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# LANDSCAPE STRUCTURE AND THE BIOLOGICAL DIVERSITY OF THE NORTH AMERICAN AVIFAUNA

By

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# ABSTRACT

# LANDSCAPE STRUCTURE AND THE BIOLOGICAL DIVERSITY OF THE NORTH AMERICAN AVIFAUNA

By

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Patterns of biological diversity are influenced by macroscale processes as well as localized ecological conditions, including the spatial distribution of landscape elements. Describing and quantifying the effect of landscape structure on ecosystem attributes such as biodiversity patterns is a research priority in modern ecology. This dissertation examines the connections between patterns of landscape structure and patterns of avian biodiversity in North America. The first goal of my dissertation was to identify metrics of landscape structure that are appropriate for describing the link between the spatial heterogeneity of landscapes and the spatial patterns of biological diversity. Then, using long-term species occurrence data from the North American Breeding Bird Survey, I tested the hypothesis that the body size distributions of species assemblages display discontinuities. I found that not only are there discontinuities, but the position of species in the body mass distribution relative to the location of the discontinuities has ecological consequences. I then used lacunarity analysis to test the hypothesis that discontinuities in landscapes structure correspond to discontinuities in body mass distributions. To accomplish this I again used species occurrence data from the Breeding Bird Survey and forested habitat distribtion data from the National Land Cover Data set. The results of this analysis suggest that the forest habitat of eastern North America is not hierarchically structured and therefore is not the likely cause of the observed discontinuities in avian

body mass distributions. Finally, I examined the hypothesis that the composition of avian species assemblages conforms to the distribution of ecoregions across North America. Using seven beta-diversity metrics to describe the species assemblages, I found that the distribution of the North American avifauna appears to be spatially autocorrelated and independent of ecoregion distribution.

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# INTRODUCTION

The spatial heterogeneity of landscape elements can affect ecological processes such as nutrient cycling, disturbance, and population dynamics (Turner et al. 2001). The study of landscape structure and its spatial patterns is based on the link between pattern and process (Gustafson 1998) with the goal of predicting ecological phenomena (Li and Wu 2004). Assessing and quantifying this structure can complement landuse statistics and enhance predictive abilities that are vital to the long term monitoring of ecosystems and the establishment of functional environmental management strategies and achievable goals (Herzog and Lausch 2001).

Patterns of biodiversity are influenced by both large-scale regional processes such as the geologic and evolutionary history of a region as well as by contemporary ecological conditions including interactions among individuals and the distribution of resources in the environment (Turner et al. 2001, Ricklefs 2004). Humans are rapidly and drastically altering the structure of landscapes on a global basis; these changes are having dramatic effects on the planet's biodiversity (Pimm and Raven 2000, Pimm 2001). Understanding the relationship between the patterns of landscape heterogeneity and patterns of biodiversity has become increasingly important to the success of regional and global conservation and ecosystem management efforts. If we can improve our ability to describe and quantify the effects of changes in landscape pattern on changes in biodiversity, it will enable us to predict the effects of environmental modifications on species assemblages, providing an opportunity to either enhance or prevent those changes. Using data from North America, this dissertation examines the connection between patterns of landscape structure and patterns of avian biodiversity.

My first chapter addresses the issue of describing landscape structure. There are many available metrics that quantify various aspects of landscape pattern, though not all metrics provide information useful to every question (Turner et al. 2001). The overall goal of my dissertation was to examine the link between patterns of spatial heterogeneity in landscapes and patterns in the distribution of species. Therefore, I have focused this first chapter on identifying those metrics that best describe aspects of landscape structure that are likely to influence the distribution of species.

The second chapter of my dissertation describes the patterns of the distribution of body sizes of birds and the ecological significance of those patterns in six physiographic regions of eastern North America (Bystrak 1981). Holling (1992) has suggested that ecosystems are hierarchically structured by only a few physical and biotic processes that each operate at different spatial and temporal scales, resulting in a discontinuous distribution of resources within a landscape. If such a resource structure exists, then the distribution of the body masses of the species using those resources should also exhibit discontinuities. Discontinuities in body mass distributions have been referred to as "zones of crisis and opportunity" (Allen et al. 1999). Using species occurrence data from the Breeding Bird Survey (BBS) (Robbins et al. 1986), I tested the hypothesis that in each assemblage body sizes are discontinuously distributed, using several different methods to identify discontinuities. To address the suggestion that discontinuities may represent either zones of crisis or opportunity, I then identified all declining and non-indigenous species within each assemblage, and tested the hypothesis that these species have body masses that place them closer to discontinuities in the body mass distribution than other species in the assemblage.

My third chapter tests a proposed connection between landscape structure and the distribution of species. As described in chapter 2, Holling (1992) has suggested that the discontinuous structure of landscapes entrains attributes of the species living in those landscapes, causing them to also be discontinuous. However, there have been no quantitative tests of this connection in terrestrial environments. Using land cover data from the U.S. Geological Survey (Vogelmann et al. 2001) and avian species occurrence data from the BBS (Robbins et al. 1986), I tested the hypothesis that discontinuities in landscape structure should correspond to discontinuities in body mass distribution. To accomplish this, I applied the technique of lacunarity analysis (Plotnick et al. 1993, Plotnick et al. 1996) to land cover and species data from six ecoregions in eastern North America (Cleland et al. 1997).

The final chapter of my dissertation addresses the presumed congruence between the distribution of ecoregions, which generally reflect geology, climate, and natural vegetation, and the distribution of other taxa (Groves et al. 2000, Olson et al. 2001). The concept of ecoregions has become a critical part of many conservation policies (Government of Canada 1996, Olson and Dinerstein 1998, Groves et al. 2000), in part because of their presumed correspondence to the patterns of distribution of other types of taxa (Spector 2002). In this chapter I used land cover data from the U.S. Geological Survey (Vogelmann et al. 2001) and avian species occurrence data from the BBS (Robbins et al. 1986) to test the hypothesis that the distribution of avian species composition corresponds to the distribution of ecoregions in the continental United

States. I used seven beta-diversity metrics to assess this correspondence, and compared the performance of these different beta-diversity metrics to determine if they differently assessed the correspondence of species composition to ecoregion distribution.

# CHAPTER 1

# QUANTIFYING ECOLOGICALLY MEANINGFUL LANDSCAPE STRUCTURE

## Pattern and Process

Ecologists have long argued that the spatial heterogeneity of landscape elements has a significant influence on ecological processes such as nutrient transfer, gas flux, evapotranspiration, and primary production across landscapes, as well as on species abundances, population persistence, metapopulation dynamics, and local community structure (Forman and Godron 1986, Turner 1989, Dunning et al. 1992). However, despite this awareness of the interactions between landscape structure and ecological processes, little progress has been made in developing a body of theory to explain the link between pattern and process (Gustafson 1998, Wiens 2002, Li and Wu 2004).

The relationship between pattern and process can be reciprocal; the pattern of landscape elements can affect the rate of a process and that same process can affect the spatial distribution of landscape elements in both ecological and evolutionary time (McCoy and Bell 1991, Li and Wu 2004). However, the connection between landscape patterns and ecological processes is not always reciprocal, and there are undoubtedly many spatial patterns in landscapes that are biologically meaningless (Li and Wu 2004), or at least irrelevant to a particular ecological process (Gustafson 1998). A tendency to focus on descriptive studies of landscape structure without linking this to quantitative measurements of the functioning of any ecological process has slowed the maturation of the discipline of landscape ecology (Hargrove and Pickering 1992, Li and Wu 2004).

The description of landscape pattern and the subsequent influence of that pattern on ecosystem processes has been referred to as one of the fundamental themes of ecology and as a research priority of landscape ecology (Levin 1992, Wu and Hobbs 2002). Landscape metrics provide a means of quantifying landscape pattern, but linking pattern with process has proven to be more difficult. One challenge facing landscape ecologists is the inability to conduct randomized and replicated experiments at the relatively large scale of most landscapes and the consequent need to rely on pseudoreplication and inference instead of unambiguously establishing causal links between pattern and process (Hargrove and Pickering 1992, Noon and Dale 2002). Though analysis of simulated landscapes may partially alleviate this problem, these artificial landscapes may not accurately reflect the configurations found in natural systems (Schumaker 1996). Additionally, although the connection between a process and the relative value of a landscape structure metric may be known, there is often no ecological interpretation for any given absolute value of a metric (Gustafson 1998). Li and Wu (2004) suggest three general topics that may be contributing to this difficulty: flaws in pattern analysis, limitations of landscape structure indices, and improper use of those indices. To develop the ability to predict likely trajectories of ecosystem processes, we must acquire an understanding of the relationship between pattern and process.

## Patterns of Biodiversity

As the Earth's biodiversity continues to decline (Wilson 1992, Pimm and Raven 2000), many regional and global conservation efforts aimed at monitoring and preserving biodiversity have been developed (Scott 1993, Olson and Dinerstein 1998, Groves et al.

2000, Myers et al. 2000). All of these efforts require some assessment of the biodiversity present in an area before a conservation or restoration plan can be developed. However, such assessments are often difficult to accomplish in a timely manner due to lack of funding, lack of taxonomic expertise, and the logistical constraints of weather, political upheaval, and access to remote locations.

Patterns of biodiversity, the spatial distribution of species, are influenced by the structure of landscapes. From an evolutionary perspective these patterns are also linked to macroevolutionary, geomorphological, and biogeographical events. However, in ecological time the proximate factor involved is the dynamics of populations; the distribution, movement, and persistence of organisms in a landscape. The formation of species assemblages is affected by the availability of suitable resources (e.g. habitat types) in patches of the appropriate size and shape, and distributed across the landscape in such a way as to facilitate the ability of organisms to move, forage, and reproduce.

Describing the structure of landscape elements and understanding the influence of that structure on ecosystem characteristics such as biodiversity patterns is an important aspect of modern ecological research (Levin 1992, Ricklefs 2004). Structure refers to the spatial pattern, including size, shape, and configuration of all biotic and abiotic components of a landscape (Turner and Gardner 1991). All landscapes exhibit a heterogeneous spatial pattern at some scale; even barren sand dunes are composed of a heterogeneity of sand grain sizes and chemical composition. This heterogeneity results in landscapes with complex structure, defined by the types and abundances of resources and their spatial distribution across the landscape (With et al. 1997) and influenced by the interactions of biotic, abiotic, and human social forces in the region (Turner 1989).

## Quantifying Landscape Structure

Geographic information systems (GIS) are widely used to describe and analyze land cover and land use across landscapes (Bolstad 2002). Using GIS, immense data sets based on sources such as aerial photography, census information, and remote sensing can be characterized by a variety of metrics that can be used to monitor ecological change across broad geographic regions (O'Neill et al. 1988a, Zheng et al. 1997). There are two commonly used formats for presenting data in a GIS, raster and vector (Clarke 1999). A raster map uses a grid, where each grid cell is equivalent to one map unit and has only one attribute value (e.g. land cover type or land use). A vector-based map represents features as points on an x-y plane. Lines (sequences of points) create polygons that can be characterized by a particular attribute value.

There are several publications containing broad overviews of metrics for describing landscape structure and spatial pattern (Forman and Godron 1986, McGarigal and Marks 1995, Haines-Young and Chopping 1996, Gustafson 1998, Turner et al. 2001). Some metrics are specific to categorical data, while others require point data. Landscapes are typically described using categorical variables, although conditions within any given habitat patch are rarely uniform, and the transition from one type of patch to another might be more accurately represented as a gradient (ecotone) than as a hard boundary (Gustafson 1998). However, most landscape metrics are designed for use with categorical variables. Some metrics focus on characteristics of the landscape (*e.g.* habitat diversity and contagion), while others describe individual landscape elements (*e.g.* patch cohesion, mean patch size) (Tischendorf 2001).

Not all landscape metrics provide information useful to understanding biodiversity patterns (Li and Wu 2004). A landscape is best described by a small number of non-redundant and independent metrics that both quantify different aspects of pattern and structure and have a relationship with the ecological pattern or process of interest (O'Neill et al. 1988a, Riitters et al. 1995, Li and Wu 2004). Many metrics, such as evenness and dominance (Turner et al. 2001), or edge density and contagion (Hargis et al. 1998) are derived from similar calculations; there is little advantage to including all of them in an analysis as they provide redundant information. Riitters et al. (1995) used factor analysis and principle components analysis to reduce an initial set of 55 metrics to six, representing independent and orthogonal axes in metric state space. Similarly, McGarigal and Marks (1995) used principle components analysis to select a subset of measurements from an initial set of 30 metrics. To simplify the comparison of landscapes over space and time, O'Neill et al. (1996) combined their selected metrics of dominance, contagion, and fractal dimension into one geometric distance measurement. Although the subsets of metrics selected in these studies may not fully describe the important aspects of pattern for all landscapes, the methods used to select non-redundant metrics are broadly applicable.

Patterns of biodiversity are influenced by population dynamics; the distribution, movement, and persistence of organisms in a landscape. There are many metrics quantifying aspects of landscape structure that likely influence the formation and maintenance of species assemblages in a landscape (Table 1.1). These metrics are conventionally divided into two categories - those that characterize non-spatial landscape composition and those that characterize spatial configuration of landscapes.

### ***Landscape composition***

#### *Diversity indices*

A variety of metrics can be used to quantify the diversity (richness, dominance, and evenness) of land cover (habitat) types that occur in a landscape, such as Simpson's index and the Shannon-Wiener function (Krebs 1989, Riitters et al. 1995). Metrics such as these can be used to describe the general ability of a landscape to support organisms. For example, the persistence of populations in a landscape will depend on the presence of a sufficient quantity of one or several particular habitat types. The lack of large amounts of unsuitable habitat may be equally important to population persistence.

Diversity comprises both richness (number of types present) and evenness (relative area of each type), each of which can be quantified separately (Romme 1982, Krebs 1989). Complementing evenness is dominance, which measures the deviation of an area from the maximum possible diversity, or the extent to which one or a few land cover types dominate the area (O'Neill et al. 1988a). The richness of land cover types in a region is a measure of habitat availability. Habitat availablity influences resource availability, and therefore is related to the biodiversity of a landscape. Evenness may be an important metric to consider when assessing the availability of some critical resource for a species (O'Neill et al. 1988a, Li and Reynolds 1994). However, these metrics – diversity, richness, evenness, and dominance – are limited in their analytic value because they are redundant; landscapes with very different compositions may have nearly identical diversity and dominance values (Turner et al. 2001).

A relatively new diversity metric is mosaic diversity, *m*, which is used to measure landscape complexity (Istock and Scheiner 1987). Mosaic diversity allows distinction between simple landscapes (dominated by only a few species and controlled by a few environmental gradients) and more complex landscapes because it is a function of the variation in species richness among communities and the variation in evenness among species (Istock and Scheiner 1987, Scheiner 1992). Mosaic diversity is potentially important in diversity analyses because it allows a quantitative assessment of gamma diversity, which is a combination of both alpha and beta diversity describing the species richness of a large region (Sweeney and Cook 2001). Mosaic diversity also permits the comparison of compositional pattern diversity, or the arrangement of communities across landscapes (Scheiner 1992, Alard and Poudevigne 2000).

The mosaic diversity index has been used to characterize spatial patterns of diversity in a variety of aquatic and terrestrial regions (Istock and Scheiner 1987, Nicholls 1994, Scheiner and Rey Benayas 1994, Farnsworth and Ellison 1996, Qian et al. 1998, Alard and Poudevigne 2000, Ma et al. 2000, Sweeney and Cook 2001, Rey Benayas and Scheiner 2002). However, there has been little critical assessment of the relationship between $m$ and underlying landscape complexity. Nicholls (1994) found only weak correlations between mosaic diversity and the two environmental factors likely responsible for structuring the landscape in his study region, casting some doubt on Scheiner's (1992) interpretation of the correlation of mosaic diversity values and landscape complexity. The interpretation of $m$ must be clarified before the mosaic diversity metric can be of real use in the management of landscapes.

### *Spatial configuration*

#### *Patch area, shape & perimeter*

Metrics concerning the size and shape of habitat patches in a landscape can provide information on the likelihood that organisms will use these individual habitat elements. For some species patch size may be a crucial landscape characteristic. In forested landscapes with small patch sizes area-sensitive bird species have been shown to have low diversity, increased variability in diversity, and higher extinction rates than non-area-sensitive species (Boulinier et al. 1998, 2001). Patch size can also influence the response of vegetation to a disturbance, and disturbances will influence both patch size and shape (Franklin and Forman 1987, Li and Archer 1997). Although mean patch size can be used to describe the grain of the landscape (Herzog and Lausch 2001), simply calculating the arithmetic average could result in a misleading descriptor of patch size because patch sizes are often not normally distributed across a landscape, but instead have a skewed distribution with many small patches and only a few large ones. A better metric is an area-weighted average patch size (Turner et al. 2001), or alternatively, a metric that weights each patch size by the probability that patches of that size would randomly occur in a given number of locations in a landscape (Li and Archer 1997). This weighted mean patch size (WMPS) index can be used to characterize the response of a landscape across multiple scales to disturbance. Over time, changes in ecosystem function or landscape organization should result in changes to the index value.

Patch shape, as well as area, can influence the movement of organisms because depending on the direction of movement, shape can affect an organism's perception of the apparent size of the patch (Game 1980, Stamps et al. 1987). There are a variety of metrics assessing patch shape (Patton 1975, Game 1980, Carrere 1990, Baker and Cai

1992, Gustafson and Parker 1992). Patch shape can also indicate general characteristics of the landscape that could affect the types and numbers of species than can be found there. Landscapes that are dominated by agricultural land cover types tend to have simple geometric patch shapes while more complex shapes are found in regions with varied topography or convoluted borders, such as coastlines (O'Neill et al. 1988a). Shape and area combine to affect the amount of edge habitat that is present in a patch. Edge habitat, or ecotones, influence species by impacting microclimates (Chen et al. 1992), the movement of organisms (Turner 1989), risk of predation and brood parasitism (Robinson et al. 1995), and the amount of forest interior habitat (Pickett and Rogers 1997). Though there are metrics to measure the amount of edge in a landscape, such as edge density (Hargis et al. 1998), the value of simply quantifying the amount of edge for a particular landscape is debatable. Organisms will perceive and respond to edge habitats individually, depending on their actual and realized movement abilities and the scale at which they interact with their environment (Lidicker and Koenig 1996).

Patch perimeter, in various combinations with patch area, provides useful descriptions of the shape complexity of patches in the landscape and their edge characteristics (Forman and Godron 1986, Turner et al. 2001). These perimeter:area ratios are sensitive to patch area as two patches of the same shape but different areas will have different ratio values. However, these ratios can be standardized to account for shapes of varying size (Baker and Cai 1992). Other indices derived from perimeter measures include core area metrics, measurements of distance from the edge to the interior of patches (Gustafson and Parker 1992, Gustafson 1998), and comparison of patch shapes to shapes of equal diameter (isodiametric) (Herzog and Lausch 2001).

### *Adjacency*

The probability that two land cover types, *i* and *j*, occupy adjacent grid cells, *Pij*, can be used to describe the finer details of the spatial pattern of a landscape and the likelihood that an organism can move from one habitat patch to another. The probability of adjacency of grid cells of the same or different land cover types can be calculated directionally to look for directionality (anisotropy) in the spatial pattern, or the average probability of having cover type *j* adjacent to *i* in any direction can be determined (Turner et al. 2001).

### *Proximity and isolation indices*

The proximity of habitat patches to other patches in the landscape (or conversely, their isolation from other patches) is important to many population processes such as migration, juvenile dispersal and foraging. The distance between habitat patches is an important aspect of two major approaches to the study of population dynamics, island biogeography theory and metapopulation theory (MacArthur and Wilson 1967, Hanski and Gilpin 1997). The importance of the proximity of habitat patches will vary with the perceptive and movement abilities of the organism of interest. For example, in general birds are highly vagile organisms, easily moving through a variety of habitat types to reach preferred habitat patches. However, movement ability is not constant across all species. Some forest birds will not cross a patch of non-forest habitat to colonize a further patch of suitable forest (Diamond 1972). Organisms that can move through non-preferred habitats may only do so if the distance is relatively small or if the target patch can be identified from the occupied patch. Many metrics have been developed to assess proximity, including the proximity index (Gustafson and Parker 1992), and various distance and area based measures (McGarigal and Marks 1995). Bender et al. (2003)

present a detailed review of patch isolation studies and a comparison of the usefulness of patch proximity and isolation metrics in predicting dispersal. One of the most commonly used metrics is nearest neighbor distance, which reflects the spatial configuration of a cluster of patches (Hargis et al. 1998). However, nearest neighbor distance is somewhat limited in its applicability as a proximity metric because it does not describe the entire landscape and comparisons between landscapes can be made only if the data are of a similar extent and grain (Hargis et al. 1998).

### *Contagion*

Contagion characterizes overall landscape patterns by describing the degree of aggregation of any given land cover type, thereby quantifying both landscape composition and spatial configuration which influences the ability of organisms to move through a landscape (O'Neill et al. 1988a, O'Neill et al. 1988b, Turner 1989, Li and Reynolds 1993, O'Neill et al. 1996). As more land cover types are added to the landscape, the landscape becomes more dissected and the contagion decreases. For species that are restricted to one or a few habitat types, landscapes exhibiting low contagion can present formidable barriers to population processes such as foraging and dispersal. Contagion can also be used to assess the potential for disturbance to spread across the landscape; disturbances that only spread within a single habitat type will have a higher likelihood of propagation in a landscape exhibiting high contagion (Turner 1989).

To determine the contagion of a landscape, attribute adjacency values must be calculated using one of two methods. The order of grid cells in each pair can either be preserved (ordered) or not preserved (unordered). The method chosen can impact the sensitivity of the resulting contagion index to landscape composition and configuration (Li and Reynolds 1993, Riitters et al. 1996). The contagion metric will exhibit high values for landscapes in which there is a high frequency of adjacency between grid cells of the same land cover type or any two land cover types (Riitters et al. 1996). This can make interpretation difficult since high contagion values may reflect true aggregation of a land cover type or unequal land cover type frequencies (Riitters et al. 1996).

He et al. (2000) have developed another method of describing the aggregation of land cover types, the aggregation index. This index is based on a ratio of the actual number of shared edges to the possible number of shared edges (unlike contagion, which is a function of the area:perimeter ratio of patches (Hargis et al. 1998)). It is independent of map unit, allowing the comparison of aggregation values among land cover types from the same or different landscapes. However, it is possible for two land cover types to have the same aggregation index value and yet have different spatial patterns. The limitations of these contagion and aggregation metrics emphasize the importance of using multiple, non-redundant metrics to accurately describe spatial pattern.

### *Connectivity*

There are two distinct concepts of connectivity in landscape ecology: structural and functional (Tischendorf and Fahrig 2000b). Structural connectivity refers to the physical contiguity of habitat across a landscape, regardless of its suitability for any given species. Functional connectivity describes the relationship between the spatial pattern of habitat and the ability of organisms to respond to this pattern and move through the landscape (Taylor et al. 1993). If an organism's movement is limited to only one habitat type, then the structural connectivity of this habitat within the landscape is synonymous with functional connectivity. However, because the congruence of structural and functional connectivity is not a universal phenomenon, any effort to detect a relationship between patterns of landscape connectivity and processes involving the movement of organisms through that landscape must focus on assessing functional, not structural, connectivity.

Functional landscape connectivity results from the spatial pattern of the landscape and the response of organisms to that pattern and is therefore both a species- and landscape-specific phenomenon that can influence the ability of populations to persist (Fahrig and Merriam 1985, With et al. 1997, Tischendorf and Fahrig 2000b). Functional connectivity is typically measured by quantifying dispersal success (number of successful immigrants) or search time (number of movements during dispersal) for a number of individuals in a study population (Schumaker 1996, Tischendorf and Fahrig 2000a). However, these data, which would require tracking multiple individuals and generations across landscapes, are logistically difficult to obtain (Tischendorf and Fahrig 2000b). Schumaker (1996) examined the ability of nine commonly used metrics of landscape pattern to predict landscape connectivity. He found only weak correlations between simulated dispersal success and the measurement of pattern in real landscapes, suggesting that these metrics would be poor substitutes for actual dispersal data. Instead, Schumaker (1996) developed a new index, patch cohesion, based on patch perimeter:area ratio and a shape index (see also Gustafson 1998). He found that patch cohesion performed better at predicting landscape connectivity.

Other methods for assessing landscape connectivity include graph theory and ring statistics (Wiegand et al. 1999, Urban and Keitt 2001). Graph theory applications are relatively new to landscape ecology although they are widely used in other disciplines such as geography and computer science. Graph theory represents landscapes as binary systems (habitat and non-habitat). Patches of habitat (nodes) are depicted as connected by lines (edges), creating systems and sub-systems of nodes that are connected by pathways of varying length. The connecting edges do not have to reflect Euclidean distances between patches, but instead can represent species-specific processes, such as the probability of dispersal between patches. By adding or removing nodes and edges to evaluate subsequent effects on the connectivity of the graph, graph theory can be used to assess the potential effects on population dynamics of gaining or losing habitat patches or dispersal corridors. The advantages of graph theory are that it requires only a minimum of demographic data and can be used to analyze landscapes with large numbers of patches as powerful algorithms have already been developed that can easily be modified for use in addressing ecological questions (Bunn et al. 2000, Urban and Keitt 2001). Landscape connectivity can also be described with ring statistics, which do not rely on a binary patch-based analysis and provide a means of assessing connectivity at multiple spatial scales (Wiegand et al. 1999). Using raster GIS data the connectivity of grid cells of suitable habitat or the interspersion of suitable habitat with unsuitable or poor quality habitat can be described, providing an assessment of the ability of a species of interest to move through the landscape. A ring of radius $r$ is chosen such that $r$ corresponds to the perceptual or movement abilities of the species of interest and the probability that a grid cell of habitat type $j$ is located at distance $r$ from a cell of habitat type $i$ is calculated.

### *Lacunarity*

Lacunarity analysis, first introduced by Mandelbrot (1983), has been developed as a method of describing the "texture" or "gappiness" of a landscape; it measures the distribution of gaps between habitat patches across a landscape (Plotnick et al. 1993). This measurement provides a scale-dependent quantification of the spatial heterogeneity of a landscape. The heterogeneity of a landscape, and the variation of the pattern of this heterogeneity with changes in scale, affects the ecological processes that occur in the landscape (Turner et al. 2001).

Lacunarity analysis is primarily conducted with binary data, though it can also be applied to quantitative data (Plotnick et al. 1996). Using a mean:variance ratio, lacunarity assesses the deviance of the landscape from translational invariance (objects that are self-similar at all scales are translationally invariant), or how similar different parts of a landscape are to each other (Plotnick et al. 1996). Although there are several methods of calculating lacunarity (see references in Plotnick et al. 1993), typically the gliding-box algorithm is used (Allain and Cloitre 1991). This is a moving window analysis that measures the density of the habitat of interest within the window as it moves across the landscape. The lacunarity value is dependent on the size of the box used, the fraction of the map occupied by the habitat of interest, and the geometry of the map (Plotnick et al. 1993). By using a variety of box sizes a lacunarity curve can be plotted as log(lacunarity) vs. log(box size); the curve can be standardized to allow comparisons among landscapes (Plotnick et al. 1996, Dale 2000). The shape of this curve depends only on the spatial pattern of the habitat and not its density in the landscape; habitat density is reflected in the position of the curve (Plotnick et al. 1993). Sudden changes in the slope of the lacunarity curve indicate shifts in the spatial pattern of landscape heterogeneity (Plotnick et al. 1996).

## Influence of Scale

The concept of spatial scale, which includes both grain (the resolution of the data) and extent (the spatial coverage of the data) is critical to understanding and predicting the interaction between landscape patterns and processes (Wu and Qi 2000). Temporal scale is also important (Gustafson 1998), but is not considered explicitly here. The scale at which landscape structure data are collected (e.g. satellite imagery at 1 km vs. 30 m resolution) can influence the interpretation of those data. The spatial extent of a landscape that is considered at any given time will influence what spatial patterns are observed (Turner et al. 1989, Haines-Young and Chopping 1996). For example, in its entirety a meadow may appear homogeneous, but within the meadow there may be many irregularly spaced clumps of grasses and other herbaceous plants interspersed with small patches of bare ground. The processes determining landscape pattern vary with area (O'Neill and King 1998). Biotic interactions may be more important at structuring the landscape at a local level, while geomorphological processes are more important across broad regions (Meisel and Turner 1998). The scale at which data are collected and analyzed can also influence the amount of information that can be gained. For example, small dispersed patches of habitat can not be detected as the grain of data is increased (Turner 1989, Haines-Young and Chopping 1996). Analyses conducted using low resolution (large grain) data may underestimate the diversity of land cover types and the number of habitat patches present in a landscape. To address this, O'Neill et al. (1996) suggest that the resolution of the collected data should be two to five times smaller than the smallest feature of interest, and the sample size (or area over which a metric is calculated) should be two to five times larger than the largest land cover patch in the landscape.

Many population dynamic and source-sink models condense the true variability of real landscapes into two land cover types, suitable and unsuitable habitat, or habitat and neutral matrix (Wiegand et al. 1999). Although a meta-analysis of 61 studies (Mazerolle and Villard 1999) found that both landscape composition and configuration variables were important predictors of species presence and abundance, solely considering composition and configuration may not be enough to accurately assess the functionality of a landscape for a particular species (Taylor et al. 1993). Instead, the ability of organisms to perceive and respond to the heterogeneity present in a landscape at a given scale must also be incorporated into population dynamic models. Organisms interact with different components of their environment based on their movement capabilities, resource requirements, and ability to use available resources (O'Neill et al. 1988b, Milne et al. 1989, Holling 1992). For any given pattern of spatial heterogeneity, organisms of distinct species will respond differently because of their differential ability to detect and respond to this heterogeneity (With 1994, Riitters et al. 1997). Therefore, landscape structure must be observed and its patterns analyzed at a scale (both extent and resolution) that is appropriate to the organism of interest.

As the field of landscape ecology has developed, researchers have realized the importance of changing their focus from human-defined landscapes (kilometers across) to landscapes whose extent is defined by the organisms and processes being studied (Wiens 1989, Wiens and Milne 1989). Typically, this landscape size is larger than an individual organism's home range and smaller than the geographic range of the species (Dunning et al. 1992). However, the resolution of data collection is often determined by available technology instead of an attempt to match the resolution with which the organism perceives the environment. Additionally, to reduce analysis time researchers may aggregate their data to a coarser resolution than the scale of observation. Neither of these practices will necessarily lead to incorrect conclusions, but changes in scale should be noted and tested for potential impacts on conclusions.

Many contemporary issues in science and public policy require a broad-scale approach (Peterson and Parker 1998, Wu and Qi 2000). The resources required to establish regionally coordinated environmental monitoring and data collection efforts are substantial. The obvious alternative is the “scaling-up” of information collected at small scales or in studies of “microlandscapes” to explain large-scale phenomena (Wiens 1989, Wiens and Milne 1989, King 1991, Johnson et al. 1992, Wiens et al. 1993). For example, the dynamics of populations – their reproduction, foraging, dispersal, and mortality – are dependent on the movement of individuals through the landscape (Wiens et al. 1995). A characterization of individual movements through a heterogeneous landscape can be translated across scales to describe and predict the distribution of a population (Turchin 1991, Johnson et al. 1992, Wiens et al. 1995, Turchin 1996).

However, translating information across scales is not simple, nor is it always advisable (Wiens 1989, Schneider 1998). The relationship between pattern and process may remain constant or change linearly only within certain domains of scale. The extrapolation of information from one scale to another within such a domain is valid. Separating these domains are transitions, or scale-breaks, across which relationships may exhibit sudden changes (Wiens 1989). Information cannot be extrapolated across domains, as this changes the observed level of organization, known as a transmutation (aggregation) error (O'Neill and King 1998). For example, With and Crist (1996) found that extrapolating average individual grasshopper movement patterns did not accurately simulate observed population distributions.

Transitions between domains of scale can result in sudden changes in the responding ecological process; these are called critical thresholds (Turner and Gardner 1991). Such thresholds have been found in the response of species to changes in the contagion (habitat fragmentation) and connectivity of landscapes, affecting dispersal and population persistence (Gardner et al. 1987, With and Crist 1995). Understanding these thresholds is important for accurately assessing the viability of populations in fragmented landscapes.

There are a variety of methods for detecting scale breaks in a landscape and characterizing its multi-scale structure (Turner et al. 1991, Gardner 1998, Wu et al. 2000). Multi-scale methods include scale variance, semivariance analysis, and lacunarity analysis. Scale breaks can also be detected indirectly by re-sampling data at different scales and repeatedly computing landscape metrics (such as contagion or perimeter:area ratios). Analysis of real landscape data has shown that some landscape metrics display predictable and simple changes with changes in scale, while others have more complex or even erratic responses (Wu et al. 2000, Wu et al. 2002, Wu 2004). The variance of calculated values will also fluctuate with changes in scale (Wiens 1989).

## Conclusion

As monitoring and managing the environment at the scale of landscapes has become increasingly common, the importance of adequately predicting the effect of variation in environmental heterogeneity on ecological processes has become apparent (Stewart et al. 2000). The complex phenomenon of landscape structure can be described and quantified with many available landscape metrics. When used appropriately, these metrics can provide a powerful means of linking landscape patterns with ecological processes, such as the formation and maintenance of species assemblages, that influence patterns of biodiversity. However, a better understanding of the limitations, sensitivities, and the range of potential values for landscape metrics needs to be developed (Haines-Young and Chopping 1996, Hargis et al. 1998). The ability to develop functional and successful conservation and ecosystem management strategies require the integration of landscape ecology with spatially explicit models of population dynamics (Wiens et al. 1993). As anthropogenically induced changes in landscape structure increase in magnitude and extent, gaining the ability to understand and predict the effect of these changes on patterns of species distribution has become crucial to the efficiency and long-term success of ecosystem management and conservation efforts.

Table 1.1. Metrics quantifying aspects of landscape structure that likely influence the formation and maintenance of species assemblages.

| Metric | Primary Literature |
|---|---|
| Landscape Composition | |
| Diversity indices | |
| Richness | Krebs (1989), Riitters et al. (1995) |
| Evenness | Krebs (1989), Riitters et al. (1995) |
| Dominance | O'Neill et al. (1988a) |
| Mosaic diversity | Istock & Scheiner (1987), Scheiner (1992), Nicholls (1994) |
| Landscape Configuration | |
| Patch area | Li & Archer (1997), Herzog & Lausch (2001) |
| Patch shape & perimeter | Game (1980), Carrere (1990), Baker & Cai (1992), Gustafson & Parker (1992) |
| Adjacency | Turner et al. (2001) |
| Proximity & isolation | Gustafson & Parker (1992), Bender et al. (2003) |
| Contagion | O'Neill et al. (1988a), Li & Reynolds (1993), He et al. (2000) |
| Connectivity | Tischendorf & Fahrig (2000a, 2000b), Wiegand et al. (1999), Urban & Keitt (2001), Schumaker (1996) |
| Lacunarity | Mandelbrot (1983), Plotnick et al. (1993), Plotnick et al. (1996) |

# CHAPTER 2

# THE ECOLOGICAL SIGNIFICANCE OF DISCONTINUITIES IN BODY MASS DISTRIBUTIONS

## Introduction

Typically, the mean body sizes of species within an assemblage are not evenly distributed along a continuum of possible body sizes (see references within Holling 1992, Havlicek and Carpenter 2001). Rather, these distributions typically contain significant discontinuities that indicate species of certain size ranges do not exist within the assemblage (Holling 1992). Discontinuous body size distributions appear to be relatively common in natural assemblages, though the position and number of discontinuities varies among ecosystems and taxa (Schwinghamer 1981, Holling 1992, Allen et al. 1999, Havlicek and Carpenter 2001). This implies that ecosystems vary in their ability to support organisms of particular sizes, and may reflect the heterogeneity of environmental structure (Holling 1992).

The size of an organism determines the manner in which it interacts with its environment, and therefore what constitutes available resources (Holling 1992, Milne et al. 1992). The combination of the structure of the environment and the ability of an organism of a particular size to use and respond to that structure will influence population dynamics (Milne et al. 1992, Cuddington and Yodzis 2002). This ultimately determines which species can have self-sustaining populations in any given geographic region and will therefore contribute to the body size frequency distribution of that assemblage.

Holling (1992) proposed that a small number of biotic and abiotic processes, each of which operates at a particular spatial and temporal scale, govern the structure of terrestrial landscapes. These scale-specific processes create discontinuously structured landscapes. Organisms can only interact with their environment at a single scale at any given time, although some species may have the ability to shift their interactions between two scales (Holling et al. 1996, Allen and Saunders 2002). Using this approach, Holling (1992) suggested that organisms living in a discontinuously distributed landscape will exhibit attributes, such as range size or body size, that are also discontinuously distributed due to the hierarchical structure of resources in their environment.

This study examines the relationship between several characteristics of landscapes across eastern North America and the avian species assemblages within them in order to address three hypotheses. First, a species assemblage within an ecosystem will have identifiable discontinuities in its body size spectrum. Since discontinuities in the body size spectrum represent body sizes for which suitable resources are not accessible in that landscape (Holling et al. 1996), species that are declining or present in very low numbers in that landscape should be found close to discontinuities in the size spectrum. Human impacts on landscapes result in changes in landscape structure, and therefore resources. Second, the pattern of discontinuities in the body size spectrum will respond to the alterations in landscape structure caused by human activities. It has also been suggested that these changes will cause species turnover in an ecosystem, beginning with species occurring close to discontinuities in the size spectrum as these areas are "zones of crisis and opportunity" (Allen et al. 1999). This leads to the third hypothesis, that in ecosystems that have been impacted by human activities, not only will declining species occur close to discontinuities, but non-indigenous species will also be found there.

## The Species Assemblage

In North America, birds are widespread in every ecosystem and their characteristics are well known. North American ecosystems (north of Mexico) have been represented by "physiographic regions" delineated for the North American Breeding Bird Survey (BBS) (Bystrak 1981). These physiographic regions were delineated based on physical characteristics and land use. Therefore, it is assumed that each region represents a relatively uniform biotic area, as required by Holling's (1992) hypothesis. Of the 73 physiographic regions described by the BBS, only 10 are sampled by more than 100 BBS routes. Of these 10 regions, six that are located almost entirely within the eastern United States were selected in which to examine size structure (Figure 2.1). BBS routes consist of 50 sampling points located 0.8 km apart along secondary roads. Surveys are conducted once per year during June, and all birds seen or heard at each sampling point are recorded (Robbins et al. 1986).

A species list was compiled for each physiographic region based on all observations of terrestrial birds made on each route in that region over the course of the BBS. These regions are relatively small compared to the size of the geographic range of many bird species, and in many cases are adjacent to one another, resulting in overlap among the species assemblages of different regions. The similarity of these species assemblages was assessed with a hierarchical agglomerative cluster analysis. The average linkage (UMPGA) cluster analysis performed better than a Ward's cluster analysis (cophenetic correlations 0.87 and 0.79, respectively), though they differed only in the placement of region 31, the Till Plains. The dendrogram (Figure 2.2) shows that the species assemblages of the two coastal regions (3 and 4) are quite similar. The assemblages of the four non-coastal regions, especially the two mountainous regions (13 and 24) are also similar. Despite these similarities among regions, no two regions are inhabited by exactly the same complement of species.

The body size of birds can be measured with a variety of univariate and multivariate methods, but the best single descriptor is probably adult body mass (Rising and Somers 1989). Although using body mass as an estimator of overall size can be problematic because of seasonal and intra-specific variation (Gaston and Blackburn 2000), it also has distinct advantages. Body masses can be compared among taxa, unlike other size metrics such as wing-span or tarsus length. They can be used to estimate many other species characteristics, such as metabolic and reproductive rates (Peters 1983). Body masses have been documented for many of the world's bird species. These analyses use the masses provided by Dunning (1993).

The six selected regions have experienced varying degrees of human modification. The native vegetation of the Allegheny Plateau (24) and Ridge and Valley (13) ecosystems both consist primarily of upland deciduous forest. The Coastal Flatwoods (3) contains sand dunes, maritime forest, marsh, bottomland hardwoods, and pine. The slightly more interior Upper Coastal Plain region (4) is predominantly a mixture of upland pine forest and bottomland hardwoods. The Great Lakes Plain (16) is dominated by glacial topography, and contains broadleaf forest, oak savannah, and prairie interspersed in the landscape. The Till Plains (31) are a mosaic of tall-grass prairie, savannah, and forest.

The species list for each region was analyzed to determine which species were exotic or declining (Table 1.1). Non-indigenous species were defined as those introduced by humans from some other locality, such as the European starling (*Sturnus vulgaris*), or in eastern North America, the house finch (*Carpodacus mexicanus*). The term "declining" refers to those species that are at risk of extinction or local extirpation. In some cases the abundance of a species may actually be increasing due to conservation efforts, though still below historical levels. Declining species were identified by consulting lists of protected species for each state that intersected a physiographic region. Species in the three highest risk categories (state endangered, state threatened, and species of special concern) were considered to be declining. If a state's natural resource agency did not maintain a list of state-protected species, then the information was obtained from the state's natural heritage program. Because each physiographic region is intersected by multiple states it was possible, though not typical, for a species to be defined as declining within the region even though it was considered to be at-risk by only one state in the region. Every state has a different process for determining at-risk species; each of these processes is also influenced by local politics. As a result, the definition of a declining species used in this study may not accurately reflect the regional biological status of a species in all cases. However, the use of state lists is a practical method of describing species status. Additionally, for each ecosystem the state lists that were used to generate the regional list of declining species were remarkably similar.

## Identification and Measurement of Discontinuities

Discontinuities in the body mass spectrum can be identified with several methods (Holling and Allen 2002). Each method has its strengths and weaknesses, and therefore criticism can be leveled at any particular method (e.g. Manly 1996, Siemann and Brown 1999). Confidence in the accuracy of identified discontinuities is increased if multiple methods produce the same result. Consequently, the following six methods were used to identify the discontinuities in the avian body size spectrums. Only the native species of an ecosystem were used in these analyses, in order to determine where discontinuities exist in the recent historical fauna of a region (Allen et al. 1999).

### *Holling index*

Holling (1992) described an index to measure how similar a species is to those species closest to it in size,

$$HI = \frac{M_{n+1} - M_{n-1}}{(M_n)^k}$$

where $Mn$ is the body mass (g) of the $n$th species in order of increasing size and $k$ is a constant that detrends the data. Holling found this constant to be taxon-specific; equivalent to 1.3 for birds and 1.1 for mammals. A large value of HI indicates a species is quite different from those ranked closest to it in size. To determine how large an index value must be to represent a true discontinuity in the distribution, a criterion line is placed at the average index value plus one standard error (Holling 1992). Discontinuities in the distribution are identified by those index values that are greater than the criterion (Figure 2.3A).

### *Siemann & Brown index*

Siemann and Brown (1999) also developed a body mass difference index,

$$SI = \log_{10}\left(\frac{M_{n+1}}{M_n}\right)$$

They argued that this is a more precise metric than the Holling Index, and it requires no *a posteriori* defined exponent to correct the data.

### *Robust indices*

Because of the concern that the beginning and ending values in each body mass spectrum were producing artifactual high index values that would result in the identification of false discontinuities, a robust version of the two indices was created. Exceptionally high index values at each end of the distribution were identified visually, removed from the calculation of the average index value, and the criterion line for determining if a discontinuity was significant was recalculated (Figure 2.3B).

### *Lump analysis-gap rarity index*

The lump analysis-gap rarity index (Restrepo et al. 1997) uses the gap rarity index statistic (GRI), which is the probability that the observed discontinuities in the body size spectrum occur by chance alone. The GRI was calculated by comparing the actual data with a null distribution. The null distribution was generated by using log-transformed body masses to estimate a continuous unimodal kernel distribution (Silverman 1981, 1986). This null distribution was then sampled repeatedly and an absolute discontinuity value,

$$d_n = \log_{10}\left(\frac{M_{n+1}}{M_n}\right)$$

was calculated for each species in each simulation. The distribution of the differences for the *n*th largest species from the simulations was compared to the actual value obtained from the original data. The GRI for each species in the actual assemblage is the proportion of the simulated discontinuity values that were smaller than the observed discontinuity value. The significance of each GRI value was then determined by testing the null hypothesis that the value was drawn from a continuous distribution with an alpha of $< 0.05$. Significant GRI values represent discontinuities in the body size distribution.

### *Cluster analysis*

Hierarchical cluster analysis using PROC CLUSTER (SAS Institute 1999) was also used to identify the "clumps" in the body mass spectrum. Ward's minimum variance clustering method (Ward 1963), based on a within-cluster least squares criterion, was used because of its high performance compared to other clustering methods (Milligan 1981). Determining the appropriate number of clusters is difficult, but can be aided by looking for consensus among the three criteria calculated by PROC CLUSTER: the psuedo F-statistic, the psuedo $t^2$ statistic, and the cubic clustering criterion (CCC). The clusters formed in this way represent a sequence of clusters from one containing the smallest species to one containing the largest species. Boundaries between clusters are formed by species that are next to one another in ranked body size. A discontinuity can then be defined as existing between species adjacent to one another in ranked body size, but belonging to different clusters.

Discontinuities identified by the Holling and Siemann & Brown indices, as well as their robust versions, were compared. Consensus discontinuities were defined as those identified by a majority (at least three) of these four methods (Table 2.2), and were used in further analyses. For three ecosystems, these consensus discontinuities were also compared with the results from the lump analysis-gap rarity index and the cluster analysis. In general, the six methods were quite comparable. Other studies (Holling et al. 1996, Holling and Allen 2002) have found that several additional methods will also identify the same discontinuities in a dataset. These methods include the split moving window index (Cornelius and Reynolds 1991), the Silverman difference index (Silverman 1986), a kernel estimator (Chambers et al. 1983, Silverman 1986), and classification and regression tree analyses (Clark and Pregibon 1992).

The structure of body mass distributions can be described in terms of the distance of each species in an assemblage to the nearest discontinuity (*e.g.*, Figure 2.4). To determine these distances, species that defined the edges of a discontinuity were assigned a value of zero. Any species that occurred in a discontinuity was also given a value of zero. Values for all other species were calculated as the absolute value of the difference between the mass of that species and the mass of the closest discontinuity edge. The untransformed body size distributions were positively skewed, causing the distribution of distances to nearest discontinuity to also be positively skewed. Before log-transforming the distance to nearest discontinuity metric, a small constant of 1/6 was added to each value to allow the use of zero distances (Tukey 1977).

## The Patterns

The expectations for the patterns of the body mass spectra were partially fulfilled. In each of the six physiographic regions, discontinuities in the body mass spectra were identified with several methods, providing further support for Holling's (1992) hypothesis. Data from other taxa, locations, and scales have also been shown to support this hypothesis – birds and mammals of North American boreal forests and the short-grass prairies of Alberta (Holling 1992); birds, mammals, and herpetofauna of the Everglades, cave bats of Mexico, and birds and mammals of Mediterranean-climate Australia (Allen et al. 1999, Allen and Saunders 2002), and marine sediment assemblages (Raffaelli et al. 2000); but see also Manly (1996), Siemann and Brown (1999) and Leaper et al.(2001).

### *Discontinuity structure*

The overall pattern of discontinuities in the six physiographic regions is shown in Figure 2.4. The smallest species in each body mass spectrum was the ruby-throated hummingbird (*Archilochus colubris*) at the left of the graph, while the largest species was the wild turkey (*Melleagris gallopavo*). There were consistently more discontinuities at smaller body sizes than at large; this reflects the larger number of small species in each assemblage.

With a few exceptions, discontinuities were located at the same point in the body mass spectrum, regardless of ecosystem. In the two regions with fewer discontinuities, the Coastal Flatwoods (3) and the Till Plains (31), the discontinuities that were not observed were those at the smaller body sizes. This observation illustrates two points. First, at a large spatial scale (represented by large body sizes) the discontinuity structure should be similar across ecosystems within a biome, as the underlying large-scale geomorphological processes will also be similar. Discontinuities at smaller spatial scales would be expected to be similar across forested ecosystems within a biome, because the small-scale structure of leaves and twigs is similar regardless of tree species. However, the small-scale structure would be expected to be different between forested and nonforested ecosystems. The Coastal Flatwoods and Till Plains regions may have fewer discontinuities at small body sizes because the forest component of these ecosystems differs from the other four. Related to this, a change in the discontinuity structure suggests that there has been a change in the complexity of the landscape (Holling et al. 1996). Due to differences in vegetation composition and the impact of human activities, the landscapes of the Coastal Flatwoods and Till Plains may have less complexity in their structure, and therefore fewer discontinuities in their body size spectra.

### *Declining species*

For the six regions, there was a slight trend for the declining species to be closer to discontinuities than the other native species (average of 52% of the declining species were closer to discontinuities than the median distance to nearest discontinuity). The same pattern was also found for declining species in the Everglades (Allen et al. 1999).

Over half (42 out of 72) of the declining species that are found in multiple ecosystems had the same distance to nearest discontinuity, regardless of ecosystem (Figure 2.5). The different distance measurements for 30 of the declining species reflect the slight changes in discontinuity structure from region to region (Figure 2.4).

### *Non-indigenous species*

Unlike the study by Allen et al. (1999), which also looked at the arrangement of invasive and declining species in the body size spectrum, here non-indigenous species were not associated with the discontinuities in the body mass distribution. Cumulative distribution functions of the distances to nearest discontinuities for each of the regions showed that an average of 72% (range of 43% to 83%) of the non-indigenous species were further away from discontinuities than the median distance (Figure 2.6).

It is also apparent from these cumulative distribution plots that, as with the declining species, the occurrence of non-indigenous species in relation to the discontinuity structure was consistent from ecosystem to ecosystem. The house finch (*Carpodacus mexicanus*) is widely distributed in all six ecosystems and was consistently located at the edge of a discontinuity in each distribution. The house sparrow (*Passer domesticus*) and the European starling (*Sturnus vulgaris*) are also widely distributed in all regions but these species were always found near the median distance to the nearest discontinuity. The Eurasian collared-dove[1] (*Streptopelia decaocta*), ringed turtle-dove (*S. risoria*), rock dove (*Columba livia*), gray partridge (*Perdix perdix*), and the ring-necked

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[1] This non-indigenous species was actually introduced into the Bahamas and then invaded Florida.

pheasant, *Phasianus colchicus*, had the largest distance to the nearest discontinuity in each region.

### *Body size*

The positively skewed distribution of body sizes in each ecosystem means that there are far more small species than large species. Similarly, the pattern of discontinuity occurrence in the distributions (Figure 2.4) shows that most discontinuities occurred at small body sizes. As a result of these patterns, large-bodied species were usually farther from the nearest discontinuity than small-bodied species. This is evident in a plot of the average distance to nearest discontinuity for non-indigenous species (Figure 2.7), and in a similar plot for declining species (Figure 2.8). However, it is worthwhile to examine those species that appear to be outliers and consider what may make them unique.

The plot of average distance to nearest discontinuity for non-indigenous species (Figure 2.7) shows that based on its body size, the monk parakeet (*Myiopsitta monachus*) was located closer to a discontinuity than expected in the one region in which it occurs. In fact, this species was actually located within a discontinuity. Unlike the other non-indigenous species, which are all ground gleaners (Ehrlich et al. 1988), the monk parakeet can utilize a variety of foraging strategies (South and Pruett-Jones 2000). The house sparrow (*Passer domesticus*) is widely distributed in all six ecosystems, and was always found near the median distance to the nearest discontinuity. However, its similarly sized congener, the Eurasian tree sparrow (*Passer montanus*) was found within a discontinuity. Although the Eurasian tree sparrow has been quite successful in its region of introduction, it has not expanded its range in North America since its arrival in 1870.

The trend of increasing average distance to nearest discontinuity with increasing body size is even clearer for the more numerous declining species (Figure 2.8). However, there are some species that were much closer to discontinuities than expected for their body size. Interestingly, the opposite pattern does not appear. Many of these species defined the edges of a discontinuity in all regions in which they occur. These include the Swainson's hawk (*Buteo swainsoni*) and the greater prairie-chicken (*Tympanuchus cupido*), which occur in only one region, as well as the cliff swallow (*Petrochelidon pyrrhonota*), whip-poor-will (*Caprimulgus vociferous*), eastern meadowlark (*Sturnella magna*), long-eared owl (*Asio otus*), and the barred owl (*Strix varia*), which are declining in multiple regions. Other species, such as the common nighthawk (*Chordeiles minor*), red-shouldered hawk (*Buteo lineatus*), peregrine falcon (*Falco peregrinus*), and northern goshawk (*Accipiter gentilis*) defined discontinuity edges in some ecosystems but not in others.

### ***Region-species interactions***

A combined plot of the cumulative distribution functions of the distance to nearest discontinuity for all ecosystems (Figure 2.9) shows that most ecosystems have a very similar probability structure. However, the Till Plains were strikingly different. In this region there was relatively little probability of a non-indigenous species occurring only a short distance from a discontinuity, but at distances greater than the median distance to nearest discontinuity, the probability increased rapidly. The Upper Coastal Plain appeared to be somewhat intermediate between the Till Plains and the other ecosystems. There was a significant interaction between region and species type (non-indigenous or declining;

maximum likelihood contingency table analysis, $\chi^2 = 11.42$, df = 5, P = 0.04). Generally, a small proportion of the non-indigenous species in each ecosystem were found at a distance less than the median distance to nearest discontinuity, and a relatively high proportion of declining species were found at a distance less than the median (Figure 2.10). However, this relationship was reversed in the Till Plains.

This analysis of the body mass distributions of terrestrial breeding birds across six ecosystems of eastern North America resulted in several clear patterns. Discontinuities in the body mass spectra were clearly present in all six ecosystems. The distribution of these discontinuities in each body mass spectrum was similar across ecosystems. Declining species were generally closer to discontinuities than expected, while non-indigenous species were generally farther from discontinuities than expected. Body size generally increased with increasing distance to nearest discontinuity. There is an ecological significance to the structure of these discontinuities, evidenced by the fact that there are consistent patterns across ecosystems, and there are clear differences between successful invasive and declining native species in an ecosystem.

## Mechanisms Underlying Discontinuities

With so much environmental heterogeneity present among these six ecosystems, it is difficult to envision a simple underlying mechanism. Yet the discontinuities in the assemblages are non-randomly located, and the species react to these discontinuities in a non-random manner, which suggests that there must be some common underlying mechanism. One possibility is that the mechanism consists of the identifiable effects that the template of landscape structure has on population dynamics.

### *The landscape template*

The composition of any landscape is a result of the past and present co-occurrence of biotic and abiotic elements in a certain spatial configuration. Climate, geology, topography, competition, predation, disturbance, and succession all interact to influence the components of an ecosystem. The structure of a landscape is described by the geometries of the biologic and geologic components (Turner et al. 2001, Noon and Dale 2002). The presence and configuration of certain elements in a landscape will influence the characteristics of the ecosystem that exists in that landscape (Wiens 1995).

The structure of the landscape is scaled in an hierarchical manner by the temporal and spatial pattern of a few key processes (Holling 1992). For example, the dynamics of boreal forests and their insect defoliators are governed by four dominant cycles. Each of these cycles operates over a specific time period and spatial extent, such as the relatively fast, small-scale interaction between insects and needles, and the slower cycle of pest outbreaks that cause tree mortality over large areas (Holling 1992). This hierarchical structure is linked to the distribution of available resources. Any given resource exists at only one scale in the landscape. Landscapes that differ in structure will have differently scaled resources. This discontinuous structure forms a template upon which the geographic ranges of species are overlaid. The template is both spatially and temporally dynamic, as the types and abundances of resources change between locations and time periods.

The template of landscape structure is influenced by natural disturbances in the environment. Natural disturbances can be biotic (the grazing of large herbivores) or abiotic (fire, wind, drought). The spatial scale of disturbances varies over orders of magnitude; a raindrop will only impact one seedling (Begon et al. 1990), while a drought may affect a large geographic region. A small disturbance may create only an opening in the landscape (tree canopy gaps), while a large disturbance can reset the successional stage of the community. Natural disturbances also vary temporally, with occurrences ranging from frequent (tidal cycles) to very rare (volcanic eruptions). Disturbances that happen often enough can invoke selection pressures on populations (Begon et al. 1990). The impacts of disturbance can be assessed by measures of ecological resilience (Holling 1973).

Although landscapes have always been impacted by natural disturbances, anthropogenic disturbances are becoming increasingly common. Currently, most changes in landscape pattern are a result of human activities, including deforestation, conversion to agriculture, and urbanization (Turner et al. 2001). Many of the anthropogenic changes to ecosystems are not unlike natural changes that have occurred over evolutionary time. Indeed, humans have influenced the structure of landscapes for millennia by changing the relative abundances of species (especially plants), altering the geographic ranges of species, aiding the invasion of non-native species, altering soil composition, and changing the distribution of cover types (Delcourt 1987). However, anthropogenic changes to ecosystems, including biological invasions and extinctions, are now occurring at a much faster pace than ever before (Vitousek et al. 1997).

As with other continents, human impacts in North America have been substantial. Forest clearing in the east began with the original Native American inhabitants, and then increased dramatically after the arrival of European settlers. In the late 1800s eastern forests were being lost at a rate of 200,000 km$^2$/yr. With the abandonment of farms in the early 1900s and subsequent reforestation, rate of forest loss slowed to about 96,000 km$^2$/yr (Williams 1990). In the last 300 years, North America has lost about seven percent of its forests (Richards 1990), although almost every forest in the east has been cut at some point (Pimm and Askins 1995).

The structures of the six physiographic regions analyzed in this study (Figure 2.1) have been affected in various ways by human activities. In many areas, not only has native vegetation been replaced by crops, but mixed crops have been replaced by single-crop monocultures, further reducing the structural heterogeneity of the landscape (Warner 1994). The Till Plains ecosystem historically consisted of a mosaic of prairie, savannah and forest, but currently almost 70% of this landscape has been converted to annual row crops (corn and soybeans) (Fitzgerald et al. 2000). About 15% of the region remains as some sort of pasture/grassland habitat, but the composition has been altered here too. For example, the amount of land planted with a homogeneous monoculture of alfalfa has increased in recent years. Only a small amount of the original habitat is estimated to remain (Fitzgerald et al. 2000). Land conversion for agriculture and urbanization, especially along the coastline, has led to the loss of a large fraction of native habitat in the Coastal Flatwoods region (Hunter et al. 2001). Most forested wetlands have been harvested and fragmented, and intense development along the coast has led to the loss of maritime forest, dune and marsh. The eastern portion of the Upper Coastal Plain has been converted to annual row crops (corn or soybeans) across approximately one-third of its area. Most of the historically widespread southern pine habitat has been cut and converted to pine plantations or non-forest uses (Hunter et al. 2001). Almost the entire original savannah habitat in the Great Lakes Plain is gone, as well as over 80% of the forest. Croplands (corn, soybeans, hay, pasture, grains) are now the dominant landcover (Knutson et al. 2001).

The influence of humans on ecosystems has been dramatic and pervasive. Urbanization and conversion to agriculture homogenize both the structure of landscapes as well as the genetic, population, and species diversity of biota within them (Matson et al. 1997, Vitousek et al. 1997, August et al. 2002). Agricultural practices have substantial effects on ecosystem processes, including the activities of soil biota, nitrogen and other nutrient cycling, and hydrological cycles (Matson et al. 1997). It is likely that as human activities continue to cause additions and deletions in regional species assemblages that ecosystem functioning will be changed. These changes may reduce the resistance and resilience of communities to future alterations to the landscape template (Chapin et al. 1997).

### *The population response*

In a broad sense, the pattern of environmental structure across the landscape affects the response of species living in the landscape through variation in resources. This influences the ability of species to survive and successfully maintain populations in a region. Species vary in their requirements and ability to utilize resources; each species has a unique niche (Hutchinson 1957). Because of this, each species will exhibit a unique response to the landscape. Any given landscape will be capable of supporting only a subset of species at any given time. Additionally, species and even life-stages within species differ in their capacity to resist and recover from disturbances. For example, species with high reproductive capabilities and broad environmental tolerances will often recover their former population levels relatively quickly. However, species with lower reproductive capabilities and narrower tolerances will be slower to recover.

The species assemblage present in a region is the sum of the overlapping geographic ranges of species that occur in that region. A species' geographic range is located where the conditions (biotic and abiotic) of the environment match the requirements of the species, allowing it to maintain populations across the landscape. The geographic range is characterized by spatially autocorrelated gradients in population abundance and density that decrease from the center to the periphery of the range, though sometimes this gradient is cut off by a "hard" range boundary set by some physical barrier, competition, or predator-prey interactions (Brown 1984, Brown et al. 1996, Curnutt et al. 1996). Underlying these gradients is spatial autocorrelation in the suitability of the environment for a species, which also decreases from the center to the periphery of the range (Brown 1984). The variability of population abundances is relatively low at the center of the range, and relatively high at the periphery of the range (Pimm 1986, Curnutt et al. 1996). Combined with lower abundances and densities, this increased variability increases the likelihood of extinction for population at the edge of its range. The boundary of a range has been generally defined as the point at which populations cease to contribute to the next generation (Caughley et al. 1988); the exact position of the boundary is determined by the interaction of population processes with the spatial and temporal variation in the environment (Brown et al. 1996).

The geographic range of a species commonly extends over more than one distinct ecosystem (99 out of 206 species were found in all six ecosystems in this study). The ability of species to maintain successful, stable populations within any given ecosystem is influenced by the relationship between the structure of the geographic range and the template of landscape structure. Each population within the geographic range of a species has distinct demographic characteristics because each is influenced by a unique set of environmental factors. The dynamics of a local population can be described by the stochastic logistic population model,

$$\frac{1}{N} \cdot \frac{dN}{dt} = r - uN + \sigma z$$

where $N$ is population abundance, $r$ is the maximum per capita rate of increase, $u$ is the negative acceleration on population growth due to intraspecific competition, $z$ is a white (Gaussian) noise random variable with mean zero and variance one, and $\sigma$ is a scale factor that represents the size of random fluctuations in the per capita rate of change (Dennis and Patil 1984, Dennis and Costantino 1988, Dennis 1989). Spatial variation in population dynamics can be modeled by assuming that the maximum per capita rate of increase ($r$) and the effects of intraspecific competition ($u$) are spatially explicit parameters. The influence of the environment causes these parameters to covary across the geographic range of the species (Maurer and Taper 2002). At the center of the geographic range, where populations are typically abundant and stable, the maximum per capita rate of increase is high and decreases with distance from the range center. Conversely, the effect of intraspecific competition typically has the lowest effect on populations at the range center and increases with distance.

The biological complexity caused by the ecological individuality of species in a spatially and temporally varying environment can be described by combining the effects generated by hierarchical environmental structure and the effects generated by the position of populations within the species' geographic range on local population processes. The relative unsuitability of resources near the periphery of a species' geographic range will influence the dynamics of populations occurring there; they will exhibit relatively low per capita rates of increase (*r*), and relatively large negative effects of intraspecific competition (*u*), (Figure 2.10). This scarcity of resources should be reflected in the structure of the body size spectra for ecosystems near geographic range edges; a species in an ecosystem at the edge of its range will likely occur near a discontinuity in the body size spectrum for that ecosystem. Consider the hypothetical landscape depicted in Figure 2.12B. The geographic range of species A is centered on Ecosystem 1. The environmental conditions for A are most suitable at the center of its range (Brown 1984), with appropriate resources to meet species requirements, and therefore populations of A in Ecosystem 1 will likely be stable. This stability is depicted in Figure 2.11, where populations of A exhibit high maximum per capita rates of increase (*r*) and low effects of intraspecific competition (*u*) at the range center (Maurer and Taper 2002). As shown in Figure 2.12A, species A is relatively small, and is located at the center of a lump in the body size spectrum, far from discontinuities. Moving towards the boundary of the geographic range of species A, into Ecosystem 2, the suitability of the environment and the availability of resources decrease. This decline is reflected in the position of species A in the body mass spectrum; in Ecosystem 2, species A is located at the edge of a discontinuity. At the scale at which species A is able to interact with the landscape of Ecosystem 2, resources are scarce or inaccessible (Holling et al. 1996). Consequently, in this region populations of A are likely to be relatively small and scattered, as compared with those in Ecosystem 1 (Brown 1984). They are also likely to be unstable, exhibit low maximum per capita rates of increase, large effects of intraspecific competition, and relatively high variability (Figure 11), (Maurer and Taper 2002).

Species B is larger than species A (note its relative position in the body mass spectra), and interacts with the landscape differently. Having different requirements, its geographic range is centered on Ecosystem 2. Here its populations are stable, with high per capita rates of increase and little negative effect from intraspecific competition (Figure 2.11). In Ecosystem 2, Species B is located in the center of a lump in the body mass spectrum. Species B also occurs in Ecosystem 1, but its range boundary intersects this region. Consequently, here its populations are relatively unstable with lower per capita rates of increase and greater negative effects of intraspecific competition (Figure 2.11). In Ecosystem 1, at the edge of its geographic range, Species B is located at the edge of a discontinuity in the body mass spectrum.

Species C is intermediate in size to A and B. However, it is a widely ranging species whose geographic range boundary intersects neither of the two ecosystems depicted here. Consequently, all populations of C in these two ecosystems have sufficient resources available to them. Species C is not located near a discontinuity in either body mass spectrum, but instead has stable populations throughout both regions with high rates of increase and few negative effects from intraspecific competition.

The actual population mechanism that determines the geographic range boundary for any species varies both spatially and temporally across populations, resulting in a varying pattern of extinctions and colonizations across the landscape (Maurer and Taper 2002). The overriding factor influencing the demography of any population at any point in time could be the maximum per capita rate of increase (*r*), the negative effect of intraspecific competition (*u*), or both.

## Conclusions

The discontinuous structure of the landscape influences geographic variation in the abundances of species and therefore the composition of species assemblages. The discontinuities in landscape structure represent areas of scarce or highly variable resources (Allen and Saunders 2002) where species can maintain only low abundance populations and are typically at the edge of their geographic range. This suggests that there is an element of risk for those species that occur at the edge of discontinuities in a body mass spectrum. Even those that are not currently declining (as defined by state lists of protected species) or at the edge of their breeding range may be at risk in the future if there is sufficient change in the landscape.

However, the discontinuities in the body size spectrum can also provide a zone of opportunity (Allen et al. 1999) for introduced species. Although these results show that most non-indigenous species were farther from discontinuities than the median distance (Figure 2.6), the house finch (*Carpodacus mexicanus*) was the exception in all six ecosystems. The house finch is a recent and widespread invader of eastern North America (Elliott and Arbib 1953, Veit and Lewis 1996). It is important to note that this is a species whose range is still expanding. As such, its population dynamics may be interacting differently with the landscape than a non-indigenous species that has stopped expanding its range (Maurer et al. 2001). It is quite possible that in their native western landscapes house finches are not located at the edge of discontinuities in the body mass spectra.

Another logical, though currently untestable, conjecture is that perhaps when the geographic range stabilizes in the east, natural selection will move the house finches away from discontinuities by an increase or decrease in body size.

The alteration of a landscape through human activities will likely disrupt the spatial pattern of population processes that occur in that landscape. Disturbed landscapes commonly see an increase in the number of non-indigenous species (Vitousek et al. 1997, Western 2001). As with the house finch across eastern North America, when these non-indigenous species are still in the invasive stage, they might be found close to discontinuities in the body mass spectrum where they can take advantage of opportunities present at that scale. Although declining species are typically located near discontinuities in the body mass spectra, they are occasionally found far from discontinuities, as in the Till Plains (31) region (Figure 2.10). There are two possible explanations for this anomalous result. First, the region may be adjusting to recent (and likely anthropogenic) environmental changes that resulted in a scarcity of once common resources. The species assemblage is in transition, although the discontinuity structure of the region's body mass spectrum has not yet changed. As the altered landscape causes additions and deletions to the species pool, the structure of the body mass spectrum will change and declining species will then display the typical pattern of placement close to the discontinuities. Alternatively, those declining species that are located far from discontinuities could simply be exhibiting a lagged response to some past change in the environment. However, this second scenario seems unlikely in light of the results from the six ecosystems analyzed to date (see Figure 2.8 and Figure 2.10).

The scarcity of suitable resources for populations at the edge of their geographic range affects their population dynamics (low maximum per capita rates of increase, high effects of intraspecific competition) as well as their position in the body mass spectrum for the ecosystem. In the body mass spectrum, those species that are at the edge of their geographic range in that ecosystem will be located close to discontinuities. This interaction between local population processes, the discontinuous structure of the environment, and the structure of the geographic range means that for any ecosystem, the relative values of population demographic parameters can be predicted from descriptions of the body mass spectrum of the ecosystem and the geographic ranges of the species in the assemblage.

Holling (1992) outlined a research agenda for the analysis of cross-scale dynamics in ecosystems (see also Holling and Allen 2002), that should ultimately lead to an understanding of how a specific hierarchical landscape structure leads to a specific discontinuous pattern of body sizes (Holling et al. 1996). The results from these six ecosystems suggest that the structural complexity of a landscape may be the key to understanding the discontinuity pattern of its species assemblage. The connection between the architecture of the landscape and the species residing in that landscape has important implications for ecosystem management and conservation. Holling (1992, Holling et al. 1996) suggested that this relationship could be used to form an "ecoassay". That is, the knowledge that a landscape is changing at a particular scale, either due to intentional or unintentional activities, could be used to predict which species in an assemblage are likely to be affected. The opposite is also true; the knowledge that a group of species of a particular body size are being similarly affected (*e.g.* population declines) can be used to predict the scale at which a landscape is changing (Lambert and Holling 1998).

Table 2.1. Summary of species lists for the six physiographic regions.

| Region | Non-indigenous Species | Declining Native Species | Total Species |
|---|---|---|---|
| Coastal Flatwoods | 6 | 18 | 130 |
| Upper Coastal Plain | 9 | 52 | 163 |
| Ridge and Valley | 6 | 64 | 158 |
| Great Lakes Plain | 6 | 43 | 158 |
| Allegheny Plateau | 5 | 44 | 157 |
| Till Plains | 7 | 18 | 129 |

Table 2.2. Gaps identified by six methods for the Coastal Flatwoods dataset. Consensus gaps are based only on the Holling (HI) and Siemann & Brown (SB) indices and their robust versions.

| Body Size Range (g) | HI | Robust HI | SB | Robust SB | GRI | Cluster Analysis | Consensus Gaps (g) |
|---|---|---|---|---|---|---|---|
| 3 - 8 | Y | N | Y | N | Y | Y | |
| 8 – 8.5 | N | N | N | Y | N | N | |
| 8.8 – 9.4 | Y | Y | N | Y | N | N | 8.8 – 9.4 |
| 11 – 11.9 | Y | Y | N | N | N | N | |
| 13.2 – 14.1 | N | Y | N | Y | Y | Y | |
| 15 – 15.9 | N | N | N | Y | N | N | |
| 17 - 18 | Y | Y | N | Y | N | N | 17 – 18 |
| 21.6 – 23.6 | Y | Y | Y | Y | Y | Y | 21.6 – 23.6 |
| 38.7 – 41.7 | Y | Y | N | Y | N* | N | 38.7 – 41.7 |
| 55.3 – 61.5 | Y | Y | Y | Y | Y | Y | 55.3 – 61.5 |
| 86.8 - 102 | Y | Y | Y | Y | Y | Y | 86.8 – 102 |
| 245 - 300 | Y | Y | Y | Y | Y | Y | 245 – 300 |
| 632 - 1028 | Y | Y | Y | Y | Y | Y | 632 – 1028 |
| 2172 - 4130 | Y | N | Y | N | N | N | |

*This GRI value is slightly less than the criterion for significance.

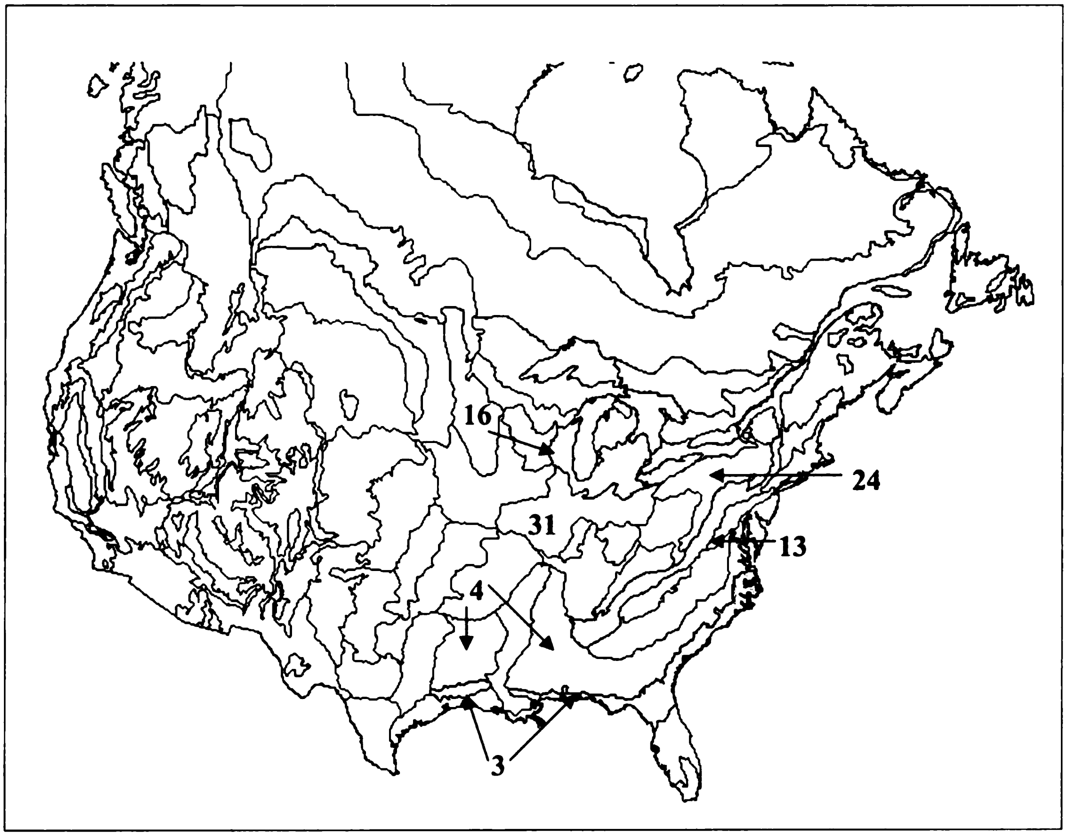


Figure 2.1. Physiographic regions delineated for the North American Breeding Bird Survey (Bystrak 1981). 3 – Coastal Flatwoods, 4 – Upper Coastal Plain, 13 – Ridge and Valley, 16 – Great Lakes Plain, 24 – Allegheny Plateau, 31 – Till Plains.

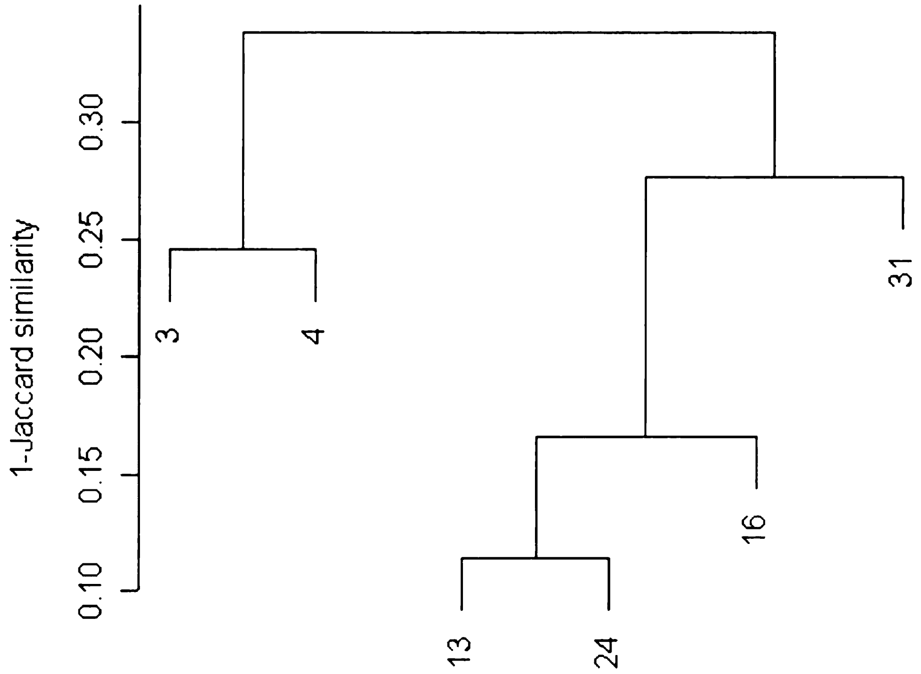
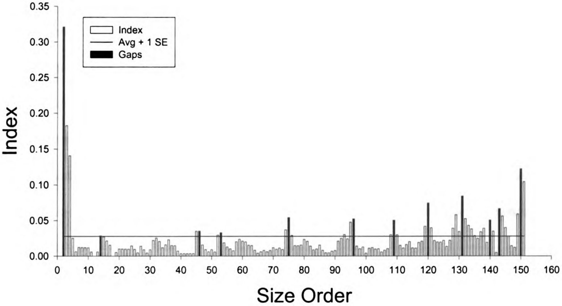


Figure 2.2. Average linkage cluster analysis for the species lists of the six physiographic regions based on Jaccard similarity values (cophenetic correlation = 0.87, agglomerative coefficient = 0.43). Regions are numbered as in Figure 2.1.

**A.**



**B.**

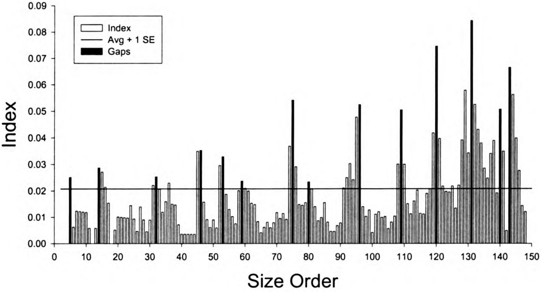


Figure 2.3. **A.** Size-ordered Holling Index values for the Ridge and Valley ecosystem. Criterion line has been placed at the average native species index value, plus 1 standard error. **B.** Robust size-ordered Holling Index values for the Ridge and Valley ecosystem. The 3 smallest and 3 largest species have been removed and the criterion line re-adjusted.

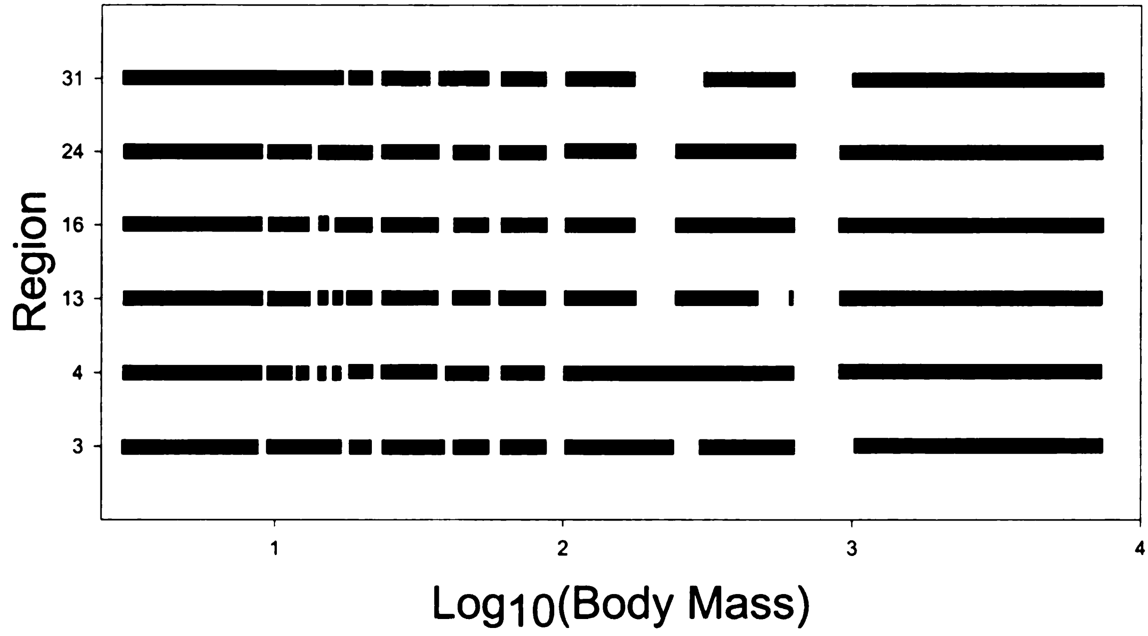


Figure 2.4. Location of discontinuities in the body-mass spectra for the six physiographic regions. Regions are numbered as in Figure 2.1.

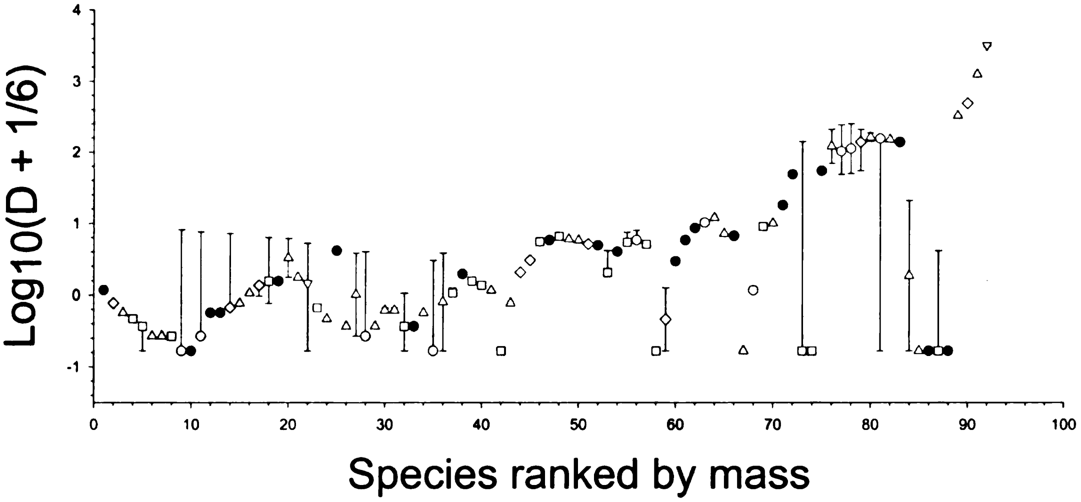


Figure 2.5. Median distance to nearest discontinuity for declining species across all six ecosystems. Error bars represent the range of values for those species whose distance to nearest gap varied across ecosystems. ● Species occurring in only 1 region (n=21), △ species occurring in 2 regions (n=30), □ species occurring in 3 regions (n=20), ◇ species occurring in 4 regions (n=9), ○ species occurring in 5 regions (n=10), and ▽ species occurring in 6 regions (n=2). Shaded vertical columns represent approximate locations of discontinuities in the body size spectra.

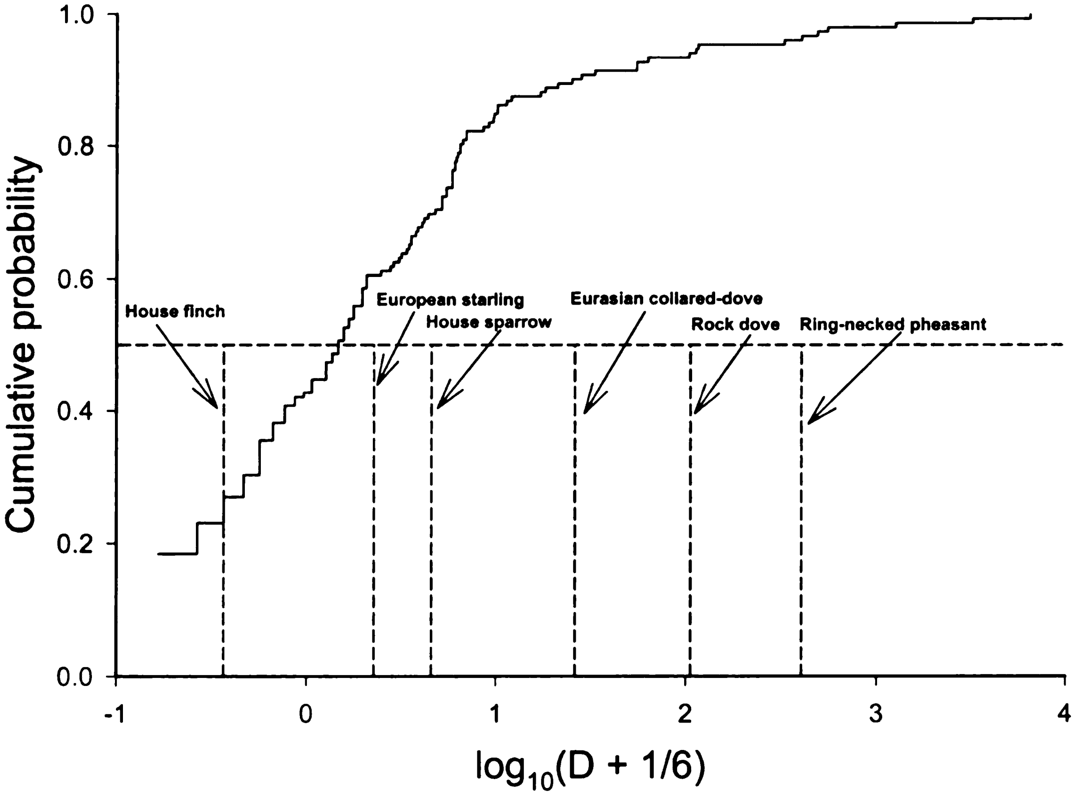


Figure 2.6. Empirical distribution function of distance to nearest discontinuity for all species in the Ridge and Valley region (13). The horizontal line denotes the median probability. Five of the six non-indigenous species have a distance to nearest discontinuity that is greater than the median distance for this region.

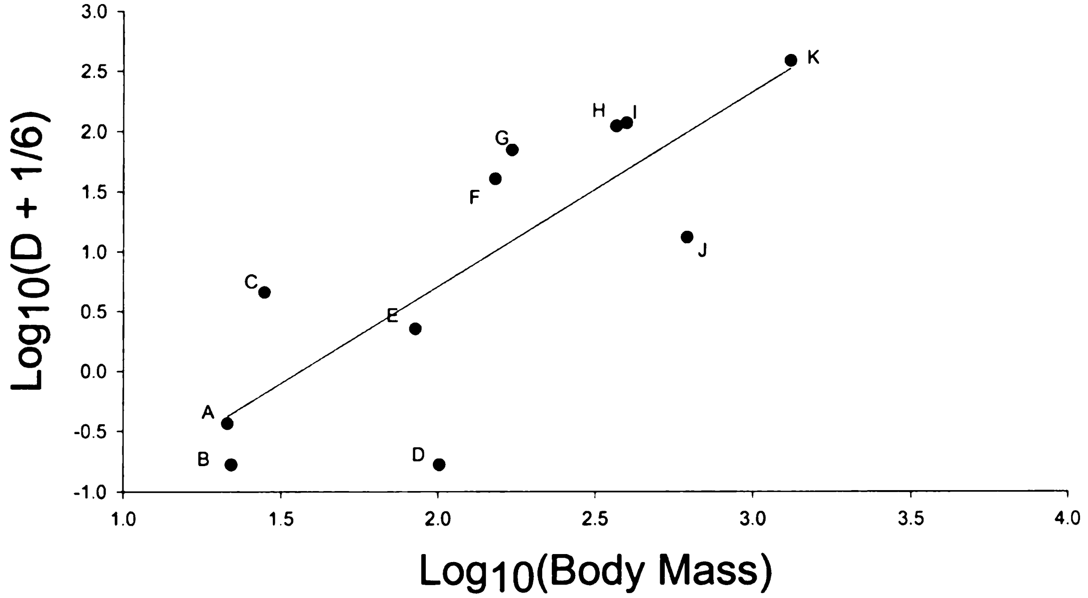


Figure 2.7. Average distance to nearest discontinuity for non-indigenous species (n=11) across all six ecosystems with least squares regression line ($r^2$ = 0.65). Names and (number of regions of occurrence): A – house finch (6), B – Eurasian tree sparrow (1), C – house sparrow (6), D – monk parakeet (1), E – European starling (6), F – Eurasian collared-dove (3), G – ringed turtle-dove (2), H – rock dove (6), I – gray partridge (2), J – chukar (1), K – ring-necked pheasant (5).

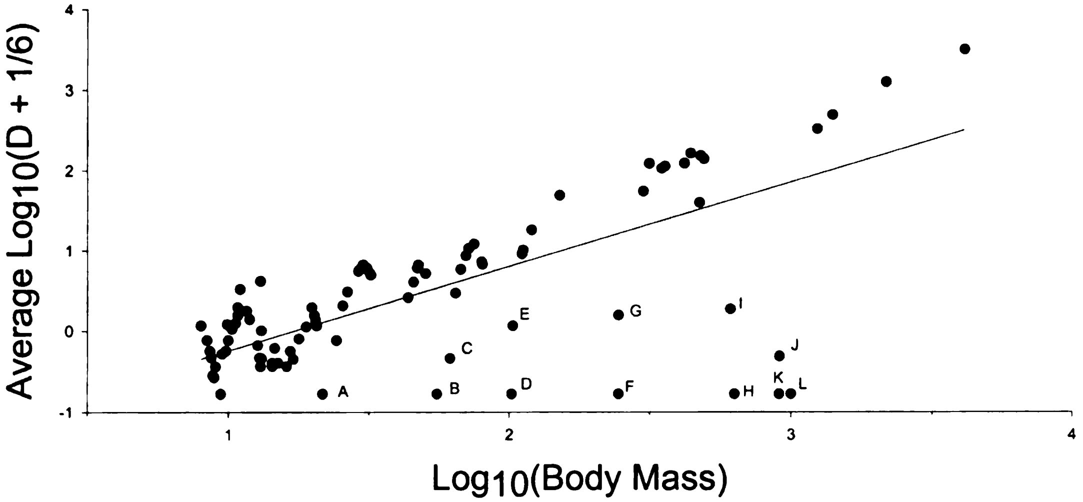


Figure 2.8. Average distance to nearest discontinuity for declining species (n = 92) across all six ecosystems with least squares regression line ($r^2$ = 0.55). Species with unusually low distances to nearest discontinuity are (number of regions where the species is declining in parentheses): A – cliff swallow (3), B – whip-poor-will (3), C – common nighthawk (4), D – eastern meadowlark (2), E – sharp-shinned hawk (5), F – long-eared owl (3), G – Mississippi kite (3), H – barred owl (2), I – peregrine falcon (2), J – northern goshawk (3), K – Swainson's hawk (1), L – greater prairie-chicken (1).

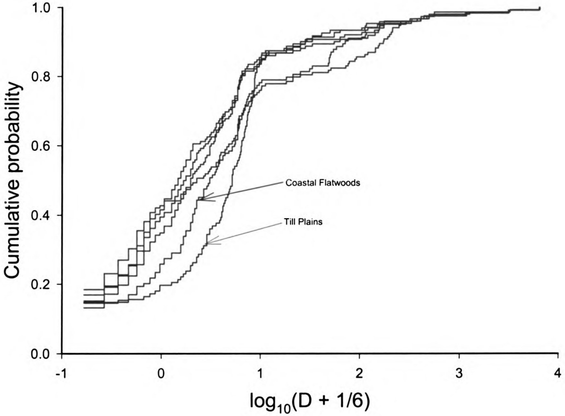


Figure 2.9. Empirical distribution functions of distance to nearest discontinuity for all six ecosystems. These distributions are significantly different (Kolmogorov-Smirnov statistic = 0.11, n = 856, p < 0.005).

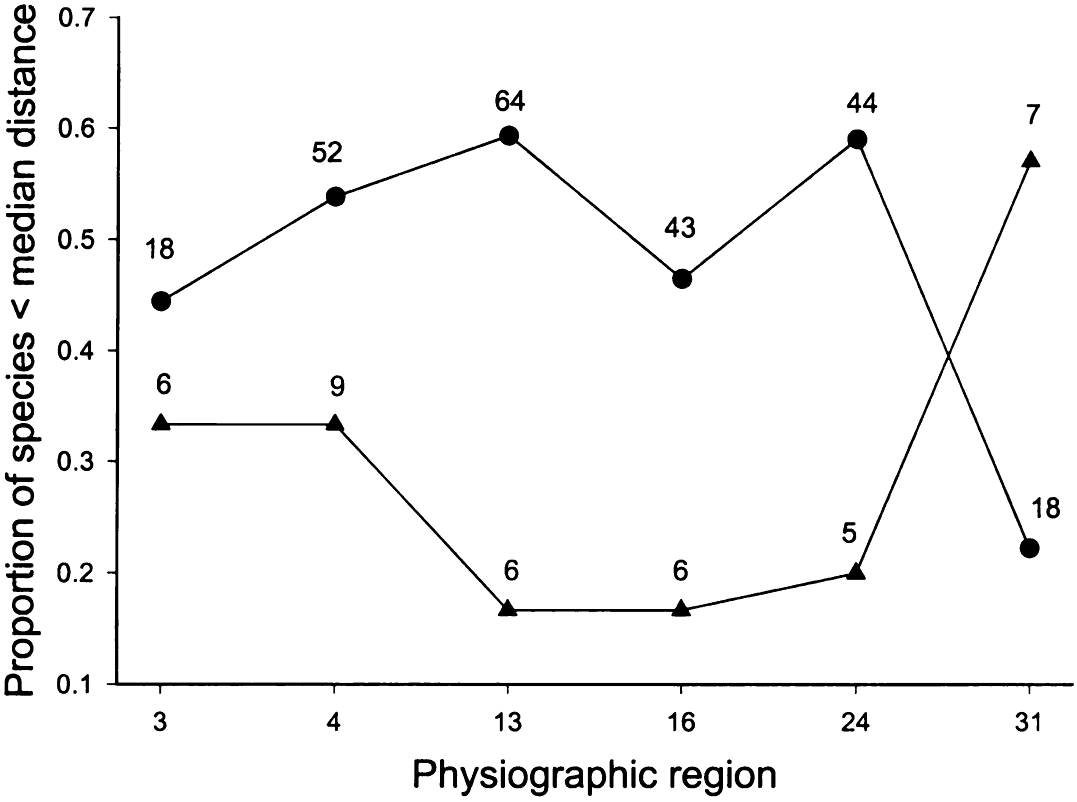


Figure 2.10. Proportion of non-indigenous (▲) and declining (●) species in each ecosystem that occur at less than the median distance to nearest discontinuity. Sample size indicated above each point. Regions are numbered as in Figure 2.1.

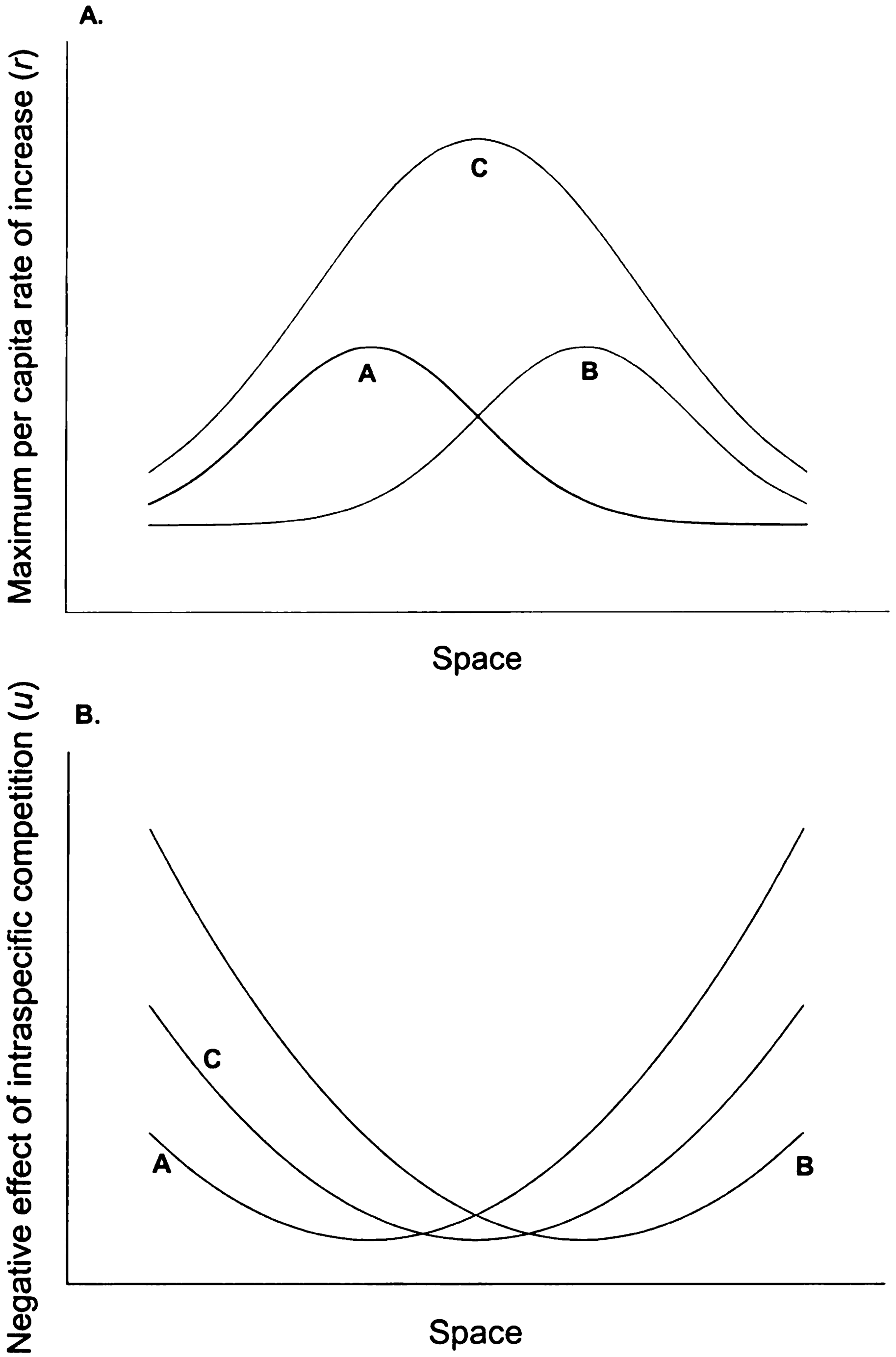


Figure 2.11. Schematic representation of (**A**) the variation of the maximum per capita rate of increase and (**B**) the negative effect of intraspecific competition across the geographic ranges of two narrowly distributed species (A and B), and one widely distributed species (C). The *x*-axis corresponds to the horizontal transect in Figure 2.12.

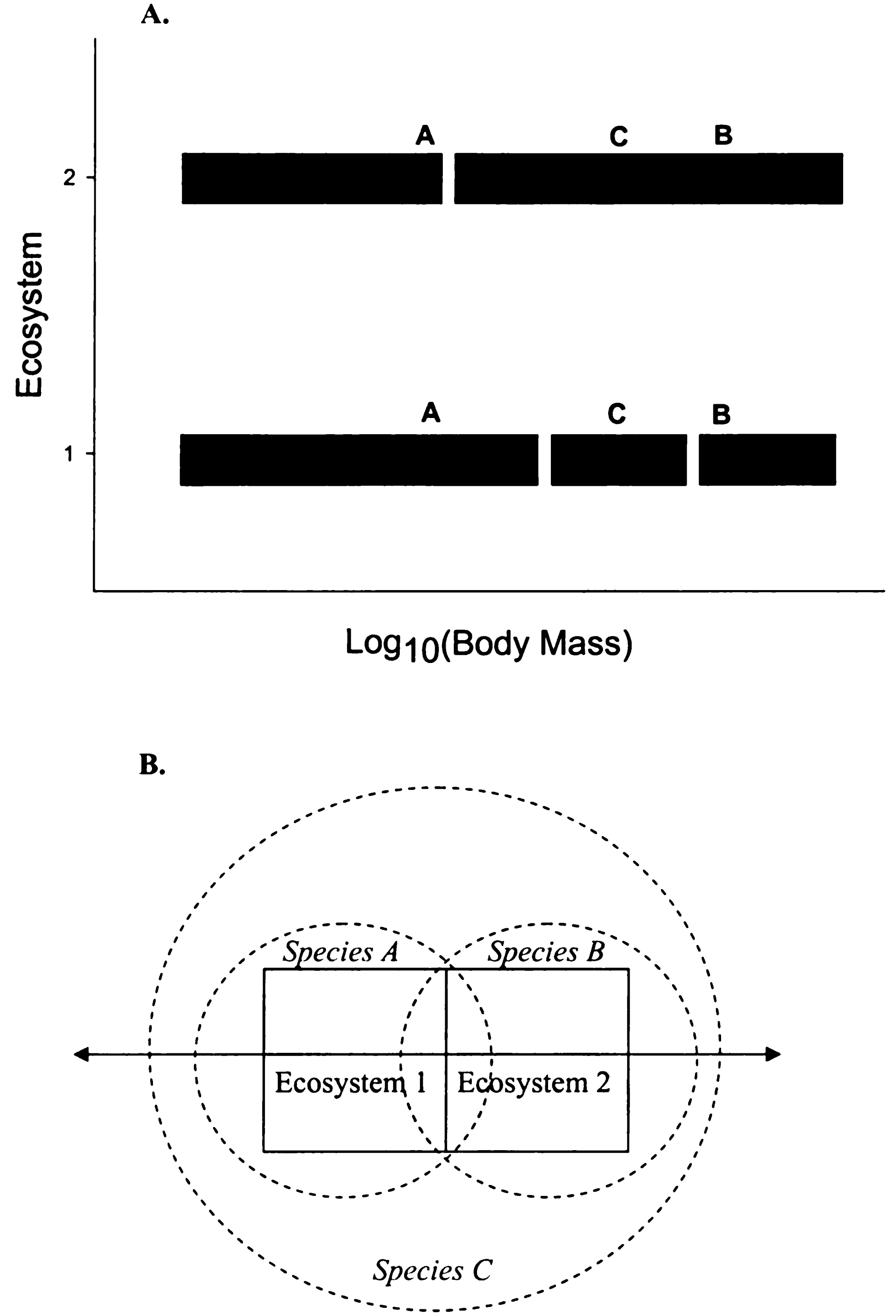


Figure 2.12. **(A)** A stylized representation of the discontinuous body mass spectra for two ecosystems, with the position of species A, B and C indicated. **(B)** Schematic representation of the geographic ranges of species A, B and C in relation to two distinct ecosystems. The linear transect across the ecosystems corresponds to the $x$-axis in Figure 2.11.

# CHAPTER 3

# LINKING LANDSCAPE STRUCTURE WITH THE BODY SIZE DISTRIBUTIONS OF SPECIES ASSEMBLAGES

## Introduction

The composition of species assemblages is determined by the dynamics within and among populations that lead to the coexistence of species. The dynamics of populations are influenced by interactions among individuals as well as the spatial heterogeneity of the environment in which these individuals live (Kareiva 1990). Recognizing the importance of the heterogeneous structure of landscape elements, models of population dynamics are increasing in complexity to incorporate spatially explicit landscape data (e.g. Liu 1993, Wiegand et al. 1999). Holling (1992) suggested that the presence of some species, and the corresponding absence of others, was a reflection of the texture of the landscape.

Holling (1992) proposed that a small number of biotic and abiotic processes, each of which operates at a particular spatial and temporal scale, govern the texture of terrestrial landscapes. The scales at which these processes operate are discrete, causing discontinuities in landscape structure, or changes in landscape pattern with changes in scale, to arise. Organisms can only interact with and obtain resources from their environment at a single scale at any given time (Holling et al. 1996, Allen and Saunders 2002); therefore, Holling (1992) suggested that organisms living in a discontinuously structured landscape will exhibit attributes, such as home range size or body size, that are also discontinuously distributed. Holling (1992) hypothesized that these discontinuities in organismal attributes correspond to scale changes in the underlying structure of the landscape. These scale changes, or breaks, represent scales at which suitable resources are not available for organisms of a particular size, therefore preventing the occurrence of species of that size in the landscape.

Holling's initial observations that assemblages of boreal bird and mammal species exhibit discontinuous body mass distributions (Holling 1992) are supported by studies of a variety of taxa, including frugivorous birds of the Andes (Restrepo et al. 1997), terrestrial birds of eastern North America (Chapter 2), birds of Mediterranean-climate Australia (Allen and Saunders 2002), mammals, birds, and herpetofauna of the Florida Everglades (Allen et al. 1999), two North American Pleistocene mammalian faunas (Lambert and Holling 1998), cave-dwelling bats of Mexico (Allen et al. 1999), marine invertebrates (Schwinghamer 1981, 1988, Raffaelli et al. 2000, Leaper et al. 2001), and phytoplankton, zooplankton, and fish of North American temperate lakes (Havlicek and Carpenter 2001). However, Holling's (1992) suggestion that discontinuities in body mass distributions correspond to discontinuities in landscape structure has been more difficult to test, due both to the difficulty of experimenting with landscape structure and the variety of spatial patterns encompassed in the term "structure".

Two tests of Holling's hypothesis using experimentally tractable marine sediment fauna have given conflicting results. The first study manipulated the composition of the species assemblage but did not change environmental structure (Raffaelli et al. 2000). This resulted in no changes in the distribution of body size discontinuities, providing indirect support for Holling's proposal. The second study did change environmental structure, with replicates of uniformly sized artificial substrate as well as controls (Leaper et al. 2001). This study found no consistency in the distribution of body size discontinuities across identical treatment groups or control groups suggesting that, at least at these small scales, the distribution of body sizes may be influenced by some factor other than habitat architecture. Restrepo et al. (1997) also investigated the correspondence of body mass discontinuities with landscape structure, though in a non-quantitative manner. They compared the body mass discontinuities of frugivorous Andean birds across elevational zones (a gradient of vertical vegetative structure and growth form diversity), and across sites within elevational zones with varying amounts of human disturbance (a gradient of horizontal vegetative structure). They found that both vertical and horizontal gradients in vegetation structure seemed to influence the distribution of body mass discontinuities, though this preliminary study could not rule out other possibilities (Restrepo et al. 1997).

Holling's original study (Holling 1992) provided little guidance as to what aspect of landscape structure is key to the body size patterns in species assemblages. However, he suggested that mesoscale processes should produce landscape-specific patterns of textural and body mass discontinuities. The spatial pattern of land cover types is the result of such a process. Though influenced through evolutionary time by macroscale geomorphological processes, the distribution of cover types within ecosystems is strongly dependent on the actions of other organisms (including humans), and abiotic disturbances such as fire, wind, and water. The concept of lacunarity provides a means of quantifying the discontinuities in landscape structure (Chapter 1). Lacunarity is a measure of the distribution of gap sizes in some spatial phenomenon of interest, such as the occurrence of patches of a particular land cover type, and can be used to detect the presence of hierarchical structure (Plotnick et al. 1993). Here I propose to quantitatively test the correspondence between the distribution of body mass discontinuities and the discontinuities in landscape structure predicted by Holling's (1992) hypothesis using avian species assemblages from eastern North America (similar to those studied in Chapter 2) in conjunction with land cover data derived from satellite imagery.

Based on Holling's (1992) hypothesis and previous studies the following predictions can be developed. First, different landscapes that have different spatial processes occurring within them will vary in structure. Second, this variation in structure among landscapes means that they will support species assemblages with varying body mass distributions. Third, these body mass distributions will not be continuous, but instead will exhibit discontinuities. Finally, the discontinuities in the body mass distributions will correspond to scale changes in landscape structure.

## Methods

### *Study area*

The terrestrial habitats of the United States can be divided into biological units using the ecoregion classification scheme devised by Bailey (1988) and subsequently modified for use in the National Ecological Unit Hierarchy (Cleland et al. 1997). In this system, the contiguous United States is divided into 35 provinces comprised of 163 sections. Six small sections in eastern North America consisting of predominantly forest and/or agricultural land cover were selected for this study (Figure 3.1, Table 3.1).

### *Land cover*

The vegetation occurring in these sections is described by the National Land Cover Data set (NLCD) from the U.S. Geological Survey. The NLCD covers the coterminous United States with a consistent classification scheme and time period of data collection (Vogelmann et al. 2001). This raster dataset has a resolution of 30 m and is based on Landsat 5 Thematic Mapper satellite imagery from the early 1990s, primarily 1992. Of the 21 land cover classes identified in the NLCD, 20 occur in the selected six study areas (Table 3.2).

### *Structure*

The structural characteristics of the six sections can be broadly characterized by a comparison of the richness, diversity, and dominance of land cover types in each section. Land cover type diversity was assessed with Shannon's diversity index (Legendre and Legendre 1998), which is the negative sum across $n$ land cover types of the proportion of the landscape, $p_i$, occupied by that type multiplied by the natural log of that proportion.

$$H = -\sum_{i=1}^{n} p_i \ln p_i$$

Dominance measures the deviation of the proportions of land cover types in a landscape from the expectation that all cover types are present in equal proportions (O'Neill *et al.* 1988a).

$$D = \ln n + \sum_{i=1}^{n} p_i \ln p_i$$

Lacunarity is a landscape metric that allows the detection of hierarchical structure and the presence of changes in the scale of that structure. Lacunarity analysis also enables the comparison of the structure of multiple landscapes. Lacunarity was calculated using the software package APACK Version 2.22 (Mladenoff and DeZonia 2002). Calculating lacunarity with APACK requires a rectangular map. For each section, the smallest rectangle encompassing the section was set as the area of analysis. The NLCD land cover data for the six sections was re-classified as binary data: forest and non-forest. This division was chosen because since the time that these species assemblages came into existence until relatively recently, much of eastern North America was forested (Williams 1990). The forest category included only upland forest (deciduous, evergreen, and mixed) located within each section. The non-forest category included all other land cover types within each section and all areas of the map between the section boundary and the encompassing rectangle, regardless of land cover type (Figure 3.2). Two sections, 133 and 153, are each composed of two noncontiguous portions (Figure 3.1). Lacunarity analysis was conducted on only the western portion of section 153 and separately on the eastern and western portions of section 133. Lacunarity analysis was not conducted on section 170 or the eastern portion of section 153 due to their large size.

APACK uses the gliding-box algorithm (Allain and Cloitre 1991) to calculate lacunarity. A window with dimensions $s$ x $s$ is moved one pixel at a time across the area of analysis. At each window position, the density of each habitat category (forest and non-forest) is calculated. For each window size, $s$, the lacunarity is:

$$\Lambda_s \equiv 1 + \frac{\mathrm{var}\, \mathit{of\ forest\ density}}{\mathit{mean\ of\ forest\ density}^2}$$

With multiple window sizes a lacunarity curve can be plotted (Figure 3.7). Changes in the slope of the curve indicate shifts in the spatial pattern of heterogeneity (Plotnick et al. 1996). Window sizes were chosen to range from $s = 60$ m to approximately one quarter the extent of the smallest landscape ($s = 27390$ m), evenly spaced on a log scale. The same set of window sizes was used for each area analyzed ($s = 60$, 90, 120, 150, 210, 270, 390, 510, 690, 930, 1290, 1740, 2370, 3210, 4350, 5940, 8040, 10950, 14850, 20160, and 27390 m).

### *Species assemblages*

A species list was compiled for each section (Tables A.1 – A. 6) based on all observations of birds made on each route lying completely within that section over the course of the North American Breeding Bird Survey (BBS). The BBS is an annual survey conducted by experienced volunteers throughout Canada and the United States. Surveys began in 1966, though not all routes have been surveyed yearly since the inception of the BBS. BBS routes consist of 50 sampling points located 0.8 km apart along secondary roads. Surveys are conducted once per year during June, and all birds seen or heard within 0.4 km of each sampling point during a 3 min period are recorded (Robbins et al. 1986).

Water birds and shorebirds were excluded from the final species lists, as were any species recorded as "unidentified" (*e.g.* unid. *Empidonax*). Additionally, several taxonomic changes have occurred since the inception of the BBS; therefore some names and American Ornithological Union (AOU) codes for these species have been changed from those originally reported to the BBS (Table B.1).

### *Body masses*

Body masses (g) for most species on the final species lists were obtained from a digital version of Dunning's *CRC Handbook of Avian Body Masses* (1993) provided by the National Center for Ecological Analysis and Synthesis Body Size Working Group. In instances where a variety of masses for separate subspecies were provided, the mass for the subspecies most likely to occur within that geographic area was used.

### *Finding discontinuities*

Discontinuities in the body mass spectrum can be identified with several methods (Holling and Allen 2002). Confidence in the accuracy of identified discontinuities is increased if multiple methods produce the same result. Consequently, five methods were used to identify the discontinuities in the avian body size spectrums. Only the native species of an ecosystem were used in these analyses in order to determine where discontinuities exist in the recent historical fauna of a region (Allen et al. 1999).

#### *Method 1 – Holling index*

Holling (1992) described an index that measures how similar a species is to those species closest to it in size,

$$HI = \frac{M_{n+1} - M_{n-1}}{(M_n)^k}$$

where $M_n$ is the body mass (g) of the $n$th species in order of increasing size and $k$ is a constant that detrends the data. Holling found this constant to be taxon-specific; equivalent to 1.3 for birds and 1.1 for mammals. A large value of HI indicates a species is quite different from those ranked closest to it in size. In order to determine how large an index value must be to represent a true discontinuity in the distribution, a criterion value is calculated as the average index value plus one standard error (Holling 1992). Discontinuities in the distribution are identified by those index values that are greater than the criterion and greater than the index value of the preceding and following species (Figure 3.3).

*Method 2 – Siemann & Brown index*

Siemann and Brown (1999) also developed a body mass difference index,

$$SI = \log_{10}\left(\frac{M_{n+1}}{M_n}\right)$$

They argued that this is a more precise metric than the Holling Index, and it requires no *a posteriori* defined exponent to correct the data. A criterion value and discontinuities are identified in the same manner as with the Holling Index.

*Methods 3 and 4 – robust indices*

Because of the concern that the beginning and ending values in each body mass spectrum were producing artifactual high index values that would result in the identification of false discontinuities, a robust version of the both the Holling Index (RH) and the Siemann & Brown Index (RS) was created. The clusters of index values at each end of the distribution were identified visually, removed from the calculation of the average index value, and the criterion line recalculated (Figure 3.3). This new criterion value was used to identify discontinuities for the RH and RS indices.

*Method 5 – cluster analysis*

A hierarchical cluster analysis using agglomerative nesting (AGNES) with Ward's method was also used to identify discontinuities in the body mass distributions. This analysis was conducted using the cluster package in R version 2.0.0 (Kaufman and Rousseeuw 1990, R Development Core Team 2004). Dendrograms of the clustering results were used to depict the species (in order of increasing body mass) in a series of nested clusters. Discontinuities were defined as existing between species adjacent to each other in the body mass spectrum but belonging to different terminal clusters.

Discontinuities identified by the five methods were then compared. Consensus discontinuities were defined as those identified by at least three of the five methods (Tables C.1 – C.6). In some cases, three or more methods identified non-identical but overlapping discontinuities. In these cases, only the overlapping portion of the discontinuity was considered to be the consensus discontinuity (for example, see the discontinuities at body mass range 21.6 – 23.6 and 21.6 – 25.5 in Table C.1). In general the five methods detected comparable discontinuities in the body mass distributions.

### *Linking lacunarity with body mass*

The fourth prediction tested by this study is that discontinuities in body mass distributions will correspond to scale changes in landscape structure. Discontinuities in landscape structure are indicated by changes in the slope of the lacunarity curve. However, the locations of discontinuities in the body mass distribution of species assemblages were measured in grams, while discontinuities in landscape structure were measured in meters. This discrepancy in measurement units was corrected by using known allometric relationships between the body size of an organism and its home range size (Peters 1983, Calder 1996). Discontinuities in the body mass distribution of each section were converted to discontinuities in home range size using the regression relationship for both passerine and nonpasserine birds, $H \propto M^{1.16}$ (Schoener 1968). Holling (1992) expanded and reanalyzed Schoener's (1968) bird data, finding an exponent of ~1.36 for avian carnivores, omnivores, and herbivores, suggesting the possibility that the slope of the regression relating home range size to body size in birds might be as high as 1.3 instead of closer to the mammalian exponent of 1.1. Holling hypothesized that this higher exponent could be a function of the three-dimensional use of space by birds, as opposed to mammals which primarily move in only two dimensions. Based on this, discontinuities in the body mass distribution of each section were also converted using a higher exponent, $H \propto M^{1.3}$. Home ranges were assumed to be approximately circular in shape, and the diameter of each home range was used as a representation of the spatial extent of the landscape sampled by a species.

## Results

### *Landscape structure*

The six landscapes analyzed here, despite all being located in the humid temperate domain of the eastern United States (Cleland et al. 1997) are not uniform in their structural characteristics. They vary in area (8790 – 97840 km$^2$; Table 3.1), shape, and topography (Figure 3.1). Sections 59 and 172 are relatively small and narrow, oriented northeast-southwest along the Appalachian Mountains. Sections 133 and 170 are located in the southern coastal flatwoods, with section 133 completely bisected by the lower Arkansas and Mississippi River valleys and section 170 nearly so. The final two sections, 47 and 153, are located in the Great Plains. However, section 153 is divided into two noncontiguous portions, with the larger area adjacent to section 47 and the smaller area more than 450 km to the west.

The number of land cover types occurring in the six sections is relatively consistent, with land cover richness varying only from 15 –19 (Tables 3.1 and 3.2).

However, the proportions of these cover types present in any given section are different. Aggregating the cover types into five general categories (agriculture, upland forest, urban, water/wetland, and other) revealed that each section is dominated by either agricultural or upland forest cover types (Figure 3.5, Table 3.2). Sections 47 and 153 consist primarily of agricultural land (76% and 84% of total land cover, respectively), while sections 59, 133, 170, and 172 are composed mostly of upland forest (66%, 65%, 65%, and 71%, respectively). Urban, water/wetland, and "other" land cover types do not make up a significant portion of total land cover in any section, with two exceptions. In both sections 133 and 170, water/wetland cover types are present in approximately the same proportions as agricultural cover (section 133: 16% and 13%, section 170: 12% and 19%). Using the original 20 land cover types, the diversity and dominance of each section was calculated (Figure 3.6). The two sections consisting primarily of agricultural cover types, sections 47 and 153, had the lowest land cover type diversity and highest dominance, while the remaining sections had relatively similar diversity and dominance values.

### *Discontinuities in body mass distributions*

The avian species assemblages (Tables A.1 – A.6) of the six sections were broadly similar, with terrestrial species richness varying from 94 – 107 (Table 3.1), and 73 of these species occurring in all six sections. When arrayed in order of increasing mass, all sections were identical in their smallest (ruby-throated hummingbird, *Archilochus colubris*, 3 g) and largest species (wild turkey, *Meleagris gallopavo*, 7400 g). Analysis of the avian species assemblages of the six sections with five different methods showed that, as predicted, there are detectable discontinuities in the body mass structure of each assemblage (Tables C.1 – C.6, Figure 3.4).

The number of discontinuities identified in each section was similar, varying from 11 – 15. The position of these discontinuities was also quite similar across sections (Figure 3.4). Three discontinuities (21.6 – 23.6 g, 86.8 – 102 g, and 148 – 174 g) were identical in all six sections, while four other discontinuities had similar zones of overlap in all sections (~ 200 g, 400 g, 800 g, and 3000 g), though starting and ending points varied slightly. The patterns of discontinuities varied slightly among sections. Section 172 had more evenly spaced discontinuities at smaller body sizes (< 100 g) and fewer discontinuities at larger body sizes (> 174 g) than section 59, though these two sections adjoin each other and are both composed primarily of upland forest (Figures 3.1 and 3.5). The species assemblage of section 153 exhibited more discontinuities (seven) at small body sizes than the other sections, while the assemblage of section 133 had the most discontinuities (seven) at larger body sizes.

### *Correspondence of assemblage discontinuities with landscape discontinuities*

Lacunarity values were calculated and curves plotted for both forest and non-forest within each section (Figures 3.7 – 3.12). The forest curves have the highest lacunarity values at the smallest window sizes and then decrease relatively smoothly as window size increases. The curves for sections 47 and 153 west (Figures 3.7 and 3.11) are nearly straight (linear regression $r^2 = 0.999$ and 0.9949, respectively). In contrast, the non-forest curves display the highest lacunarity values at intermediate window sizes and exhibit many changes in slope. The non-forest curves for sections 47 and 153 west are quite similar in shape, with the two largest slope changes occurring at the sixth and eighth largest window sizes ($s$ = 270 m and $s$ = 510 m). Sections 59 and 172 (Figures 3.8 and 3.12) also have similar non-forest lacunarity curves; section 59 has its largest slope changes at the seventh and tenth window sizes ($s$ = 390 m and $s$ = 930 m) while section 172 has large slope changes at the sixth and ninth window sizes ($s$ = 270 m and $s$ = 690 m). The eastern and western portions of section 133 (Figures 3.9 and 3.10), despite being considered part of the same ecological section, display major slope changes at different window sizes, though the overall shape of the non-forest lacunarity curves is quite similar. The largest slope changes in section 133 east occur at the ninth and twelfth largest window sizes ($s$ = 690 m and $s$ = 1740 m) while in 133 west they occur at the seventh and ninth window sizes ($s$ = 390 m and $s$ = 690 m).

Sections 47 and 153 west have the largest range of lacunarity values for forest habitat (Figures 3.7 and 3.11; log-lacunarity varies from 0.137 – 0.897 for section 47 and from 0.194 – 1.533 for section 153 west), showing that although these areas consist primarily of agricultural land (Table 3.2, Figure 3.5), the forest structure that is present is more heterogeneous than that of other sections. The gaps, or distances between patches of forest habitat in the remaining sections have less variation than that present in sections 47 and 153 west. The lacunarity values for forest habitat in sections 59, 133 east, 133 west, and 172 have a lower maximum and span a smaller range of value, indicating that the forest habitat has a more homogeneous structure (Figures 3.8 – 3.10 and 3.12). Sections 59 and 172, which are primarily forest (Table 3.2, Figure 3.5), have the largest range of lacunarity values for the non-forest category (Figures 3.8 and 3.12; log-lacunarity varies from 0.099 – 0.614 in section 59 and from 0.128 – 0.622 in section 172). This indicates that the structure of non-forest habitat is more heterogeneous in these two sections than in the remaining sections. Sections 133 east and 133 west, which also consist primarily of forest land cover types (Table 3.2, Figure 3.5), have similar ranges of lacunarity values for both forest and non-forest habitat (Figures 3.9 and 3.10), indicating that both habitat categories display a similar degree of heterogeneity in their structure.

Discontinuities in the body mass distributions were converted to discontinuities in the distribution of home range size diameters. The location of these discontinuities is overlaid on the lacunarity curves for each section (Figures 3.7 – 3.12). There are many more discontinuities in the avian home range size distributions than there are obvious changes in slope for either the forest or the non-forest lacunarity curves.

## Discussion

The six sections analyzed here are broadly distributed across eastern North America in areas of widely differing topography and geologic history. These diverse geographic settings indicate that the structure of these landscapes is likely to differ, though each section predominantly consists of either agricultural or upland forest land cover. Calculations of the dominance and diversity of the land cover types in the six sections show that the sections currently composed mostly of human originated land cover types (agriculture) have very high dominance and low diversity values. In contrast, those sections consisting primarily of non-anthropogenic land cover types (upland forest) have very low dominance and high diversity values.

Though there is some upland forest present in each section (Table 3.2), the distribution of this forest differs between the highly human-modified, agriculturally dominated sections and the forest dominated areas. Interestingly, the large range of lacunarity values for forest habitat in sections 47 and 153 west, both consisting predominantly of agriculture, show that there is much more heterogeneity in the distribution of forest land cover in these sections than in the remaining sections. The forest land cover in sections 47 and 153 west appears to be located primarily along waterways, roads, and in patches along field edges, a distribution in which the gaps between forest patches are quite varied in size. However, the other sections contain large tracts of continuous forest and so have little heterogeneity in gap size.

Although avian species richness did not vary significantly across the six sections, and there were 73 species that occurred in every section, there was variation in the body mass distributions of these sections. As expected based on studies of other taxa, the species assemblages of these six sections also clearly exhibit discontinuities in their distributions of body masses. However, there is no clear pattern to the structure of these body mass distributions (Figure 3.4). In contrast to the results described in Chapter 2, here the most heavily human modified areas, sections 47 and 153, displayed conflicting results in terms of body mass discontinuities. The species assemblage of section 47 had a very simple structure, with only 11 identified discontinuities, while the assemblage of section 153 had the most complex structure with 15 discontinuities. This discrepancy in results may reflect the differences in the total area of analysis. The study described in Chapter 2 used data from much larger physiographic regions (Bystrak 1981), which had correspondingly higher species richness values, than the smaller National Ecological Unit Hierarchy sections (Cleland et al. 1997) used here.

To quantitatively test Holling's (1992) hypothesis that the heterogeneity in the structure of a landscape entrains the attributes of species living in that landscape, this study aimed to assess the correspondence between discontinuities in the distribution of land cover types and discontinuities in body mass distributions (converted to home range size distributions). The age of North American avian species assemblages is unknown. The continent has been in an interglacial period for approximately 10,000 years, so these species assemblages could date back thousands of years. However, substantial habitat changes in the past 300 years (Pimm and Askins 1995) could also have resulted in recent changes to the composition of these assemblages. If the species assemblages of these sections have been in existence much longer than the presence of European settlements in North America, then the distribution of many of the anthropogenic land cover types (*e.g.* agricultural and urban cover types) listed in Table 3.2 may not be appropriate predictors of species body mass distributions. Much of eastern North America was heavily forested prior to European settlement (Williams 1990) so it is likely that if these species assemblages have remained relatively unchanged, they would have co-evolved in primarily forested landscapes. However, lacunarity analyses of upland forest land cover types show that there are very few discontinuities in the structure of this habitat (lacunarity curves have very few changes in slope) and therefore little correspondence to discontinuities in home range size. There are more instances of correspondence between discontinuities in non-forest habitat and home range size, though in each section there are many more discontinuities in the distribution of home range sizes than in non-forest habitat. Since home range size discontinuities exist without a corresponding discontinuity in non-forest habitat structure, it is unlikely that the heterogeneity of non-forest structure is the key factor influencing the structure of avian assemblages.

This lack of any correspondence between discontinuities in the structure of the species assemblages and the current forest structure of the landscape does not provide support for Holling's hypothesis. However, out of necessity this analysis used relatively recent land cover data. If these species assemblages arose prior to European settlement, the composition and configuration of forest patches across eastern North America is likely different than it was when the assemblages originated, even if the land cover types have remained relatively consistent. For example, since most eastern forests have been logged at some point in the past 300 years (Pimm and Askins 1995), it is likely that the structure of this second- or third-growth forest is now different from the pristine forests that once existed. Additionally, many forests are now actively managed for timber production; these forests may consist of even-aged stands of only one or a few species with little undergrowth and architectural diversity. The NLCD data set used here does not discriminate between highly human modified forested areas and naturally regenerated forest.

It is probably more likely that the habitat changes that have occurred in the past few centuries have also caused changes in the composition of species assemblages. If this is true, that species assemblages have changed in response to environmental change, then the expectation is that there should be a correlation between the current composition of species assemblages and landscape structure. No such correspondence was found between discontinuities in home range size and discontinuities in upland forest habitat. Although it is possible that a correspondence might be found using some other subset of the land cover types listed in Table 3.2, the results of the present analysis are inconsistent with Holling's (1992) hypothesis.

The requirements of the software APACK (Mladenoff and DeZonia 2002) used to conduct the lacunarity analyses likely affected the results depicted in Figures 3.7 – 3.12. All the sections analyzed here have irregular boundaries, but APACK requires a rectangular map. The irregular shapes of these sections meant that analyzing the largest possible rectangular area that could be placed completely within the section boundaries would result in the loss of data from a large proportion of each section, especially from the areas near the section boundaries. In order to use all the data from each section, the area of analysis was defined as the smallest rectangle that encompassed the entire section (Figure 3.2). However, this definition resulted in a large proportion of each area of analysis being populated by continuous areas of non-forest habitat. Therefore, many of the habitat density calculations, especially at the smaller window sizes, resulted in a zero density of forest habitat (or conversely for the non-forest lacunarity analysis, a window saturated with non-forest habitat). These consistent density values may be artificially depressing the lacunarity curves at small window sizes; the true structure could be more heterogeneous than it appears.

The occurrence of discontinuities in body mass distributions is pervasive across taxa and geographic locations, suggesting that there must be some common causal explanation for the pattern. The importance of environmental structure in the dynamics of populations, and therefore the composition of species assemblages, is well known. In light of this, Holling's textural discontinuity hypothesis seems reasonable, though it was not supported by this study. Holling's hypothesis is difficult to test given the challenge of finding an appropriate quantification of landscape structure. Lacunarity is a promising metric because of its ability to detect hierarchical structure in a landscape. The insights gained from this study suggest several possible avenues for future investigations, including modifying the APACK software to remove the requirement for a rectangular map, testing other subsets of land cover types, and choosing study areas in regions that have been little impacted by human activities and therefore more closely represent conditions under which the species assemblage arose.

Table 3.1. Summary statistics for the National Ecological Unit Hierarchy sections used in this analysis.

| Section No. | Section Name | Area (1000 km$^2$) | No. Land Cover Types | No. Bird Species |
|---|---|---|---|---|
| 47 | Central Till Plains, Oak-Hickory | 41.43 | 18 | 107 |
| 59 | Central Ridge and Valley | 12.97 | 15 | 100 |
| 133 east | Coastal Plains and Flatwoods, Western Gulf | 8.79 | 16 | 94 |
| 133 west | Coastal Plains and Flatwoods, Western Gulf | 24.91 | 18 | |
| 153 east | Central Loess Plains | 93.50 | 19 | 101 |
| 153 west | Central Loess Plains | 24.39 | 18 | |
| 170 | Mid Coastal Plains, Western | 97.84 | 17 | 106 |
| 172 | Southern Cumberland Plateau | 22.53 | 15 | 105 |

Table 3.2. Land cover types identified by the National Land Cover Data Set and their percent of occurrence in each section. A * indicates that cover type makes up < 0.01% of the total land cover within that section.

| Land Cover Type | 47 | 59 | 133e | 133w | 153e | 153w | 170 | 172 |
|---|---|---|---|---|---|---|---|---|
| Open water | 1.54 | 2.70 | 2.84 | 3.32 | 0.97 | 0.95 | 2.66 | 2.28 |
| Perennial ice/snow | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Low intensity residential | 1.03 | 2.01 | 0.48 | 0.66 | 0.70 | 0.37 | 0.98 | 1.26 |
| High intensity residential | 0.32 | 0.38 | 0.02 | 0.18 | 0.42 | * | 0.25 | 0.28 |
| Commercial/ industrial /transportation | 0.48 | 1.15 | 0.17 | 0.65 | 0.53 | 0.46 | 0.74 | 0.79 |
| Bare rock/sand/clay | 0.03 | 0.02 | 0.01 | 0.10 | 0.02 | 0.01 | 0.09 | * |
| Quarries/strip mines /gravel pits | 0.18 | 0.09 | 0.05 | 0.06 | 0.04 | 0.02 | 0.14 | 0.35 |
| Transitional | 0.02 | 0.61 | 3.19 | 4.41 | * | 0 | 1.64 | 0.95 |
| Deciduous forest | 14.02 | 25.92 | 16.72 | 11.14 | 8.90 | 2.81 | 19.40 | 32.59 |
| Evergreen forest | 0.52 | 18.76 | 33.70 | 32.03 | 0.25 | 0.08 | 23.91 | 14.65 |
| Mixed forest | 0.41 | 21.24 | 15.62 | 20.97 | 0.07 | 0.02 | 21.71 | 23.61 |
| Shrubland | 0.01 | 0 | 0 | * | * | 0.02 | 0 | 0 |
| Orchards/vineyards /other | 0 | 0 | 0 | 0 | 0.01 | 0 | 0 | 0 |
| Grasslands/ herbaceous | 0.97 | 0 | 0 | 0.09 | 0.49 | 15.75 | 0.09 | 0 |
| Pasture/hay | 37.18 | 21.14 | 1.89 | 7.94 | 13.37 | 11.73 | 15.95 | 14.48 |

Table 3.2 (cont'd).

| Land Cover Type | 47 | 59 | 133e | 133w | 153e | 153w | 170 | 172 |
|---|---|---|---|---|---|---|---|---|
| Row crops | 37.28 | 4.65 | 9.78 | 4.58 | 71.98 | 61.27 | 2.90 | 7.41 |
| Small grains | 1.17 | 0 | 0.42 | 1.35 | 0.19 | 5.12 | 0.17 | 0 |
| Fallow | 0 | 0 | 0 | 0 | 0 | 0.01 | 0 | 0 |
| Urban/recreational Grasses | 0.79 | 1.07 | 0.06 | 0.11 | 0.59 | 0.16 | 0.17 | 0.43 |
| Woody wetlands | 3.72 | 0.20 | 14.57 | 11.52 | 1.22 | 0.15 | 8.43 | 0.82 |
| Emergent herbaceous wetlands | 0.31 | 0.07 | 0.47 | 0.88 | 0.24 | 1.05 | 0.76 | 0.10 |

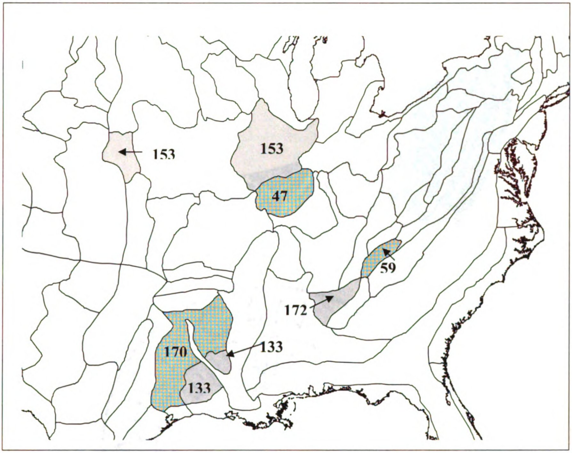


Figure 3.1. Sections of the eastern United States delineated by an ecoregion classification scheme (Bailey 1988, Cleland et al. 1997). Sections analyzed in this study are (47) Central Till Plains, Oak-Hickory; (59) Central Ridge and Valley; (133) Coastal Plains and Flatwoods, Western Gulf; (153) Central Loess Plains; (170) Mid Coastal Plains, Western; and (172) Southern Cumberland Plateau.

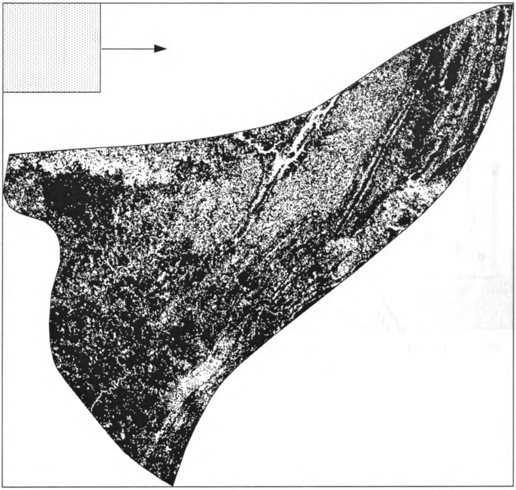


Figure 3.2. Binary classification of section 172 for lacunarity analysis showing section boundary and the boundary of the area of analysis (rectangle encompassing section). Dark areas of the map indicate forest habitat within the section boundary. White areas indicate non-forest habitat within the section boundary and all area between section boundary and analysis boundary. Stippled square represents a moving window of size *s* used in lacunarity analysis.

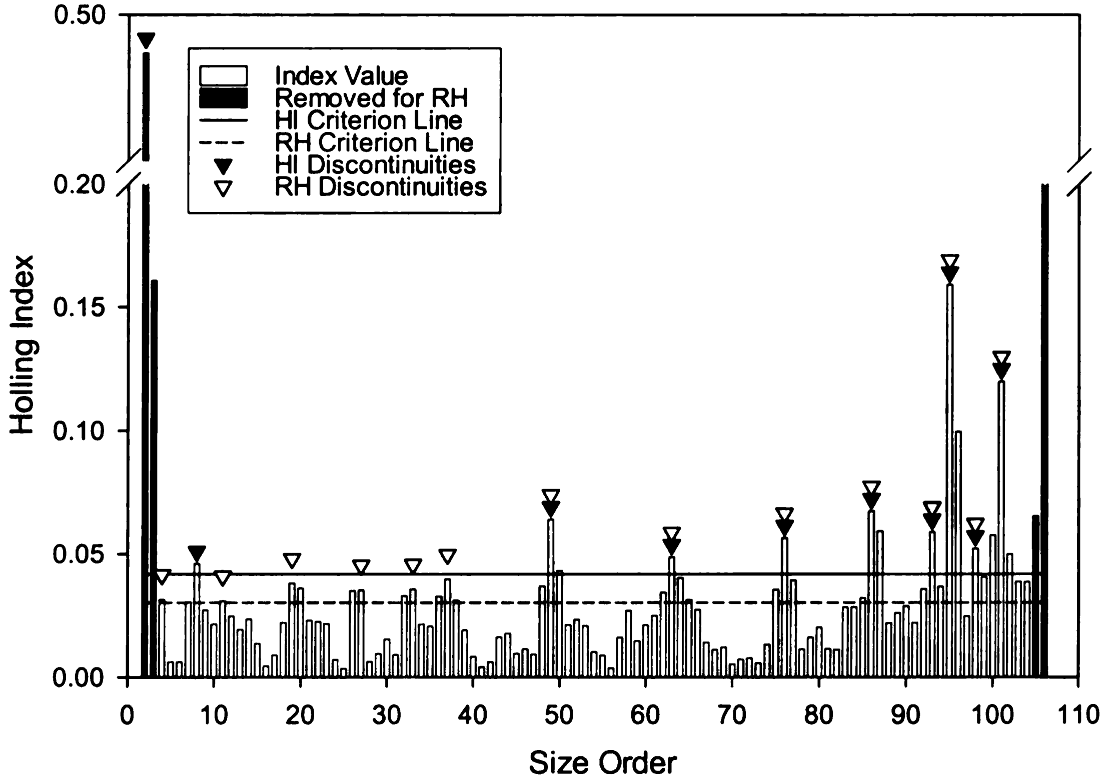


Figure 3.3. Size-ordered Holling Index values for the native terrestrial avian species of Section 47. Black bars indicate index values removed for the calculation of the Robust Holling Index. Criterion lines have been placed at the average index value plus one standard error. Arrows indicate discontinuities identified by the Holling Index (HI) and the Robust Holling index (RH).

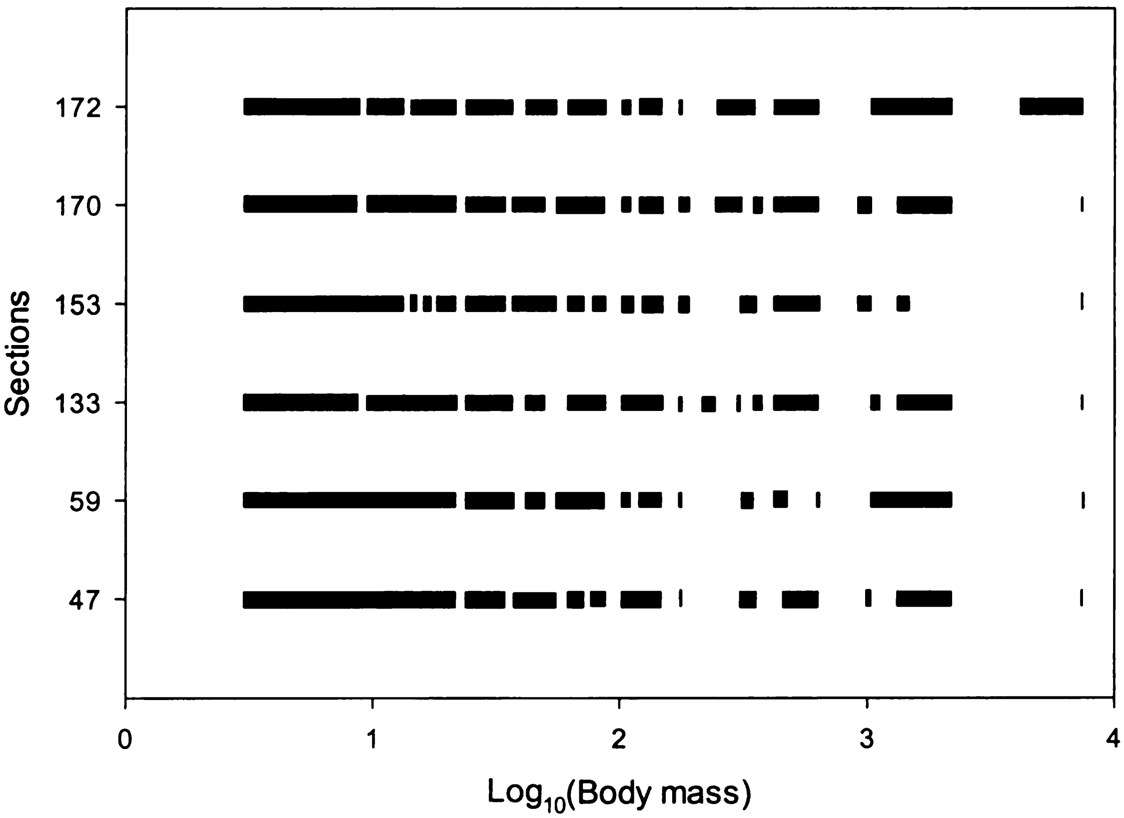


Figure 3.4. Distribution of species clusters (dark bars) and discontinuities (white spaces) in body masses of the six sections.

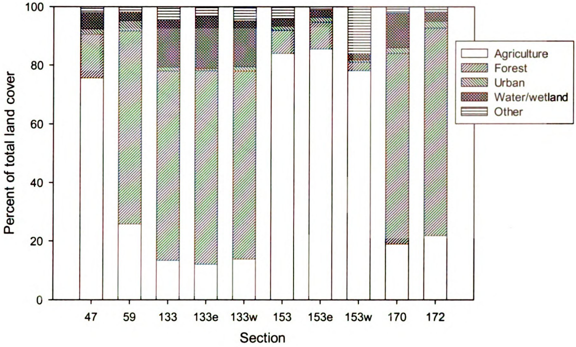


Figure 3.5. Percentage of land cover types across the six sections (with the disjunct areas of sections 133 and 153 displayed separately) in each of five broad categories (agriculture, upland forest, urban, water/wetland, and other), aggregated from the 20 land cover types present in these sections (Table 3.2).

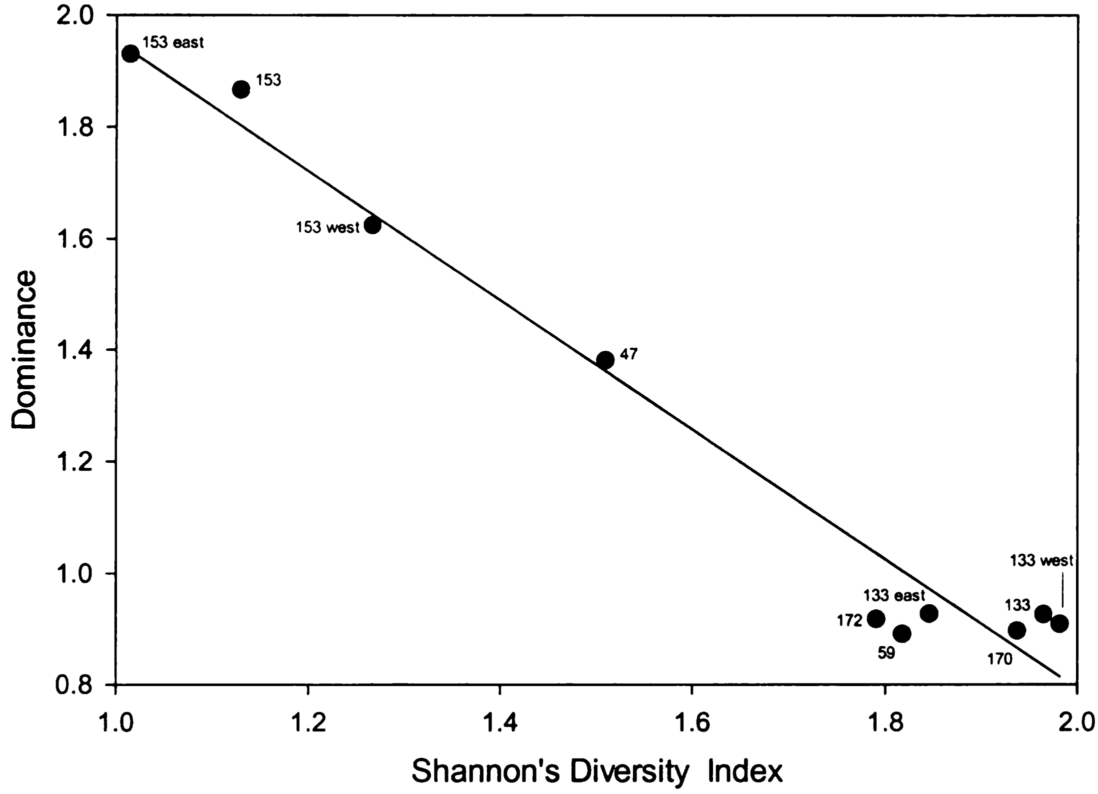


Figure 3.6. Dominance vs. diversity of land cover types in the six sections with least squares regression line ($r^2 = 0.969$).

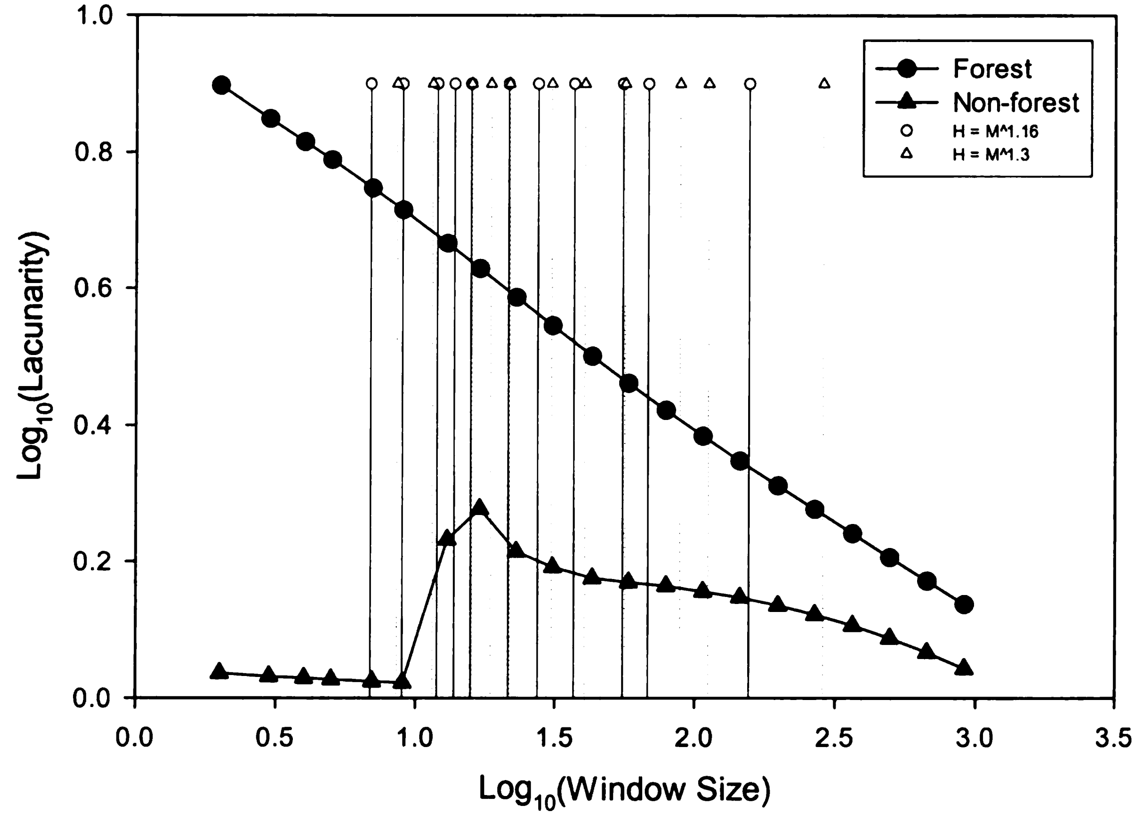


Figure 3.7. Lacunarity curves for the forest (●) and non-forest (▲) categories of section 47. Locations of discontinuities in home range size distribution as calculated by two allometric equations are indicated by vertical lines.

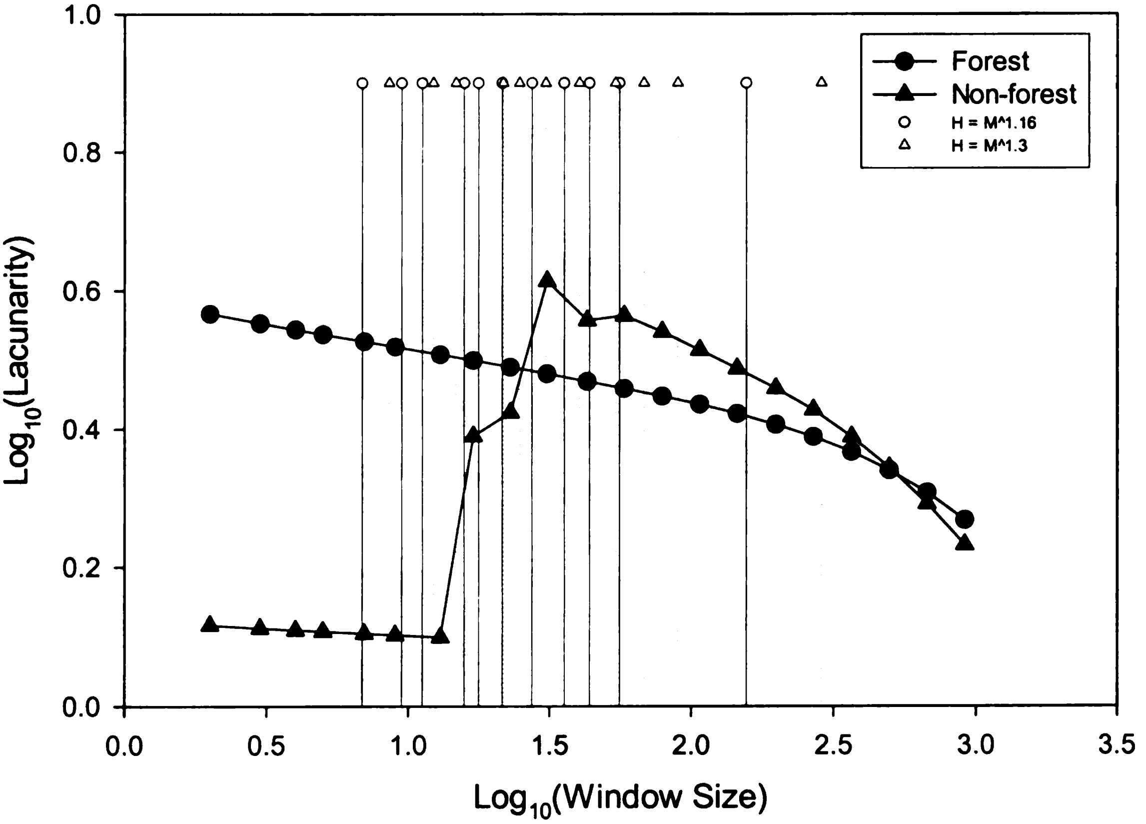


Figure 3.8. Lacunarity curves for the forest (●) and non-forest (▲) categories of section 59. Locations of discontinuities in home range size distribution as calculated by two allometric equations are indicated by vertical lines.

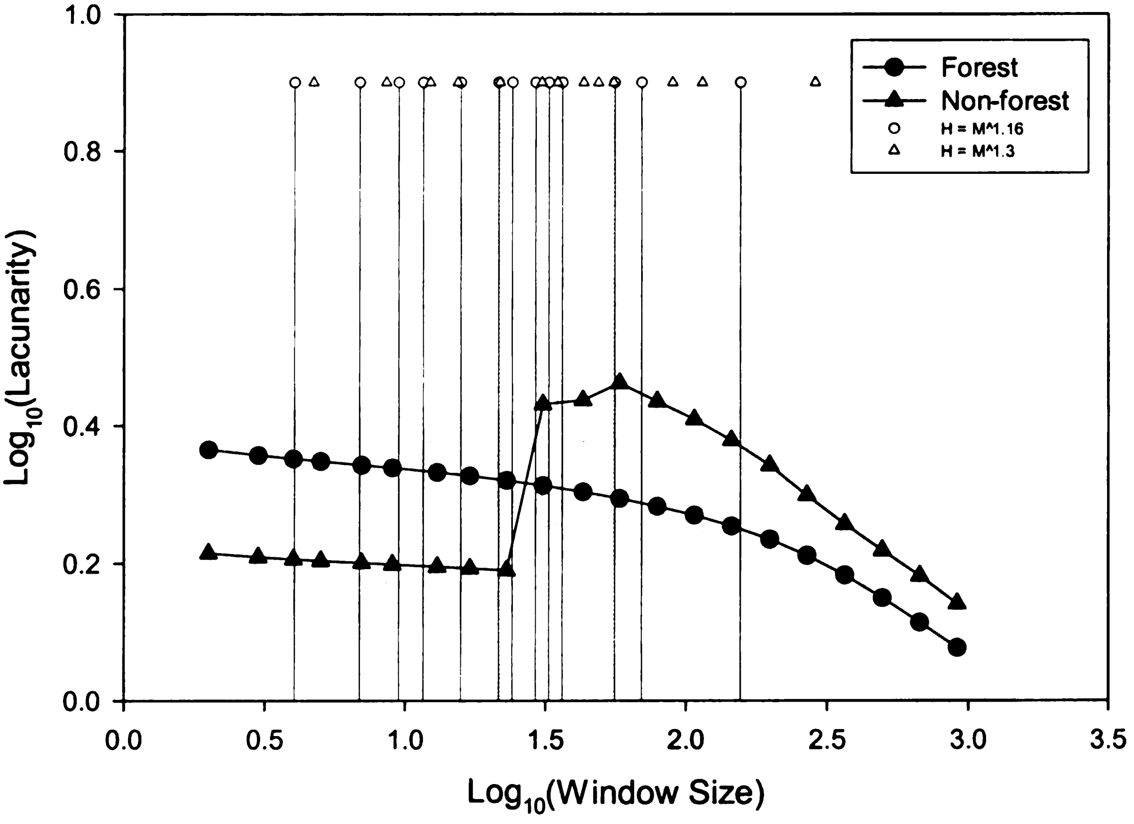


Figure 3.9. Lacunarity curves for the forest (●) and non-forest (▲) categories of section 133 east. Locations of discontinuities in home range size distribution as calculated by two allometric equations are indicated by vertical lines.

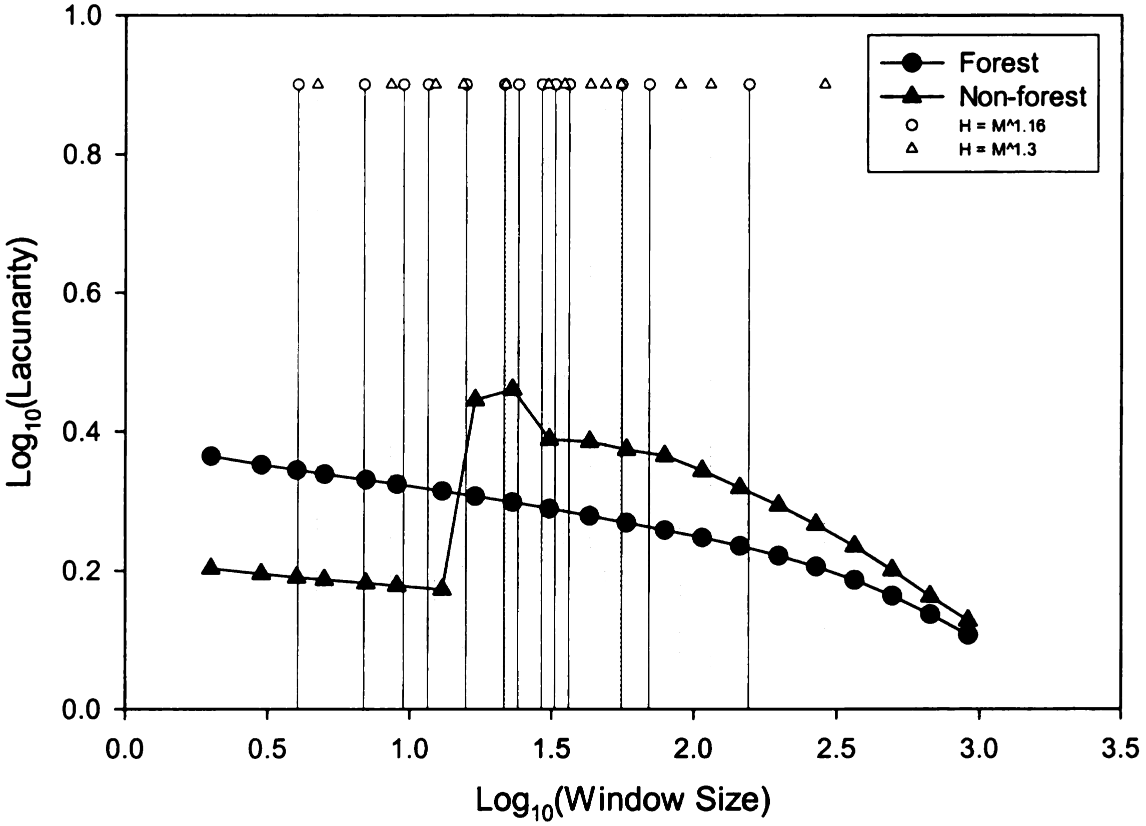


Figure 3.10. Lacunarity curves for the forest (●) and non-forest (▲) categories of section 133 west. Locations of discontinuities in home range size distribution as calculated by two allometric equations are indicated by vertical lines.

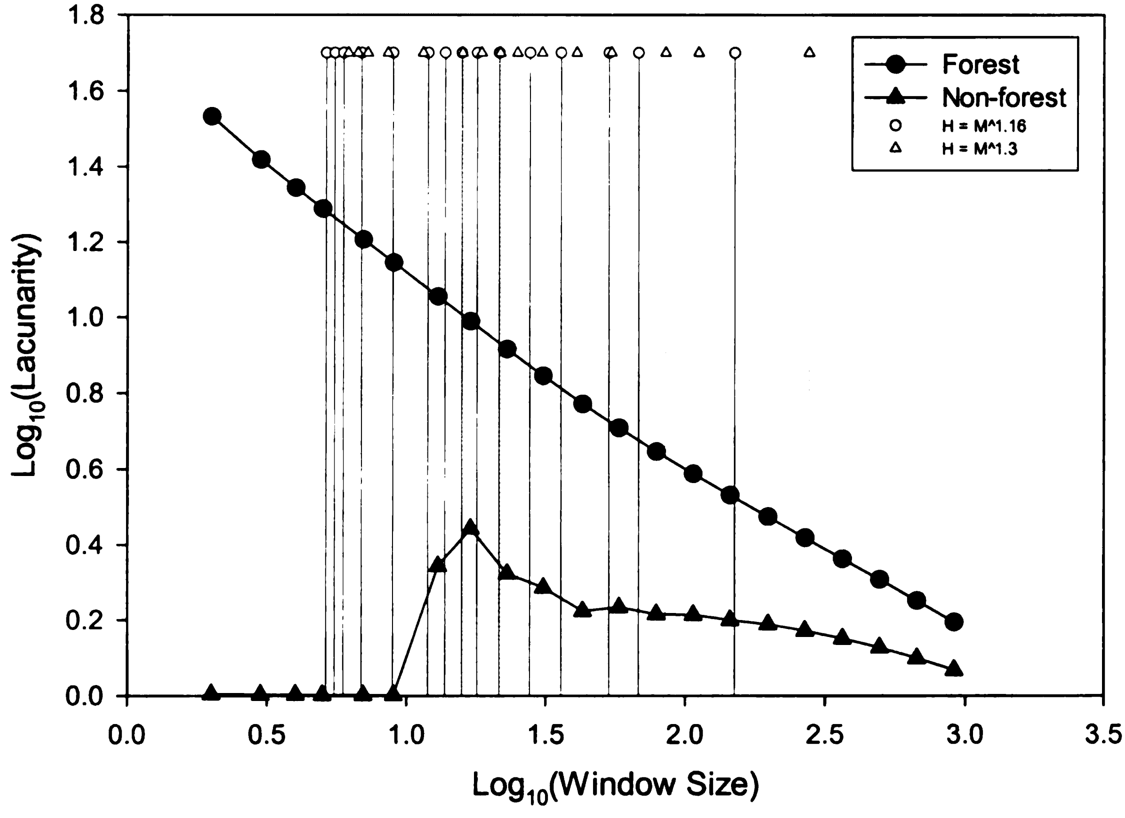


Figure 3.11. Lacunarity curves for the forest (●) and non-forest (▲) categories of section 153 west. Locations of discontinuities in home range size distribution as calculated by two allometric equations are indicated by vertical lines.

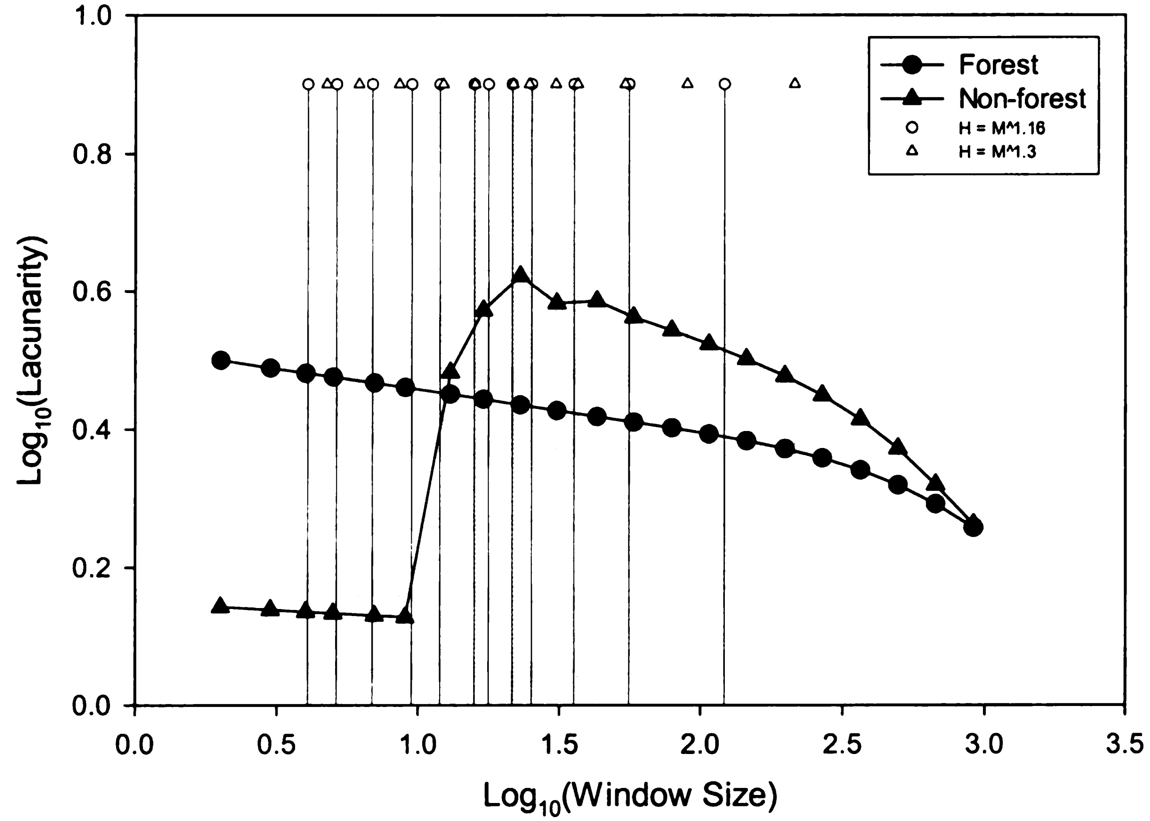


Figure 3.12. Lacunarity curves for the forest (●) and non-forest (▲) categories of section 172. Locations of discontinuities in home range size distribution as calculated by two allometric equations are indicated by vertical lines.

# CHAPTER 4

# AVIAN SPECIES COMPOSITION AND NORTH AMERICAN ECOREGIONS

## Introduction

Environmental management and conservation policies are increasingly being constructed around the framework of ecoregions; however, the factors that influence the distribution of ecoregions may not always be key influences on the distribution of taxa inhabiting those ecoregions (Goldstein 1999, Margules and Pressey 2000). Humans often describe landscapes with arbitrary sociopolitical boundaries, although we also have a long history of attempting to divide landscapes along more natural boundaries (Omernik 1995, Bailey 1996). These boundaries typically delineate areas of similar climate and resources and contain similar ecosystems (Omernik 1995, Bailey 2002). Different systems for delineating ecoregions have developed, as there is not universal agreement (Golledge et al. 1982, Hart 1982b, a, 1983, Healey 1983). Ecoregions have traditionally been delineated with a combination of quantitative and qualitative methods (Omernik 1995, Bailey 1996, Olson et al. 2001). This lack of quantitative purity has led to some controversy over the validity over the concept of ecoregions (Gering 2004, Magnusson 2004).

As ecosystem-based approaches to conservation and management have become more predominant, ecoregions have become a critical part of the framework of resource management and conservation policies worldwide (Government of Canada 1996, Olson and Dinerstein 1998, Groves et al. 2000). Ecoregions have become an important focus of conservation efforts as they are large enough to define areas that can preserve not only populations and genetic diversity, but also critical ecological and evolutionary processes (Groves et al. 2000, Olson et al. 2001). For example, the Native Seed Network affiliated with the U.S. Bureau of Land Management uses ecoregions as a substitute for empirical data on the genetic makeup of metapopulations of native plants (Native Seed Network 2005).

One of the often cited benefits of framing management policies around ecoregions is that ecoregion boundaries not only represent areas of distinct geological landforms and potential natural vegetation, but also likely reflect the distribution of both vertebrate and invertebrate taxa (Groves et al. 2000, Olson et al. 2001). Although ecoregions are undoubtedly more accurate representations of ecological landscape units than political divisions (Olson and Dinerstein 1998, Groves et al. 2000, Magnusson 2004), their delineation is still often at least partially based on human interpretations of the landscape and therefore subject to the question of whether these divisions reflect actual natural entities (Goldstein 1999). Ecoregions are often delineated based on some subset of variables including potential natural vegetation, soil types, and climatic variables (Bystrak 1981, Omernik 1995, Cleland et al. 1997, Williams and Pashley 1999, Olson et al. 2001). One of the assumptions underlying the use of ecoregions in conservation planning is that diverse taxa are thought to exhibit similar patterns in relation to ecoregion boundaries because they are subject to common influences of geology, climate, and structure (Spector 2002). However, several authors have pointed out that it is unlikely that any single system of dividing the landscape into regions will adequately represent the distribution of all taxa (Olson et al. 2001, Magnusson 2004).

Conservation planning usually involves choosing a surrogate taxon or a few taxa to represent the biodiversity of an area. Vascular plants, birds, or butterflies are often used as surrogate taxa because their taxonomic and distribution status are relatively well known world wide (Ricketts et al. 1999, Margules and Pressey 2000). Natural vegetation is perhaps the most commonly used criterion in defining landscape units, although there have been relatively few studies looking at whether divisions based on vegetation structure have meaning for other taxa (Goldstein 1999). Those studies that have been conducted show inconsistent results (Poynton and Boycott 1996, Mac Nally et al. 2002, Gering et al. 2003). This study tests the hypothesis that the distribution of avian species composition corresponds to the distribution of ecoregions in the continental United States. That is, bird community assemblages in ecoregions composed of comparable soils, climate, and vegetation are predicted to be similar to each other, and dissimilar to assemblages in ecoregions with different characteristics.

Assessing the correspondence of species assemblages to ecoregion distribution requires a method of measuring similarity and dissimilarity. The dissimilarity of species assemblages has commonly been described by three measures of diversity: alpha, beta, and gamma (Whittaker 1975). Of these, beta diversity measures the turnover, or change in the species composition between two communities. Multiple measures of beta diversity have been proposed (Koleff et al. 2003), each emphasizing different aspects of community structure. These differences among beta diversity metrics should result in different assessments of the correspondence of bird community assemblages to ecoregion distribution.

## Methods

### *Data sources*

This study used the National Ecological Unit Hierarchy (Cleland et al. 1997) which is a classification of ecological units encompassing spatial scales ranging from < 50 hectares to millions of square kilometers. In order of increasing size, the ecological units are landtype phase, landtype, landtype association, subsection, section, province, division, and domain. Two units within this hierarchy were used in this study, provinces and sections. Provinces are delineated primarily by continental weather patterns, and are characterized by similar soil orders and potential natural vegetation. Provinces are composed of sections, which are distinguished by similar sub-regional climates, geology, and potential natural vegetation. Only provinces (n = 35) and sections (n = 163) within the contiguous United States were included (Table D.1, Figure 4.1). The Channel Islands off the coast of southern California were excluded from analysis. A GIS coverage of this ecoregion classification scheme was obtained from the U.S. Forest Service (USDA Forest Service Inventory and Monitoring Institute 2005).

The composition of bird community assemblages across the continental United States was determined using species occurrence data from the North American Breeding Bird Survey (Sauer et al. 2001). Species occurrence data from all routes within the continental United States from 1966-2000 were included. BBS routes consist of 50 sampling points located 0.8 km apart along secondary roads. Surveys are conducted once per year during June, and all birds seen or heard at each sampling point are recorded (Robbins et al. 1986). A GIS coverage of all survey routes monitored by the BBS was obtained from the National Atlas of the United States® (U.S. Department of the Interior 2005).

Species lists for each of the 35 provinces and 163 sections were generated using ArcView 3.2 (Environmental Systems Research Institute Inc. 1992-1999) to identify the BBS routes occurring within each province and section. Routes that crossed province and section boundaries were excluded from province and section species lists, respectively. However, routes that crossed section boundaries within a province were included in the list for that province. Consequently a species list for a province could contain more species than any of the component section lists, but not fewer. The Northern Rio Grande Intermontane section (43) contained no BBS routes entirely within its boundaries. Consequently a species list could not be generated for this section.

### *Data analysis*

To compare the adequacy of BBS sampling across sections and provinces of varying area, species-area plots were created based on avian species lists at both the section and province level (Figures 4.3 and 4.4). Species richness was also plotted against sampling intensity, calculated as the number of BBS routes per km$^2$ in both sections and provinces (Figures 4.5 and 4.6).

Seven beta-diversity metrics (Table 4.1) were used to assess the differences between the bird community assemblages at two spatial scales, provinces and sections. These seven metrics represent the four categories of metrics described by Koleff et al. (2003): measures of continuity and loss, species richness gradients, continuity, and gain and loss. The seven selected also include metrics commonly used in diversity studies (βw, βj, and βso) as well as those metrics which have been shown to perform well in terms of ability to reflect community turnover, additivity, and independence from alpha diversity and sample size (βw and βt) (Wilson and Shmida 1984, Chao et al. 2005). Jaccard's similarity index, βj, here expressed as a diversity index, is widely used and easily calculated. Values of βj are strongly dependent on matching component *a* (Figure 4.2, Koleff et al. 2003) and weight all species equally, which contributes to its poor performance when the species assemblage contains a large proportion of rare species (Chao et al. 2005). Values of Simpson's diversity index, βsi, depend on matching component *a* as well as the relative magnitude of *b* and *c* (Koleff et al. 2003). Unlike βj, βsi is weighted towards common species and so may be inappropriate for assemblages with a large component of rare species (Gering et al. 2003). Local species richness gradients do not affect calculated values of βsi (Lennon et al. 2001). Ruggiero et al. (1998) developed a similarity index, βrlb, here expressed as a diversity index, which is the only metric to fall into the category of continuity and loss (Koleff et al. 2003). Values for βrlb are dependent on matching components *a* and *c*. βgl is a measure of local species richness gradients, and as such has been used to test the performance of other beta-diversity metrics (Lennon et al. 2001). Values for βgl depend solely on matching components *b* and *c* (Koleff et al. 2003). Sørensen's similarity index, βso, here expressed as a diversity metric, is also widely used and easily calculated. As with βj, βso weights all species equally and so is inappropriate for assemblages containing many rare species (Chao et al. 2005). Unlike βsi, βso is affected by local species richness gradients (Lennon et al. 2001). Whittaker's diversity index, βw, is probably the most widely used beta-diversity metric (Koleff et al. 2003). Values of βw decrease with increases in the value of matching component *a*. As with βso, βw is affected by local species richness gradients (Lennon et al. 2001). Wilson and Shmida (1984) developed a measure of beta turnover, βt, that has also become widely used, perhaps because it is often more easily interpretable than βw. Like βw, βt also decreases with increases in matching component *a* (Koleff et al. 2003).

Using the equations presented in Koleff et al. (2003), which compare species occurrence data based on some or all of the components depicted in Figure 4.2, distance matrices were calculated for these seven beta-diversity metrics. All calculations and analyses were conducted with the R statistical package (R Development Core Team 2004) unless otherwise indicated.

The Nearest Features ArcView extension (Jenness 2004) was used to calculate the actual geographic distance between section edges of all possible pairs of the 163 sections. Adjoining sections were defined as having a distance of zero. All small coastal polygons (*e.g.* barrier islands) were excluded from these calculations. For noncontiguous sections such as the Central Loess Plains, which is composed of two distinct polygons, the smaller of the two distances between the Central Loess Plains polygons and any other section was retained in the geographic distance matrix. The resulting 163x163 section geographic distance matrix was also condensed into a 35x35 province geographic distance matrix. The inter-province distance for each possible pair of provinces was defined as the smallest distance between all possible pairs of sections comprising each province.

At the scale of both sections and provinces, the beta-diversity and geographic distance matrices were classified using a hierarchical agglomerative technique, unweighted arithmetic average clustering (UPGMA) (Legendre and Legendre 1998), implemented in R (R Development Core Team 2004) using the cluster package (Rousseeuw et al. 2004). The beta-diversity matrices were also classified using a divisive method, partitioning around medoids (PAM), at each spatial scale (Kaufman and Rousseeuw 1990). Each of the seven beta-diversity matrices based on section species lists (n = 162) was partitioned into 35 clusters since there are 35 provinces in the contiguous United States (Cleland et al. 1997). At the province level, each of the seven beta-diversity matrices based on province species lists (n = 35) was partitioned into 19 clusters since there are 19 divisions in the contiguous United States (Cleland et al. 1997).

Mantel tests with 1000 permutations were used to assess the congruence of the seven beta-diversity matrices with each other and with the corresponding geographic distance matrices at both the section and province spatial scales (Legendre and Legendre 1998). A sectional species lists could not be generated for the Northern Rio Grande Intermontane section (43); therefore, for the Mantel tests at the section level all geographic distance data associated with this section were deleted, creating a section geographic distance matrix with the same dimensions (162x162) as the beta-diversity matrices.

## Results

The 163 sections of the contiguous United States vary in area from 100 km$^2$ to 1170 km$^2$ (Table D.1). The species richness of the 162 sections for which species lists could be generated varies from 54 to 259 (Figure 4.3). The 35 provinces vary in area from 120 km$^2$ to 6702 km$^2$, while species richness varies from 115 to 314 species (Figure

4.4). Although the number of species does increase with increases in province area ($r^2$ = 0.461), at the section level there is no significant change in species richness with increases in area ($r^2$ = 0.001, $F_{1,160}$ = 0.0994, p = 0.753). Species richness increases with increases in sampling intensity at the section level (Figure 4.5; $r^2$ = 0.313), but there is no significant change in species richness with changes in sampling intensity across provinces (Figure 4.6; $r^2$ = 0.001, $F_{1,33}$ = 0.037, p = 0.849). Sampling intensity decreases with area for both sections and provinces (Figures 4.7 and 4.8; $r^2$ = 0.273 and 0.248, respectively).

UPGMA cluster analysis of the beta-diversity matrices from both section and province species lists produced dendrograms that were all similarly correlated with the original data (Table 4.2). However, clustering based on section species lists consistently had lower cophenetic correlations and higher root mean squared errors than those based on provinces, while the clustering of the geographic distance matrix based on sections had a higher cophenetic correlation and lower root mean squared error than that based on provinces.

Three of the seven dendrograms produced by UPGMA analysis of the beta-diversity matrices based on section species lists, ßso, ßw, and ßt, were identical, with pairwise correlations of cophenetic distances equal to 1.00 (Table 4.3). The dendrogram based on the ßj matrix was very similar, with differences in the grouping of only a few sections. The remaining three dendrograms, ßrlb, ßgl, and ßsi were each distinct, with the ßgl dendrograms being notable for its particularly short branch lengths.

Six of the seven dendrograms produced by UPGMA analysis of the beta-diversity matrices based on province species lists were broadly similar in that the largest two clusters (n = 16 and n = 19) were composed of the same provinces. Within these largest clusters, however, the ßrlb and ßsi dendrograms had a different pattern of aggregation than in the other four dendrograms. The clustering patterns of the ßso, ßw, and ßt dendrograms were identical (Table 4.4). The ßj dendrogram was very similar to the dendrograms of ßso, ßw, and ßt; only the branch lengths varied slightly. The pattern of aggregation in the ßgl dendrogram was distinct from all other section dendrograms. The largest two clusters were unbalanced in size (n = 30 and n = 5), and neither was identical in composition to clusters in any other dendrogram.

Mantel tests comparing dissimilarity matrices based on section species lists indicate that, with two exceptions (the comparison of ßsi to ßgl, $p = 0.938$, and ßgl to geographic distance, $p = 0.313$), the beta-diversity distance matrices were similar both to each other and the geographic distance matrix ($p < 0.001$) (Table 4.5). At the province level, with three exceptions (the comparison of ßgl to ßsi, $p = 1$, ßgl to ßrlb, $p = 0.055$, and ßgl to geographic distance, $p = 0.206$), the beta-diversity matrices were again highly correlated with each other and with the geographic distance matrix ($p < 0.001$) (Table 4.6).

The results of the PAM analysis for the species lists based on sections (n = 162) show a consistently high rate of misclassification across all seven beta-diversity metrics (misclassification rate ranged from 0.89 to 1.0). Of the 35 provinces that the 162 species lists were expected to cluster into, only one was classified correctly in multiple analyses. The six sections of province 47 (Southwest Plateau and Plains Dry Steppe and Shrub) were grouped together by the cluster analysis of the ßj, ßso, ßw, and ßt beta-diversity matrices. In all other instances at least one of the sections comprising a province was placed in a group with sections from another province. The results of the PAM analysis for the species lists based on provinces (n = 35) show a slightly lower level of misclassification (rate ranged from 0.58 to 0.79), with more provinces that were correctly grouped together into divisions by multiple distance matrices (Table 4.7).

## Discussion

The use of BBS data introduces several potential sources of bias. The BBS survey methods are not equally successful for all bird species; for example, populations of nocturnal species are not well-described by BBS data. Although the species lists generated from BBS data may not accurately represent the complete species assemblage of a section or province, the biases are likely to be consistent across all regions. The number of species observed in an area commonly increases with the size of the area surveyed (MacArthur and Wilson 1967). Although this trend was present at the province level (Figure 4.4), it did not emerge at the section level (Figure 4.3). Larger provinces tend to be composed of more sections than smaller provinces, and therefore contain more habitat types, which increases species richness. BBS sampling effort is not constant across the contiguous United States. When sampling effort is expressed as route density (routes/km$^2$), species richness increases with increasing sampling intensity at the section level (Figure 4.5), but there is no change in species richness with sampling intensity at the province level (Figure 4.6). This suggests that, at the province level, the BBS survey data adequately captures richness; that is, adding more routes within a province is not likely to increase species richness unless sampling methods are also changed. However, within sections increasing sampling effort does increase the number of observed species, perhaps by increasing the likelihood of finding individuals of species more commonly found in neighboring sections within the province.

Although there are many metrics that describe beta-diversity, this study was limited to those appropriate for presence/absence data. Four of these metrics, ßj, ßso, ßw, and ßt, were categorized by Koleff et al. (2003) as measures of continuity, or “broad-sense” turnover, which focus on differences in composition but not on the relative magnitude of species gains or losses. Variation in the values of these measures depends primarily on differences in the matching component $a$ (Figure 4.2). Reflecting this common influence the ßj, ßso, ßw, and ßt distance matrices based on both section and province species lists performed almost identically in UPGMA cluster analysis, Mantel tests, and PAM cluster analysis (Tables 4.2 and 4.5 – 4.7). The ßj distance matrix clustered only a few sections differently in the UPGMA analysis of section species lists.

Of the other three beta-diversity metrics, ßrlb was described by Koleff et al. (2003) as a measure of continuity and loss, depending on the values of both $a$ and $c$ (Figure 4.2). Though originally formulated to create an equiprobabilistic map based on species occurrences across multiple quadrats (Ruggiero et al. 1998), it was re-expressed by Koleff et al. (2003) to reflect only a single pair-wise comparison. In this re-expressed form it is mathematically comparable to the other metrics, though in practice cophenetic correlations tended to be low and root mean square error tended to be high (Table 4.2). ßsi was categorized as a measure of gain and loss (Koleff et al. 2003), or “narrow-sense” turnover that focuses on changes in species composition rather than changes in species richness. Unlike the “broad-sense” turnover measures, variation in ßsi depends on both the value of $a$ and the relative magnitude of $b$ and $c$.

The last metric, ßgl, is distinct from the other six. Described by Koleff et al. (2003) as a species richness gradient measure, it was not originally intended as a measure of beta-diversity but rather as a measure of local richness gradients, or alpha diversity (Lennon et al. 2001). As such, it is not surprising that at the spatial scale of this study ßgl performed rather poorly. The ßgl distance matrices were relatively poorly correlated with the original data (Table 4.2) and with the geographic distance matrices (Tables 4.3 and 4.4).

The scale of a study also can affect beta-diversity values. As the sampling grain increases, species richness tends to increase (MacArthur and Wilson 1967), and as the spatial extent of a study area increases, diversity between observations also tends to increase (Nekola and White 1999). A study of birds and butterflies in the North American Great Basin demonstrated empirically that as sampling grain increased, the similarity of the species composition of two assemblages also increased (Mac Nally et al. 2004). The range of the sampling grain in this Great Basin study – sites, canyons, and mountain ranges – covered about five orders of magnitude. The smallest sample size (sites) assessed the distribution of individuals while the largest sample size (mountain ranges) assessed the distribution of populations. Similarly to Mac Nally et al. (2004), the present study of North American ecoregions does not have a consistent scale as sizes of both sections and provinces vary. However, the size variation from the smallest section (100 $km^2$) to the largest province (6702 $km^2$) is less than two orders of magnitude. This relatively small amount of variation in sampling grain is unlikely to affect the calculated beta-diversity values. Additionally, the section and province species lists generated from BBS survey data describe the distribution of populations and species, not individuals, over a much longer time frame than that in the Great Basin study (Mac Nally et al. 2004). The results of the Great Basin study are much more likely to have been influenced by short-term local ecological conditions, whereas the results of this study of North American ecoregions are more likely to represent long-term regional ecological conditions.

Ecoregions are frequently used as the foundation of conservation planning, based in part on the assumption that ecoregions likely represent the distribution of taxa (Groves et al. 2000, Olson et al. 2001). Under this assumption, a comparison of the composition of the section species lists should enable the recreation of provinces. With a divisive classification method like PAM, the expectation was that partitioning the 162 section species lists into 35 clusters would result in clusters that conformed to the 35 provinces found in the contiguous United States. However, such correspondence was the exception rather than the rule. The ßrlb matrix was the most successful, correctly matching four groups of species lists to their respective provinces. The ßgl matrix was the least successful, with no provinces correctly identified. Only one province, the Southwest Plateau and Plains Dry Steppe and Shrub, was correctly classified using the data from multiple beta-diversity matrices. At a larger spatial scale, the results were slightly better. Using PAM, the expectation was that partitioning the 35 province species lists into 19 clusters would result in clusters that conformed to the 19 divisions found in the contiguous United States. Though there were more correct classifications by multiple beta-diversity matrices (Table 4.7), the error rate was still > 50% for each beta-diversity metric.

For the birds of North America, it appears that avian beta diversity does not correspond to biogeographic regions based on soils, climate, and vegetation. Instead, the results of this study suggest that the geographic distance between species assemblages is a stronger influence on their composition. With the exception of the ßgl matrix, all beta-diversity matrices were strongly correlated with the geographic distance matrix (Mantel tests, $p < 0.001$). This fits with other work that has shown the distribution of North American bird species to be spatially autocorrelated (Brown et al. 1995). Many sections that are grouped together into a province by the National Ecological Unit Hierarchy (Cleland et al. 1997) actually occur over a wide geographic area. For example, the ten sections of the Great Plains-Palouse Dry Steppe Province are distributed over a 1300 km swath from the Canadian border south to northern Texas while the seven sections of the Outer Coastal Plain Mixed Forest Province range over 1500 km from the Atlantic coast west to southeastern Texas.

The validity of the concept of ecoregions can only be assessed by addressing complex issues such as human and non-human perceptions of landscape characteristics, the permeability of boundaries between landscapes for various species, and the dynamic nature of landscape characteristics. However, the results of this study do provide insight into the utility of ecoregions for a particular purpose, environmental management and conservation planning. The provinces and sections of the National Ecological Unit Hierarchy, which are based on continental weather patterns, soils, and potential natural vegetation, do not seem to reflect the distribution of birds in North America, though they may be adequate for other taxa (Gering et al. 2003). The distribution of bird species across North America may follow a Gleasonian continuum pattern, where the range of occurrence of each species is independent of the co-occurrence of a particular plant association or ecoregion (Barbour et al. 1987). Although some species within a particular avian assemblage may indeed have distributions that correspond to ecoregion boundaries, the results of this study suggest that overall, North American avian species are distributed independently of the distribution of ecoregion landscape units.

Table 4.1. Beta-diversity metrics used in analyses; equations as presented in Koleff et al. (2003).

| β-Diversity Metric | Equation |
|---|---|
| Jaccard | $\beta j = 1 - [a / (a + b + c)]$ |
| Simpson | $\beta si = [\min\{b,c)] / [(\min(b,c)) + a]$ |
| Ruggiero et al. | $\beta rlb = 1 - [a / (a + c)]$ |
| Lennon et al. | $\beta gl = 2( \lvert b - c\rvert ) / (2a + b + c)$ |
| Sorenson | $\beta so = 1 - [2a / (2a + b + c)]$ |
| Whittaker | $\beta w = (a + b + c) / [(2a + b + c) / 2]$ |
| Wilson & Shmida | $\beta t = (b + c) / (2a + b + c)$ |

Table 4.2. Hierarchical agglomerative clustering (UPGMA) results for species lists based on sections (n = 162) and provinces (n = 35), and geographic distance between sections (n = 163) and provinces (n = 35).

| β-Diversity | Cophenetic Correlation | | Root Mean Square Error | |
|---|---|---|---|---|
| Matrix | Section | Province | Section | Province |
| βj | 0.857343 | 0.8726094 | 0.0853477 | 0.07726224 |
| βsi | 0.8163491 | 0.8298172 | 0.1078507 | 0.09663368 |
| βrlb | 0.7500869 | 0.7657905 | 0.1261695 | 0.1225102 |
| βgl | 0.748039 | 0.8808222 | 0.1318996 | 0.1067753 |
| βso | 0.8267704 | 0.8498973 | 0.09590017 | 0.0818542 |
| βw | 0.8267704 | 0.8498973 | 0.09590017 | 0.0818542 |
| βt | 0.8267704 | 0.8498973 | 0.09590017 | 0.0818542 |
| Geographic distance | 0.699514 | 0.6650709 | 695068.6 | 706924 |

Table 4.3. Correlation of cophenetic distances for each of the beta-diversity matrices based on section species lists (n = 162).

| | βj | βsi | βrlb | βgl | βso | βw | βt |
|---|---|---|---|---|---|---|---|
| βj | | | | | | | |
| βsi | 0.885891 | | | | | | |
| βrlb | 0.839922 | 0.862965 | | | | | |
| βgl | 0.141615 | 0.030986 | 0.052162 | | | | |
| βso | 0.988724 | 0.896334 | 0.855323 | 0.129944 | | | |
| βw | 0.988724 | 0.896334 | 0.855323 | 0.129944 | 1.000000 | | |
| βt | 0.988724 | 0.896334 | 0.855323 | 0.129944 | 1.000000 | 1.000000 | |

Table 4.4. Correlation of cophenetic distances for each of the beta-diversity matrices based on province species lists (n = 35).

| | βj | βsi | βrlb | βgl | βso | βw | βt |
|---|---|---|---|---|---|---|---|
| βj | | | | | | | |
| βsi | 0.879076 | | | | | | |
| βrlb | 0.864968 | 0.894623 | | | | | |
| βgl | 0.186577 | 0.021726 | 0.047332 | | | | |
| βso | 0.996568 | 0.899755 | 0.877283 | 0.176228 | | | |
| βw | 0.996568 | 0.899755 | 0.877283 | 0.176228 | 1.000000 | | |
| βt | 0.996568 | 0.899755 | 0.877283 | 0.176228 | 1.000000 | 1.000000 | |

Table 4.5. P-values for comparisons of beta-diversity matrices based on section species lists and the section geographic distance matrix using Mantel tests with 1000 replicates.

|  | βj | βsi | βrlb | βgl | βso | βw | βt | GeoDist |
|---|---|---|---|---|---|---|---|---|
| βj |  |  |  |  |  |  |  |  |
| βsi | <0.001 |  |  |  |  |  |  |  |
| βrlb | <0.001 | <0.001 |  |  |  |  |  |  |
| βgl | <0.001 | 0.938 | <0.001 |  |  |  |  |  |
| βso | <0.001 | <0.001 | <0.001 | <0.001 |  |  |  |  |
| βw | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |  |  |  |
| βt | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |  |  |
| GeoDist | <0.001 | <0.001 | <0.001 | 0.313 | <0.001 | <0.001 | <0.001 |  |

Table 4.6. P-values for comparisons of beta-diversity matrices based on province species lists and the section geographic distance matrix using Mantel tests with 1000 replicates.

| | βj | βsi | βrlb | βgl | βso | βw | βt | GeoDist |
|---|---|---|---|---|---|---|---|---|
| βj | | | | | | | | |
| βsi | <0.001 | | | | | | | |
| βrlb | <0.001 | <0.001 | | | | | | |
| βgl | <0.001 | 1.000 | 0.055 | | | | | |
| βso | <0.001 | <0.001 | <0.001 | <0.001 | | | | |
| βw | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | | | |
| βt | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | | |
| GeoDist | <0.001 | <0.001 | <0.001 | 0.206 | <0.001 | <0.001 | <0.001 | |

Table 4.7. Province species lists (n = 35) correctly classified by PAM into 19 divisions for each of the seven beta-diversity matrices (Note: Division 19 is located outside the contiguous United States).

| Division | βj | βsi | βrlb | βgl | βso | βw | βt |
|---|---|---|---|---|---|---|---|
| 1 | | | ✓ | | | | |
| 2 | | | | ✓ | | | |
| 3 | | | | | | | |
| 4 | ✓ | ✓ | ✓ | | ✓ | ✓ | ✓ |
| 5 | ✓ | ✓ | ✓ | | ✓ | ✓ | ✓ |
| 6 | | ✓ | ✓ | | | | |
| 7 | | ✓ | ✓ | | | | |
| 8 | | | ✓ | | | | |
| 9 | | | | | | | |
| 10 | ✓ | | | | ✓ | ✓ | ✓ |
| 11 | | | ✓ | | | | |
| 12 | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ |
| 13 | ✓ | | | | ✓ | ✓ | ✓ |
| 14 | | | ✓ | ✓ | | | |
| 15 | ✓ | | | | ✓ | ✓ | ✓ |
| 16 | | | | ✓ | | | |
| 17 | | | | | | | |
| 18 | | | | | | | |
| 20 | ✓ | | | | ✓ | ✓ | ✓ |

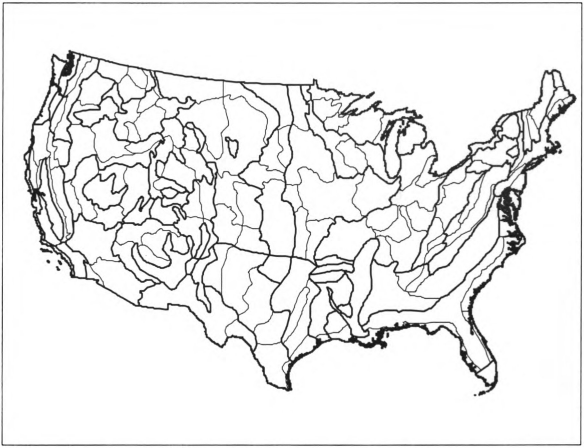


Figure 4.1. Provinces (bold lines) and sections of the contiguous United States delineated by the National Ecological Unit Hierarchy (Cleland et al. 1997).

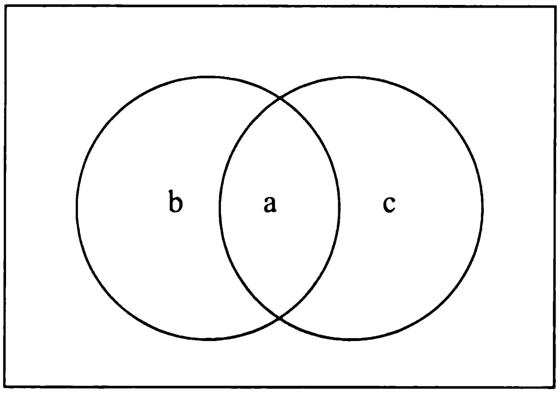


Figure 4.2. The matching/mismatching components used in pairwise comparisons of presence/absence data: (a) the total number of species common to both regions, (b) the number of species that occur only in the neighboring region, and (c) the number of species that occur only in the focal region.

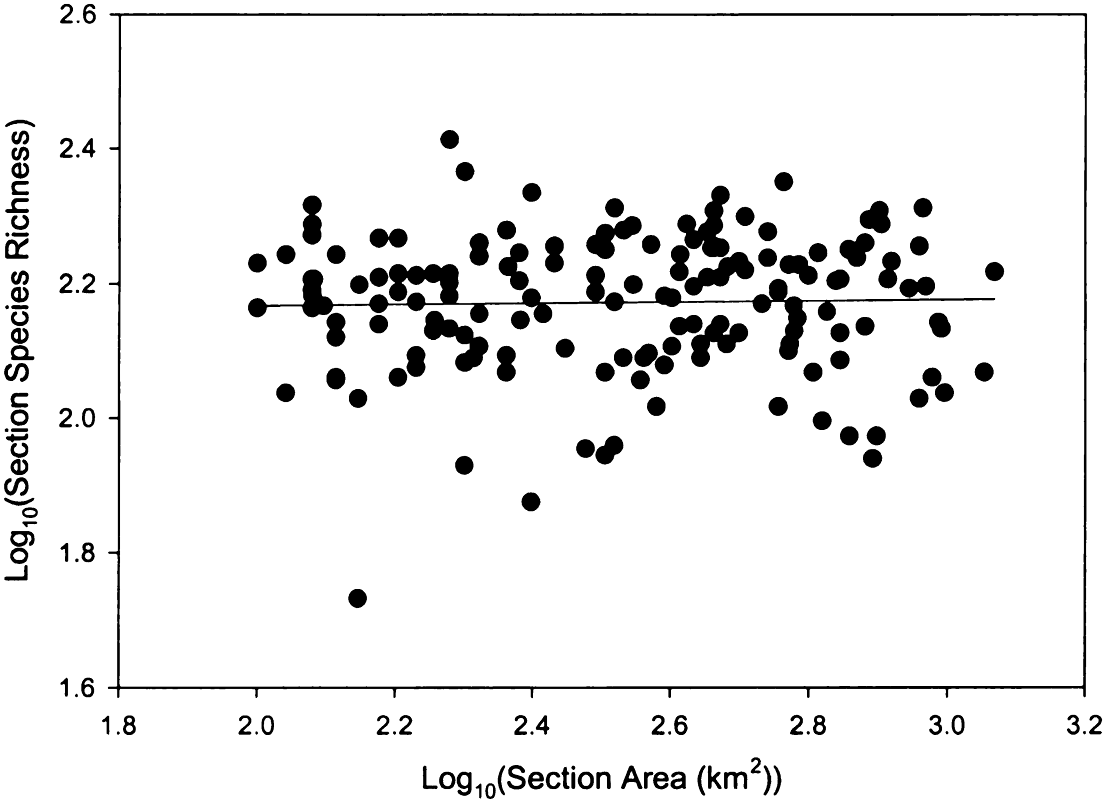


Figure 4.3. Section species richness vs. area (km$^2$) (n = 162) with least squares linear regression ($r^2$ = 0.001).

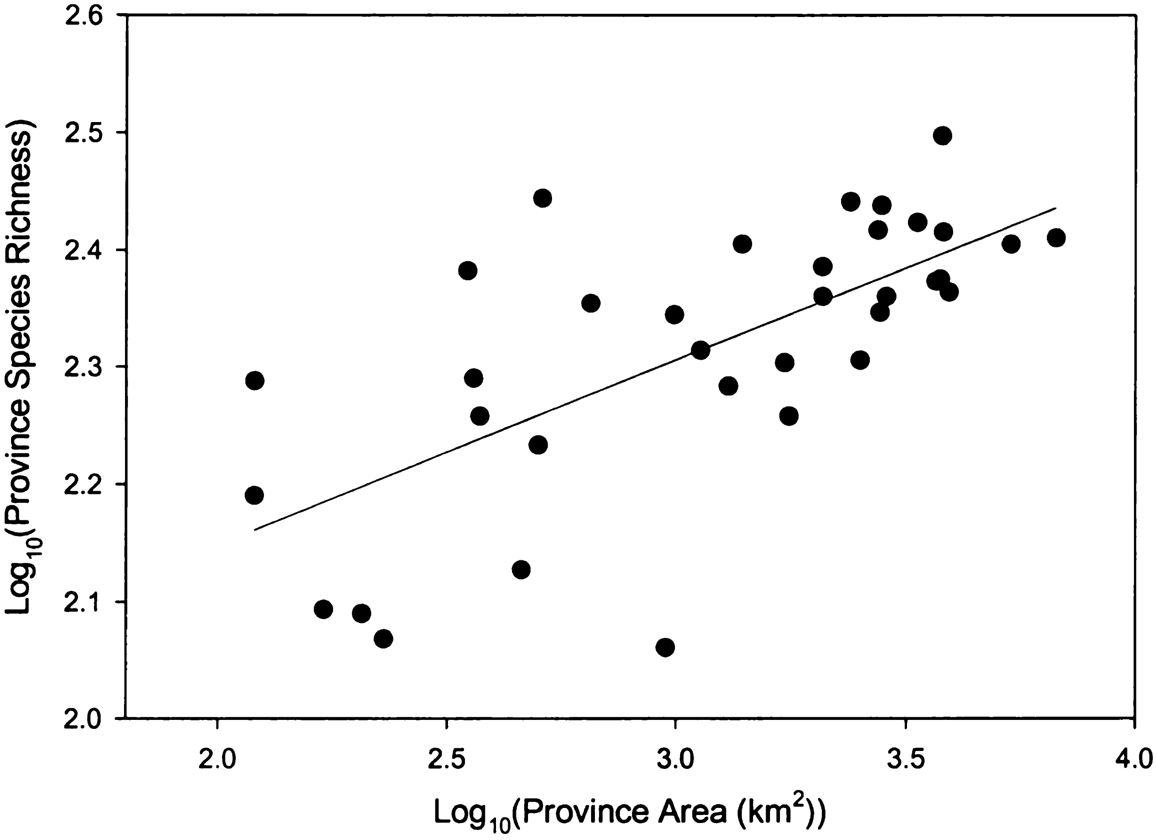


Figure 4.4. Province species richness vs. area ($km^2$) (n = 35) with least squares linear regression ($r^2 = 0.461$).

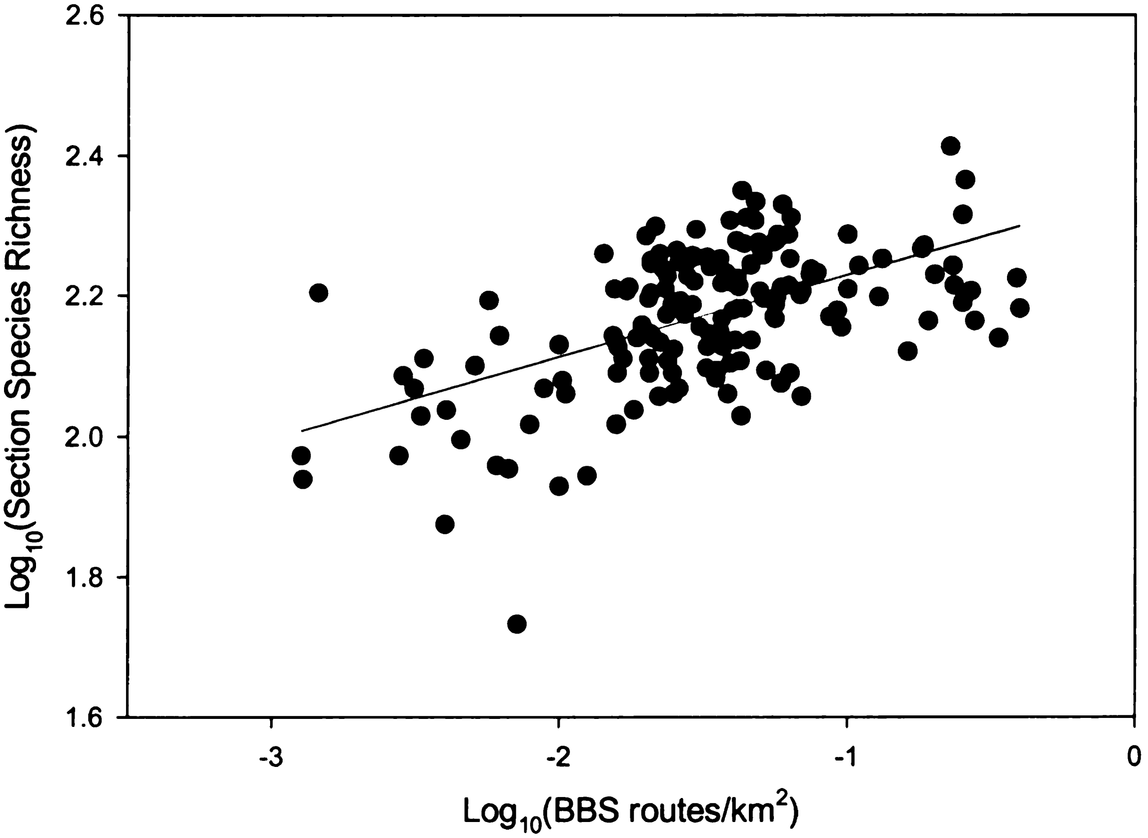


Figure 4.5. Species richness and sampling intensity (BBS routes/km$^2$) for sections (n = 162) with least squares linear regression ($r^2 = 0.313$).

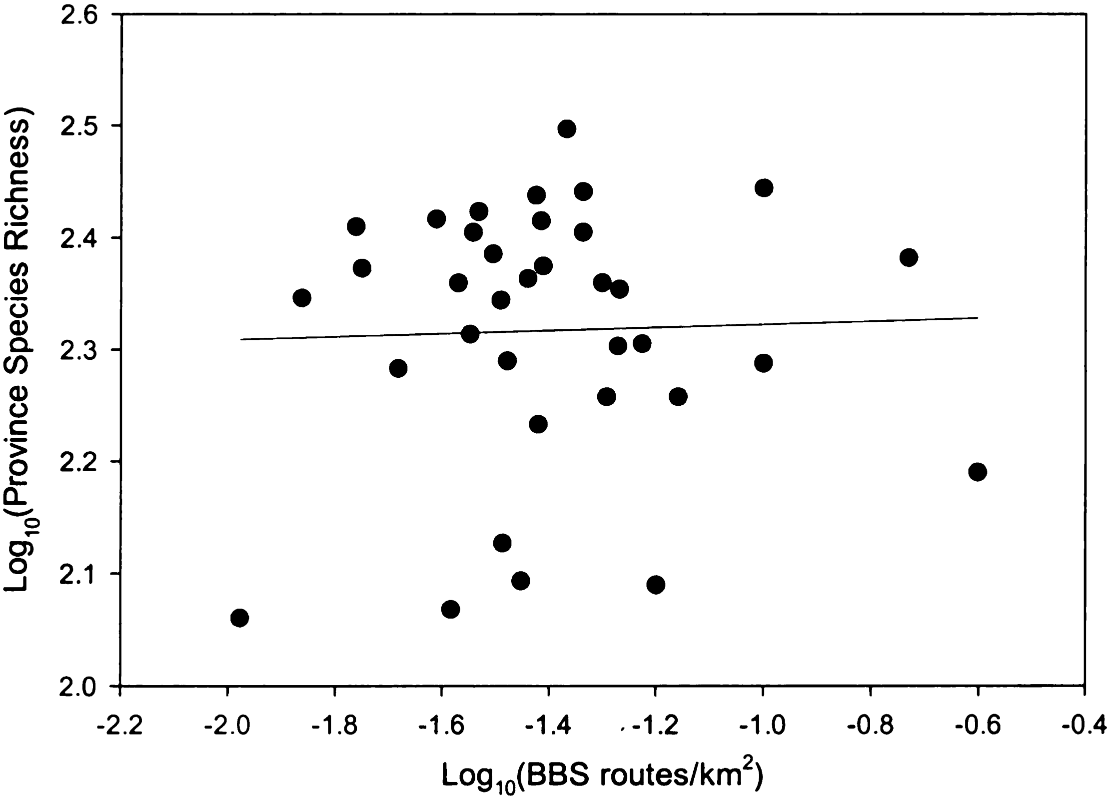


Figure 4.6. Species richness and sampling intensity (BBS routes/km$^2$) for provinces (n = 35) with least squares linear regression ($r^2 = 0.001$).

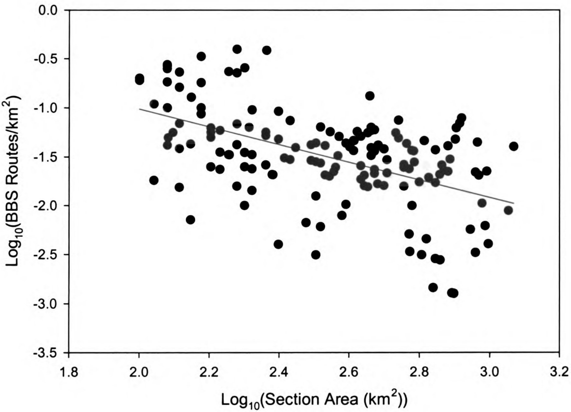


Figure 4.7. Sampling intensity (BBS routes/km$^2$) vs. area for sections (n = 162) with least squares linear regression ($r^2 = 0.273$).

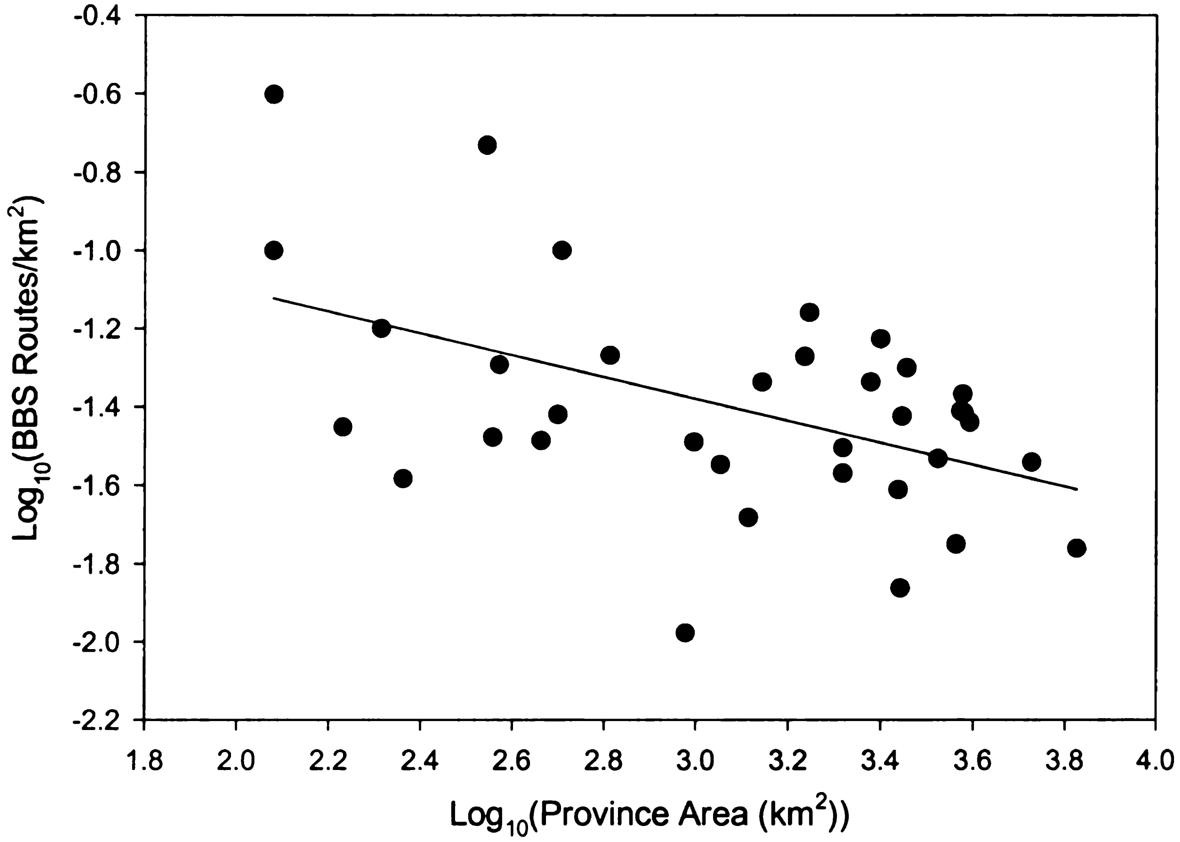


Figure 4.8. Sampling intensity (BBS routes/km$^2$) vs. area for provinces (n = 35) with least squares linear regression ($r^2$ = 0.248).

# CONCLUSIONS

## Patterns of Biological Diversity

The results of my dissertation illustrate several patterns of biological diversity. In both Chapter 2 and 3, avian species assemblages from eastern North America were shown to exhibit discontinuous distributions of body masses. These patterns are robust; with similar discontinuities identified using multiple methods. In Chapter 2 I identified the potential ecological correlates of discontinuities in body mass distributions for the birds of these assemblages. Declining species typically had body masses that placed them near the discontinuities in the body mass spectra. This suggests that in a species assemblage, having such a body mass presents challenges to maintaining a viable population. Non-indigenous species typically had body masses that placed them far from discontinuities in the body mass spectra, suggesting that the body mass of a species may be a factor in determining the ability of a species to successfully invade an ecosystem. The species composition of birds across the contiguous United States was analyzed in Chapter 4. Using seven different beta-diversity metrics, I compared the composition of species assemblages in 162 sections. The results showed that the distribution of bird species is spatially autocorrelated, with sections closer together having assemblages that are more similar in composition than those of sections that are farther apart.

## Patterns of Landscape Structure

The structure of landscapes can be described with many different metrics, not all of which are useful to understanding patterns of biodiversity. Chapter 1 identifies those metrics that are most likely to affect the formation and maintenance of species assemblages. Using some of these metrics (diversity, dominance, and lacunarity), the land cover of six sections of eastern North America was characterized in Chapter 3. As described in Chapter 2, the activities of humans tend to homogenize landscapes. The results of Chapter 3 showing that agriculturally dominated landscapes had the lowest diversity and highest dominance values were not surprising. Lacunarity, which can identify the presence of hierarchical structure in landscapes, was used to describe the heterogeneity of the distribution of forest and non-forest habitat in eastern North America. Forest habitat was found to be quite homogeneously distributed in most sections, but more heterogeneously distributed in areas dominated by agriculture. Unlike the non-forest habitat lacunarity curves, the forest habitat lacunarity curves were all quite smooth, indicating that there were few discontinuities in the structure of forest habitat in any of the areas analyzed.

## Correspondence of Landscape Structure and Biodiversity

Though it has long been known that the spatial pattern of landscape elements can affect ecological processes occurring in landscapes, it has been difficult to quantify these links between pattern and process. Lacunarity analysis provided me with a means of testing such a proposed link, the entrainment of species attributes by the structure of the landscape. In Chapter 3 I used lacunarity to test the hypothesis that the distribution of discontinuities in body mass would correspond to the discontinuities in landscape structure. Though the results presented in Chapter 3 do not support such a correspondence, they do suggest several directions for future research. In Chapter 4 I tested the hypothesis that the spatial distribution of ecoregions corresponds to the distribution of avian taxa. I found that ecoregions could not be recreated based on the composition of avian species assemblages, showing that the distribution of North American bird species is independent of the distribution of ecoregions defined on the basis of climate, soils, and natural vegetation.

## Future Directions

The results of this dissertation suggest several directions for future research. I am interested in determining if the ecological consequences of discontinuities in the body mass distributions identified in Chapter 2 will be found in other regions and with other taxa. Analysis of different types of non-indigenous species (*e.g.* those that are established vs. those that are still actively invading, "natural" invaders vs. human-introduced species) and declining species (*e.g.* those that have already been extirpated from a region vs. those that are currently declining) may reveal different patterns. The results of Chapter 2 suggested that ecological consequences may vary depending on the amount of human impact and landscape homogenization, but this has not yet been quantitatively investigated.

The use of lacunarity analysis to quantify the link between landscape structure and biodiversity patterns is promising. However, based on the results of Chapter 3, modifying the APACK software program used to calculate lacunarity could more accurately reflect the spatial pattern of habitat in the landscape of interest. Additionally, the spatial distribution of habitat types other than upland forest should also be examined.

# APPENDIX A: SPECIES LISTS

Table A.1. Species list for section 47, the Central Till Plains, Oak-Hickory Section.

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 02890 | Northern Bobwhite | *Colinus virginianus* | 178.0 |
| 03050 | Greater Prairie-Chicken | *Tympanuchus cupido* | 999.0 |
| 03091 | Ring-necked Pheasant | *Phasianus colchicus* | 1317.0 |
| 03100 | Wild Turkey | *Meleagris gallopavo* | 7400.0 |
| 03131 | Rock Dove | *Columba livia* | 369.0 |
| 03160 | Mourning Dove | *Zenaida macroura* | 123.0 |
| 03250 | Turkey Vulture | *Cathartes aura* | 1467.0 |
| 03310 | Northern Harrier | *Circus cyaneus* | 358.0 |
| 03330 | Cooper's Hawk | *Accipiter cooperii* | 349.0 |
| 03370 | Red-tailed Hawk | *Buteo jamaicensis* | 1028.0 |
| 03390 | Red-shouldered Hawk | *Buteo lineatus* | 475.0 |
| 03600 | American Kestrel | *Falco sparverius* | 111.0 |
| 03680 | Barred Owl | *Strix varia* | 632.0 |
| 03730 | Eastern Screech-Owl | *Otus asio* | 174.0 |
| 03750 | Great Horned Owl | *Bubo virginianus* | 1318.0 |
| 03870 | Yellow-billed Cuckoo | *Coccyzus americanus* | 64.0 |
| 03880 | Black-billed Cuckoo | *Coccyzus erythropthalmus* | 51.1 |
| 03900 | Belted Kingfisher | *Ceryle alcyon* | 148.0 |
| 03930 | Hairy Woodpecker | *Picoides villosus* | 70.0 |
| 03940 | Downy Woodpecker | *Picoides pubescens* | 27.0 |

Table A.1 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04050 | Pileated Woodpecker | *Dryocopus pileatus* | 308.0 |
| 04060 | Red-headed Woodpecker | *Melanerpes erythrocephalus* | 71.6 |
| 04090 | Red-bellied Woodpecker | *Melanerpes carolinus* | 67.2 |
| 04120 | Northern Flicker | *Colaptes auratus* | 135.0 |
| 04170 | Whip-poor-will | *Caprimulgus vociferus* | 55.3 |
| 04200 | Common Nighthawk | *Chordeiles minor* | 61.5 |
| 04230 | Chimney Swift | *Chaetura pelagica* | 23.6 |
| 04280 | Ruby-throated Hummingbird | *Archilochus colubris* | 3.0 |
| 04440 | Eastern Kingbird | *Tyrannus tyrannus* | 43.6 |
| 04470 | Western Kingbird | *Tyrannus verticalis* | 39.6 |
| 04520 | Great Crested Flycatcher | *Myiarchus crinitus* | 33.5 |
| 04560 | Eastern Phoebe | *Sayornis phoebe* | 19.8 |
| 04610 | Eastern Wood-Pewee | *Contopus virens* | 14.1 |
| 04650 | Acadian Flycatcher | *Empidonax virescens* | 12.9 |
| 04660 | Willow Flycatcher | *Empidonax traillii* | 13.1 |
| 04670 | Least Flycatcher | *Empidonax minimus* | 10.3 |
| 04740 | Horned Lark | *Eremophila alpestris* | 31.9 |
| 04770 | Blue Jay | *Cyanocitta cristata* | 86.8 |
| 04880 | American Crow | *Corvus brachyrhynchos* | 458.0 |
| 04930 | European Starling | *Sturnus vulgaris* | 84.7 |

Table A.1 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04940 | Bobolink | *Dolichonyx oryzivorus* | 47.0 |
| 04950 | Brown-headed Cowbird | *Molothrus ater* | 49.0 |
| 04970 | Yellow-headed Blackbird | *Xanthocephalus xanthocephalus* | 79.7 |
| 04980 | Red-winged Blackbird | *Agelaius phoeniceus* | 63.6 |
| 05010 | Eastern Meadowlark | *Sturnella magna* | 102.0 |
| 05011 | Western Meadowlark | *Sturnella neglecta* | 112.0 |
| 05060 | Orchard Oriole | *Icterus spurius* | 19.6 |
| 05070 | Baltimore Oriole | *Icterus galbula* | 34.3 |
| 05110 | Common Grackle | *Quiscalus quiscula* | 127.0 |
| 05190 | House Finch | *Carpodacus mexicanus* | 21.4 |
| 05290 | American Goldfinch | *Carduelis tristis* | 13.2 |
| 05400 | Vesper Sparrow | *Pooecetes gramineus* | 26.5 |
| 05420 | Savannah Sparrow | *Passerculus sandwichensis* | 20.6 |
| 05460 | Grasshopper Sparrow | *Ammodramus savannarum* | 17.0 |
| 05520 | Lark Sparrow | *Chondestes grammacus* | 29.0 |
| 05600 | Chipping Sparrow | *Spizella passerina* | 12.3 |
| 05630 | Field Sparrow | *Spizella pusilla* | 12.5 |
| 05810 | Song Sparrow | *Melospiza melodia* | 21.0 |
| 05870 | Eastern Towhee | *Pipilo erythrophthalmus* | 41.7 |
| 05930 | Northern Cardinal | *Cardinalis cardinalis* | 45.4 |

Table A.1 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 05950 | Rose-breasted Grosbeak | *Pheucticus ludovicianus* | 45.6 |
| 05970 | Blue Grosbeak | *Guiraca caerulea* | 29.3 |
| 05980 | Indigo Bunting | *Passerina cyanea* | 14.9 |
| 06040 | Dickcissel | *Spiza americana* | 29.3 |
| 06080 | Scarlet Tanager | *Piranga olivacea* | 28.6 |
| 06100 | Summer Tanager | *Piranga rubra* | 28.2 |
| 06110 | Purple Martin | *Progne subis* | 49.4 |
| 06120 | Cliff Swallow | *Hirundo pyrrhonota* | 21.6 |
| 06130 | Barn Swallow | *Hirundo rustica* | 16.2 |
| 06140 | Tree Swallow | *Tachycineta bicolor* | 20.1 |
| 06160 | Bank Swallow | *Riparia riparia* | 14.6 |
| 06170 | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* | 15.9 |
| 06190 | Cedar Waxwing | *Bombycilla cedrorum* | 30.6 |
| 06220 | Loggerhead Shrike | *Lanius ludovicianus* | 47.4 |
| 06240 | Red-eyed Vireo | *Vireo olivaceus* | 16.7 |
| 06270 | Warbling Vireo | *Vireo gilvus* | 14.8 |
| 06280 | Yellow-throated Vireo | *Vireo flavifrons* | 18.0 |
| 06310 | White-eyed Vireo | *Vireo griseus* | 11.4 |
| 06330 | Bell's Vireo | *Vireo bellii* | 8.5 |
| 06360 | Black-and-white Warbler | *Mniotilta varia* | 11.0 |

Table A.1 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06370 | Prothonotary Warbler | *Protonotaria citrea* | 14.3 |
| 06410 | Blue-winged Warbler | *Vermivora pinus* | 8.4 |
| 06480 | Northern Parula | *Parula americana* | 8.6 |
| 06520 | Yellow Warbler | *Dendroica petechia* | 9.8 |
| 06580 | Cerulean Warbler | *Dendroica cerulea* | 9.5 |
| 06630 | Yellow-throated Warbler | *Dendroica dominica* | 9.4 |
| 06710 | Pine Warbler | *Dendroica pinus* | 11.9 |
| 06730 | Prairie Warbler | *Dendroica discolor* | 8.0 |
| 06740 | Ovenbird | *Seiurus aurocapillus* | 19.4 |
| 06770 | Kentucky Warbler | *Oporornis formosus* | 14.3 |
| 06810 | Common Yellowthroat | *Geothlypis trichas* | 10.1 |
| 06830 | Yellow-breasted Chat | *Icteria virens* | 25.5 |
| 06840 | Hooded Warbler | *Wilsonia citrina* | 10.8 |
| 06870 | American Redstart | *Setophaga ruticilla* | 8.5 |
| 06882 | House Sparrow | *Passer domesticus* | 28.0 |
| 06883 | Eurasian Tree Sparrow | *Passer montanus* | 22.0 |
| 07030 | Northern Mockingbird | *Mimus polyglottos* | 48.5 |
| 07040 | Gray Catbird | *Dumetella carolinensis* | 36.9 |
| 07050 | Brown Thrasher | *Toxostoma rufum* | 68.8 |
| 07180 | Carolina Wren | *Thryothorus ludovicianus* | 18.7 |

Table A.1 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 07210 | House Wren | *Troglodytes aedon* | 10.9 |
| 07240 | Sedge Wren | *Cistothorus platensis* | 9.0 |
| 07270 | White-breasted Nuthatch | *Sitta carolinensis* | 21.1 |
| 07310 | Tufted Titmouse | *Parus bicolor* | 21.6 |
| 07350 | Black-capped Chickadee | *Parus atricapillus* | 10.8 |
| 07360 | Carolina Chickadee | *Parus carolinensis* | 10.5 |
| 07510 | Blue-gray Gnatcatcher | *Polioptila caerulea* | 6.0 |
| 07550 | Wood Thrush | *Hylocichla mustelina* | 47.8 |
| 07610 | American Robin | *Turdus migratorius* | 77.3 |
| 07660 | Eastern Bluebird | *Sialia sialis* | 31.6 |
| 03260 | Black Vulture | *Coragyps atratus* | 2172.0 |
| 05470 | Henslow's Sparrow | *Ammodramus henslowii* | 13.1 |
| 06760 | Louisiana Waterthrush | *Seiurus motacilla* | 19.8 |

Table A.2. Species list for section 59, the Central Ridge and Valley Section.

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 02890 | Northern Bobwhite | *Colinus virginianus* | 178.0 |
| 03000 | Ruffed Grouse | *Bonasa umbellus* | 621.0 |
| 03100 | Wild Turkey | *Meleagris gallopavo* | 7400.0 |
| 03131 | Rock Dove | *Columba livia* | 369.0 |
| 03160 | Mourning Dove | *Zenaida macroura* | 123.0 |
| 03250 | Turkey Vulture | *Cathartes aura* | 1467.0 |
| 03260 | Black Vulture | *Coragyps atratus* | 2172.0 |
| 03320 | Sharp-shinned Hawk | *Accipiter striatus* | 103.0 |
| 03330 | Cooper's Hawk | *Accipiter cooperii* | 349.0 |
| 03370 | Red-tailed Hawk | *Buteo jamaicensis* | 1028.0 |
| 03390 | Red-shouldered Hawk | *Buteo lineatus* | 475.0 |
| 03430 | Broad-winged Hawk | *Buteo platypterus* | 420.0 |
| 03600 | American Kestrel | *Falco sparverius* | 111.0 |
| 03680 | Barred Owl | *Strix varia* | 632.0 |
| 03730 | Eastern Screech-Owl | *Otus asio* | 174.0 |
| 03750 | Great Horned Owl | *Bubo virginianus* | 1318.0 |
| 03870 | Yellow-billed Cuckoo | *Coccyzus americanus* | 64.0 |
| 03900 | Belted Kingfisher | *Ceryle alcyon* | 148.0 |
| 03930 | Hairy Woodpecker | *Picoides villosus* | 70.0 |
| 03940 | Downy Woodpecker | *Picoides pubescens* | 27.0 |

Table A.2 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04050 | Pileated Woodpecker | *Dryocopus pileatus* | 308.0 |
| 04060 | Red-headed Woodpecker | *Melanerpes erythrocephalus* | 71.6 |
| 04090 | Red-bellied Woodpecker | *Melanerpes carolinus* | 67.2 |
| 04120 | Northern Flicker | *Colaptes auratus* | 135.0 |
| 04160 | Chuck-will's-widow | *Caprimulgus carolinensis* | 120.0 |
| 04170 | Whip-poor-will | *Caprimulgus vociferus* | 55.3 |
| 04200 | Common Nighthawk | *Chordeiles minor* | 61.5 |
| 04230 | Chimney Swift | *Chaetura pelagica* | 23.6 |
| 04280 | Ruby-throated Hummingbird | *Archilochus colubris* | 3.0 |
| 04440 | Eastern Kingbird | *Tyrannus tyrannus* | 43.6 |
| 04520 | Great Crested Flycatcher | *Myiarchus crinitus* | 33.5 |
| 04560 | Eastern Phoebe | *Sayornis phoebe* | 19.8 |
| 04610 | Eastern Wood-Pewee | *Contopus virens* | 14.1 |
| 04650 | Acadian Flycatcher | *Empidonax virescens* | 12.9 |
| 04660 | Willow Flycatcher | *Empidonax traillii* | 13.1 |
| 04740 | Horned Lark | *Eremophila alpestris* | 31.9 |
| 04770 | Blue Jay | *Cyanocitta cristata* | 86.8 |
| 04880 | American Crow | *Corvus brachyrhynchos* | 458.0 |
| 04930 | European Starling | *Sturnus vulgaris* | 84.7 |
| 04950 | Brown-headed Cowbird | *Molothrus ater* | 49.0 |

Table A.2 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04980 | Red-winged Blackbird | *Agelaius phoeniceus* | 63.6 |
| 05010 | Eastern Meadowlark | *Sturnella magna* | 102.0 |
| 05060 | Orchard Oriole | *Icterus spurius* | 19.6 |
| 05070 | Baltimore Oriole | *Icterus galbula* | 34.3 |
| 05110 | Common Grackle | *Quiscalus quiscula* | 127.0 |
| 05190 | House Finch | *Carpodacus mexicanus* | 21.4 |
| 05290 | American Goldfinch | *Carduelis tristis* | 13.2 |
| 05460 | Grasshopper Sparrow | *Ammodramus savannarum* | 17.0 |
| 05600 | Chipping Sparrow | *Spizella passerina* | 12.3 |
| 05630 | Field Sparrow | *Spizella pusilla* | 12.5 |
| 05810 | Song Sparrow | *Melospiza melodia* | 21.0 |
| 05870 | Eastern Towhee | *Pipilo erythrophthalmus* | 41.7 |
| 05930 | Northern Cardinal | *Cardinalis cardinalis* | 45.4 |
| 05950 | Rose-breasted Grosbeak | *Pheucticus ludovicianus* | 45.6 |
| 05970 | Blue Grosbeak | *Guiraca caerulea* | 29.3 |
| 05980 | Indigo Bunting | *Passerina cyanea* | 14.9 |
| 06040 | Dickcissel | *Spiza americana* | 29.3 |
| 06080 | Scarlet Tanager | *Piranga olivacea* | 28.6 |
| 06100 | Summer Tanager | *Piranga rubra* | 28.2 |
| 06110 | Purple Martin | *Progne subis* | 49.4 |

Table A.2 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06130 | Barn Swallow | *Hirundo rustica* | 16.2 |
| 06140 | Tree Swallow | *Tachycineta bicolor* | 20.1 |
| 06160 | Bank Swallow | *Riparia riparia* | 14.6 |
| 06170 | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* | 15.9 |
| 06190 | Cedar Waxwing | *Bombycilla cedrorum* | 30.6 |
| 06220 | Loggerhead Shrike | *Lanius ludovicianus* | 47.4 |
| 06240 | Red-eyed Vireo | *Vireo olivaceus* | 16.7 |
| 06280 | Yellow-throated Vireo | *Vireo flavifrons* | 18.0 |
| 06290 | Blue-headed Vireo | *Vireo solitarius* | 16.6 |
| 06310 | White-eyed Vireo | *Vireo griseus* | 11.4 |
| 06360 | Black-and-white Warbler | *Mniotilta varia* | 11.0 |
| 06370 | Prothonotary Warbler | *Protonotaria citrea* | 15.0 |
| 06380 | Swainson's Warbler | *Limnothlypis swainsonii* | 18.9 |
| 06390 | Worm-eating Warbler | *Helmitheros vermivorus* | 13.0 |
| 06410 | Blue-winged Warbler | *Vermivora pinus* | 8.4 |
| 06420 | Golden-winged Warbler | *Vermivora chrysoptera* | 8.7 |
| 06480 | Northern Parula | *Parula americana* | 8.6 |
| 06520 | Yellow Warbler | *Dendroica petechia* | 9.8 |
| 06580 | Cerulean Warbler | *Dendroica cerulea* | 9.5 |
| 06630 | Yellow-throated Warbler | *Dendroica dominica* | 9.4 |

Table A.2 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06670 | Black-throated Green Warbler | *Dendroica virens* | 8.8 |
| 06710 | Pine Warbler | *Dendroica pinus* | 11.9 |
| 06730 | Prairie Warbler | *Dendroica discolor* | 8.0 |
| 06740 | Ovenbird | *Seiurus aurocapillus* | 19.4 |
| 06760 | Louisiana Waterthrush | *Seiurus motacilla* | 19.8 |
| 06770 | Kentucky Warbler | *Oporornis formosus* | 14.3 |
| 06810 | Common Yellowthroat | *Geothlypis trichas* | 10.1 |
| 06830 | Yellow-breasted Chat | *Icteria virens* | 25.5 |
| 06840 | Hooded Warbler | *Wilsonia citrina* | 10.8 |
| 06870 | American Redstart | *Setophaga ruticilla* | 8.5 |
| 06882 | House Sparrow | *Passer domesticus* | 28.0 |
| 07030 | Northern Mockingbird | *Mimus polyglottos* | 48.5 |
| 07040 | Gray Catbird | *Dumetella carolinensis* | 36.9 |
| 07050 | Brown Thrasher | *Toxostoma rufum* | 68.8 |
| 07180 | Carolina Wren | *Thryothorus ludovicianus* | 18.7 |
| 07190 | Bewick's Wren | *Thryomanes bewickii* | 9.9 |
| 07210 | House Wren | *Troglodytes aedon* | 10.9 |
| 07270 | White-breasted Nuthatch | *Sitta carolinensis* | 21.1 |
| 07310 | Tufted Titmouse | *Parus bicolor* | 21.6 |
| 07360 | Carolina Chickadee | *Parus carolinensis* | 10.5 |

Table A.2 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 07510 | Blue-gray Gnatcatcher | *Polioptila caerulea* | 6.0 |
| 07550 | Wood Thrush | *Hylocichla mustelina* | 47.8 |
| 07610 | American Robin | *Turdus migratorius* | 77.3 |
| 07660 | Eastern Bluebird | *Sialia sialis* | 31.6 |

Table A.3. Species list for section 133, the Coastal Plains and Flatwoods, Western Gulf Section.

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 02890 | Northern Bobwhite | *Colinus virginianus* | 178.0 |
| 03100 | Wild Turkey | *Meleagris gallopavo* | 7400.0 |
| 03131 | Rock Dove | *Columba livia* | 369.0 |
| 03160 | Mourning Dove | *Zenaida macroura* | 123.0 |
| 03210 | Inca Dove | *Columbina inca* | 47.5 |
| 03250 | Turkey Vulture | *Cathartes aura* | 1467.0 |
| 03260 | Black Vulture | *Coragyps atratus* | 2172.0 |
| 03270 | Swallow-tailed Kite | *Elanoides forficatus* | 442.0 |
| 03290 | Mississippi Kite | *Ictinia mississippiensis* | 245.0 |
| 03330 | Cooper's Hawk | *Accipiter cooperii* | 349.0 |
| 03370 | Red-tailed Hawk | *Buteo jamaicensis* | 1028.0 |
| 03390 | Red-shouldered Hawk | *Buteo lineatus* | 475.0 |
| 03430 | Broad-winged Hawk | *Buteo platypterus* | 420.0 |
| 03600 | American Kestrel | *Falco sparverius* | 111.0 |
| 03620 | Crested Caracara | *Caracara plancus* | 1117.0 |
| 03680 | Barred Owl | *Strix varia* | 632.0 |
| 03730 | Eastern Screech-Owl | *Otus asio* | 174.0 |
| 03750 | Great Horned Owl | *Bubo virginianus* | 1318.0 |
| 03850 | Greater Roadrunner | *Geococcyx californianus* | 376.0 |
| 03870 | Yellow-billed Cuckoo | *Coccyzus americanus* | 64.0 |

Table A.3 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 03900 | Belted Kingfisher | *Ceryle alcyon* | 148.0 |
| 03930 | Hairy Woodpecker | *Picoides villosus* | 70.0 |
| 03940 | Downy Woodpecker | *Picoides pubescens* | 27.0 |
| 03950 | Red-cockaded Woodpecker | *Picoides borealis* | 43.6 |
| 04050 | Pileated Woodpecker | *Dryocopus pileatus* | 308.0 |
| 04060 | Red-headed Woodpecker | *Melanerpes erythrocephalus* | 71.6 |
| 04090 | Red-bellied Woodpecker | *Melanerpes carolinus* | 67.2 |
| 04120 | Northern Flicker | *Colaptes auratus* | 135.0 |
| 04160 | Chuck-will's-widow | *Caprimulgus carolinensis* | 120.0 |
| 04200 | Common Nighthawk | *Chordeiles minor* | 61.5 |
| 04230 | Chimney Swift | *Chaetura pelagica* | 23.6 |
| 04280 | Ruby-throated Hummingbird | *Archilochus colubris* | 3.0 |
| 04430 | Scissor-tailed Flycatcher | *Tyrannus forficatus* | 43.2 |
| 04440 | Eastern Kingbird | *Tyrannus tyrannus* | 43.6 |
| 04520 | Great Crested Flycatcher | *Myiarchus crinitus* | 33.5 |
| 04560 | Eastern Phoebe | *Sayornis phoebe* | 19.8 |
| 04610 | Eastern Wood-Pewee | *Contopus virens* | 14.1 |
| 04650 | Acadian Flycatcher | *Empidonax virescens* | 12.9 |
| 04770 | Blue Jay | *Cyanocitta cristata* | 86.8 |
| 04880 | American Crow | *Corvus brachyrhynchos* | 458.0 |

Table A.3 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04900 | Fish Crow | *Corvus ossifragus* | 300.0 |
| 04930 | European Starling | *Sturnus vulgaris* | 84.7 |
| 04950 | Brown-headed Cowbird | *Molothrus ater* | 49.0 |
| 04980 | Red-winged Blackbird | *Agelaius phoeniceus* | 63.6 |
| 05010 | Eastern Meadowlark | *Sturnella magna* | 102.0 |
| 05060 | Orchard Oriole | *Icterus spurius* | 19.6 |
| 05070 | Baltimore Oriole | *Icterus galbula* | 34.3 |
| 05110 | Common Grackle | *Quiscalus quiscula* | 127.0 |
| 05130 | Boat-tailed Grackle | *Quiscalus major* | 214.0 |
| 05190 | House Finch | *Carpodacus mexicanus* | 21.4 |
| 05460 | Grasshopper Sparrow | *Ammodramus savannarum* | 17.0 |
| 05520 | Lark Sparrow | *Chondestes grammacus* | 29.0 |
| 05600 | Chipping Sparrow | *Spizella passerina* | 12.3 |
| 05630 | Field Sparrow | *Spizella pusilla* | 12.5 |
| 05750 | Bachman's Sparrow | *Aimophila aestivalis* | 20.2 |
| 05870 | Eastern Towhee | *Pipilo erythrophthalmus* | 41.7 |
| 05930 | Northern Cardinal | *Cardinalis cardinalis* | 45.4 |
| 05970 | Blue Grosbeak | *Guiraca caerulea* | 29.3 |
| 05980 | Indigo Bunting | *Passerina cyanea* | 14.9 |
| 06010 | Painted Bunting | *Passerina ciris* | 16.1 |

Table A.3 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06040 | Dickcissel | *Spiza americana* | 29.3 |
| 06100 | Summer Tanager | *Piranga rubra* | 28.2 |
| 06110 | Purple Martin | *Progne subis* | 49.4 |
| 06120 | Cliff Swallow | *Hirundo pyrrhonota* | 21.6 |
| 06130 | Barn Swallow | *Hirundo rustica* | 16.2 |
| 06170 | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* | 15.9 |
| 06220 | Loggerhead Shrike | *Lanius ludovicianus* | 47.4 |
| 06240 | Red-eyed Vireo | *Vireo olivaceus* | 16.7 |
| 06270 | Warbling Vireo | *Vireo gilvus* | 14.8 |
| 06280 | Yellow-throated Vireo | *Vireo flavifrons* | 18.0 |
| 06310 | White-eyed Vireo | *Vireo griseus* | 11.4 |
| 06360 | Black-and-white Warbler | *Mniotilta varia* | 11.0 |
| 06370 | Prothonotary Warbler | *Protonotaria citrea* | 15.0 |
| 06380 | Swainson's Warbler | *Limnothlypis swainsonii* | 18.9 |
| 06390 | Worm-eating Warbler | *Helmitheros vermivorus* | 13.0 |
| 06480 | Northern Parula | *Parula americana* | 8.6 |
| 06630 | Yellow-throated Warbler | *Dendroica dominica* | 9.4 |
| 06710 | Pine Warbler | *Dendroica pinus* | 11.9 |
| 06730 | Prairie Warbler | *Dendroica discolor* | 8.0 |
| 06760 | Louisiana Waterthrush | *Seiurus motacilla* | 19.8 |

Table A.3 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06770 | Kentucky Warbler | *Oporornis formosus* | 14.3 |
| 06810 | Common Yellowthroat | *Geothlypis trichas* | 10.1 |
| 06830 | Yellow-breasted Chat | *Icteria virens* | 25.5 |
| 06840 | Hooded Warbler | *Wilsonia citrina* | 10.8 |
| 06870 | American Redstart | *Setophaga ruticilla* | 8.5 |
| 06882 | House Sparrow | *Passer domesticus* | 28.0 |
| 07030 | Northern Mockingbird | *Mimus polyglottos* | 48.5 |
| 07040 | Gray Catbird | *Dumetella carolinensis* | 36.9 |
| 07050 | Brown Thrasher | *Toxostoma rufum* | 68.8 |
| 07180 | Carolina Wren | *Thryothorus ludovicianus* | 18.7 |
| 07270 | White-breasted Nuthatch | *Sitta carolinensis* | 21.1 |
| 07290 | Brown-headed Nuthatch | *Sitta pusilla* | 10.2 |
| 07310 | Tufted Titmouse | *Parus bicolor* | 21.6 |
| 07360 | Carolina Chickadee | *Parus carolinensis* | 10.5 |
| 07510 | Blue-gray Gnatcatcher | *Polioptila caerulea* | 6.0 |
| 07550 | Wood Thrush | *Hylocichla mustelina* | 47.8 |
| 07610 | American Robin | *Turdus migratorius* | 77.3 |
| 07660 | Eastern Bluebird | *Sialia sialis* | 31.6 |

Table A.4. Species list for section 153, the Central Loess Plains Section.

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 02881 | Gray Partridge | *Perdix perdix* | 398.0 |
| 02890 | Northern Bobwhite | *Colinus virginianus* | 178.0 |
| 03050 | Greater Prairie-Chicken | *Tympanuchus cupido* | 999.0 |
| 03091 | Ring-necked Pheasant | *Phasianus colchicus* | 1317.0 |
| 03100 | Wild Turkey | *Meleagris gallopavo* | 7400.0 |
| 03131 | Rock Dove | *Columba livia* | 369.0 |
| 03160 | Mourning Dove | *Zenaida macroura* | 123.0 |
| 03250 | Turkey Vulture | *Cathartes aura* | 1467.0 |
| 03310 | Northern Harrier | *Circus cyaneus* | 358.0 |
| 03320 | Sharp-shinned Hawk | *Accipiter striatus* | 103.0 |
| 03330 | Cooper's Hawk | *Accipiter cooperii* | 349.0 |
| 03370 | Red-tailed Hawk | *Buteo jamaicensis* | 1028.0 |
| 03390 | Red-shouldered Hawk | *Buteo lineatus* | 475.0 |
| 03420 | Swainson's Hawk | *Buteo swainsoni* | 908.0 |
| 03430 | Broad-winged Hawk | *Buteo platypterus* | 420.0 |
| 03600 | American Kestrel | *Falco sparverius* | 111.0 |
| 03670 | Short-eared Owl | *Asio flammeus* | 315.0 |
| 03680 | Barred Owl | *Strix varia* | 632.0 |
| 03730 | Eastern Screech-Owl | *Otus asio* | 174.0 |
| 03750 | Great Horned Owl | *Bubo virginianus* | 1318.0 |

Table A.4 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 03870 | Yellow-billed Cuckoo | *Coccyzus americanus* | 64.0 |
| 03880 | Black-billed Cuckoo | *Coccyzus erythropthalmus* | 51.1 |
| 03900 | Belted Kingfisher | *Ceryle alcyon* | 148.0 |
| 03930 | Hairy Woodpecker | *Picoides villosus* | 70.0 |
| 03940 | Downy Woodpecker | *Picoides pubescens* | 27.0 |
| 04050 | Pileated Woodpecker | *Dryocopus pileatus* | 308.0 |
| 04060 | Red-headed Woodpecker | *Melanerpes erythrocephalus* | 71.6 |
| 04090 | Red-bellied Woodpecker | *Melanerpes carolinus* | 67.2 |
| 04120 | Northern Flicker | *Colaptes auratus* | 135.0 |
| 04170 | Whip-poor-will | *Caprimulgus vociferus* | 55.3 |
| 04200 | Common Nighthawk | *Chordeiles minor* | 61.5 |
| 04230 | Chimney Swift | *Chaetura pelagica* | 23.6 |
| 04280 | Ruby-throated Hummingbird | *Archilochus colubris* | 3.0 |
| 04430 | Scissor-tailed Flycatcher | *Tyrannus forficatus* | 43.2 |
| 04440 | Eastern Kingbird | *Tyrannus tyrannus* | 43.6 |
| 04470 | Western Kingbird | *Tyrannus verticalis* | 39.6 |
| 04520 | Great Crested Flycatcher | *Myiarchus crinitus* | 33.5 |
| 04560 | Eastern Phoebe | *Sayornis phoebe* | 19.8 |
| 04570 | Say's Phoebe | *Sayornis saya* | 21.2 |
| 04610 | Eastern Wood-Pewee | *Contopus virens* | 14.1 |

Table A.4 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04650 | Acadian Flycatcher | *Empidonax virescens* | 12.9 |
| 04660 | Willow Flycatcher | *Empidonax traillii* | 13.1 |
| 04661 | Alder Flycatcher | *Empidonax alnorum* | 12.7 |
| 04670 | Least Flycatcher | *Empidonax minimus* | 10.3 |
| 04740 | Horned Lark | *Eremophila alpestris* | 31.9 |
| 04750 | Black-billed Magpie | *Pica pica* | 189.0 |
| 04770 | Blue Jay | *Cyanocitta cristata* | 86.8 |
| 04880 | American Crow | *Corvus brachyrhynchos* | 458.0 |
| 04930 | European Starling | *Sturnus vulgaris* | 84.7 |
| 04940 | Bobolink | *Dolichonyx oryzivorus* | 47.0 |
| 04950 | Brown-headed Cowbird | *Molothrus ater* | 49.0 |
| 04970 | Yellow-headed Blackbird | *Xanthocephalus xanthocephalus* | 79.7 |
| 04980 | Red-winged Blackbird | *Agelaius phoeniceus* | 63.6 |
| 05010 | Eastern Meadowlark | *Sturnella magna* | 102.0 |
| 05011 | Western Meadowlark | *Sturnella neglecta* | 112.0 |
| 05060 | Orchard Oriole | *Icterus spurius* | 19.6 |
| 05070 | Baltimore Oriole | *Icterus galbula* | 34.3 |
| 05110 | Common Grackle | *Quiscalus quiscula* | 127.0 |
| 05190 | House Finch | *Carpodacus mexicanus* | 21.4 |
| 05210 | Red Crossbill | *Loxia curvirostra* | 36.5 |

Table A.4 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 05290 | American Goldfinch | *Carduelis tristis* | 13.2 |
| 05400 | Vesper Sparrow | *Pooecetes gramineus* | 26.5 |
| 05420 | Savannah Sparrow | *Passerculus sandwichensis* | 20.6 |
| 05460 | Grasshopper Sparrow | *Ammodramus savannarum* | 17.0 |
| 05470 | Henslow's Sparrow | *Ammodramus henslowii* | 13.1 |
| 05520 | Lark Sparrow | *Chondestes grammacus* | 29.0 |
| 05600 | Chipping Sparrow | *Spizella passerina* | 12.3 |
| 05610 | Clay-colored Sparrow | *Spizella pallida* | 12.0 |
| 05630 | Field Sparrow | *Spizella pusilla* | 12.5 |
| 05810 | Song Sparrow | *Melospiza melodia* | 21.0 |
| 05840 | Swamp Sparrow | *Melospiza georgiana* | 17.0 |
| 05870 | Eastern Towhee | *Pipilo erythrophthalmus* | 41.7 |
| 05930 | Northern Cardinal | *Cardinalis cardinalis* | 45.4 |
| 05950 | Rose-breasted Grosbeak | *Pheucticus ludovicianus* | 45.6 |
| 05970 | Blue Grosbeak | *Guiraca caerulea* | 29.3 |
| 05980 | Indigo Bunting | *Passerina cyanea* | 14.9 |
| 06040 | Dickcissel | *Spiza americana* | 29.3 |
| 06050 | Lark Bunting | *Calamospiza melanocorys* | 37.6 |
| 06080 | Scarlet Tanager | *Piranga olivacea* | 28.6 |
| 06100 | Summer Tanager | *Piranga rubra* | 28.2 |

Table A.4 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06110 | Purple Martin | *Progne subis* | 49.4 |
| 06120 | Cliff Swallow | *Hirundo pyrrhonota* | 21.6 |
| 06130 | Barn Swallow | *Hirundo rustica* | 16.2 |
| 06140 | Tree Swallow | *Tachycineta bicolor* | 20.1 |
| 06160 | Bank Swallow | *Riparia riparia* | 14.6 |
| 06170 | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* | 15.9 |
| 06190 | Cedar Waxwing | *Bombycilla cedrorum* | 30.6 |
| 06220 | Loggerhead Shrike | *Lanius ludovicianus* | 47.4 |
| 06240 | Red-eyed Vireo | *Vireo olivaceus* | 16.7 |
| 06270 | Warbling Vireo | *Vireo gilvus* | 14.8 |
| 06280 | Yellow-throated Vireo | *Vireo flavifrons* | 18.0 |
| 06310 | White-eyed Vireo | *Vireo griseus* | 11.4 |
| 06330 | Bell's Vireo | *Vireo bellii* | 8.5 |
| 06360 | Black-and-white Warbler | *Mniotilta varia* | 11.0 |
| 06370 | Prothonotary Warbler | *Protonotaria citrea* | 14.3 |
| 06410 | Blue-winged Warbler | *Vermivora pinus* | 8.4 |
| 06480 | Northern Parula | *Parula americana* | 8.6 |
| 06520 | Yellow Warbler | *Dendroica petechia* | 9.8 |
| 06580 | Cerulean Warbler | *Dendroica cerulea* | 9.5 |
| 06590 | Chestnut-sided Warbler | *Dendroica pensylvanica* | 9.8 |

Table A.4 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06630 | Yellow-throated Warbler | *Dendroica dominica* | 9.4 |
| 06730 | Prairie Warbler | *Dendroica discolor* | 8.0 |
| 06740 | Ovenbird | *Seiurus aurocapillus* | 19.4 |
| 06760 | Louisiana Waterthrush | *Seiurus motacilla* | 19.8 |
| 06770 | Kentucky Warbler | *Oporornis formosus* | 14.3 |
| 06810 | Common Yellowthroat | *Geothlypis trichas* | 10.1 |
| 06830 | Yellow-breasted Chat | *Icteria virens* | 25.5 |
| 06840 | Hooded Warbler | *Wilsonia citrina* | 10.8 |
| 06870 | American Redstart | *Setophaga ruticilla* | 8.5 |
| 06882 | House Sparrow | *Passer domesticus* | 28.0 |
| 06883 | Eurasian Tree Sparrow | *Passer montanus* | 22.0 |
| 07030 | Northern Mockingbird | *Mimus polyglottos* | 48.5 |
| 07040 | Gray Catbird | *Dumetella carolinensis* | 36.9 |
| 07050 | Brown Thrasher | *Toxostoma rufum* | 68.8 |
| 07180 | Carolina Wren | *Thryothorus ludovicianus* | 18.7 |
| 07190 | Bewick's Wren | *Thryomanes bewickii* | 9.9 |
| 07210 | House Wren | *Troglodytes aedon* | 10.9 |
| 07240 | Sedge Wren | *Cistothorus platensis* | 9.0 |
| 07250 | Marsh Wren | *Cistothorus palustris* | 11.9 |
| 07260 | Brown Creeper | *Certhia americana* | 8.4 |

Table A. 4 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 07270 | White-breasted Nuthatch | *Sitta carolinensis* | 21.1 |
| 07310 | Tufted Titmouse | *Parus bicolor* | 21.6 |
| 07350 | Black-capped Chickadee | *Parus atricapillus* | 10.8 |
| 07360 | Carolina Chickadee | *Parus carolinensis* | 10.5 |
| 07510 | Blue-gray Gnatcatcher | *Polioptila caerulea* | 6.0 |
| 07550 | Wood Thrush | *Hylocichla mustelina* | 47.8 |
| 07610 | American Robin | *Turdus migratorius* | 77.3 |
| 07660 | Eastern Bluebird | *Sialia sialis* | 31.6 |

Table A.5. Species list for section 170, the Mid Coastal Plains, Western Section.

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 02890 | Northern Bobwhite | *Colinus virginianus* | 178.0 |
| 03100 | Wild Turkey | *Meleagris gallopavo* | 7400.0 |
| 03131 | Rock Dove | *Columba livia* | 369.0 |
| 03160 | Mourning Dove | *Zenaida macroura* | 123.0 |
| 03210 | Inca Dove | *Columbina inca* | 47.5 |
| 03250 | Turkey Vulture | *Cathartes aura* | 1467.0 |
| 03260 | Black Vulture | *Coragyps atratus* | 2172.0 |
| 03290 | Mississippi Kite | *Ictinia mississippiensis* | 245.0 |
| 03320 | Sharp-shinned Hawk | *Accipiter striatus* | 103.0 |
| 03330 | Cooper's Hawk | *Accipiter cooperii* | 349.0 |
| 03370 | Red-tailed Hawk | *Buteo jamaicensis* | 1028.0 |
| 03390 | Red-shouldered Hawk | *Buteo lineatus* | 475.0 |
| 03420 | Swainson's Hawk | *Buteo swainsoni* | 908.0 |
| 03430 | Broad-winged Hawk | *Buteo platypterus* | 420.0 |
| 03600 | American Kestrel | *Falco sparverius* | 111.0 |
| 03680 | Barred Owl | *Strix varia* | 632.0 |
| 03730 | Eastern Screech-Owl | *Otus asio* | 174.0 |
| 03750 | Great Horned Owl | *Bubo virginianus* | 1318.0 |
| 03850 | Greater Roadrunner | *Geococcyx californianus* | 376.0 |
| 03870 | Yellow-billed Cuckoo | *Coccyzus americanus* | 64.0 |

Table A.5 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 03900 | Belted Kingfisher | *Ceryle alcyon* | 148.0 |
| 03930 | Hairy Woodpecker | *Picoides villosus* | 70.0 |
| 03940 | Downy Woodpecker | *Picoides pubescens* | 27.0 |
| 03950 | Red-cockaded Woodpecker | *Picoides borealis* | 43.6 |
| 04050 | Pileated Woodpecker | *Dryocopus pileatus* | 308.0 |
| 04060 | Red-headed Woodpecker | *Melanerpes erythrocephalus* | 71.6 |
| 04090 | Red-bellied Woodpecker | *Melanerpes carolinus* | 67.2 |
| 04120 | Northern Flicker | *Colaptes auratus* | 135.0 |
| 04160 | Chuck-will's-widow | *Caprimulgus carolinensis* | 120.0 |
| 04170 | Whip-poor-will | *Caprimulgus vociferus* | 55.3 |
| 04200 | Common Nighthawk | *Chordeiles minor* | 61.5 |
| 04230 | Chimney Swift | *Chaetura pelagica* | 23.6 |
| 04280 | Ruby-throated Hummingbird | *Archilochus colubris* | 3.0 |
| 04430 | Scissor-tailed Flycatcher | *Tyrannus forficatus* | 43.2 |
| 04440 | Eastern Kingbird | *Tyrannus tyrannus* | 43.6 |
| 04470 | Western Kingbird | *Tyrannus verticalis* | 39.6 |
| 04520 | Great Crested Flycatcher | *Myiarchus crinitus* | 33.5 |
| 04560 | Eastern Phoebe | *Sayornis phoebe* | 19.8 |
| 04610 | Eastern Wood-Pewee | *Contopus virens* | 14.1 |
| 04650 | Acadian Flycatcher | *Empidonax virescens* | 12.9 |

Table A.5 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04740 | Horned Lark | *Eremophila alpestris* | 31.9 |
| 04770 | Blue Jay | *Cyanocitta cristata* | 86.8 |
| 04880 | American Crow | *Corvus brachyrhynchos* | 458.0 |
| 04900 | Fish Crow | *Corvus ossifragus* | 300.0 |
| 04930 | European Starling | *Sturnus vulgaris* | 84.7 |
| 04950 | Brown-headed Cowbird | *Molothrus ater* | 49.0 |
| 04980 | Red-winged Blackbird | *Agelaius phoeniceus* | 63.6 |
| 05010 | Eastern Meadowlark | *Sturnella magna* | 102.0 |
| 05060 | Orchard Oriole | *Icterus spurius* | 19.6 |
| 05070 | Baltimore Oriole | *Icterus galbula* | 34.3 |
| 05110 | Common Grackle | *Quiscalus quiscula* | 127.0 |
| 05120 | Great-tailed Grackle | *Quiscalus mexicanus* | 191.0 |
| 05190 | House Finch | *Carpodacus mexicanus* | 21.4 |
| 05290 | American Goldfinch | *Carduelis tristis* | 13.2 |
| 05460 | Grasshopper Sparrow | *Ammodramus savannarum* | 17.0 |
| 05520 | Lark Sparrow | *Chondestes grammacus* | 29.0 |
| 05600 | Chipping Sparrow | *Spizella passerina* | 12.3 |
| 05630 | Field Sparrow | *Spizella pusilla* | 12.5 |
| 05750 | Bachman's Sparrow | *Aimophila aestivalis* | 20.2 |
| 05870 | Eastern Towhee | *Pipilo erythrophthalmus* | 41.7 |

Table A.5 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 05930 | Northern Cardinal | *Cardinalis cardinalis* | 45.4 |
| 05970 | Blue Grosbeak | *Guiraca caerulea* | 29.3 |
| 05980 | Indigo Bunting | *Passerina cyanea* | 14.9 |
| 06010 | Painted Bunting | *Passerina ciris* | 16.1 |
| 06040 | Dickcissel | *Spiza americana* | 29.3 |
| 06080 | Scarlet Tanager | *Piranga olivacea* | 28.6 |
| 06100 | Summer Tanager | *Piranga rubra* | 28.2 |
| 06110 | Purple Martin | *Progne subis* | 49.4 |
| 06120 | Cliff Swallow | *Hirundo pyrrhonota* | 21.6 |
| 06130 | Barn Swallow | *Hirundo rustica* | 16.2 |
| 06140 | Tree Swallow | *Tachycineta bicolor* | 20.1 |
| 06170 | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* | 15.9 |
| 06190 | Cedar Waxwing | *Bombycilla cedrorum* | 30.6 |
| 06220 | Loggerhead Shrike | *Lanius ludovicianus* | 47.4 |
| 06240 | Red-eyed Vireo | *Vireo olivaceus* | 16.7 |
| 06270 | Warbling Vireo | *Vireo gilvus* | 14.8 |
| 06280 | Yellow-throated Vireo | *Vireo flavifrons* | 18.0 |
| 06310 | White-eyed Vireo | *Vireo griseus* | 11.4 |
| 06330 | Bell's Vireo | *Vireo bellii* | 8.5 |
| 06360 | Black-and-white Warbler | *Mniotilta varia* | 11.0 |

Table A.5 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06370 | Prothonotary Warbler | *Protonotaria citrea* | 15.0 |
| 06380 | Swainson's Warbler | *Limnothlypis swainsonii* | 18.9 |
| 06390 | Worm-eating Warbler | *Helmitheros vermivorus* | 13.0 |
| 06480 | Northern Parula | *Parula americana* | 8.6 |
| 06580 | Cerulean Warbler | *Dendroica cerulea* | 9.5 |
| 06630 | Yellow-throated Warbler | *Dendroica dominica* | 9.4 |
| 06710 | Pine Warbler | *Dendroica pinus* | 11.9 |
| 06730 | Prairie Warbler | *Dendroica discolor* | 8.0 |
| 06740 | Ovenbird | *Seiurus aurocapillus* | 19.4 |
| 06760 | Louisiana Waterthrush | *Seiurus motacilla* | 19.8 |
| 06770 | Kentucky Warbler | *Oporornis formosus* | 14.3 |
| 06810 | Common Yellowthroat | *Geothlypis trichas* | 10.1 |
| 06830 | Yellow-breasted Chat | *Icteria virens* | 25.5 |
| 06840 | Hooded Warbler | *Wilsonia citrina* | 10.8 |
| 06870 | American Redstart | *Setophaga ruticilla* | 8.5 |
| 06882 | House Sparrow | *Passer domesticus* | 28.0 |
| 07030 | Northern Mockingbird | *Mimus polyglottos* | 48.5 |
| 07040 | Gray Catbird | *Dumetella carolinensis* | 36.9 |
| 07050 | Brown Thrasher | *Toxostoma rufum* | 68.8 |
| 07180 | Carolina Wren | *Thryothorus ludovicianus* | 18.7 |

Table A.5 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 07190 | Bewick's Wren | *Thryomanes bewickii* | 9.9 |
| 07210 | House Wren | *Troglodytes aedon* | 10.9 |
| 07270 | White-breasted Nuthatch | *Sitta carolinensis* | 21.1 |
| 07290 | Brown-headed Nuthatch | *Sitta pusilla* | 10.2 |
| 07310 | Tufted Titmouse | *Parus bicolor* | 21.6 |
| 07360 | Carolina Chickadee | *Parus carolinensis* | 10.5 |
| 07510 | Blue-gray Gnatcatcher | *Polioptila caerulea* | 6.0 |
| 07550 | Wood Thrush | *Hylocichla mustelina* | 47.8 |
| 07610 | American Robin | *Turdus migratorius* | 77.3 |
| 07660 | Eastern Bluebird | *Sialia sialis* | 31.6 |

Table A.6. Species list for section 172, the Southern Cumberland Plateau Section.

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 02890 | Northern Bobwhite | *Colinus virginianus* | 178.0 |
| 03100 | Wild Turkey | *Meleagris gallopavo* | 7400.0 |
| 03131 | Rock Dove | *Columba livia* | 369.0 |
| 03160 | Mourning Dove | *Zenaida macroura* | 123.0 |
| 03200 | Common Ground-Dove | *Columbina passerina* | 30.1 |
| 03250 | Turkey Vulture | *Cathartes aura* | 1467.0 |
| 03260 | Black Vulture | *Coragyps atratus* | 2172.0 |
| 03290 | Mississippi Kite | *Ictinia mississippiensis* | 245.0 |
| 03320 | Sharp-shinned Hawk | *Accipiter striatus* | 103.0 |
| 03330 | Cooper's Hawk | *Accipiter cooperii* | 349.0 |
| 03370 | Red-tailed Hawk | *Buteo jamaicensis* | 1028.0 |
| 03390 | Red-shouldered Hawk | *Buteo lineatus* | 475.0 |
| 03430 | Broad-winged Hawk | *Buteo platypterus* | 420.0 |
| 03520 | Bald Eagle | *Haliaeetus leucocephalus* | 4130.0 |
| 03600 | American Kestrel | *Falco sparverius* | 111.0 |
| 03640 | Osprey | *Pandion haliaetus* | 1403.0 |
| 03680 | Barred Owl | *Strix varia* | 632.0 |
| 03730 | Eastern Screech-Owl | *Otus asio* | 174.0 |
| 03750 | Great Horned Owl | *Bubo virginianus* | 1318.0 |
| 03870 | Yellow-billed Cuckoo | *Coccyzus americanus* | 64.0 |

Table A.6 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 03880 | Black-billed Cuckoo | *Coccyzus erythropthalmus* | 51.1 |
| 03900 | Belted Kingfisher | *Ceryle alcyon* | 148.0 |
| 03930 | Hairy Woodpecker | *Picoides villosus* | 70.0 |
| 03940 | Downy Woodpecker | *Picoides pubescens* | 27.0 |
| 03950 | Red-cockaded Woodpecker | *Picoides borealis* | 43.6 |
| 04050 | Pileated Woodpecker | *Dryocopus pileatus* | 308.0 |
| 04060 | Red-headed Woodpecker | *Melanerpes erythrocephalus* | 71.6 |
| 04090 | Red-bellied Woodpecker | *Melanerpes carolinus* | 67.2 |
| 04120 | Northern Flicker | *Colaptes auratus* | 135.0 |
| 04160 | Chuck-will's-widow | *Caprimulgus carolinensis* | 120.0 |
| 04170 | Whip-poor-will | *Caprimulgus vociferus* | 55.3 |
| 04200 | Common Nighthawk | *Chordeiles minor* | 61.5 |
| 04230 | Chimney Swift | *Chaetura pelagica* | 23.6 |
| 04280 | Ruby-throated Hummingbird | *Archilochus colubris* | 3.0 |
| 04440 | Eastern Kingbird | *Tyrannus tyrannus* | 43.6 |
| 04520 | Great Crested Flycatcher | *Myiarchus crinitus* | 33.5 |
| 04560 | Eastern Phoebe | *Sayornis phoebe* | 19.8 |
| 04610 | Eastern Wood-Pewee | *Contopus virens* | 14.1 |
| 04650 | Acadian Flycatcher | *Empidonax virescens* | 12.9 |
| 04740 | Horned Lark | *Eremophila alpestris* | 31.9 |

Table A.6 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 04770 | Blue Jay | *Cyanocitta cristata* | 86.8 |
| 04880 | American Crow | *Corvus brachyrhynchos* | 458.0 |
| 04900 | Fish Crow | *Corvus ossifragus* | 300.0 |
| 04930 | European Starling | *Sturnus vulgaris* | 84.7 |
| 04950 | Brown-headed Cowbird | *Molothrus ater* | 49.0 |
| 04980 | Red-winged Blackbird | *Agelaius phoeniceus* | 63.6 |
| 05010 | Eastern Meadowlark | *Sturnella magna* | 102.0 |
| 05060 | Orchard Oriole | *Icterus spurius* | 19.6 |
| 05070 | Baltimore Oriole | *Icterus galbula* | 34.3 |
| 05110 | Common Grackle | *Quiscalus quiscula* | 127.0 |
| 05190 | House Finch | *Carpodacus mexicanus* | 21.4 |
| 05290 | American Goldfinch | *Carduelis tristis* | 13.2 |
| 05460 | Grasshopper Sparrow | *Ammodramus savannarum* | 17.0 |
| 05600 | Chipping Sparrow | *Spizella passerina* | 12.3 |
| 05630 | Field Sparrow | *Spizella pusilla* | 12.5 |
| 05750 | Bachman's Sparrow | *Aimophila aestivalis* | 20.2 |
| 05810 | Song Sparrow | *Melospiza melodia* | 21.0 |
| 05870 | Eastern Towhee | *Pipilo erythrophthalmus* | 41.7 |
| 05930 | Northern Cardinal | *Cardinalis cardinalis* | 45.4 |
| 05970 | Blue Grosbeak | *Guiraca caerulea* | 29.3 |

Table A.6 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 05980 | Indigo Bunting | *Passerina cyanea* | 14.9 |
| 06040 | Dickcissel | *Spiza americana* | 29.3 |
| 06080 | Scarlet Tanager | *Piranga olivacea* | 28.6 |
| 06100 | Summer Tanager | *Piranga rubra* | 28.2 |
| 06110 | Purple Martin | *Progne subis* | 49.4 |
| 06120 | Cliff Swallow | *Hirundo pyrrhonota* | 21.6 |
| 06130 | Barn Swallow | *Hirundo rustica* | 16.2 |
| 06140 | Tree Swallow | *Tachycineta bicolor* | 20.1 |
| 06160 | Bank Swallow | *Riparia riparia* | 14.6 |
| 06170 | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* | 15.9 |
| 06190 | Cedar Waxwing | *Bombycilla cedrorum* | 30.6 |
| 06220 | Loggerhead Shrike | *Lanius ludovicianus* | 47.4 |
| 06240 | Red-eyed Vireo | *Vireo olivaceus* | 16.7 |
| 06280 | Yellow-throated Vireo | *Vireo flavifrons* | 18.0 |
| 06290 | Blue-headed Vireo | *Vireo solitarius* | 16.6 |
| 06310 | White-eyed Vireo | *Vireo griseus* | 11.4 |
| 06360 | Black-and-white Warbler | *Mniotilta varia* | 11.0 |
| 06370 | Prothonotary Warbler | *Protonotaria citrea* | 15.0 |
| 06380 | Swainson's Warbler | *Limnothlypis swainsonii* | 18.9 |
| 06390 | Worm-eating Warbler | *Helmitheros vermivorus* | 13.0 |

Table A.6 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 06410 | Blue-winged Warbler | *Vermivora pinus* | 8.4 |
| 06480 | Northern Parula | *Parula americana* | 8.6 |
| 06520 | Yellow Warbler | *Dendroica petechia* | 9.8 |
| 06580 | Cerulean Warbler | *Dendroica cerulea* | 9.5 |
| 06630 | Yellow-throated Warbler | *Dendroica dominica* | 9.4 |
| 06670 | Black-throated Green Warbler | *Dendroica virens* | 8.8 |
| 06710 | Pine Warbler | *Dendroica pinus* | 11.9 |
| 06730 | Prairie Warbler | *Dendroica discolor* | 8.0 |
| 06740 | Ovenbird | *Seiurus aurocapillus* | 19.4 |
| 06760 | Louisiana Waterthrush | *Seiurus motacilla* | 19.8 |
| 06770 | Kentucky Warbler | *Oporornis formosus* | 14.3 |
| 06810 | Common Yellowthroat | *Geothlypis trichas* | 10.1 |
| 06830 | Yellow-breasted Chat | *Icteria virens* | 25.5 |
| 06840 | Hooded Warbler | *Wilsonia citrina* | 10.8 |
| 06870 | American Redstart | *Setophaga ruticilla* | 8.5 |
| 06882 | House Sparrow | *Passer domesticus* | 28.0 |
| 07030 | Northern Mockingbird | *Mimus polyglottos* | 48.5 |
| 07040 | Gray Catbird | *Dumetella carolinensis* | 36.9 |
| 07050 | Brown Thrasher | *Toxostoma rufum* | 68.8 |
| 07180 | Carolina Wren | *Thryothorus ludovicianus* | 18.7 |

Table A.6 (cont'd).

| AOU Code | Common Name | Scientific Name | Mass (g) |
|---|---|---|---|
| 07210 | House Wren | *Troglodytes aedon* | 10.9 |
| 07270 | White-breasted Nuthatch | *Sitta carolinensis* | 21.1 |
| 07290 | Brown-headed Nuthatch | *Sitta pusilla* | 10.2 |
| 07310 | Tufted Titmouse | *Parus bicolor* | 21.6 |
| 07360 | Carolina Chickadee | *Parus carolinensis* | 10.5 |
| 07510 | Blue-gray Gnatcatcher | *Polioptila caerulea* | 6.0 |
| 07550 | Wood Thrush | *Hylocichla mustelina* | 47.8 |
| 07610 | American Robin | *Turdus migratorius* | 77.3 |
| 07660 | Eastern Bluebird | *Sialia sialis* | 31.6 |
| 22860 | Eurasian Collared-Dove | *Streptopelia decaocto* | 152.0 |

# APPENDIX B: TAXONOMIC CHANGES

Table B.1. Changes made to species names from those originally reported to the BBS.

| Former Name | | Current Name | |
|---|---|---|---|
| Yellow-shafted Flicker | | Northern Flicker | *Colaptes auratus* |
| Red-shafted Flicker | | Northern Flicker | *Colaptes auratus* |
| unid. Flicker subsp. | | Northern Flicker | *Colaptes auratus* |
| Black-crested Titmouse | | Tufted Titmouse | *Parus bicolor* |
| Slate-colored Junco | | Dark-eyed Junco | *Junco hyemalis* |
| unid. Junco subsp. | | Dark-eyed Junco | *Junco hyemalis* |
| Solitary Vireo | | Blue-headed Vireo | *Vireo solitarius* |
| Crested Caracara | *Caracara plancus* | Crested Caracara | *Caracara cheriway* |
| Rufous-sided towhee | | Eastern Towhee | *Pipilo erythrophthalmus* |
| Ringed turtle-dove | *Steptopelia risoria* | Eurasian collared-dove | *Streptopelia decaocta* |

# APPENDIX C: DISCONTINUITIES IN BODY SIZE DISTRIBUTIONS

Table C.1. Discontinuities in body size distribution identified by five methods (HI = Holling Index, SI = Siemann & Brown Index, RH = robust Holling Index, RS = robust Siemann & Brown Index, AG = agglomerative nesting cluster analysis, Y = discontinuity identified, N = discontinuity not identified) for the Section 47 dataset.

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 3 - 6 | N | Y | N | N | N | N |
| 3 – 8 | Y | N | N | N | N | N |
| 8 – 8.5 | N | N | Y | N | N | N |
| 8.6 – 9.4 | Y | N | N | N | N | N |
| 9.5 – 10.1 | N | N | Y | N | N | N |
| 11 – 11.4 | N | N | N | N | Y | N |
| 11 – 11.9 | N | N | Y | N | N | N |
| 13.2 – 14.1 | N | N | N | Y | N | N |
| 13.2 – 14.3 | N | N | Y | N | N | N |
| 14.9 – 15.9 | N | N | N | Y | N | N |
| 14.9 – 16.2 | N | N | Y | N | N | N |
| 17 – 18 | N | N | N | N | Y | N |
| 17 – 18.7 | N | N | Y | N | N | N |
| 21.6 – 23.6 | N | Y | N | Y | N | Y |
| 21.6 – 25.5 | Y | N | Y | N | N | N |
| 23.6 – 25.5 | N | N | N | N | Y | N |
| 34.3 – 36.9 | N | N | N | Y | Y | Y |
| 34.3 – 39. | Y | N | Y | N | N | N |
| 51.1 – 55.3 | N | N | N | N | Y | N |

Table C.1 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 51.1 – 61.5 | Y | N | Y | N | N | N |
| 55.3 – 61.5 | N | Y | N | Y | N | Y |
| 71.6 – 77.3 | N | Y | N | Y | Y | Y |
| 79.7 – 102 | Y | N | Y | N | N | N |
| 86.8 – 102 | N | Y | N | Y | Y | Y |
| 112 – 123 | N | Y | N | Y | N | N |
| 135 – 174 | Y | N | Y | N | N | N |
| 148 – 174 | N | Y | N | Y | Y | Y |
| 174 – 308 | Y | N | Y | N | N | N |
| 178 – 308 | N | Y | N | Y | Y | Y |
| 349 – 458 | Y | N | Y | N | N | N |
| 358 – 458 | N | Y | N | Y | Y | Y |
| 475 – 999 | Y | N | Y | N | N | N |
| 632 – 999 | N | Y | N | Y | Y | Y |
| 1028 – 1318 | N | Y | N | Y | Y | Y |
| 1067 – 2172 | N | N | N | N | Y | N |
| 1467 – 7400 | Y | N | N | N | N | N |
| 2172 – 7400 | N | Y | N | N | Y | Y |

Table C.2. Discontinuities in body size distribution identified by five methods (HI = Holling Index, SI = Siemann & Brown Index, RH = robust Holling Index, RS = robust Siemann & Brown Index, AG = agglomerative nesting cluster analysis, Y = discontinuity identified, N = discontinuity not identified) for the Section 59 dataset.

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 3 – 6 | N | Y | N | N | N | N |
| 3 – 8 | Y | N | N | N | N | N |
| 8.7 – 9.4 | N | N | Y | N | N | N |
| 8.8 – 9.4 | N | N | N | Y | N | N |
| 10.1 – 10.8 | N | N | Y | N | N | N |
| 11 – 11.4 | N | N | N | N | Y | N |
| 11 – 11.9 | N | N | Y | N | N | N |
| 13.2 – 14.1 | N | N | N | Y | N | N |
| 13.2 – 14.3 | N | N | Y | N | N | N |
| 15 – 16.2 | N | N | Y | N | N | N |
| 17 – 18 | N | N | N | N | Y | N |
| 17 – 18.7 | N | N | Y | N | N | N |
| 21.6 – 23.6 | N | Y | N | Y | N | Y |
| 21.6 – 25.5 | Y | N | Y | N | N | N |
| 23.6 – 25.5 | N | N | N | N | Y | N |
| 34.3 – 41.7 | Y | N | Y | N | N | N |
| 36.9 – 41.7 | N | Y | N | Y | Y | Y |
| 49.4 – 55.3 | N | Y | N | Y | N | Y |
| 49.4 – 61.5 | Y | N | Y | N | N | N |

Table C.2 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 55.3 – 61.5 | N | N | N | N | Y | N |
| 71.6 – 77.3 | N | N | N | N | Y | N |
| 77.3 – 102 | Y | N | Y | N | N | N |
| 86.8 – 102 | N | Y | N | Y | Y | Y |
| 103 – 120 | N | N | Y | N | N | N |
| 111 – 120 | N | N | N | Y | Y | Y |
| 127 – 135 | N | N | N | N | Y | N |
| 135 – 174 | Y | N | Y | N | N | N |
| 148 – 174 | N | Y | N | Y | Y | Y |
| 174 – 308 | Y | N | Y | N | N | N |
| 178 – 308 | N | Y | N | Y | Y | Y |
| 349 – 420 | N | Y | N | Y | Y | Y |
| 458 – 621 | Y | N | Y | N | N | N |
| 475 – 621 | N | Y | N | Y | Y | Y |
| 621 – 1028 | Y | N | Y | N | N | N |
| 632 – 1028 | N | Y | N | Y | Y | Y |
| 1467 – 2172 | N | N | N | N | Y | N |
| 1467 – 7400 | Y | N | N | N | N | N |
| 2172 – 7400 | N | Y | N | N | Y | Y |

Table C.3. Discontinuities in body size distribution identified by five methods (HI = Holling Index, SI = Siemann & Brown Index, RH = robust Holling Index, RS = robust Siemann & Brown Index, AG = agglomerative nesting cluster analysis, Y = discontinuity identified, N = discontinuity not identified) for the Section 133 dataset.

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 3 – 8 | Y | Y | N | N | N | N |
| 8.6 – 9.4 | N | Y | N | Y | N | Y |
| 8.6 – 10.1 | Y | N | Y | N | N | N |
| 11 – 11.9 | N | N | Y | N | N | N |
| 12.9 – 14.1 | N | N | Y | N | N | N |
| 13 – 14.1 | N | N | N | Y | Y | N |
| 17 – 18.7 | N | N | Y | N | N | N |
| 21.6 – 23.6 | N | Y | N | Y | Y | Y |
| 21.6 – 25.5 | Y | N | Y | N | N | N |
| 29.3 – 31.6 | N | N | N | Y | N | N |
| 29.3 – 33.5 | N | N | Y | N | N | N |
| 34.3 – 41.7 | Y | N | Y | N | N | N |
| 36.9 – 41.7 | N | Y | N | Y | Y | Y |
| 49 – 61.5 | Y | N | Y | N | N | N |
| 49.4 – 61.5 | N | Y | N | Y | Y | Y |
| 71.6 – 77.3 | N | N | N | N | Y | N |
| 77.3 – 102 | Y | N | Y | N | N | N |
| 86.8 - 102 | N | Y | N | Y | Y | Y |
| 111 – 120 | N | N | N | N | Y | N |

Table C.3 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 127 –135 | N | N | N | N | Y | N |
| 135 – 174 | Y | N | Y | N | N | N |
| 148 – 174 | N | Y | N | Y | Y | Y |
| 178 – 214 | N | Y | N | Y | Y | Y |
| 214 – 300 | Y | N | Y | N | N | N |
| 245 – 300 | N | Y | N | Y | Y | Y |
| 308 – 349 | N | Y | N | Y | Y | Y |
| 376 – 420 | N | Y | N | Y | Y | Y |
| 475 – 632 | N | N | N | N | Y | N |
| 475 – 1028 | Y | N | Y | N | N | N |
| 632 – 1028 | N | Y | N | Y | Y | Y |
| 1117 – 1318 | N | Y | N | Y | Y | Y |
| 1467 – 2172 | N | N | N | N | Y | N |
| 1467 – 7400 | Y | N | N | N | N | N |
| 2172 – 7400 | N | Y | N | N | Y | Y |

Table C.4. Discontinuities in body size distribution identified by five methods (HI = Holling Index, SI = Siemann & Brown Index, RH = robust Holling Index, RS = robust Siemann & Brown Index, AG = agglomerative nesting cluster analysis, Y = discontinuity identified, N = discontinuity not identified) for the Section 153 dataset.

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 3 – 6 | N | Y | N | N | N | N |
| 3 – 8 | Y | N | N | N | N | N |
| 8 – 8.4 | N | N | N | Y | N | N |
| 8.6 – 9.4 | Y | N | Y | N | N | N |
| 11 – 11.9 | N | N | Y | N | N | N |
| 13.2 – 14.1 | N | Y | N | Y | N | Y |
| 13.2 – 14.3 | N | N | Y | N | N | N |
| 14.9 – 15.9 | N | Y | N | Y | N | Y |
| 14.9 – 16.2 | N | N | Y | N | N | N |
| 17 – 18 | N | N | N | Y | Y | Y |
| 17 – 18.7 | Y | N | Y | N | N | N |
| 21.6 – 23.6 | N | Y | N | Y | N | Y |
| 21.6 – 25.5 | Y | N | Y | N | N | N |
| 23.6 – 25.5 | N | N | N | N | Y | N |
| 29.3 – 31.6 | N | N | Y | N | N | N |
| 31.9 – 33.5 | N | N | N | Y | N | N |
| 33.5- 36.5 | N | N | Y | N | N | N |
| 34.3 – 36.5 | N | Y | N | Y | Y | Y |
| 37.6 – 39.6 | N | N | N | Y | N | N |

Table C.4 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 37.6 – 41.7 | N | N | Y | N | N | N |
| 55.1 – 55.3 | N | N | N | N | Y | N |
| 51.1 – 61.5 | Y | N | Y | N | N | N |
| 55.3 – 61.5 | N | Y | N | Y | N | Y |
| 71.6 – 77.3 | N | Y | N | Y | Y | Y |
| 79.7 – 102 | Y | N | Y | N | N | N |
| 86.8 – 102 | N | Y | N | Y | Y | Y |
| 103 – 111 | N | Y | N | Y | N | N |
| 112 – 123 | N | Y | N | Y | Y | Y |
| 112 – 127 | N | N | Y | N | N | N |
| 135 – 148 | N | N | N | N | Y | N |
| 135 – 174 | Y | N | Y | N | N | N |
| 148 – 174 | N | Y | N | Y | Y | Y |
| 178 – 308 | Y | N | Y | N | N | N |
| 189 – 308 | N | Y | N | Y | Y | Y |
| 315 – 349 | N | Y | N | Y | N | N |
| 358 – 420 | N | Y | N | Y | Y | Y |
| 358 – 458 | Y | N | Y | N | N | N |
| 475 – 632 | N | N | N | N | Y | N |
| 475 – 908 | Y | N | Y | N | N | N |

Table C.4 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 632 – 908 | N | Y | N | Y | Y | Y |
| 999 – 1318 | Y | N | N | N | N | N |
| 1028 – 1318 | N | Y | N | N | Y | Y |
| 1318 – 7400 | Y | N | N | N | N | N |
| 1467 – 7400 | N | Y | N | N | Y | Y |

Table C.5. Discontinuities in body size distribution identified by five methods (HI = Holling Index, SI = Siemann & Brown Index, RH = robust Holling Index, RS = robust Siemann & Brown Index, AG = agglomerative nesting cluster analysis, Y = discontinuity identified, N = discontinuity not identified) for the Section 170 dataset.

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 3 – 6 | N | Y | N | N | N | N |
| 3 – 8 | Y | N | N | N | N | N |
| 8 – 8.5 | N | N | N | Y | N | N |
| 8 – 8.6 | N | N | Y | N | N | N |
| 8.5 – 9.4 | Y | N | Y | N | N | N |
| 8.6 – 9.4 | N | Y | N | Y | N | Y |
| 9.5 – 10.1 | N | N | Y | N | N | N |
| 11 – 11.9 | N | N | Y | N | N | N |
| 11.9 – 12.3 | N | N | N | N | Y | N |
| 13 – 14.1 | N | N | Y | N | N | N |
| 13.2 – 14.1 | N | N | N | Y | N | N |
| 15 – 15.9 | N | N | N | Y | N | N |
| 15 – 16.1 | N | N | Y | N | N | N |
| 17 – 18.7 | N | N | Y | N | N | N |
| 21.6 – 23.6 | N | Y | N | Y | N | Y |
| 21.6 – 25.5 | Y | N | Y | N | N | N |
| 23.6 – 25.5 | N | N | N | N | Y | N |
| 34.3 – 36.9 | N | Y | N | Y | N | Y |
| 34.3 – 39.6 | Y | N | Y | N | N | N |

Table C.5 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 36.9 – 39.6 | N | N | N | N | Y | N |
| 49.4 – 55.3 | N | Y | N | Y | N | Y |
| 49.4 – 61.5 | Y | N | Y | N | N | N |
| 55.3 – 61.5 | N | N | N | N | Y | N |
| 71.6 – 77.3 | N | N | N | N | Y | N |
| 77.3 - 102 | Y | N | Y | N | N | N |
| 86.8 - 102 | N | Y | N | Y | Y | Y |
| 103 - 120 | N | N | Y | N | N | N |
| 111 - 120 | N | Y | N | Y | Y | Y |
| 127 - 135 | N | N | N | N | Y | N |
| 135 - 174 | Y | N | Y | N | N | N |
| 148 - 174 | N | Y | N | Y | Y | Y |
| 191 – 245 | N | Y | N | Y | Y | Y |
| 191 – 300 | Y | N | Y | N | N | N |
| 308 – 349 | N | Y | N | Y | Y | Y |
| 308 – 376 | N | N | Y | N | N | N |
| 376 – 420 | N | Y | N | Y | Y | Y |
| 376 – 458 | N | N | Y | N | N | N |
| 475 – 632 | N | N | N | N | Y | N |
| 475 – 908 | Y | N | Y | N | N | N |

Table C.5 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 632 – 908 | N | Y | N | Y | Y | Y |
| 1028 – 1318 | N | Y | N | Y | Y | Y |
| 1467 – 2172 | N | N | N | N | Y | N |
| 1467 – 7400 | Y | N | N | N | N | N |
| 2172 – 7400 | N | Y | N | N | Y | Y |

Table C.6. Discontinuities in body size distribution identified by five methods (HI = Holling Index, SI = Siemann & Brown Index, RH = robust Holling Index, RS = robust Siemann & Brown Index, AG = agglomerative nesting cluster analysis, Y = discontinuity identified, N = discontinuity not identified) for the Section 172 dataset.

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 3 – 6 | N | Y | N | N | N | N |
| 3 – 8 | Y | N | N | N | N | N |
| 8 – 8.5 | N | N | Y | N | N | N |
| 8.6 – 9.4 | Y | N | Y | N | N | N |
| 8.8 – 9.4 | N | N | N | Y | N | Y |
| 9.5 – 10.1 | N | N | Y | N | N | N |
| 11 – 11.9 | N | N | Y | N | N | N |
| 13 – 14.1 | N | N | Y | N | N | N |
| 13.2 – 14.1 | N | N | N | Y | Y | Y |
| 15 – 16.2 | N | N | Y | N | N | N |
| 17 – 18.7 | N | N | Y | N | N | N |
| 21.6 – 23.6 | N | Y | N | Y | N | Y |
| 21.6 – 25.5 | Y | N | Y | N | N | N |
| 23.6 – 25.5 | N | N | N | N | Y | N |
| 34.3 – 41.7 | Y | N | Y | N | N | N |
| 36.9 – 41.7 | N | Y | N | Y | Y | Y |
| 51.1 – 61.5 | Y | N | Y | N | N | N |
| 55.3 – 61.5 | N | Y | N | Y | Y | Y |
| 71.6 – 77.3 | N | N | N | N | Y | N |

Table C.6 (cont'd).

| Discontinuity Location (g) | HI | SI | RH | RS | AG | Consensus Discontinuity |
|---|---|---|---|---|---|---|
| 77.3 – 102 | Y | N | Y | N | N | N |
| 86.8 – 102 | N | Y | N | Y | Y | Y |
| 103 – 120 | N | N | Y | N | N | N |
| 111 – 120 | N | N | N | Y | Y | Y |
| 127 – 135 | N | N | N | N | Y | N |
| 135 – 174 | Y | N | Y | N | N | N |
| 148 – 174 | N | Y | N | Y | Y | Y |
| 178 – 245 | N | Y | N | Y | Y | Y |
| 178 – 300 | Y | N | Y | N | N | N |
| 245 – 300 | N | N | N | N | Y | N |
| 308 – 420 | Y | N | Y | N | N | N |
| 349 – 420 | N | Y | N | Y | Y | Y |
| 475 – 632 | N | N | N | N | Y | N |
| 475 – 1028 | Y | N | Y | N | N | N |
| 632 – 1028 | N | Y | N | Y | Y | Y |
| 1028 – 1318 | N | N | N | N | Y | N |
| 1467 – 2172 | N | N | N | N | Y | N |
| 1467 – 4130 | Y | N | N | N | N | N |
| 2172 – 4130 | N | Y | N | N | Y | Y |

# APPENDIX D: ECOREGIONS OF THE CONTINENTAL UNITED STATES

Table D.1. Provinces (in bold) and their component sections of the contiguous United States delineated by the National Ecological Unit Hierarchy (Cleland et al. 1997) with corresponding numeric codes and areas (km$^2$).

| Name | Code | Area (km$^2$) |
|---|---|---|
| **Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow Province** | **1** | **1720.00** |
| Adirondack Highlands Section | 1 | 270.00 |
| Catskill Mountains Section | 2 | 640.00 |
| Green, Taconic, Berkshire Mountains Section | 3 | 190.00 |
| New England Piedmont Section | 4 | 160.00 |
| White Mountains Section | 5 | 460.00 |
| **American Semi-Desert and Desert Province** | **5** | **350.00** |
| Mojave Desert Section | 12 | 120.00 |
| Sonoran Colorado Desert Section | 13 | 130.00 |
| Sonoran Mojave Desert Section | 14 | 100.00 |
| **Arizona-New Mexico Mountains Semi-Desert-Open Woodland-Coniferous Forest-Alpine Meadow Province** | **7** | **1300.00** |
| Sacramento-Monzano Mountain Section | 16 | 390.00 |
| White Mountain-San Francisco Peaks Section | 17 | 910.00 |
| **Black Hills Coniferous Forest Province** | **9** | **950.00** |
| Black Hills Section | 21 | 950.00 |
| **California Coastal Chaparral Forest and Shrub Province** | **11** | **360.88** |
| Central California Coast Section | 24 | 240.11 |
| Southern California Coast Section | 25 | 120.77 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| **California Coastal Range Open Woodland-Shrub-Coniferous Forest-Meadow Province** | **12** | **650.00** |
| Central California Coast Ranges Section | 26 | 320.00 |
| Southern California Mountains and Valleys Section | 27 | 330.00 |
| **California Coastal Steppe-Mixed Forest-Redwood Forest Province** | **13** | **120.07** |
| Northern California Coast Section | 28 | 120.07 |
| **California Dry Steppe Province** | **14** | **500.15** |
| Great Valley Section | 29 | 500.15 |
| **Cascade Mixed Forest-Coniferous Forest-Alpine Meadow Province** | **15** | **1391.22** |
| Eastern Cascades Section | 30 | 580.00 |
| Oregon and Washington Coast Ranges Section | 31 | 411.21 |
| Western Cascades Section | 32 | 400.01 |
| **Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow Province** | **16** | **1760.00** |
| Allegheny Mountains Section | 33 | 250.00 |
| Blue Ridge Mountains Section | 34 | 540.00 |
| Northern Cumberland Mountains Section | 35 | 140.00 |
| Northern Ridge & Valley Section | 36 | 830.00 |
| **Chihuahuan Semi-Desert Province** | **17** | **510.00** |
| Basin and Range Section | 37 | 190.00 |
| Stockton Plateau Section | 38 | 320.00 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| **Colorado Plateau Semi-Desert Province** | **19** | **2770.00** |
| Grand Canyon Lands Section | 41 | 590.00 |
| Navajo Canyonlands Section | 42 | 570.00 |
| Northern Rio Grande Intermontane Section | 43 | 910.00 |
| Painted Desert Section | 44 | 250.00 |
| Tonto Transition Section | 45 | 450.00 |
| **Eastern Broadleaf Forest (Continental) Province** | **20** | **6702.00** |
| Central Till Plains, Beech-Maple Section | 46 | 700.00 |
| Central Till Plains, Oak-Hickory Section | 47 | 410.00 |
| Erie and Ontario Lake Plain Section | 48 | 481.53 |
| Interior Low Plateau, Bluegrass Section | 49 | 400.00 |
| Interior Low Plateau, Highland Rim Section | 50 | 760.00 |
| Interior Low Plateau, Shawnee Hills Section | 51 | 370.00 |
| Lake Agassiz, Aspen Parklands Section | 52 | 880.00 |
| Minnesota & NE Iowa Morainal, Oak Savannah Section | 53 | 760.00 |
| North Central U.S. Driftless and Escarpment Section | 54 | 430.00 |
| Ozark Highlands Section | 55 | 120.00 |
| South Central Great Lakes Section | 56 | 650.47 |
| Southwestern Great Lakes Morainal Section | 57 | 460.00 |
| Upper Gulf Coastal Plain Section | 58 | 280.00 |
| **Eastern Broadleaf Forest (Oceanic) Province** | **21** | **3912.60** |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| Central Ridge and Valley Section | 59 | 130.00 |
| Hudson Valley Section | 60 | 150.00 |
| Lower New England Section | 61 | 801.92 |
| Northern Appalacian Piedmont Section | 62 | 210.08 |
| Northern Cumberland Plateau Section | 63 | 360.00 |
| Southern Cumberland Mountains Section | 64 | 990.00 |
| Southern Unglaciated Allegheny Plateau Section | 65 | 820.00 |
| Upper Atlantic Coastal Plain Section | 66 | 140.59 |
| Western Glaciated Allegheny Plateau Section | 67 | 310.00 |
| **Everglades Province** | **22** | **205.96** |
| Everglades Section | 68 | 205.96 |
| **Great Plains Steppe and Shrub Province** | **23** | **460.00** |
| Redbed Plains Section | 69 | 460.00 |
| **Great Plains Steppe Province** | **24** | **2080.00** |
| Nebraska Sand Hills Section | 70 | 480.00 |
| North-Central Great Plains Section | 71 | 430.00 |
| Northeastern Glaciated Plains Section | 72 | 720.00 |
| South-Central Great Plains Section | 73 | 150.00 |
| Western Glaciated Plains Section | 74 | 300.00 |
| **Great Plains-Palouse Dry Steppe Province** | **25** | **3780.00** |
| Arkansas Tablelands Section | 75 | 610.00 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| Central High Plains Section | 76 | 600.00 |
| Central High Tablelands Section | 77 | 670.00 |
| Northern Glaciated Plains Section | 78 | 700.00 |
| Northwestern Glaciated Plains Section | 79 | 110.00 |
| Northwestern Great Plains Section | 80 | 200.00 |
| Palouse Prairie Section | 81 | 170.00 |
| Powder River Basin Section | 82 | 120.00 |
| Southern High Plains Section | 83 | 440.00 |
| Upper Rio Grande Basin Section | 84 | 160.00 |
| **Intermountain Semi-Desert and Desert Province** | **27** | **3660.00** |
| Bonneville Basin Section | 86 | 730.00 |
| Lahontan Basin Section | 87 | 660.00 |
| Mono Section | 88 | 260.00 |
| Northeastern Great Basin Section | 89 | 330.00 |
| Northern Canyon Lands Section | 90 | 390.00 |
| Southeastern Great Basin Section | 91 | 380.00 |
| Uinta Basin Section | 92 | 910.00 |
| **Intermountain Semi-Desert Province** | **28** | **3800.00** |
| Bear Lake Section | 93 | 790.00 |
| Bighorn Basin Section | 94 | 200.00 |
| Central Basin and Hills Section | 95 | 410.00 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| Columbia Basin Section | 96 | 550.00 |
| Greater Green River Basin Section | 97 | 510.00 |
| High Lava Plains Section | 98 | 210.00 |
| Northwestern Basin and Range Section | 99 | 120.00 |
| Owyhee Uplands Section | 100 | 740.00 |
| Snake River Basalts Section | 101 | 270.00 |
| **Laurentian Mixed Forest Province** | **29** | **5336.66** |
| Aroostook Hills & Lowlands Section | 102 | 970.00 |
| Central Maine Coastal & Interior Section | 103 | 124.71 |
| Fundy Coastal & Interior Section | 104 | 592.73 |
| Maine & New Brunswick Foothills & Central Lowlands Section | 105 | 170.00 |
| Northern Glaciated Allegheny Plateau Section | 106 | 550.00 |
| Northern Great Lakes Section | 107 | 797.02 |
| Northern Minnesota & Ontario Section | 108 | 240.00 |
| Northern Minnesota Drift & Lake Plains Section | 109 | 310.00 |
| Northern Superior Uplands Section | 110 | 180.75 |
| Northern Unglaciated Allegheny Plateau Section | 111 | 150.00 |
| Southern Superior Uplands Section | 112 | 921.26 |
| St. Lawrence Valley Section | 113 | 120.19 |
| Western Superior Section | 114 | 210.00 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| **Lower Mississippi Riverine Forest Province** | **30** | **120.00** |
| Mississippi Alluvial Basin Section | 115 | 120.00 |
| **Middle Rocky Mountain Steppe-Coniferous Forest-Alpine Meadow Province** | **31** | **2740.00** |
| Beaverhead Mountains Section | 116 | 510.00 |
| Belt Mountains Section | 117 | 320.00 |
| Bitterroot Valley Section | 118 | 200.00 |
| Blue Mountains Section | 119 | 450.00 |
| Challis Volcanics Section | 120 | 140.00 |
| Idaho Batholith Section | 121 | 430.00 |
| Rocky Mountain Front Section | 122 | 690.00 |
| **Nevada-Utah Mountains-Semi-Desert-Coniferous Forest-Alpine Meadow Province** | **32** | **1130.00** |
| Central Great Basin Mountains Section | 123 | 630.00 |
| Tavaputs Plateau Section | 124 | 180.00 |
| Utah High Plateaus and Mountains Section | 125 | 320.00 |
| **Northern Rocky Mountain Forest-Steppe-Coniferous Forest-Alpine Meadow Province** | **33** | **990.00** |
| Bitterroot Mountains Section | 126 | 330.00 |
| Flathead Valley Section | 127 | 210.00 |
| Northern Rockies Section | 128 | 110.00 |
| Okanogan Highlands Section | 129 | 340.00 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| **Ouachita Mixed Forest - Meadow Province** | **34** | **230.00** |
| Ouachita Mountains Section | 130 | 230.00 |
| **Outer Coastal Plain Mixed Forest Province** | **35** | **3741.64** |
| Atlantic Coastal Flatlands Section | 131 | 607.53 |
| Coastal Plains and Flatwoods, Lower Section | 132 | 231.20 |
| Coastal Plains and Flatwoods, Western Gulf Section | 133 | 1130.00 |
| Florida Coastal Lowlands (Eastern) Section | 134 | 601.02 |
| Florida Coastal Lowlands (Western) Section | 135 | 351.50 |
| Louisiana Coast Prairies and Marshes Section | 136 | 364.24 |
| Middle Atlantic Coastal Plain Section | 137 | 456.15 |
| **Ozark Broadleaf Forest - Meadow Province** | **36** | **170.00** |
| Boston Mountains Section | 138 | 170.00 |
| **Pacific Lowland Mixed Forest Province** | **39** | **372.75** |
| Willamette Valley and Puget Trough Section | 147 | 372.75 |
| **Prairie Parkland (Subtropical) Province** | **40** | **2081.05** |
| Blackland Prairies Section | 148 | 340.00 |
| Central Gulf Prairies and Marshes Section | 149 | 241.05 |
| Cross Timbers and Prairie Section | 150 | 930.00 |
| Oak Woods and Prairies Section | 151 | 570.00 |
| **Prairie Parkland (Temperate) Province** | **41** | **2860.00** |
| Central Dissected Till Plains Section | 152 | 180.00 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| Central Loess Plains Section | 153 | 1170.00 |
| Flint Hills Section | 154 | 440.00 |
| North-Central Glaciated Plains Section | 155 | 130.00 |
| Osage Plains Section | 156 | 470.00 |
| Red River Valley Section | 157 | 470.00 |
| **Sierran Steppe-Mixed Forest-Coniferous Forest-Alpine Meadow Province** | **44** | **2390.00** |
| Klamath Mountains Section | 160 | 420.00 |
| Modoc Plateau Section | 161 | 250.00 |
| Northern California Coast Ranges Section | 162 | 160.00 |
| Northern California Interior Coast Ranges Section | 163 | 700.00 |
| Sierra Nevada Foothills Section | 164 | 230.00 |
| Sierra Nevada Section | 165 | 470.00 |
| Southern Cascades Section | 166 | 160.00 |
| **Southeastern Mixed Forest Province** | **45** | **2510.00** |
| Arkansas Valley Section | 167 | 200.00 |
| Coastal Plains, Middle Section | 168 | 150.00 |
| Eastern Gulf Prairies and Marshes Section | 169 | 590.00 |
| Mid Coastal Plains, Western Section | 170 | 980.00 |
| Southern Appalachian Piedmont Section | 171 | 190.00 |
| Southern Cumberland Plateau Section | 172 | 230.00 |

Table D.1 (cont'd).

| Name | Code | Area (km$^2$) |
|---|---|---|
| Southern Ridge and Valley Section | 173 | 170.00 |
| **Southern Rocky Mountain Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province** | **46** | **3340.00** |
| Bighorn Mountains Section | 174 | 130.00 |
| North-Central Highlands Section | 175 | 310.00 |
| Northern Parks and Ranges Section | 176 | 470.00 |
| Overthrust Mountains Section | 177 | 460.00 |
| South-Central Highlands Section | 178 | 460.00 |
| Southern Parks and Ranges Section | 179 | 190.00 |
| Uinta Mountains Section | 180 | 190.00 |
| **Southwest Plateau and Plains Dry Steppe and Shrub Province** | **47** | **2792.02** |
| Edwards Plateau Section | 183 | 570.00 |
| Pecos Valley Section | 184 | 500.00 |
| Rio Grande Plain Section | 185 | 770.00 |
| Rolling Plains Section | 186 | 100.00 |
| Southern Gulf Prairies and Marshes Section | 187 | 722.02 |
| Texas High Plains Section | 188 | 130.00 |

# LITERATURE CITED

Alard, D., and I. Poudevigne. 2000. Diversity patterns in grasslands along a landscape gradient in northwestern France. Journal of Vegetation Science **11**:287-294.

Allain, C., and M. Cloitre. 1991. Characterizing the lacunarity of random and deterministic fractal sets. Physical Review A **44**:3552-3558.

Allen, C. R., E. A. Forys, and C. S. Holling. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. Ecosystems **2**:114-121.

Allen, C. R., and D. A. Saunders. 2002. Variability between scales: predictors of nomadism in birds of an Australian Mediterranean-climate ecosystem. Ecosystems **5**:348-359.

August, P., L. Iverson, and J. Nugranad. 2002. Human conversion of terrestrial habitats. Pages 198-224 *in* K. J. Gutzwiller, editor. Applying landscape ecology in biological conservation. Springer, New York City, New York.

Bailey, R. G. 1988. Ecogeographic analysis: a guide to the ecological division of land for resource management. Misc. Publ. No. 1465. USDA Forest Service, Washington, D.C.

Bailey, R. G. 1996. Ecosystem geography. Springer, New York.

Bailey, R. G. 2002. Ecoregion-based design for sustainability. Springer, New York.

Baker, W. L., and Y. Cai. 1992. The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. Landscape Ecology **7**:291-302.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. Terrestrial Plant Ecology, 2nd edition. The Benjamin/Cummings Publishing Company, Inc., Menlo Park, California.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: individuals, populations and communities, 2nd edition. Blackwell Scientific, London.

Bender, D. J., L. Tischendorf, and L. Fahrig. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology **18**:17-39.

Bolstad, P. 2002. GIS Fundamentals: A first text on geographic information systems. Eider Press, White Bear Lake, Minnesota.

Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 1998. Higher temporal variability of forest breeding bird communities in fragmented landscapes. Proceedings of the National Academy of Sciences, United States of America **95**:7497-7501.

Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. Ecology **82**:1159-1169.

Brown, J. H. 1984. On the relationship between distribution and abundance. The American Naturalist **124**:255-279.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology **76**:2028-2043.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics **27**:597-623.

Bunn, A. G., D. L. Urban, and T. H. Keitt. 2000. Landscape connectivity: A conservation application of graph theory. Journal of Environmental Management **59**:265-278.

Bystrak, D. 1981. The North American Breeding Bird Survey. Studies in Avian Biology **6**:34-41.

Calder, W. A. 1996. Size, function, and life history. Dover Publications, Inc., Mineola NY.

Carrere, V. 1990. Development of multiple source data processing for structural analysis at a regional scale. Photogrammetric Engineering and Remote Sensing **56**:587-595.

Caughley, G., D. Grice, R. J. Barker, and B. Brown. 1988. The edge of the range. Journal of Animal Ecology **57**:771-785.

Chambers, J. M., W. S. Cleveland, K. Beat, and P. A. Tukey. 1983. Graphical methods for data. Duxbury Press, Boston, Massachusetts.

Chao, A., R. L. Chazdon, R. K. Colwell, and T.-J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters **8**:148-159.

Chapin, F. S., III, B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science **277**:500-504.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications **2**:387-396.

Clark, J. S., and D. Pregibon. 1992. Three-based models. Pages 377-419 *in* J. M. Chambers and T. J. Hastie, editors. Statistical models in S. Wadsworth & Brooks/Cole, Pacific Grove, California.

Clarke, K. C. 1999. Getting Started with Geographic Information Systems. Prentice Hall, Upper Saddle River, New Jersey.

Cleland, D. T., P. E. Avers, H. McNab, M. E. Jensen, R. G. Bailey, T. King, and W. E. Russell. 1997. National hierarchical framework of ecological units. *in* M. S. Boyce and A. Haney, editors. Ecosystem management applications for sustainable forest and wildlife resources. Yale University Press, New Haven, CT.

Cornelius, J. M., and J. F. Reynolds. 1991. On determining the statistical significance of discontinuities within ordered ecological data. Ecology **72**:2057-2070.

Cuddington, K., and P. Yodzis. 2002. Predator-prey dynamics and movement in fractal environments. The American Naturalist **160**:119-134.

Curnutt, J. L., S. L. Pimm, and B. A. Maurer. 1996. Population variability of sparrows in space and time. Oikos **76**:131-144.

Dale, M. R. T. 2000. Lacunarity analysis of spatial pattern: A comparison. Landscape Ecology **15**:467-478.

Delcourt, H. R. 1987. The impact of prehistoric agriculture and land occupation on natural vegetation. Trends in Ecology & Evolution **2**:39-44.

Dennis, B. 1989. Stochastic differential equations as insect population models. Pages 219-238 *in* L. McDonald, B. Manly, J. Lockwood, and J. Logan, editors. Estimation and analysis of insect populations. Springer-Verlag, Berlin.

Dennis, B., and R. F. Costantino. 1988. Analysis of steady-state populations with the gamma-abundance model - application to Tribolium. Ecology **69**:1200-1213.

Dennis, B., and G. P. Patil. 1984. The gamma-distribution and weighted multimodal gamma-distributions as models of population abundance. Mathematical Biosciences **68**:187-212.

Diamond, J. M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. Proceedings of the National Academy of Sciences, United States of America **69**:3199-3203.

Dunning, J. B., Jr., editor. 1993. CRC Handbook of Avian Body Masses. CRC Press, Boca Raton, Florida.

Dunning, J. B., Jr., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169-175.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon & Schuster, New York.

Elliott, J. J., and R. S. Arbib, Jr. 1953. Origin and status of the house finch in the eastern United States. The Auk **70**:31-37.

Environmental Systems Research Institute Inc. 1992-1999. ArcView GIS 3.2. Redmond, California.

Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology **66**:1762-1768.

Farnsworth, E. J., and A. M. Ellison. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecological Monographs **66**:45-66.

Fitzgerald, J. A., J. R. Herkert, and J. D. Brawn. 2000. Partners in Flight bird conservation plan for the Prairie Peninsula (physiographic area 31). Partners in Flight, Brentwood, Missouri.

Forman, R. T. T., and M. Godron. 1986. Landscape Ecology. John Wiley & Sons., New York.

Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecology **1**:5-18.

Game, M. 1980. Best shape for nature reserves. Nature **287**:630-632.

Gardner, R. H. 1998. Pattern, process, and the analysis of spatial scales. Pages 17-34 *in* D. L. Peterson and V. T. Parker, editors. Ecological scale: theory and applications. Columbia University Press, New York.

Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology **1**:19-28.

Gaston, K. J., and T. M. Blackburn. 2000. Pattern and process in macroecology. Blackwell Science, Oxford.

Gering, J. C. 2004. Reply to "Ecoregion as a pragmatic tool". Conservation Biology **18**:5-6.

Gering, J. C., T. O. Crist, and J. A. Veech. 2003. Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conservation Biology **17**:488-499.

Goldstein, P. Z. 1999. Functional ecosystems and biodiversity buzzwords. Conservation Biology **13**:247-255.

Golledge, R. G., R. Church, J. Dozier, J. E. Estes, J. Michaelsen, D. S. Simonett, R. Smith, T. Smith, A. H. Strahler, and W. R. Tobler. 1982. Commentary on "The highest form of the geographer's art". Annals of the Association of American Geographers **72**:557-558.

Government of Canada. 1996. The state of Canada's environment - 1996. Government of Canada, Ottawa.

Groves, C., L. Valutis, D. Vosick, B. Neely, K. Wheaton, J. Touval, and B. Runnels. 2000. Designing a geography of hope: a practitioner's handbook for ecoregional conservation planning. The Nature Conservancy, Arlington, Virginia.

Gustafson, E. J. 1998. Quantifying landscape spatial pattern: what is state of the art? Ecosystems **1**:143-156.

Gustafson, E. J., and G. R. Parker. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecology **7**:101-110.

Haines-Young, R., and M. Chopping. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. Progress in Physical Geography **20**:418-445.

Hanski, I., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York, New York.

Hargis, C. D., J. A. Bissonette, and J. L. David. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. Landscape Ecology **13**:167-186.

Hargrove, W. H., and J. Pickering. 1992. Pseudoreplication: a *sine qua non* for regional ecology. Landscape Ecology **6**:251-258.

Hart, J. F. 1982a. Comment in reply. Annals of the Association of American Geographers **72**:559.

Hart, J. F. 1982b. The highest form of the geographer's art. Annals of the Association of American Geographers **72**:1-29.

Hart, J. F. 1983. More gnashing of false teeth. Annals of the Association of American Geographers **73**:441-443.

Havlicek, T. D., and S. R. Carpenter. 2001. Pelagic species size distributions in lakes: Are they discontinuous? Limnological Oceanography **46**:1021-1033.

He, H. S., B. E. DeZonia, and D. J. Mladenoff. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. Landscape Ecology **15**:591-601.

Healey, R. G. 1983. Regional geography in the computer age: a further commentary on "The highest form of the geographer's art". Annals of the Association of American Geographers **73**:439-441.

Herzog, F., and A. Lausch. 2001. Supplementing land-use statistics with landscape metrics: some methodological considerations. Environmental Monitoring and Assessment **72**:37-50.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4**:1-23.

Holling, C. S. 1992. Cross-scale morphologies, geometry, and dynamics of ecosystems. Ecological Monographs **62**:447-502.

Holling, C. S., and C. R. Allen. 2002. Adaptive inference for distinguishing credible from incredible patterns in nature. Ecosystems **5**:319-328.

Holling, C. S., G. Peterson, P. Marples, J. Sendzimir, K. H. Redford, L. Gunderson, and D. Lambert. 1996. Self-organization in ecosystems: lumpy geometries, periodicities and morphologies. Pages 346-384 *in* B. Walker and W. Steffen, editors. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, Massachusetts.

Hunter, W. C., L. H. Peoples, and J. A. Collazo. 2001. South Atlantic coastal plain Partners in Flight bird conservation plan (physiographic area #03). U.S. Fish and Wildlife Service in cooperation with Partners in Flight, Atlanta, Georgia.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Q. Biol. **22**:415-427.

Istock, C. A., and S. M. Scheiner. 1987. Affinities and high-order diversity within landscape mosaics. Evolutionary Ecology **1**:11-29.

Jenness, J. 2004. Nearest features (nearfeat.avx) extension for ArcView 3.x, v. 3.8. Jenness Enterprises.

Johnson, A. R., J. A. Wiens, B. T. Milne, and T. O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology **7**:63-75.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London, Series B **330**:175-190.

Kaufman, L., and P. J. Rousseeuw. 1990. Finding groups in data: an introduction to cluster analysis. John Wiley & Sons, Inc., New York.

King, A. W. 1991. Translating models across scales in the landscape. Pages 479-517 *in* M. G. Turner and R. H. Gardner, editors. Quantitative Methods in Landscape Ecology: Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York.

Knutson, M. G., G. Butcher, J. Fitzgerald, and J. Shieldcastle. 2001. Partners in Flight bird conservation plan for the Upper Great Lakes Plain (physiographic area 16). USGS Upper Midwest Environmental Sciences Center in cooperation with Partners in Flight, LaCrosse, Wisconsin.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology **72**:367-382.

Krebs, C. J. 1989. Ecological Methodology. Harper Collins Publishers, New York, New York.

Lambert, W. D., and C. S. Holling. 1998. Causes of ecosystem transformation at the end of the Pleistocene: evidence from mammal body-mass distributions. Ecosystems **1**:157-175.

Leaper, R., D. Raffaelli, C. Emes, and B. F. J. Manly. 2001. Constraints on body-size distributions: an experimental test of the habitat architecture hypothesis. Journal of Animal Ecology **70**:248-259.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2001. The geographic structure of British bird distributions: diversity, spatial turnover and scale. Journal of Animal Ecology **70**:966-979.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943-1967.

Li, B.-L., and S. Archer. 1997. Weighted mean patch size: a robust index for quantifying landscape structure. Ecological Modelling **102**:353-361.

Li, H., and J. F. Reynolds. 1993. A new contagion index to quantify spatial patterns of landscapes. Landscape Ecology **8**:155-162.

Li, H., and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology **75**:2446-2455.

Li, H., and J. Wu. 2004. Use and misuse of landscape indices. Landscape Ecology **19**:389-399.

Lidicker, W. Z., Jr., and W. D. Koenig. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. Pages 85-109 *in* D. R. McCullough, editor. Metapopulations and Wildlife Conservation. Island Press, Washington, D.C.

Liu, J. 1993. ECOLECON: an ECOLogical-ECONomic model for species conservation in complex forest landscapes. Ecological Modelling **70**:63-87.

Ma, K.-M., B.-J. Fu, X.-D. Gue, and H.-F. Zhou. 2000. Finding spatial regularity in mosaic landscapes: two methods integrated. Plant Ecology **149**:195-205.

Mac Nally, R., A. F. Bennett, G. W. Brown, L. F. Lumsden, A. Yen, S. Hinkley, P. Lillywhite, and D. Ward. 2002. How well do ecosystem-based planning units represent different components of biodiversity? Ecological Applications **12**:900-912.

Mac Nally, R., E. Fleishman, L. P. Bulluck, and C. J. Betrus. 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. Journal of Biogeography **31**:917-929.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Magnusson, W. E. 2004. Ecoregion as a pragmatic tool. Conservation Biology **18**:4-5.

Mandelbrot, B. B. 1983. The Fractal Geometry of Nature. W.H. Freeman, San Francisco, California.

Manly, B. F. J. 1996. Are there clumps in body-size distributions? Ecology **77**:81-86.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature **405**:243-253.

Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. 1997. Agricultural intensification and ecosystem properties. Science **277**:504-509.

Maurer, B. A., E. T. Linder, and D. E. Gammon. 2001. A geographical perspective on the biotic homogenization process: implications from the macroecology of North

American birds. Pages 157-177 *in* J. L. Lockwood and M. L. McKinney, editors. Biotic Homogenization. Kluwer Academic/Plenum Publishers, New York City, New York.

Maurer, B. A., and M. L. Taper. 2002. Connecting geographical distributions with population processes. Ecology Letters **5**:223-231.

Mazerolle, M. J., and M.-A. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: A review. EcoScience **6**:117-124.

McCoy, E. D., and S. S. Bell. 1991. Habitat structure: The evolution and diversification of a complex topic. Pages 3-27 *in* S. S. Bell, E. D. McCoy, and H. R. Mushinsky, editors. Habitat Structure: The physical arrangement of objects in space. Chapman and Hall.

McGarigal, K. M., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW-351.

Meisel, J. E., and M. G. Turner. 1998. Scale detection in real and artificial landscapes using semivariance analysis. Landscape Ecology **13**:347-362.

Milligan, G. W. 1981. A review of Monte Carlo tests of cluster analysis. Multivariate Behavioral Research **16**:379-407.

Milne, B. T., K. M. Johnston, and R. T. T. Forman. 1989. Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model. Landscape Ecology **2**:101-110.

Milne, B. T., M. G. Turner, J. A. Wiens, and A. R. Johnson. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. Theoretical Population Biology **41**:337-353.

Mladenoff, D. J., and B. E. DeZonia. 2002. APACK 2.22 User's Guide.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853-858.

Native Seed Network. 2005. Ecoregion Information: http://www.nativeseednetwork.org. Corvallis, Oregon.

Nekola, J. C., and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography **26**:867-878.

Nicholls, A. O. 1994. Variation in mosaic diversity in the forests of coastal northern New South Wales. Pacific Conservation Biology **1**:177-182.

Noon, B. R., and V. H. Dale. 2002. Broad-scale ecological science and its application. Pages 34-52 *in* K. J. Gutzwiller, editor. Applying landscape ecology in biological conservation. Springer, New York, New York.

Olson, D. M., and E. Dinerstein. 1998. The global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biology **12**:502-515.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience **51**:933-938.

Omernik, J. M. 1995. Ecoregions: A spatial framework for environmental management. Pages 49-65 *in* W. S. Davis and T. P. Simon, editors. Biological assessment and criteria: tools for water resource planning and decision making. CRC Press, Boca Raton, FL.

O'Neill, R. V., C. T. Hunsaker, S. P. Timmins, B. L. Jackson, K. B. Jones, K. H. Riitters, and J. D. Wickham. 1996. Scale problems in reporting landscape pattern at the regional scale. Landscape Ecology **11**:169-180.

O'Neill, R. V., and A. W. King. 1998. Homage to St. Michael; or, why are there so many books on scale? Pages 3-15 *in* D. L. Peterson and V. T. Parker, editors. Ecological Scale: Theory and Applications. Columbia University Press, New York.

O'Neill, R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and R. L. Graham. 1988a. Indices of landscape pattern. Landscape Ecology **1**:153-162.

O'Neill, R. V., B. T. Milne, M. G. Turner, and R. H. Gardner. 1988b. Resource utilization scales and landscape pattern. Landscape Ecology **2**:63-69.

Patton, D. R. 1975. A diversity index for quantifying habitat "edge". Wildlife Society Bulletin **3**:171-173.

Peters, R. H. 1983. The ecological implications of body size, 1st edition. Press Syndicate of the University of Cambridge, Cambridge.

Peterson, D. L., and V. T. Parker. 1998. Dimensions of scale in ecology, resource management, and society. Pages 499-522 *in* D. L. Peterson and V. T. Parker, editors. Ecological scale: theory and applications. Columbia University Press, New York.

Pickett, S. T. A., and K. H. Rogers. 1997. Patch dynamics: the transformation of landscape structure and function. Pages 101-127 *in* J. A. Bissonette, editor. Wildlife and Landscape Ecology: Effects of Pattern and Scale. Springer, New York.

Pimm, S. L. 1986. Community stability and structure. Pages 309-329 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusetts.

Pimm, S. L. 2001. The world according to Pimm: a scientist audits the Earth. R.R. Donnelley & Sons.

Pimm, S. L., and R. A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. Proceedings of the National Academy of Sciences, United States of America **92**:9343-9347.

Pimm, S. L., and P. Raven. 2000. Extinction by numbers. Nature **403**:843-845.

Plotnick, R. E., R. H. Gardner, W. H. Hargrove, K. Prestegaard, and M. Perlmutter. 1996. Lacunarity analysis: A general technique for the analysis of spatial patterns. Physical Review E **53**:5461-5468.

Plotnick, R. E., R. H. Gardner, and R. V. O'Neill. 1993. Lacunarity indices as measures of landscape texture. Landscape Ecology **8**:201-211.

Poynton, J. C., and R. C. Boycott. 1996. Species turnover between Afromontane and eastern African lowland faunas: patterns shown by amphibians. Journal of Biogeography **23**:669-680.

Qian, H., K. Klinka, and G. J. Kayahara. 1998. Longitudinal patterns of plant diversity in the North American boreal forest. Plant Ecology **138**:161-178.

R Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raffaelli, D., S. Hall, C. Emes, and B. F. J. Manly. 2000. Constraints on body size distributions: an experimental approach using a small-scale system. Oecologia **122**:389-398.

Restrepo, C., L. M. Renjifo, and P. Marples. 1997. Frugivorous birds in fragmented neotropical montane forests: landscape pattern and body mass distribution. Pages 616 *in* W. F. Laurance and R. O. Bierregaard, Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois.

Rey Benayas, J. M., and S. M. Scheiner. 2002. Plant diversity, biogeography and environment in Iberia: Patterns and possible causal factors. Journal of Vegetation Science **13**:245-258.

Richards, J. F. 1990. Land transformation. Pages 163-178 *in* B. L. Turner, II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, editors. The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years. Cambridge University Press, Cambridge, Massachusetts.

Ricketts, T. H., E. Dinerstein, D. M. Olson, and C. Loucks. 1999. Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. BioScience **49**:369-381.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters **7**:1-15.

Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. Landscape Ecology **10**:23-39.

Riitters, K. H., R. V. O'Neill, and K. B. Jones. 1997. Assessing habitat suitability at multiple scales: A landscape-level approach. Biological Conservation **81**:191-202.

Riitters, K. H,, R. V. O'Neill, J. D. Wickham, and K. B. Jones. 1996. A note on contagion indices for landscape analysis. Landscape Ecology **11**:197-202.

Rising, J. D., and K. M. Somers. 1989. The measurement of overall body size in birds. The Auk **106**:666-674.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. U.S. Fish Wild. Serv. Resour. Publ. 157.

Robinson, S. K., F. R. Thompson, III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987-1990.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs **52**:199-221.

Rousseeuw, P. J., A. Struyf, and M. Hubert. 2004. Cluster: functions for clustering. R package version 1.9.6.

Ruggiero, A., J. H. Lawton, and T. M. Blackburn. 1998. The geographic ranges of mammalian species in South America: spatial patterns in environmental resistnace and anisotropy. Journal of Biogeography **25**:1093-1103.

SAS Institute. 1999. SAS User's Guide: Statistics, Version 5 Edition. SAS Institute, Inc., Cary, North Carolina.

Sauer, J. R., J. E. Hines, and J. Fallon. 2001. The North American Breeding Bird Survey, results and analysis 1966-2000. Version 2001.2. USGS Patuxent Wildlife Research Center, Laurel, MD.

Scheiner, S. M. 1992. Measuring pattern diversity. Ecology **73**:1860-1867.

Scheiner, S. M., and J. M. Rey Benayas. 1994. Global patterns of plant diversity. Evolutionary Ecology **8**:331-347.

Schneider, D. C. 1998. Applied scaling theory. Pages 253-269 *in* D. L. Peterson and V. T. Parker, editors. Ecological Scale: Theory and Applications. Columbia University Press, New York.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology **49**:123-141.

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. Ecology **77**:1210-1225.

Schwinghamer, P. 1981. Characteristic size distributions of integral benthic communities. Can. J. Fish. Aquat. Sci. **38**:1255-1263.

Schwinghamer, P. 1988. Influence of pollution along a natural gradient and in a mesocosm experiment on biomass-size spectra of benthic communities. Marine Ecology Progress Series **46**:199-206.

Scott, J. M. 1993. A geographical approach to protection of biological diversity. Wildlife Monographs:1-41.

Siemann, E., and J. H. Brown. 1999. Gaps in mammalian body size distributions reexamined. Ecology **80**:2788-2792.

Silverman, B. W. 1981. Using kernel density estimates to investigate multimodality. Journal of the Royal Statistical Society, B **43**:97-99.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman & Hall, London.

South, J. M., and S. Pruett-Jones. 2000. Patterns of flock size, diet, and vigilance of naturalized monk parakeets in Hyde Park, Chicago. The Condor **102**:848-854.

Spector, S. 2002. Biogeographic crossroads as priority areas for biodiversity conservation. Conservation Biology **16**:1480-1487.

Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. The American Naturalist **129**:533-552.

Stewart, A. J. A., E. A. John, and M. J. Hutchings. 2000. The world is heterogeneous: ecological consequences of living in a patchy environment. Pages 1-8 *in* M. J. Hutchings, E. A. John, and A. J. A. Stewart, editors. The ecological consequences of environmental heterogeneity. British Ecological Society, Oxford, England.

Sweeney, B. A., and J. E. Cook. 2001. A landscape-level assessment of understory diversity in upland forests of North-Central Wisconsin, USA. Landscape Ecology **16**:55-69.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos **68**:571-573.

Tischendorf, L. 2001. Can landscape indices predict ecological processes consistently? Landscape Ecology **16**:235-254.

Tischendorf, L., and L. Fahrig. 2000a. How should we measure landscape connectivity? Landscape Ecology **15**:633-641.

Tischendorf, L., and L. Fahrig. 2000b. On the usage and measurement of landscape connectivity. Oikos **90**:7-19.

Tukey, J. W. 1977. Exploratory data analysis. Addison-Wesley, Reading, Massachusetts.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology **72**:1253-1266.

Turchin, P. 1996. Fractal analyses of animal movement: a critique. Ecology **77**:2086-2090.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics **20**:171-197.

Turner, M. G., and R. H. Gardner. 1991. Quantitative methods in landscape ecology: an introduction. Pages 3-14 *in* M. G. Turner and R. H. Gardner, editors. Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice. Springer, New York, NY.

Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne. 1989. Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecology **3**:153-162.

Turner, S. J., R. V. O'Neill, W. Conley, M. R. Conley, and H. C. Humphries. 1991. Pattern and scale: Statistics for landscape ecology. Pages 17-49 *in* M. G. Turner and R. H. Gardner, editors. Quantitative Methods in Landscape Ecology: Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York.

U.S. Department of the Interior. 2005. National Atlas of the United States: http://www.nationalatlas.gov. Washington, D.C.

Urban, D., and T. H. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology **82**:1205-1218.

USDA Forest Service Inventory and Monitoring Institute. 2005. Ecoregions: http://www.fs.fed.us/institute/ecolink.html. Fort Collings, Colorado.

Veit, R. R., and M. A. Lewis. 1996. Dispersal, population growth, and the Allee effect: dynamics of the House finch invasion of eastern North America. The American Naturalist **148**:255-274.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melilo. 1997. Human domination of Earth's ecosystems. Science **277**:494-499.

Vogelmann, J. E., S. M. Howard, L. Yang, C. R. Larson, B. K. Wylie, and N. Van Driel. 2001. Completion of the 1990s National Land Cover Data Set for the coterminous United States from Landsat Thematic Mapper data and ancillary data sources. Photogrammetric Engineering and Remote Sensing **67**:650-652.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association **58**:236-244.

Warner, R. E. 1994. Agricultural land use and grassland habitat in Illinois: future shock for midwestern birds? Conservation Biology **8**:147-156.

Western, D. 2001. Human-modified ecosystems and future evolution. Proceedings of the National Academy of Sciences of the United States of America **98**:5458-5465.

Whittaker, R. H. 1975. Communities and ecosystems. Macmillan, New York.

Wiegand, T., K. A. Moloney, J. Naves, and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. The American Naturalist **154**:605-627.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1-26 *in* L. Hansson, L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman & Hall, London.

Wiens, J. A. 2002. Central concepts and issues of landscape ecology. Pages 3-21 *in* K. J. Gutzwiller, editor. Applying Landscape Ecology in Biological Conservation. Springer-Verlag, New York, NY.

Wiens, J. A., T. O. Crist, K. A. With, and B. T. Milne. 1995. Fractal patterns of insect movement in microlandscape mosaics. Ecology **76**:663-666.

Wiens, J. A., and B. T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology **3**:87-96.

Wiens, J. A., N. C. Stenseth, B. Van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos **66**:369-380.

Williams, E. J., and D. N. Pashley. 1999. Designation of conservation planning units. *in* R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, editors. Strategies for bird conservation: the Partners in Flight planning process. Cornell Lab of Ornithology, <http://birds.cornell.edu/pifcapemay>.

Williams, M. 1990. Forests. Pages 179-201 *in* B. L. Turner, II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, editors. The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years. Cambridge University Press, Cambridge, Massachusetts.

Wilson, E. O. 1992. The Diversity of Life. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Wilson, M. V., and A. Shmida. 1984. Measuring beta diversity with presence-absence data. Journal of Ecology **72**:1055-1064.

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology **9**:25-36.

With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology **76**:2446-2459.

With, K. A., and T. O. Crist. 1996. Translating across scales: Simulating species distributions as the aggregate response of individuals to heterogeneity. Ecological Modelling **93**:125-137.

With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos **78**:151-169.

Wu, J. 2004. Effects of changing scale on landscape pattern analysis: Scaling relations. Landscape Ecology **19**:125-138.

Wu, J., and R. J. Hobbs. 2002. Key issues and research priorities in landscape ecology: An idiosyncratic synthesis. Landscape Ecology **17**:355-365.

Wu, J., D. E. Jelinski, M. Luck, and P. T. Tueller. 2000. Multiscale analysis of landscape heterogeneity: Scale variance and pattern metrics. Geographic Information Sciences **6**:6-19.

Wu, J., and Y. Qi. 2000. Dealing with scale in landscape analysis: an overview. Geographic Information Sciences **6**:1-5.

Wu, J., W. Shen, W. Sun, and P. T. Tueller. 2002. Empirical patterns of the effects of changing scale on landscape metrics. Landscape Ecology **17**:761-782.

Zheng, D., D. O. Wallin, and Z. Hao. 1997. Rates and patterns of landscape change between 1972 and 1988 in the Changbai Mountain area of China and North Korea. Landscape Ecology **12**:241-254.