff, Scott Winterstein, and David MacFarlane, for their valuable assistance with this work. Additionally, I must express my extreme gratitude to my fellow lab-mates in the QWC (past and present, in no particular order): Chad Parent, Amy Dechen Quinn, Bryan Stevens, Heather Porter, Nathan Snow, Andrea Bowling, Jodi Kreuser, Marta Jarzyna (Vegetable), David Williams, Sonja Christensen, Kathryn Frens, Rebecca Cain, Chris Hoving, Jon Cook, Jennifer Smith, and Leslie Skora. I could not have asked for a better group of people to work with these past five years.

Dr. Mike Walters from the Department of Forestry and Dr. Jiangua (Jack) Liu from the Center for Systems Integration and Sustainability at Michigan State University generously provided the data used in this research. Dr. Walters also provided invaluable advice concerning the details of the data. Appreciation also goes to Dr. Pen Holland from the University of York for generously supplying me with the Python and R code for simulating landscapes with spatially correlated pixel values.

Finally, and most importantly, I need to thank my family for their love and support. My wonderful wife Andrea and our beautiful son Sebastian; Mom and Dad (who set me on my path

supported me the entire way); and my brother and sisters who kept me honest by asking (continually) when I was going to be done with school. Thank you all.

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PROLOGUE

Over the past several decades there has been a shift in the focus of natural resource management towards a more holistic, ecologically-based approach generally referred to as ecosystem management (Christensen et al., 1996; Fuhlendorf et al., 2012). Ecosystem management is a landscape-level approach to planning for the management of natural resources that emphasizes a central goal of maintaining the sustainability of the ecological system (Christensen et al., 1996; Haufler et al., 2002). The ecosystem management paradigm can be traced back to the writings of Aldo Leopold, who developed the idea of conservation as a way of utilizing natural resources while still maintaining the integrity of the biotic community (Leopold, 1949; Fuhlendorf et al., 2012). Leopold viewed conservation as a scientifically-based form of management that preserved all of the constituent parts of the system (Leopold, 1949). Leopold's view underlies one of the central goals of ecosystem management, which is the conservation of biological diversity.

Ecosystem management and the conservation of biodiversity is central to the practice of sustainable forestry (Carey and Curtis, 1996). As such, the importance of maintaining biodiversity is reflected in the standards of sustainable forestry certification programs such as the Sustainable Forestry Initiative (SFI, 2015) and the Forest Stewardship Council (FSC, 2010). Regional biodiversity is driven by many ecological factors that can be affected by management across a range of spatial and temporal scales (Levin, 2000; Bestelmeyer et al., 2003). Therefore, if sustainable forestry certification standards are to be met it is vital that forest managers understand how ecosystems respond to management decisions across multiple scales (Bestelmeyer et al., 2003).

Ecosystems are heterogeneous in space and time, and ecosystem composition and structure are determined by processes occurring at multiple spatial and temporal scales (Levin, 2000; Fuhlendorf et al., 2006). The dynamics of these processes impact the diversity and complexity of the ecosystem as well as the amount and distribution of resources that species depend on for survival (Wiens, 1976). Ecologists recognize that patterns of spatial and temporal heterogeneity are critical factors determining ecosystem function and sustainability, and provide the underlying basis for maintaining biological diversity (Christensen, 1997; Levin, 2000; Fuhlendorf et al., 2006). The fact that processes determining these patterns of heterogeneity operate at multiple scales means that diversity patterns change across scales as well (Levin, 2000; Crist et al., 2003) which has important implications for landscape-scale conservation planning when biodiversity conservation is a goal.

Biodiversity is a complex idea encompassing many aspects of the ecosystem, but generally refers to the variety of species and the interactions among them across all scales and levels of biological organization (Noss, 1990; Hooper et al., 2005). In concrete terms, changes in biodiversity involve changes in the distribution and abundance of organisms at any scale. These changes can have profound effects on ecosystem properties, functioning, and resilience, and so the human-induced alteration of biodiversity is of primary concern for the continuing production of ecosystem goods and services (Folke et al., 2004; Hooper et al., 2005). The importance of maintaining biodiversity to the functioning and resilience of ecosystems makes it vital to the sustainability of managed forests (Lindenmayer et al., 2000).

In ecosystem management, conservation of biodiversity is usually thought of in terms of preventing reductions in species richness and changes in composition across a region of concern (Carey and Curtis, 1996). Within this context, maintaining the richness and diversity of bird

species on managed forest landscapes has been a continuing focus in forest conservation (Hansen et al., 1991; Sallabanks and Arnett, 2002; Mahon et al., 2016). Birds provide many ecologically and economically important functions in forested ecosystems, such as nutrient transfer, insect control, and seed distribution (Sekercioglu, 2006), as well as being important indicators of ecological conditions and ecosystem integrity (Canterbury et al., 2000; O'Connell et al., 2000). The distribution of bird species and communities across a forested landscape is partly determined by spatial patterns of forest composition and structure (Verschuyl et al., 2008; Mahon et al., 2016), and forest management systems impact these patterns across multiple spatial and temporal scales (Boutin and Hebert, 2002). Therefore, forest management affects bird community diversity at multiple scales, which is an important aspect of sustainable forest management planning.

The effect of pattern and scale on our understanding of how species diversity is established and maintained is a longstanding problem in ecology (Wiens, 1989; Levin, 1992; Levin, 2000). Whittaker (1960) first articulated the link between spatial scale and species diversity by defining alpha (α ; within-unit), beta (β ; among-unit), and gamma (γ ; total) diversity (Gering et al., 2003). The relative contributions of these components to regional diversity can change at different spatial scales, reflecting differences in ecological patterns across scales (Crist et al., 2003). Because patterns of diversity change across scales, the way we define and measure species diversity, and at what spatial scales, is central to our understanding of how management will affect biodiversity. This means that managing forests with the objective of maintaining regional biodiversity (gamma diversity) requires knowledge of how species and communities respond to landscape patterns across multiple spatial scales; from stand-level forest conditions (alpha diversity) to the distribution of community types and successional stages among

landscapes, ownerships, and ecoregions (reflecting beta diversity across multiple spatial scales). Despite this need, there is little research on how patterns of forest conditions across multiple scales affect regional species diversity.

My overall research goal was to investigate the response of bird community diversity to patterns of forest composition and structure across multiple spatial scales on a managed forest landscape. I estimated avian distribution and abundance and forest composition and structure across a range of ecosystem types present in the western Upper Peninsula of Michigan, USA. At the stand level, I focused on attributes of the vegetation that described forest community type and successional stage. At the landscape level, I focused on patterns of heterogeneity in those attributes. The results of my research are presented in 3 separate chapters.

The first chapter investigates how patterns of heterogeneity in stand-level attributes impact patterns of bird community diversity across multiple spatial scales. The problem of pattern and scale pervades our understanding of ecological relationships (Wiens, 1989; Levin, 1992), and different patterns and drivers of diversity emerge at different spatial scales (Levin, 2000; Crist et al., 2003). Therefore, understanding the drivers of regional species diversity requires disentangling the effects of environmental conditions, landscape pattern, and spatial scale. My objective was to investigate how regional bird community diversity was impacted by spatial patterns of vegetation composition and structure across four spatial scales in a managed forest landscape. Specifically, I looked at which spatial scales had the biggest influence on diversity and how environmental heterogeneity within and among spatial units at different spatial scales affected their contribution to regional bird species diversity.

The second chapter demonstrates a novel application of the conservation filters strategy to maintaining avian diversity on managed forests. The coarse filter conservation strategy

focuses on retaining the full range of vegetation community types on the landscape as a way to conserve the vast majority of species, while the mesofilter strategy seeks to maintain important structural features of ecosystems to increase biodiversity on managed areas (Hunter, 2005).

Coarse filters and mesofilters are 2 of the primary strategies used by planners to aid in managing for biodiversity conservation (Schulte et al., 2006). However, these strategies operate at different spatial scales and are traditionally applied independently. In chapter 2 I proposed applying an integrated coarse filter-mesofilter conservation strategy to the problem of maintaining regional bird diversity on a managed forest landscape. This application uses the diversity contribution approach of Lu et al. (2007) to prioritize ecosystem types for conservation (the coarse filter scale) and estimate the compositional and structural attributes of forest stands that have a high relative contribution to regional diversity (the mesofilter scale). My objective was to evaluate a strategy for multi-scale management planning that would aid in the maintenance of biodiversity.

The third chapter looks at monitoring beta diversity in bird communities as an alternative paradigm to species-level strategies for tracking changes in regional biodiversity. Approaches to biodiversity monitoring have typically been focused at the species level, with a great deal of controversy over which species can act as indicators of regional biodiversity (Manley et al., 2004; Noon et al., 2012). Monitoring of beta diversity at multiple scales offers an alternative that focuses on how patterns of diversity change across scales, reflecting environmental changes that drive these patterns (Marsh and Ewers, 2013). I propose a system that focuses on species-level monitoring of bird communities for the estimation of beta diversity using a hierarchical sampling design. More specifically, I investigate the link between beta diversity and environmental heterogeneity and compare the abilities of different sampling designs to estimate patterns of beta diversity across scales. Being able to effectively monitor changes in diversity patterns across

scales is a key to understanding if management systems are accomplishing the objective of maintaining regional diversity.

Collectively, these chapters address questions that are fundamental to the problem of maintaining regional biodiversity on managed forest landscapes. The research presented here represents a step forward in our understanding of how forest management decisions might impact regional bird species diversity. By improving our understanding of how forest patterns at multiple scales impact biodiversity, I have begun to address a critical knowledge gap for making management decisions under the ecosystem management paradigm.

CHAPTER 1

DIFFERENTIAL IMPACTS OF LANDSCAPE PATTERN ON BIODIVERSITY ACROSS MULTIPLE SPATIAL SCALES

ABSTRACT

Addressing the issue of pattern and scale is critical to our understanding of the factors governing the maintenance of biodiversity across the landscape. I examined how patterns of bird species diversity changed across spatial scales in a managed northern forest landscape and investigated how heterogeneity affected the contribution of individual spatial units at multiple scales to regional diversity. I estimated bird community occupancy and abundance for individual sampling plots within a 4000 km² area in the western Upper Peninsula of Michigan, USA. Using a hierarchical sampling design, I applied additive partitioning of species diversity at 4 nested spatial scales: 50-m-radius sampling plots, ecological neighborhoods (1–3 km²), management areas (100–1000 km²), and ecoregions (1000–3000 km²) to determine the scales most important for driving regional diversity. I further estimated the relative contribution of individual spatial units to regional diversity across scales and analyzed how within-unit environmental heterogeneity related to diversity contribution and bird community beta diversity. I found that beta diversity among plots and neighborhoods provided the largest relative contribution to regional diversity. Uniqueness of a sampling plot relative to mean conditions, in terms of vegetation structure and composition, had a significant positive correlation with diversity contribution. Within-neighborhood heterogeneity was positively correlated with beta diversity but showed no relationship to diversity contribution. Conversely, heterogeneity within management areas was positively correlated with diversity contribution. My results illustrate that the effect of landscape pattern on regional species diversity changes across scales, and that

variation in pattern as well as in habitat conditions is important to the maintenance of regional biodiversity.

1.1 INTRODUCTION

The problem of pattern and scale in ecology has long presented challenges to our understanding of how species diversity is established and maintained across the landscape (Wiens, 1989; Levin, 1992; Levin, 2000). The primary issue is that the patterns observed in ecology depend to a large degree on the scales at which they are viewed (Wiens, 1989). Ecosystems are heterogeneous in space and time, and patterns of heterogeneity are determined by processes operating at multiple spatial and temporal scales (Fuhlendorf et al., 2006). The dynamics of these processes determine the amount and distribution of resources that species depend on for survival, and so provide the underlying basis for maintaining biological diversity (Levin, 2000; Fuhlendorf et al., 2006). Because the processes that drive patterns operate at multiple scales, diversity is not distributed evenly across space or time and different patterns and drivers of diversity emerge at different spatial and temporal scales (Levin, 2000; Crist et al., 2003). As a result, addressing the issue of pattern and scale is critical to our understanding of the factors governing the distribution of biodiversity across landscapes (Wiens, 1989; Bestelmeyer et al., 2003).

Whittaker (1960) first articulated the link between spatial scale and species diversity by defining alpha (α ; within-unit), beta (β ; among-unit), and gamma (γ ; total) diversity (Gering et al., 2003). Gamma diversity can be additively partitioned into the alpha and beta components ($\alpha + \beta = \gamma$) so that the contributions of each can be directly compared (Lande, 1996). This approach treats alpha diversity as the average within-unit diversity at a given scale and beta as the average diversity among all units (Lu et al., 2007), and makes it possible to estimate the

relative contributions of alpha and beta diversity across multiple spatial scales (Fig. 1.1; Lande, 1996; Gering et al., 2003). Beta diversity, then, represents the spatial component of diversity and describes the proportion of gamma diversity contributed at a given scale (Gering et al., 2003; Marsh and Ewers, 2013). This means that spatial scales with greater beta diversity have a greater contribution to overall (gamma) diversity, and so heterogeneity among units at those scales should be an important driver of regional diversity. However, diversity is not distributed evenly among units and so the contributions of individual units to total diversity at any scale are not equal (Wagner and Edwards, 2001; Lu et al., 2007).

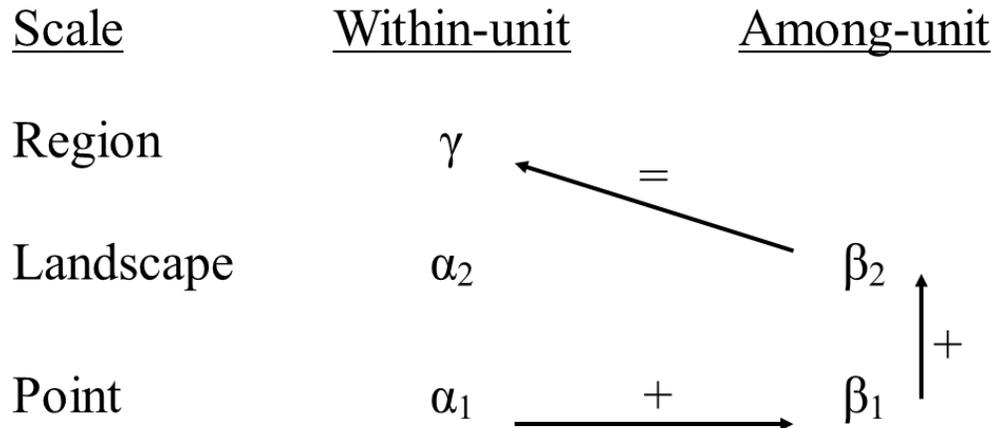


Figure 1.1. Diagram of additive partitioning of species diversity across multiple scales. At the smallest scale, α_1 is the mean within-point diversity and β_1 is diversity among points. Points are nested into landscapes, and so α_2 is the mean within-landscape diversity and $\alpha_1 + \beta_1 = \alpha_2$. The relative contribution of each scale to overall diversity is described by $\alpha_1 + \beta_1 + \beta_2 = \gamma$. Adapted from Gering et al. (2003).

The relative contribution of a spatial unit at a given scale to regional (gamma) diversity depends in part on species richness within that unit (an index of alpha diversity) and in part on how distinct the species composition is from other units at the same scale, which is an aspect of beta diversity (Lu et al., 2007). At the smallest spatial scales, marginality of a spatial unit in terms of habitat conditions may have a large impact on diversity contribution. Marginality refers

to how different the habitat conditions are relative to average conditions among all units. Marginal habitats are likely to support more uncommon species (Wagner and Edwards, 2001; Heino and Gronroos, 2014), thus making them more distinctive in terms of species composition (Fig. 1.2A). At larger scales, there are two potentially contradictory hypotheses about how patterns of heterogeneity influence regional diversity (Fig. 1.2B). On one hand, past research has shown that there is a positive correlation between within-unit environmental heterogeneity and beta diversity (Fuhlendorf et al., 2006; Astorga et al., 2014), and so more heterogeneous units may contribute more to regional diversity through increased niche diversity and greater overall species richness. On the other hand, homogeneous landscapes have been shown to support more specialist species (Devictor et al., 2008; Katayama et al., 2014), which may increase their diversity contribution through greater distinctiveness. It is also possible that the effect of environmental heterogeneity on diversity contribution is scale-dependent, and so different relationships may emerge at different scales. Therefore, understanding the drivers of regional species diversity (gamma diversity) requires disentangling the effects of environmental conditions, landscape pattern, and spatial scale.

The goal of my research was to investigate the impacts of landscape pattern and spatial scale on regional biodiversity. Specifically, I investigated how regional bird community diversity was impacted by spatial patterns of vegetation composition and structure across four spatial scales in a managed forest landscape. My objectives were to examine how regional bird species diversity was partitioned across scales, and investigate how patterns of heterogeneity influenced the contributions of individual spatial units to overall diversity at multiple scales. I hypothesized that marginality of a spatial unit in terms of habitat conditions would be positively correlated

with diversity contribution. I also examined two competing hypotheses (Fig. 1.2B) about the effect of environmental heterogeneity on diversity contribution at 2 different spatial scales.

$$\text{Species richness} + \text{Species distinctiveness} = \text{Diversity Contribution}$$

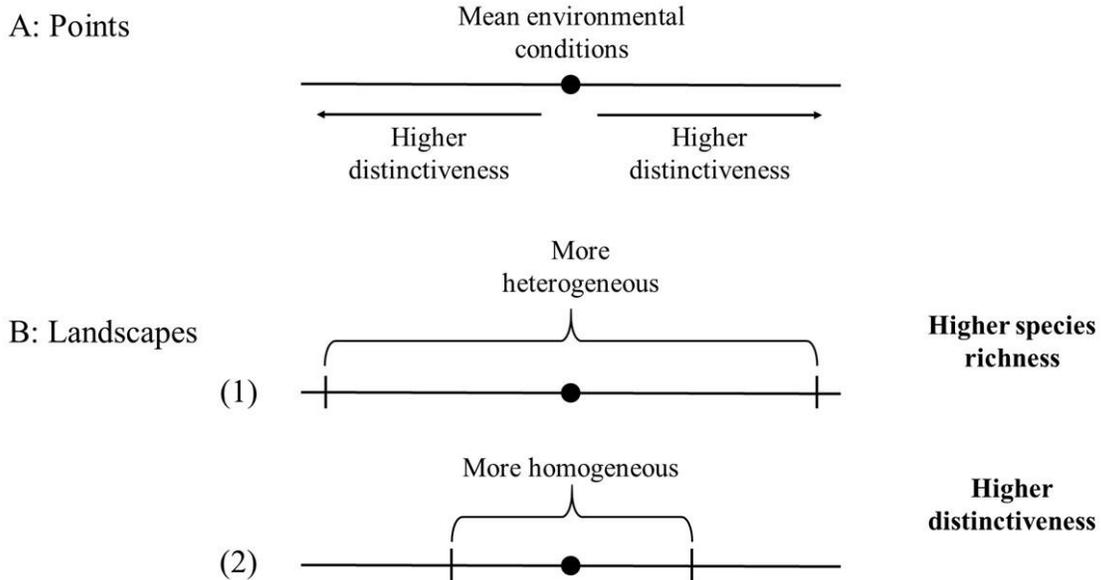


Figure 1.2. Hypotheses about the effect of environmental conditions and heterogeneity on the contribution of a spatial unit to overall regional diversity, where diversity contribution is an additive result of species richness and distinctiveness. A: at the point level, greater distance from mean environmental conditions may increase distinctiveness, leading to higher diversity contribution. B: Competing hypotheses, (1) more heterogeneous landscapes are more diverse, leading to higher species richness and therefore increased contribution, and (2) homogeneous landscapes favor more specialist species, leading to higher distinctiveness and therefore increased diversity contribution.

1.2 METHODS

1.2.1. Study area and sampling design

My study was conducted in a 4000-km² area in the western upper peninsula of Michigan, USA (Fig. 1.3). This is an ecologically-diverse northern forest landscape, with variability driven by glacial topography, soil, and differences in deer browse and forest management across ownerships (Laurent et al., 2005). The region is dominated by upland northern hardwood forests, and also includes upland and lowland conifer, early-successional, and upland mixed forest types

(Millington et al., 2011). Dominant tree species include sugar maple (*Acer saccharum*) in the northern hardwood types, red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) in the upland conifer types, northern white cedar (*Thuja occidentalis*) in lowland forest areas, and aspen (*Populus spp.*) and white birch (*Betula papyrifera*) in the early-successional areas. The majority of the land is state-owned or private industrial forest managed for timber production. The most prominent management practice is selective cutting of northern hardwoods, primarily sugar maple, however plantation management for pine and clear-cut management of aspen also occur (Millington et al., 2011).

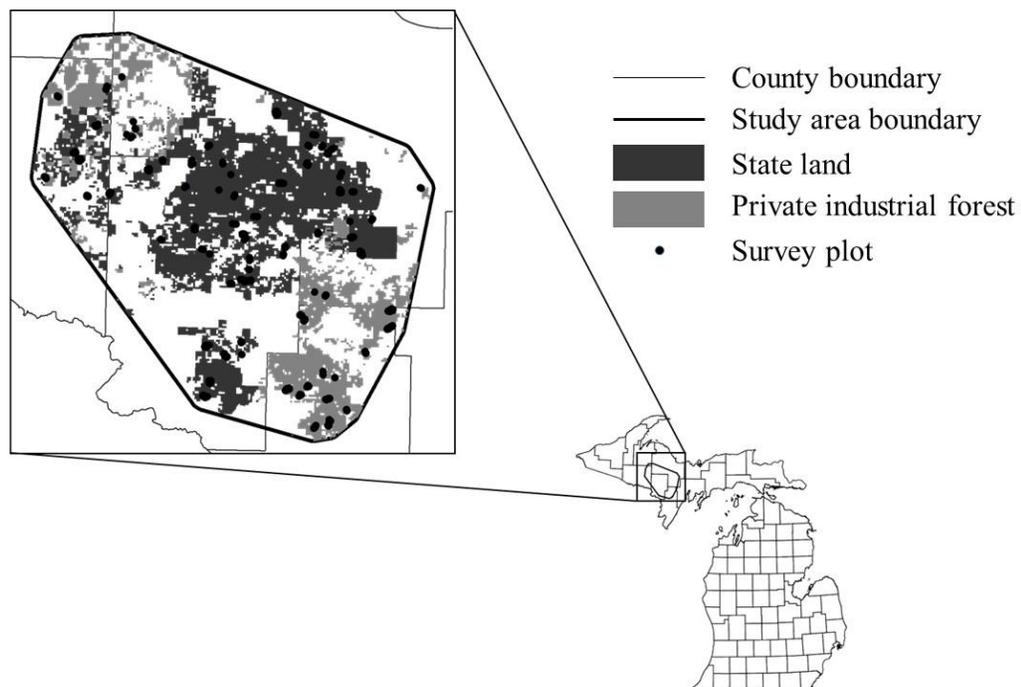


Figure 1.3. Location of the 4000 km² study area in the western Upper Peninsula of Michigan, USA, where bird community and vegetation data were collected in 2001–2003.

I used data on bird species and vegetation variables collected in 2001-2003 from a regional study of bird species in forested habitats (Laurent et al., 2005; Millington et al., 2011). Sample plots were selected according to what was known as the GRAIN protocol (Laurent et al., 2005), where the landscape was gridded into ~1,000 ha sections and 2-8 plots were placed within

randomly selected sections. See Laurent et al. (2005) for more detail on the plot selection protocol. This plot selection system allowed me to impose a hierarchical study design on the data (Fig. 1.4). In this design, individual plots were clustered into ecological neighborhoods where each plot was ≤ 1000 m from at least one other plot. Neighborhoods were nested into management areas defined by the state management system or by private industrial landowners, and management areas were further nested into ecological subsections as defined by McNab et al. (2007), hereafter referred to as ecoregions.

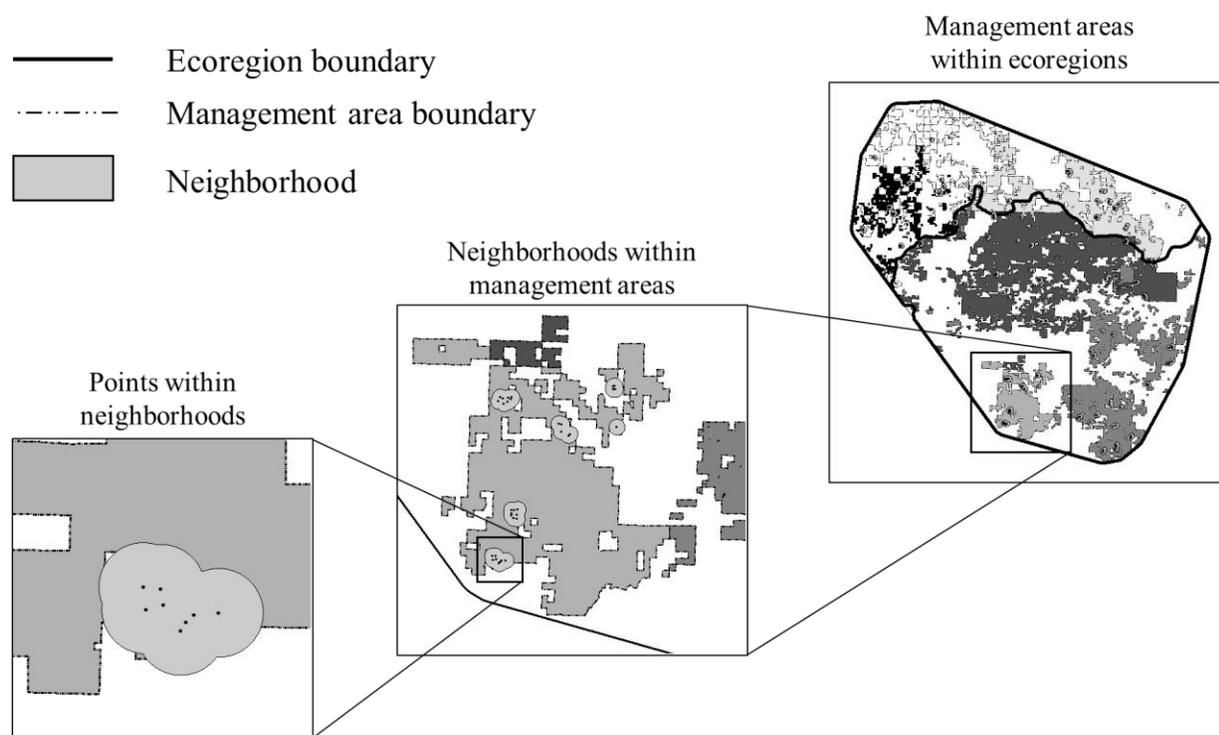


Figure 1.4. Hierarchical cluster sampling design used for estimating bird community diversity across four spatial scales: 50-m-radius sampling plots; ecological neighborhoods where each plot is ≤ 1000 m from at least one other plot; management areas defined by the Michigan Department of Natural Resources or private industrial forest owners; and ecological subsections (here referred to as ecoregions) defined by McNab et al. (2007) nested within the 4000 km² study area.

1.2.2. Bird community data

To characterize bird communities, I used data from fixed-radius point counts (Ralph et al., 1995) collected from all sampling plots in 2001–2003. Each plot was sampled 3–4 times

between June 4 and July 3 (1 plot was visited twice) in either 2001, 2002, or 2003 between sunrise and 5 hr post-sunrise. All birds detected within a 10-min timeframe were recorded to species. I limited my analysis to birds that were detected within 50m of the plot center. Because my objective was to model resident species that could be indicative of community structure and habitat conditions within a plot, I excluded large raptors (families *Accipitridae*, *Cathartidae*, *Falconidae*, *Strigidae*), and large corvids (*Corvus corax* and *C. brachyrhynchos*), because their large home ranges and ubiquitous distributions make their status as residents questionable (Crosby et al., 2015). I also considered species that were detected at <1% of plots, as well as waterfowl (family *Anatidae*) to be incidentals and excluded them from the analysis (Crosby et al., 2015; Mahon et al., 2016).

1.2.3. Forest composition and structure data

I characterized forest composition and structure within each plot using 11 variables derived from measurements taken at the plots concurrent with the bird data and from remotely-sensed elevation data. Basal area (BA; m²/ha) for trees ≥10 cm diameter at breast height (DBH) was measured using a 10-factor prism at 3 subplots within each plot located at the vertices of an equilateral triangle surrounding the plot center. The first point of the triangle was placed 15 m from the center at a random azimuth, and the succeeding points were 25 m from the initial point and 15 m from the center (Laurent, 2005). From the prism measurements I also estimated proportion of BA in conifers, proportion of BA in deciduous trees other than maple, and stem density (trees/ha) of snags ≥25 cm DBH and large trees ≥50 cm DBH (sensu McGee et al., 1999; Millington et al., 2011). Canopy openness was measured at each of the three subplots using a spherical densitometer and calculated as the average of measurements taken while facing in each of 4 directions (north, south, east, and west) (Comeau et al., 1998). Stem density of trees <10 cm

DBH was measured using 5-tree distance sampling (Lessard et al., 2002) at 9 subplots spaced on a 3x3 grid centered on the plot center, with subplots 16 m apart (Laurent, 2005). From this I calculated stems/m² of seedlings (trees ≥ 25 cm tall and < 1.5 m tall) and canopy recruits (trees ≥ 1.5 m tall and < 10 cm DBH), and the proportion of seedlings that were conifers. To characterize size structure of the stand, I calculated an index of diameter distribution as the departure from an idealized even size class distribution of 20 trees per hectare in each 5-cm size class, where the value was the log-transformed chi-square value measuring departure from the idealized distribution (Tyrrell and Crow, 1994). Finally, I indexed soil moisture in each plot using a modification of the topographic wetness index called the SAGA wetness index (SWI; Olaya and Conrad, 2009), where topography was derived from the U. S. Geological Survey National Elevation Dataset 1/3 arc-second 2013 maps (<https://lta.cr.usgs.gov/NED>; accessed August 21, 2016).

1.2.4. Data analysis

To describe patterns of bird diversity, I estimated the occupancy probability and abundance of each species at each plot using a multi-species occupancy-abundance model (Appendix A). Multi-species models have been developed recently as a way to account for detection probability while retaining information on rare species and thus improve estimates of community-level parameters such as species richness (Zipkin et al., 2010; Yamaura et al., 2016). Previous versions of such models have either estimated only occupancy or used global occupancy estimates to account for undetected species and estimated site-level occupancy as a derived parameter based on the assumed mathematical relationship with abundance (Wenger and Freeman, 2008; Yamaura et al., 2016). The model that I developed, however, treats occupancy and abundance as separate but related processes and estimates them individually. There are three

important reasons for doing this. The first is that occupancy patterns and local abundance can arise from separate processes operating at different scales (Wenger and Freeman, 2008), and so may not follow assumed mathematical relationships. The second is that it allows the model to account for the covariance between global occupancy and abundance as a way to improve estimates (Royle and Dorazio, 2009). Finally, estimating occupancy explicitly allows the model to take advantage of spatial correlation in occupancy in order to discriminate between plots (Hines et al., 2010; Mattsson et al., 2013), given that no habitat variables were used in the estimation process. Through this method, I modeled occupancy explicitly at each plot using the spatial correlation among plots within 1000 m to improve estimates (*sensu* Mattsson et al., 2013). I modeled survey-specific detection probability as a linear function of standardized covariates for Julian day (linear and quadratic) and time as measured in minutes from sunrise (Zipkin et al., 2010).

I fit the model in a Bayesian framework with programs R (Version 3.3.0) and JAGS (Version 4.2.0; Plummer, 2003) using the package *runjags* with parallel chains, with uninformative prior distributions for all parameters and hyperparameters. I ran 3 chains of 300,000 iterations with a burn-in of 50,000 and a thinning ratio of 10, and assessed convergence using the Gelman and Rubin R-hat statistic (Brooks and Gelman, 1998). The occupancy-abundance analysis was performed using data from all sample plots where point counts were done. However, for the additive partitioning and beta diversity analyses described below I limited the data set to plots within neighborhoods containing ≥ 3 plots within management areas containing ≥ 3 such neighborhoods (Anderson, 2006; Marsh and Ewers, 2013).

To meet my first objective of examining how bird species diversity is partitioned across scales, I used additive diversity partitioning of species richness, Shannon diversity, and Simpson

diversity. Lande (1996) showed that an index of biodiversity can be additively partitioned across scales provided the index is strictly concave, meaning the value of the index for a pooled set of units is equal to or greater than the average value within those units (Gering et al., 2003). The overall regional diversity of an area is the sum of alpha and beta diversity when alpha is the average within-unit diversity and beta is diversity among units (Lande, 1996). If partitioning is across multiple scales, then alpha diversity at a given scale is the sum of alpha and beta diversity at the next lowest scale. In terms of my study, this means that α_1 represents the average bird species diversity within all plots, β_1 is the diversity among plots, β_2 is the diversity among neighborhoods, β_3 is diversity among management areas, and β_4 is diversity among ecoregions. Therefore, overall bird species diversity of my study area is equal to $\alpha_1 + \beta_1 + \beta_2 + \beta_3 + \beta_4$ (sensu Gering et al., 2003). The 3 indices used in my analysis give information on different aspects of diversity, where richness looks at the pure effect of species and the Shannon and Simpson indices look at combined richness and relative abundance (Gering et al., 2003). The Shannon and Simpson indices are dominance measures that differ in their sensitivity to rare species, where the Shannon index is weighted equally between common and rare species and the Simpson index is weighted towards common species (Gering et al., 2003). I used occupancy estimates to calculate species richness and abundance estimates for Shannon and Simpson Diversity

Lu et al. (2007) extended this additive partitioning approach to calculate the contribution of each spatial unit to regional diversity at each scale. They did this by decomposing diversity contribution into 2 separate components: within-unit diversity ($\alpha_{S(k)}$) and distinctiveness of the species within the unit ($\beta_{S(k)}$) for the k_{th} unit at each spatial scale so that $\alpha_{S(k)} + \beta_{S(k)} = C_{\gamma S(k)}$ where $C_{\gamma S(k)}$ is the contribution of the k_{th} unit to overall species diversity (Lu et al., 2007).

Because of the additive partitioning approach, $\sum C_{\gamma S(k)}$ at each scale is equal to overall regional diversity. Using this approach, I estimated the contribution of each spatial unit to overall regional diversity across all scales used in my sampling design using occupancy estimates.

To meet my second objective of investigating factors that make spatial units at different scales important contributors to biodiversity, I used multivariate dispersion analysis to estimate marginality of habitat conditions, environmental heterogeneity, and bird community beta diversity. Multivariate dispersion arranges environmental or species data in principal coordinate space around a group centroid, where the distance from the centroid acts as a measure of dissimilarity (Anderson, 2006). This allows environmental heterogeneity or beta diversity to be estimated as the average distance of individual units to the group centroid and provides a robust test for differences in beta diversity among spatial units (Anderson et al., 2006).

To test the hypothesis that diversity contribution is positively correlated with the habitat marginality of a plot, I estimated multivariate dispersion among all plots and calculated marginality of a plot as the distance of that plot from the overall centroid. I used linear regression to test for a significant relationship between $\ln(\text{distance to centroid})$ and $\ln(\text{diversity contribution})$. At the neighborhood and management area levels, I used multivariate dispersion analysis to estimate environmental heterogeneity and bird community beta diversity within spatial units and test for significant differences among units. I estimated environmental heterogeneity using the Euclidean distance for the normalized forest composition and structure variables, and beta diversity of bird communities using the Bray-Curtis index for multi-species abundance estimates (Anderson et al., 2006). I then used linear regression to test the hypothesized relationships of environmental heterogeneity with beta diversity and diversity contribution at the neighborhood level. My data did not meet regression assumptions at the

management area level due to a small sample size, so I calculated the correlation coefficients between the variables at this level. Correlation assumes a linear relationship between the variables and that they are drawn from a bivariate normal distribution. Because there may be a relationship between within-unit sample size and the unit's environmental heterogeneity, beta diversity, and diversity contribution I removed any possible effect by using residuals from regressions of each of the 3 estimates against the number of plots within the unit (Veech and Crist, 2007). I performed all analyses using program R. The multivariate dispersion analyses was done using the `betadisper` function in package `vegan` with `type = "centroid"` specified. Statistical significance was assessed at the $\alpha = 0.1$ level.

1.3. RESULTS

1.3.1. Bird community analysis

A total of 433 sample plots were surveyed for bird species in this study, and 59 species met my criteria for being included in the analysis. The distribution of occupancy rates among all species was strongly right-skewed, ranging from 0.015–0.823 with a median of 0.182, showing few common species and a large number of uncommon species. Mean estimated species richness among all sites was 13.869 (variance = 5.306). The subset of the data that was used for the additive partitioning and beta diversity analyses included 232 plots nested within 36 ecological neighborhoods and 5 management areas. Neighborhoods ranged from 105–313 ha with a mean of 174 ha. Management areas ranged from 12,428–75,850 ha with a mean of 45,343 ha.

1.3.2. Additive partitioning

Additive partitioning of species richness indicated that the majority of diversity was contributed at smaller spatial scales (Fig. 1.5). The largest amount of diversity in species richness came from diversity among plots (β_1 ; 37%), followed by diversity among neighborhoods (β_2 ;

34%) and within-plot diversity (α_1 ; 23%). For both the Shannon and Simpson indices the majority of diversity was accounted for by within-plot diversity, although there were differences between the indices with the Simpson index attributing a greater percentage to diversity within plots (Fig. 1.5).

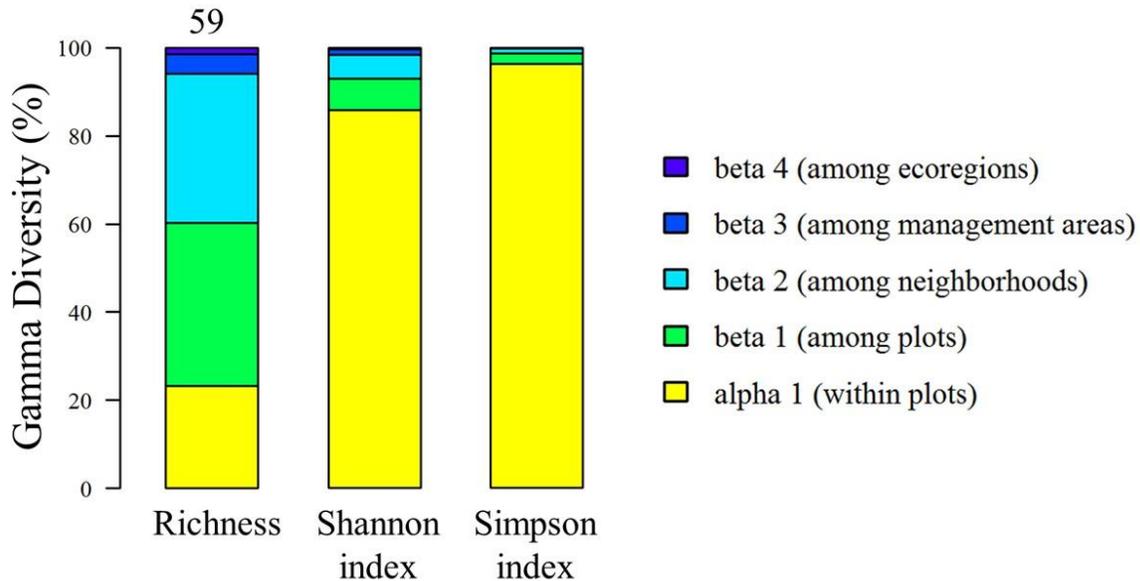


Figure 1.5. Percentages of total bird species diversity contributed by the alpha and beta components across 4 spatial scales, estimated by additive diversity partitioning, for species richness, Shannon diversity, and Simpson diversity. The number at the top of the richness bar is the total number of species detected (gamma diversity).

1.3.3. Heterogeneity and diversity

There was a significant positive relationship between the marginality of habitat conditions within a plot and the contribution of the plot to overall regional diversity ($df = 230$, $\beta = 0.186$, $P < 0.001$; Fig. 1.6), although marginality explained only a small amount of the variability in the model ($R^2 = 0.07$). The tests of multivariate dispersion showed significant differences in environmental heterogeneity among neighborhoods ($df = 35$, $F = 2.886$, $P < 0.001$) but not among management areas ($df = 4$, $F = 1.774$, $P = 0.135$). Bird community beta diversity,

on the other hand, showed significant differences in multivariate dispersion both among neighborhoods ($df = 35$, $F = 2.151$, $P = 0.001$) and among management areas ($df = 4$, $F = 3.278$, $P = 0.012$).

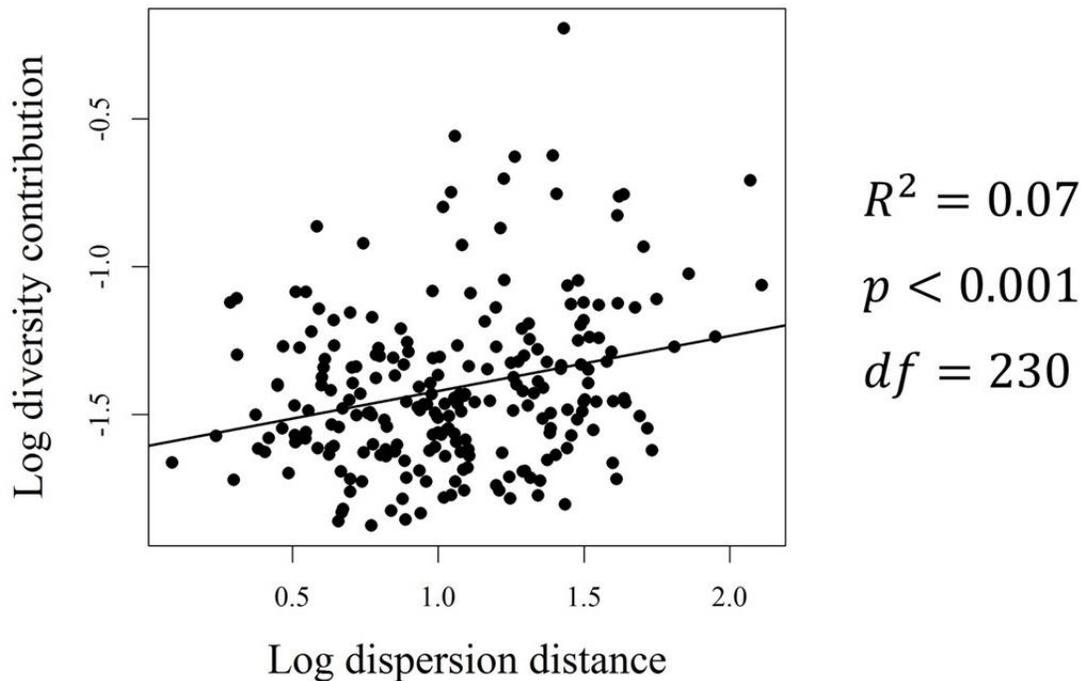


Figure 1.6. Scatterplot and best-fit line showing the relationship between the \ln distance from mean vegetation conditions (dispersion distance) for 50-m-radius plots in a multivariate dispersion analysis and the \ln of the contribution of the plot to regional bird diversity. Dispersion distance is a measure of how marginal a plot was in terms of vegetation composition and structure, relative to all measured plots.

As expected, there was a significant positive correlation between environmental heterogeneity and beta diversity within units at the neighborhood level ($df = 34$, $\beta = 0.024$, $P = 0.003$) and a strong correlation at the management area level ($r = 0.796$) (Fig 1.7). There was no apparent relationship between environmental heterogeneity and diversity contribution at the neighborhood level ($df = 34$, $\beta = -0.007$, $P = 0.938$). However, at the management area level there was a moderately strong positive correlation ($r = 0.668$) (Fig 1.7).

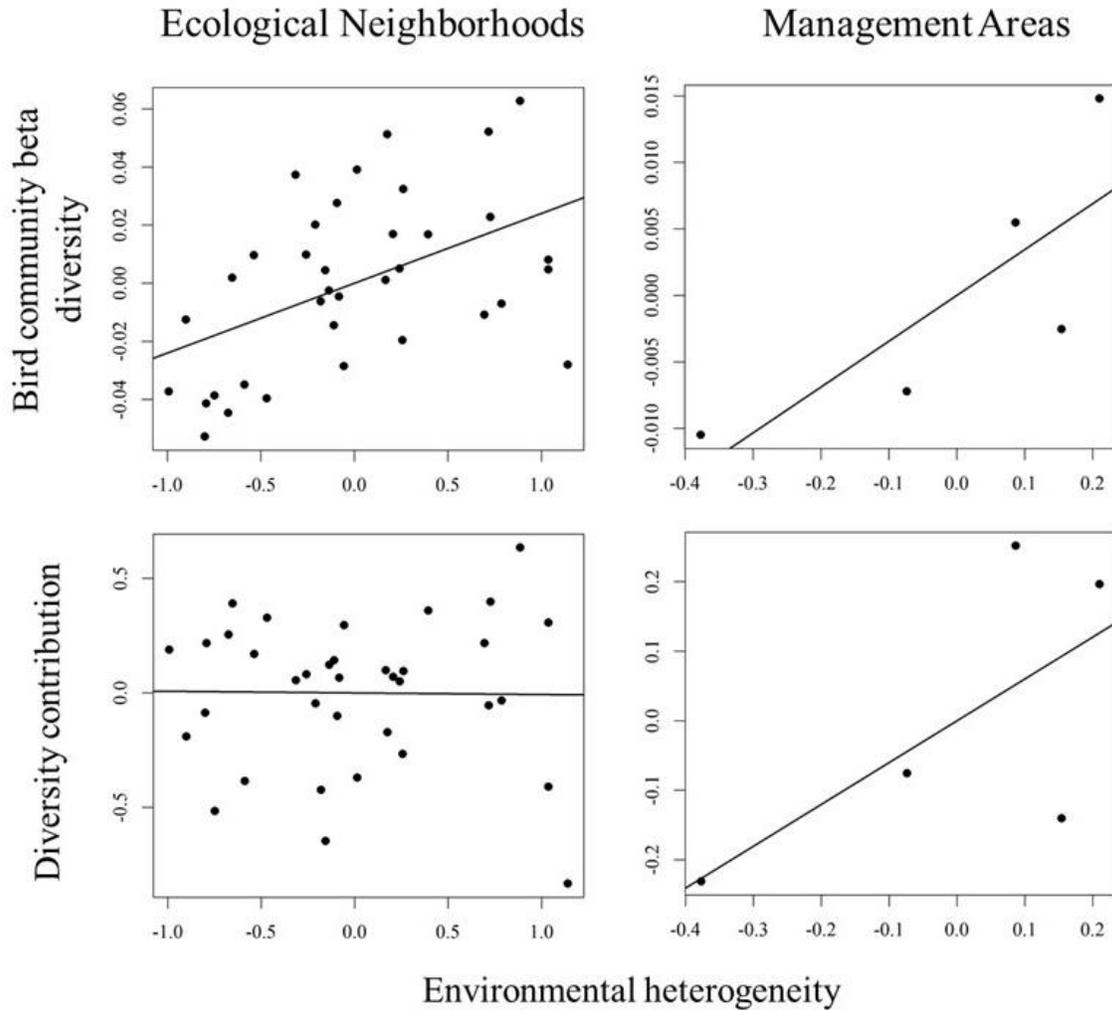


Figure 1.7. Scatterplots with best-fit lines showing the relationship of within-unit environmental heterogeneity with bird community beta diversity and the contribution of a unit to regional diversity.

1.4. DISCUSSION

Understanding how patterns of heterogeneity interact across scales to influence regional species diversity is fundamental to deciphering the processes that generate and maintain biodiversity. My study showed that regional bird species diversity is most strongly influenced by beta diversity at smaller spatial scales (among sampling plots and ecological neighborhoods), and demonstrated the scale-dependent effects of landscape pattern on regional diversity. In particular, there were differential effects of spatial heterogeneity in forest structure and

composition at different scales, illustrating how variation in heterogeneity patterns helps to maintain regional diversity.

The tests of my competing hypotheses, asking whether homogeneous or heterogeneous areas contribute more to regional biodiversity, seemed to show that it depends on the scale at which the heterogeneity is measured. This should not be considered surprising, as scale plays a powerful role in the patterns observed in ecology (Wiens, 1989; Levin, 1992). In my analysis, I did not explicitly define areas as either homogeneous or heterogeneous, but rather estimated the level of heterogeneity as a continuous variable using multivariate dispersion. As such, areas with low heterogeneity were considered more homogeneous and I tested for a correlation between diversity contribution and the level of heterogeneity within a spatial unit. Previous studies of the effects of heterogeneity on biodiversity have used different metrics, such as beta diversity (Fuhlendorf et al., 2006; Astorga et al., 2014), species richness (Morelli et al., 2013; Katayama et al., 2014), or abundance of individual species (Julliard et al., 2006; Devictor et al., 2008), and have tended to view diversity at only a single scale (but see Veech and Crist, 2007). To my knowledge, this study is the first to look at how heterogeneity affects diversity contribution across multiple scales, and illustrates the importance of pattern and scale in the maintenance of biodiversity.

At the smallest scale used in this study, that of an individual survey plot, the relative marginality of a plot in terms of its habitat had a significant impact on its contribution to regional bird species diversity. This is consistent with the results of Wagner and Edwards (2001) who found that habitat specificity values (an alternative measure of diversity contribution) were consistently higher for the least common habitat types in an agricultural matrix. The habitat types used by Wagner and Edwards (2001) were discreet classifications rather than continuous

measures, as in our study. The conclusion, however, is the same: the more marginal the habitat conditions in a spatial unit, the greater it tends to contribute to regional diversity. The fact that marginal habitat conditions support more distinctive species is also consistent with the work of Heino and Gronroos (2014) on the relationship between niche position and occupancy rates of stream invertebrates. Heino and Gronroos (2014) found that stream invertebrates that relied on more marginal habitat conditions also had much lower occupancy rates, meaning that the areas they occupied were likely to have a more distinctive species composition. This relationship between occupancy rate, habitat marginality, and diversity contribution is logically intuitive but to my knowledge has not been examined until now.

The explanatory power of the regression model of the relationship between habitat marginality and diversity contribution was low, however this is not unexpected because of the way diversity contribution is defined and estimated. This is because habitat marginality only speaks to the $\beta_{S(k)}$ component of diversity contribution, which describes the distinctiveness of species in that unit (Lu et al., 2007). The other component of diversity contribution is $\alpha_{S(k)}$, or species richness within the unit. While species distinctiveness is related to habitat marginality, species richness of an equal-sized area may not be (Wagner and Edwards, 2001; Lu et al., 2007). Therefore, it is likely that a large part of the unexplained variability in this model comes from the species richness component of diversity contribution.

At intermediate scales ($\sim 1-3 \text{ km}^2$; the ecological neighborhoods in this study), within-unit heterogeneity had the expected positive correlation with beta diversity but seemed to have no effect on the contribution of a spatial unit to overall regional diversity. This means that high within-unit beta diversity did not necessarily equate with high diversity contribution at the neighborhood scale. There are two possible explanations for this. One is that there is simply no

relationship between within-unit environmental heterogeneity and diversity contribution at the neighborhood scale. On the other hand it may indicate the opposite: that both heterogeneous and homogenous units are important for maintaining biodiversity. This post-hoc hypothesis fits with my finding that beta diversity among neighborhoods had one of the highest impacts on regional diversity in the additive partitioning analysis. The hypothesis is also consistent with the findings of Julliard et al. (2006) and Devictor et al. (2008), showing that specialist and generalist species are spatially segregated between homogenous and heterogeneous landscapes, respectively. This suggests that having both homogenous and heterogeneous units at the neighborhood scale should have a positive impact on regional species richness. If true, this would show that among-unit heterogeneity in landscape pattern at certain scales may be as important as within-unit heterogeneity in habitat conditions.

In contrast to the neighborhood scale, within-unit heterogeneity at the management area scale (~100–1000 km²) appeared to have a positive correlation with diversity contribution. While the lack of a statistical test due to the small sample size did not offer definitive evidence for this, the high correlation coefficient is noteworthy nonetheless. The fact that the relationship between the two patterns appears to change at different scales speaks directly to the scale-dependent nature of many relationships in ecology (Wiens, 1989; Levin, 1992; Levin, 2000). These results may represent an example of separate domains of scale, as proposed by Wiens (1989). Domains of scale are areas of the scale continuum along which a pattern remains constant or changes monotonically, bounded by sharp transitional zones between adjacent domains (Wiens, 1989). Such domains are defined by the scale at which the landscape changes as well as the scale at which species respond to the landscape (Wheatley, 2010). My results suggest that neighborhoods

and management areas may represent separate scale domains in terms of the effect of heterogeneity on bird community diversity contribution.

The fact that I found a difference in bird community beta diversity among management areas, but not in environmental heterogeneity, suggests that there are environmental differences driving species composition among management areas unaccounted for in my analysis. My estimate of heterogeneity using multivariate dispersion examined heterogeneity among plot-level compositional and structural features, which represents only one aspect of landscape pattern. The spatial arrangement of these features relative to each other is likely to have an impact on community composition within management areas (Fahrig, 2003), and this arrangement is not accounted for in the multivariate dispersion analysis. Another possibility is that differences in climate and landform between ecoregions impacted bird community composition enough to create differences that were not reflected in plot-level vegetation measurements.

Similar to Gering et al. (2003), my additive partitioning analysis reflected the differing influences of rare and common species on driving within-unit versus among-unit diversity. Specifically, the fact that the Shannon and Simpson indices were dominated by within-plot diversity while species richness was dominated by beta diversity suggests that common species are the primary drivers of alpha diversity while uncommon species drive beta diversity among units (Crist et al., 2003). Gering et al. (2003) and Crist et al. (2003) found similar patterns for beetle diversity while sampling over a much larger area with substantial differences among ecoregions at the largest scale. The ecological implication of this is that biodiversity is driven by patterns of heterogeneity that maintain common species while creating diversity in uncommon species among sites (Gering et al., 2003). This pattern maintains species richness as well as the functional roles driven largely by common species (Gering et al., 2003).

Variation in patterns across multiple spatial scales provides the underlying foundation for maintaining biological diversity by magnifying underlying patterns of environmental variability (Levin, 2000). Historically, however, studies of biodiversity have focused on alpha and gamma diversity at a single spatial scale with little research on how patterns occurring at different scales impact regional diversity (Marsh and Ewers, 2013). My research shows that the environmental patterns contributing to diversity change across scales, and that variability in patterns of heterogeneity is important to the maintenance of regional biodiversity.

CHAPTER 2

APPLYING CONSERVATION FILTERS TO CONSERVING BIRD DIVERSITY ON MANAGED FORESTS

ABSTRACT

Maintaining the richness and diversity of bird species on working forest landscapes has long been one of the major themes in sustainable forest management. However, managers face a great deal of uncertainty as to the impacts of management decisions on species diversity because of the difficulty of accounting for all species simultaneously. This difficulty has led to the development of conservation strategies to be used as tools in the decision-making process. Among these strategies, the use of conservation filters has been prominent over the last several decades. I demonstrate a novel application of the conservation filter strategy to the problem of maintaining bird species diversity on managed forest landscapes utilizing a diversity contribution approach. Using data on bird community composition, I estimated the relative contributions of individual plots to regional bird species diversity on a 4,000 km² area in the western Upper Peninsula of Michigan managed primarily for timber production. At the coarse filter level I was able to identify community types and areas that were priorities for conservation. At the mesofilter level, I described compositional and structural attributes of high value sites within 6 different community types relative to average sites. I identified bird species that were positively associated with high-contribution sites as well as indicator species for high value sites within the community types. I found that the conservation value of a community type was inversely proportional to its representation on the landscape. There were differences among community types in the relationship between diversity contribution and forest composition and structure variables, but the commonality was an increase in structural complexity within high value plots.

There was a significant negative relationship between species overall abundance and the probability of being positively associated with high value sites. Managers can use this application of the conservation filter strategy as a planning tool in the face of uncertainty about how management decisions affect regional biodiversity.

2.1 INTRODUCTION

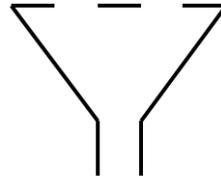
The shift in forest management goals over the past several decades to meet societal demands for more non-timber benefits, such as wildlife habitat and biodiversity conservation, has led to a move towards ecosystem-based approaches to management (Zollner et al., 2008). Ecosystem management is a landscape-level approach to planning for the management of natural resources that emphasizes a central goal of maintaining the sustainability of the ecological system (Christensen et al., 1996; Haufler et al., 2002). One of the primary ecological goals of ecosystem management is the maintenance of regional biodiversity, which is typically defined as preserving the full complement of native species and biological processes within the area of interest (Haufler et al., 2002). Meeting this objective in forests managed for timber production, however, is a complex process that requires long-term planning at multiple scales (Haufler et al., 2002; Crous et al., 2013). A large part of the difficulty of planning for the conservation of multiple species across a heterogeneous landscape is that managers are often charged with making decisions in the face of incomplete information on how those decisions might impact biodiversity (Schulte et al., 2006).

Within the ecosystem management context, maintaining the richness and diversity of bird species has continued to be one of the major themes in sustainable forest management (Hansen et al., 1991; Sallabanks and Arnett, 2002; Mahon et al., 2016). Birds provide many ecologically and economically important functions in forested ecosystems, such as nutrient transfer, insect

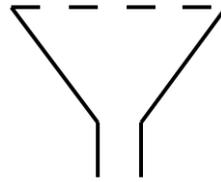
control, and seed distribution, as well as being important indicators of ecological conditions (e.g. vegetation composition and structure, landscape composition) (Canterbury et al., 2000; O'Connell et al., 2000; Sekercioglu, 2006). The distribution of bird species and communities across a forested landscape is determined by spatial patterns of forest composition and structure (Verschuyl et al., 2008; Mahon et al., 2016), and forest management systems impact these patterns across multiple spatial and temporal scales (Boutin and Hebert, 2002).

A great deal of the literature on how forest management impacts species diversity focuses on forest fragmentation and species richness (e.g. O'Connell et al., 2000; Zipkin et al., 2009), or uses coarse-resolution cover types to predict occupancy (e.g. Schwenk and Donovan, 2011; Mahon et al., 2016). As a result, there is little information on how the majority of species respond to forest composition and structure across a range of forest community types (but see Cushman and McGarigal, 2004). This lack of information makes it impossible to account for each species individually in management planning (Noss, 1987), and leads to a great deal of uncertainty about how management decisions will impact regional species diversity. Consequently, planners and managers have developed a number of scientifically-based conservation strategies that can be used as tools for conservation planning in the face of this uncertainty (Noss, 1987; Schulte et al., 2006; Zenner et al., 2010).

Coarse filter: Ecosystem type



Meso-filter: Structure



Fine filter: Species-level habitat

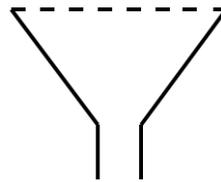


Figure 2.1. Operational scales of the conservation filter concept. The coarse filter seeks to conserve most species by retaining the full range of community types within a region. The mesofilter increases the conservation value of community types by retaining structures and processes that may be overlooked at the coarse filter level. The fine filter consists of species-level conservation efforts aimed at rare or highly specialized species that may fall through the higher-level filters (adapted from Zenner et al., 2010).

The coarse filter–fine filter approach to conservation (Fig. 2.1) has been one of the primary conservation strategies in North America since being introduced by The Nature Conservancy (TNC) in the 1980’s (Noss, 1987; Schulte et al., 2006; Beier et al., 2015). The original conception of this strategy (Noss, 1987) is based on the idea that a majority of species can be conserved by creating a reserve network that retains the full complement of native community types within a region (Hunter et al., 1988). The reserve network represents a coarse filter, and is the most commonly-applied strategy in large-scale forest conservation planning (Schulte et al., 2006). Even then, a certain number of rare or endangered species fall through this coarse filter, and thus require specialized management practices to maintain their populations (Noss, 1987). This specialized management represents the fine filter, and extends to areas outside the coarse filter network to protect vulnerable species (Hunter, 2005). Hunter (2005) introduced

the complementary idea of mesofilter conservation, which requires conserving important structural features within managed areas outside of the coarse filter reserve network. The mesofilter is seen as a way of extending coarse filter efficiencies to many species that do not warrant fine filter treatment by maintaining features and processes that increase species richness of areas within the matrix. In managed forests, these strategies are traditionally applied independently, with coarse filters applied at the regional level to ensure that all native community types are represented and the mesofilter strategy applied to stand-level structural retention (Lindenmayer et al., 2006; Villard and Jonsson, 2009). However, explicitly combining 2 or more of these strategies may offer advantages for conservation planning on managed forests.

In working forest landscapes, where the majority of the land is managed for timber production under multiple ownerships, creating a connected reserve network representing all native community types may not be a realistic goal. To address this issue, Haufler et al. (1996) proposed an alternative approach to the coarse filter as providing adequate distribution of all community types across the landscape based on their historical range and variability. The ability to maintain desired distributions of all community types within a region, however, might not be possible in regions where there are multiple, fragmented ownerships with differing priorities and management objectives. In such a case, a modified version of this coarse filter approach might be more appropriate. Because some community types may have a larger impact on biodiversity, either because of their relative scarcity or because they support higher species richness (Lindenmayer and Cunningham, 2013), the coarse filter can be re-conceived as a system of prioritizing community types in terms of their conservation value. Similarly, mesofilter strategies can go beyond simple structural elements to incorporate multiple compositional and structural attributes that increase the conservation value of an area through increased complexity or

ecological distinctiveness (Crosby, chapter 1 this dissertation; Lindenmayer et al., 2006).

Implementing a strategy that combines these modified coarse filter and mesofilter concepts requires a method for estimating the value of individual community types or areas.

Lu et al. (2007) proposed a method for estimating the contribution of individual areas to overall regional diversity as a combination of the number of species in that area (species richness) and how uncommon those species are throughout the region (distinctiveness relative to other plots). The diversity contribution approach uses data on community composition from a given taxon to estimate the additive contributions of all sampled areas to regional diversity of that taxon (Lu et al., 2007). In practice, this approach provides a quantitative method for ranking specific areas according to their importance for regional diversity. Explicitly applying the diversity contribution approach within the context of the combined filter strategy can, therefore, be used as a tool for maintaining bird species diversity on working forest landscapes.

My goal was to apply an integrated coarse filter-mesofilter conservation strategy to the problem of maintaining bird species diversity on a managed forest landscape. At the coarse filter level, my objective was to compare the conservation value of the primary community types on the landscape. At the mesofilter level, my objective was to investigate the compositional and structural features of sites with a high contribution to regional diversity relative to other sites within the same community type. Finally, at the species level my objective was to examine which species had the strongest relationship with high-contribution sites, and if any species could act as indicators of high-contribution sites within ecosystem types.

2.2 METHODS

2.2.1. Study area and plot selection

To investigate the use of the combined filter approach in forest management, I used data from a 4000-km² area in the western upper peninsula of Michigan, USA (Fig. 2.2). This is an ecologically-diverse northern forest landscape, with variability driven by glacial topography, soil, and differences in deer browse and forest management across ownerships (Laurent et al., 2005). The region is dominated by upland northern hardwood forests, and is interspersed with upland and lowland conifer, early-successional, and mixed upland forest types (Millington et al., 2011). Dominant tree species include sugar maple (*Acer saccharum*) in the northern hardwood types, red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) in the upland conifer types, northern white cedar (*Thuja occidentalis*) in lowland forest areas, and aspen (*Populus spp.*) and white birch (*Betula papyrifera*) in the early-successional areas. There are also small amounts of non-forested areas throughout the region.

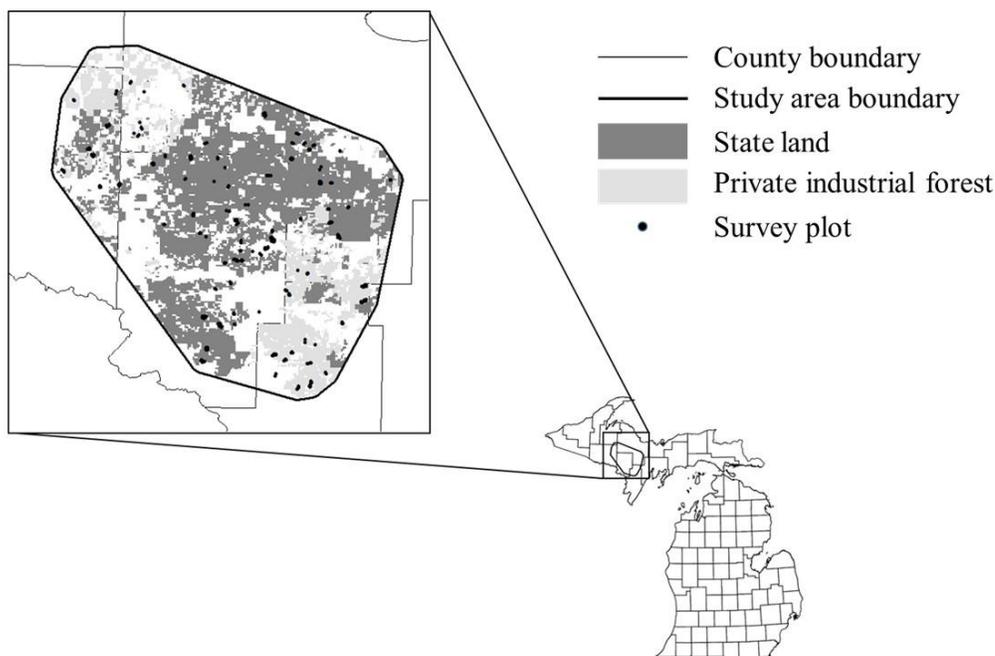


Figure 2.2. Study area in the western Upper Peninsula of Michigan, totaling 4000 km², sampled for bird species and forest composition and structure in 2001–2003.

The majority of the land is state-owned or private industrial forest managed for timber production, and northern hardwood stands are primarily mature second-growth. The most prominent management practice is selective cutting of northern hardwoods, primarily for sugar maple, although plantation management for pine and clearcut management of aspen also occurs (Millington et al., 2011). I used data on bird species and vegetation variables collected in 2001-2003 from a large-scale study of bird species in managed forests (Laurent et al., 2005; Millington et al., 2011). Sample plots were selected according to what was known as the GRAIN protocol (Laurent et al., 2005), where the landscape was gridded into ~1,000 ha sections and 2-8 plots were placed within randomly selected sections.

2.2.2. Bird community and forest data

Data on bird community composition at each plot were collected using fixed-radius point counts (Ralph et al., 1995). Each plot was sampled 3–4 times between June 4 and July 3 (1 plot was visited twice) in either 2001, 2002, or 2003. Point counts were conducted between sunrise and 5 hr post-sunrise, and all birds seen or heard within a 10-min period were recorded and assigned to distance bands of 30 m, 50 m, 100 m, and >100 m from the plot center. I limited my analysis to birds recorded within 50 m of the plot center to coincide with the scale at which vegetation data were collected. Because the purpose of my analysis was to describe bird community composition of resident species that would be indicative of habitat conditions within a plot, I considered species that were detected at <1% of plots, as well as waterfowl (family *Anatidae*), to be incidental detections and excluded them from the analysis (Crosby et al., 2015; Mahon et al., 2016). I also excluded large raptors (families *Accipitridae*, *Cathartidae*, *Falconidae*, *Strigidae*) and large corvids (*Corvus corax* and *C. brachyrhynchos*) because their

large home ranges and ubiquitous distributions make their status as residents difficult to verify (Crosby et al., 2015).

To characterize environmental conditions within each plot I estimated 6 variables describing forest composition and structure derived from measurements taken at the plots concurrent with bird surveys. Basal area (BA; m^2/ha) by species for trees ≥ 10 cm diameter at breast height (DBH) was measured using a 10 basal area factor prism at 3 subplots within each plot located at the vertices of an equilateral triangle surrounding the plot center. The first point of the triangle was placed 15 m from the center at a random azimuth, and the succeeding points were 25 m from the initial point and 15 m from the center (Laurent, 2005). From the prism measurements I estimated total BA, proportion BA in conifers, stem density (trees/ha) of snags ≥ 25 cm DBH and large trees ≥ 50 cm DBH (sensu McGee et al., 1999; Millington et al., 2011). I also estimated the proportion of BA in species of trees used to describe specific community types (see below). Stem density of trees < 10 cm DBH was measured using 5-tree distance sampling (Lessard et al., 2002) at 9 subplots spaced on a 3x3 grid centered on the plot center, with subplots 16 m apart (Laurent, 2005). From this I calculated stems/ m^2 of seedlings (trees ≥ 25 cm tall and < 1.5 m tall). To characterize size structure of the stand, I calculated an index of diameter distribution as the departure from an idealized even size class distribution of 20 trees per hectare in each 5-cm size class. where the value was the log-transformed chi-square value measuring departure from the idealized distribution (Tyrrell and Crow, 1994). This metric is an index of the distribution of trees in different size classes within the stand, and is strongly correlated with stand age among northern hardwood stands in Michigan (Tyrrell and Crow, 1994).

2.2.3. Bird species analysis and plot-level diversity contribution

I estimated the occupancy probability and abundance for each species at each plot using an integrated, multi-species occupancy-abundance model. These estimates provided plot-level occupancy and abundance estimates without the use of habitat variables (Appendix A). Previous versions of such models have either estimated only occupancy or used global occupancy estimates to account for undetected species and estimated plot-level occupancy as a derived parameter based on its assumed mathematical relationship with abundance (Wenger and Freeman, 2008; Yamaura et al., 2016). My model treats occupancy and abundance as separate but related processes, and incorporates the covariance between occupancy and abundance directly into the model (Royle and Dorazio, 2009). Through this method, I modeled occupancy explicitly at each plot using the spatial correlation among plots within 1000 m to improve estimates (*sensu* Mattsson et al., 2013). I modeled survey-specific detection probability as a linear function of standardized covariates for Julian day (linear and quadratic) and time as measured in minutes from sunrise (Zipkin et al., 2010).

I fit the model in a Bayesian framework with programs R (Version 3.3.0) and JAGS (Version 4.2.0; Plummer, 2003) using the package `runjags` with parallel chains, with uninformative prior distributions for all parameters and hyperparameters. I ran three chains of 300,000 iterations with a burn-in of 50,000 and a thinning ratio of 10, and assessed convergence using the Gelman and Rubin R-hat statistic (Brooks and Gelman, 1998). The occupancy-abundance analysis was performed using data from all sample plots where point counts were conducted. However, for further analyses we used only the subset of plots where vegetation data were collected.

To estimate the relative contribution of each plot to overall regional bird diversity, I applied my estimates of occupancy probability to the method developed by Lu et al. (2007). This method estimates the contribution of plots to regional diversity by decomposing diversity contribution into 2 separate components: within-unit diversity ($\alpha_{S(k)}$) and distinctiveness of the species within the unit ($\beta_{S(k)}$) for the k th unit so that $\alpha_{S(k)} + \beta_{S(k)} = C_{\gamma S(k)}$, where $C_{\gamma S(k)}$ is the contribution of the k th unit to overall species diversity (γ ; gamma diversity) (Lu et al., 2007). This is an additive approach, so that $\gamma = \sum C_{\gamma S(k)}$, meaning that $C_{\gamma S(k)}$ represents the diversity contribution relative to all other plots within the sample. I then designated high-contribution plots as those above the third quantile in diversity contribution scores (i.e. the top 25% of plots in terms of diversity contribution).

2.2.4. Coarse filter: identifying high-value community types

To meet my first objective of estimating the relative conservation value of different community types, I designated each plot as one of 8 primary community types found in the region. These types were derived from definitions from the Michigan Department of Natural Resources (MDNR) in the Integrated Forest Monitoring Assessment and Prescription (IFMAP) protocol (Space Imaging Solutions, 2001) as: Non-forested, Northern Hardwood Association, Upland Conifer, Upland Mixed, Early-successional, Cedar, Lowland Conifer, and Other. Non-forested areas were those with <25% canopy cover of trees. Northern Hardwood Association was defined as having a combination of maples (*Acer spp.*), American beech (*Fagus grandifolia*), basswood (*Tilia americana*), white ash (*Fraxinus canadensis*), cherry (*Prunus spp.*), and yellow birch (*Betula alleghaniensis*) >60% of the basal area. Upland conifer was defined as having a combination of balsam fir (*Abies balsamia*), European larch (*Larix decidua*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*), and

eastern hemlock (*Tsuga canadensis*) >60% of the basal area. Upland Mixed forest contained between 40% and 60% conifers. Early-successional forest had >40% of the basal area in aspen (*Populus spp.*) and white birch (*Betula papyrifera*). Cedar consisted of >50% of the basal area in Northern White Cedar, and Lowland Conifer had >50% of basal area in Tamarack (*Larix laricina*) and Black Spruce (*Picea glauca*). Other was defined as forested areas that did not fit any of the other categories.

To estimate the relative conservation value of each community type, I created an index from the ratio of the proportional representation of each community type among high-contribution plots to the proportional representation among all plots:

$$Contribution\ index_i = \frac{prop_i(High)}{prop_i(All)}$$

where “High” refers to the high-contribution plots and “All” refers to all plots, for community type *i*. If the value of the index was 1, the proportional representation of that ecosystem type among high-contribution plots was equal to its proportional representation among all plots, and it could be thought of as neutral in terms of conservation value. An index value greater than 1 would suggest an ecosystem type with high conservation value, and vice versa.

2.2.5. Mesofilter: attributes of high-contribution plots

To meet my objective of identifying important compositional and structural attributes at the mesofilter level, I compared forest measurements between high-contribution plots and the remaining plots within the 6 forested community types (Northern Hardwood, Upland Conifer, Upland Mixed, Early Successional, Cedar, and Lowland Conifer). I did not perform formal statistical tests for differences in mean values because 4 of the 6 community types were represented by fewer than 20 plots, leading to small sample sizes for comparison and a subsequent inability to meet statistical assumptions. Instead I compared medians and

interquartile ranges between high-contribution plots and the remaining plots for the 6 measured variables representing stand compositional and structural attributes. I considered there to be a strong relationship between a variable and diversity contribution if interquartile ranges did not overlap between average and high-contribution plots, and a moderate correlation if at least one of the interquartile ranges did not overlap with the median of the other category.

2.2.6. Bird species relationships to high-contribution plots

To examine the species-level relationship of birds to high-contribution plots, I tested which species had higher abundances in high-contribution plots and examined whether any species could act as indicators of high-contribution plots within each ecosystem type. I tested for a significant difference in individual species abundances between high-contribution plots and average plots using a Student's t-test with unequal variances. I also used logistic regression to test for a relationship between overall mean abundance among plots for each species and the probability of having a higher mean abundance in high-contribution plots.

To examine if species could be used as indicators of high-contribution plots within forested community types, I used indicator analysis with two-species combinations (De Cáceres et al., 2012). This technique allows for the possibility that the joint occurrence of ≥ 2 species may be a more reliable indicator than the target plot is a member of a discreet group, but includes single species in its rankings of indicator values as well (De Cáceres et al., 2012). Within each forested community type, I tested which species or combinations of species might act as indicators of high-diversity plots relative to average plots.

2.3 RESULTS

2.3.1. Bird community composition

A total of 433 sample plots were surveyed for bird species in this study, and 59 species met the criteria for being included in the analysis. There were 335 plots at which vegetation data were collected to be used in our diversity contribution analysis. The distribution of occupancy rates among these plots was strongly right-skewed, ranging from 0.007–0.894 with a median of 0.170, showing few common species and a large number of uncommon species. Mean estimated species richness among all plots was 13.767 (variance = 5.081).

2.3.2. Coarse filter: identifying high-value community types

The coarse filter analysis found large differences among community types in terms of their conservation value (Fig. 2.3). The dominant ecosystem type on the landscape was Northern Hardwoods, representing 48% of all plots in the dataset. Besides Early-successional, no other ecosystem type constituted >7% of the dataset, with the least common being Cedar (2.7%) and Lowland Conifer (2.4%). The contribution index values for each ecosystem type were inversely proportional to their representation on the landscape, although this was not a constant relationship (Fig. 2.3). Upland Conifer, Upland Mixed, Cedar, and Non-forested all had contribution index values >2, which corresponded with their low occurrence rates in the dataset. Northern Hardwoods and Early-successional both had contribution indices of <1.

The total number of high-contribution plots was not evenly distributed across community types either, however the relationship was less consistent than with the contribution index. Despite its low relative conservation value, Northern Hardwoods supplied the greatest number of high-contribution plots at 25. Early-successional, Upland Conifer, and Non-forested areas

supplied 10, 11, and 11 high-contribution plots, even though they represented 20.3%, 5.7%, and 6% of the plots, respectively.

2.3.3. Mesofilter: attributes of high-contribution plots

The comparison of forest compositional and structural attributes between high-contribution plots and the remaining plots showed a great deal of variation among community types (Table 2.1; Fig. 2.4). On the whole, high-contribution plots tended to have lower basal area than average, with the effect being most pronounced among Northern Hardwood, Cedar, and Lowland Conifer community types (Fig. 2.4). For the proportion of basal area in conifer, the only community type that showed a moderate difference was Northern Hardwoods, where the median value among average plots was 0.0 and among high-contribution plots was 0.02. Community types that had a strong conifer component showed moderate negative relationship, suggesting that greater numbers of deciduous trees had a positive effect on diversity contribution in these community types.

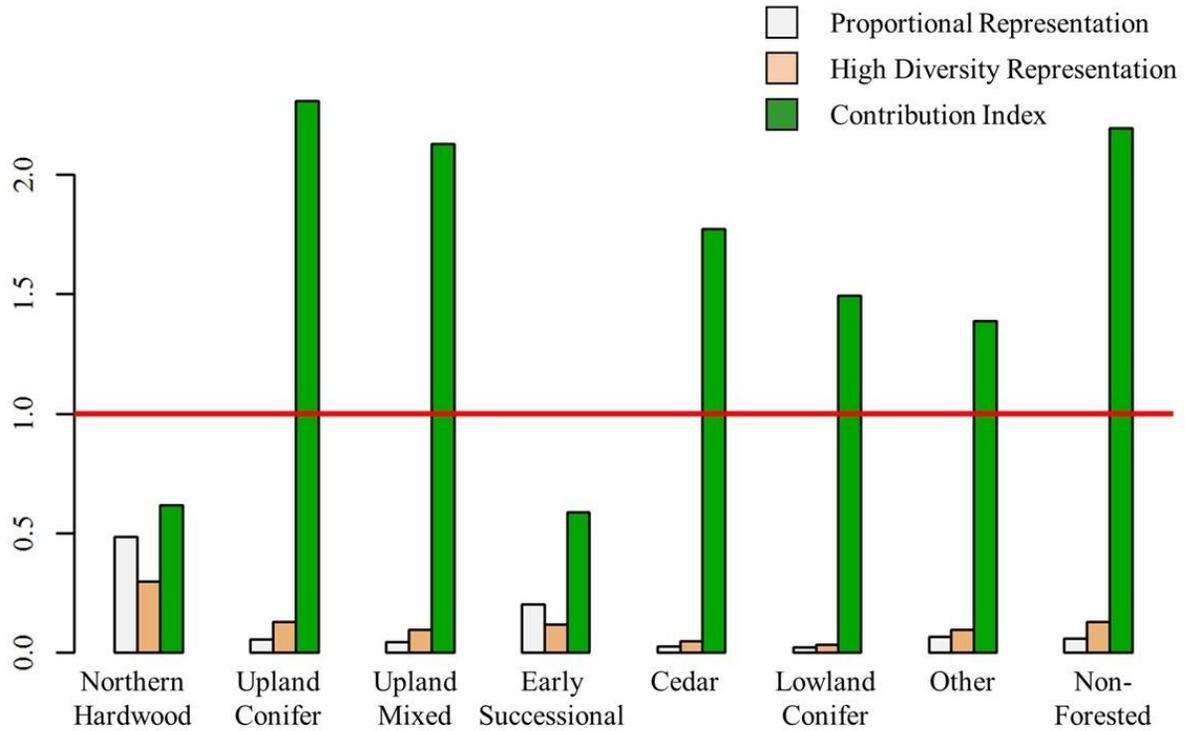


Figure 2.3. Comparison of conservation index values between forested community types in the western Upper Peninsula of Michigan relative to bird species diversity. The light gray bars represent the proportional representation of each community type in the dataset, pink bars represent their proportional representation among plots in the upper 25% of diversity contribution. Conservation value is represented by the green bars as the contribution index calculated by dividing the pink bar by the gray bar.

Community Type	Total Count	High-Contribution Count	Total Basal Area	Proportion BA in Conifer	Large Tree Density	Snag Density	Seedling Density	Diameter Distribution
Northern Hardwood	162	26	— Moderate ^a	+ Moderate	+ 0	0	+ Moderate	— Moderate
Upland Conifer	19	11	— Moderate	— Moderate	0	—	+ Moderate	+ Moderate
Upland Mixed	15	8	— Moderate	— Moderate	+ Moderate	0	+ Moderate	+ Moderate
Early-successional	68	10	+ Moderate	0 ^c	0	0	+ Moderate	— Moderate
Cedar	9	4	— Strong ^b	— Moderate	+ Moderate	+ Moderate	+ Moderate	+ Moderate
Lowland Conifer	8	3	— Strong	+ Moderate	0	0	+ Strong	— Strong

Table 2.1. Total number of plots among six primary forested community types, number of plots with a high contribution to overall regional diversity, and the direction (+ or —) and strength of the relationship between forest compositional and structural variables and diversity contributions[†].

[†]Based on the difference between median and interquartile range between high-contribution plots and average plots.

^aIndicates that at least one of the interquartile ranges did not overlap with the median of the other category.

^bIndicates that interquartile ranges did not overlap between high-contribution plots and average plots.

^cMedians of both categories were equal to zero.

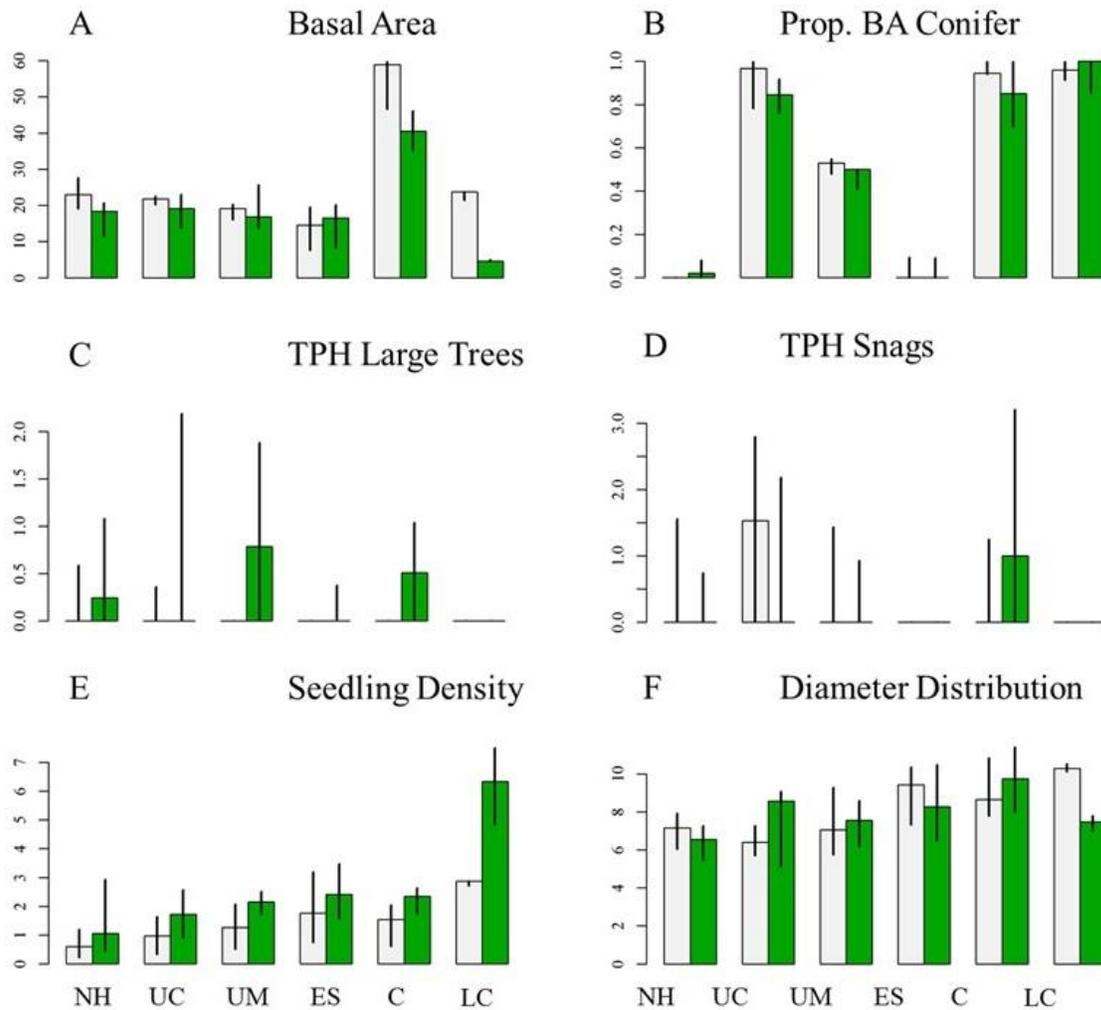


Figure 2.4. Median (bars) and interquartile range values (black lines) of forest compositional and structural variables between plots with high relative contribution to regional bird diversity (the top 25%; green bars) and remaining plots (gray bars) within the same community type. Community types are coded as: NH = Northern Hardwood; UC = Upland Conifer; UM = Upland Mixed; ES = Early-successional; C = Cedar; and LC = Lowland Conifer. Basal area (BA) is measured in m²/ha. Large trees (≥ 50 cm diameter) and snags (standing dead trees ≥ 25 cm diameter) are measured in trees per hectare. Seedling density (trees ≥ 25 cm tall and < 1.5 m tall) is measured in stems/m². Diameter distribution is the $\ln \chi^2$ departure from an idealized even distribution of 20 trees per hectare in each 5-cm size class.

The density of large trees ≥ 50 cm DBH showed a positive relationship with diversity contribution among the Northern Hardwood, Upland Mixed, and Cedar ecosystem types, however the relationship was weak in Northern Hardwoods and only moderate in the 2 others (Table 2.1). These large trees were not common in any of the community types, and median

values were 0 in 3 of the 6 types. The upper end of the interquartile range was substantially higher in high-contribution plots among all community types except Lowland Conifer (Fig. 2.4). The density of snags ≥ 25 cm DBH was lower than that of large trees (Fig. 2.4), and showed almost no relationship with diversity contribution in any of the community types. The median value was 0 in all but 2 instances and interquartile ranges showed little variation between average and high-contribution plots in any of the community types. The only exceptions were in Upland conifers, where snag density was much higher among average plots, and Cedar, where snag density was much higher among high-contribution plots, with both relationship being weak.

Seedling density showed a positive relationship with diversity contribution among all community types. The relationship with diversity contribution in Lowland Conifer was considered strong, and all others were moderate except for Early-successional and Northern Hardwoods. Median values of seedling density were, on average, 1.8 times higher in high-contribution plots and the low end of the interquartile range averaged 2.2 times higher. Finally, diameter distribution did not vary greatly between average and high-contribution plots, with the only real exception being among Lowland Conifer plots. The Lowland Conifer plots showed that high-contribution plots had smaller departure from the low-density, even-age-class distribution as measured by the chi-square value. Upland Conifer also showed a moderate effect, with high-contribution plots showing a greater departure from the idealized distribution.

Species			Mean Abundance	
AOU Code	Common Name	Scientific Name	Average Plots	High-contribution Plots
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	0.090	0.600
AMGO	American Goldfinch	<i>Spinus tristis</i>	1.662	2.545
AMRE	American Redstart	<i>Setophaga ruticilla</i>	0.683	1.828
AMRO	American Robin	<i>Turdus migratorius</i>	2.139	2.220
AMWO	American Woodcock	<i>Scolopax minor</i>	0.024	0.551
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	0.208	0.318
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	0.528	1.088
BBCU	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	0.121	0.286
BLWA	Blackburnian Warbler	<i>Setophaga fusca</i>	0.655	1.124
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	2.763	3.831
BTBW	Black-throated Blue Warbler	<i>Setophaga caeruleascens</i>	0.273	0.780
BTNW	Black-throated Green Warbler	<i>Setophaga virens</i>	2.365	2.052
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	2.642	3.194
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	0.671	0.858
BWWA	Blue-winged Warbler	<i>Vermivora cyanoptera</i>	0.121	0.339
BWHA	Broad-winged Hawk	<i>Buteo platypterus</i>	0.402	0.569
BRCR	Brown Creeper	<i>Certhia americana</i>	1.545	1.555
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	0.132	0.427
CEDW	Cedar Waxwing	<i>Bombycilla cedrorum</i>	1.555	2.389
CSWA	Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	1.423	2.713
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	0.341	0.864
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	0.203	1.255

Table 2.2. Bird species used in diversity contribution analysis from the western Upper Peninsula of Michigan, USA. Average plots are those below the third quantile of diversity contribution scores. High-contribution plots are those above the third quantile. Species in bold are those that had a significantly higher abundance in high-contribution plots ($P < 0.05$).

Table 2.2 (cont'd)

Species			Mean Abundance	
AOU Code	Common Name	Scientific Name	Average Plots	High-contribution Plots
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	0.253	0.843
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	0.446	0.342
EABL	Eastern Bluebird	<i>Sialia sialis</i>	0.187	0.397
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	0.107	0.533
EAWP	Eastern Wood-Pewee	<i>Contopus virens</i>	1.337	1.402
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	0.464	1.541
GCFL	Great-crested Flycatcher	<i>Myiarchus crinitus</i>	1.049	1.385
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	0.838	0.888
HETH	Hermit Thrush	<i>Catharus guttatus</i>	2.318	2.262
INBU	Indigo Bunting	<i>Passerina cyanea</i>	0.970	1.949
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	1.298	1.227
MAWA	Magnolia Warbler	<i>Setophaga magnolia</i>	0.707	0.985
MODO	Mourning Dove	<i>Zenaida macroura</i>	0.323	0.552
MOWA	Mourning Warbler	<i>Geothlypis philadelphia</i>	1.210	1.533
NAWA	Nashville Warbler	<i>Oreothlypis ruficapilla</i>	2.445	3.533
NOFL	Northern Flicker	<i>Colaptes auratus</i>	1.043	1.162
NOPA	Northern Parula	<i>Setophaga americana</i>	0.375	0.956
NOWT	Northern Waterthrush	<i>Parkesia noveboracensis</i>	0.193	0.343
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>	3.777	2.895
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.182	0.301
PIWA	Pine Warbler	<i>Setophaga pinus</i>	0.199	0.613
PUFI	Purple Finch	<i>Haemorhous purpureus</i>	0.331	0.619
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	0.651	1.009

Table 2.2 (cont'd)

Species			Mean Abundance	
AOU Code	Common Name	Scientific Name	Average Plots	High-contribution Plots
REVI	Red-eyed vireo	<i>Vireo olivaceus</i>	3.853	3.171
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	3.063	2.614
RTHU	Ruby-throated Hummingbird	<i>Archilochus colubris</i>	0.300	0.532
RUGR	Ruffed Grouse	<i>Bonasa umbellus</i>	0.597	0.618
SASP	Savannah Sparrow	<i>Passerculus sandwichensis</i>	0.019	0.098
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	0.896	0.743
SOSP	Song Sparrow	<i>Melospiza melodia</i>	0.191	1.004
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	0.121	0.759
VEER	Veery	<i>Catharus fuscescens</i>	0.584	0.807
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>	0.659	0.947
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	0.817	1.466
WIWR	Winter Wren	<i>Troglodytes hiemalis</i>	0.603	1.015
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	2.192	2.083
YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>	1.535	2.449

2.3.4. Species-level relationships

The Student's t-tests identified 35 of 59 species that had significantly higher mean abundance in high-diversity plots than average plots (Table 2.2). There was a significant negative correlation between the probability of having a higher mean abundance in high-contribution plots and overall mean abundance ($\beta = -0.804$; $P = 0.015$), meaning that less-common species tended to be better represented in high-contribution plots. In the indicator species analysis, 5 of the 6 forest types had single species as either the best or second-best indicator of high-contribution plots (Table 2.3). The species acting as indicators were not necessarily uncommon (e.g. Red-eyed Vireo) or strongly associated with those forest types (e.g. Eastern Kingbird in Northern Hardwoods). Positive predictive value, or the probability that the plot belonged to a specific group given that the species was found there (also called specificity), ranged from very high (>0.9 in high-contribution Lowland Conifer plots) to moderate (0.6 for high-contribution Upland Mixed plots) (Table 2.3).

Ecosystem Type	1	2	3	4	5
Northern Hardwoods	EAKI ^a (0.850)	OVEN+EAKI (0.850)	REVI+EAKI (0.850)	BTNW+EAKI (0.850)	HETH+EAKI (0.829)
Upland Conifer	CSWA (0.851)	NAWA+CSWA (0.849)	OVEN+CSWA (0.812)	RBNU (0.811)	NAWA_RBNU (0.794)
Upland Mixed	OVEN+YBSA (0.621)	OVEN (0.603)	BRCR (0.584)	OVENI+BRCR (0.584)	REVI+BRCR (0.584)
Early-successional	LEFL+NOOR (0.898)	LEFL+CSWA (0.888)	LEFL+MOWA (0.877)	SCJU (0.867)	OVENA+SCJU (0.867)
Cedar	BHVI+BLWA (0.813)	VEER (0.807)	REVI+VEER (0.807)	NAWA+VEER (0.807)	BLJA+VEER (0.807)
Lowland Conifer	CEDW (0.906)	NAWA+CEDW (0.906)	CEDW+BLJA (0.906)	REVI+CEDW (0.875)	OVEN+CEDW (0.875)

Table 2.3. Top 5 indicator species or combinations for high-contribution plots within 6 ecosystem types in the western Upper Peninsula of Michigan, USA. Numbers in parentheses are the probabilities of being a high-contribution site, given that combination of species is found there. See Table 2 for species associated with four-letter codes.

^aStandardized species codes used by the American Ornithologist's Union (AOU).

2.4. DISCUSSION

My research demonstrates that a novel application of the conservation filter strategy can be used for the prioritization of ecosystem types and habitat conditions that are critical to the maintenance of species diversity in managed landscapes. My work focused on bird community conservation in areas that are actively managed for timber production, however this method is easily applicable to other taxa and other systems. In particular, the diversity contribution approach can be used to identify areas and ecosystem types that are important for maintaining regional species diversity and provide guidelines for site-level management that will enhance biodiversity value. Combining coarse filters and mesofilters in this way facilitates the multi-scale planning that is an integral part of the ecosystem management paradigm and the effort to conserve species diversity across managed landscapes. Therefore, this novel approach provides an additional tool that managers can use in making management decisions in the face of uncertainty about the effects on biodiversity.

The diversity contribution approach I employed here was proposed a decade ago (Lu et al., 2007), and is an extension of the concept of habitat specificity (Halvorsen and Edvardsen, 2009). The idea behind habitat specificity is that individual species will be dependent to a degree on individual spatial elements (i.e. habitats) within the landscape, with specificity being measured as the proportion of occurrences of that species that fall into that spatial element (Wagner and Edwards, 2001). Thus, the contribution of an individual unit to regional diversity is the sum of the specificity scores of the species that occur there (Wagner and Edwards, 2001). Lu et al. (2007) extended this idea by decomposing diversity contribution into richness and distinctiveness components within an additive framework so that spatial units are described according to their relative contribution to regional diversity, thus providing a robust method for

ranking and prioritizing areas for conservation. To date, these methods have been applied primarily to plants and invertebrates in terrestrial systems (e.g. Halvorsen and Edvardsen, 2009; Saraiva et al., 2015), and I know of no instances where they have been employed in planning or management decisions.

My finding that the conservation value of a community type, as defined by my contribution index, is inversely proportional to its representation on the landscape (Fig. 2.3) is logically intuitive, and aligns with the idea of habitat specificity (Wagner and Edwards, 2001). This effect of proportional representation is because diversity contribution is largely determined by the distinctiveness of species within a site (Lu et al., 2007), which is strongly associated with the distinctiveness of the environmental conditions relative to the rest of the landscape (Crosby, chapter 1 this dissertation). The strong influence of uncommon species on regional diversity is an aspect of the beta component of diversity (the difference among spatial units within a region; Whittaker, 1972), which has been shown to be a major driver of diversity among birds and other taxa (Crist et al., 2003; Veech and Crist, 2007). The effect of proportional representation, however, was not constant. My results show that Upland Mixed and Upland Conifer forests both had a higher conservation value than Cedar and Lowland Conifer, even though Upland Mixed and Upland Conifer were nearly twice as common. Although I did not examine the relative influences of richness and distinctiveness on the diversity contribution scores, it is possible that Cedar and Lowland Conifer support fewer species on average. Species richness as reflected in alpha diversity is a component of diversity contribution (Lu et al., 2007), and so it is possible that lower species richness may have accounted for the lower conservation value of these community types.

It was clear at the mesofilter level that different compositional and structural attributes affected diversity contribution within different community types (Fig. 2.4), however the commonality seemed to be that they created more structural complexity within plots. For example, the proportion of BA in conifer had a positive correlation with diversity contribution in Northern Hardwood community types, but a negative correlation in Upland Conifer and Upland mixed community types (Fig. 2.4B). Similarly, high-contribution plots among Northern Hardwoods and Cedar community types had lower total basal area while basal area seemed to be neutral in Upland Conifer and Upland Mixed plots, which had lower basal area on average to begin with. The relationship between structural complexity and diversity was first demonstrated by MacArthur and MacArthur (1961), and has guided some forest conservation efforts under the concept that “diversity begets diversity” (Schulte et al., 2006; Hunter and Schmiegelow, 2011). My research suggests that increasing the compositional and structural complexity of forest stands increases not just species richness, but also the contribution to overall regional diversity, by increasing habitat specificity within those stands.

The fact that the abundance of less-common bird species was more likely to be positively related to high-contribution plots also corresponds to the idea of habitat specificity. Heino and Gronroos (2014) showed that niche marginality among stream invertebrates, which is akin to habitat specificity, had a significant negative relationship with occupancy rates. This relationship between specificity, occupancy, and diversity contribution is important for our understanding of the drivers of regional species diversity (Crosby, chapter 1 this dissertation). Knowing which species rely more strongly on high-contribution sites is important for managers in determining monitoring and habitat conservation priorities. Because these species tend to be less common regionally, they have increased importance for the maintenance of regional diversity.

In my application, the coarse filter strategy is not focused on creating reserves, as it traditionally has been (Noss, 1987; Hunter, 2005), or on maintaining a certain distribution of ecosystem types as suggested by Haufler et al. (1996). Rather, my application focuses on prioritizing community types throughout the landscape in terms of their conservation value and identifying sites of high conservation value among all community types. I then integrate the mesofilter with the coarse filter by describing those high-value sites in terms of compositional and structural attributes that set them apart from other sites within the same community type. This approach is distinctly different from the traditional practice of prioritizing areas for conservation based on species richness (Lu et al., 2007), which is problematic for a number of reasons (Palmer and White, 1994). The key here is that conservation value is defined not in terms of species richness but rather in the contribution to overall regional diversity (i.e. gamma diversity), and so emphasizes uncommon species and community types within the context of the broader biological community (Wagner and Edwards, 2001; Lu et al., 2007).

My application is based on the idea that, while all ecosystem types are important, some sites have scarcity value because of their low occurrence rates on the landscape (Wagner and Edwards, 2001). Within all ecosystem types, however, there will always be some that support more or different species because of specific compositional and structural attributes (Hunter, 2005; Crous et al., 2013). Taken together, this represents the integration of coarse filter and mesofilter strategies, and the diversity contribution approach provides a quantitative method for applying this combined strategy on managed forest landscapes.

2.5. MANAGEMENT IMPLICATIONS

At the coarse filter operational scale, it is important to be able to identify high-value ecosystem types on the landscape and ensure that these are maintained in suitable amounts. The

actual amount and distribution of such types needs to be guided by the biophysical template, as well as some sense of historical range and variability (Haufler et al., 2002; Keane et al., 2009), however forest production goals and other objectives can also play a role and may even be advantageous to both biodiversity and timber production (Zenner et al., 2010). For example, pine plantations have high economic value, but are often considered to have low value in terms of biodiversity (Bremer and Farley, 2010). In my study area, however, pine forests were relatively rare and so had high conservation value. Therefore, maintaining pine plantations in this study area could have a positive impact on regional biodiversity. This illustrates the importance for managers of recognizing and maintaining native community types that are regionally uncommon, but also shows how economic and ecological interests can be sometimes serve a common goal.

At the mesofilter scale, understanding the compositional and structural attributes of high-contribution plots within a specific community type may hold the key to increasing the overall biodiversity value throughout a region. When supplied with this knowledge, managers can use it to modify management prescriptions to increase the conservation value of forest harvesting activities and maintain diversity across the landscape. Because specific attributes, such as total basal area or percent conifer, have differential impacts among community types, it is critical for managers to understand this and be able to adjust harvest and retention guidelines based on the community type of a particular area to be harvested.

CHAPTER 3

MONITORING BETA DIVERSITY OF BIRD COMMUNITIES AS AN ALTERNATIVE PARADIGM FOR TRACKING CHANGES IN REGIONAL BIODIVERSITY

ABSTRACT

Regional monitoring of biodiversity is consistently recognized as one of the primary requirements of any long-term conservation program. Despite this recognition, examples of monitoring programs that can link changes in biodiversity to environmental changes at scales relevant to land management and conservation planning (1–1000 km²) are uncommon. To address this issue, I propose a monitoring system based on beta diversity of bird communities at multiple spatial scales. Beta diversity has been shown to reflect environmental heterogeneity in several systems, and bird community diversity in particular is reflective of ecological conditions. My proposed system focuses on species-level monitoring of bird communities for the estimation of beta diversity using a hierarchical sampling design. I analyzed bird community and habitat data from the western Upper Peninsula of Michigan collected using a hierarchical sampling design to test the link between beta diversity and environmental heterogeneity at different spatial scales. I then used simulations of species and landscapes to compare capabilities of different sampling designs for detecting patterns of diversity across multiple spatial scales. My results show a positive relationship between heterogeneity and diversity at 2 management-related scales (1–3 km² and 100–1000 km²). The hierarchical sampling design was superior to systematic, random and stratified random sampling designs because it is able to detect patterns at finer spatial scales. The fact that bird communities are relatively easy to monitor, are reflective of ecological conditions at multiple scales, and generate so much interest with the general public makes them the most appropriate taxon for regional biodiversity monitoring. The system I

propose here can provide a baseline monitoring program that is logistically feasible and ecologically useful for assessing and guiding regional conservation policy.

3.1. INTRODUCTION

Regional monitoring of biodiversity is consistently recognized as one of the primary aspects of any long-term conservation program (Yoccoz et al., 2001; White et al., 2013). Despite this recognition, examples of landscape scale species-level monitoring programs are uncommon because of the high costs of surveying a large and diverse group of species (Manley et al., 2004; Noon et al., 2012). The few broad-scale monitoring programs available, such as the North American Breeding Bird Survey (Sauer et al., 2003) or state-level breeding bird atlas programs (Zuckerberg and Porter, 2010), are too coarse-grained in both space and time to track the way typical land management activities impact biodiversity. As a result, there is little geographically extensive information that can link changes in species diversity to environmental changes at spatial and temporal scales at which management and conservation planning typically occur (1–1000km²; Bestelmeyer et al., 2003; Noon et al., 2012).

To date, most biodiversity monitoring schemes have focused on determining which few species offer the best indices of environmental conditions, and therefore may be useful as surrogates for tracking biodiversity at large spatial scales (Manley et al., 2004). While this strategy is intuitively appealing, the assumption that the status of one or a few species is indicative of broad-scale ecological conditions has often been challenged (Manley et al., 2004; Wiens et al., 2008). On the other hand, ecologists recognize that spatial and temporal patterns of heterogeneity in the environment at multiple scales are the precursor for biological diversity (Christensen, 1997; Levin, 2000), and research suggests that maintaining patterns of environmental heterogeneity should be the focus of ecosystem management and conservation

efforts (Fuhlendorf et al., 2006; Veech and Crist, 2007; Fuhlendorf et al., 2012; Astorga et al., 2014). Therefore, a monitoring system for tracking biodiversity and environmental heterogeneity across scales while still providing valuable species-level data would provide important information for our understanding of land-use impacts on biodiversity and long-term conservation planning.

Species diversity is traditionally partitioned into three components related to spatial scale, where α is within-unit diversity, β is the diversity among units, and γ as the overall regional diversity (Whittaker, 1960). Among these, β -diversity represents a useful spatial component of diversity, and can provide information about how diversity is distributed across the landscape (Marsh and Ewers, 2013). β -diversity of specific taxa has been shown to reflect compositional and structural heterogeneity within ecosystems (Fuhlendorf et al., 2006; Astorga et al., 2014), suggesting that species diversity within selected groups can act as an index of environmental heterogeneity. Lande (1996) showed how α -, β -, and γ -diversity can be additively partitioned at multiple spatial scales to investigate how diversity patterns are distributed across scales (Gering et al., 2003). Monitoring of β -diversity at multiple scales, then, offers an alternative to traditional surrogate-species approaches for tracking ecological conditions and indexing biodiversity at regional scales.

I propose that measuring beta diversity of bird communities at multiple spatial scales offers an efficient and effective way to monitor regional biodiversity. Bird community composition has been used in the past as an indicator of ecological conditions (Canterbury et al., 2000; O'Connell et al., 2000) and environmental heterogeneity (Fuhlendorf et al., 2006; Veech and Crist, 2007), and birds are known to respond strongly to land-use change (DeGraaf et al., 1998). Additionally, monitoring bird species is relatively easy and efficient compared to most

other taxa, and there is a great deal of interest within the general public for bird species conservation. My goal was to evaluate a hierarchical sampling design intended to characterize regional beta diversity at multiple spatial scales. My objectives were to test the hypothesis that bird community diversity reflects environmental heterogeneity across spatial scales and evaluate the effectiveness of different sampling designs for estimating beta diversity at multiple spatial scales. I used bird community and environmental data within a hierarchical sampling design to investigate the relationship between heterogeneity and beta diversity, and simulated landscape and community data to evaluate sampling designs. My approach demonstrates the appropriateness of birds as biodiversity indicators and offers insights into the impact that sampling designs can have on biodiversity estimates.

3.2. METHODS

3.2.1. Study area and data acquisition

To meet my first objective, I tested the link between beta diversity of bird communities and environmental heterogeneity across scales using bird community and forest data from a 4000-km² area in the western upper peninsula of Michigan, USA. This is an ecologically diverse northern forest landscape, with variability driven by glacial topography, soil, and differences in deer browse and forest management across ownerships (Laurent et al., 2005). The majority of the land is state-owned or private industrial forest managed for timber production. Upland northern hardwood forests make up the majority of the landscape, interspersed with upland and lowland conifers and areas of early successional forest. The primary species in northern hardwood stands is sugar maple (*Acer saccharum*), while red pine (*Pinus resinosa*) and white pine (*P. strobus*) dominate the upland conifer communities. Northern white cedar (*Thuja occidentalis*) is the main

tree species in lowland areas, and aspen (*Populus spp.*) and white birch (*Betula papyrifera*) cover most of the early-successional areas.

I used data on bird species and vegetation variables collected in 2001–2003 from a large-scale study of bird species in forested habitats (Laurent et al., 2005; Millington et al., 2011). Sample plots were selected according to what was known as the GRAIN protocol (Laurent et al., 2005), where the landscape was gridded into ~1,000 ha sections and 2–8 plots were placed within randomly selected sections. This plot selection system allowed me to impose a hierarchical study design on the data (Fig. 3.1). Individual plots were clustered into ecological neighborhoods where each plot was no more than 1000 m from at least one other plot. Neighborhoods were nested into management areas defined by the state forest management system or by private industrial landowner, and management areas were further nested into ecological subsections defined by McNab et al. (2007).

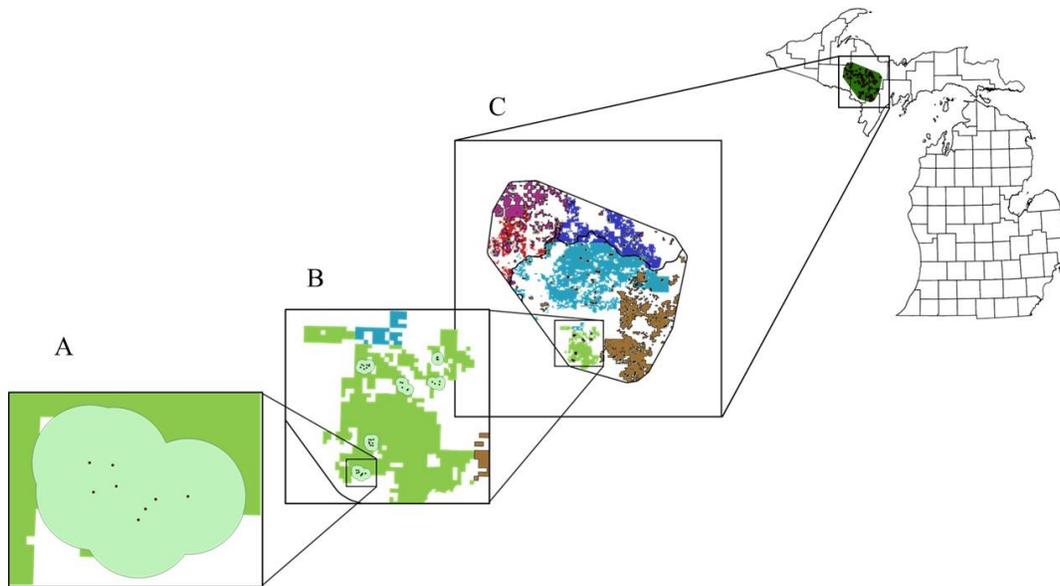


Figure 3.1. Study area and study design map showing: (A) sampling plots within ecological neighborhoods; (B) neighborhoods within management areas; (C) management areas within ecological subregions; and (D) study area location within the Upper Peninsula of Michigan, USA.

I used data from all birds detected within 50 m of the plot center during standard 10-min point counts (Ralph et al., 1995). Each plot was sampled 3–4 times between June 4 and July 3 (1 plot was visited twice) in either 2001, 2002, or 2003 between sunrise and 5 hr post-sunrise. I estimated the abundance for each species at each site using a multi-species occupancy-abundance model that provided site-level abundance estimates without the use of habitat variables (Appendix A). This model estimated occupancy and abundance as separate but related processes, and accounted for spatial correlation in occupancy within a neighborhood distance of 1000 m (sensu Mattsson et al., 2013). I modeled survey-specific detection probability as a linear function of standardized covariates for Julian day (linear and quadratic) and time as measured in minutes from sunrise (Zipkin et al., 2010). Because my purpose was to sample resident species indicative of community structure and habitat conditions, I regarded species that were detected at <1% of plots, as well as waterfowl (*family Anatidae*), as incidental detections and excluded them from the analysis (Crosby et al., 2015; Mahon et al., 2016). I also excluded large raptors (families *Accipitridae*, *Cathartidae*, *Falconidae*, *Strigidae*) and large corvids (*Corvus corax* and *C. brachyrhynchos*) because their large home ranges and ubiquitous distributions make their status as residents difficult to verify (Crosby et al., 2015). I fit the model in a Bayesian framework with programs R (Version 3.3.0) and JAGS (Version 4.2.0; Plummer, 2003) using the package *runjags* with parallel chains, with uninformative prior distributions for all parameters and hyperparameters. I ran three chains of 300,000 iterations with a burn-in of 50,000 and a thinning ratio of 10, and assessed convergence using the Gelman and Rubin R-hat statistic (Brooks and Gelman, 1998). The multi-species occupancy-abundance analysis was performed using data from all sample plots where point counts were done. However, for the beta diversity analyses

described below I limited the data set to plots within neighborhoods containing ≥ 3 plots within management area containing ≥ 3 such neighborhoods (Anderson, 2006; Marsh and Ewers, 2013).

I characterized forest composition and structure within each plot center using 11 variables derived from measurements taken at the plots concurrent with bird surveys and from remotely-sensed elevation data. Total basal area (BA; m^2/ha) for trees ≥ 10 cm diameter at breast height (DBH) was measured using a 10-factor prism at 3 subplots within each plot located at the vertices of an equilateral triangle surrounding the plot center. The first point of the triangle was placed 15 m from the center at a random azimuth, and the succeeding points were 25 m from the initial point and 15 m from the center (Laurent, 2005). From the prism measurements I also estimated proportion BA in conifers, proportion BA in deciduous trees other than sugar maple, and stem density (trees/ha) of snags ≥ 25 cm DBH and large trees ≥ 50 cm DBH (sensu McGee et al., 1999; Millington et al., 2011). Canopy openness was measured at each of the three subplots using a spherical densitometer and calculated as the average of measurements taken while facing in each of 4 directions (north, south, east, and west) (Comeau et al., 1998). Stem density of trees < 10 cm DBH was measured using 5-tree distance sampling (Lessard et al., 2002) at 9 subplots spaced on a 3x3 grid centered on the plot center, with subplots 16 m apart (Laurent, 2005). From this I calculated stems/ m^2 of seedlings (trees ≥ 25 cm tall and < 1.5 m tall) and canopy recruits (trees ≥ 1.5 m tall and < 10 cm DBH), and the proportion of seedlings that were conifers. To characterize size structure of the stand, I calculated an index of diameter distribution as the departure from an idealized even size class distribution of 20 trees per hectare in each 5-cm size class, where the value was the log-transformed chi-square value measuring departure from the idealized distribution (Tyrrell and Crow, 1994). Finally, I indexed soil moisture in each plot using a modification of the topographic wetness index called the SAGA wetness index (SWI;

Olaya and Conrad, 2009), where topography was derived from the U.S. Geological Survey National Elevation Dataset 1/3 arc-second 2013 maps (<https://ita.cr.usgs.gov/NED>; accessed August 21, 2016).

3.2.2. Environmental heterogeneity and beta diversity

I evaluated the appropriateness of my chosen environmental variables for modeling community composition by estimating the correlation among variables and testing for their influence on niche separation among species in an outlying mean index (OMI) analysis. OMI is a constrained ordination technique that estimates the niche position of species relative to average environmental conditions, and total inertia reflects the influence of the environmental variables on the species' niche separation (Dolédec et al., 2000). To test whether the chosen variables described niche separation, I employed a permutation test of the total inertia calculated from the OMI analysis using species abundance estimates at each plot for the analysis. The permutation test randomizes the communities among sites and tests the null hypothesis that the species niche separation is not influenced by the environmental variables (Dolédec et al., 2000). I ran 1000 permutations and compared the average marginality from the randomized data to the observed average marginality and evaluated significance as the proportion of permutation values higher than the observed value.

To describe the influence of environmental heterogeneity on diversity, I measured environmental heterogeneity and bird community beta diversity across scales using multivariate dispersion analysis (Anderson et al., 2006). Multivariate dispersion estimates the ecological distance of each point to a group centroid based on species composition or environmental variables, and the mean of these distances within a group can be used as a measure of beta diversity or environmental heterogeneity, respectively (Astorga et al., 2014). I estimated

environmental heterogeneity at the neighborhood and management area scales using Euclidean distance for the normalized environmental variables, and to estimate beta diversity of bird communities using the Bray-Curtis index at the same scales (Anderson et al., 2006). Because there may be a relationship between beta diversity and sampling area, I used the residuals obtained from linear regressions of beta diversity and environmental heterogeneity against the number of points in the unit for which the estimate was obtained for neighborhoods and management areas (Veech and Crist, 2007). I used linear regression to test for a relationship between environmental heterogeneity and beta diversity at the neighborhood level. Due to small sample size, my data did not meet regression assumptions at the management area level so I looked at correlations between variables among management areas. I performed all analyses using program R. The multivariate dispersion analyses was done using the `betadisper` function in package `vegan` with `type = "centroid"` specified. I considered tests to be statistically significant at $p < 0.1$.

3.2.3. Landscape and species simulation

To meet my second objective of evaluating sampling designs for monitoring beta diversity, I simulated a landscape to represent 2 separate, large-scale primary gradients, each following a different direction and changing at a different spatial scale. Within these large-scale directional gradients were small-scale secondary gradients changing in random directions at varying spatial scales, where the spatial scale was dependent on the level of aggregation within that subsection of the landscape. The full simulated landscape was 500x750 pixels. I simulated the composition of the first 2 primary gradients according to probability density functions determined by a beta distribution and configuration specified as the H-value in the midpoint displacement method (*sensu* Holland et al., 2009). The first primary gradient was composed of 3

separate 500 x 250 pixel landscapes increasing in average value and spatial aggregation from west to east according to the increasing H-value (Table 3.1). In this method, an H-value of -2.0 would represent a random landscape, but because such a landscape would be highly unlikely in nature smallest H-value used in my simulations was -0.2. The second primary gradient was composed of 4 separate 125x750 pixel landscapes decreasing in average value from north to south and unchanging in spatial aggregation (Table 3.1). The simulation of spatial aggregation created the secondary gradients, where a low level of spatial aggregation caused the secondary gradients to change over a smaller spatial scale relative to areas with higher spatial aggregation (Fig. 3.2).

Primary Gradient	α	β	H-value
1: West to East	3.0	3.0	-0.2
	5.0	3.0	0.0
	7.0	2.5	2.0
2: North to South	4.0	1.0	0.0
	3.0	2.0	0.0
	2.0	3.0	0.0
	1.0	4.0	0.0

Table 3.1. Parameters used for simulating landscape gradients, where pixel values are randomly drawn from a beta distribution with parameters α and β , and spatial correlation in parameter values specified by the H-value in the midpoint displacement method.

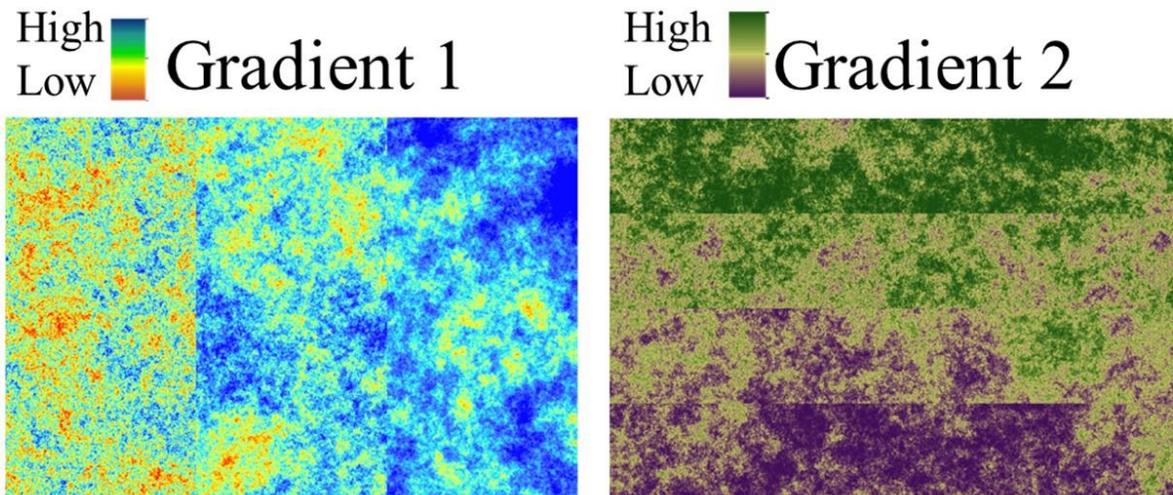


Figure 3.2. Simulated ecological gradients used for simulating species occurrence based on randomly generated beta distributions. Landscape dimensions were 500x700 pixels.

I populated the landscape by simulating 100 species with differing responses to the environmental gradients according to randomly generated beta distributions using the coenocliner package in program R version 3.1.1. The coenocliner package simulates species occurrence or abundance data along gradients according to Gaussian or beta response curves (Simpson, 2016). I drew species response parameters from random distributions to reflect a range of responses from rare to common and generalist to specialist (Table 3.2). I increased all probabilities by a factor of $x = 100$ million using the equation $1 - (1 - psi)^x$ to approximate a realistic range of occupancy probabilities in a natural bird community. I also simulated a response resembling a climate effect, where some species had a reduced occupancy probability in the northern half of the landscape. To do this, I randomly chose which species would be affected with a 0.5 probability. I then randomly assigned the strength of the effect by multiplying the initial occupancy probability by a random draw from a uniform (0.1, 0.9) distribution.

	Response parameter	Distribution
	Max psi	
	Species set 1	beta (5, 2)
	Species set 2	beta (7, 1)
Gradient 1	Modal abundance	uniform (min, max) [†]
	Range of occurrence	uniform (0.01, 0.5)
	α	uniform (0.5, 7.0)
	β	uniform (0.5, 7.0)
Gradient 2	Modal abundance	uniform (min, max) [†]
	Range of occurrence	uniform (0.01, 0.9)
	α	uniform (0.5, 7.0)
	β	uniform (0.5, 7.0)

Table 3.2. Parameters used to simulate species occurrence probabilities along 2 environmental gradients using the package *coenocliner* in program R. Parameters for each species were drawn randomly from probability distributions. Max psi represents the maximum occurrence probability, modal abundance represents the point on the gradient where maximum occurrence is achieved, and range of occurrence represents the limits of occurrence along the gradient.

[†]min and max are the minimum and maximum gradient values, respectively.

3.2.4. Sample design comparisons

I compared the effectiveness of different sample designs in estimating beta diversity across scales using additive partitioning of diversity components (Gering et al., 2003). Additive partitioning separates diversity into α , β , and γ components where $\alpha + \beta = \gamma$ provided that the diversity metric is strictly concave, meaning that the value of the metric for a pooled set of communities is \geq the average value within those communities (Lande, 1996; Gering et al., 2003). Such metrics can be partitioned across multiple scales when γ for a level is measured as the

average α -diversity at the next higher level. I used species richness as my diversity measure and separated the landscape into 5 levels corresponding to those typically used in management (Fig. 3.3). From highest to lowest levels: I vertically separated the landscape into 2 climatic zones measuring 250 x 750 pixels; each climatic zone was split into 3 regions of 250 x 250 pixels; each region was separated into 25 management areas of 50 x 50 pixels, and each management area was separated into 100 neighborhoods of 5 x 5 pixels. Each pixel was considered an individual plot.

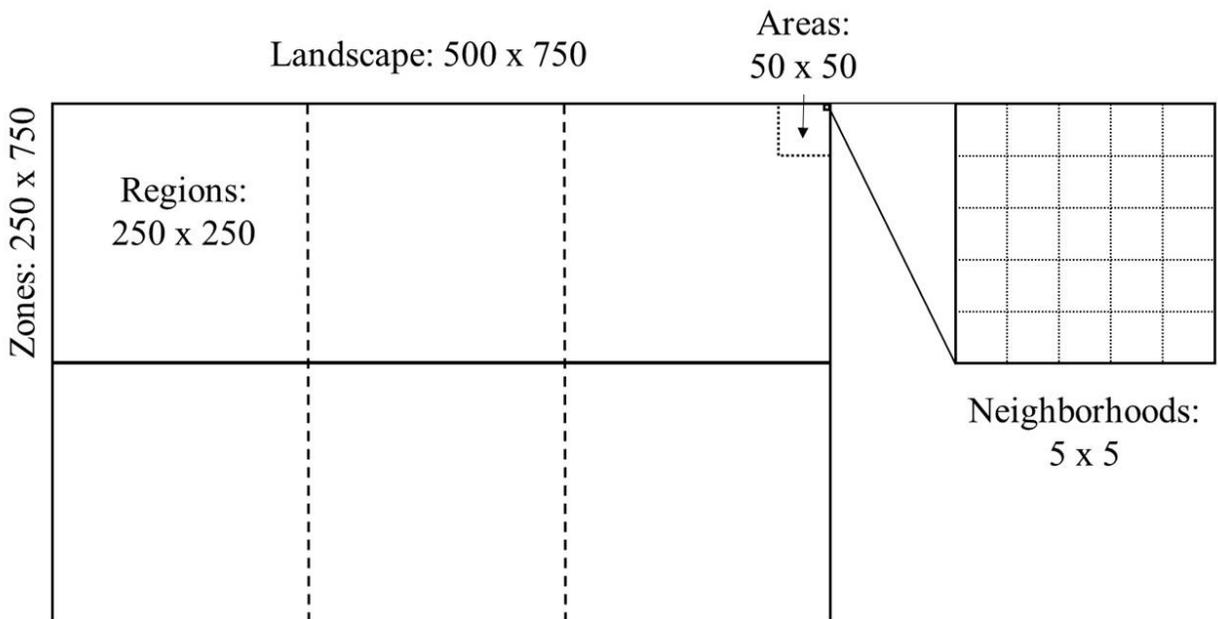


Figure 3.3. Hierarchical partitioning of simulated landscape used to compare the effectiveness of different study designs for estimating species diversity across scales.

I first calculated the known diversity at all levels using all 375,000 plots. I then estimated diversity by sampling 450 individual pixels using 4 different sampling designs: systematic, random, stratified random, and a hierarchical cluster sampling design (Thompson, 2012). The systematic sampling design was based on an 18x25 grid spaced evenly across the landscape. For

the random sample, I randomly chose plots without replacement from across the entire landscape. In the stratified random sample I randomly chose 75 plots from within each of the 6 regions. In the hierarchical cluster design, I randomly selected 5 management areas from within each region, 5 neighborhoods from within each of the management areas, and 3 plots from each of the neighborhoods. I drew 100 individual samples using each design (except for the systematic design) and compared the results at each level using means and 95% confidence intervals.

3.3. RESULTS

3.3.1. Bird community and beta diversity

The bird community analysis estimated occupancy and abundance from 433 plots. The hierarchical dataset included 232 point count plots within 36 ecological neighborhoods divided among 5 management areas and 2 ecological subsections. Neighborhoods ranged from 105–313 ha with a mean of 174 ha. Management areas ranged from 12,428–75,850 ha with a mean of 45,343 ha. There were 3 moderate correlations among the environmental variables: total BA with canopy openness (-0.542); total BA with sapling density (-0.494); and density of seedlings with density of saplings (0.437). All other correlations were between -0.4 and 0.4. The permutation test showed that the environmental variables increased total inertia by 2.33/1 over random. This increase was significant ($P = 0.003$). Bird community beta diversity was significantly correlated with environmental heterogeneity in the linear regression at the neighborhood level ($df = 34$, $\beta = 0.024$, $P = 0.003$) and showed a strong correlation at the management area level ($r = 0.796$) (Fig. 3.4).

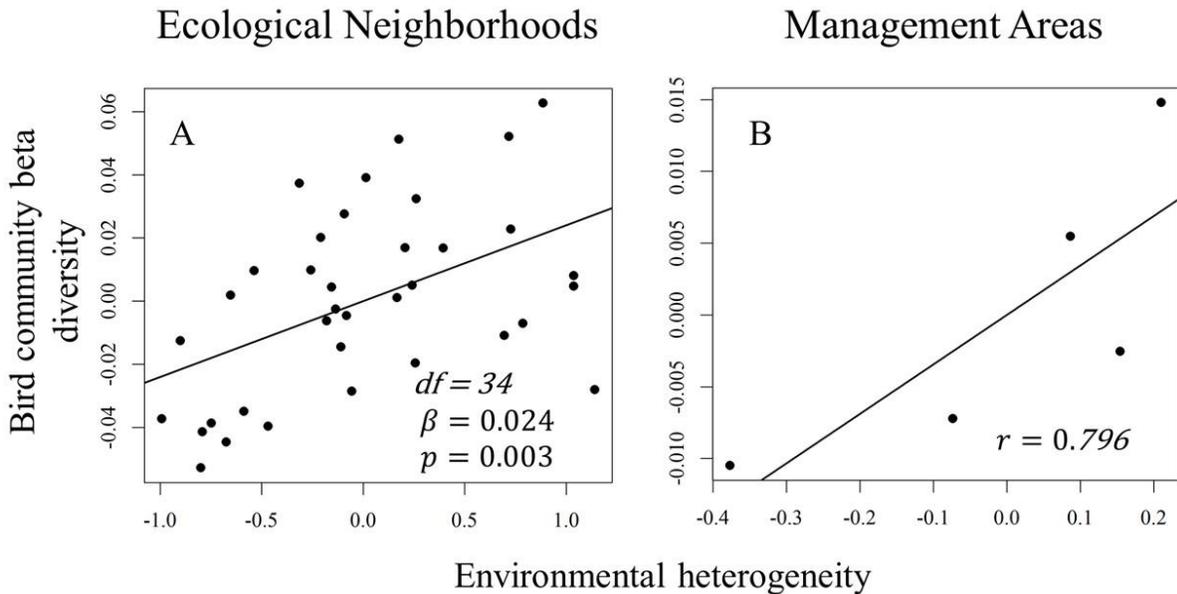


Figure 3.4. A: Linear regression of the relationship between environmental heterogeneity and bird community beta diversity within ecological neighborhoods (all points ≤ 1000 m from at least 1 other point). B: Correlation of the same relationship for forest management areas as defined by the Michigan Department of Natural Resources or private industrial forest landowners.

3.3.2. Simulation analysis

The simulation analysis showed that the hierarchical cluster design performed better than any of the other sampling designs in estimating diversity across scales. In particular the systematic, random, and stratified random designs were all unable to detect beta diversity among plots. These designs also captured an average of only 21% of the beta diversity among neighborhoods and overestimated beta diversity among management areas by an average of 2.086/1. The hierarchical cluster design gave the most accurate estimates of beta diversity at the beta.1, beta.2, and beta.3 levels and gave similar estimates to the other sampling designs for beta.4, beta.5, and gamma (Fig. 3.5). All 4 designs were able to accurately estimate plot-level alpha diversity (alpha.1), and all of them overestimated diversity at large scales (beta.4, beta.5) and underestimated gamma diversity (Fig. 3.5).

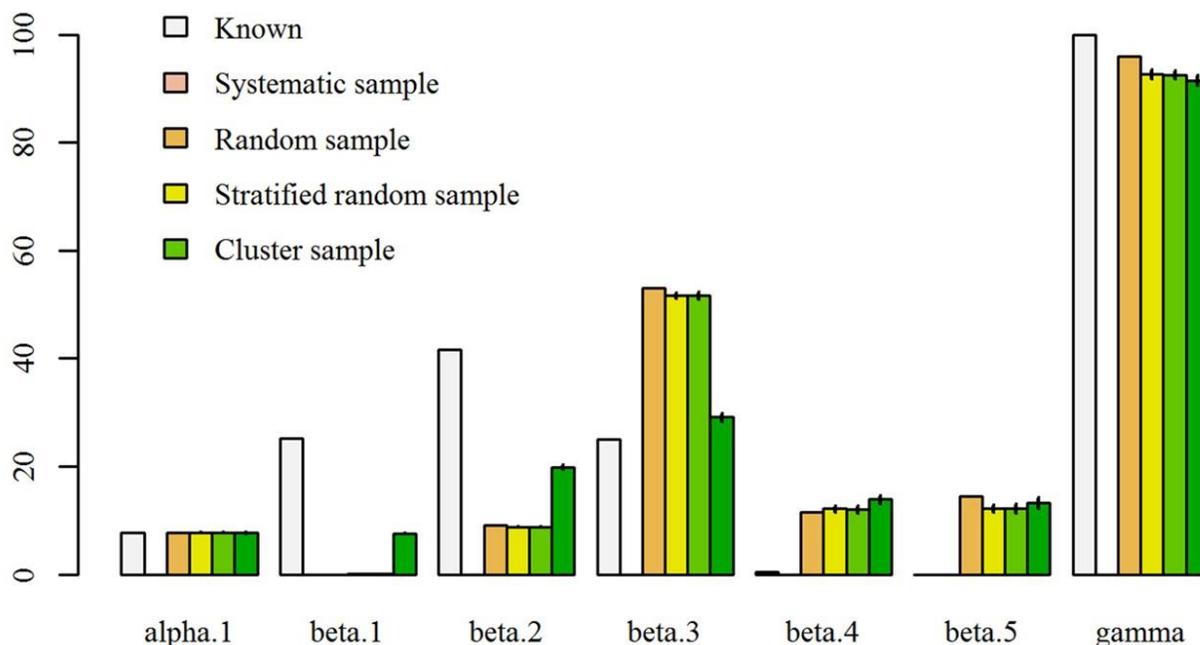


Figure 3.5. Comparison of the estimates from 4 different sampling designs to known contribution of alpha and beta components of diversity to overall gamma diversity across 5 hierarchically-partitioned spatial scales in a simulated landscape. Each design contained 450 sampling points. The systematic sample was an 18x25 grid of points spread evenly across the landscape, the stratified random sample was stratified at the beta.4 level, and the cluster sample was hierarchically partitioned across all scales.

3.4. DISCUSSION

The foundation of ecosystem management is the conservation of pattern and process, which maintains the spatial and temporal patterns of heterogeneity that underlie biodiversity conservation (Fuhlendorf et al., 2012). These patterns of diversity change across scales because the processes that drive them operate at multiple spatial and temporal scales (Levin, 2000). Therefore, the key to measuring and monitoring biodiversity at large spatial extents is using metrics that reflect heterogeneity across multiple scales. My findings show that bird community diversity reflects environmental heterogeneity at multiple spatial scales relevant to forest management, and that a hierarchical cluster sampling design estimates diversity across

scales much more accurately than the random, stratified random, and systematic sampling designs that are used more commonly in large-scale sampling. These findings illustrate the advantages of using communities rather than individual species as surrogates for biodiversity monitoring, which is that they can be used to index environmental differences among spatial units across scales. My results also show the advantage of using hierarchical sampling designs in large scale biodiversity monitoring rather than the classical designs more commonly employed by researchers.

The application of a hierarchical cluster sampling design for large-scale monitoring systems derives from 2 complementary ideas: that cluster sampling is much more efficient for sampling in large landscapes (Hines et al., 2010; Aing et al., 2011); and that a cluster-based sampling design is optimal for estimating beta diversity across multiple spatial scales (Marsh and Ewers, 2013). Cluster sampling is more efficient because it reduces travel time between sampling sites (Aing et al., 2011), and it is often done by default in monitoring programs in an effort to overcome logistical difficulties (Hines et al., 2010). Hierarchical cluster designs are better able to estimate beta diversity across scales because they naturally sample processes occurring at multiple spatial scales (Marsh and Ewers, 2013), thus providing greater resolution and accuracy of diversity patterns (Fortin et al., 1989). As in my analysis, Marsh and Ewers (2013) showed that the spatial configuration of sampling points can have a large impact on beta diversity estimates at different scales. When compared to more-common sampling designs, their fractal-based cluster design gave better estimates of beta diversity and was the only design that could successfully partition diversity at all scales (Marsh and Ewers, 2013). What my results show is that a fractal-based design is not necessary for sampling multi-scale beta diversity as long as some form of hierarchical, cluster-based design is employed.

My landscape simulation created a complex landscape with multiple gradients changing in different directions, and the scale of the gradients changing in different parts of the landscape. Such a simulation is likely to be more reflective of natural ecological conditions than the simplified, single directional gradients simulated by Marsh and Ewers (2013). Therefore I believe my analysis to be a more realistic evaluation of the ability of different sampling designs to estimate diversity at multiple scales. Given that, my additive partitioning results were not dissimilar from Marsh and Ewers (2013) with all sampling designs underestimating small-scale diversity and overestimating large-scale diversity. This result is to be expected because of the inability of any sampling design to detect all species within a region. Because the estimates are additive, any overestimation in one part must inevitably lead to an underestimation in another part. Although such inherent deficiencies can never be entirely overcome, it is likely that they can be mitigated using models that account for unobserved species in the samples such as multi-species occupancy or abundance models (Yamaura et al., 2016).

Other factors that may affect the accuracy of diversity estimates across scales are the multiple scales and directions at which ecological gradients change across the landscape. Because ecological patterns change in different directions and at different scales (Levin, 1992), and species respond to conditions individually (Taper et al., 1995), there is little possibility that any sampling design can estimate changes in diversity across large spatial scales with complete accuracy. This does not, however, preclude the benefits of obtaining the best possible estimates for use in ecological investigations, conservation planning, and management decision-making.

The link between heterogeneity and biodiversity has been investigated before with other taxa and at different scales. The hypothesis that heterogeneity is the precursor to biodiversity, and therefore should be the basis for conservation has been around for some time (Christensen,

1997; Ostfeld et al., 1997). Astorga et al. (2014) showed that habitat heterogeneity was the biggest factor driving the geographic distribution of beta diversity of stream invertebrates in New Zealand. Veech and Crist (2007) drew the link between beta diversity of bird communities and habitat and climate heterogeneity at large spatial scales (across large landscapes and ecological provinces). My analysis is also similar to the work of Fuhlendorf et al. (2006) which showed that managing for heterogeneity in rangeland systems increased bird community diversity over standard management systems, although theirs was not an explicit measure of beta diversity and did not consider multiple spatial scales. The difference in my work is that I show the usefulness of the heterogeneity-biodiversity relationship at multiple scales appropriate to management (1–1000km²; Bestelmeyer et al., 2003), using compositional and structural variables affected by management. Monitoring bird communities in this way can help researchers and managers draw the explicit link between biodiversity, forest management systems, and large-scale conservation planning.

Using bird community composition as an index of ecological conditions is not new either. Bird communities have been used in the past as indicators of biotic integrity (O'Connell et al., 2000; Glennon and Porter, 2005), and individual species have often been seen as surrogates for specific habitat types: e.g. spotted owls in the northwestern United States, (Caro and O'Doherty, 1999) or white-backed woodpeckers in Europe (Roberge et al., 2008) as indicators of old-growth forest. Bird communities have several characteristics that make them the best choice among taxa for this type of monitoring system:

1. They are known to respond to commonly-measured variables that are affected by management (DeGraaf et al., 1998).

2. Communities respond to conditions at multiple spatial scales relevant to management (Cushman and McGarigal, 2004).
3. Breeding birds are easy to monitor relative to other taxa, and can be monitored non-invasively (Ralph et al., 1995; O'Connell et al., 2000).

In addition to these advantages, there is expertise and enthusiasm among the general public for surveying birds. This is evinced by the many citizen science programs that use volunteers to collect scientifically-defensible bird community data such as the North American Breeding Bird Survey (Sauer et al., 2014) and many state-level and national breeding bird atlas projects (e.g. McGowan and Corwin, 2008; Balmer et al., 2013). Combining this expertise and enthusiasm with the proper sampling design and survey protocol could provide the most reliable and cost-effective biodiversity monitoring system available.

Under the monitoring system suggested here, changes in the amount of diversity explained within levels would indicate changes in landscape pattern. For example, if proportion of diversity explained among neighborhoods was reduced while that explained among management areas increased, that could indicate homogenization at the neighborhood levels but greater variability among management areas as a consequence of management decisions (Zollner et al., 2008). Management for contiguous areas of specific habitat types might result in such a pattern, and be beneficial to area-sensitive species such as many forest interior birds and mammals (Robbins et al., 1989; Zollner et al., 2008). On the other hand, higher diversity at small scales coupled with low diversity at large scales would suggest a highly fragmented landscape that does not change much over a large area, as in a heavily-managed area undergoing short-rotation timber harvest. Understanding these dynamics can help managers estimate how management alternatives at different scales interact to influence regional biodiversity.

While the diversity metrics described here show how bird communities can act as indicators of environmental heterogeneity, and thus as an index biodiversity, alternative analyses using the same type of data can give more specific information. For example, ordination techniques can be used to investigate which species are most vulnerable as well as which environmental conditions are most important for maintaining those species at the appropriate scales (e.g. Thuiller et al., 2005; Mahon et al., 2016). A contribution-diversity approach (Lu et al., 2007) can be applied to find which areas contribute the most to diversity across scales and what the characteristics of such areas are (Crosby, chapter 2 this dissertation). Ordinations can also be applied to data from different time periods to gauge how conditions have changed and investigate the drivers of those changes (e.g. Coppedge et al., 2001).

The appropriateness of using surrogate species for monitoring biodiversity has been debated in the literature for several decades, and the limitations of this approach are well-known and documented (Caro and O'Doherty, 1999; Lindenmayer et al., 2000; Manley et al., 2004). There are two primary issues with the use of surrogate species. First, species respond to changes in environmental conditions individually, and so the use of a few indicator species as an index of the broader community is not a viable strategy (Taper et al., 1995). Second, it cannot be assumed that the status of a few species indicates the condition of the ecosystem (Manley et al., 2004). Therefore, rather than suggesting the use of a few surrogate species whose relationship to ecological conditions is presumed to be known, we propose the use of bird community beta diversity as an efficient and effective alternative. The general monitoring system proposed here can provide regional managers with a set of metrics that act as reliable indices of environmental heterogeneity over a range of relevant spatial scales. These metrics can then be used to make

inferences about how management affects biodiversity, which is a fundamental question under the ecosystem management paradigm (Christensen et al., 1996).

It is not known how reliably bird community diversity can predict diversity in other taxa, but the few studies that have examined this question so far have shown promise (Vielliard, 2000; Aslan et al., 2015). It must be understood, though, that bird communities cannot possibly act as a perfect index of biodiversity but only of a few important aspects of it. Other information must be brought to bear if we are to better understand and predict how land management decisions will affect biodiversity conservation at large scales. The status of rare or endangered species and the continued functioning of vital ecosystem processes are other important aspects of conservation. However, monitoring bird communities using a hierarchical sampling design across appropriate spatial scales represents an ecologically sound and logistically feasible alternative to traditional approaches to biodiversity monitoring for large scale management and conservation planning.

EPILOGUE

The purpose of this dissertation was to address the problem of maintaining biodiversity on managed forest landscapes. More specifically, my goal was to investigate the response of bird communities to patterns of forest composition and structure across multiple spatial scales. In the first chapter, I investigated how patterns of heterogeneity in stand-level attributes impact patterns of bird community diversity across multiple spatial scales. In the second chapter, I demonstrated a novel application of the conservation filters strategy to maintaining avian diversity on managed forests. In the third chapter, I looked at monitoring beta diversity in bird communities as an alternative paradigm to indicator-based strategies for estimating changes in regional biodiversity.

The research in these chapters draws several conclusions that are fundamental to the problem of maintaining regional biodiversity on managed forest landscapes. The first is that the effect of environmental heterogeneity on bird community diversity changes across spatial scales. This conclusion is important to understand because forest management systems affect spatial patterns at multiple scales. Therefore, sustainable forest management planning requires an understanding of how spatial patterns at multiple scales will impact regional diversity. The second conclusion is that uncommon ecosystem types have a greater relative contribution to regional diversity, and the importance of specific compositional and structural attributes changes among types. This has important implications for how different areas are prioritized for conservation and how structural retention guidelines are written because it underlies the patterns that maintain diversity at different operational scales. Finally, quantifying beta diversity of bird communities (differences among spatial units within a region) across multiple scales, using a hierarchical cluster sampling design, reflects environmental heterogeneity and offers an efficient

and effective system for monitoring regional biodiversity. Bird community beta diversity, then, provides an alternative to species-based strategies for indexing biodiversity, and can provide an important contribution to our understanding of how and why biodiversity changes through time.

The first chapter addressed the issue of how pattern and scale impact our understanding of the factors governing the maintenance of biodiversity across the landscape. I examined how patterns of bird species diversity changed across spatial scales in a managed northern forest landscape and investigated the effect of environmental heterogeneity on the contributions of individual spatial units at multiple scales to regional diversity. I found that beta diversity at smaller spatial scales (1–300 ha) provided the largest relative contribution to regional bird diversity. Uniqueness of a sampling plot relative to mean conditions, in terms of vegetation structure and composition, had a significant positive correlation with diversity contribution. At medium scales (100–300 ha), within-unit heterogeneity was positively correlated with beta diversity but showed no relationship to diversity contribution. Conversely, within-unit heterogeneity was positively correlated with diversity contribution at large scales (100–1000 km²). Thus I were able to show the differential effects of heterogeneity patterns on diversity across scales.

Chapter 2 addressed the issue of management planning for regional bird diversity on managed forest landscapes. There is usually a great deal of uncertainty about how management decisions will impact biodiversity, and so scientifically-based strategies are often employed as tools in the planning process (Schulte et al., 2006). The coarse filter and mesofilter strategies (Hunter, 2005) are two of the most common strategies, however they are traditionally employed independently. I showed that integrating coarse filter and mesofilter conservation strategies can help prioritize ecosystem types for conservation and enhance management prescription

guidelines to increase the contribution of managed areas to regional diversity. Specifically, I employed the diversity contribution approach of Lu et al. (2007) to prioritize ecosystem types for conservation, and described compositional and structural attributes of high-contribution sites relative to other sites within the same ecosystem type. This represented a novel application of the conservation filter strategy in managed forests where reserve designation is not a viable option. My application is an extension of the approach proposed by Haufler et al. (1996), which viewed the coarse filter as maintaining the historical distributions of ecosystem types within a region. My application is more appropriate in working forest landscapes with multiple ownerships and diverse management objectives, as is the case in many regions.

In chapter 3, I addressed the issue of regional biodiversity monitoring. Historically, biodiversity monitoring recommendations have focused on using one or a few species as indicators of overall species diversity (Manley et al., 2004; Noon et al., 2012). Estimating beta diversity (differences among spatial units), on the other hand, can be used as an indicator of patterns of heterogeneity at multiple scales, which is strongly linked with biodiversity (Benton et al., 2003). I proposed a monitoring system that focuses on species-level monitoring of bird communities for the estimation of beta diversity using a hierarchical cluster sampling design. I showed that beta diversity in bird communities is correlated with environmental heterogeneity across multiple scales. Additionally, using simulated data, I were able to show that the hierarchical sampling design is superior to more traditional designs for estimating beta diversity across multiple scales.

The research presented in this dissertation offers an expanded and integrated view of the problem of maintaining biodiversity on managed forests. In the first place, I demonstrated that maintaining the mix of generalist and specialist species that leads to high regional diversity

requires maintaining heterogeneity at multiple scales. This means that large-scale management systems must explicitly address how forest planning will impact patterns at multiple scales simultaneously, and maintain both homogenous and heterogeneous landscapes at the appropriate scales. Secondly, I showed the utility of using the diversity contribution approach to the application of an integrated conservation filter strategy for maintaining regional bird diversity on a managed forest landscape. Such an approach can be very important for making management decisions in the face of uncertainty about how those decisions will impact biodiversity. Third, I showed that monitoring bird communities using a hierarchical cluster sampling design offers a viable alternative to traditional indicator species approaches to monitoring regional biodiversity. My work offers an integrated set of guidelines for biodiversity conservation on managed forests that explicitly accounts for the multiple scales at which biodiversity is generated and maintained. I believe that this research provides ecologists, land managers, and planners with an improved framework for managing forests under the ecosystem management paradigm.

APPENDICES

APPENDIX A

MULTI-SPECIES OCCUPANCY-ABUNDANCE MODEL

Model description for a zero-inflated multi-species occupancy-abundance model accounting for spatial correlation in occupancy by incorporating an autologistic parameter into the probability of occupancy (sensu Mattsson et al., 2013). The model utilizes an augmented dataset (a set of all-zero encounter histories) to account for unobserved species, and accounts for the covariance between occupancy and abundance (sensu Royle and Dorazio, 2009).

Ecological model for occupancy:

Parameters:

ψ_{ij} = the probability that species i occurs at site j

$$\text{logit}(\psi_{ij}) = \varphi_i + \alpha_i A_{ij}$$

$$w_i = \begin{cases} 1, & \text{if species } i \text{ is included in the sample of all sites (will always be 1 for} \\ & \text{observed species)} \\ 0, & \text{otherwise} \end{cases}$$

$$w_i \sim \text{Bernoulli}(\Omega)$$

φ_i = logit intercept for species i , representing the mean probability of occupancy for that species among all sites.

$$\varphi_i \sim \text{Normal}(\mu_u, \sigma_u^2)$$

α_i = the spatial weights parameter, representing the change in the logit occupancy probability conditional on the spatial weight assigned to species i at site j .

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \tau_\alpha)$$

$$A_{ij} = \frac{\sum_r z_{ir}}{R_j} \quad \text{where } A_{ij} \text{ is the proportion of sites } r \text{ neighboring } j \text{ that are occupied by species } i.$$

$$z_{ij} = \begin{cases} 1, & \text{if species } i \text{ is present at site } j \text{ (will always be 1 for} \\ & \text{observed species at site } j) \\ 0, & \text{otherwise} \end{cases}$$

$$z_{ij} | w_i \sim \text{Bernoulli}(\psi_{ij})$$

Hyperparameters:

$\Omega \sim \text{Uniform}(0, 1)$ This parameter describes the inclusion probability of any species randomly chosen from the augmented dataset. The probability will be \geq

n/n_{spec} , where n is the number of observed species and $n_{\text{spec}}=n$ +the number of added zeros in the augmented dataset.

$\mu_u \sim \text{Normal}(0, 0.001)$ The mean and variance of the mean logit occupancy probability
 $\sigma_u \sim \text{Unifrom}(0, 10)$ across all species
 $\tau_u = 1 / \sigma_u^2$

$\mu_\alpha \sim \text{Normal}(0, 0.0001)$ The mean and variance of the spatial weights parameter across
 $\tau_\alpha \sim \text{Gamma}(0.1, 0.1)$ all species

Ecological model for abundance:

Parameters:

λ_{ij} = the mean abundance of species i at site j .

$$*\log(\lambda_{ij}) = \delta_i$$

δ_i = the log abundance intercept for species i , representing the mean abundance for that species among all sites.

Covariance between occupancy and abundance:

To account for the known relationship between occupancy and abundance, we specify the covariance between these 2 parameters. We let $u_i = \text{logit}(\psi_i)$ and $v_i = \log(\lambda_i)$ and specify heterogeneity in the parameters among species with a bivariate normal distribution:

$$\begin{pmatrix} u_i \\ v_i \end{pmatrix} \sim \text{Normal} \left(\begin{pmatrix} \beta \\ \alpha \end{pmatrix}, \Sigma \right)$$

where Σ is a 2 x 2 matrix with diagonal element σ_u^2 and σ_v^2 and whose off-diagonal elements, σ_{uv} is the covariance between the diagonal elements (Royle and Dorazio, 2009). Parameters β and α represent the logit- and log-scale mean probability of occupancy and mean abundance, respectively, among all species.

$$^\dagger v_i = \mu_v + (\rho \times \sigma_v / \sigma_u) \times (\varphi_i - \mu_u)$$

$$\delta_i \sim \text{Normal}(v_i, \sigma_\eta^2)$$

[†]Equations drawn from Kéry and Royle (2009)

N_{ij} = The abundance of species i at site j

$$N_{ij} | z_{ij} \sim \text{Poisson}(\lambda_{ij})$$

The zero-inflated abundance estimate

Hyperparameters:

$\mu_v \sim \text{Normal}(0, 0.0001)$ The mean and variance of mean log abundance across all

$\sigma_v \sim \text{Unifrom}(0, 10)$ species

$$\tau_v = 1 / \sigma_v^2$$

$\rho \sim \text{uniform}(-1, 1)$ The covariance parameter between ψ and λ
 $\sigma_\eta^2 = \tau_v / (1 - \rho^2)$ The variance of δ_i (the log mean abundance for species i)

Detection model

Parameters:

p_{ijk} = the probability of detection species i at site j .

$$\text{logit}(p_{ijk}) = \pi_i + \boldsymbol{\beta}_i x'_{jk}$$

π_i = the logit detection probability intercept for species i , representing the mean probability of detection for that species among all sites.

$$\pi_i \sim \text{Normal}(\mu_y, \sigma_y^2)$$

x'_{jk} = the covariate values at site j during survey k that affect detection probability.

$\boldsymbol{\beta}_i$ = the covariate coefficients for species i affecting detection probability during a survey.

$$\boldsymbol{\beta}_i \sim \text{Normal}(\mu_\beta, \sigma_\beta^2)$$

Y_{ijk} = the number of individuals of species i detected at site j during survey k .

$$Y_{ijk} \sim \text{Binomial}(N_{ij}, p_{ijk})$$

Hyperparameters:

$\mu_y \sim \text{Normal}(0, 0.0001)$ The mean and variance of mean logit detection probability across

$\sigma_y \sim \text{Uniform}(0, 10)$ all species

$$\tau_y = 1 / \sigma_v^2$$

APPENDIX B

MULTI-SPECIES OCCUPANCY-ABUNDANCE MODEL CODE

```
# -----  
# Zero-inflated Poisson-binomial Multi-species Abundance Model (ZIP-MSAM), where  
# occupancy and abundance are modeled separately and there is spatial correlation in  
# the probability of occupancy for each species at each site. Correlation is specified  
# with an autologistic parameter based on the number of sites within a 1km neighborhood  
# of the site where the species was detected .  
# Author: Andrew D. Crosby  
#           Quantitative Wildlife Center  
#           Michigan State University  
#           480 Wilson Road, Room 13 NR  
#           East Lansing, Michigan 48824  
# Date: 10 April 2016  
# -----  
  
# The point count data is a 3-dimensional array of sampling points x surveys x species  
# nstats is the number of sampling points  
# nspec is the number of species (including the augmented all-zero encounter histories)  
# K is a vector of the number of surveys done at each sampling point  
# day is Julian day, day2 is day-squared, time is minutes from sunrise  
# weights is a sample points x species matrix of the proportion of sample points within the  
# neighborhood surrounding each sample point where the species was detected  
  
# The code for the initial values was derived from Zipkin et al. (2010), and is very important  
# for model performance and convergence  
  
data = list(nstats=nstats, Y=bird.comm.data, nspec=nspec, K=nsurvs,  
           day=day, day2=day2, time=time, weights=as.matrix(weights_aug))  
  
params = c("N", "z", "Ntot", "zmean", "psi", "alpha")  
Nst <- matrix(nrow=nstats, ncol=nspec)  
for (j in 1:nstats) {  
  for (i in 1:nspec) {  
    Nst[j, i] <- max(bird.comm.data[j, ,i], na.rm=T)  
  }  
}  
  
zinit <- matrix(nrow=nstats, ncol=nspec)  
for (j in 1:nstats) {  
  for (i in 1:nspec) {  
    zinit[j, i] <- min(1, max(bird.comm.data[j, ,i], na.rm=TRUE))  
  }  
}
```

```

}

inits = function() {
  omegaGuess = runif(1, n/(nspec), 1)
  psi.meanGuess = runif(1, .25,1)
  lambda.meanGuess = runif(1, .25,1)
  pi.meanGuess = runif(1, .25,1)
  rhoGuess = runif(1, 0,1)
  sigma.uGuess = runif(1,0,1.5)
  sigma.vGuess = runif(1,0,1.5)
  sigma.piGuess = runif(1,0,1.5)
  list(omega=omegaGuess, mu.u=psi.meanGuess, mu.v=lambda.meanGuess,
       mu.pi=pi.meanGuess, sigma.u=sigma.uGuess,
       sigma.v=sigma.vGuess,sigma.pi=sigma.piGuess,
       rho=rhoGuess, w=c(rep(1, n), rbinom(nz, size=1, prob=omegaGuess)),
       z=zinit, N=Nst, phi=rnorm(nspec, psi.meanGuess, sigma.uGuess),
       delta=rnorm(nspec, lambda.meanGuess, sigma.vGuess),
       pi=rnorm(nspec, pi.meanGuess, sigma.piGuess),
       alpha=rnorm(nspec), beta1.pi=rnorm(nspec), beta2.pi=rnorm(nspec),
       beta3.pi=rnorm(nspec))
}
sink("zip_msam_spatial.txt")
cat("
model{

# -----#
# Hyper-priors on community parameters#
# -----#

      # The ecological process
      # -----
# Hyper-parameter for inclusion probability
omega ~ dunif(0, 1)

# Hyper-parameter for occupancy random species effect
mu.u ~ dnorm(0, 0.0001)I(-5, 5)
sigma.u ~ dunif(0, 10)
tau.u <- pow(sigma.u, -2)

# Hyper-parameter for abundance random species effect
mu.v ~ dnorm(0, 0.0001)I(-5, 5)
sigma.v ~ dunif(0, 10)
tau.v <- pow(sigma.v, -2)

# Hyper-parameter for detection probability random species effect
mu.pi ~ dnorm(0, 0.0001)I(-5, 5)

```

```

sigma.pi ~ dunif(0, 10)
tau.pi <- pow(sigma.pi, -2)

# Hyper-parameters on the covariance matrix of psi and lambda
rho ~ dunif(-1,1)
var.delta <- tau.v/(1-pow(rho,2))

# Priors on the spatial weights parameter
mu.alpha ~ dnorm(0, 0.001)
tau.alpha ~ dgamma(0.1, 0.1)

# The detection process
# -----
mu.beta1.pi ~ dnorm(0, 0.001)
mu.beta2.pi ~ dnorm(0, 0.001)
mu.beta3.pi ~ dnorm(0, 0.001)

tau.beta1.pi ~ dgamma(0.1, 0.1)
tau.beta2.pi ~ dgamma(0.1, 0.1)
tau.beta3.pi ~ dgamma(0.1, 0.1)

for(i in 1:nspec){
# Species-specific priors drawn from the hyper-priors
# -----

# Priors on the ecological processes
w[i] ~ dbern(omega) # Inclusion parameter for species i
phi[i] ~ dnorm(mu.u, tau.u) # Mean species occupancy probability
alpha[i] ~ dnorm(mu.alpha, tau.alpha) # Spatial weights parameter

# Priors on the covariance matrix of psi and lambda
mu.delta[i] <- mu.v + (rho*sigma.v/sigma.u)*(phi[i]-mu.u)
delta[i] ~ dnorm(mu.delta[i], var.delta)

# Priors on the detection process
pi[i] ~ dnorm(mu.pi, tau.pi) # Mean species detection probability
beta1.pi[i] ~ dnorm(mu.beta1.pi, tau.beta1.pi)
beta2.pi[i] ~ dnorm(mu.beta2.pi, tau.beta2.pi)
beta3.pi[i] ~ dnorm(mu.beta3.pi, tau.beta3.pi)

# Ecological model for occupancy and abundance
for (j in 1:nstats) {
lpsi[j,i]<-phi[i]+alpha[i]*weights[j,i] # logit occupancy probability
psi[j,i]<-exp(lpsi[j,i])/(1+exp(lpsi[j,i])) # occupancy probability
}
}

```

```

      mu.psi[j,i]<-min(0.999, max(0.001, psi[j,i]))*w[i] # occupancy probability conditional
on species inclusion probability
      z[j,i]~dbern(mu.psi[j,i]) # Occupancy
indicator (1 or 0)

      log(lambda[j,i])<-delta[i] # log mean abundance
      lam.eff[j,i]<-z[j,i]*lambda[j,i] # mean abundance
conditional on occupancy
      N[j,i] ~ dpois(lam.eff[j,i]) # Abundance estimate

# Detection process model
for (k in 1:K[j]) {
  lp[j,k,i]<-pi[i] + beta1.pi[i]*day[j,k] + beta2.pi[i]*day2[j,k] + beta3.pi[i]*time[j,k]
  p[j,k,i]<-min(0.999, max(0.001, exp(lp[j,k,i])/(1+exp(lp[j,k,i]))))
  Y[j,k,i] ~ dbin(p[j,k,i],N[j,i])
}
}
Ntot[i]<-sum(N[,i])
zmean[i]<-mean(z[,i])
}

},fill=TRUE)
sink()

ni<-2000
nc<-3
nb<-10000
nt<-50

system.time({
zip_msam_spat1000_full_parallel<-run.jags(model="zip_msam_spatial_full.txt",
monitor=params,
data=data, n.chains=nc, inits=inits, burnin=nb, sample=ni,
thin=nt, method="parallel", n.sims=3)
})

```

APPENDIX C

PYTHON CODE FOR LANDSCAPE SIMULATION

```
# Python code for simulating landscapes with spatially correlated pixel values
#     according to the diamond-square improvement on the midpoint displacement
#     method. Code was generously supplied by:

# Dr Pen Holland
# Ecology Teaching Fellow
# Department of Biology
# University of York
# Heslington
# York
# YO10 5DD
# UK
# Tel: work 01904 328734
# pen.holland@york.ac.uk

# For an example of the application of this code, see:
# Holland, E.P., Aegerter, J.N., Dytham, C., 2009. Comparing resource representations and
#     choosing scale in heterogeneous landscapes. Landscape Ecology 24, 213-227.

# This version of the code creates landscape value according to the beta distribution

# H is the value for the level of spatial correlation

# -----
# -----

# Python code for running the landscape simulation code (see below)
import diasq_beta
reload(diasq_beta)

H = 0.2
N = 7

maxdim = 50
ydim = 100
a = 7.0
b = 2.5

folder = str(maxdim) + "_" + str(a) + "_" + str(b) + "_" + str(H)

surface = diasq_beta.make_landscape(H, N, maxdim, ydim)
pixellandscape = diasq_beta.revalue(surface, a, b)
```

```

diasq_beta.save_landscape(pixellandscape, maxdim, ydim, "for_age_" + folder + ".txt")

# -----
# -----

# Code for simulating the landscape; referred to as "diasq_beta" in the code to run the simulation
# (see above)
import math, random

def randomdisplace(disheight):
    return random.random()*disheight-0.5*disheight

def displacevals(p, disheight):
    if len(p)==4:
        pcentre = 0.25*sum(p)+randomdisplace(disheight)
    elif len(p) == 3:
        pcentre = sum(p)/3 + randomdisplace(disheight)
    return pcentre

def check_diamond_coords(diax,diay,dim,i2):
    if diax < 0 or diax > dim or diay <0 or diay > dim:
        return []
    if diax-i2 < 0:
        return [(diax+i2,diay),(diax,diay-i2),(diax,diay+i2)]
    if diax + i2 >= dim:
        return [(diax-i2,diay),(diax,diay-i2),(diax,diay+i2)]
    if diay-i2 < 0:
        return [(diax+i2,diay),(diax-i2,diay),(diax,diay+i2)]
    if diay+i2 >= dim:
        return [(diax+i2,diay),(diax-i2,diay),(diax,diay-i2)]
    return [(diax+i2,diay),(diax-i2,diay),(diax,diay-i2),(diax,diay+i2)]

#hlist = [-2.0, -1.0, -0.71, -0.43, -0.14, 0.0, 0.14, 0.28, 0.43, 0.71, 1.0, 2.0]

def make_landscape(H, N, maxdim, ydim):

    displacementheight = 2.0

    dim = 2**N + 1

    if H == -2.0:
        surface={}
        for x in xrange(dim):
            for y in xrange(dim):

```

```

        surface[x,y] = random.random()
else:
    surface={}
    for x in xrange(dim):
        for y in xrange(dim):
            surface[x,y] = randomdisplace(displacementheight)

    inc = dim-1
    while inc > 1:

        i2 = inc/2
        #print 'inc', inc, 'i2', i2
        # print 'square'
        for x in range(0,dim-1,inc):
            for y in range(0,dim-1,inc):
                # this fills in the centre of the square
                surface[x+i2,y+i2] =
displacevals([surface[x,y],surface[x+inc,y],surface[x+inc,y+inc],surface[x,y+inc]],displacement
height)

        #print 'diamond'
        for x in range(0, dim-1, inc):
            for y in range(0, dim-1,inc):
                #print '*****', x, y, '*****'
                #print x+i2,y
                diaco = check_diamond_coords(x+i2,y,dim,i2)
                # print diaco
                diavals = []
                for co in diaco:
                    diavals.append(surface[co])
                surface[x+i2,y] = displacevals(diavals,displacementheight)

                # print x,y+i2

                diaco = check_diamond_coords(x,y+i2,dim,i2)
                # print diaco
                diavals = []
                for co in diaco:
                    diavals.append(surface[co])
                surface[x,y+i2] = displacevals(diavals,displacementheight)

                # print x+inc, y+i2
                diaco = check_diamond_coords(x+inc,y+i2,dim,i2)
                # print diaco
                diavals = []

```

```

        for co in diaco:
            diavals.append(surface[co])
        surface[x+inc,y+i2] = displacevals(diavals,displacementheight)

        # print x+i2, y+inc
        diaco = check_diamond_coords(x+i2,y+inc,dim,i2)
        # print diaco
        diavals = []
        for co in diaco:
            diavals.append(surface[co])
        surface[x+i2,y+inc] = displacevals(diavals,displacementheight)

    displacementheight = displacementheight*2**(-H)
    inc = inc/2

# maxdim = 40
if dim < maxdim:
    maxdim =dim

trimmedsurf = {}
for x in xrange(ydim):
    for y in xrange(maxdim):
        # print x, y
        if surface.has_key((x,y)):
            trimmedsurf[x,y] = surface[x,y]
## fileout = open("surfconf.txt",'w',-1)
## for x in xrange(maxdim):
##     thisline = ""
##     for y in xrange(maxdim):
##         if surface.has_key((x,y)):
##             thisline = thisline + str(surface[x,y]) + '\t'
##         else:
##             thisline = thisline + '0\t'
##     thisline = thisline + '\n'
##     fileout.write(thisline)
## fileout.close()

return trimmedsurf

def save_landscape(surface, maxdim, ydim, fileoutname):
    fileout = open(fileoutname,'w',-1)
    for x in xrange(ydim):
        thisline = ""
        for y in xrange(maxdim):
            if surface.has_key((x,y)):

```

```
        thisline = thisline + str(surface[x,y]) + '\t'
    else:
        thisline = thisline + '0\t'
    thisline = thisline + '\n'
    fileout.write(thisline)
fileout.close()
```

```
def revalue(surface,a,b):
```

```
    oldvals = surface.values()
    oldvals.sort()

    newvals = [random.betavariate(a,b) for i in xrange(len(oldvals))]
    newvals.sort()

    newsurface = {}
    for k in surface.keys():
        newsurface[k] = newvals[oldvals.index(surface[k])]
    return newsurface
```

```
# -----
# -----
```

APPENDIX D

R CODE FOR SPECIES SIMULATION

```
library(raster)
library(coenocliner)
library(reshape2)

memory.limit(size=20000) # This program can use a great deal of memory

# Create the location matrix from the text files representing the ecological gradients (i.e. raster
# maps)
matrix1<-as.matrix(read.table("TABLE_NAME.txt"))
matrix2<-as.matrix(read.table("TABLE_NAME.txt"))

matrix1.vec<-sort(matrix1, index.return=TRUE)
matrix2.vec<-sort(matrix2, index.return=TRUE)
loc1<- matrix1.vec$x
loc2<- matrix2.vec$x

# Simulate 50 spp using beta distribution
M<-50 # Number of species
A0 <- rbeta(M, 0.5, 1) # max occupancy rate
m <- runif(M, min(loc1), max(loc1)) # location on gradient of modal abundance
r <- runif(M, 0.01, 0.5) # species range of occurrence on gradient
alpha<-round(runif(M, 0.5, 7), 1) # shape parameter
gamma<-round(runif(M, 0.5, 7), 1) # shape parameter
alpha
gamma
pars<-list(A0=A0, m=m, r=r, alpha=alpha, gamma=gamma)

pbern<-coenocline(loc1, responseModel = "beta", params = pars, countModel = "bernoulli",
  expectation=TRUE)
pbern

## plot
plot(pbern, type = "p", pch = 1) # a random realisation
lines(pbern, lty = "solid") # probability of occurrence

# Save the output as a matrix
trial.out<-pbern[1:length(loc1),1:M]

prob<-cbind(loc1, trial.out)
```

```

data<-matrix(0, length(loc1), M)
for(i in 1:dim(data)[1]){
  for(j in 1:dim(data)[2]){
    data[i,j]<-rbinom(1, 1, trial.out[i,j])
  }
}

# Add the second gradient
# -----
m2 <- runif(M, min(loc2), max(loc2))# location on gradient of modal abundance
r2 <- runif(M, 0.01, 0.9)           # species range of occurrence on gradient
alpha2<-round(runif(M, 0.5, 7), 1) # shape parameter
gamma2<-round(runif(M, 0.5, 7), 1) # shape parameter
pars2<-list(m=m2, r=r2, alpha=alpha2, gamma=gamma2)

params2<-list(px=pars, py=pars2)

# Create the location points for the individual grid sections
maxdim<-50
xdim<-dim(matrix1)[2]/maxdim
ydim<-dim(matrix1)[1]/maxdim
d<-f<-0
for(i in 1:xdim){
  d<-0
  for(j in 1:ydim){
    assign(paste("loc1.", j, i, sep=""), sort(matrix1[(d+1):(d+maxdim),(f+1):(f+maxdim)],
index.return=TRUE))
    assign(paste("loc2.", j, i, sep=""), sort(matrix2[(d+1):(d+maxdim),(f+1):(f+maxdim)],
index.return=TRUE))
    d<-d+maxdim
  }
  f<-f+maxdim
}

# Run the simulations on each individual grid section
system.time({
for(i in 1:xdim){
  for(j in 1:ydim){
    locs<-expand.grid(x=get(paste("loc1.", j, i, sep=""))$x, y=get(paste("loc2.", j, i, sep=""))$y)
    assign(paste("pbern2.", j, i, sep=""), coenocline(locs, responseModel = "beta", params =
params2,
countModel = "bernoulli", expectation=TRUE))
  }
}
}

```

```
)
```

```
pbern2.11
```

```
# -----  
# Return values to matrix  
# -----  
  
# Re-cast all of the simulation output into arrays indexed by loc1 and loc2 values  
for(i in 1:xdim){  
  for(j in 1:ydim){  
    t<-cbind(expand.grid(x=get(paste("loc1.", j, i, sep=""))$x, y=get(paste("loc2.", j, i,  
sep=""))$y), get(paste("pbern2.", j, i, sep=""))) )  
    t.m<-melt(t, id=c("x", "y"), measured=seq(1, 10, 1))  
    assign(paste("t.cast_", j, i, sep=""), acast(t.m, x~y~variable))  
  }  
}  
  
f<-0  
for(i in 1:xdim){  
  d<-0  
  for(j in 1:ydim){  
    mat1<-matrix1[(d+1):(d+maxdim),(f+1):(f+maxdim)]  
    mat2<-matrix2 [(d+1):(d+maxdim),(f+1):(f+maxdim)]  
    g<-array(NA, dim=c(maxdim, maxdim, M))  
    for(l in 1:maxdim){  
      for(m in 1:maxdim){  
        x<-which(dimnames(get(paste("t.cast_", j, i, sep="")))[[1]]==mat1[l,m])  
        y<-which(dimnames(get(paste("t.cast_", j, i, sep="")))[[2]]==mat2[l,m])  
        for(k in 1:M){  
          z<-get(paste("t.cast_", j, i, sep=""))[x,y,k]  
          g[l,m,k]<-z  
        }  
      }  
    }  
    assign(paste("bird.comm_", j, i, sep=""), g)  
    d<-d+maxdim  
  }  
  f<-f+maxdim  
}  
  
# Save all of the arrays  
for(i in 1:xdim){  
  for(j in 1:ydim){
```

```

x<-get(paste("bird.comm_", j, i, sep=""))
save(x, file=paste("bird.comm_", j, i, ".Rdata", sep=""))
}
}

# Re-load all of the tables
for(i in 1:xdim){
  for(j in 1:ydim){
    load(paste("bird.comm_", j, i, ".Rdata", sep=""))
    assign(paste("bird.comm_", j, i, sep=""), x)
  }
}

# Combine the individual arrays into the entire map
library(abind)

birds.north<-abind(bird.comm_11, bird.comm_12, bird.comm_13, along=2)
birds.south<-abind(bird.comm_21, bird.comm_22, bird.comm_23, along=2)
birds.psimap<-abind(birds.north, birds.south, along=1)
dim(birds.south)
dim(birds.psimap)

# Create occupancy map
birds.zmap<-array(NA, dim=c(dim(birds.psimap)[1], dim(birds.psimap)[2],
dim(birds.psimap)[3]))
for(i in 1:dim(birds.zmap)[1]){
  for(j in 1:dim(birds.zmap)[2]){
    for(k in 1:dim(birds.zmap)[3]){
      birds.zmap[i,j,k]<-rbinom(1, 1, birds.psimap[i,j,k])
    }
  }
}
hist(apply(birds.zmap, 3, sum)/15000)

# Increase occupancy probabilities
birds.psimap_new<-1-(1-birds.psimap)^100000000
hist(birds.psimap_new)

# Create occupancy map

```

```

birds.zmap_new<-array(NA, dim=c(dim(birds.psimap)[1], dim(birds.psimap)[2],
dim(birds.psimap)[3]))
for(i in 1:dim(birds.zmap)[1]){
  for(j in 1:dim(birds.zmap)[2]){
    for(k in 1:dim(birds.zmap)[3]){
      birds.zmap_new[i,j,k]<-rbinom(1, 1, birds.psimap_new[i,j,k])
    }
  }
}
apply(birds.zmap_new, 3, sum)/15000
hist(apply(birds.zmap_new, 3, sum)/15000)

birds.zmap<-birds.zmap_new

# Add in the north/south climate gradient
C<-0.5 # The probability that the species is not affected by the gradient
clim<-rep(0, M)
for(i in 1:M){
  clim[i]<-1*(runif(1) < C)
}
clim
clim.eff<-round(runif(M, 0.1, 0.9), 1)
clim.eff

# Re-do the north-half occupancy matrix using the climate filter
birds.north.zmap<-array(NA, dim=c(dim(birds.north)[1], dim(birds.north)[2], M))
for(i in 1:dim(birds.north)[1]){
  for(j in 1:dim(birds.north)[2]){
    for(k in 1:M){
      birds.north.zmap[i,j,k]<-birds.zmap[i,j,k]*1*(runif(1) > clim[k]*clim.eff[k])
    }
  }
}

birds.clim.zmap<-abind(birds.north.zmap, birds.zmap[51:100,,], along=1)
dim(birds.clim.zmap)
apply(birds.clim.zmap, 3, sum)/15000
hist(apply(birds.clim.zmap, 3, sum)/15000)

save(birds.clim.zmap, file="birds.clim.zmap_1.Rdata")

```

```
# -----  
# Create a new map using both data frames  
# -----  
  
# Bring in both arrays  
load("birds.clim.zmap_1.Rdata")  
load("birds.clim.zmap_3.Rdata")  
  
hist(apply(birds.clim.zmap_1, 3, sum)/15000)  
hist(apply(birds.clim.zmap, 3, sum)/15000)  
  
# Combine both species arrays  
birds.clim.zmap_full<-abind(birds.clim.zmap_1, birds.clim.zmap, along=3)  
dim(birds.clim.zmap_full)  
apply(birds.clim.zmap_full, 3, sum)/15000  
hist(apply(birds.clim.zmap_full, 3, sum)/15000)
```

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