

ABSTRACT

Title of Dissertation: DYNAMICS OF THE SHORT TERM AND LONG TERM AVIAN DISTRIBUTIONS IN NORTH AMERICA - THE ROLES OF VEGETATION HEIGHT HETEROGENEITY AND CLIMATIC FACTORS

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Understanding how biodiversity spatially distribute over both the short term and long term, and what factors are affecting the distribution, are critical for modeling the spatial pattern of biodiversity as well as for promoting effective conservation planning and practices. This dissertation aims to examine factors that influence short-term and long-term avian distribution from the geographical sciences perspective.

The research develops landscape level habitat metrics to characterize forest height heterogeneity and examines their efficacies in modelling avian richness at the continental scale. Two types of novel vegetation-height-structured habitat metrics are created based on second order texture algorithms and the concepts of patch-based habitat metrics. I correlate the height-structured metrics with the richness of different forest guilds, and also examine their efficacies in multivariate richness models. The results suggest that height heterogeneity, beyond canopy height alone, supplements

habitat characterization and richness models of two forest bird guilds. The metrics and models derived in this study demonstrate practical examples of utilizing three-dimensional vegetation data for improved characterization of spatial patterns in species richness.

The second and the third projects focus on analyzing centroids of avian distributions, and testing hypotheses regarding the direction and speed of these shifts. I first showcase the usefulness of centroids analysis for characterizing the distribution changes of a few case study species. Applying the centroid method on 57 permanent resident bird species, I show that multi-directional distribution shifts occurred in large number of studied species. I also demonstrate, plain birds are not shifting their distribution faster than mountain birds, contrary to the prediction based on climate change velocity hypothesis. By modelling the abundance change rate at regional level, I show that extreme climate events and precipitation measures associate closely with some of the long-term distribution shifts.

This dissertation improves our understanding on bird habitat characterization for species richness modelling, and expands our knowledge on how avian populations shifted their ranges in North America responding to changing environments in the past four decades. The results provide an important scientific foundation for more accurate predictive species distribution modeling in future.

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DISTRIBUTIONS IN NORTH AMERICA - THE ROLES OF VEGETATION
HEIGHT HETEROGENEITY AND CLIMATIC FACTORS

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Dedication

To my parents,

Qijun Huang and Ming Xu

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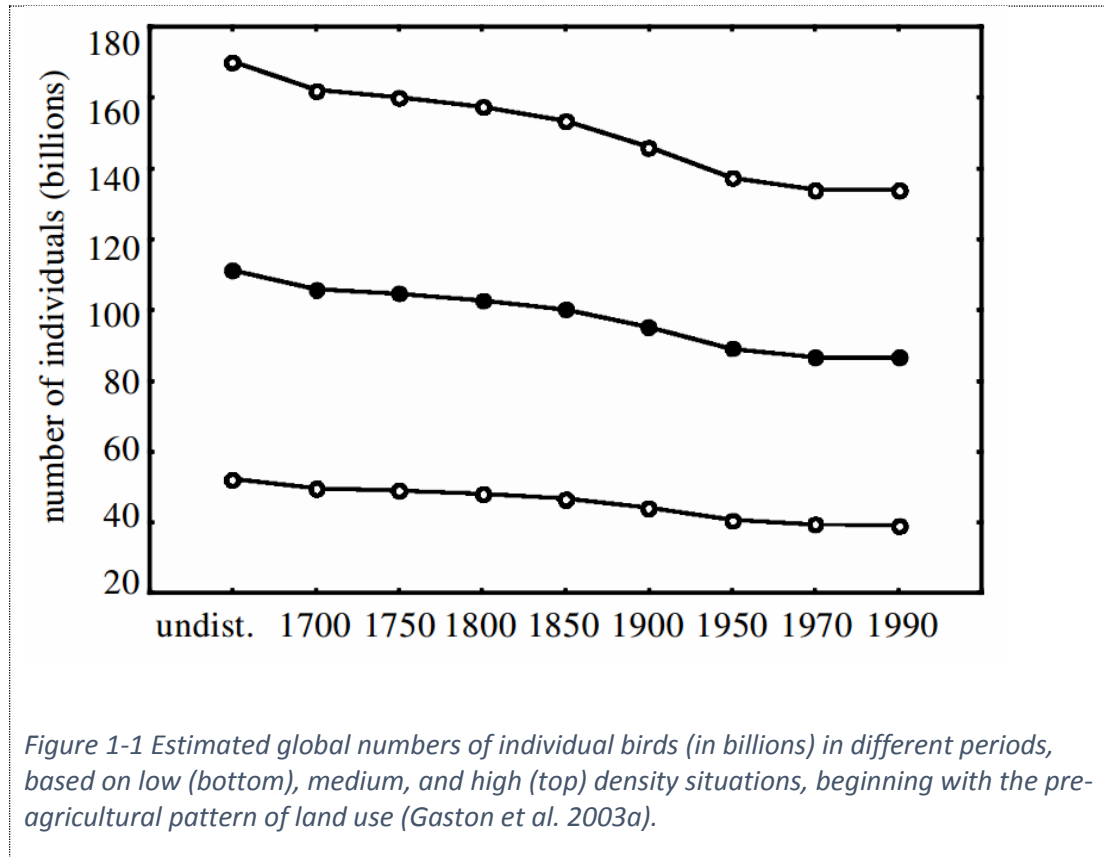
Chapter 1. Introduction

1.1 Motivation & Background

Since the Industrial Revolution, between one-third to one-half of the Earth's land surface has been transformed by human actions. As a result, approximately one-quarter of avian species have gone extinct (Vitousek et al. 1997). The questions of how wildlife communities interact with changing habitat, and how species are adapting to anthropogenic environmental changes such as habitat conversion and climate change, are of increasing urgency. For endangered species whose distributions are restricted to fragmented habitats, understanding the dynamics of species distribution and its relationship with changing environments will provide a critical scientific foundation for accurate prediction of future distributions, and promote more cost-effective conservation planning and practices (Pereira et al. 2010).

Birds are excellent research subjects for studying responses of biodiversity distribution to environmental changes because they have a relatively well documented record, are ecologically diverse, are distributed widely, and are highly responsive to changes such as climate and habitat changes (Araújo and Pearson 2005). Many of the global avian populations have been undergoing dramatic decline, mostly due to habitat conversion (Gaston et al. 2003) (Figure 1-1). Particularly in the U.S., the avian populations undergone significant changes during the past few decades, although the area of forested land has remained relatively stable since the 1950s (United States Forest Service 2001). Most neotropical migrant bird species populations have declined in the

eastern U.S. and Canada in the 1970s and 1980s dramatically (Robbins et al. 1989b, Sauer et al. 2014). Similar declines are observed and confirmed by numerous studies a local scale as well (Holmes and Sherry 2001, Holmes 2007).



Understanding the landscape-level factors that determine biodiversity patterns in the short term and the factors driving species distribution shifts over the long term are priority inquiries in addressing not only the declining avian diversity but general biodiversity at risk. However, the current knowledge on avian biodiversity and range distribution is limited in two domains.

Firstly, in the short term, the distribution of biodiversity is considered stationary, and is predominantly controlled by environmental conditions, most dominantly habitat characteristics. Vertical characteristics of the habitat, particularly the vegetation's vertical characteristics, however have not been adequately considered when we explain the patterns of bird biodiversity distributions. The traditional methods to model avian species richness have relied predominantly on quantifying habitats' horizontal characteristics. As remote sensing and GIS techniques become increasingly prevalent, many aspects of habitats' horizontal characteristics have been explored. For example the normalized vegetation index (NDVI) as a measure of primary productivity (Oindo and Skidmore 2002), land-cover types heterogeneity as an indicator of habitat heterogeneity (Gould 2000) and habitat fragmentation (Luoto et al. 2004) have all been used to relate to habitat quality and species richness. However the third-dimension of vegetation- the habitat height structure, is just as important to biodiversity as the horizontal characteristics (Bergen et al. 2009).

Bird species in particular, are known to have structural habitat requirements and preferences (MacArthur and MacArthur 1961). As recent developments in active remote sensing technology advance, emerging systems such as Light Detection And Ranging (lidar) and Radio Detection And Ranging (Radar) have shown great capability in mapping the vertical dimensions of vegetation structure with high accuracies(Lefsky et al. 2002, Bergen et al. 2009). The three-dimensional vegetation information derived from these systems has been applied to a few studies (e.g. Goetz et al. 2007, Swatantran et al. 2012). Most of the studies focused on the local or

regional relationship between avian biodiversity and forest height structure. The applicability of vegetation height structure and heterogeneity to continental-scale avian species richness models remains uncertain. Also most studies have emphasized only simple summary statistics of height values, such as the mean, maximum and minimum vegetation height value within the studied scenes. Those metrics are easy to obtain, however they cannot capture complex spatial variation of vegetation height structure.

Secondly, in the long term, the shift of species distributions is considered a major fingerprint of global climate change. However very few studies have examined the patterns of the avian geographical range shift at continental scale in North America. Although it has been hypothesized that global warming has driven the poleward and elevationally upward movement across taxonomic groups (Parmesan et al. 1999, La Sorte and Thompson 2007), methodologies identifying systematic shift of species distribution mostly focus at the edge of species ranges. In particular, the inferred edge of the range can be a somewhat crude index to characterize changes in species distributions (Gaston et al. 2003), as regional studies at the outermost limit of species occurrence are not robust to exclusion or inclusion of outliers (Santelmann 1991, Van Rossum et al. 1997). There lacks a method to quantify the change of species distribution more systematically, especially at the continental scale. Additionally many of the hypotheses have been proposed to predict the direction and the speed of the distribution shifts, few of which, however, has been tested. Little research has been done to examine the effect of non-climatic factors, or to compare the influences of different climatic factors on changing species

distributions. The paucity of the research on species' range shift and the factors driving them, likely stems from the difficulties of collecting standardized species data-often at the continental scale(Parmesan 2006). As a result, climate envelop models (often referred to as species distribution models), which assume plants and animals are always at equilibrium with their suitable climatic conditions (Guisan and Thuiller 2005), are still the primary tools used to project species and biomes' distribution shift (Pereira et al. 2010). This is a limited approach because, among other concerns, species with drastically different biological attributes are treated the same when modeled for future distribution, and almost all the climatic variables are fed into the statistical model as equally important variables. Additionally, most of the climate variables used in those models are average measures of seasonal or annual temperature and precipitation, which might not be linked with species distribution ecologically. Insufficient studies on species' distribution change pattern and what environmental factors have driven such changes limit the accuracy and the usefulness of existing models' predictions (Pereira et al. 2010).

1.2 Objectives & Outlines

1.2.1 Objectives

The overall goal of my dissertation is to understand the impact of vegetation height, climatic and non-climatic factors on the short term and long term avian biodiversity distribution in the U.S.

In particular, I seek to achieve 3 objectives (Figure 1-2):

1. Develop landscape level habitat metrics to characterize forest height heterogeneity, and examine their efficacy on short term avian richness models at the continental scale.
2. Develop a distribution centroid metric to characterize avian spatial distribution, and demonstrate the efficacies of the centroid analysis in associating with drastic distribution shifts.
3. Examine the direction and speed of climate change fingerprint among permanent resident birds in the U.S. to test the multidirectionality of distribution shifts, to test the prediction based on climate change velocity hypothesis, and to evaluate the influence of different climatic factors on population changes for species with significant shifts.

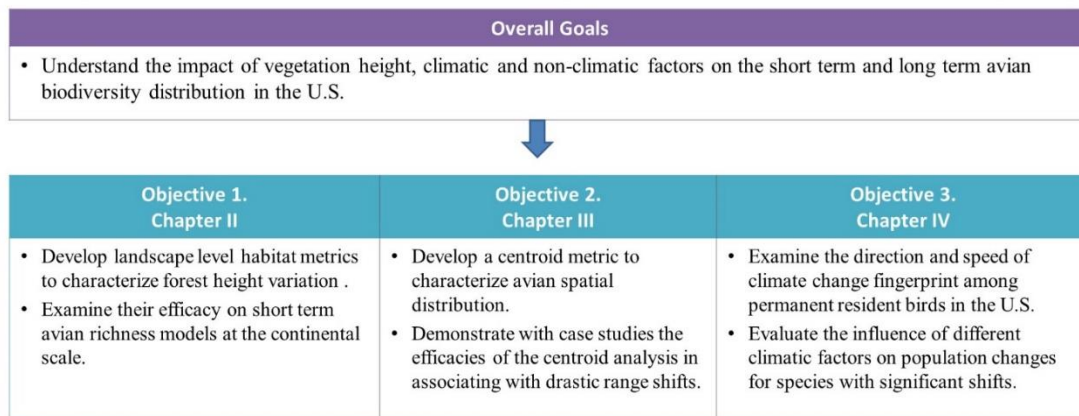


Figure 1-2 Organization of Dissertation chapters.

1.2.2 Outlines

1.2.2.1 Chapter 2. The Influence of Vegetation Height Heterogeneity on Forest and Woodland Bird Species Richness across the United States.

The focus of this part of the dissertation is to demonstrate practical ways of creating habitat metrics that incorporate vegetation height heterogeneity, and to test the efficacies of the height-structure metrics in avian richness modeling. Doing so will improve our understanding on the relationship between avian biodiversity and habitat structure. To achieve this I develop two groups of height-incorporated habitat metrics: the height-structured patch-based metrics and second-order texture metrics. I examine how individual metric correlates with the richness of three forest bird guilds, and how the addition of the selected height-structured metrics can improve the multivariate bird richness models using traditional metrics.

1.2.2.2 Chapter 3. A Centroid Model of Species Distribution with Applications to the Carolina Wren (*Thryothorus Ludovicianus*) and House Finch (*Haemorhous Mexicanus*) in the United States

Chapter 3 introduces a distribution centroid as a population descriptor to characterize the annual spatial distribution of bird species. The foundation of the centroid analysis is a Bayesian model that reliably model individual species population change at the regional level. I provide detailed descriptions on the hierarchical Bayesian model and the procedures of producing centroids based

on modeled abundance indices. Then as case studies, I derive annual centroids for the Carolina wren and house finch in their ranges in the U.S. Lastly, I evaluate the correlation between species' centroid movement and changes in winter severity and total population abundance. The case studies highlight the usefulness and applicability of the centroid method in reflecting changes of species distributions affected by factors such as environmental stressors and invasive colonization process.

1.2.2.3 Rapid Multi-directional Climate Change Fingerprint in North American Bird Distributions Associated with Multi-faceted Climate Change

This chapter is built on the methodological foundation of chapter 3. I use the centroid method developed in the previous chapter to quantify the direction and speed of 57 permanent resident birds in North America. I document the ratio of species that experienced significant centroid shift in four directions (north, south, east, and west), and their corresponding population status. I first utilize the analysis to test the multi-directionality of the distribution shifts. I then test a prediction based on climate velocity hypothesis that the species occurring in flat regions will shift their distributions at a faster rate than species in mountainous regions. The prediction is founded because the low topographic variability in flat areas leads to low temperature gradient which will require species to shift longer distance in order to maintain constant temperature condition. Lastly, to explore the relative influence of different climatic factors behind the significant distribution shifts, I model the regional abundance change rate that constitute the shift of distributions. I used temperature, precipitation, average climate, and extreme climate models to

explain the abundance change rate for the species with significant shift of distribution. Model performances and are evaluated in two pair-wise comparisons (temperature vs. precipitation, average climate vs. extreme climate).

1.2.3 The North American Breeding Bird Survey Data

Throughout this dissertation, I used the North American Breeding Survey (BBS) Data to model avian richness, species range centroid, and regional abundance indices. Because of its extensive geographical and temporal coverage, the BBS provides a unique opportunity for analyzing continental scale distribution of avian diversity and changes in avian distributions. The BBS started in 1966, and by 1968 it was established in the contiguous U.S. and southern Canada. It is an annual roadside survey with > 5000 routes along secondary roads covering the contiguous United States, southern Canada, and northern Mexico. Each route is 39.43 km in length and has 50 sample points evenly spread out along the route path. Each year, competent volunteers survey routes during breeding season using a protocol of 3 min point counts at each sample point. Birds heard and seen within 0.4 km radius are recorded (Robbins et al. 1986, Sauer et al. 2014). The numbers of routes surveyed and consistency of coverage has increased throughout the survey period, but few routes have been surveyed every year since the beginning of the BBS (Link and Sauer 2002).

1.3 Summary

Although my dissertation focuses on multiple aspects of avian distributions at different temporal scales, the ultimate purpose is to understand the dynamics of avian distribution in North America, and ultimately to provide insight into the nature of short term and long term distribution of other wildlife. Through examination of how current environmental structures determine the spatial distribution of species and biodiversity, and how these distributions respond to environmental changes, we can establish more accurate ecological theories and models to predict future distribution of biodiversity. Specifically, by incorporating vegetation height heterogeneity, and by utilizing the centroid method, I expand the methodologies on habitat characterization, species richness modeling, and long term species range monitoring. The information generated from this dissertation can help to establish better predictive species distribution models and provide a foundation upon which effective conservation planning and practices rely.

Chapter 2. The influence of vegetation height heterogeneity on forest and woodland bird species richness across the United States

2.1 Abstract

Avian diversity is under increasing pressures. It is thus critical to understand the ecological variables that contribute to large scale spatial distribution of avian species diversity.

Traditionally, studies have relied primarily on two-dimensional habitat structure to model broad scale species richness. Vegetation vertical structure is increasingly used at local scales. However, the spatial arrangement of vegetation height has never been taken into consideration. Our goal was to examine the efficacies of three-dimensional forest structure, particularly the spatial heterogeneity of vegetation height in improving avian richness models across forested ecoregions in the U.S. We developed novel habitat metrics to characterize the spatial arrangement of vegetation height using the National Biomass and Carbon Dataset for the year 2000 (NBCD). The height-structured metrics were compared with other habitat metrics for statistical association with richness of three forest breeding bird guilds across U.S. Breeding Bird Survey (BBS) routes: a broadly grouped woodland guild, and two forest breeding guilds with preferences for forest edge and for interior forest. Parametric and non-parametric models were built to examine the improvement of predictability. Height-structured metrics had the strongest associations with species richness, yielding improved predictive ability for the woodland guild richness models ($r^2 \sim 0.53$ for the parametric models, 0.63 the non-parametric model) and the forest edge guild models ($r^2 \sim 0.34$ for the parametric models, 0.47 the non-parametric model).

All but one of the linear models incorporating height-structured metrics showed significantly

higher adjusted- r^2 values than their counterparts without additional metrics. The interior forest guild richness showed a consistent low association with height-structured metrics. Our results suggest that height heterogeneity, beyond canopy height alone, supplements habitat characterization and richness models of forest bird species. The metrics and models derived in this study demonstrate practical examples of utilizing three-dimensional vegetation data for improved characterization of spatial patterns in species richness.

2.2 Introduction

Avian diversity has been under increasing pressure from anthropogenic disturbances such as habitat loss and fragmentation (Gaston et al. 2003). Successful conservation planning relies upon understanding how the distribution of avian richness responds to existing and potential changes in environmental conditions which influence their distributions. Discovering the drivers of large-scale spatial variation of species richness has been a central debate in ecology (Palmer 1994, Rosenzweig 1995, Gaston 2000, Gaston and Spicer 2004), and many hypotheses have been proposed to address this issue (Waide et al. 1999, Rahbek and Graves 2001, Willig et al. 2003, Hawkins et al. 2003, Colwell et al. 2004, Currie et al. 2004). One major hypothesis suggests that habitat heterogeneity is a key factor because it leads to greater spatial variability of habitat physical conditions, and therefore permits greater niche specialization resulting in more species richness (Kerr and Packer 1997, Kerr et al. 2001, Koh et al. 2006, Davies et al. 2007).

Particularly in North America, habitat heterogeneity theory predicted the richness of some faunas significantly better than the species-energy theory (Kerr and Packer 1997, Rahbek and Graves 2001, Kerr et al. 2001). This latter theory also has widespread support, and hypothesizes that

productive energy through food webs or species physiological constraints to ambient energy determines species richness (Waide et al. 1999, Gaston 2000, Hawkins et al. 2003, Evans et al. 2005).

Traditionally large scale habitat heterogeneity has been quantified mostly as topographical variability (Richerson and Lum 1980, Kerr and Packer 1997, Rahbek and Graves 2001) or two dimensional habitat characteristics derived from remote sensing products (Turner et al. 1988, Duro et al. 2007). Vertical habitat structure may also lead to niche generalization, and as such be an important element of habitat heterogeneity affecting biodiversity (Bergen et al. 2009). However, it has rarely been used to explain species richness at broad scales. The incorporation of vertical heterogeneity is especially important for avian richness models where vertical habitat structure at local scales has long been recognized as a critical factor influencing bird life history (Robinson and Holmes 1984, Kelly 1993, Halaj et al. 2000) and abundance (MacArthur and MacArthur 1961, Whittaker et al. 2001).

Until recently, there have been relatively few studies utilizing three-dimensional habitat information due to difficulties of acquiring measurements of vertical vegetation structure beyond the plot scale over extended geographical areas (Bergen et al. 2009). This has changed significantly since the emergence of active remote sensing systems such as Light Detection and Ranging (lidar) and Radio Detection and Ranging (radar) which provide capability to map the vertical dimension of vegetation at local to regional scales (Lefsky et al. 2002, Bergen et al. 2009). There is an increasing number of studies using lidar and radar derived three-dimensional vegetation structure to model biodiversity, many of which have revealed significant association between vegetation vertical structure, habitat quality, species richness and abundance (Imhoff et al. 1997, Bergen et al. 2007, Goetz et al. 2007, Swatantran et al. 2012, Culbert et al. 2013,

Zellweger et al. 2013). However, none of the existing habitat metrics sufficiently characterize the spatial arrangement of vegetation height (i.e. the heterogeneity of height), nor its potential for predicting avian richness distributions over large geographical extents.

Related advances have been made in the development of statistical fusion models that provide a means to effectively combine remotely sensed data from radar, lidar, optical remote sensing systems and forest inventory data, yielding wall-to-wall high resolution vegetation structure maps at the continental scale (Walker et al. 2007, Kellndorfer et al. 2010, 2011, Saatchi et al. 2011, Baccini et al. 2012). The production of these maps not only enables the creation of habitat metrics that capture rich vegetation height heterogeneity, but also the comparison of the predictive abilities in various forms of these metrics. Our study is designed to embrace these opportunities by examining the relationship between forest bird richness, height-structured habitat metrics and avian richness models involving various degrees of forest height heterogeneity.

The overall goal of our study is to examine the potential of three-dimensional habitat structure in improving avian richness models at broad geographical scales. In doing so we hope to expand our understanding of the relationship between habitat structure and the spatial distribution of avian species richness, and to lay the foundation for constructing habitat metrics that better utilize increasingly available three-dimensional habitat data. Specifically we address the following questions:

1. How do the height-structured metrics compare with traditional habitat metrics in their ability to associate and predict forest bird richness in the forested ecoregion of the U.S.? Does

incorporating the height-structured metrics improve the explanatory ability of avian richness models that use traditional habitat metrics?

2. How does the predictive skill of richness models vary among forest bird guilds with contrasting preferences to habitat edges?

First, we introduce the conceptual similarities and differences between traditional habitat metrics and two types of height-structured metrics. Next, we describe the data and the methods we used to create the habitat metrics in this study. We then use correlation analysis and multivariate regression models to examine the relationships between different combinations of metrics and the species richness of three forest breeding guilds. Lastly, we examine the models' explanatory abilities and the importance of individual metrics in predicting the richness of the three guilds.

2.3 Background

Traditional habitat metrics are based primarily on two-dimensional habitat structure, such as land cover types, patch size and shape statistics. Developing such metrics generally depends on two steps: a) classifying scene space into binary habitat and non-habitat land cover types; b) delineating habitat patches based on the rule of contiguity (Figure 2-1) (Girvetz and Greco 2007). There have been numerous studies using habitat patch metrics and derivative habitat edge and contrast metrics to associate with ecological attributes such as species richness, reproductive success and individual fitness of birds (Strelke and Dickson 1980, Robbins et al. 1989a, Helzer and Jelinski 1999). However vegetation height information generally plays little role in the process of delineating habitat patches and characterizing their properties.

Some studies have applied three-dimensional habitat information in habitat quality and species diversity models (Hill et al. 2004, Broughton et al. 2006, Goetz et al. 2007, Hinsley et al. 2009,

Swatantran et al. 2012, Culbert et al. 2013). Usually, these applications rely on simple summary statistics such as mean, maximum, minimum and standard deviation to characterize three-dimensional vegetation structure. Summary statistics are straightforward and easy to obtain, but they cannot fully capture the heterogeneity of vegetation vertical structure. To give an example, one can have two forested landscapes with the same mean, maximum, minimum and standard deviation of tree height but with greatly different spatial arrangements of trees (e.g. tall trees can cluster in a few locations or can randomly distribute over the landscape which would have very different ecological implications for bird communities).

To account for more height heterogeneity, we created two groups of height-structured habitat metrics, the first of which integrates vegetation height information into the habitat patch framework while the second one characterizes canopy height distribution directly using second-order texture algorithms.

At the canopy level, vertical differences in vegetation create boundaries that segment contiguous habitats into smaller patches, each with similar height values (Figure 2-1). We first classified height pixels into a few height classes to characterize vertical edges and patches. Next, we grouped adjacent pixels from the same height class into patches. We treated the boundaries dividing those vertical patches as vertical edges (Figure 2-1). We also weighted the vertical edges by their depth (the height difference between two sides of a vertical edge) to capture the contrast of the height values of neighboring patches. By doing so, we could adapt a wide range of conventional habitat patch and edge metrics to account for complex spatial variability of canopy height.

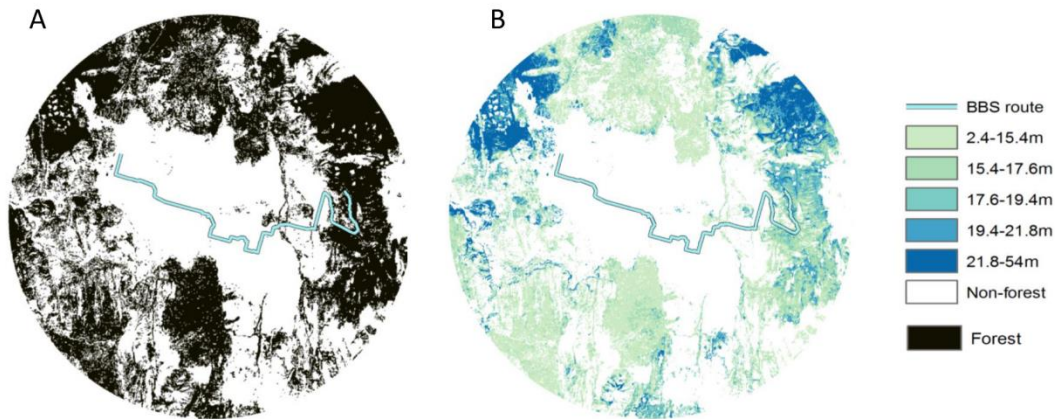


Figure 2-1 An example of the delineation of habitat patches at one BBS location. A two-dimensional vegetation map (A) and a vegetation map segmented by height structure (B) are shown. The pixel-based segmentation method (

Appendix I-6) is used to segmented by height structure (B) are shown. The pixel-based segmentation method (

Appendix I-6) is used to segment two dimensional habitat maps by using height thresholds.

Besides utilizing habitat patch and edge metrics to capture vegetation height heterogeneity, the second approach we introduce here involves calculation of the second-order (co-occurrence) texture statistics (Haralick et al. 1973) directly from the gridded vegetation height maps. Second-order texture measures indicate the probabilities of each combination of pixel values co-occurring in a specific direction and distance (Haralick et al. 1973). These metrics can quantify spatial heterogeneity in terms of the spatial distribution and dependencies of height values (Coburn and Roberts 2004) through grey level co-occurrence matrix. Texture measures are conventionally extracted from individual bands of remotely sensed imagery and aerial photographs to assist object or land cover type discriminations (Franklin et al. 2000, Coburn and Roberts 2004). Normally a small moving window is used to calculate the grey level co-occurrence matrix in specified neighborhoods. Texture measures extracted from optical remote

sensing imageries have been used to infer broadly defined habitat heterogeneity that includes various environmental factors (e.g. land cover type, vegetation type, soil condition as well as vertical structure). This type of habitat structural information has been linked to avian species richness in many studies (St-Louis et al. 2006, St-Louis et al. 2009, Culbert et al. 2012). Here we derived the second-order texture metrics from gridded canopy height maps to associate them with variation in avian richness.

2.4 Datasets and Methods

2.4.1 Avian Data

The study area includes 21 predominately forested ecological regions (provinces) (Bailey 1995) across the conterminous U.S. (Appendix I-1) (Figure 2-2). We used avian records from the Breeding Bird Survey (BBS) to model species richness over the entire study range. BBS is an annual road side survey organized by U.S. Geological Survey (USGS) (Robbins et al. 1986, 1989a). Initiated in 1966, BBS has over 4000 survey routes located on secondary roads across the continental U.S. and Canada. Each survey route is 39.4 km long. Every year, during the avian breeding season, surveys are conducted by competent volunteers using the protocol of three-minute point count at 50 stops at 0.8km intervals. All birds seen or heard within 0.37 km radius are recorded (Sauer et al. 2011). We removed the records whose survey procedures or associated data are not acceptable by BBS standard. We also removed the records surveyed by first year observers to minimize observer bias (Kendall et al. 1996). We selected 134 broadly grouped woodland breeding birds species (here after “woodland guild”) based on the USGS species groupings (U.S. Geological Survey 2012). We also selected 26 and 49 bird species as the forest breeding guilds with preference for interior forest habitat and forest edge habitat respectively

(here after “interior forest guild” and “forest edge guild”) based on the classification of Boulinier et al.1998 (Boulinier et al. 1998). A complete list of birds involved in this study and their guild assignment are given in Appendix I-2. Because most of the interior forest and forest edge bird species are distributed in the Eastern U.S., we limited our analysis on these two guilds to the 10 forested ecoregions in the east (Figure 2-2).

Table 2-1 List of all metrics developed in the study.

Data	Metrics type (Set)	Metric name (Abbreviation)
NBCD vegetation height map	Summary height statistics (A)	Mean height (MEAN)
		Standard deviation of height (SD)
		Minimum height (Min)
		Maximum height (Max)
Two-dimensional vegetation cover map	Traditional patch-based metrics (B)	Number of patches(B.NP)
		Mean patch area (B.Area.MN)
		Standard deviation of patch area (B.Area.SD)
		Edge density (B. ED)
		Total edge (B.TE)
		Mean fractal dimension index (B.FRAC.MN)
		Standard deviation of fractal dimension index (B.FRAC.SD)
Vegetation cover map segmented by height structure	Height-structured patch-based metrics (C)	Number of patches(C.NP)

		Mean patch area (C.Area.MN)
		Standard deviation of patch area (C.Area.SD)
		Total edge (C.TE)
		Mean fractal dimension index (C.FRAC.MN)
		Standard deviation of fractal dimension index (C.FRAC.SD)
		Contrast weighted edge density (C.CWED)
		Mean of edge contrast index(C.ECON.MN)
		Standard deviation of edge contrast index (C.ECON.SD)
		Shannon's diversity index (C.SHDI)
NBCD vegetation height map	Second-order texture metrics (D)	Entropy
		Contrast
		Angular second moment (ASM)
		Homogeneity
		Dissimilarity

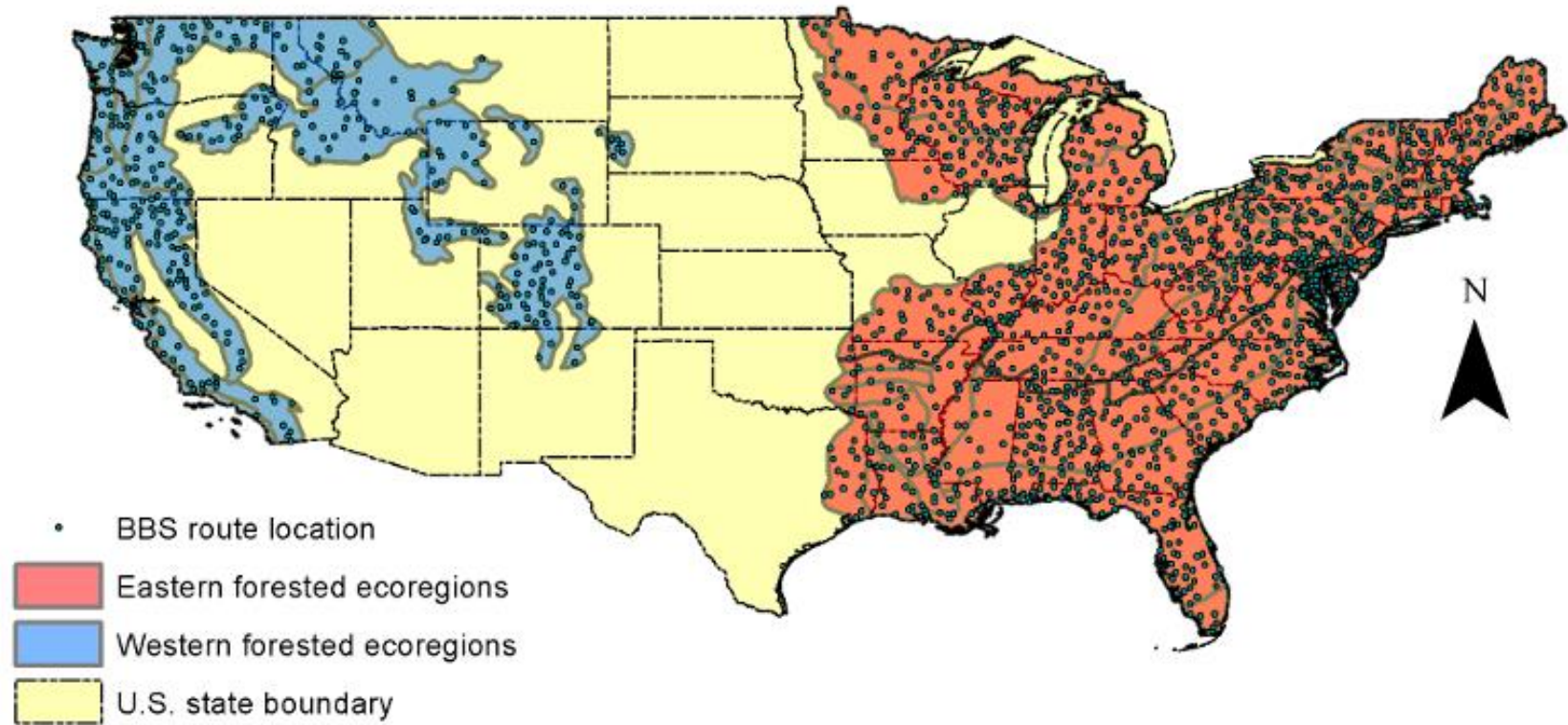


Figure 2-2 Distribution of BBS routes through the primarily forested ecoregions in the U.S. The richness models for the woodland guild were built using data from both eastern and western forested ecoregions. The forest edge and interior forest bird richness was modeled in the eastern forested ecoregions only.

Adjustments were made to take into account the detection probability bias (Kéry and Schmid 2004). We used the “fossil” package (Vavrek 2011) in the R statistical program (R Development Core Team 2011) to calculate the adjusted species richness using a first-order jackknife estimator (Burnham and Overton 1978, 1979). This estimator is based on multiple recapture studies in closed populations, which allows detection probability to vary among species. It is also the basic estimator underlying the species richness adjustments used by a USGS-developed BBS pre-processing program called COMDYN (Hines et al. 1999). We averaged the available first-order jackknife richness within the five years period between 1998 and 2002 to temporally approximate the acquisition time of the radar data which played a key role in developing the vegetation height maps as discussed in the following section. The resulting mean avian richness is the richness we refer to in the rest of the study.

2.4.2 Forest Height Data and Habitat Metrics

The National Biomass and Carbon Database of the year 2000 (NBCD) (Kellndorfer et al. 2011) provides an estimate of vegetation height distribution and variation at fine resolution for the continental U.S. The dataset is based on combined information from U.S. Department of Agriculture’s Forest Service Forest Inventory and Analysis data, high-resolution Interferometric Synthetic Aperture Radar data acquired from 2000 Shuttle Radar Topography Mission and optical remote sensing data from the Landsat ETM+ sensor. Products from the USGS’ National Land Cover Dataset 2001 and the Landscape Fire and Resource Management Planning Tools Project were also used during the process as input to build the empirical model for tree height estimation. The basal area weighted tree height (hereafter, “tree height”) maps produced by the

model gives spatially explicit vegetation vertical structure maps over the conterminous U.S. of 30 m-resolution.

We adapted a method to use 19 km (~half the length of a BBS route) radius buffers placed on the centroid of each BBS route, encompassing ~1100 km² areas to characterize the surrounding habitat around BBS locations (Pidgeon et al. 2007, Rittenhouse et al. 2012, Culbert et al. 2013).

We created habitat metrics on 1751 such circular landscapes where there are available BBS species richness data. (A), (B), (C) and (D) four metric sets incorporating a total of 26 metrics were calculated for each landscape (Table 2-1). The methods to produce each set of metrics are described in more details in the

Appendix I-6. The first two metric sets, embedded with little to no vegetation height heterogeneity, included (A) summary height statistics (hereafter “summary statistics”) and (B) traditional patch-based metrics. The other two metric sets incorporated height heterogeneity: (C) patch metrics characterizing vertical patches and edges (hereafter, “height-structured patch-based metrics”), and (D) second-order texture metrics capturing vertical heterogeneity of height distributions (Table 2-1). The metric sets (A) and (B) were created as baselines to compare with the height-structured metric sets (C) and (D).

All the metrics created are listed in Table 2-1, and the detailed formula and descriptions for each metric are presented in Appendix I-3. In order to differentiate the metrics with the same name from metrics set (B) and (C), capital letter “B” or “C” were given as prefixes to metrics’ acronym to indicate metric set membership.

2.4.3 Species Richness Models

We first explored the statistical correlation between richness of the three avian guilds and the predictive habitat metric to evaluate the association between individual habitat metrics and the richness of different guilds. The woodland species richness models were based on data of all 21 forested ecoregions, and the interior forest and forest edge guild models were limited to data of the 10 forested ecoregions from Eastern U.S. as noted earlier.

We selected 2 metrics from each of metric set (C) and (D) that on average had the best association with the richness of the three guilds as the best performing height-structured metrics (BPHMs). These four BPHMs were later combined with the traditional habitat metrics in multivariable models for comparisons of improvement. We limited our choice to only the four best metrics to avoid subsequent overfitting of our multivariate models while still maintaining enough representativeness.

We next constructed 6 multivariate linear models to explain each guild's richness. The first 4 models were created using the complete list of metrics from set (A), (B), (C), and (D) respectively. They served to compare the explanatory abilities of models that characterize habitat condition with very different approaches. The two other models combined metric set (A) and (B) individually with the 4 BPHMs. We created the combined models to examine the impacts of adding spatial arrangement of height in richness models characterizing habitat in traditional ways.

We used a bootstrapping technique to provide the mean value and confidence intervals for the richness models' adjusted r^2 value and AIC values to assess models' explanatory ability and goodness of fit as well as the variability of these measures. The bootstrap resampling was repeated 3000 times for each model. To examine the significance level of model improvements

the 95% confidence interval of adjusted r^2 value and AIC values were obtained with the bias-corrected and accelerated (BCA) bootstrap algorithm (Efron 1987) to make the interval's median unbiased and adjusted for skewness.

Lastly we explored the effect of combining the 26 metrics from all four metric sets using a non-parametric Random Forest (RF) model. The RF model (Breiman 2001) can incorporate large number of input variables well without overfitting (Biau 2012). It is also well-suited for our study because the model allows for covariance between predictor variables, which commonly exists between different habitat metrics. The RF model also provides a mechanism for assessing predictor variable importance using a measure of cross-validated mean square error (out of bag mean square error (OOB MSE)). The higher the increase of OOB MSE (IncMSE) is, the more important a specific metric is. More detailed introduction of Random Forest model is described in the

Appendix I-6. We also ran 6 RF models on the same combinations of metrics used by the linear models to compare the differences between linear and RF models. We set the number of trees to be 2000 for all models to allow for the mean residual error to converge. In our study the RF models were built with Random Forests package (Liaw and Wiener 2002) in the R statistical program (R Development Core Team 2011).

2.5 Results

2.5.1 Predictor Metric Correlation

The predictor metrics that correlate best with bird species richness varied among guilds. For woodland species richness, (D) the second order texture metrics generally had the greatest

predictive ability, followed by the traditional patch-based metrics, and height-structured patch metrics. For forest edge bird richness, the metrics with the strongest correlation were (C) the height-structured patch-based metrics followed by (D) the second order texture metrics and (A) the summary height statistics (Figure 2-3). Interior forest bird species richness in general had consistently low correlation with any metrics. Among all the metrics developed (Table 2-1, Appendix I-3), the metric with the greatest predictive capability for this guild was mean vegetation height. ASM had the strongest average predictive capability over the richness models for three guilds, followed by entropy, C.TE, homogeneity, and C.CWED (Figure 2-3), all of which are height-structured metrics. We selected ASM, entropy, C.TE and C.CWED as the four BPHMs to be combined with models relied on the traditional metrics.

The direction of the correlation between metrics and the bird richness was generally consistent across three guild types except for metrics with weak correlation (Appendix I-4). Among the variables with highest average correlation, ASM and homogeneity both had negative correlation with the richness of all three guilds. Conversely, entropy, C.TE, C.CWED all showed strong positive correlation for each guild's richness (Figure 2-3, Appendix I-4).

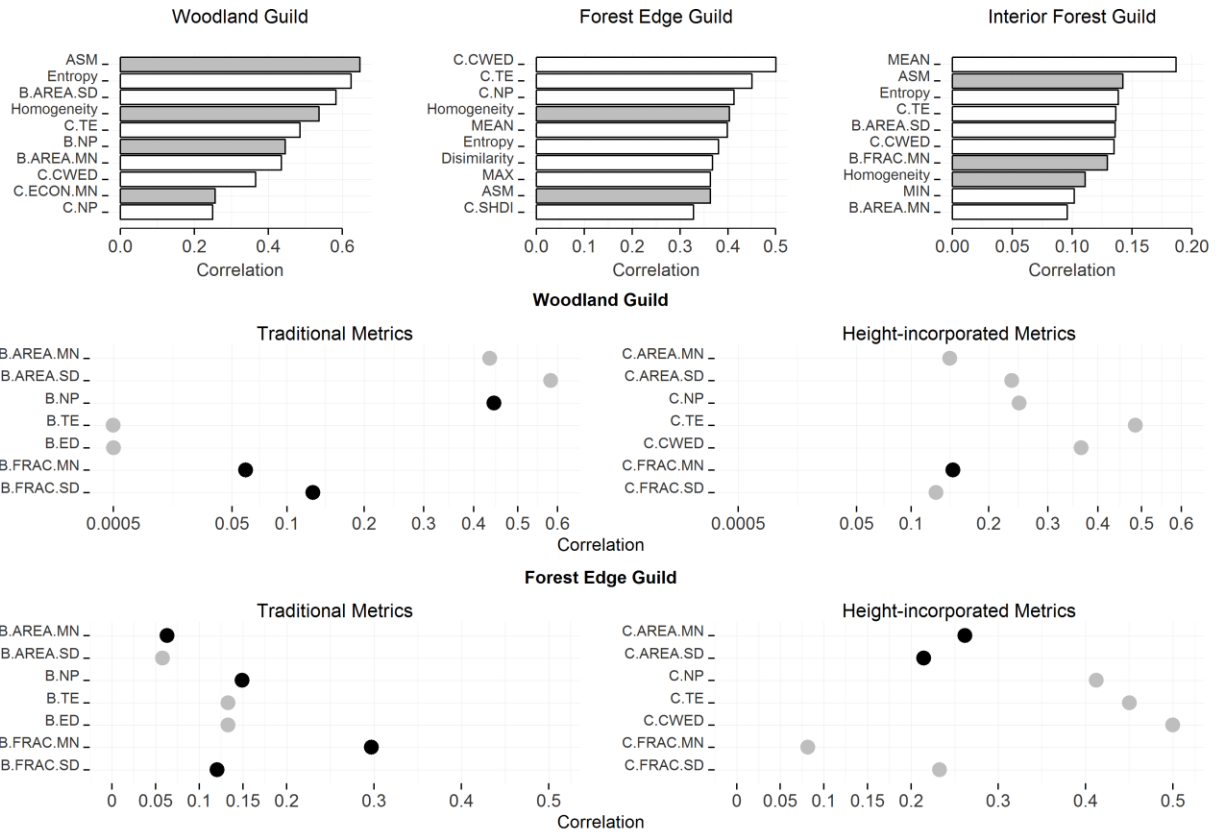


Figure 2-3 Guild richness associations with various metrics. (Top row): correlation bar plots of the most predictive metrics and species richness by guild. White bars represent a positive correlation and grey indicate a negative correlation. (Bottom rows): correlation comparisons between comparable patch-based metrics with and without considering the vertical patches and edges for the woodland and forest edge guild. The left panels show traditional metrics without accounting for height-heterogeneity; the right panels are height-structured counterparts. The black dots indicate a negative correlation and the grey ones indicate a positive correlation.

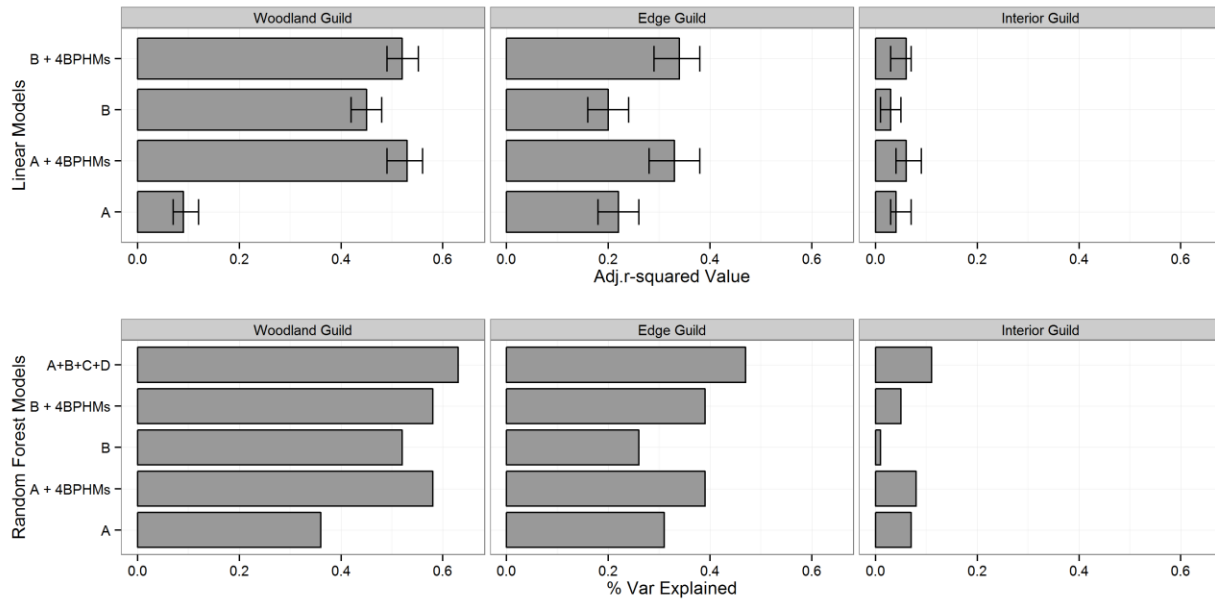


Figure 2-4 Predictive ability of multivariable models. A, B, C, and D are the four habitat metric sets, and 4BPHMs are the four best predictive height-structured metrics. Each of the top panels shows four linear models with whiskers giving 95% confidence interval of adjusted r² values. The length of the bar represents the mean adjusted r² for these models. The lower panels show the explained variance of the comparable random forest (RF) models. Uniquely the top bars are the results from the models employed all metrics from the four metric sets.

After incorporating vegetation height heterogeneity in patch-based metrics, the metrics characterizing patch number and area (AREA.MN, AREA.SD, and NP) showed a decreased correlation with the woodland guild richness. Conversely, the strength of the correlation between edge metrics (ED, TE) and the woodland guild richness increased. For the forest edge species both the patch and edge related metrics showed a prominent increase of correlation after incorporating vegetation height heterogeneity. The direction of the correlation for some patch-based metrics also changed. The NP metric showed an exceptionally large change for the woodland guild richness: from -0.45 to 0.25 after incorporating vertical patches (Appendix I-4, Figure3).

2.5.2 Predictive Models

The non-parametric RF models combining all 26 metrics (all-inclusive models) from the four metric sets were the ones with greatest ability to predict species richness for each guild (Figure 2-4, Appendix I-5). Among those models the lowest species richness variability was explained for the interior forest guild ($r^2=0.11$), but the forest edge guild richness was predicted moderately well ($r^2=0.47$) and the predictive model was strong for the woodland guild ($r^2=0.63$) (Figure 2-5). The most important variable for predicting the woodland guild richness were two traditional patch-based metrics (B.AREA.MN and B.AREA.SD) followed by two second order texture metrics (entropy and ASM). The forest edge species richness model was most dependent on two height-structured patch metrics (C.CWED and C.NP) followed by two summary height statistics (MAX and MEAN). The most important predictive metrics for the interior forest guild model were MEAN followed by B.AREA.MN and B.AREA.SD (Figure 2-5).

For the RF models, our results consistently showed that adding height-structured metrics improved the model predictive ability. Specifically, the explained variance of the all-inclusive RF models for woodland and forest edge guild were up to 0.27 and 0.21 higher respectively than the RF models with only traditional habitat metrics. In addition for these two guilds, when the RF models were combined with the four BPHMs, the improvement for explained variance values were up to 0.21 (woodland guild) and 0.13 (forest edge guild). The interior forest guild however showed only minor improvements when combined with any height-structured metrics. In general for woodland and forest edge guild, RF models' predictabilities were higher than the comparable linear models by a prominent margin. (See Figure 2-4, and Appendix I-5).

The linear models had a lower explanatory ability than their RF counterparts. For a specific combination of habitat metrics, the linear models explained the most amount of variation in the woodland guild richness and the least in the interior forest guild richness. The one exception was the model using summary statistics of height (set A), which showed the highest predictability for forest edge guild richness, followed by woodland guild richness, and then the interior forest guild richness (Figure 2-4, Appendix I-5). In every guild, the models incorporating the four BPHMs showed consistently higher predictability than the models without (Figure 2-4,).

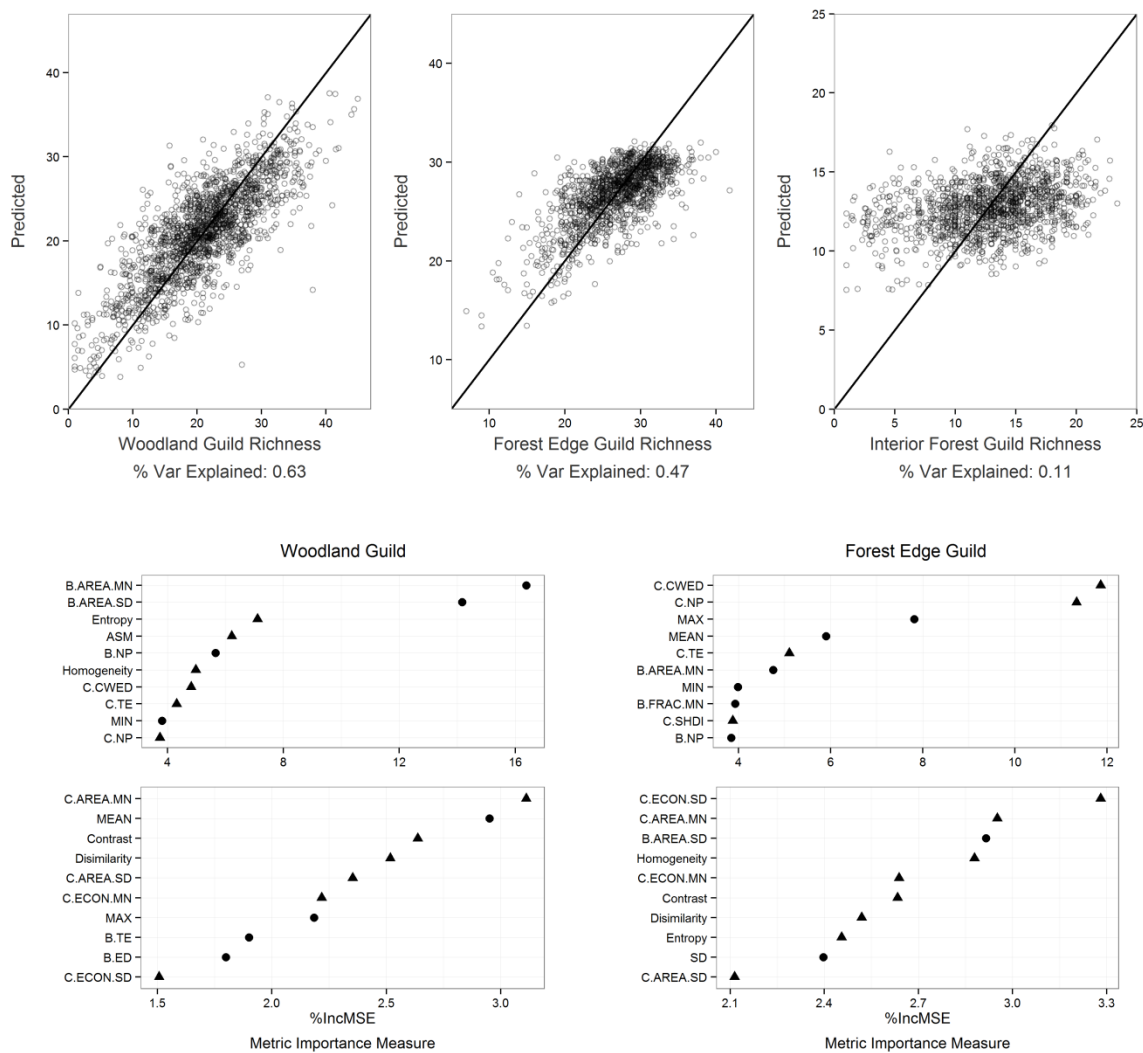


Figure 2-5 Random Forest model results. (Top row): Modeled vs. actual species richness for three guilds using all-inclusive random forest models. (Below the scatter plots): variable importance plots show the percent increase in mean square error (%IncMSE) of the top 20 most influential metrics in the woodland guild richness model and the forest edge guild richness model (note different scales on X-axes). The metrics characterizing vegetation height heterogeneity are plotted with triangles and the rest of the metrics are circles.

Combining the BPHMs with the summary height statistics resulted in significantly higher adjusted- r^2 values in the woodland and forest edge models (Figure 2-4). The AIC value for the woodland richness model also improved significantly. In comparison, when combined with traditional patch-based metrics, the BPHMs significantly increased the adjusted- r^2 for the forest edge guild model, while significantly improving the AIC values for both the forest edge and woodland guild models (Appendix I-5).

2.6 Discussion

A large number of hypotheses have been proposed to explain the spatial patterns of species richness over broad geographical scales (Palmer 1994, Guégan et al. 1998, Waide et al. 1999, Gaston 2000, Hawkins et al. 2007, Rahbek et al. 2007). While it is unlikely that there is one single mechanism that can explain species richness patterns completely, a large portion of the literature testing habitat heterogeneity hypothesis has focused on the association between species richness and two dimensional habitat structure, often combined with land cover type composition and distribution (Griffiths and Lee 2000, Donovan and Flather 2002, Pidgeon et al. 2007, Rittenhouse et al. 2012). On the other hand other studies testing species-energy hypothesis have relied on covariates related to ecosystem productivity and energy such as evapotranspiration and photosynthetic capacity indices like the normalized difference vegetation index (NDVI) (Hurlbert and Haskell 2003, Seto et al. 2004, Phillips et al. 2008) to explain large scale species

richness patterns. Studies to associate habitat vertical structure with species richness are, however, often focused at local scale (Culbert et al. 2013), which limited the efficacies of habitat heterogeneity models to explain species richness at broad scale.

Only recently was vegetation height information assessed as a predictor of avian species richness across the conterminous U.S. in two studies (Culbert et al. 2013, Goetz et al. 2014). One of these (Culbert et al. 2013) used the same NBCD data we employed here, but they explored only summary statistics of vegetation height and biomass combined with land cover type composition and distribution. The other used sparsely sampled height metrics from a satellite lidar system that is no longer operating, and included climatic data as predictive variables (Goetz et al. 2014).

Although our models employed only vegetation structural distribution, with no input from the land cover other than vegetation type or climatic data, their explanatory ability for the woodland guild was comparable to these recent results ($r^2=0.70$ for the forest guild model (Culbert et al. 2013), and $r^2=0.60$ for the open woodland model (Goetz et al. 2014)). We found that models combining only vegetation vertical and horizontal structure can explain a significant amount of species richness for the broadly grouped woodland guild and the forest breeding guild with preferences for the forest edge habitat. More importantly, our results showed that incorporating vegetation vertical heterogeneity, and not just mean and standard deviation of height, greatly improves the ability to explain variability in avian richness for the two guilds. The spatial arrangement of vegetation height plays an important role in associating the quality of habitat condition and diversity of ecological niches for bird species within the two groups.

Traditionally habitat edges are thought to affect species movement, interaction, mortality and community dynamics (Fagan et al. 1999). The summary height statistics are considered indicators of habitat diversity and forest successional stage (Morgan and Freedman 1985, North et al. 1999,

Bergen et al. 2009). The traditional way of characterizing habitat through two-dimensional habitat patch distribution and summary height statistics still play important roles in our multivariate richness models. The large pool of traditional patch-based metrics provides a well-known framework to readily incorporate vertical height distribution once habitat patches are segmented by height. Both traditional and our height-structured metrics contribute to explanation of the variance of avian richness, although the importance of individual metrics in the models varies from guild to guild. Thus, our study shows that for the woodland avian guild and forest edge guild, the species richness is highly sensitive to the vegetation height heterogeneity, and the addition of the spatial arrangement of vegetation height provides significantly improved estimates of species richness for the two guilds. The patch-based height-structured metrics and the second order texture metrics thereby supplement and extend common methods of characterizing habitat condition and predicting avian species richness.

We note the BBS data is collected along roadways where volunteers can easily and regularly traverse, thus the areas along the survey routes could be subject to disturbances such as motor vehicle traffic or habitat conversion (Keller and Scallan 1999, Griffith et al. 2010); i.e. they may not be representative samplings of forest spatial and vertical variability. This characteristic of the data set could pose a challenge for systematical sampling of interior forest bird species in the surrounding areas and is likely one of the contributing factors for the consistently low species richness and weak correlations with our metrics and models in the case of the interior forest guild. Alternatively, forest edge habitats are relatively more exposed to stressors such as wind damages and human disturbances. They normally exhibit higher vertical structure diversity than the interior forest areas (Whitehurst et al. 2013). It may be that interior birds are less adapted to habitat structure heterogeneity, and thus exhibit limited sensibility to habitat structure metrics.

Lastly the results could also be attributed to the different ways members of avian guilds utilize habitat. Forest edge and majority of woodland bird species tend to use a wide range of habitat for foraging, and their degree of co-existence can vary in a broad spectrum over space. In comparison the interior forest guild, composed mostly of forest specialists that avoid other habitat types(Hagan et al. 1996) with overlapping ecological niches, are more likely to face greater interspecific competition which limits species richness despite diverse height structure across landscapes(Cody 1974). However while the species richness models see low association between height heterogeneity metrics and richness, there are still likely more specific vertical structure preferences associated with individual species (Goetz et al. 2010, Swatantran et al. 2012).

While four BPHMs highlighted in our study showed a good ability to associate with species richness and to improve broad scale avian richness modeling, it is reasonable to assume that height-structured metrics have potential to be improved further given the large number of options that remained unexplored. First, the pixel-based segmentation method used in our study (Appendix I-6) is one of the simplest algorithms to delineate vertical patches and edges. The method is based on a set of global threshold values while not considering neighboring heterogeneity (Schiewe 2002). The process of setting up the threshold values and weight matrix (for contrast metrics) inevitably involves somewhat arbitrary decisions. More complex segmentation methods such as edge and region-based methods can be performed readily with commercial and open-source software packages that potentially may produce more efficacious vertical patches and be less arbitrary (Baatz et al. 2003). Secondly, there are many untested texture measures (Haralick et al. 1973). The relationship between texture metrics and the avian richness varies as the size of moving window changes (St-Louis et al. 2006). More work is

needed to understand the impact of those methodological options for further improving species richness models.

2.7 Conclusion

As active remote sensing technologies like radar and lidar mature and become more widely available, data sets characterizing vegetation vertical structure should become increasingly useful for biodiversity applications and management. Our study showed that vegetation height heterogeneity is associated with habitat diversity and species richness for some forest avian guilds. Thus, while recognizing the advances conveyed by incorporating height information, there is an imperative to explore in more depth the role of such heterogeneity. Furthermore we suggest not just height, but vertical canopy heterogeneity, e.g. foliar profiles and layering, will provide an even richer source of information from which to develop new metrics and models (Swatantran et al. 2012, Whitehurst et al. 2013). Incorporating such information will require data on not only canopy height but canopy vertical structure, the latter of which is unavailable at continental scales. Nonetheless, the metrics and models used in our analyses provide a means to incorporate and utilize three-dimensional habitat information, with the goal of better understanding the controls on avian species richness and habitat use.

Chapter 3. A Centroid Model of Species Distribution with Applications to the Carolina Wren (*Thryothorus ludovicianus*) and House Finch (*Haemorhous mexicanus*) in the United States

3.1 Abstract

Drastic shifts in species distributions are a cause of concern for ecologists. Such shifts pose great threat to biodiversity especially under unprecedented anthropogenic and natural disturbances. Many studies have documented recent shifts in species distributions. However, most of these studies are limited to regional scales, and do not consider the abundance structure within species ranges. Developing methods to detect systematic changes in species distributions over their full ranges is critical for understanding the impact of changing environments and for successful conservation planning. Here, we demonstrate a centroid model for range-wide analysis of distribution shifts using the North American Breeding Bird Survey. The centroid model is based on a hierarchical Bayesian framework which models population change within physiographic strata while accounting for several factors affecting species detectability. Yearly abundance-weighted range centroids are estimated. As case studies, we derive annual centroids for the Carolina Wren and House Finch in their ranges in the U.S. We further evaluate the first-difference correlation between species' centroid movement and changes in winter severity, total population abundance. We also examined associations of change in centroids between sub-ranges. Change in full-range centroid movements of Carolina Wren significantly correlate with snow cover days ($r=-0.58$). For both species, the full-range centroid shifts also have strong correlation with total abundance ($r=0.65$, and 0.51 respectively). The movements of the full-range centroids of the two species are correlated strongly (up to $r=0.76$) with that of the sub-

ranges with more drastic population changes. Our study demonstrates the usefulness of centroids for analyzing distribution changes in a two-dimensional spatial context. Particularly it highlights applications that associate the centroid with factors such as environmental stressors, population characteristics, and progression of invasive species. Routine monitoring of changes in centroid will provide useful insights into long-term avian responses to environmental changes.

3.2 Introduction

Species distributions have been changing drastically because of unprecedented anthropogenic disturbance (Vitousek et al. 1997, Brooks et al. 2002) and climate change (Nakicenovic and Swart 2000, Reilly et al. 2001). Examples of recent northward or upward shifts in species ranges from many taxa have been documented (Thomas and Lennon 1999, Parmesan et al. 1999, Parmesan 2006, La Sorte and Jetz 2012). Understanding how species distributions are shifting and how such changes relate to environmental covariates are of great importance for conservation (Parmesan 2006, Pereira et al. 2010).

Most of the previous studies focusing on changes in species ranges have been based on evidence across small sections of a range boundary or on regional species' composition (Parmesan 2006). For instance, the geographical location of northern range limits have been estimated to study distribution changes for a variety of avian and insect species (Pollard 1979, Thomas and Lennon 1999, Hickling et al. 2005, Hitch and Leberg 2007). Parmesan et al. (1999) compared the differences in the ratio of extinction to colonization at the northern and southern range margin for a group of non-migratory European butterflies. For some montane species with isolated populations, range related studies have compared species compositions at the plot level across elevational gradients (Pounds et al. 1999, Beaver et al. 2003). Results based on portions of

species distributions have limitations because the abundance structure within species boundaries is often not accounted for. In particular, the inferred edge of the range can be a somewhat crude index to characterize changes in species distributions (Gaston 2003), as regional studies at the outermost limit of species occurrence are not robust to exclusion or inclusion of outliers (Santelmann 1991, Van Rossum et al. 1997). The lack of methodologies that permit evaluation of species abundance information over their entire ranges makes it difficult to characterize systematic shifts in distribution especially for species with extensive ranges.

A systematic approach that uses range-wide data is particularly needed to examine the changes of avifauna distribution because they are widely distributed, ecologically diverse, and highly responsive to environmental change (Walther et al. 2002). More importantly range-wide analysis can take advantage of the broad spatial and temporal coverage of many existing avian data sets (Gaston 2003, Araújo and Pearson 2005). Using a range centroid as a summary statistics to synthesize and visualize avian range-wide distribution can fulfill these requirements. In general the centroid characterizes the central tendency of geographically referenced elements (e.g. regions) while capable of weighting the contribution (e.g. abundance) of individual elements differently. The change of centroid location over time quantifies the direction and magnitude of relative changes happening among all elements. Centroids are commonly used in GIS and cartographical practices (Environmental Systems Research Institute 1999), biological studies (Batschelet 1981), as well as U.S. population analysis (US Census Bureau 2010). However few studies have employed the centroid concept to investigate avian distribution shifts (but see La Sorte and Thompson 2007, Niven and Butcher 2009, La Sorte et al. 2013). None of these studies have estimated range centroids using the wealth of avian information documented by the North America Breeding Bird Survey (BBS) (Sauer et al. 2014). Analysis of the BBS also provides an

opportunity to capture a reliable and comprehensive picture of distribution shifts, given the standardized data collection procedures and long time-series of information (the survey was started in 1966) from the BBS. Also during breeding season, avian species in general have stricter habitat requirements, and thus their breeding ranges are relatively less malleable than winter distributions (Root 1988).

The goal of this study is to present an approach to quantify changes in the centroids of species distributions using BBS data and for the purpose of monitoring changes in long term avian species distribution. We employ this approach to characterize and visualize the long term centroid of the ranges of the Carolina Wren (*Thryothorus ludovicianus*) and the House Finch (*Haemorhous mexicanus*) as case studies. Carolina Wren populations in the Eastern U.S. have exhibited rapid growth followed by precipitous declines in portions of their range (most prominently during the mid-1970s) (Link and Sauer 2007), where their populations encounter severe winter conditions (Sauer et al. 1996). House Finches are native to Western United States, but were introduced to Eastern United States in the 1930s. They have been rapidly colonizing and establishing new ranges since. Because both species have undergone distributional changes in the past few decades, they represent good test cases for our method. In particular we seek to demonstrate the efficacy of a centroid model in characterizing distribution changes, especially those that result from large scale environmental stressors such as severe winter conditions and from invasive colonization processes.

Using the calculated range centroids of the two case studies, we first examine the statistical association between the centroid movement and a winter severity index for Carolina Wren. We then correlate the centroid movement with a total population abundance index. Furthermore, we assess the correlation among centroids derived from different ranges. For the House Finch, the

native western population and the invasive eastern population have had disjunct ranges during most of the 20th century, thus emphasis is placed on implications of centroid analysis on species with contrasting populations dynamics or with disjoint ranges. We also examined two null cases, i.e. species with less pronounced distribution change, to provide a baseline for centroid movement. The range centroids of Bushtit (*Psaltriparus minimus*) and Dusky Flycatcher (*Empidonax oberholseri*) were then calculated and visualized. Extending from the case studies, we discuss the characteristics and applicability of the centroid model aimed towards facilitating the potential implementation of the model on broader lists of species and other survey data.

3.3 Data & Methods

3.3.1 The North American Breeding Bird Survey & Study Areas

Because of its extensive geographical and temporal coverage, the BBS provides a unique opportunity for analyzing continental scale changes in avian distributions. The BBS started in 1966, and by 1968 it was established in the contiguous U.S. and southern Canada. It is an annual roadside survey with >5000 routes along secondary roads covering the contiguous United States, Southern Canada, and Northern Mexico. Each route is 39.4 km in length and has 50 sample points evenly spread out along the route path. Every year competent volunteers survey routes during breeding season using a protocol of three minute point counts at each sample point. Birds heard and seen within 0.4 km radius are recorded (Robbins et al. 1986, Sauer et al. 2011). The numbers of routes surveyed and consistency of coverage has increased throughout the survey period, but few routes have been surveyed every year since the beginning of the BBS (Link and Sauer 2002, Sauer et al. 2011). For each species, the sum of counts from the 50 sample points was used as a measure of abundance at a route for a specific year. We used the count values to

model stratum-specific abundance indices. We included all data from routes where the species of interest was observed at least once.

To summarize the method of calculating the range centroid from BBS data, we first divided the species ranges into strata. We then used a hierarchical Bayesian model to estimate the annual species abundance indices within each stratum. Finally the annual centroid coordinates were calculated as the average coordinates of all strata centroids weighted by their respective abundance indices. Because the Markov chain Monte Carlo (MCMC) method is used for fitting hierarchical Bayesian models, it produces posterior distributions for both directly estimated parameters and derived parameters such as the centroid coordinates (Lunn et al. 2000). Posterior distributions are used to estimate statistical attributes of the centroid locations and form the basis for additional statistical inference.

Although the BBS has an extensive geographic range, it still does not cover entire ranges of many species, and the analysis must be viewed as conditional to the surveyed area. In this analysis, we limited the scope to the contiguous United States, as this area has the most consistent BBS coverage. The range of the Carolina Wren is almost entirely within the contiguous United States (only 10 surveys encountered the species in Ontario); while House Finch are encountered at low abundances in eastern and western Canada. Scale of the stratification can have significant influence on BBS results and thus on variability of centroid location. In general, dividing strata more finely provides a more local scale for estimation of the centroid. More importantly, the extent of the ecological processes underpinning the distribution change affects one's choice of stratification scheme. For the BBS, strata have historically been delineated by the union of the U.S. states and Bird Conservation Region (BCR) boundaries (Sauer et al. 2003) (Figure 3-1). BCRs are ecologically distinct regions having similar bird

community and habitat conditions, and BBS surveys are organized by state coordinators. The resulting state/BCR strata allow us to model the species abundance index within relatively small and homogenous regions. (Sauer et al. 2003) (Figure 3-1). We only included strata with more than 4 BBS routes to ensure adequate samples in each stratum. All geographically referenced maps were projected to USA Contiguous Equidistant Conic projection. For computation of species distribution centroids, ArcGIS (Environmental Systems Research Institute 1999) was used to calculate the X-coordinate (easting) and Y-coordinate (northing) (unit: meter) of each stratum's centroid.

3.3.2 Hierarchical Models for Stratum-specific Abundance Index

Summarizing accurate bird abundance values from BBS data is challenging because, like many other index surveys, BBS survey methods do not directly account for imperfect detection of birds (Link and Sauer 2002). Directly using count values is problematic since a variety of factors such as regional differences, observer, and year can significantly influence detection rates, and thus the count values (Robbins et al. 1986, Sauer et al. 1994, 1995). We adapted a hierarchical Bayesian model from Link and Sauer (2002) to accommodate these complications. The stratum-specific abundance indices are then estimated by the model as the measurements of abundance in each region.

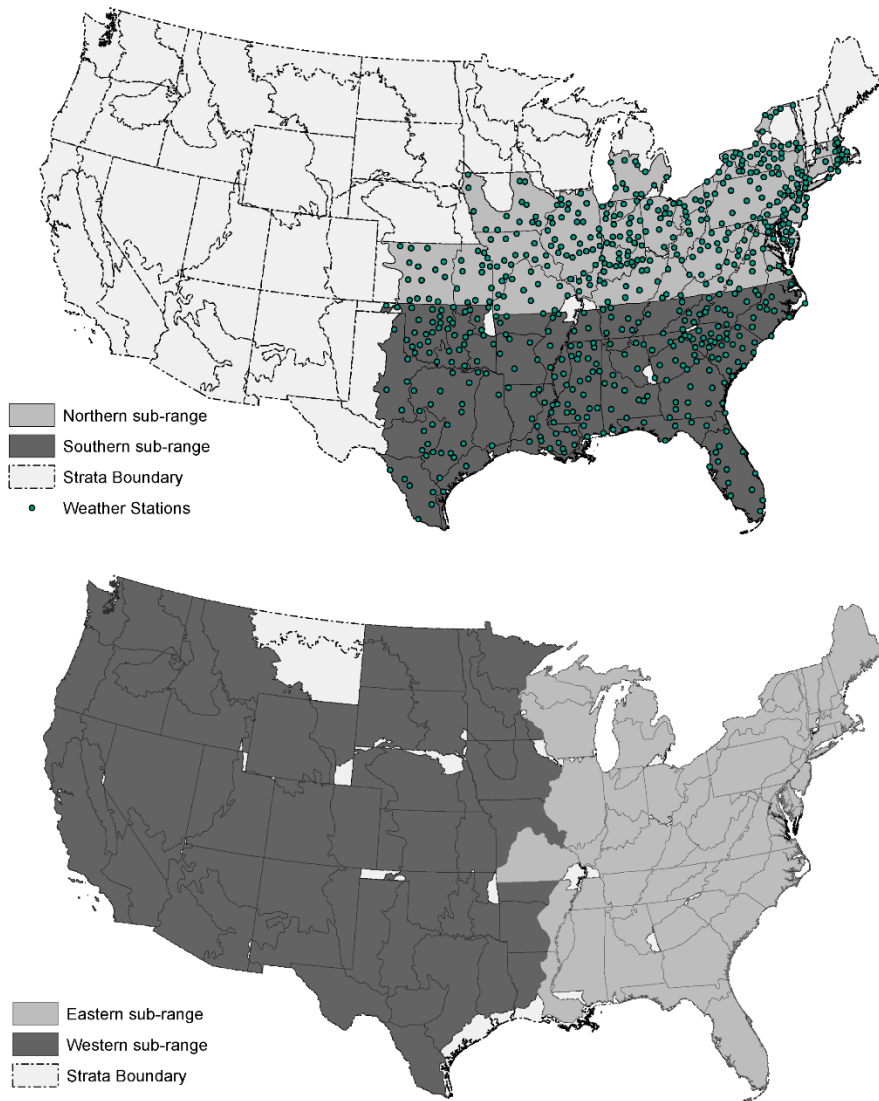


Figure 3-1 Study area and sub-ranges of Carolina Wren and House Finch. The top map shows the range of Carolina Wren in the contiguous U.S. The range was divided into northern and southern sub-ranges for analysis at the sub-ranges scale. Weather stations used for snow depth data are shown as circles in the map. Similarly, the bottom map shows the range of House Finch in the contiguous U.S., divided into eastern and western sub-ranges for subsequent analysis.

The hierarchical Bayesian model we use is an overdispersed Poisson regression model which accounts for overdispersion in BBS count data and controls for the variability in the skills of

BBS observers (Link and Sauer 2002). In our adaptation, we modeled the expected values $\lambda_{i,j,t}$ of BBS route counts $Y_{i,j,t}$ (i indexes stratum, j indexes observer within route, and t indexes year). The model is a log-linear function of the explanatory variables including stratum-specific intercept, slope, and year effects (S_i , β_i , and $\gamma_{i,t}$), observer/route effect (ω_j), and overdispersion term ($\varepsilon_{i,j,t}$). In the formula t^* denotes a baseline year, η is the first year effect, and $I(j, t)$ is a binary variable indicating whether the survey was done by a first year observer:

$$\log(\lambda_{i,j,t}) = S_i + \beta_i(t - t^*) + \omega_j + \eta I(j, t) + \gamma_{i,t} + \varepsilon_{i,j,t}. \quad \text{Formula 1}$$

We followed Link and Sauer (2002) in defining the prior distribution of model parameters, as well as hyperparameters. We mostly used diffuse (essentially flat) priors for the hyperparameters, S_i , β_i , and η set as normally distributed with mean of 0 and standard deviation of 1000. The year effects, observer effects, and overdispersion effects ($\gamma_{i,t}$, ω_j , and $\varepsilon_{i,j,t}$) were all specified as having a normal distribution with mean zero. However they differed in that the variance of the year effects ($\sigma_{\gamma,i}^2$) was allowed to vary between strata, whereas the observer effects and overdispersion effects were identically distributed, having the same variances across strata (σ_{ω}^2 and σ_{ε}^2 respectively). The prior distributions of these variances were also set as diffuse distributions, following an inverse gamma distribution, having mean of 1 and variance of 1000 (Link and Sauer 2002).

After the model was established, we then calculated the stratum-specific annual abundance indices as

$$N_{i,t} = A_i * z_i * \exp(S_i + \beta_i(t - t^*) + \gamma_{i,t}). \quad \text{Formula 2}$$

This formula included two weights that were multiplied to scale the local abundance term ($\exp(S_i + \beta_i(t - t^*) + \gamma_{i,t})$). The first weight z_i is the proportion of routes in stratum i , on which the species was ever encountered. It was applied to account for the fact that in some strata the species were never observed on some surveyed routes. The other weight A_i is the ratio of the stratum area over the area of all strata where the species is ever present. It is worth noting that the species abundance index ($N_{i,t}$) is a relative measurement. The hierarchical model analysis controls for detection rates and makes them comparable among themselves, but they are not actual abundance and density values.

3.3.3 Fitting the Hierarchical Model and Centroid Calculations

We used the R2winbugs package (Sturtz et al. 2005) in the R language for statistical computing and graphics (R Development Core Team 2011) to call the Winbugs program (Lunn et al. 2000, Spiegelhalter et al. 2003) to fit the hierarchical models. Winbugs is a commonly used software for formulating and customizing Bayesian statistical models. It uses MCMC methods to produce a large number of samples from a joint posterior distribution (Kéry 2010).

For each species we generated three independent Markov chains. Each chain had 30,000 iterations, the first 15,000 of which were discarded (burn-in samples). After the first 15,000 iterations, posterior samples were collected every 50 iterations (thinning rate of 50) so that estimates of posterior distribution were based on the 900 (3 chains \times 15,000 iterations / 50 thinning rate) sample values. We used $t^*=1987$ as the baseline year for scaling results. The R code to generate the posterior samples of $N_{i,t}$ and other parameters in the model are provided in the Appendix II-1.

Annual centroid locations of distribution for a species, defined in terms of X_t and Y_t coordinates, were calculated as yearly weighted mean of strata centroids (x_i and y_i):

$$X_t = \frac{\sum_i N_{i,t} * x_i}{\sum_i N_{i,t}}, \quad Y_t = \frac{\sum_i N_{i,t} * y_i}{\sum_i N_{i,t}} \quad \text{Formula 3}$$

The stratum-specific annual abundance indices ($N_{i,t}$) modeled by hierarchical Bayesian models served as the weights in this process. Because the abundance indices were all based on 900 sample values from posterior distributions, the posterior distributions of X_t and Y_t can be computed directly in the MCMC, and credible intervals are computed for both coordinates.

3.3.4 Case Studies

We demonstrate the yearly centroid for Carolina Wren and House Finch in the U.S. and analyzed the relationship between centroid locations and some environmental and population metrics.

Carolina Wren

Carolina Wren populations in portions of the Eastern U.S. exhibit rapid growth and precipitous declines closely associated with winter conditions (Sauer et al. 1996, Link and Sauer 2007).

Since the species relies primarily on ground-foraging, extended periods of snow cover caused by heavy snow precipitation can lead to starvation and drastic population declines (Mehlman 1997).

We hypothesized that the Y-coordinates of the Carolina Wren's range centroid should decrease as winter severity increases. The Y-coordinates were also hypothesized to be correlated with the total population size within the range.

Carolina Wren's entire range in the U.S. covers 73 strata (Figure 3-1). We first calculated the annual centroid locations for the full range. We used first-difference correlation to associate the changes in Y-coordinates of the centroid with the changes in an index of winter severity: the

average number of snow-cover days within full range. We used daily snow depth data from National Oceanic and Atmospheric Administration's United States Historical Climatology Network (USHCN) dataset (Easterling et al. 1999). The snow-cover days were defined as the days when the snow depth measured by a weather station was at least 5.08 cm (≥ 2 inches). The number of snow-cover days was counted for a specific year between January 1st and March 31st. We calculated the average number of snow-cover days per station from a pool of 616 stations within the Carolina Wren's range (Figure 3-1). Some stations did not report snow depth information in the years when there was no significant snow accumulation, so the actual number of stations with available snow depth data varies from year to year. Lastly we evaluated the first-difference correlation between the Y-coordinate of the range centroids and the Carolina Wren's total abundance indices across the full range. If the stressor is acting in the Y dimension, then we would expect that overall abundance changes would be correlated with changes in that dimension.

Throughout this study we used the first-difference correlation to measure the statistical association between two series of data over time (Anderson 1994), to enable calculation of the correlation with minimum impacts of autocorrelations exhibited in time series data (Barker and Sauer 1992). Correlation of first differences (from here on "correlation") does not examine relationships between absolute values, but instead correlates changes in value from year to year (Thompson and Page 1989). It is commonly used to detrend (reduce autocorrelated effects) time series data, so that the correlation is based on annual changes rather than long-term changes in the variables (Barker and Sauer 1992).

Carolina Wren is distributed over a large extent in the eastern U.S. Several important environmental gradients in the region are likely to influence Carolina Wren abundance,

particularly change in yearly snow-depth patterns across latitudes. We split the Carolina Wren's full range in the U.S. into northern and southern sub-ranges with approximately equal number of strata, to examine the centroid behavior across geographical gradients, and more importantly to evaluate the relationship between centroid and the population dynamic at different scales. The division ensured that both sub-ranges are of comparable sizes and that they cover a similar range of longitudes. There are significant differences in winter condition between the sub-ranges because of the latitudinal differences (Figure 3-1). We calculated the centroids and total abundance indices (sum of $N_{i,t}$ among all strata within the range) for each sub-range. We then examined the correlation of the Y-coordinates of the centroids of different ranges, as well as the correlation between the sub-ranges' total abundance indices and their respective Y-coordinates. We hypothesized that the correlation between snow-cover days and the Y-coordinates of the centroid will be stronger for southern sub-range. This is because the population at the low latitude region would not be affected significantly by the range-wide snow-cover index due to the warm and mostly snow free winters. In comparison, snow storms are likely to have greatest impact, in terms of reducing regional abundance measures, at the mid latitude region around the south-north sub-range division, as the Carolina Wren has relatively big baseline populations there, and they are vulnerable to fluctuations of winter storms from year to year. Therefore for the southern sub-range, the contrasting winter conditions and responses to snow-cover index were hypothesized to cause more changes in centroid movements.

House Finch

House Finches are native to the western United States, but were imported to eastern United States from California in the 1930s and 1940s (Elliott and Arbib 1953). The invasion and colonization in the east was accelerated by illegal release of captive birds after a ban on their

importation for the pet trade in the 1940s. House Finches are particularly common in human modified habitats. Their populations multiplied and expanded rapidly since their introduction in the East Coast (Veit and Lewis 1996), and much of the expansion in the east has occurred after the BBS was initiated. Our intention was to evaluate how the range centroid reflects explosive population growth and rapid colonization of an invasive species such as House Finch. House Finch also serves as an example that demonstrates the application of the centroid model on species with contrasting disjunct populations (western and eastern populations). We excluded the first three years of BBS data from our analysis, because of the lack of systematic survey over the range of House Finch during these years. The full range of the species covered 124 strata (Figure 3-1).

Native and invasive House Finch populations have been geographically separated on the eastern and western U.S., although in recent years the eastern population has almost expanded to the Great Plains, in direct contact with regions occupied by native population. To analyze centroid characteristics of the two populations and to compare the behavior of centroids at different scales, we divided the entire range into eastern and western sub-ranges. Most strata in the eastern sub-range had no record of House Finch when the BBS started in the 1967. Additionally the two sub-ranges of House Finch cover similar range of latitudes. We calculated the annual centroid locations and the total population abundance indices of House Finch for the entire range and for the sub-ranges between 1969 and 2012. Unlike Carolina Wrens, where the latitudinal (Y) directions are of interest due to climate, House Finch distributions were hypothesized to change in the longitudinal (X) dimensions. We correlated the X-coordinates of centroids derived from different ranges to compare the similarity of their movement pattern. We also examined the

correlation between the X-coordinates and total population abundance indices within different ranges.

3.3.5 Null Cases

We selected Bushtit and Dusky Flycatcher as null cases, because their populations did not change significantly since 1968 in any of the four geographical regions at different scales: the entire U.S., western BBS region, central BBS region, or the whole BBS region (including U.S. and Southern Canada) (Sauer et al. 2014). Both species have less pronounced distribution changes. We calculated and plotted their centroids between 1969 and 2012.

3.4 Results

The Y-coordinates of the centroid of the Carolina Wren distribution exhibited significant fluctuation over the course of 47 years (Figure 3-2). The centroid consistently shifted northward during the years with mild winters with relatively few snow-cover days (Figure 3-2). In contrast it shifted dramatically to the south in the later 1970s, early 1990s, and late 2000s, coincident with severe winters (with extended snow-cover days). The largest southward shift of the centroid was in the year of 1977 (Figure 3-2) when the extreme cold winter dominated much of the eastern U.S. (Namias 1978).

We analyzed the statistical association between centroid coordinates and environmental stressor. The number of snow-cover days was strongly correlated with the Carolina Wren's Y-coordinates of the full-range centroids (mean correlation -0.58, (95% CI of -0.51 ~ -0.66)). The relationship at the sub-range in the south remained significantly negative (mean correlation -0.32, (95% CI -0.45 ~ -0.19)) while in the northern sub-range it showed no significant correlation (mean

correlation -0.08, (95% CI -0.21 ~ 0.05)) (Table 3-1) (the change of the y-coordinates of the sub-range centroids can be seen in Figure 3-3).

Table 3-1 First-difference correlation Table

	Carolina Wren			House Finch		
	Pairs of Comparisons	Correlation	95% CI	Pairs of Comparisons	Correlation	95% CI
Centroid coordinates vs. snow-cover days	Y-coor. & Snow-cover Days (Full range)	-0.58	-0.51 ~ -0.66	-	-	-
	Y-coor. & Snow-cover Days (Northern sub-range)	-0.08	-0.21 ~ 0.05	-	-	-
	Y-coor. & Snow-cover Days (Southern sub-range)	-0.32	-0.45 ~ 0.19	-	-	-
Centroid coordinates vs. abundance indices of different ranges	Y-coor. & Abundance Indices (Full range)	0.65	0.57 ~ 0.72	X-coor. & Abundance Indices (Full-range)	0.51	0.26 ~ 0.70
	Y-coor. & Abundance Indices (Northern sub-range)	0.05	-0.09 ~ 0.18	X-coor. & Abundance Indices (Eastern sub-range)	-0.24	-0.12 ~ -0.38
	Y-coor. & Abundance Indices (Southern sub-range)	0.43	0.28 ~ 0.59	X-coor. & Abundance Indices (Western sub-range)	0.15	-0.13 ~ 0.42
Between centroid coordinates of different ranges	Y-coor.North & Y-coor.Full-range	0.13	-0.04 ~ 0.30	X-coor.East & X-coor.Full-range	-0.12	-0.31 ~ 0.09
	Y-coor.South & Y-coor.Full-range	0.76	0.67 ~ 0.83	X-coor.West & X-coor.Full-range	0.38	0.13 ~ 0.58
	Y-coor.North & Y-coor.South	0.09	-0.12 ~ 0.30	X-coor.East & X-coor.West	-0.03	-0.29 ~ 0.23

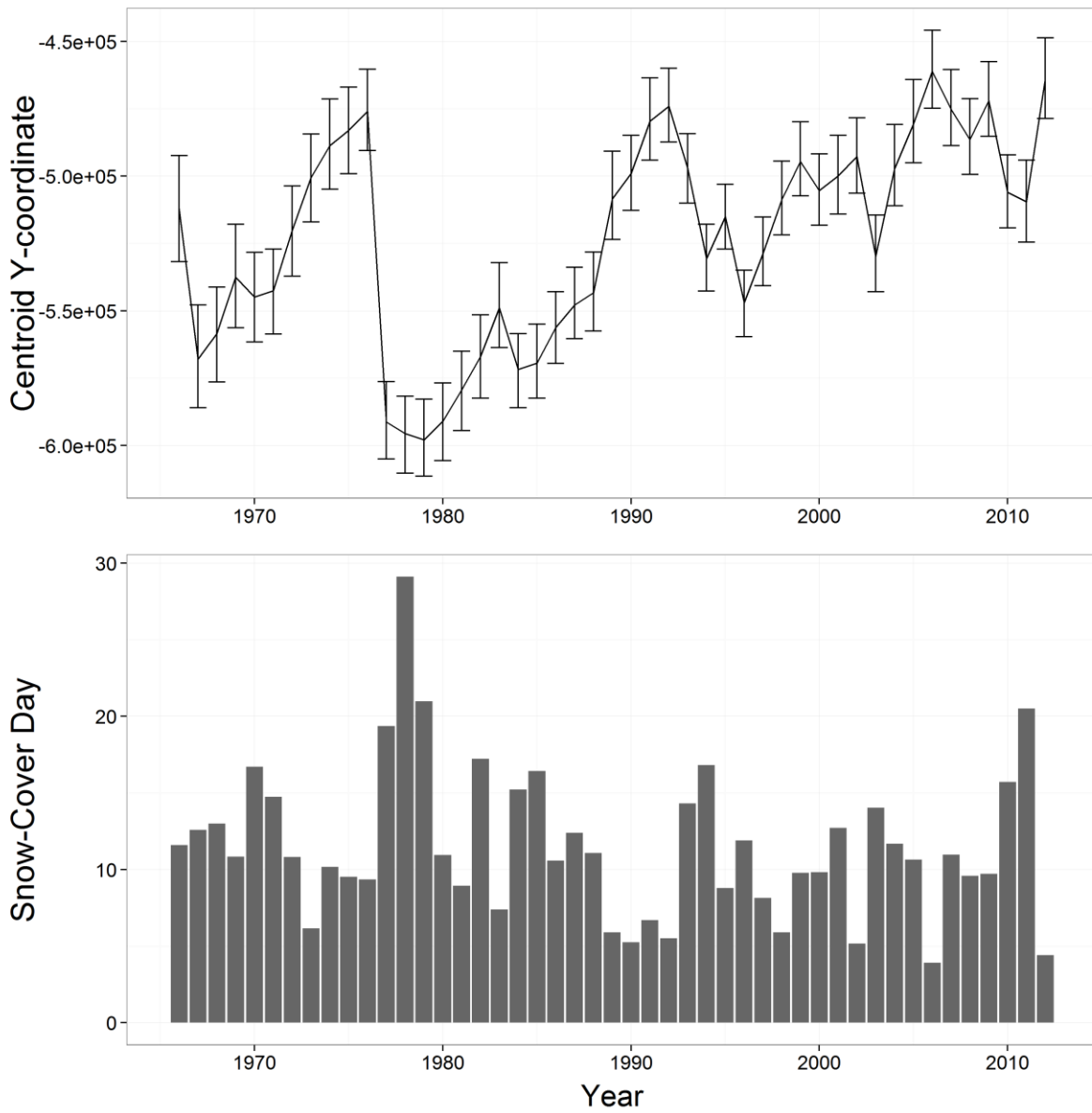


Figure 3-2 The Y-coordinates of Carolina Wren’s full-range centroid and number of snow-cover days. The Y-coordinates (meters) of Carolina Wren’s full-range centroid was plotted (top panel) with 95% credible interval. As can be seen, a significantly negative correlation exists between the Y-coordinate values and the average number of snow-cover days (bottom panel).

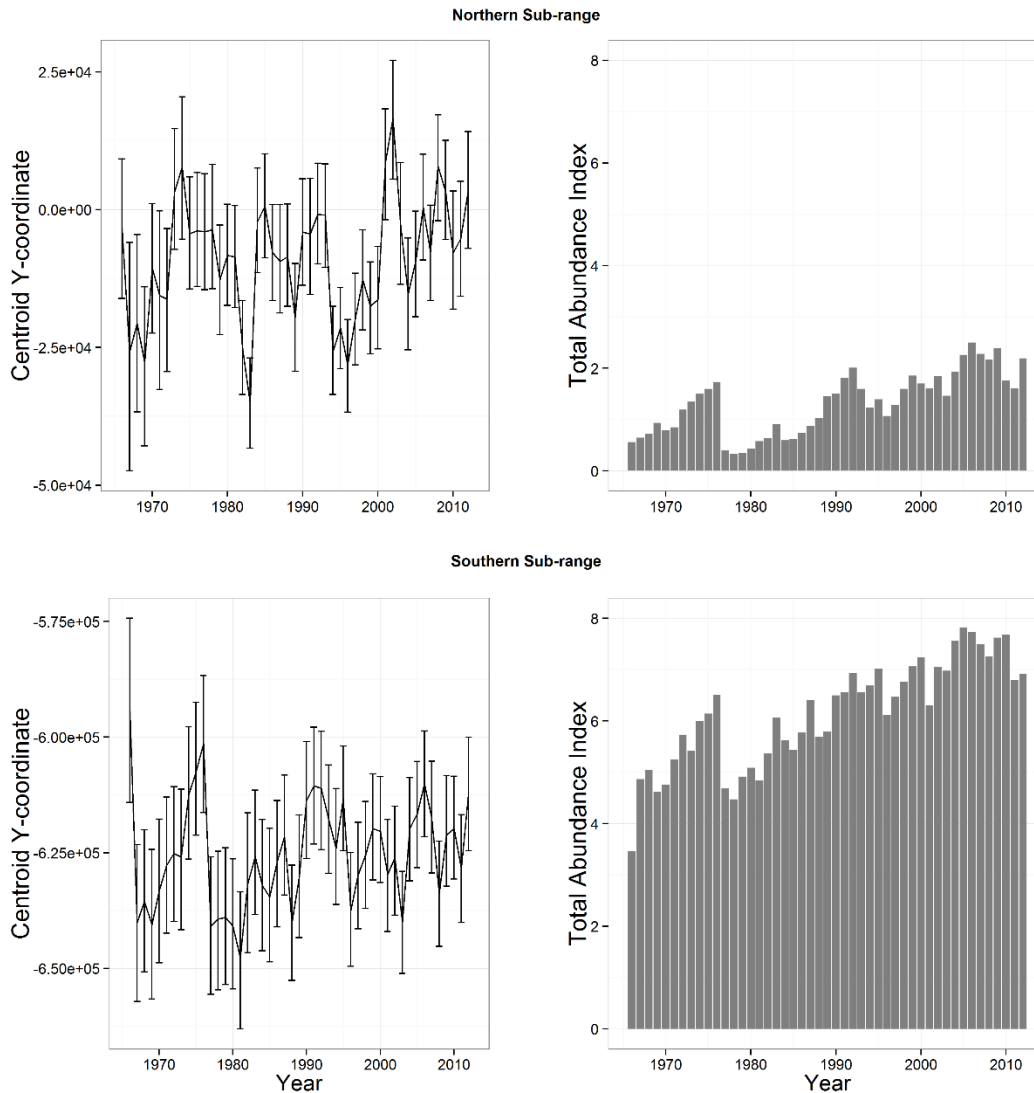


Figure 3-3 The Centroids' Y-coordinates movement and the total population abundance indices in Carolina Wren's northern and southern sub-ranges. The Y-coordinates of the centroids derived on the southern and northern sub-range with whiskers giving 95% credible interval (Left two plots). The two plots on the right side show the total abundance indices in each sub-range over the study period. Significant positive correlation exists between the Y-coordinate and total abundance index in the southern sub-range. The relationship is not significant in the northern sub-range.

The House Finch's full-range centroids summarize the combined distribution of the eastern and western populations which had been two disjunct distributions until the late 1990s. The full-

range centroid shifted significantly over the course of the study period (Figure 3-4). The most rapid change of centroid location took place in the late 1980s and early 1990s when the centroid showed prominent eastward movement. Specifically between 1985 and 1995, the centroid shifted at least 50 km eastward annually (Figure 3-4, Figure 3-5). In comparison during the 1970s and 2000s the distribution of House Finch was relatively stable: full-range centroids were close to their neighbors in the previous and following years and with largely overlapping CI (Figure 3-4).

As hypothesized, full-range centroid coordinates (Y-coordinates for Carolina Wren and X-coordinates for House Finch) associated strongly with the total population abundance indices. The mean correlation for Carolina Wren was 0.65 (95% CI 0.57 ~ 0.72), whereas the one for House Finch was 0.51 (95% CI 0.26 ~ 0.70). The relationship between total population abundance and the coordinates of centroid remained moderate in one of the sub-ranges for each species (southern sub-range for Carolina Wren (mean correlation 0.43, (95% CI 0.28~0.59)) (Figure 3-3), and eastern sub-range for House Finch (mean correlation -0.24, (95% CI -0.12 ~ -0.38)) (Figure 3-5)). The relationships for the rest of the sub-ranges were not significantly different from zero (Table 1).

Lastly, as expected, moderate to strong correlation also existed between coordinates of centroids derived from different ranges. For the Carolina Wren, the relationship was the strongest between the Y coordinates of the full-range centroid and that of the southern range centroid (mean correlation 0.76, 95% CI 0.67 ~ 0.83) (Figure 3-3), whereas for House Finch the association was closest between the X-coordinates of the full-range centroid and that of the eastern sub-range (mean correlation 0.38, 95% CI 0.13 ~ 0.58) (Figure 3-5).

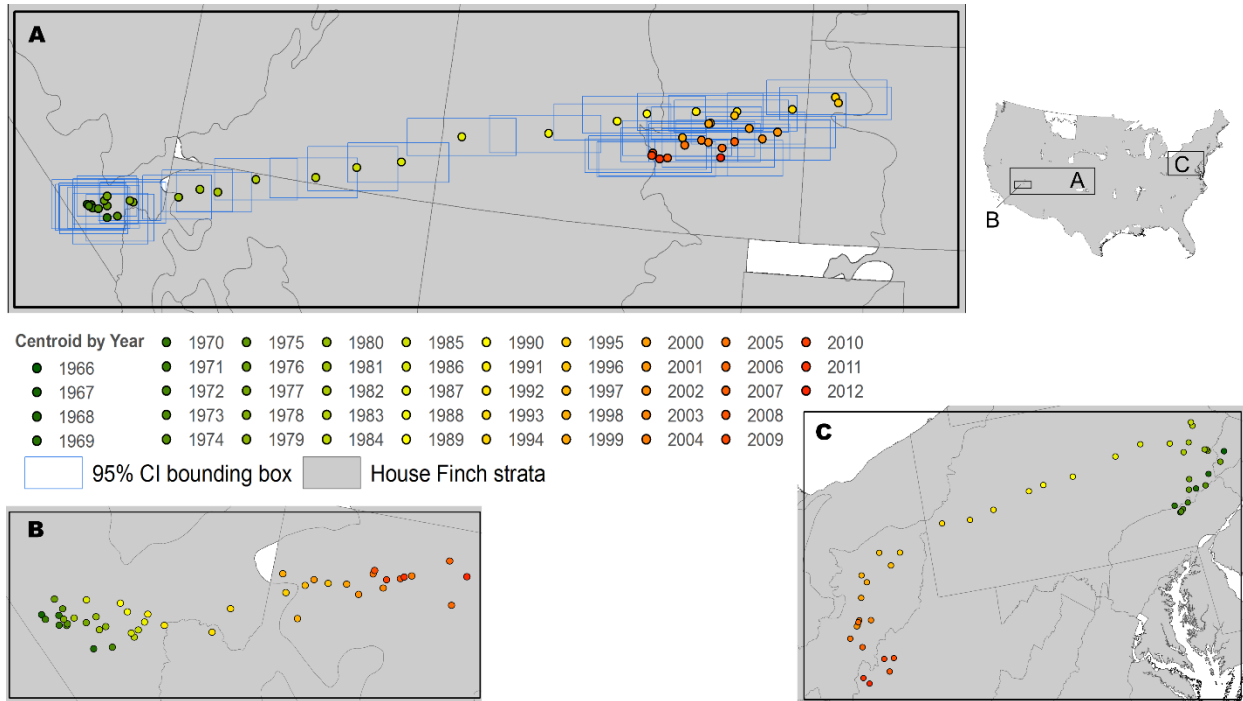


Figure 3-4 The spatial location of House Finch centroids in the entire range, eastern and western sub-ranges. Panel A, B and C show the centroid movement within the entire range, western and eastern sub-ranges respectively. The color of the circle from dark green to red represent the progression of time from year 1969 ~ 2012. As can be seen, both the full-range and eastern sub-range centroids have shifted significantly, whereas the western sub-range centroids are clustered and have shifted with less magnitude.

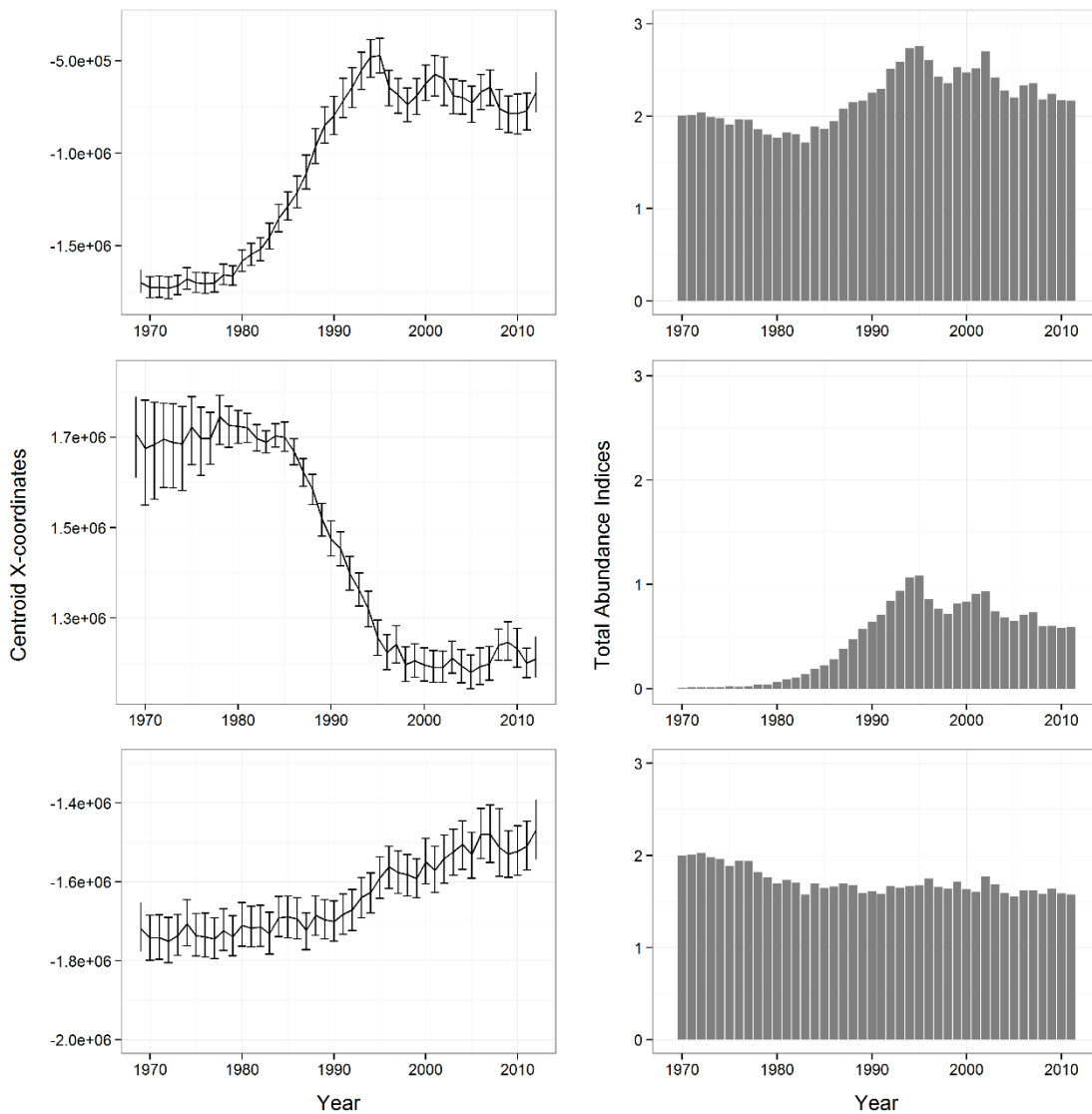


Figure 3-5 The X-coordinates of House Finch centroids and total population abundance indices in different ranges. The top, middle and bottom panel show the X-coordinates (left) of centroids and abundance indices (right) in the entire range, eastern and western sub-ranges respectively. It shows strong correlation between the centroid X-coordinates and total abundance indices in the full range and the eastern sub-range.

The yearly range centroids for the null cases, Bushtit and Dusky Flycatcher, showed tightly distributed centroids with largely overlapping CIs between 1969 and 2012 (Figure 3-6). Dusky Flycatcher showed exceptionally clustered centroids, which is associated with particularly stable populations in the four regions of interest.

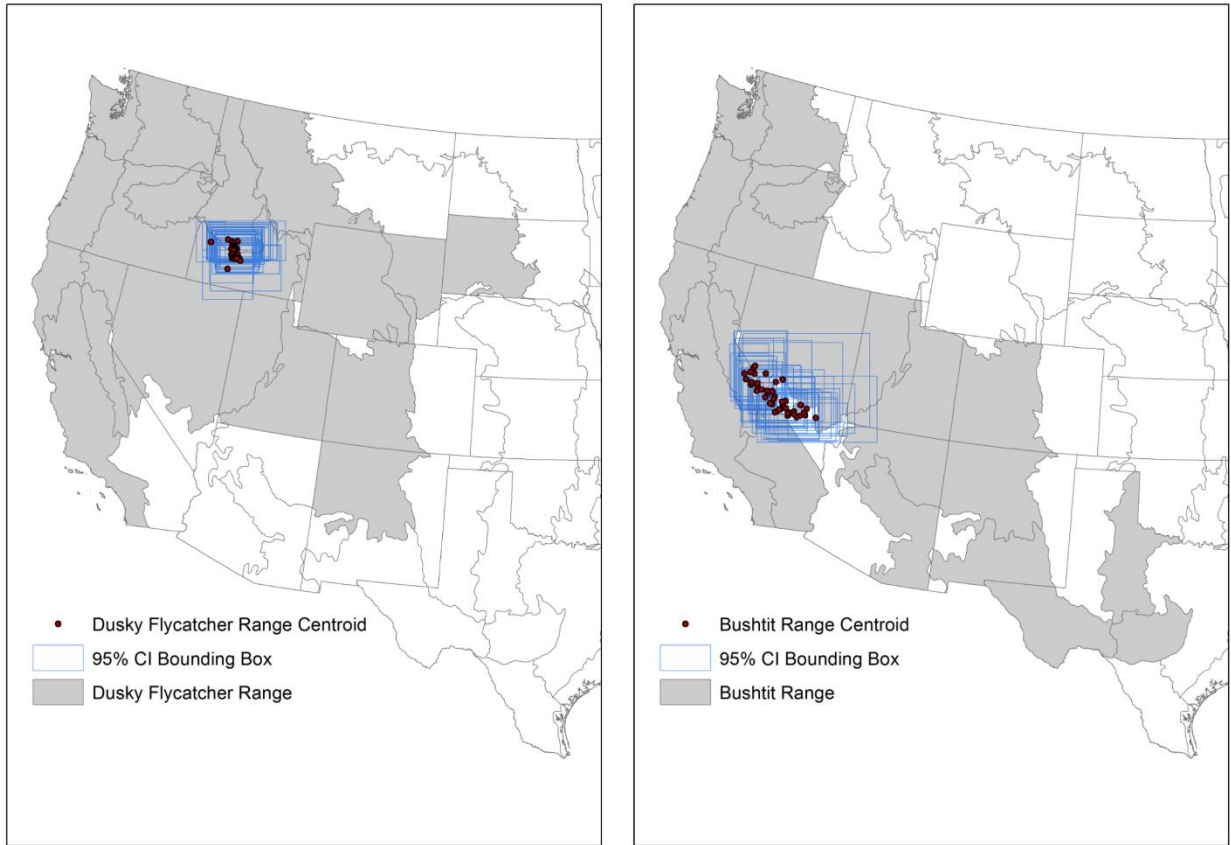


Figure 3-6 Range centroids of Bushtit and Dusky Flycatcher between 1968 and 2012.

3.5 Discussion

3.5.1 Species Patterns

Carolina Wren’s latitudinal distribution is strongly correlated with winter conditions. The number of snow-cover days is strongly associated with reduction in the population size at different scales. As predicted, winter conditions have stronger impacts on the southern and full-range centroid than the northern sub-range, manifested by the stronger correlation between the centroid Y-coordinate and the number of snow-cover days in the ranges. The relatively weak influence of winter conditions on the centroid in the northern sub-range could be because the Carolina Wren routinely encounters deep snows in the northern states, and survival in even

normal winters are mediated by reliable food sources (i.e., feeders). Thus, over the northern sub-range the severe winters have relatively small and similar impact on their food sources as well as on their already small population sizes. Much larger mortality often occurs further south, where the species is more abundant and unaccustomed to heavy snowfall. The population there can survive in moderate winters in natural habitats away from feeders. But extreme heavy snow can thus result in starvation and drastic population decline (Link and Sauer 2007).

Interpretation of the movements of the full-range centroid for House Finch requires an understanding of the history of the eastern and western sub-populations. The eastward movement of the full-range centroid of House Finch is determined mainly by a relatively stable western population and a prominent population growth in the east (before the late 1990s) where introduced House Finches rapidly colonized new areas. After the introduction of House Finch in New York area, by the 1960s the populations had spread to New Jersey and Connecticut. The fast southwest movement of the eastern centroid in the late 1980s and early 1990s was coincident with the most rapid regional population growth (Figure 3-5). During the period, the House Finch population expanded its range quickly to occupy most of the Great Lake region and Southern Appalachian region (Figure 3-7) (Veit and Lewis 1996). The eastern sub-range's centroid changes provide an informative summary of this colonization process.

Interestingly, in the 1990s a severe conjunctivitis caused by a parasitic bacterium *Mycoplasma gallisepticum* became widespread in the eastern House Finch population (Dhondt et al. 1998). The disease was first documented in the Washington D.C. area in 1993 and was believed to affect House Finches the most in areas with established large populations (mainly in the north) (Dhondt et al. 1998, Hochachka and Dhondt 2000). The epidemic of the density dependent disease may have contributed to the decline of the total House Finch population in the eastern

sub-range (Figure 3-5); moreover, the rapid southwest shift of the House Finch range centroid in the eastern sub-range in the 1990s could also be attributed to the disease since during such period the disease disproportionately affected the established northern population along the coast, while the population growth in the frontier regions was unhampered.

It is not surprising that for both species, centroid movements of the full range correlate significantly with their counterpart in one of the sub-ranges. Although they are not independent, i.e., sub-range centroids were calculated on part of the shared data. It does indicate that changes in the overall centroid may indicate important ecological changes occurring in sub-ranges.

However, understanding the geographic structuring that divides the population will clearly lead to more informative inferences regarding the unique population dynamics taking place at specific regions.

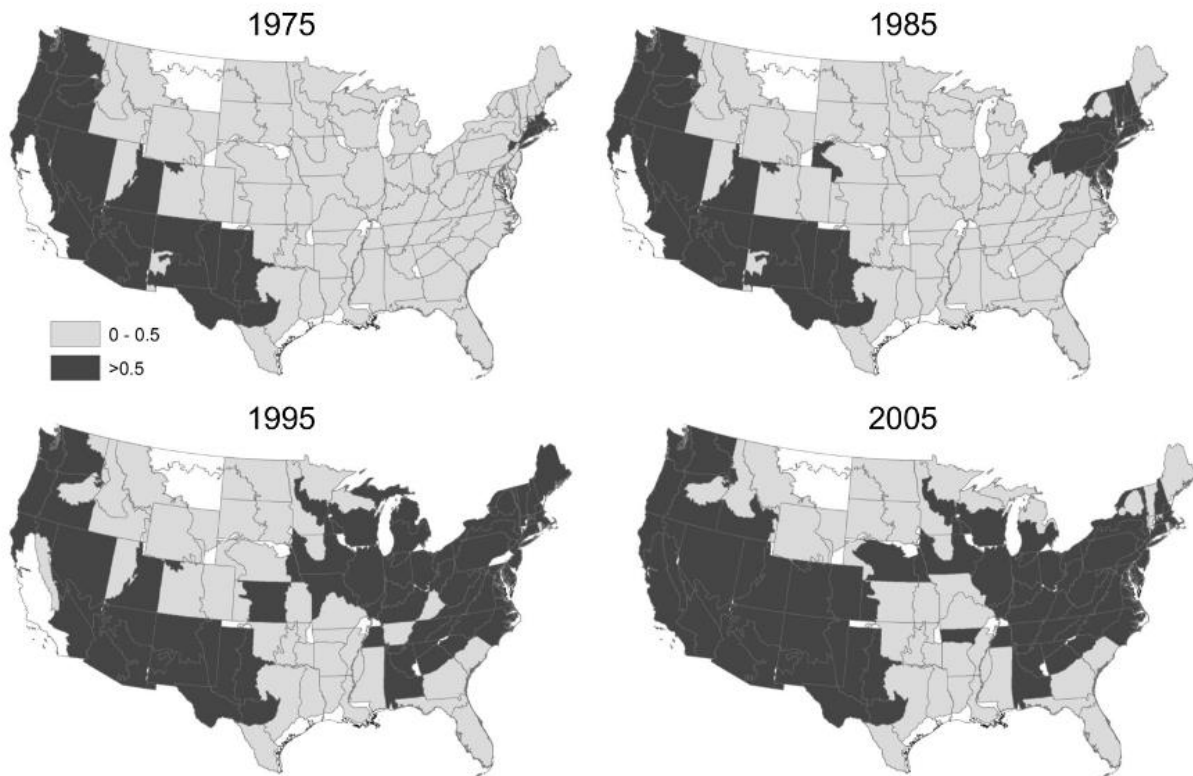


Figure 3-7 The distribution of House Finch population over the contiguous U.S. between 1975 ~ 2005. For each stratum we calculated House Finch's density indices (it is the stratum-specific abundance indices divided by the weight of area: $N_{i,t}/A_i$). The darker areas highlight the strata with density indices larger than 0.5.

In comparison, for the null cases, the centroids of Bushtit and Dusky Flycatcher were tightly clustered (Figure 3-6). This clustering is consistent with the summarized population trends that show stable populations for both species across their ranges (Sauer et al. 2014). Similar clustering is observed in the case of the House Finch during the earliest and the latest decades of the survey when population changes were slow (Figure 3-4). These patterns could represent null case scenarios within a shorter time period.

3.5.2 Range Statistics

The centroid of a species' distribution is a useful summary statistic of the population's central tendency in a spatial context. Our study demonstrated that the centroid model is a very useful tool to characterize the long term changes of avian distribution, while the log-linear Bayesian model ensures that the abundance measures at the strata level are controlled for varying detection rates that occur in the raw data. The efficacy of centroids as descriptors lies within the fact they condense large scale species distributional information into spatially referenced points. They enable the visualization of population change and interpretation of results in a straightforward and intuitive way. In essence, the shift of centroids reflects asymmetrical changes of population in two dimensional spaces. Centroids always move toward the direction with relatively rapid growth or away from the direction of rapid population reduction or a mixture of both. They are closely related to population trends and yet compliment population abundance measurements, as the shifting of centroids reveals two dimensional information regarding the general direction and magnitude of population changes.

Many hypotheses associated with distributional changes can be reasonably expressed in a single dimension. For simplicity purposes, we primarily focused our analysis for both case studies on a single dimension (either latitudinal or longitudinal) that had more significant changes. However, the natural description of centroids is in two dimensions, both for display and for many distribution change cases. It is thus reasonable to combine both X and Y-coordinates together, when changes take place in both directions. One striking example is showed for Eurasian Collared-Dove (*Streptopelia decaocto*) in Figure 3-8 Eurasian Collared-Dove is an invasive species in the U.S. It was first observed by BBS surveyors in Florida in 1986 and then quickly expanded its range to the northern and western states (Bled et al. 2011). The centroid model effectively characterizes the magnitude and the direction of such colonization process on two-dimensional space. Our qualitative description of the effects of conjunctivitis on the eastern House Finch population is another example of this. It would be useful to obtain information on the geographic distribution of conjunctivitis and evaluate the associations between the disease and House Finch populations in two dimensions.

3.5.3 Effect of Range Delineation and Scale

The disparity in centroids' movement patterns between sub-ranges shows that while the composite range centroid derived at the continental scale can be an effective mechanism for characterizing changes, it may not reflect population changes taking place at individual sub-ranges and strata. Clear interpretation of the changes requires some degree of contextual information on the ground. Multiple scenarios (e.g. population growth, decline, colonizing new range, and local extinction) can result in similar patterns of centroid movements. The calculation and visualization of population abundance indices at different scales as demonstrated in this study may help to further examine the sources of changes on the ground. Cautions are needed for

species with disjunct distributions, as they are more likely to have contrasting population dynamics. Therefore, meaningful centroid analyses require strategic delineation of range boundaries which are informed by specific research questions. However, as shown by the Carolina Wren example, if environmental factors that influence distributional change vary from year to year, distinct boundaries for relevant sub-populations may not be unique to delineate.

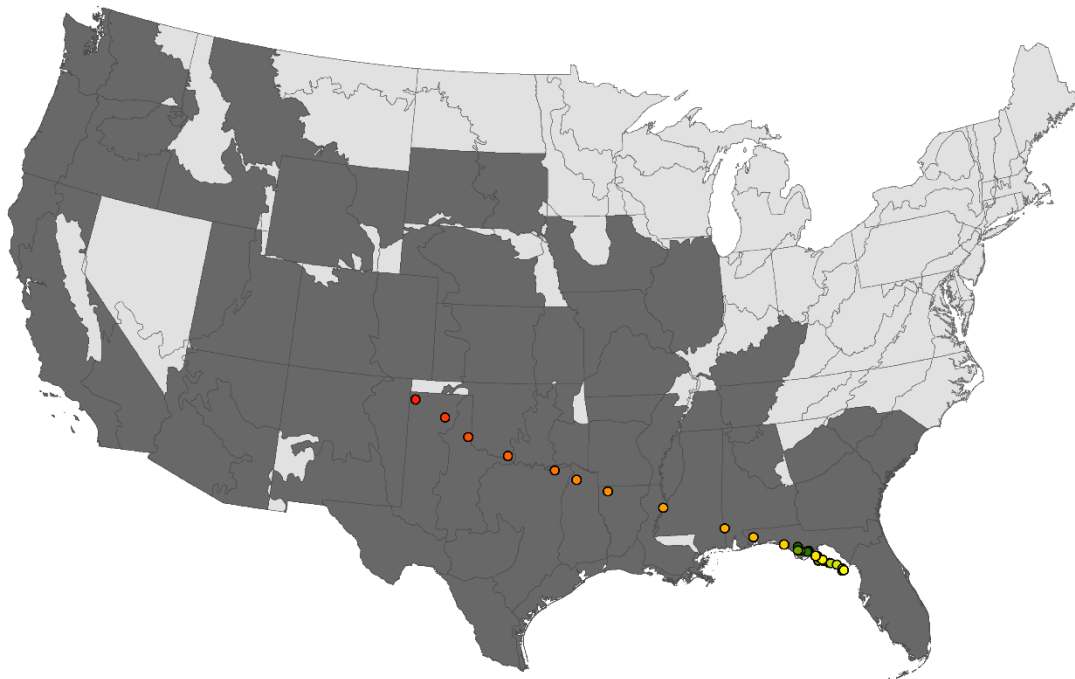
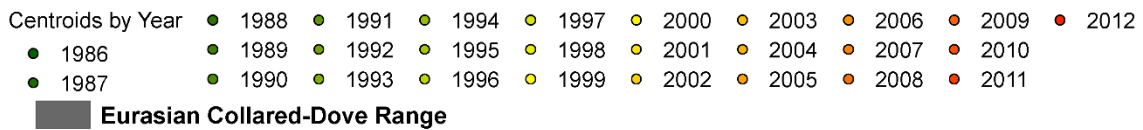


Figure 3-8 Range centroid shift of Eurasian Collared-Dove.

Natural or artificial range boundaries play an important role in shaping centroid movements. Such boundaries can result from un-surveyed regions or geographical barriers such as oceans and mountains. For example, even though the BBS has extensive spatial coverage, it still does not survey the full ranges of many species(Sauer et al. 2014); we can only model the portion of the

range with data, and we should be sensitive to the possibilities of artifacts in summary analysis that might occur as consequence of working with partial ranges. The characteristics of centroid movements sometimes reflect the spatial pattern of the delineated ranges. For instance, the sharp turns of the centroid in House Finch's eastern sub-range (e.g. turning from northeast to southwest around late 1980s, and from southwest to south around early 2000s (Figure 3-4)) are mostly the consequences of the range boundaries chosen for our study. The centroid changed course significantly because in one area House Finch population reached equilibrium when it expanded to the range boundary; at the same time, the population continued to grow and expand in other directions which drove the centroid in new trajectories. Despite the sharp turns, at the continental scale, in the north, the invasive House Finch population crossed the U.S. border into southern Canada (Sauer et al. 2011), whereas in the west, the population continued to spread further west which potentially facilitated the expansion of the population to several strata in the western sub-range (Figure 3-4, Figure 3-7).

The scales of ranges upon which centroids are derived can have significant effect on the variability of centroid location. Specifically, broader ranges can be related to larger potential variability in centroid location. This is intuitive because the potential variability of centroid is always restrained by the spatial extents of components they represent. They are always located between the minimum and maximum coordinate of the components. More importantly, larger geographical ranges also encompass larger environmental gradients which have the capacity to result in more diverse population dynamics across strata, and thus greater potential variability in centroid locations. This was evident when comparing the Carolina Wren's full-range centroid versus that of the southern or northern sub-ranges. Working with full scale or relatively large range centroids thus has advantages in interpreting population trends influenced by large scale

environmental forces (Figure 3-1, Figure 3-2). However, when comparing the magnitude of centroid shifts between species with different ranges, methods to account for the extents of ranges may be required.

3.5.4 Scale of Implementation of Centroid Models

It is worth noting that we implemented our centroid models using strata as basic units, which are structured by the intersection of physiographic regions and U.S. states. We modeled stratum-specific abundance indices that required at least 5 surveyed routes within each stratum. This model was driven by our intention to summarize the population spatial characteristics at the continental scale. However, the method could be applied at other spatial scales. Bled et al. (2013), for example, employed a spatial model that permitted estimation of population change on a regular grid system. The grid system, which is scalable, provides a reasonable alternative framework for computing centroids of distribution at regional scale.

Alternatively, localized survey information such as bird atlas data can be suitable for local implementation of centroid models. Atlas data sets are available for many countries, states, and provinces (Harding 1979, Andrle and Carroll 1988, Brewer et al. 1991, Brauning et al. 1992, Sharrock 2010), and they also have more regular sampling schemes and finer scale (Gaston 2003). Of particular use would be atlases that provide relative abundance estimates. Similar centroid methods can be readily applied on such survey data at the regional or local scales. Moreover, the centroid approach can also work in conjunction with site occupancy models (Royle and Link 2006, Royle and Kéry 2007) which normally provide presence and absence information regarding the species distribution. Analysis at the regional scale would particularly emphasize relationships between species distributions and localized influences such as

conservation policy, habitat structure and land cover land use patterns (Donald et al. 2007, Pidgeon et al. 2007, Huang et al. 2014).

3.6 Conclusion

There are a variety of methods for analyzing changes in the geographic distributions of species. However incorporating range-wide abundance heterogeneity while accounting for variability and constraints embedded in large scale surveys has been a difficult task (Link and Sauer 1998, 2002, Gaston 2003). Our centroid analysis based on hierarchical Bayesian models demonstrated a framework to address such concerns while utilizing the long term BBS data set at the continental scale. By incorporating the abundance structure over the whole range, our method provides a valuable descriptor to characterize and analyze species long-term spatial distribution changes. Particularly the results show the value of the centroid model in examining avian interaction with large scale environmental covariates as well as in summarizing rapid change in species' ranges and population. Future studies should be done to examine the pattern of centroid shifts for large groups of avian species and possibly extended to other taxa. Such centroid analysis at the community level will provide valuable empirical observations regarding recent species range changes. It will also lend insight on the interactions between a variety of changing environmental forces and systematic species distribution changes.

Chapter 4. Rapid Multi-directional Climate Change

Fingerprint in North American Bird Distributions Associated with Multi-Faceted Climate Change

4.1 Abstract

The shift of species' distribution as a major fingerprint of climate change is of great interest to conservationists and ecologists. Many hypotheses have been proposed regarding the direction and the speed of species' distribution shifts. However, few have been tested with data of recent distribution shifts at the continental scale. Additionally, the relative influences of temperature, precipitation, average climate, and extreme climate conditions on the shifting distributions are not clear. In this study, we quantify the directions and speed in the geographical distributions of 57 North American permanent resident birds using a distribution centroid method. We first test the multi-directionality of these shifts. We then compare the speed of the shifts between birds occurring primarily in mountainous regions and flat regions, to test a hypothesis based on climate change velocity hypothesis. Lastly, for the species with significant distribution changes, we compare the influence of two pairs of climatic factors (temperature with precipitation, and extreme climate with average climate condition) by modelling species population change rate using different sets of climatic data. Our results show that, over the past four decades, 36 of 57 bird species shifted their distribution significantly. There is strong evidence that the climate change fingerprint in avian distribution is multi-directional. Our findings do not support the climate velocity prediction and show that the speed of the distribution shifts for the plain birds is not significantly faster than that of the mountain birds. For most species, the average climate model and the temperature model have stronger associations with the population change rate

than the precipitation and extreme climate models. For some species, however, the extreme climate model and the precipitation models have considerable advantages in explaining their shifting distributions, and they show great potential to supplement and extend the study of species distribution which traditionally focuses on average temperature measures. Our study improves the understanding of the extent and characteristics of the recent climate change fingerprint. It also presents a complex picture of how species respond to recent environmental changes at the continental scale. The results highlight the need for a more species-specific approach to examine the contributing factors to such rapid changes and the need for comprehensive conservation planning and practices for adaptation. Furthermore the study also emphasizes the values of climatological records with fine temporal resolution on which the extreme climate events can be better characterized.

4.2 Introduction

Global climate has rapidly changed in the past century and is projected to change further at an unprecedented rate (IPCC 2014). This poses a great threat to global biodiversity because the rate of climate change will most likely outpace the ability of species to relocate or adapt (Walther et al. 2002, Parmesan and Yohe 2003, Loarie et al. 2009). Shift in species distribution is considered one of the major fingerprints of climate change, and thus has been of great interest to ecologists and conservation practitioners (Parmesan and Yohe 2003). Recent meta-analyses have concluded that a wide range of animal and plant species have been exhibiting shifts in their distribution (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Chen et al. 2011). Most prior studies have focused on latitudinally poleward and elevationally upward shift of species distributions (Thomas and Lennon 1999, Parmesan et al. 1999, Hickling et al. 2006, Hitch and Leberg 2007). This is, in part, because latitude and elevation are broadly correlated with surface

temperature, the biological responses to which are relatively better understood and more predictable for most species (Root et al. 2003). However, temperature, particularly the average temperature metrics used by many climate change studies, is not the only climatic factor that has a profound impact on species distributions. Other factors such as precipitation and the combination of temperature and precipitation can be closely related to shifts in species' geographical distributions, and the resulted changes could also be multi-directional (Gillings et al. 2015). However, evidence to support such hypotheses are mostly based on model projections or regional studies (Tingley et al. 2009, VanDerWal et al. 2013, Gillings et al. 2015) which utilize only limited amount of data and are not idea to be used to examine multi-directional distribution shifts. A systematic analysis that examines the multi-directionality of the recent climate change fingerprint at the continental scale is lacking.

A major recent contribution defines the speed of climate change fingerprint based on the concept of climate change velocity (Loarie et al. 2009), a minimum distance required at a specific location to catch up with climate change. I was hypothesized that greater topographic variability in mountainous areas leads to a greater spatial gradient of surface temperature which in turn results in lower climate change velocity. Therefore, it was hypothesized that smaller geographical displacements (slower speed of distribution change) are required for species in mountainous regions to keep pace with increasing temperature (Loarie et al. 2009). In contrast, faster speeds of distribution change are required in relative flat regions. To improve our understanding on how species respond to the changing environments, there is a need to better understand the speed of climate change fingerprint and to test existing hypotheses. Evaluating the speed of recent climate change fingerprint on a large number of species and testing the climate change velocity hypothesis would provide valuable information to this end.

Furthermore, most of the studies examining the impact of global climate change, including the climate velocity hypothesis, have focused on the effect of climatic conditions derived on monthly or seasonal weather data, such as mean seasonal or annual temperature (Guisan and Zimmermann 2000, Root et al. 2003, Parmesan 2006, Alexander et al. 2006, Pereira et al. 2010). Climate-based species distribution models also rely heavily on mean seasonal climate conditions as predictive variables (Guisan and Zimmermann 2000, Pearson and Dawson 2003, Hijmans and Graham 2006, Pereira et al. 2010). However, there is an increasing number of studies that showed the frequency and intensity of extreme climate events could have great impacts on species ecology and spatial distribution (Karl et al. 1999, Parmesan et al. 2000, Easterling et al. 2000). Recent studies also show that the decrease in frequency of extreme cold weather events have enabled a few species to increase abundances in poleward direction where they used to be limited by winter condition (Crozier 2003, Cavanaugh et al. 2014). However, little is known about the relative influences of average and extreme climate events on the changing distributions of avian species. The selection of climatic predictors in the species distribution models is an important source of model uncertainty (Braunisch et al. 2013, Barbet-Massin and Jetz 2014). However very few studies have examined the most relevant and influential climatic predictors at large spatial scale for a wide group of species (Barbet-Massin and Jetz 2014). Our study is seeking to examine the impact of different sets of climatic metrics on changing distribution shifts.

The overall goal of this study is to understand the direction and speed of the recent climate change fingerprint in avian species distributions in North America and to examine the influence of different climatic factors on such changes. Specifically the objectives of this study are three fold. We first test the multi-directionality of the climate change fingerprint in avian distributions by quantifying the cardinal direction of recent distribution shifts of 57 North American

permanent resident birds. We then test the hypothesis that species in mountainous regions shift their distributions slower than species in the plain regions. Finally we contrast the influence of two pairs of climatic factors, temperature with precipitation, and extreme climate with average climate condition on species distribution shifts that showed significant change. We utilize 44 years of Breeding Bird Survey (BBS) data and characterize the direction and speed of the distribution shifts using a centroid method (Huang et al. 2015). Birds are classified into mountain and plain species based on their primary ranges, and shift characteristics are compared between two classes. Four climate models: average climate, extreme climate, temperature, and precipitation models, are established to explain the regional abundance changes of species with significant distribution shifts (Figure 4-1).

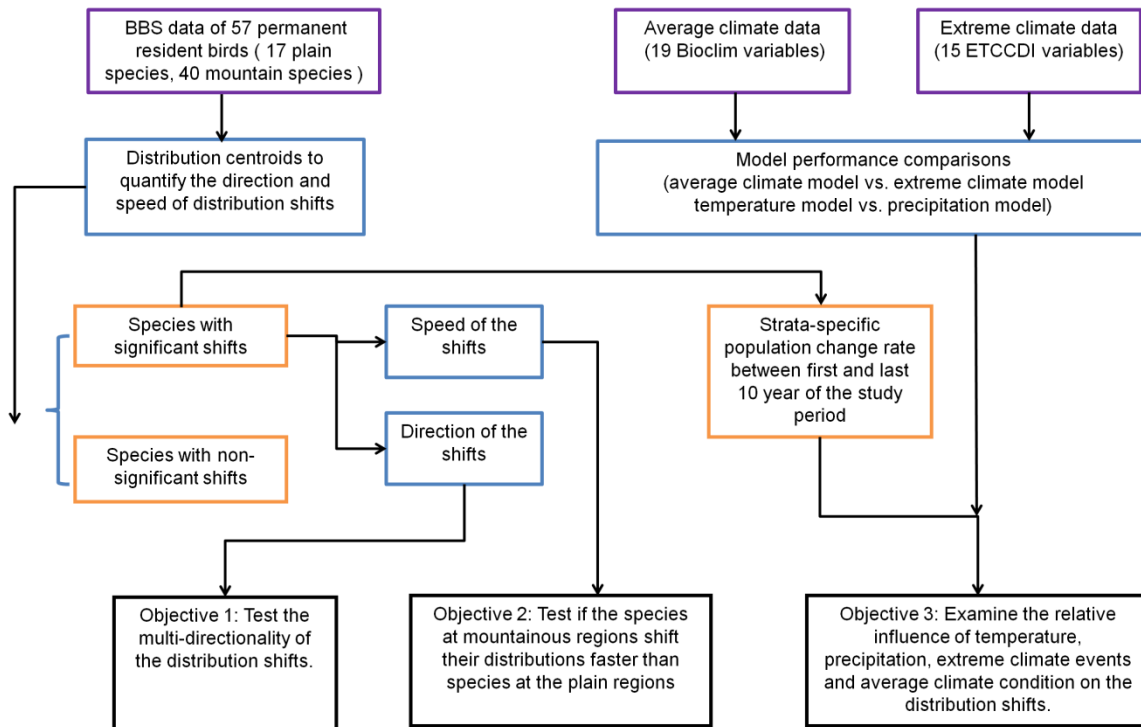


Figure 4-1 Flow chart showing data, methods, hypotheses, and research question in chapter 4.

4.3 Data & Methods

4.3.1 Bird Data

We used the North American Breeding Bird Survey (BBS) data to estimate the avian distribution shifts. BBS is an annual road side survey with more than 5000 routes covering the contiguous United States, southern Canada, and northern Mexico. Since the beginning of the survey in 1966, every year during the breeding season, competent volunteers survey routes using a protocol of 3 minute point counts at each of the 50 sample points along the 39.43km long route. Birds heard and seen within 0.4 km radius are recorded (Robbins 1986, Sauer et al. 2014). We included the 43 years (1969-2012) of BBS data in the contiguous U.S. and southern Canada for our analysis, because the spatial and temporal coverage of the data are more consistent for the selected regions and period. We analyzed the distributions of 57 permanent resident bird species using a centroid method (Appendix III-1). Species are classified as plain species if more than 50% of their ranges are within plain or lowland ecoregions with small topographic variability, otherwise the species are classified as mountain species. The classification resulted in 17 plain species and 40 mountain species (Appendix III-1).

4.3.2 Bird Distribution Centroid

The annual centroids of bird distributions were calculated following methods outlined in Huang et al. (2015). The method divided each bird species range into a list of physiographic strata which were delineated by the union of the U.S. states, Canadian provinces, and Bird Conservation Region (BCR) boundaries. A hierarchical Bayesian model was used to calculate the stratum-specific population abundance N_{it} each year (Link and Sauer 2002, Huang et al. 2015). The annual centroid was calculated as the yearly mean of strata centroids weighted by N_{it}

(See Chapter 3 for detailed description of the model). The sum of population abundance indices over all strata is also estimated as an index for total population of each species.

Inferences for both directly estimated and derived parameters (e.g. centroid coordinates and population abundance indices) in the analysis are based on posterior distributions, because we used the Markov Chain Monte Carlo (MCMC) method to fit the hierarchical Bayesian models. In this study, we created 3 independent Markov chains. Each chain had 20,000 iterations, the first 10,000 of which were discarded (burn-in samples). After the first 10,000 iterations, posterior samples were collected every 50 iterations (thinning rate of 50) so that estimates of posterior distribution were based on the 600 (3 chains \times 10,000 iterations/50 thinning rate) sample values. Based on prior testing and procedures in Huang et al. (2015), this setting is sufficient for characterizing significant changes of distribution. We consistently collected the same number of posterior samples for each N_{it} and centroid coordinates. The posterior samples were used to estimate statistical attributes such as median value and confidence interval (CI) of parameters. For each species, we regressed annual centroids' latitudinal and longitudinal coordinates against year. We then fitted 600 linear regression models. The species were identified as having a significant distribution shift in one of the four directions (northward, eastward, southward, and westward) if the regression slope was significantly larger or lower than 0. A 95% CI value was used to determine statistical significance. For example a significantly positive slope in latitudinal direction indicates significant northward distribution shift.

The speed of the distribution change (km/y) was characterized as the average distance between consecutive annual distribution centroids. Widespread species with more distant physiographic strata tend to have larger potential variability in centroid locations (Huang et al. 2015). To

account for the differences of range sizes, we calculated the ratio of annual shift speed to the average maximum distance across range to measure the speed while accounting for range sizes.

4.3.3 Average Climate Indices

Average climate conditions were characterized by using Bioclimatic indices (hereafter bioclim variables). The indices were derived based on monthly temperature and precipitation data. The indices are commonly used in ecological niches models/ species distribution models, and primarily depict annual trends and seasonality measured at relatively coarse temporal scales (e.g. mean temperature of the warmest month, precipitation of the driest quarter). We used the station-based monthly data from United States Historical Climatology Network (USHCH) version 2.5 serial (Williams, Jr., et al. 2006, Menne et al. 2009). Then we used the “dismo” package (Hijmans et al. 2015) on R statistical program (R Development Core Team 2011) to calculate 19 bioclim variables using data from each weather station (Table 1). Out of 19 bioclim variables, 11 were temperature indices, while 7 were precipitation indices (Table 1). Stations were selected if they consistently had climate record over the periods of 1969-1978 and 2003-2012. The change of mean and standard deviation of the index values between the two periods were tabulated in each station.

4.3.4 Extreme Climate Indices

We used the indices defined by the Expert Team on Climate Change Detection and Indices (ETCCDI) to capture change of climate extremes (Sillmann and Roeckner 2007). The ETCCDI indices were derived from daily temperature and precipitation data that support more detailed measurement of extreme climate events such as the annual frequency of days with temperatures below 0 degree Celsius and the maximum number of dry spell days. We used the station-based

15 ETCCDI extreme climate indices (Table 1) modeled and reanalyzed by Coupled Model Intercomparison Project Phase 5 (CMIP5)(Sillmann et al. 2013). Among the 15 ETCCDI indices, 7 of them measure temperature related events, and 8 of them measure precipitation related events (Table 1). Station data in the United States were selected, again, if they had the full coverage of the specific ETCCDI index values over the periods of 1969-1978 and 2003-2012. The change of a specific index's mean and standard deviation value between two periods were calculated for each station.

4.3.5 Population Change Rate & Climatic Models

For each stratum the changes of climatic conditions were summarized as the maximum, minimum, median value of the climatic metrics of all available weather stations. This generated 57 (19×3) bioclimatic metrics and 45 (15×3) extreme climatic metrics for each stratum. To prepare for comparing the effect of temperature and precipitation, we also grouped all temperature metrics (54) and precipitation metrics (45).

Species with significant shift in at least one direction were selected for population change rate modeling utilizing different sets of metrics. We calculated the stratum-specific population change rates for each species. The growth rate r_i was defined as the natural logarithm of the ratio of the average abundance indices in 2003-2012 to the average abundance indices in 1969-1978. The 10 year mean was used to average out the short term variability of population and climatic fluctuations.

$$r_i = \log_e \frac{Ni_{2003-2012}}{Ni_{1969-1978}}$$

A positive r indicates an increasing population, whereas a negative r , a declining population. Six hundred posterior samples of population change rates were calculated at each stratum based on the posterior samples of population abundance indices.

We established four climate models to evaluate the influences of the changes of different types of climatic factors on the population change rate across strata for the species with significant shifts. The average climate, extreme climate, temperature, and precipitation models were built utilizing 54 temperature metrics (33 bioclim metrics & 21 extreme climate metrics), 45 precipitation metrics (21 bioclim metrics & 24 extreme climate metrics), 57 average climate metrics, and 45 extreme climate metrics, respectively. To maintain the consistent data coverage of these climatic data, we only modeled the population change rate with the strata in the U.S.

We used the random forests (RF) algorithm to model the population change rate at different strata for each species. The RF model is known to perform well with small number of observations and large number of predictive variables without overfitting (Breiman 2001). Specifically, when building a random forest model, about 37% of data are randomly drawn as the out-of-bag (OOB) observations and excluded in the model construction. The OOB error estimation provides a cross-validation mechanism, thus normally test sets or extra cross-validation is not necessary. The performance of the random forest models was estimated using percent of variance explained (% var. explained or PVE from hereafter) = $1 - \text{MSE} / \text{observed variance}$, where MSE is mean square error between OOB predictions (Breiman 2001, Wei et al. 2010). The measure of PVE, ranging from 0 to 1, works similarly as the r -squared value in measuring model performances. However if the OOB-predicted MSE is larger than the variance of the observed response, as happens when the predictors perform poorly to predict the responses, the PVE can be negative. Overall the RF model is especially well suited for our study because

the model is robust even with significant covariance between predictive variables (Breiman 2001, Biau 2012), which commonly exists between a variety of climatic and habitat metrics (Huang et al. 2014).

We used the RandomForest R package (Liaw and Wiener 2002) in the R statistical program (R Development Core Team 2011) to build RF models. For each species and each type of climate model, we built 600 iterative RF models based on the number of posterior samples. We set the number of trees to be 4000 for all RF models to allow convergence of mean residual error so the PVE remained stable regardless of the random seed used. The values of the mean PVE were averaged among 600 models. The models with negative average PVE cannot significantly explain the variability of population change rate, and thus are marked as accounting for zero average PVE. We then compared the model performance differences (differences in average PVE) between 2 pairs of models (average climate model with extreme climate model, temperature model with precipitation model).

Table 4-1 Climatic metrics used in the analysis. The average climate conditions are characterized by the 19 Bioclim metrics, and the extreme climate conditions are characterized by the 15 ETCCDI metrics. Each metric set contains both the temperature metrics (Temp) and precipitation metrics (Precp).

Bioclim Metrics	Definition	Class	ETCCDI Metrics	Definition	Class
Bio1	Annual mean temperature	Temp	FD	Number of frost days: Annual count of days when TN (daily minimum temperature) < 0°C.	Temp
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Temp	SU	Number of summer days: Annual count of days when TX (daily maximum temperature) > 25°C.	Temp
Bio3	Isothermality (BIO2/BIO7) (* 100)	Temp	ID	Number of icing days: Annual count of days when TX (daily maximum temperature) < 0°C.	Temp
Bio4	Temperature Seasonality (standard deviation *100)	Temp	TR	Number of tropical nights: Annual count of days when TN (daily minimum temperature) > 20°C.	Temp
Bio5	Max Temperature of Warmest Month	Temp	GSL	Growing season length: Annual count between first span of at least 6 days with daily mean temperature TG (daily mean temperature)>5°C and first span after July 1st of 6 days with TG<5°C.	Temp
Bio6	Min Temperature of Coldest Month	Temp	WSDI	Warm spell duration index: Annual count of days with at least 6 consecutive days when TX > 90th percentile	Temp
Bio7	Temperature annual range (bio5-bio6)	Temp	CSDI	Cold spell duration index: Annual count of days with at least 6 consecutive days when TN < 10th percentile	Temp
Bio8	Mean Temperature of Wettest Quarter	Temp	SDII	Simple precipitation intensity index	Precp
Bio9	Mean Temperature of Driest Quarter	Temp	R10mm	Annual count of days when PRCP≥ 10mm	Precp
Bio10	Mean Temperature	Temp	R20mm	Annual count of days when PRCP≥	Precp

	of Warmest Quarter			20mm	
Bio11	Mean Temperature of Coldest Quarter	Temp	CDD	Maximum length of dry spell, maximum number of consecutive days with RR(daily precipitation) < 1mm	Precp
Bio12	Annual precipitation	Precp	CWD	Maximum length of wet spell, maximum number of consecutive days with RR ≥ 1mm	Precp
Bio13	Precipitation of Wettest Month	Precp	R95P	Annual total PRCP when RR > 95p	Precp
Bio14	Precipitation of Driest Month	Precp	R99P	Annual total PRCP when RR > 99p	Precp
Bio15	Precipitation Seasonality (Coefficient of Variation)	Precp	DRCPtot	Annual total precipitation in wet days	Precp
Bio16	Precipitation of Wettest Quarter	Precp			
Bio17	Precipitation of Driest Quarter	Precp			
Bio18	Precipitation of Warmest Quarter	Precp			
Bio19	Precipitation of Coldest Quarter	Precp			

4.4 Results

We first report the summary of the species with significant distribution shifts, and show the direction and speed of these shifts. Secondly we report the differences of shift characteristics between mountain bird and plain bird classes. Finally, for species with significant shifts, we show the relative performance between the two pairs of climatic models (temperature model with precipitation model, and the extreme climate model with average climate model) in explaining the variability of population change rate across strata.

4.4.1 Multi-directionality

Among the 57 permanent resident species selected, 63% (36) showed significant centroid shifts in at least one direction (Figure 4-2,

Table 4-2,). 19 of these 36 species moved northward, while 3 shifted southward. In the longitudinal direction, 16 of the significant shifts occurred eastward, while 17 westward. Note that the latitudinal and longitudinal directional shifts are not mutually exclusive (Figure 4-3,

Table 4-2).

Species with a significant increase in total population accounted for the greatest number (44% (16)) of the significant centroid shifts, followed by species with a significant decline of total population (31% (11)), and the ones with stable population (25% (89)) (Table 4-3). The species with increased populations accounted for the largest number of shifts in all directions except the southward shift, which did not include any species with growing population (Table 4-3).

Table 4-2 36 species with significant distribution shifts. The direction columns (north, south, east, and west) indicating whether a species was identified having significant distribution shift over the specific direction. The species population status (increased, stable, and decreased total population), guild membership (whether the species is primarily distributed in flat regions), distribution shift speed (raw speed and standardized speed using speed-to-range-width ratio) are also presented.

ID	Scientific Name	Common Name	north	south	east	west	population status	Plain Index	Speed (km/y)	speed to range width ratio
0	<i>Colinus virginianus</i>	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	TRUE	36.3	0.0158
1	<i>Callipepla californica</i>	California Quail	FALSE	FALSE	TRUE	FALSE	Increased	FALSE	57.0	0.0421
2	<i>Meleagris gallopavo</i>	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	FALSE	30.0	0.0091
3	<i>Columbina passerina</i>	Common Ground-Dove	FALSE	FALSE	FALSE	TRUE	Stable	TRUE	21.7	0.0109
4	<i>Columbina inca</i>	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	TRUE	26.4	0.0197
5	<i>Coragyps atratus</i>	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	FALSE	31.5	0.0130
6	<i>Bubo virginianus</i>	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	FALSE	29.6	0.0066
7	<i>Geococcyx californianus</i>	Greater Roadrunner	FALSE	TRUE	TRUE	FALSE	Stable	TRUE	27.4	0.0154
8	<i>Picoides villosus</i>	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	FALSE	22.0	0.0048
9	<i>Picoides pubescens</i>	Downy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	FALSE	23.3	0.0051
10	<i>Dryocopus pileatus</i>	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	FALSE	20.4	0.0053
11	<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	TRUE	10.8	0.0050
12	<i>Cyanocitta stelleri</i>	Steller's Jay	TRUE	FALSE	FALSE	TRUE	Stable	FALSE	13.5	0.0074
13	<i>Aphelocoma californica</i>	Western Scrub-Jay	TRUE	FALSE	FALSE	TRUE	Stable	FALSE	16.6	0.0085
14	<i>Corvus corax</i>	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	FALSE	20.1	0.0045
15	<i>Corvus ossifragus</i>	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	TRUE	12.1	0.0065
16	<i>Quiscalus</i>	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	FALSE	10.7	0.0056

	<i>mexicanus</i>									
17	<i>Cardinalis cardinalis</i>	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	TRUE	7.2	0.0023
18	<i>Mimus polyglottos</i>	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	FALSE	27.0	0.0077
19	<i>Toxostoma curvirostre</i>	Curve-billed Thrasher	TRUE	FALSE	FALSE	FALSE	Decreased	FALSE	11.2	0.0082
20	<i>Thryothorus ludovicianus</i>	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	TRUE	28.6	0.0137
21	<i>Sitta carolinensis</i>	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	FALSE	46.4	0.0123
22	<i>Baeolophus bicolor</i>	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	TRUE	20.1	0.0090
23	<i>Poecile atricapillus</i>	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	FALSE	62.6	0.0153
24	<i>Poecile carolinensis</i>	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	TRUE	13.0	0.0072
25	<i>Poecile gambeli</i>	Mountain Chickadee	TRUE	FALSE	FALSE	TRUE	Decreased	FALSE	47.8	0.0251
26	<i>Poecile rufescens</i>	Chestnut-backed Chickadee	FALSE	FALSE	TRUE	FALSE	Decreased	FALSE	16.6	0.0115
27	<i>Psaltriparus minimus</i>	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	FALSE	52.8	0.0247
28	<i>Auriparus flaviceps</i>	Verdin	FALSE	TRUE	TRUE	FALSE	Decreased	FALSE	28.7	0.0224
29	<i>Callipepla squamata</i>	Scaled Quail	FALSE	FALSE	FALSE	TRUE	Decreased	TRUE	22.4	0.0175
30	<i>Tympanuchus phasianellus</i>	Sharp-tailed Grouse	FALSE	FALSE	TRUE	FALSE	Stable	TRUE	33.5	0.0190
31	<i>Spinus psaltria</i>	Lesser Goldfinch	TRUE	FALSE	FALSE	TRUE	Stable	FALSE	44.8	0.0212
32	<i>Aimophila ruficeps</i>	Rufous-crowned Sparrow	TRUE	FALSE	FALSE	TRUE	Decreased	FALSE	17.5	0.0112
33	<i>Cardinalis sinuatus</i>	Pyrrhuloxia	TRUE	FALSE	FALSE	TRUE	Decreased	TRUE	12.3	0.0112
34	<i>Catherpes mexicanus</i>	Canyon Wren	FALSE	FALSE	FALSE	TRUE	Stable	FALSE	28.1	0.0138
35	<i>Sitta pusilla</i>	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	TRUE	8.3	0.0059

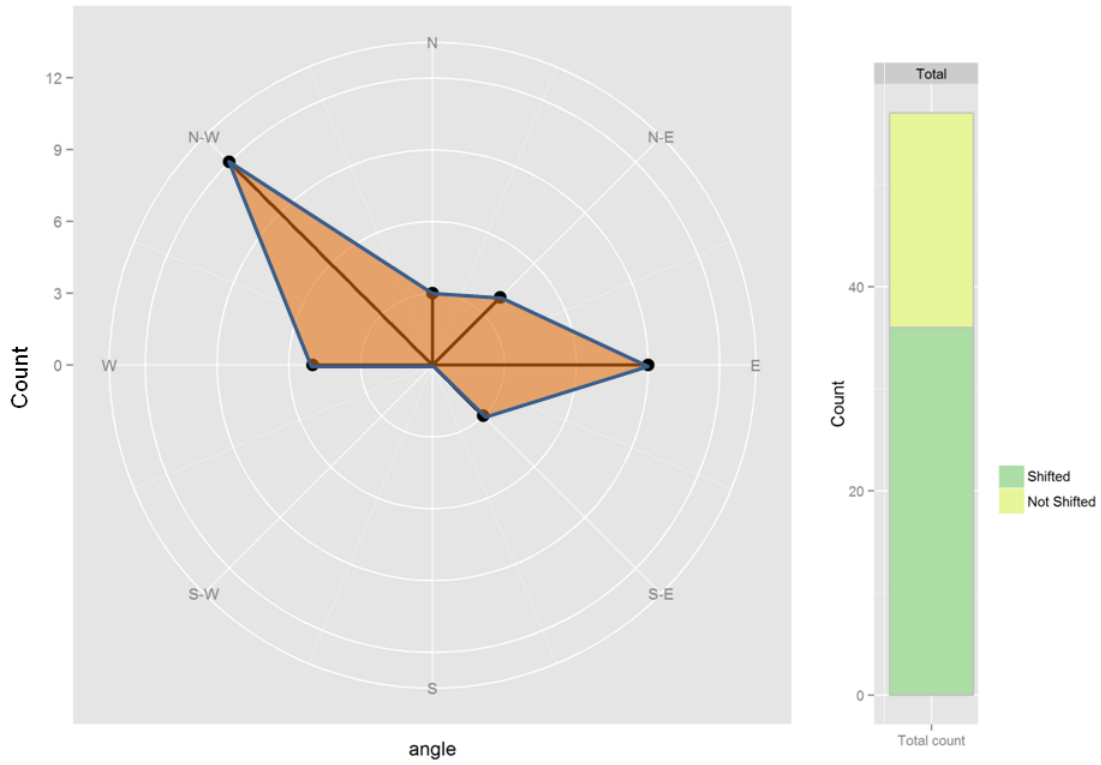


Figure 4-2 Right: the number of species with and without significant distribution shifts. Left: The number of species that experienced significant shifts in different directions.

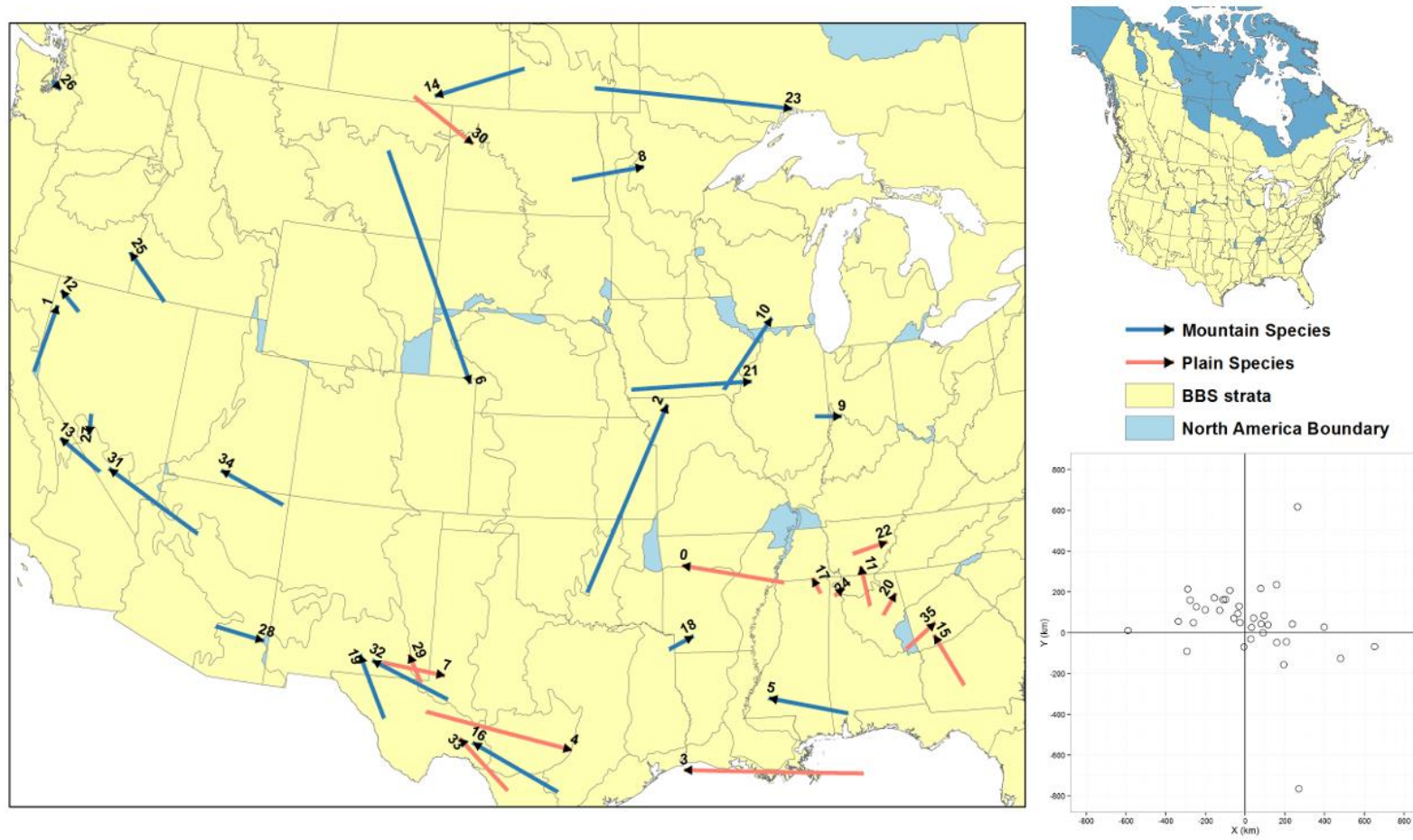


Figure 4-3 Left: the directions and magnitudes of the centroid movement between 1969 and 2012 for 36 species with significant shifts. The arrows point from the 1969 centroids to the 2012 centroids. The color of the arrows denotes the type of biomes in which the species are predominately distributed. The labeled numbers associate with the species ID listed in Table 2. The plot at the lower right shows the magnitude of the shifts where the center point (0, 0) represents the centroids of all species in 1969; the circles represent their shifted centroid in 2012.

Table 4-3 The comparison of the numbers and percentage of species with significant centroid shift and with increased, decreased, or stable total population. The percentage values represent the proportion of the numbers over total number of species (36) with significant centroid shifts.

Shifted direction	Increased total population	Stable total population	Decreased total population
Northward (19, 53%)	8 (22%)	4 (11%)	7 (19%)
Southward (3, 8%)	0 (0%)	1 (3%)	2 (6%)
Eastward (16, 44%)	9 (25%)	4 (11%)	3 (8%)
Westward (17, 47%)	7 (19%)	5 (14%)	5 (14%)
Total Species shifted (36, 100%)	16 (44%)	9 (25%)	11 (31%)

4.4.2 Speed of Climate Change Fingerprint

Speed wise, the species with significant northward shifts had the slowest average speed, 21.5 km/y. In contrast, the species with significant eastward movements shifted the fastest (31.6 km/y), followed by the species that shifted southward (28.6 km/y), and those that shifted westward (22.5 km/y) (Figure 4-4). The speed-to-range-width ratio also showed that the species with significant northward shifts had the slowest average speed in comparison to species that shifted in other directions (Figure 4-4).

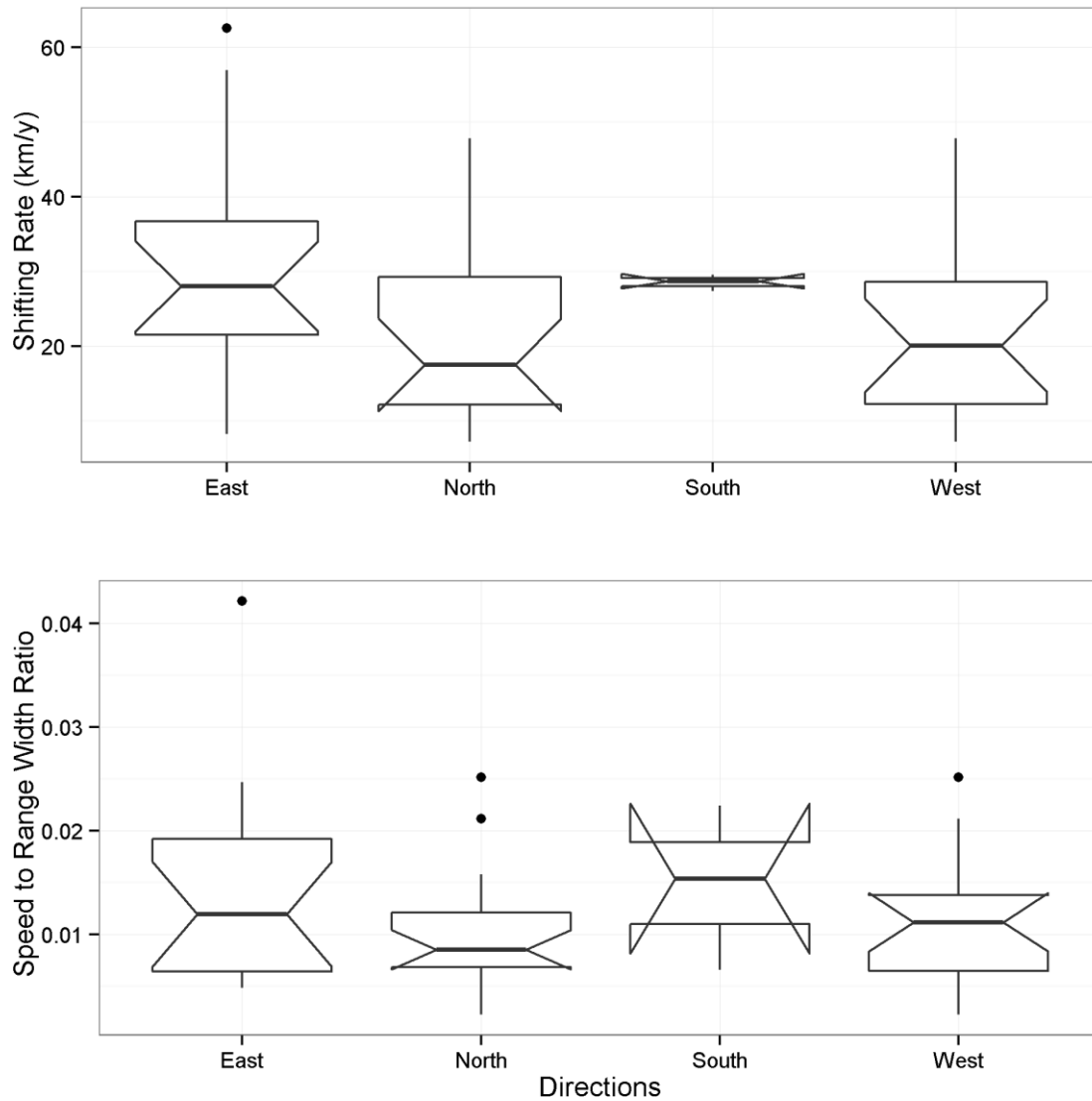


Figure 4-4 Top: the speeds of the distribution shift in four directions. Bottom: the speed of the distribution shift measured in speed-t- range-width ratio accounting for the size of the species ranges. The notches denote $1.58 * \text{Inter quintile range} (25-75) / \text{sqrt}(n)$.

4.4.3 Mountain Birds vs Plain Birds

In all directions plain species consistently had a higher proportion of species that experienced significant distribution shift than that of the mountain group. For the plain species, the highest proportion occurred in the northward direction, 53% (14) shifted significantly, followed by westward direction, eastward direction, and southward direction (respectively with 47% (8), 29%

(5), 6% (1) shifted significantly) (Table 4). For the mountain species, the highest proportion occurred at the eastward direction with 28% (11) shifted significantly, followed by northward, westward, and southward direction (respectively with 28% (11), 23% (9), 5% (2) shifted significantly) (Table 4). Overall, 82% (14) of plain species shifted significantly in at least one direction, whereas the number is 55% (22) for mountainous species.

Table 4-4 The percentage (number) of species in the plain species and mountainous guilds that exhibited significant shifts in different directions.

	North	South	East	West	Total Species Shifted
Plain species (17)	53% (9)	6% (1)	29% (5)	47% (8)	82% (14)
Mountainous Species (40)	25% (10)	5% (2)	28% (11)	23% (9)	55% (22)

Among species that had significant centroid shift, the average speed of the centroid for the plain species was 20 km/y. The average speed was 30 km/y for mountainous species, slightly faster than that of the plain species, although the difference is not statistically significant (Figure 4-5). Considering the size of the range, although the average speed-to-range-width ratio for plain species is slightly faster than the mountain species, the difference is still not statistically significant (Figure 4-5).

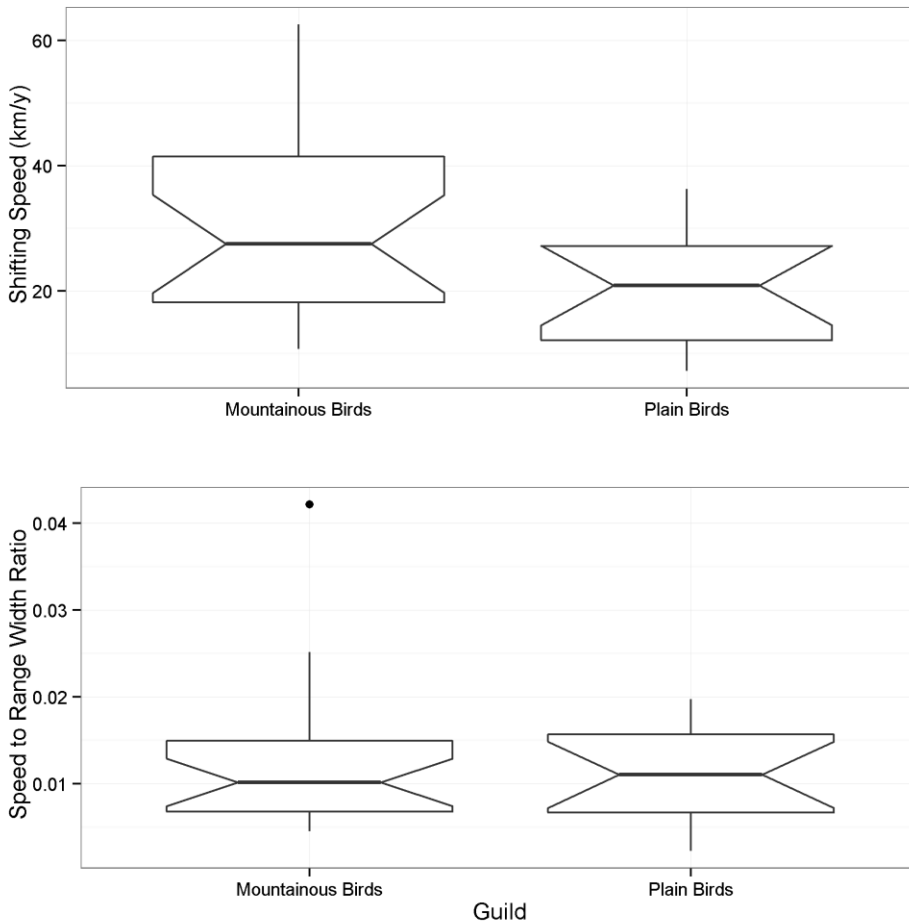


Figure 4-5 Speed of the centroid shifts between mountainous birds (40) and plain birds (17) that have significant distribution changes. The mountain birds' annual centroid movement with or without taking into consideration of range width, is not significantly slower than that of the plain birds (Both *t*-test and Wilcoxon- test used with 95% confidence interval). Top: comparison in speed (km/y). Bottom: comparison in speed-to-range-width ratio accounting for the size of the ranges. The notches show $1.58 * \text{Inter quintile range (25-75)} / \text{sqrt}(n)$.

4.4.4 Influence of Different Climatic Factors on Shifting Distributions

Among the 36 species with significantly centroid shifts, 22 species were influenced by the average climate or extreme climate model - with positive average PVE in at least one of the model (Appendix III-2). The average climate models explained 13.2% of the variability of the population change rate, whereas the extreme climate models explained 9.2%. Similarly, 23 species have larger than 0 PVE in either the temperature model or the precipitation model. The

temperature models on average accounted for 14% of population change rate variability, whereas the precipitation models explained 12%.

Pair comparisons between models showed large variability of model performance across species. The average climate model had a higher PVE than the extreme climate model for 16 species, most of which had increased populations during the study period (Figure 4-6). The biggest margin was 23.1% for Tufted Titmouse (ID 22) whose population increased significantly during the study period (Figure 4-6). The average climate model explained many of the fastest shifting distribution better than the extreme climate model (e.g. ID=6, ID=2 in Figure 4-6).

Comparatively the extreme climate model had higher PVE for 7 species; however, the margins were in general smaller. The biggest margin was 10.1% for the Curve-billed Thrasher (ID 19), which had a decreased population.

Correspondingly, when comparing the model performances between the temperature model and the precipitation model, most of species (n=13) showed a higher PVE by the temperature model (Figure 4-7). The species with relatively high differences between the two models' performance were mostly centered in the south (Figure 4-7). The biggest margin was 34.6% for Northern Cardinal (ID 17). On the other hand, 10 species had higher PVE by the precipitation model. However almost all the differences were very small (< 3%) with the exception of Inca Dove (ID 4), for which the precipitation model explained 31.0% more variance of the population change rate than the temperature model (Figure 4-7).

Detailed examination of the individual models with prominent differences of PVE showed that the agreement between observed and predicted values improved mostly over the sections of intermediate population change rate. In most models (Figure 4-6, Figure 4-7), the population

change rates tend to be over-predicted and under-predicted at the lower and upper end of the range respectively (Figure 4-8). Although some models showed a strong ability to predict overall variability of the growth rate (e.g. Figure 4-8), they appeared unable to predict both population growth and decline. For instance, all four models in Figure 4-8 predicted no population declines (negative r), which occurred in small number of regions. In comparison, for Northern Bobwhite, a species with predominantly declining population, none of the models predicted population increases that were present within small part of the strata (whose plot is not shown here).

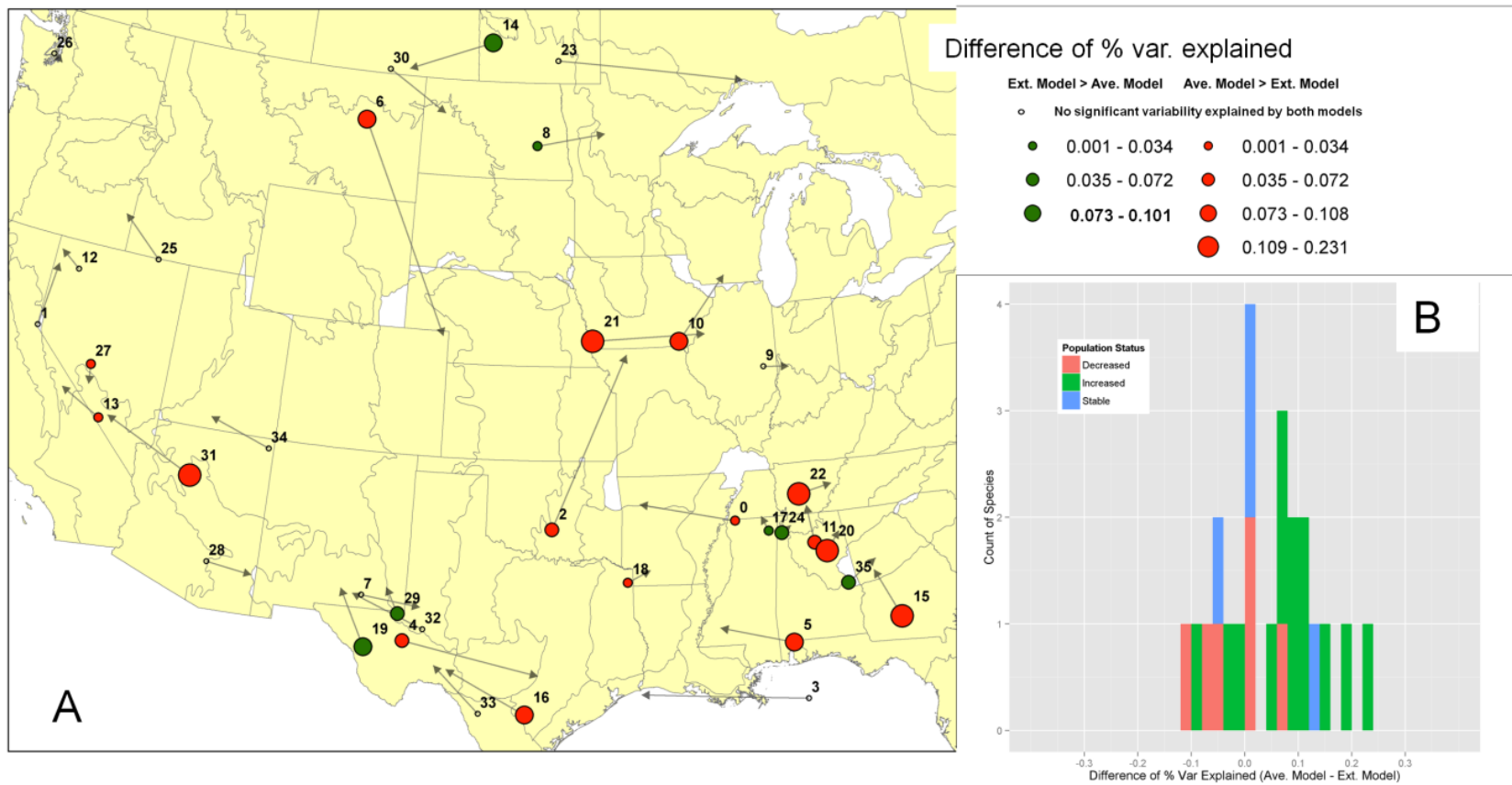


Figure 4-6 The differences of % variance explained between the extreme climate models and average climate models. The colors of the circles represent the direction of the differences (either the extreme climate model or the average climate model performs better). The sizes of the circle indicate the margin of the differences. B: The frequencies of model differences and the population status of the species involved.

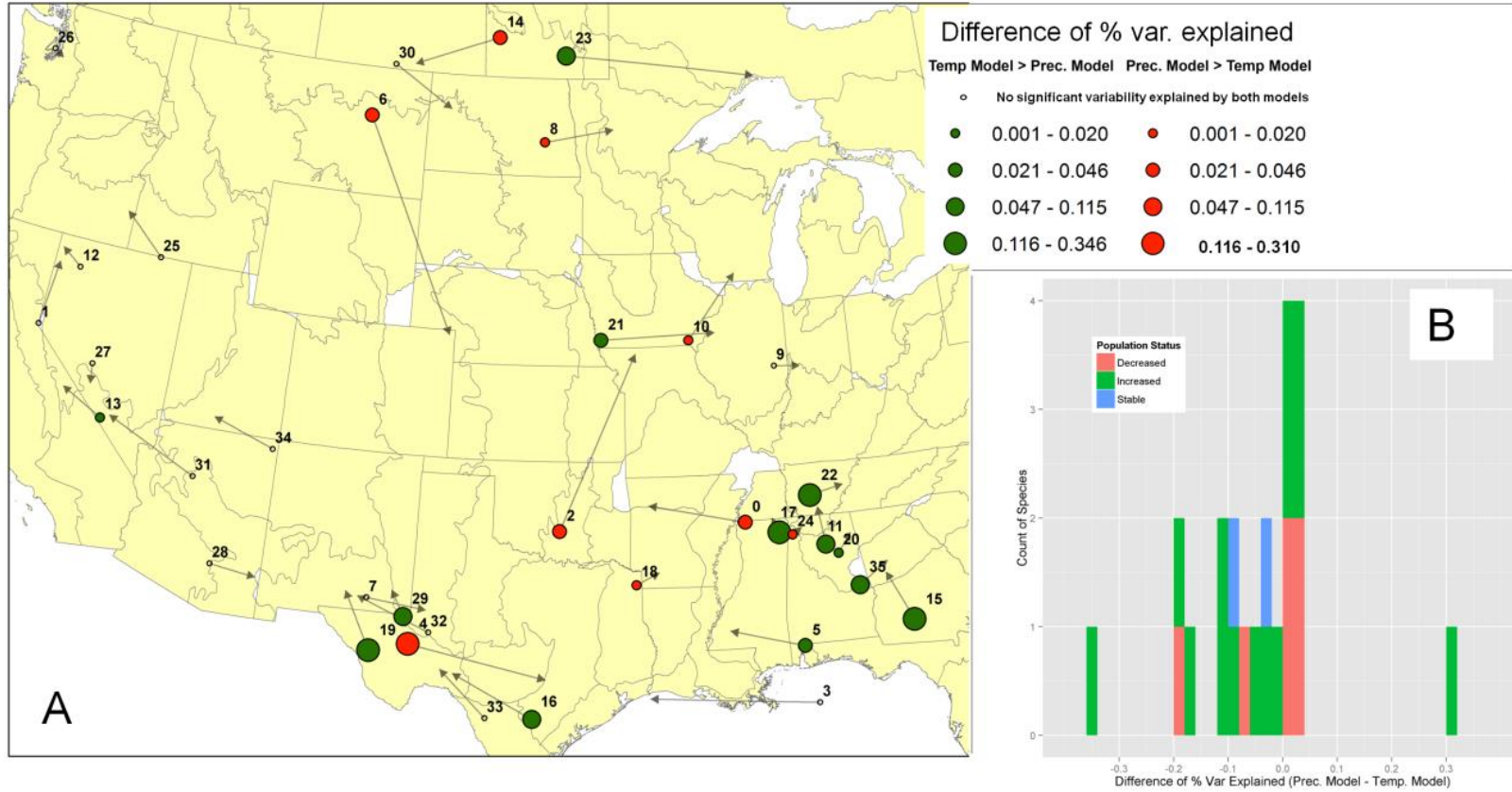


Figure 4-7 A: The differences of % variance explained between the temperature models and precipitation models. B: The frequencies of model differences and the population status of the species involved.

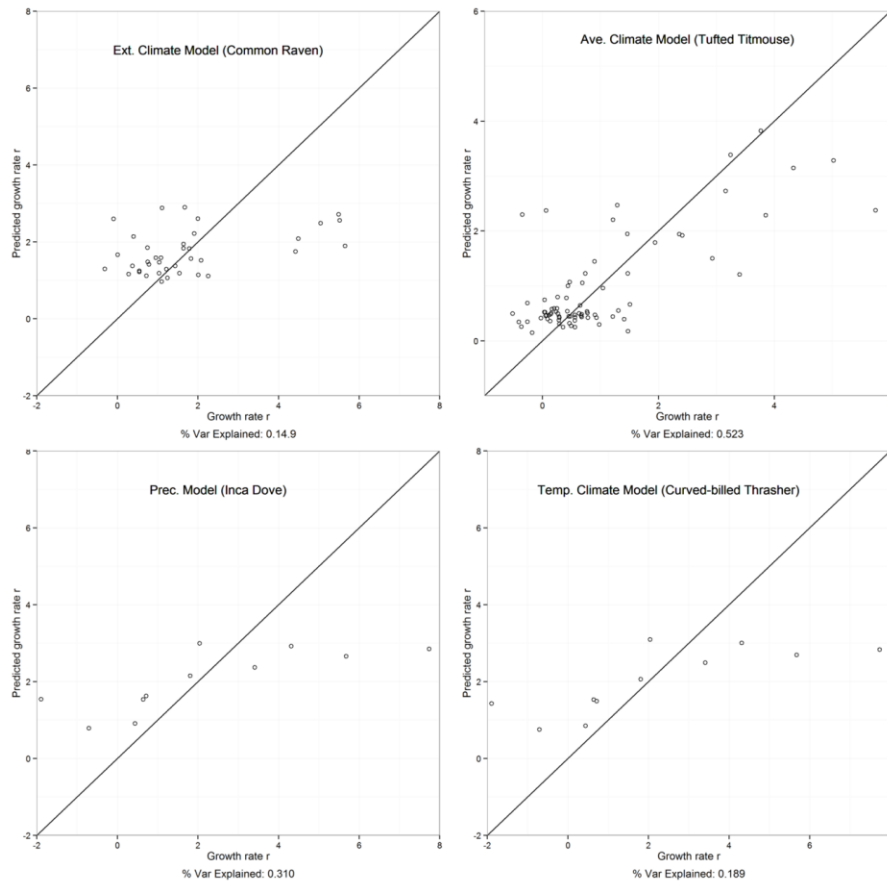


Figure 4-8 Modeled vs. actual population change rate for four species with high margin of percent variance explained compared with their counterpart models.

4.5 Discussion

Avian species, being highly vagile, can respond quickly to changes in climate conditions (Tingley et al. 2009). Previously, the multi-directional climate change fingerprint was only hypothesized based on model projection (VanDerWal et al. 2013) or observed at regional scales (Tingley et al. 2009, Gillings et al. 2015), which does not inform the pattern of continental scale movement of species geographical distributions. Our study provides the first evidence to support such hypothesis based on analysis of recent North American bird distributions at the continental scale. The multi-directionality could likely be the results of combinations of different climatic factors and different ecological processes at various regions. We discuss in more detail below.

Our finding showed similar speed of distribution shift between mountain birds and plain birds which do not support the prediction based on climate change velocity hypothesis (Loarie et al. 2009). Prior studies on non-avian species demonstrated that the speed of the distribution changes does not always keep pace with the climate change velocity (Lenoir et al. 2008). Although avian species have great mobility, many constraints could still be associated with the delayed shift of species distributions following the change of climatic conditions (Gear and Huntley 1991, Hill et al. 1999). The distributions of suitable habitat and biotic factors such as prey and predator would likely be key limiting factors. Alternatively, since topographic variability closely associates with habitat heterogeneity (Kerr and Packer 1997, Huang et al. 2014), the habitat in mountainous biomes tends to be more heterogeneous. Suitable habitat niches, which feature not only suitable mean temperature and precipitation, but also habitat and biotic attributes, could be further away in these biomes, and thus could result in faster distribution shifts. Interestingly, we did observe a greater percentage of plain species exhibited significant distribution shifts, which might reflect drastic environmental changes in flat biomes that disproportionally affect grassland bird populations (Peterjohn and Sauer 1999, Brennan et al. 2005).

Classical ecological theories hypothesize that along a key environmental gradient, species appear to be physically constrained in one direction and biologically constrained in the other (Brown et al. 1996, Guisan and Thuiller 2005). Regardless of the type of forces in play, the predominant northward shifts and rare southward shifts observed in our study show that the factors constraining population in the northern and southern ranges have been disproportionally affected. The stressors limiting species' northern population seem to have weakened, while those in the southern ranges remained relatively unchanged. This appears to agree with conventional theories that wintering birds northern distributions are limited primarily by ambient temperature in winter

(Root 1988) which can be lifted by warming climate (Jeffree and Jeffree 1994). On the other hand, the southern distribution are believed to be limited mostly by other climatic factors and biotic interaction and their connection with climate change is less straightforward (Gaston 2003, Sagarin et al. 2006). Most interestingly, in the longitudinal direction, the results show that the environmental forces that limit species distributions might be highly susceptible to changing climate conditions. Species distribution are shifting eastward and westward as rapidly as the northward shifts.

The selection of appropriate predictive climatic variables is critical in terms of establish accurate and transferable species distribution models (Barbet-Massin and Jetz 2014). The predictor selection issue is also something that received little attention, and most studies just include all 19 bioclimatic metrics which are the most available and widely used climatic predictors. Our research here is an attempt to separate and examine the relative influence of different types of climatic predictors on avian distribution shifts. Most prior studies have attributed the poleward shifts of avian distributions to the increase in average temperature (Williamson 1975, Thomas and Lennon 1999, Hitch and Leberg 2007, La Sorte and Thompson 2007, Maclean et al. 2008). Here, we compared the influences of the average, extreme climate conditions, precipitation and temperature on the multi-directional shifts of avian distribution. It is particularly worth noting that extreme climate conditions are known to have a profound impact on terrestrial ecosystems. These extreme conditions have been documented to directly or indirectly affect species distribution, community structure, abundance, and many life history traits such as morphology, and reproduction (Parmesan et al. 2000, Rittenhouse et al. 2010, Cavanaugh et al. 2014). The influence of extreme climate on species distribution can also be multi-directional, because one extreme climate event can often have opposite effects among different species or even among

subspecies in the same habitat (Parmesan et al. 2000). Although extreme climate events in large magnitude and frequency would eventually affect the measurement of average climate metrics (they are thus correlated to some extent), species that are directly affected by extreme climate associate more closely with metrics and models based on frequencies and severity of weather events (Cavanaugh et al. 2014), and will be better modeled by using extreme climate metrics and models. Our study demonstrated that compared with averaged seasonal or annual weather metrics the variability in daily climatological record can have more direct influence on long-term population dynamics and distribution shift for some avian species. Thus, it supplements and extends common methods of modeling species distribution based solely on average climate metrics such as bioclim variables or on temperature measures. Future research is needed to determine the link between those ecological processes and species-specific ecological responses. Our study highlights the importance of documentation, digitization and quality-control of not just temperature but also precipitation at fine temporal scale which will be one of the critical links to understand how species respond to climate change and to future endeavors in prognostic modeling of species distributions.

The change of land cover, human population and housing density are closely related to resources and disturbances available to wildlife (Thuiller et al. 2006, Midgley et al. 2006, Rittenhouse et al. 2012), and thus are possible alternative factors that can lead to systematic shifts of species distributions. In tests of alternative hypotheses, for the shift of permanent resident bird ranges, we also tested the explanatory power of a non-climatic model utilizing changes of land cover types (urban, forest, grassland, barren, agriculture, and wetland) coverage and changes of rural and urban human population and housing density (See Appendix III-3 for detailed description about the method). We used the National Land Cover Databases 1992-2001 and 2011 (Fry et al.

2009, Homer et al. 2015) and U.S. census data of 1990 and 2010 (Minnesota Population Center 2011). We sought to determine if habitat conversion and human population and housing density could be linked with some shifts of species distributions. The model performance of non-climatic models were compared with the 4 climate models based on climate data between 1988-1997 and 2003-2012. The analysis showed that the non-climatic model did have better performances than the climatic models for a few species (e.g. pileated woodpecker, pyrrhuloxia, white-breasted nuthatch, and chestnut-backed chickadee) (Appendix III-4). For the majority of species, however, non-climatic models did not explain more variability of the population change rate than the best performing climatic model (Appendix III-4).

While there is likely no single climatic metric that explains shifts of species distributions completely, different types of climatic and non-climatic factors might also be involved. Our results showed that, despite the considerable explanatory ability of the models utilizing single type of climatic metrics, they appeared to have limited ability to address both population increase and decrease. This might suggest that different ecological processes govern the growth and decline of most of populations on different fronts. For instance, as we explained before, if the northern range of a species is limited by winter condition, then the change of population in other parts of the range would likely be explained by alternative factors such as biotic interaction, or habitat conversion. Such multi-faceted population changes are suitable to be modeled using non-parametric models such as RF, as they do not fit all data with a universal distribution or relationship. More importantly, in future models combining multiple aspects of climatic and non-climatic environmental factors will be more useful in modelling and predicting multi-faceted population change and distribution shifts over broad scales.

Almost all the birds included in our study are wide spread species, and are not in immediate danger of extinction. However, the high ratio of multi-directional shifts suggests a high level of environmental changes that push to redistribute population across broad scale. If the trend is consistent across taxonomic groups, it would pose even greater threat to the conservation of rare species that have limited distribution and fragmented habitat (Walther et al. 2002, Songer et al. 2012). In general, rare species are more likely to be specialists, highly dependent on specialized habitat and climate niches, and with limited dispersal ability. The combination of these factors makes them less likely to benefit from newly emerged suitable habitat and more vulnerable to drastic environmental changes, as they tend to have no means of relocation, or have few places to relocate to.

4.6 Conclusion

Our study show statistically significant distribution shifts in 36 of the 57 North American permanent resident bird species over the past 44 years. Our study provides strong evidence to support that the climate change fingerprint in avian distribution is multi-directional. It also shows that species distributions in flat ecoregions have been shifting no faster than the ones in the mountainous ecoregions, which did not support the prediction based on climate change velocity hypothesis. The trend holds even after controlling the size of the ranges. For most shifting species, the average climate model and the temperature model had stronger associations with the population change rate, but the extreme climate model and the precipitation models had considerable advantages in explaining shifting distributions for some species.

As the anthropogenic climate change and other environmental changes continue to alter the earth ecosystem at an unprecedented rate, it is increasingly critical to understand how species

distributions respond to drastic changes at broad geographical scale. Our study provides insight into the direction and speed of the recent climate change fingerprint associated with multi-faceted climatic factors. The study presents a complex challenge for biodiversity conservation. It calls for more species-specific conservation planning and practices that must establish resilient wildlife habitat and reserve systems to prepare and adapt for such multi-directional and rapid changes of species distributions.

Chapter 5. Conclusion

The development of remote sensing technologies, powerful computation capabilities, and sophisticated modeling approaches has presented new opportunities to the study of species distribution, particularly at broad geographical scales (Gaston 2003). My dissertation demonstrates that the combining physical geography methods with spatially explicit environmental data and long-term species records at continental scale can be a productive way to new discoveries in this field. This dissertation advances our existing knowledge regarding how avian species are distributed across heterogeneous landscapes, how these distributions have been changing, and what type of habitat or climatic factors have been closely associated with these distributions over short and long term. In doing so, my goal was to not only examine the new dimensions in habitat heterogeneity and evaluate recent fingerprint of climate change and the driving climatic factors, but also develop practical tools that can be used for future species richness modelling and species distribution monitoring.

Specifically, the dissertation is composed of two parts. The first part (Chapter 2) focuses on the concept of habitat heterogeneity, a key ecosystem component that has long been hypothesized to determine species richness at different scales. The traditional ecological theory states that the diverse physical condition of habitat condition would lead to greater niche specialization, and eventually result in high species richness. However, due to the limitation of previous studies (e.g. limited availability of vegetation height data, lack of broad scale study, and limited habitat metric options), my first step was to develop a set of habitat metrics that could capture the spatial heterogeneity of vegetation height. Derived from gridded vegetation height maps across the continental U.S., I was able to characterize spatial arrangement of vegetation height information

using two methods. The first method relied on point-based segmentation algorithm to introduce height-structured habitat patches and edges. They coupled with a set of traditional patch-based habitat metrics to describe landscape level spatial arrangement of forest height. The second method directly applied the algorithms of second-order texture metrics on gridded height maps with a defined moving window.

Although the correlation between avian richness and different height-structured metrics varied considerably across the spectrum of metrics created, some metrics consistently showed high association with the richness of woodland and forest edge guild. The results of the multivariate richness model also showed that when adding the selected four height-structured habitat metrics to the models using the traditional metrics, most of woodland and forest edge bird richness models' performance were improved significantly. Despite that the interior forest bird richness had low correlation with habitat metrics and low model performances regardless of the metrics or models involved, the study demonstrated that for some specific forest breeding bird guilds, the information of vegetation height heterogeneity imbedded in height-structured habitat metrics are highly efficient at characterizing their habitat conditions and modeling their species richness. The metrics used in this study also demonstrated practical ways of applying gridded vegetation height information to habitat suitability and species richness modeling for other species.

While extracting height-structured habitat patches and habitat edges is a straight-forward way of relating vegetation height structure with well-understood ecological metrics, future research could address some methodological limitations of this study. The method in this dissertation relies on a point-based segmentation algorithm (a set of global thresholds) to classify continuous forest area into smaller patches with similar height values. The segmentation algorithm is not computationally intensive, and takes a relatively short amount of time to compute. More

sophisticated vertical patches and edges can be delineated by using segmentation algorithms that group pixels based not only on absolute values but the variation of neighboring values. Such region-based or object-based segmentation method can be conducted using commercial software such as Ecognition (Baatz et al. 2003) or open access packages such as EBImage (Pau et al. 2010) built on R statistical program. Once the segmentation process is done, instead of using Fragstats to calculate the patch-based metrics, an efficient alternative would be using R packages such as SDMTools (VanDerWal et al. 2011) in R statistical program. The incorporation of image segmentation and metrics calculation using a script-based platform like R can allow a more automated and reproducible process, and it will enable a smooth and organized project flow by combining pre-processing, metrics calculation, and results analysis together. Additionally, R also supports parallel computation, which is necessary for computationally expensive projects involving a large number of landscapes.

Examining four decades' of avian distribution changes in North America, the second part of the dissertation (Chapter 3 and Chapter 4) focuses on the direction and speed of long-term avian distribution shifts and evaluating the environmental factors associated with such shifts. These two chapters are motivated by large number of studies that emphasize poleward distribution shifts and the effect of rising average temperature as the main climate change fingerprint. The lack of systematic method to quantify the distribution shifts limited the ability to test the multi-directionality of the climate change fingerprint and other hypotheses regarding the direction and speed of the shifts. In Chapter 3, I combined Hierarchical Bayesian models with centroid analysis to extract the direction and speed of the long term bird distribution shifts. I used two bird species as case studies to demonstrate that the centroid model built upon the Breeding Bird Survey data is sensitive to asymmetrical and drastic changes of population at broad geographical

scale. Additionally, two null cases were briefly presented too. I showed that the centroid method is a useful tool to quantify changes of birds' distribution related to potentially a variety of factors such as climate, land cover change, and invasive colonization process.

In Chapter 4, I used the centroid model on 57 North American permanent resident bird species to test a few hypotheses regarding the direction and speed of distribution shifts. The results of these analyses first showed that the large proportion of the analyzed permanent resident birds have experienced significant distribution shifts. The directions of the distribution changes are not limited to the north, which strongly support the multi-directionality hypothesis. Additionally, the species in mountainous ecoregions with large elevational variability have showed distribution shifts as fast, if not faster, as the species in the flat ecoregions. The observation does not support the hypothesis based on the climate change velocity hypothesis which stated that to maintain a constant average temperature, species at flat regions must shift longer distance (faster) than species at mountainous regions under global warming. Lastly, my study has also showed that the change of regional abundance for the species with significant distribution shifts are predominately explained better using average climate and temperature metrics compared with extreme climate and precipitation metrics respectively. However, the extreme climate and precipitation do outperform their counterparts in some cases. These results provide important evidence to show that the change of precipitation as well as extreme climatic conditions are sometimes driving forces behind climate change fingerprints, and they are not always replaceable by correlated measure of average temperature conditions. The influence of extreme climate condition showed in this study also highlights the importance of the documentation and projection of climatological data with fine temporal resolution.

This part of the dissertation seeks to generalize how species respond to climate change based on the analyses of the 57 permanent resident bird species. I tried to select as many permanent resident species to represent the changes experienced by avian and wildlife communities in general. However the selected species do share some characteristics; for example they are all wide spread species, and almost all have relatively healthy population. These similarities, however, should not discount the trend discovered in the study. In fact the results I present here are possibly good case scenarios, because compared with other wildlife avian species have relatively high mobility and are less affected by habitat fragmentation. Given the magnitude of the changes documented in this study, climate change, particularly extreme climate events could pose a greater threat to species with limited dispersal ability and are limited by habitat distribution or particular climatic niches. These populations in general have low resilience to large scale stressors and have difficulty to relocate to suitable environments.

A potential limitation of this part of the research is the exceptionally large variability of the population change rates estimated at the strata level. Such level of variability resulted that for some species, a considerable number of the 600 iterative models built for each climate model yielded negative percent variance explained. We used the average PVE when evaluating different climate model performances while assigned the models with negative average PVE having 0 percent variance explained. The average PVE albeit being a reasonable metric to compare model performances, was only showing the central tendency of model performances and provided little information regarding the variability of the measurement and significance of the differences between different values. Future studies could focus on ways of stabilizing the population change rate estimate which will be likely to provide a more robust way of comparing model differences such as using confidence interval of the PVE. The variability of population

change metrics stems from the data and Bayesian models variability, which is affected by a variety of factors including the data coverage (spatial and temporal), the variability of the species abundance observed, number of iteration for each Markov chain, the burn-in and thinning number. Although the data coverage and variability are not something we can change, it is reasonable to experiment with acquiring larger number of posterior samples by reducing the thinning number. Alternatively, generating longer Markov chains (bigger iteration number) and starting to collect posterior samples later (larger burn-in number) during the iteration processes could also be possible options to help with the data stabilization.

Furthermore, my analysis only groups the climatic variables into large categories, and compare the relative performance of a specific climatic group against the other. I did not focus on selecting individual variables, because there is likely no single factor that explains shifts of species distributions completely. Nevertheless the results of my study can help guide future studies in narrowing down the ecological mechanisms that underpin the dramatic distribution shifts of avian species. Such studies will have to be species-specific and will likely require extensive field observations and controlled experiments to examine how species fitness, survival rate, fecundity, dispersal, and other physiological and ecological attributes are affected by different aspects of climate change.

The design and format of the BBS makes its data suitable for depicting a snapshot of avian distribution during breeding season. However, other dimensions of the ecological fingerprint of climate change such as phenology changes (e.g. the timing of migration for migratory birds) and winter distributions are not directly reflected by the BBS data. Alternatively, other continental scale species records, particularly the ones collected by a large number of citizen scientists with loosely defined survey locations and times (e.g. eBird) could provide useful insights into these

aspects. Most of the citizen-scientists-based wildlife databases were established relatively recently and have not yet collected data over long period of time. But as more wildlife enthusiasts from different places are joining in and more and more data are collected over time, these datasets will be valuable assets in future studies.

One of the major, and arguably the most important, driving forces, behind the ongoing studies of species distribution is concern about future species distribution drastically affected by environmental changes. The development of Species Distribution Models (SDMs) has been a milestone in this field. While SDMs were conceived in the early twentieth century (Good 1931), it has only been recently that the technical capability and extensive environmental data exist to implement the large scale distribution prediction and modeling (Gaston 2003). SDMs have been able to help ecologists understand how species have evolved to have the current characteristics of their distribution, how invasive species can potentially spread in new environment, and how species will distributed in future (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Hijmans and Graham 2006, Lawler et al. 2006). However some of the basic assumptions of SDMs still need to be tested with empirically observed data. For instance, one of the key assumptions of SDMs is that the distribution of specific species is always at equilibrium with climate conditions. Although this is generally true over long term, and is widely confirmed with prehistoric records (Martínez-Meyer et al. 2004), it is not clear how long it will take habitat suitability to catch up with climatic changes, and whether it is possible to have species at equilibrium with their climatic niches in ecosystems so fragmented by anthropogenic activities.

Organized by the Intergovernmental Panel on Climate Change, most of the existing general circulation models do not project climate scenarios beyond the end of twenty-first century. The limitation of these datasets dictate that most of the prognostic SDMs studies have similar

projecting range: almost all focus on predicting changes occurring at the end of this century. These predictions can, at best, be interpreted as the future distribution of potential climate niche, and they have very limited implications on the realized niche, and actual distributions of species. My dissertation reinforces this point by showing that realized niche of avian species in North America is bounded closely to the multiple aspects of habitat condition. For the long term study the extreme climate conditions and precipitation are actively involved in affecting the redistribution of realized niche.

In conclusion, the patterns I discovered consistently through all three research projects are that the avian richness and species distributions are affected heavily by environmental heterogeneity. Many of the existing theories and model predictions rely on highly simplified characterization of environment (e.g. characterizing habitat as a binary property without considering vegetation height, characterizing climate conditions using only average temperature) which might have limited ability to explain the actual patterns of richness and distribution shifts observed by our long term survey data. As we develop more extensive and sophisticated monitoring networks to survey more and more details of earth environment, it becomes imperative to incorporate the new dimensions of habitat and climatic conditions into the modelling and prediction processes. The multidirectional and rapid shifts in species distributions discovered in the last part of the research in particular emphasize the necessity and urgency of developing better prognostic species distribution models and predictions that could withstand the test of empirical data and provide accountable suggestions to adaptive conservation planning and practices. There are challenges ahead involving how to accurately predict habitat and climate at fine spatial and temporal resolution, and how to incorporate the granular level environment heterogeneity into predictive species distribution models. Nevertheless, this dissertation provides valuable insight

on improved continental scale modeling and monitoring of avian richness and distribution shifts.

Towards this end, I hope my dissertation has provided some forward progress.

Appendices

Appendix I

Appendix I-1 Ecological provinces involved and the sub-region assignment.

Division	Province	Sub-region
Warm Continental Division	Laurentian Mixed Forest Province	Eastern
Hot Continental Division	Eastern Broadleaf Forest (Oceanic) Province	Eastern
Hot Continental Division	Eastern Broadleaf Forest (Continental) Province	Eastern
Warm Continental Regime Mountains	Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow Province	Eastern
Hot Continental Regime Mountains	Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow Province	Eastern
Subtropical Division	Southeastern Mixed Forest Province	Eastern
Subtropical Division	Outer Coastal Plain Mixed Forest Province	Eastern
Subtropical Division	Lower Mississippi Riverine Forest Province	Eastern
Hot Continental Regime Mountains	Ozark Broadleaf Forest - Meadow Province	Eastern
Savanna Division	Everglades Province	Eastern
Marine Division	Pacific Lowland Mixed Forest Province	Western

Mediterranean Division	California Coastal Chapparral Forest and Shrub Province	Western
Mediterranean Division	California Coastal Steppe-Mixed Forest-Redwood Forest Province	Western
Marine Regime Mountains	Cascade Mixed Forest-Coniferous Forest-Alpine Meadow Province	Western
Mediterranean Regime Mountains	Sierran Steppe-Mixed Forest-Coniferous Forest-Alpine Meadow Province	Western
Mediterranean Regime Mountains	California Coastal Range Open Woodland-Shrub-Coniferous Forest-Meadow Province	Western
Temperate Steppe Regime Mountains	Southern Rocky Mountain Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province	Western
Temperate Steppe Regime Mountains	Middle Rocky Mountain Steppe-Coniferous Forest-Alpine Meadow Province	Western
Temperate Steppe Regime Mountains	Northern Rocky Mountain Forest-Steppe-Coniferous Forest-Alpine Meadow Province	Western
Temperate Steppe Regime Mountains	Black Hills Coniferous Forest Province	Western

Appendix I-2 Species list and guild classification

English_name	Scientific_Name	USGS habitat	Sensitivity to
Barred Owl	<i>Strix varia</i>	Woodland	Forest Edge
Eastern Screech-Owl	<i>Megascops asio</i>	Woodland	Forest Edge
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	Woodland	Forest Edge
Black-billed Cuckoo	<i>Coccyzus</i>	Woodland	Forest Edge
Downy Woodpecker	<i>Picoides pubescens</i>	Woodland	Forest Edge
Chuck-will's-widow	<i>Caprimulgus carolinensis</i>	Woodland	Forest Edge
Whip-poor-will	<i>Antrostomus vociferus</i>	Woodland	Forest Edge
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	Woodland	Forest Edge
Eastern Wood-Pewee	<i>Contopus virens</i>	Woodland	Forest Edge
Yellow-throated Vireo	<i>Vireo flavifrons</i>	Woodland	Forest Edge
Blue-headed Vireo	<i>Vireo solitarius</i>	Woodland	Forest Edge
Prothonotary Warbler	<i>Protonotaria citrea</i>	Woodland	Forest Edge
Magnolia Warbler	<i>Setophaga magnolia</i>	Woodland	Forest Edge
Yellow-throated Warbler	<i>Setophaga dominica</i>	Woodland	Forest Edge
Black-throated Green Warbler	<i>Setophaga virens</i>	Woodland	Forest Edge
Pine Warbler	<i>Setophaga pinus</i>	Woodland	Forest Edge
Hooded Warbler	<i>Setophaga citrina</i>	Woodland	Forest Edge
American Redstart	<i>Setophaga ruticilla</i>	Woodland	Forest Edge
Brown Creeper	<i>Certhia americana</i>	Woodland	Forest Edge
Brown-headed Nuthatch	<i>Sitta pusilla</i>	Woodland	Forest Edge
Black-capped Chickadee	<i>Poecile atricapillus</i>	Woodland	Forest Edge
Carolina Chickadee	<i>Poecile carolinensis</i>	Woodland	Forest Edge
Mourning Dove	<i>Zenaida macroura</i>	NA	Forest Edge
Blue Jay	<i>Cyanocitta cristata</i>	NA	Forest Edge
European Starling	<i>Sturnus vulgaris</i>	NA	Forest Edge

Common Grackle	<i>Quiscalus quiscula</i>	NA	Forest Edge
American Robin	<i>Turdus migratorius</i>	NA	Forest Edge
American Goldfinch	<i>Spinus tristis</i>	NA	Forest Edge
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	NA	Forest Edge
Northern Cardinal	<i>Cardinalis cardinalis</i>	NA	Forest Edge
Indigo Bunting	<i>Passerina cyanea</i>	NA	Forest Edge
White-eyed Vireo	<i>Vireo griseus</i>	NA	Forest Edge
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	NA	Forest Edge
Prairie Warbler	<i>Setophaga discolor</i>	NA	Forest Edge
Common Yellowthroat	<i>Geothlypis trichas</i>	NA	Forest Edge
Yellow-breasted Chat	<i>Icteria virens</i>	NA	Forest Edge
Gray Catbird	<i>Dumetella carolinensis</i>	NA	Forest Edge
Carolina Wren	<i>Thryothorus ludovicianus</i>	NA	Forest Edge
House Wren	<i>Troglodytes aedon</i>	NA	Forest Edge
Northern Bobwhite	<i>Colinus virginianus</i>	NA	Forest Edge
Red-tailed Hawk	<i>Buteo jamaicensis</i>	NA	Forest Edge
Great Horned Owl	<i>Bubo virginianus</i>	NA	Forest Edge
Red-headed Woodpecker	<i>Melanerpes</i>	NA	Forest Edge
Northern Flicker	<i>Colaptes auratus</i>	NA	Forest Edge
Common Raven	<i>Corvus corax</i>	NA	Forest Edge
Fish Crow	<i>Corvus ossifragus</i>	NA	Forest Edge
Brown-headed Cowbird	<i>Molothrus ater</i>	NA	Forest Edge
Baltimore Oriole	<i>Icterus galbula</i>	NA	Forest Edge
Cedar Waxwing	<i>Bombycilla cedrorum</i>	NA	Forest Edge
Dusky Grouse	<i>Dendragapus obscurus</i>	Woodland	NA
Sooty Grouse	<i>Dendragapus fuliginosus</i>	Woodland	NA
Ruffed Grouse	<i>Bonasa umbellus</i>	Woodland	NA
Wild Turkey	<i>Meleagris gallopavo</i>	Woodland	NA
Band-tailed Pigeon	<i>Patagioenas fasciata</i>	Woodland	NA

Swallow-tailed Kite	<i>Elanoides forficatus</i>	Woodland	NA
Sharp-shinned Hawk	<i>Accipiter striatus</i>	Woodland	NA
Cooper's Hawk	<i>Accipiter cooperii</i>	Woodland	NA
Northern Goshawk	<i>Accipiter gentilis</i>	Woodland	NA
Broad-winged Hawk	<i>Buteo platypterus</i>	Woodland	NA
Merlin	<i>Falco columbarius</i>	Woodland	NA
Western Screech-Owl	<i>Megascops kennicottii</i>	Woodland	NA
Northern Pygmy-Owl	<i>Glaucidium gnoma</i>	Woodland	NA
Red-cockaded Woodpecker	<i>Picoides borealis</i>	Woodland	NA
Ladder-backed Woodpecker	<i>Picoides scalaris</i>	Woodland	NA
Nuttall's Woodpecker	<i>Picoides nuttallii</i>	Woodland	NA
White-headed Woodpecker	<i>Picoides albolarvatus</i>	Woodland	NA
Black-backed Woodpecker	<i>Picoides arcticus</i>	Woodland	NA
American Three-toed Woodpecker	<i>Picoides dorsalis</i>	Woodland	NA
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	Woodland	NA
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	Woodland	NA
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	Woodland	NA
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	Woodland	NA
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	Woodland	NA
Golden-fronted Woodpecker	<i>Melanerpes aurifrons</i>	Woodland	NA
Vaux's Swift	<i>Chaetura vauxi</i>	Woodland	NA
Black-chinned Hummingbird	<i>Archilochus alexandri</i>	Woodland	NA
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	Woodland	NA
Rufous Hummingbird	<i>Selasphorus rufus</i>	Woodland	NA
Calliope Hummingbird	<i>Stellula calliope</i>	Woodland	NA
Brown-crested Flycatcher	<i>Myiarchus tyrannulus</i>	Woodland	NA
Olive-sided Flycatcher	<i>Contopus cooperi</i>	Woodland	NA
Western Wood-Pewee	<i>Contopus sordidulus</i>	Woodland	NA
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	Woodland	NA

Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	Woodland	NA
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	Woodland	NA
Least Flycatcher	<i>Empidonax minimus</i>	Woodland	NA
Hammond's Flycatcher	<i>Empidonax hammondii</i>	Woodland	NA
Dusky Flycatcher	<i>Empidonax oberholseri</i>	Woodland	NA
Vermilion Flycatcher	<i>Pyrocephalus rubinus</i>	Woodland	NA
Steller's Jay	<i>Cyanocitta stelleri</i>	Woodland	NA
Gray Jay	<i>Perisoreus canadensis</i>	Woodland	NA
Clark's Nutcracker	<i>Nucifraga columbiana</i>	Woodland	NA
Evening Grosbeak	<i>Coccothraustes</i>	Woodland	NA
Pine Grosbeak	<i>Pinicola enucleator</i>	Woodland	NA
Purple Finch	<i>Carpodacus purpureus</i>	Woodland	NA
Cassin's Finch	<i>Carpodacus cassinii</i>	Woodland	NA
Red Crossbill	<i>Loxia curvirostra</i>	Woodland	NA
White-winged Crossbill	<i>Loxia leucoptera</i>	Woodland	NA
Pine Siskin	<i>Spinus pinus</i>	Woodland	NA
Dark-eyed Junco	<i>Junco hyemalis</i>	Woodland	NA
Bachman's Sparrow	<i>Peucaea aestivalis</i>	Woodland	NA
Black-headed Grosbeak	<i>Pheucticus</i>	Woodland	NA
Western Tanager	<i>Piranga ludoviciana</i>	Woodland	NA
Hepatic Tanager	<i>Piranga flava</i>	Woodland	NA
Philadelphia Vireo	<i>Vireo philadelphicus</i>	Woodland	NA
Warbling Vireo	<i>Vireo gilvus</i>	Woodland	NA
Cassin's Vireo	<i>Vireo cassinii</i>	Woodland	NA
Plumbeous Vireo	<i>Vireo plumbeus</i>	Woodland	NA
Hutton's Vireo	<i>Vireo huttoni</i>	Woodland	NA
Swainson's Warbler	<i>Limnothlypis swainsonii</i>	Woodland	NA
Tennessee Warbler	<i>Oreothlypis peregrina</i>	Woodland	NA
Cape May Warbler	<i>Setophaga tigrina</i>	Woodland	NA

Yellow-rumped Warbler	<i>Setophaga coronata</i>	Woodland	NA
Bay-breasted Warbler	<i>Setophaga castanea</i>	Woodland	NA
Blackpoll Warbler	<i>Setophaga striata</i>	Woodland	NA
Blackburnian Warbler	<i>Setophaga fusca</i>	Woodland	NA
Grace's Warbler	<i>Setophaga graciae</i>	Woodland	NA
Townsend's Warbler	<i>Setophaga townsendi</i>	Woodland	NA
Hermit Warbler	<i>Setophaga occidentalis</i>	Woodland	NA
Winter Wren	<i>Troglodytes hiemalis</i>	Woodland	NA
Red-breasted Nuthatch	<i>Sitta canadensis</i>	Woodland	NA
Pygmy Nuthatch	<i>Sitta pygmaea</i>	Woodland	NA
Black-crested Titmouse	<i>Baeolophus atricristatus</i>	Woodland	NA
Oak Titmouse	<i>Baeolophus inornatus</i>	Woodland	NA
Juniper Titmouse	<i>Baeolophus ridgwayi</i>	Woodland	NA
Mountain Chickadee	<i>Poecile gambeli</i>	Woodland	NA
Boreal Chickadee	<i>Poecile hudsonicus</i>	Woodland	NA
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	Woodland	NA
Golden-crowned Kinglet	<i>Regulus satrapa</i>	Woodland	NA
Ruby-crowned Kinglet	<i>Regulus calendula</i>	Woodland	NA
Townsend's Solitaire	<i>Myadestes townsendi</i>	Woodland	NA
Gray-cheeked Thrush	<i>Catharus minimus</i>	Woodland	NA
Swainson's Thrush	<i>Catharus ustulatus</i>	Woodland	NA
Hermit Thrush	<i>Catharus guttatus</i>	Woodland	NA
Varied Thrush	<i>Ixoreus naevius</i>	Woodland	NA
Western Bluebird	<i>Sialia mexicana</i>	Woodland	NA
Red-shouldered Hawk	<i>Buteo lineatus</i>	Woodland	Interior Forest
Hairy Woodpecker	<i>Picoides villosus</i>	Woodland	Interior Forest
Pileated Woodpecker	<i>Dryocopus pileatus</i>	Woodland	Interior Forest
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	Woodland	Interior Forest
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	Woodland	Interior Forest

Acadian Flycatcher	Empidonax virescens	Woodland	Interior Forest
Rose-breasted Grosbeak	Pheucticus ludovicianus	Woodland	Interior Forest
Scarlet Tanager	Piranga olivacea	Woodland	Interior Forest
Summer Tanager	Piranga rubra	Woodland	Interior Forest
Red-eyed Vireo	Vireo olivaceus	Woodland	Interior Forest
Black-and-white Warbler	Mniotilta varia	Woodland	Interior Forest
Worm-eating Warbler	Helminthos vermivorum	Woodland	Interior Forest
Northern Parula	Setophaga americana	Woodland	Interior Forest
Black-throated Blue Warbler	Setophaga caerulescens	Woodland	Interior Forest
Cerulean Warbler	Setophaga cerulea	Woodland	Interior Forest
Ovenbird	Seiurus aurocapilla	Woodland	Interior Forest
Northern Waterthrush	Parkesia noveboracensis	Woodland	Interior Forest
Louisiana Waterthrush	Parkesia motacilla	Woodland	Interior Forest
Kentucky Warbler	Geothlypis formosa	Woodland	Interior Forest
Canada Warbler	Cardellina canadensis	Woodland	Interior Forest
White-breasted Nuthatch	Sitta carolinensis	Woodland	Interior Forest
Tufted Titmouse	Baeolophus bicolor	Woodland	Interior Forest
Blue-gray Gnatcatcher	Poliotilta caerulea	Woodland	Interior Forest
Wood Thrush	Hylocichla mustelina	Woodland	Interior Forest
Veery	Catharus fuscescens	Woodland	Interior Forest
American Crow	Corvus brachyrhynchos	NA	Interior Forest

Appendix I-3 Metric descriptions.

Data used	Metrics type	Metrics name	Description	Notes
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NBCD vegetation height map	Summary statistics (A)	Mean	$\frac{\sum x_k}{K}$	x_k = height values of forested pixels in the landscape. K = the number of those pixels in the landscape.
		Standard deviation (SD)	$\sqrt{\frac{\sum (x_k - Mean)^2}{K}}$	N/A
		Minimum (Min)	MIN $\{X_k\}$	N/A
		Maximum (Max)	MAX $\{X_k\}$	N/A
Two-dimensional vegetation cover map	Traditional patch-based metrics (B)	Number of patches(B.NP)	Total number of patches in the landscape	N/A
		Mean patch area (B.Area.MN)	$\frac{\sum x_i}{N}$	x_i = patch area across all patches in the landscape. N = total number of patches.
		Standard deviation of patch area (B.Area.SD)	$\sqrt{\frac{\sum (x_i - Area.MN)^2}{N}}$	N/A
		Edge density (B. ED)	$\frac{\sum_{k=1}^m e_{ik}}{A} (10,000)$	e_{ik} = total length of edge in landscape between height class i and k. A = total landscape area (m ²).
		Total edge (B.TE)	Total length (m) of edge in landscape	N/A
		Mean fractal dimension index (B.FRAC.MN)	$\frac{\sum 2\ln(0.25p_i)/\ln a_i}{N}$	p_i = perimeter of patch i. a_i = area of patch i.

		Standard deviation of fractal dimension index (B.FRAC.SD)	$\sqrt{\frac{\sum (f_i - FRAC.MN)^2}{N}}$	f_i = fractal dimension index across all patches.
Vegetation cover map segmented by height structure	Height-incorporated patch-based metrics (C)	Number of patches(C.NP)	Total number of patches in the landscape	patches and edges referred to for height-incorporated patch-based metrics (C) include vertical patches and edges.
		Mean patch area (C.Area.MN)	$\frac{\sum x_i}{N}$	x_i = patch area across all patches in the landscape. N = total number of patches.
		Standard deviation of patch area (C.Area.SD)	$\sqrt{\frac{\sum (x_i - Area.MN)^2}{N}}$	N/A
		Total edge (C.TE)	Total length (m) of edge in landscape	N/A
		Mean fractal dimension index (C.FRAC.MN)	$\frac{\sum 2\ln(0.25p_i)/\ln a_i}{N}$	p_i = perimeter of patch i. a_i = area of patch i.
		Standard deviation of fractal dimension index (C.FRAC.SD)	$\sqrt{\frac{\sum (f_i - FRAC.MN)^2}{N}}$	f_i = fractal dimension index across all patches.
		Contrast weighted edge density (C.CWED)	$\frac{\sum \sum e_{ik} * d_{ik}}{A} (10,000)$	e_{ik} = total length of edge in landscape between height class i and k. d_{ik} = contrast weight

				between class i and k. A = total landscape area.
		Mean of edge contrast index(C.ECON.MN)	$\frac{\sum \frac{\sum p_{ijk} * d_{ijk}}{P_{ij}}}{N} (100)$	p_{ijk} =length of edge of patch ij adjacent to height class k. d_{ijk} = edge contrast weight between height class i and k. P_{ij} =length of perimeter of patch ij.
		Standard deviation of edge contrast index (C.ECON.SD)	$\sqrt{\frac{\sum (ECON_i - ECON.MN)^2}{N}}$	$ECON_i$ =edge contrast index of patch i.
		Shannon's diversity index (C.SHDI)	$-\sum Pr_i * \ln Pr_i$	Pr_i = proportion of the landscape occupied by height class i.
NBCD vegetation height map	Second-order texture measures (D)	Entropy	$-\sum_i \sum_j p(i,j) \log(p(i,j))$	$p(i,j)$ is the (i,j)th entry of the normalized GLCM matrix.
		Contrast	$\sum_{n=0}^{N-1} n^2 \left\{ \sum_{i=1}^N \sum_{j=1}^N p(i,j) \right\}_{ i-j =n}$	N/A
		Angular second moment (ASM)	$\sum_i \sum_j \{p(i,j)\}^2$	N/A
		Homogeneity	$\sum_i \sum_j \frac{p(i,j)}{1 + i-j }$	N/A
		Dissimilarity	$\sum_{n=0}^{N-1} n \left\{ \sum_{i=1}^N \sum_{j=1}^N p(i,j) \right\}$	N/A

Appendix I-4 Metrics correlation with species richness.

	Woodland Guild		Forest Edge Guild		Interior Forest guild		Metric Set
	Correlation	P-value	Correlation	P-value	Correlation	P-value	
MIN	0.11	0.00	0.00	0.92	0.10	0.00	A
MAX	0.04	0.06	0.36	0.00	0.04	0.14	A
MEAN	0.20	0.00	0.40	0.00	0.19	0.00	A
SD	-0.02	0.34	0.14	0.00	-0.05	0.05	A
B.NP	-0.45	0.00	-0.15	0.00	-0.06	0.02	B
B.TE	0.00	0.98	0.13	0.00	-0.05	0.05	B
B.ED	0.00	0.98	0.13	0.00	-0.05	0.05	B
B.AREA.MN	0.44	0.00	-0.06	0.02	0.10	0.00	B
B.AREA.SD	0.58	0.00	0.06	0.03	0.14	0.00	B
B.FRAC.MN	-0.06	0.01	-0.30	0.00	-0.13	0.00	B
B.FRAC.SD	-0.13	0.00	-0.12	0.00	-0.06	0.04	B
C.NP	0.25	0.00	0.41	0.00	0.08	0.01	C
C.TE	0.49	0.00	0.45	0.00	0.14	0.00	C
C.AREA.MN	0.15	0.00	-0.26	0.00	0.02	0.56	C
C.AREA.SD	0.24	0.00	-0.21	0.00	0.01	0.75	C
C.FRAC.MN	-0.15	0.00	0.08	0.00	0.00	0.87	C
C.FRAC.SD	0.13	0.00	0.23	0.00	0.03	0.27	C
C.CWED	0.37	0.00	0.50	0.00	0.14	0.00	C
C.ECON.MN	-0.26	0.00	0.08	0.00	-0.03	0.29	C
C.ECON.SD	-0.21	0.00	0.11	0.00	-0.04	0.11	C

C.SHDI	0.03	0.21	0.33	0.00	0.04	0.14	C
Contrast	0.08	0.00	0.32	0.00	0.04	0.16	D
Entropy	0.62	0.00	0.38	0.00	0.14	0.00	D
ASM	-0.65	0.00	-0.36	0.00	-0.14	0.00	D
Homogeneity	-0.54	0.00	-0.40	0.00	-0.11	0.00	D
Disimilarity	0.22	0.00	0.37	0.00	0.04	0.15	D

Appendix I-5 Model performances for different multivariable models.

Model (number of variables)	Model Type	Measurement name	Woodland guild	Forest edge guild	Interior forest guild
D (5)	Linear	adj. r-squared	0.48	0.26	0.06
		adj. r-squared 95% CI	0.45	0.22	0.03
			0.52	0.30	0.08
		AIC	10783.64	7642.58	7721.88
		AIC 95% CI	10663.48	7543.14	7626.97
			10919.38	7772.84	7827.75
C (10)	Linear	adj. r-squared	0.45	0.30	0.04
		adj. r-squared 95% CI	0.41	0.25	0.02
			0.49	0.34	0.06
		AIC	10886.77	7579.35	7745.47
		AIC 95% CI	10776.59	7491.13	7655.00
			11031.62	7708.06	7864.19
A (4)	Linear	adj. r-squared	0.09	0.22	0.04
		adj. r-squared 95% CI	0.07	0.18	0.02
			0.12	0.26	0.07
		AIC	11768.01	7713.44	7737.10
		AIC 95% CI	11650.73	7612.97	7645.61

			11894.79	7832.26	7845.43
B (7)	Linear	adj. r-squared	0.45	0.20	0.03
		adj. r-squared 95% CI	0.42	0.16	0.01
			0.48	0.24	0.05
		AIC	10894.73	7754.34	7757.22
		AIC 95% CI	10779.40	7645.87	7661.07
			11030.33	7881.45	7864.17
A+4BPHM (8)	Linear	adj. r-squared	0.52	0.33	0.06
		adj. r-squared 95% CI	0.48	0.28	0.04
			0.56	0.38	0.09
		AIC	10642.09	7505.54	7713.40
		AIC 95% CI	10515.22	7407.62	7621.75
			10792.03	7632.99	7825.33
B+4BPHM (11)	Linear	adj. r-squared	0.52	0.34	0.06
		adj. r-squared 95% CI	0.49	0.29	0.03
			0.55	0.38	0.07
		AIC	10648.74	7494.67	7727.33
		AIC 95% CI	10544.73	7402.19	7636.25
			10795.68	7622.01	7839.27
A+B+C+D (26)	Random Forest	% variance explained	0.63	0.47	0.11
A (4)	Random Forest	% variance explained	0.37	0.31	0.07
A+4BPHM (8)	Random Forest	% variance explained	0.58	0.39	0.08
B (7)	Random Forest	% variance explained	0.52	0.26	0.01
B+4BPHM (11)	Random Forest	% variance explained	0.58	0.39	0.05
C (10)	Random Forest	% variance explained	0.58	0.39	0.06

D (5)	Random Forest	% variance explained	0.50	0.23	~0.00
-------	---------------	----------------------	------	------	-------

Appendix I-6 Supporting Information

Metrics development methods

Summary statistics

The summary statistics used in this study included, mean, standard deviation (SD), minimum value (Min), and maximum value (Max) of tree height (Appendix I-3). All the metrics were computed in a GIS environment using ArcGIS 9.3 (Environmental Systems Research Institute 1999).

Patch-based metrics

Patch-based metrics based on two-dimensional vegetation distribution were derived by classifying the NBCD forest height maps into binary forest-non-forest maps. Vegetation height values larger than 0 were assigned as habitat and the rest of the cells as non-habitat, and vertical height information were discarded (Figure 2-1). Within each landscape a set of patch-based metrics (Appendix I-3) were calculated using Fragstats (McGarigal et al. 2002). The metrics in this group included patches (NP), mean patch area (Area.MN), standard deviation of patch area (Area.SD), mean fractal dimension index (FRAC.MN), standard deviation of fractal dimension (FRAC.SD), total edge (TE) and edge density (ED) where fractal dimension index was a measure of complexity of shape based on perimeter-area relationships.

Height-structured patch-based metrics

We used a pixel-based segmentation approach to create vertical patches and edges within continuous habitat patches. The pixel-based approach relies on a set of global thresholds to classify pixels into different groups, and then spatially connected pixels from the same group are segmented from the surrounding areas and assigned with different group memberships. The classification process only depends on the attribute value of a specific pixel. It is a relatively simple method compared with edge-based and region-based methods which consider variation of attribute values in the neighboring regions when assigning group memberships (Darwish et al. 2003). We selected a set of thresholds using quintile classification based on frequency of height values across 1751 landscapes. The forest height values were classified into five groups using four thresholds: 20, 40, 60, and 80 percentile values at 15.4, 17.6, 19.4, and 21.8 m respectively (Figure 2-1).

A set of metrics similar to the ones in metric set (B) was then derived. A diversity index (Shannon's diversity index (SHDI)) was included to measure the richness of height classes, and a contrast weight matrix (see Table below) was used to calculate four adjacent contrast metrics. The contrast matrix is symmetrical with weights ranging from 0 (no contrast) to 1 (maximum contrast). When adjacent areas have great height differences, vertical edges separating the areas are weighted heavily and thus have a large contribution to the weighted edge measurements (Appendix I-3). The resulting contrast weighted edge density (CWED) was derived from sum of weighted edges at the landscape level. Mean and standard deviation of an edge contrast index (ECON.MN & ECON.SD)) summarizes the distribution of weighted edge lengths of all patches, including vertical patches within a specific landscape (McGarigal et al. 2002).

Second-order texture metrics

We calculated a set of second-order texture metrics using the texture filter in ENVI 4.7 (Exelis Visual Information Solutions Boulder, Colorado). A variety of texture metrics have been used to characterize habitat structure (St-Louis et al. 2006). We developed five texture measures: angular second moment (ASM), contrast, homogeneity, entropy, and dissimilarity. The metrics were developed by processing the NBCD tree height map with a 3×3 moving window. For our purposes, non-forest land cover types were reclassified as having 0 height value.

Random Forest Model

In essence, RF model is an ensemble machine learning technique which consists of a compilation of multiple regression trees, a method proven to be better than the single regression tree analysis (Hamza and Larocque 2005). The regression tree method seeks to construct a set of binary splits on the predictor variables; the dependent variable is predicted through recursive partitioning. The selected splits are the ones that maximize the homogeneity of the two resulting groups. In comparison, each tree in random forests method is built with a subset of variables randomly chosen. At each node, the number of predictors tested for the best split is also randomized. Like bagging trees method (Breiman 1996), the trees are grown to maximum size without pruning.

About 37% of data are randomly drawn as the out-of-bag (OOB) observations and excluded in the construction of every tree. The OOB error estimation provides a cross-validation mechanism, thus test sets or extra cross-validation is not necessary. The performance of the random forest models was estimated using percent of variance explained: $R^2 = 1 - \text{MSE} / \text{observed variance}$, where MSE is mean square error between OOB predictions and observations (Breiman 2001, Wei et al. 2010).

Table. Contrast matrix for weighted edge metrics

Forest Height Class	NO.1	NO.2	NO.3	NO.4	NO.5	Non-forest
NO.1	0	0.25	0.5	0.75	1	0.25
NO.2	-	0	0.25	0.5	0.75	0.5
NO.3	-	-	0	0.25	0.5	0.75
NO.4	-	-	-	0	0.25	1
NO.5	-	-	-	-	0	1
Non-forest	-	-	-	-	-	0

Appendix II

Appendix II-1 The R code to generate the posterior samples of $N_{i,t}$ and other parameters using Hierarchical Bayesian model

```
#### We are presenting here the R code for calling Winbugs to produce the strata specific abundance
indices for Carolina Wren(aou=7180)

## importing and orgnizing data tables

aoupick<-7180

indextable<-
read.csv(paste("F:/project/BBS_winbugs_2/index_rawdata/indexed",aoupick,".csv",sep=""),header=T)

# the first data table keeps the pre-processed BBS survey data. strata and observer/route have been
indexed

weighttable<-
read.csv(paste("F:/project/BBS_winbugs_2/index_rawdata/weight_z/Weightfactor",aoupick,".csv",sep=
""),header=T)

#the second data table stores a list of strata that composed the species range. The table includes the X-
and Y-coordinates of the strata centroids and the Zi and Ai weights for the stratum
```

```
indextable<-indextable[order(indextable$BCRstate,indextable$RTENO,indextable$Year),]
```

```
weighttable<-weighttable[order(weighttable$BCRstate),]
```

```
## setting up and saving the code for Winbugs program
```

```
setwd("F:/project/BBS_winbugs_2/index_rawdata/winbugsfiles/")
```

```
sink(paste("winbugsfile",aoupick,".txt",sep=""))
```

```
cat("
```

```
  model{
```

```
    ##----priors for identically distributed parameters
```

```
    ## observer/route effect Wj
```

```
    for (k in 1:n.obs.rt){
```

```
      Wj[k]~dnorm(0.0,tauW )
```

```
    }
```

```
    tauW~dgamma(0.001,0.001)
```

```
    sdW<-1/pow(tauW,0.5)
```

```

##overdispersion E

for (m in 1:n){

Eijt[m]~dnorm(0.0,tauE)

}

tauE~dgamma(0.001,0.001)

sdE<-1/pow(tauE,0.5)

## novice observer effect etha,

## identically distributed

etha~dnorm(0.0,0.000001)

##----priors for the stratum specific parameters

for (j in 1:n.strata){

Si[j]~dnorm(0.0,0.000001)

Bi[j]~dnorm(0.0,0.000001)

```

```

tauR[j]~dgamma(0.001,0.001)

sdR[j]<-1/pow(tauR[j],0.5)

for (k in 1: n.year){

Rit[k,j]~dnorm(0.0,tauR[j])

}

}

#likelihood

for (i in 1: n){

Y[i]~dpois(lambda[i])

log(lambda[i])<-Si[index.stra[i]]+Bi[index.stra[i]]*(yearfrom65[i]-
22)+Wj[index.ObsRT[i]]+etha*Firstyear[i]

+Rit[yearfrom65[i],index.stra[i]]

+Eijt[i]

}

```

```

#summary statistics derived variables

for (j in 1:n.strata){

for (k in 1: n.year){

n.d[j,k]<-weightZ[j]*exp(Si[j]+Bi[j]*(k-22)+Rit[k,j])

N.d[j,k]<-weightA[j]*n.d[j,k]

}

}

}

",fill=TRUE)

sink()

##Bundle data

#----- transfer R value to variables needed for winbugs

n<-dim(indextable)[1] # total number of data points

n.strata<-length(unique(indextable$BCRstate)) # number of strata

n.obs.rt<-length(unique(indextable$ObsRT)) # number of observer/route combinations

```

```

strata.list<-unique(indextable$BCRstate) # unique list of strata id

n.year<-max(indextable$Year)-1965 # number of years available in the data

Y<-indextable$SpeciesTotal # count value to be modeled

index.stra<-as.numeric(indextable$index.stra) # strata index

index.ObsRT<-as.numeric(indextable$index.ObsRT) # observer/route index

Firstyear<-as.numeric(indextable$Firstyear) # the binary index to indicate whether it was surveyed by
1st year observer

weightZ<-round(weighttable[,"Zi"],digits=6)

weightA<-round(weighttable[,"Ai"], digits=6)

yearfrom65<-as.numeric(indextable$yearfrom65)

#-----

win.data<-
list(n=n,Y=Y,index.stra=index.stra,n.strata=n.strata,index.ObsRT=index.ObsRT,n.obs.rt=n.obs.rt,Firstyear
=Firstyear

```

```

    , n.year=n.year

    ,yearfrom65=yearfrom65

    ,weightZ=weightZ

    ,weightA=weightA

)

##~~~~~Bundle data finished

#setting up initial values for the parameters

inits<-function(){list(Si=rep(0,n.strata),Bi=rep(0,n.strata),tauW=1,etha=0

    ,tauR=rep(1,n.strata)

    ,tauE=1

)}

# parameters to estimate

params<-c( #"Si", "Bi",

    #"Wj", "tauW", "etha", "Eijt", "Rit",

    "sdE", "sdW",

```



```

    #"n.d" # a lot more parameters can be estimated and saved but for the sake of speed we are
only saving 3 of them

    "N.d"

)

#MCMC settings

nc<-3 # number of chain

ni<-30000 #total number of iterations

nb<-15000 # number of burn-in iterations

nt<-50 # thinning rate

## starting the R2WinBUGS package and start running Winbugs program

library(R2WinBUGS)

out<-
bugs(data=win.data,inits=inits,parameters.to.save=params,model.file=paste("winbugsfile",aoupick,".txt"
,sep=""),n.thin=nt,n.chains=nc,n.burnin=nb,n.iter=ni,debug=FALSE,bugs.directory="F:/WinBUGS14")

print ("finished saving Rdata")

## saving the result

```

```
setwd("F:/project/BBS_winbugs_2/index_rawdata/output/")
```

```
save(out,file=paste(aoupick,"-",Sys.Date(),".Rdata",sep=""))
```

Appendix III

Appendix III-1 57 permanent resident bird species included in the study and their attributes

English Common Name	Scientific Name	aou	Nit change	north shift	south shift	east shift	west shift	shift at all	plain bird
Northern Bobwhite	Colinus virginianus	2890	Decrease d	TRUE	FALSE	FALSE	TRUE	TRUE	TRUE
Scaled Quail	Callipepla squamata	2930	Decrease d	FALSE	FALSE	FALSE	TRUE	TRUE	TRUE
California Quail	Callipepla californica	2940	Increase d	FALSE	FALSE	TRUE	FALSE	TRUE	FALSE
Gambel's Quail	Callipepla gambelii	2950	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Ruffed Grouse	Bonasa umbellus	3000	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Sharp-tailed Grouse	Tympanuchus phasianellus	3080	Stable	FALSE	FALSE	TRUE	FALSE	TRUE	TRUE
Wild Turkey	Meleagris gallopavo	3100	Increase d	TRUE	FALSE	TRUE	FALSE	TRUE	FALSE
Common Ground-Dove	Columbina passerina	3200	Stable	FALSE	FALSE	FALSE	TRUE	TRUE	TRUE
Inca Dove	Columbina inca	3210	Increase d	FALSE	FALSE	TRUE	FALSE	TRUE	TRUE
Black Vulture	Coragyps atratus	3260	Increase d	TRUE	FALSE	FALSE	TRUE	TRUE	FALSE
Barred Owl	Strix varia	3680	Increase d	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Eastern Screech-Owl	Megascops asio	3730	Decrease d	FALSE	FALSE	FALSE	FALSE	FALSE	TRUE
Great Horned Owl	Bubo virginianus	3750	Decrease d	FALSE	TRUE	TRUE	FALSE	TRUE	FALSE
Northern Pygmy-Owl	Glaucidium gnoma	3790	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Greater Roadrunner	Geococcyx californianus	3850	Stable	FALSE	TRUE	TRUE	FALSE	TRUE	TRUE
Hairy Woodpecker	Picoides villosus	3930	Increase d	FALSE	FALSE	TRUE	FALSE	TRUE	FALSE
Downy Woodpecker	Picoides pubescens	3940	Increase d	FALSE	FALSE	TRUE	FALSE	TRUE	FALSE

Ladder-backed Woodpecker	Picoides scalaris	3960	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Black-backed Woodpecker	Picoides arcticus	4000	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
American Three-toed Woodpecker	Picoides dorsalis	4010	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Pileated Woodpecker	Dryocopus pileatus	4050	Increase d	TRUE	FALSE	TRUE	FALSE	TRUE	FALSE
Red-bellied Woodpecker	Melanerpes carolinus	4090	Increase d	TRUE	FALSE	FALSE	TRUE	TRUE	TRUE
Black Phoebe	Sayornis nigricans	4580	Increase d	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Black-billed Magpie	Pica hudsonia	4750	Decrease d	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Steller's Jay	Cyanocitta stelleri	4780	Stable	TRUE	FALSE	FALSE	TRUE	TRUE	FALSE
Western Scrub-Jay	Aphelocoma californica	4810	Stable	TRUE	FALSE	FALSE	TRUE	TRUE	FALSE
Gray Jay	Perisoreus canadensis	4840	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Common Raven	Corvus corax	4860	Increase d	FALSE	FALSE	FALSE	TRUE	TRUE	FALSE
Chihuahuan Raven	Corvus cryptoleucus	4870	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	TRUE
Fish Crow	Corvus ossifragus	4900	Increase d	TRUE	FALSE	FALSE	TRUE	TRUE	TRUE
Clark's Nutcracker	Nucifraga columbiana	4910	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Pinyon Jay	Gymnorhinus cyanocephalus	4920	Decrease d	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Great-tailed Grackle	Quiscalus mexicanus	5120	Increase d	FALSE	FALSE	FALSE	TRUE	TRUE	FALSE
Boat-tailed Grackle	Quiscalus major	5130	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	TRUE
Lesser Goldfinch	Spinus psaltria	5300	Stable	TRUE	FALSE	FALSE	TRUE	TRUE	FALSE
Rufous-crowned Sparrow	Aimophila ruficeps	5800	Decrease d	TRUE	FALSE	FALSE	TRUE	TRUE	FALSE
Canyon Towhee	Melospiza fusca	5910	Decrease d	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Northern Cardinal	Cardinalis cardinalis	5930	Increase d	TRUE	FALSE	FALSE	TRUE	TRUE	TRUE
Pyrrhuloxia	Cardinalis sinuatus	5940	Decrease d	TRUE	FALSE	FALSE	TRUE	TRUE	TRUE
American Dipper	Cinclus mexicanus	7010	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Northern Mockingbird	Mimus polyglottos	7030	Decrease d	TRUE	FALSE	FALSE	FALSE	TRUE	FALSE

Curve-billed Thrasher	Toxostoma curvirostre	7070	Decrease d	TRUE	FALSE	FALSE	FALSE	TRUE	FALSE
Cactus Wren	Campylorhynchus brunneicapillus	7130	Decrease d	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Canyon Wren	Catherpes mexicanus	7170	Stable	FALSE	FALSE	FALSE	TRUE	TRUE	FALSE
Carolina Wren	Thryothorus ludovicianus	7180	Increase d	TRUE	FALSE	FALSE	TRUE	TRUE	TRUE
Bewick's Wren	Thryomanes bewickii	7190	Decrease d	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
White-breasted Nuthatch	Sitta carolinensis	7270	Increase d	FALSE	FALSE	TRUE	FALSE	TRUE	FALSE
Brown-headed Nuthatch	Sitta pusilla	7290	Stable	TRUE	FALSE	TRUE	FALSE	TRUE	TRUE
Pygmy Nuthatch	Sitta pygmaea	7300	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Tufted Titmouse	Baeolophus bicolor	7310	Increase d	TRUE	FALSE	TRUE	FALSE	TRUE	TRUE
Black-capped Chickadee	Poecile atricapillus	7350	Increase d	FALSE	FALSE	TRUE	FALSE	TRUE	FALSE
Carolina Chickadee	Poecile carolinensis	7360	Decrease d	TRUE	FALSE	FALSE	FALSE	TRUE	TRUE
Mountain Chickadee	Poecile gambeli	7380	Decrease d	TRUE	FALSE	FALSE	TRUE	TRUE	FALSE
Boreal Chickadee	Poecile hudsonicus	7400	Stable	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
Chestnut-backed Chickadee	Poecile rufescens	7410	Decrease d	FALSE	FALSE	TRUE	FALSE	TRUE	FALSE
Bushtit	Psaltriparus minimus	7430	Stable	FALSE	FALSE	TRUE	FALSE	TRUE	FALSE
Verdin	Auriparus flaviceps	7460	Decrease d	FALSE	TRUE	TRUE	FALSE	TRUE	FALSE

Appendix III-2 Model performance comparison between the climatic models (BIOCLIM, EXTRE, TEMP, and PREC). The climatic models are derived based on climatic changes between periods of 1969 – 1978 and 2003 – 2012. The table shows the species having at least one of the four models with positive percent variance explained (% var. explained). The negative % var. explained are assigned to explain 0 % var. explained.

model	% var. explained adjusted	common.name	north shift	south shift	east shift	west shift	Nit change	% var. explained original
BIOCLIM	0.320469748	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.32047
EXTRE	0.3164923	Northern	TRUE	FALSE	FALSE	TRUE	Decreased	0.316492

	84	Bobwhite						
PREC	0.317585205	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.317585
TEMP	0.289590286	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.28959
TOTO	0.329348707	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.329349
BIOCLIM	0.103670516	Scaled Quail	FALSE	FALSE	FALSE	TRUE	Decreased	0.103671
EXTRE	0.148649203	Scaled Quail	FALSE	FALSE	FALSE	TRUE	Decreased	0.148649
PREC	0.087666393	Scaled Quail	FALSE	FALSE	FALSE	TRUE	Decreased	0.087666
TEMP	0.152411343	Scaled Quail	FALSE	FALSE	FALSE	TRUE	Decreased	0.152411
TOTO	0.132023923	Scaled Quail	FALSE	FALSE	FALSE	TRUE	Decreased	0.132024
BIOCLIM	0.056024624	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0.056025
EXTRE	0.007126261	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0.007126
PREC	0.081705035	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0.081705
TEMP	0.054804713	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0.054805
TOTO	0.054618816	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0.054619
BIOCLIM	0.125576297	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0.125576
EXTRE	0.054069392	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0.054069
PREC	0.31033048	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0.31033
TEMP	0	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	-0.12281
TOTO	0.037573828	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0.037574
BIOCLIM	0.092094982	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0.092095
EXTRE	0	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	-0.14451
PREC	0	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	-0.05983
TEMP	0.023502414	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0.023502
TOTO	0.046695262	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0.046695
BIOCLIM	0.076346263	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.076346
EXTRE	0	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	-0.02121

PREC	0.0420620 32	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.042062
TEMP	0.0186821 82	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.018682
TOTO	0.0356153 18	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.035615
BIOCLIM	0.0210359 18	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.021036
EXTRE	0.0235269 54	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.023527
PREC	0.0479279 78	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.047928
TEMP	0.0443852 67	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.044385
TOTO	0.0602810 47	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.060281
BIOCLIM	0.1578761 04	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.157876
EXTRE	0.0497646 65	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.049765
PREC	0.0931925 14	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.093193
TEMP	0.0929173 09	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.092917
TOTO	0.1148106 23	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.114811
BIOCLIM	0.2410958 93	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.241096
EXTRE	0.1795752 39	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.179575
PREC	0.1113757 85	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.111376
TEMP	0.2266682 04	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.226668
TOTO	0.2218014 72	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.221801
BIOCLIM	0.0176203 92	Western Scrub-Jay	TRUE	FALSE	FALSE	TRUE	Stable	0.01762
EXTRE	0	Western Scrub-Jay	TRUE	FALSE	FALSE	TRUE	Stable	-0.22789
PREC	0	Western Scrub-Jay	TRUE	FALSE	FALSE	TRUE	Stable	-0.11913
TEMP	0.0200212 24	Western Scrub-Jay	TRUE	FALSE	FALSE	TRUE	Stable	0.020021
TOTO	0	Western Scrub-Jay	TRUE	FALSE	FALSE	TRUE	Stable	-0.07952
BIOCLIM	0.0499694 3	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.049969
EXTRE	0.1487110 96	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.148711
PREC	0.1184357	Common	FALSE	FALSE	FALSE	TRUE	Increased	0.118436

	57	Raven						
TEMP	0.089081566	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.089082
TOTO	0.095553957	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.095554
BIOCLIM	0.188959675	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0.18896
EXTRE	0	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	-0.08735
PREC	0	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	-0.23926
TEMP	0.193807399	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0.193807
TOTO	0.115481595	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0.115482
BIOCLIM	0.112270375	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.11227
EXTRE	0.013764865	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.013765
PREC	0	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	-0.17937
TEMP	0.110895941	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.110896
TOTO	0.023553331	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.023553
BIOCLIM	0.134650642	Lesser Goldfinch	TRUE	FALSE	FALSE	TRUE	Stable	0.134651
EXTRE	0	Lesser Goldfinch	TRUE	FALSE	FALSE	TRUE	Stable	-0.04829
PREC	0	Lesser Goldfinch	TRUE	FALSE	FALSE	TRUE	Stable	-0.10193
TEMP	0	Lesser Goldfinch	TRUE	FALSE	FALSE	TRUE	Stable	-0.01702
TOTO	0	Lesser Goldfinch	TRUE	FALSE	FALSE	TRUE	Stable	-0.00849
BIOCLIM	0.334447733	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.334448
EXTRE	0.368619491	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.368619
PREC	0.065176112	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.065176
TEMP	0.411335435	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.411335
TOTO	0.39055261	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.390553
BIOCLIM	0.008302715	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.008303
EXTRE	0	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	-0.0212
PREC	0.011655742	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.011656
TEMP	0	Northern	TRUE	FALSE	FALSE	FALSE	Decreased	-0.04347

		Mockingbird						
TOTO	0.019403264	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.019403
BIOCLIM	0	Curve-billed Thrasher	TRUE	FALSE	FALSE	FALSE	Decreased	-0.14555
EXTRE	0.101420888	Curve-billed Thrasher	TRUE	FALSE	FALSE	FALSE	Decreased	0.101421
PREC	0	Curve-billed Thrasher	TRUE	FALSE	FALSE	FALSE	Decreased	-0.28514
TEMP	0.188872058	Curve-billed Thrasher	TRUE	FALSE	FALSE	FALSE	Decreased	0.188872
TOTO	0.058952096	Curve-billed Thrasher	TRUE	FALSE	FALSE	FALSE	Decreased	0.058952
BIOCLIM	0.339184512	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.339185
EXTRE	0.223330902	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.223331
PREC	0.255713561	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.255714
TEMP	0.265123527	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.265124
TOTO	0.302957917	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.302958
BIOCLIM	0.153585931	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.153586
EXTRE	0	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	-0.02483
PREC	0.031708005	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.031708
TEMP	0.077736571	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.077737
TOTO	0.090349751	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.09035
BIOCLIM	0	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	-0.1104
EXTRE	0.054544293	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	0.054544
PREC	0	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	-0.17139
TEMP	0.080543258	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	0.080543
TOTO	0	Brown-	TRUE	FALSE	TRUE	FALSE	Stable	-0.00187

		headed Nuthatch						
BIOCLIM	0.522785997	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.522786
EXTRE	0.291465624	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.291466
PREC	0.188550599	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.188551
TEMP	0.355258704	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.355259
TOTO	0.343951936	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.343952
BIOCLIM	0	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	-0.02243
EXTRE	0	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	-0.06099
PREC	0	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	-0.1023
TEMP	0.085173863	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	0.085174
TOTO	0.066742532	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	0.066743
BIOCLIM	0	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	-0.01819
EXTRE	0.064510892	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0.064511
PREC	0.057824174	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0.057824
TEMP	0.0574594	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0.057459
TOTO	0.067124279	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0.067124
BIOCLIM	0.005483204	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	0.005483
EXTRE	0	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	-0.03815
PREC	0	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	-0.15591
TEMP	0	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	-0.03633
TOTO	0	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	-0.06485

Appendix III-3 The description of the methods used to characterize the change of non-climatic factors

We used county level data of the U.S. census data of 1990 and 2010 (Minnesota Population Center 2011) to capture the population and housing density changes. The metrics included are: person in urbanized area, person in rural area, rural housing units, total population, and total housing units. The county areas are calculated. Based on the geographic location of county centroids to BBS strata, each county was assigned to a BBS stratum (the one it falls within or closest to). Lastly, the change of population or housing density is calculated as the change of total metric values of the counties within each BBS strata divided by the total area of these counties.

The land cover types included are: open water, barren land, grassland, agriculture, forest, wetland, and urban. The percentage change of each land cover type by stratum were calculated. We used the National Land Cover Databases 1992-2001 and 2011 (Fry et al. 2009, Homer et al. 2015) respectively to calculate the total area of each land cover type in 1992 and 2011. The change was then calculated as the percentage change of the land cover type within each stratum.

Appendix III-4 Model performance comparison between the climatic models (BIOCLIM, EXTRE, TEMP, and PREC) and the non-climatic models(LC_CEN). The climatic models are derived based on climatic changes between periods of 1988 – 1997 and 2003 – 2012. The non-climatic models are based on U.S. census data of 1990 and 2010, as well as the National Land Cover Databases 1992-2001 and 2011. The table shows the species having at least one of the five models with positive percent variance explained (% var. explained). The negative % var. explained are assigned to explain 0 % var. explained.

aou	model	% var. explained original	common name	north shift	south shift	east shift	west shift	Nit change	% var. explained adjusted
2890	BIOCLIM	0.258183	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.258183
2890	EXTRE	0.200208	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.200208
2890	LC_CEN	0.295541	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.295541

2890	PREC	0.270322	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.270322
2890	TEMP	0.194028	Northern Bobwhite	TRUE	FALSE	FALSE	TRUE	Decreased	0.194028
3100	BIOCLIM	0.010061	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0.010061
3100	EXTRE	-0.04013	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0
3100	LC_CEN	0.043283	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0.043283
3100	PREC	-0.02811	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0
3100	TEMP	-0.04089	Wild Turkey	TRUE	FALSE	TRUE	FALSE	Increased	0
3210	BIOCLIM	0.170088	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0.170088
3210	EXTRE	-0.05508	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0
3210	LC_CEN	-0.02755	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0
3210	PREC	0.107988	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0.107988
3210	TEMP	-0.14529	Inca Dove	FALSE	FALSE	TRUE	FALSE	Increased	0
3260	BIOCLIM	0.097393	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0.097393
3260	EXTRE	-0.05969	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0
3260	LC_CEN	-0.00738	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0
3260	PREC	-0.16771	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0
3260	TEMP	0.119107	Black Vulture	TRUE	FALSE	FALSE	TRUE	Increased	0.119107
3750	BIOCLIM	0.05475	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.05475
3750	EXTRE	0.059777	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.059777
3750	LC_CEN	-0.03946	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0
3750	PREC	0.040775	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.040775
3750	TEMP	0.065866	Great Horned Owl	FALSE	TRUE	TRUE	FALSE	Decreased	0.065866
3930	BIOCLIM	0.005299	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.005299
3930	EXTRE	-0.01895	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0

3930	LC_CEN	-0.09463	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0
3930	PREC	0.039545	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.039545
3930	TEMP	0.032113	Hairy Woodpecker	FALSE	FALSE	TRUE	FALSE	Increased	0.032113
4050	BIOCLIM	0.148034	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.148034
4050	EXTRE	0.024415	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.024415
4050	LC_CEN	0.231802	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.231802
4050	PREC	0.005053	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.005053
4050	TEMP	0.068072	Pileated Woodpecker	TRUE	FALSE	TRUE	FALSE	Increased	0.068072
4090	BIOCLIM	0.092153	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.092153
4090	EXTRE	0.288771	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.288771
4090	LC_CEN	-0.05257	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0
4090	PREC	0.240265	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.240265
4090	TEMP	0.189896	Red-bellied Woodpecker	TRUE	FALSE	FALSE	TRUE	Increased	0.189896
4860	BIOCLIM	0.045339	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.045339
4860	EXTRE	0.190016	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.190016
4860	LC_CEN	0.128284	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.128284
4860	PREC	-0.02927	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0

4860	TEMP	0.01638	Common Raven	FALSE	FALSE	FALSE	TRUE	Increased	0.01638
4900	BIOCLIM	-0.00612	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0
4900	EXTRE	-0.10548	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0
4900	LC_CEN	0.050005	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0.050005
4900	PREC	-0.1057	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0
4900	TEMP	-0.13274	Fish Crow	TRUE	FALSE	FALSE	TRUE	Increased	0
5120	BIOCLIM	0.185072	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.185072
5120	EXTRE	0.026136	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.026136
5120	LC_CEN	-0.19591	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0
5120	PREC	0.202739	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.202739
5120	TEMP	0.009449	Great-tailed Grackle	FALSE	FALSE	FALSE	TRUE	Increased	0.009449
5930	BIOCLIM	0.340832	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.340832
5930	EXTRE	0.406515	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.406515
5930	LC_CEN	0.126437	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.126437
5930	PREC	0.105311	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.105311
5930	TEMP	0.392576	Northern Cardinal	TRUE	FALSE	FALSE	TRUE	Increased	0.392576
5940	BIOCLIM	-0.22529	Pyrrhuloxia	TRUE	FALSE	FALSE	TRUE	Decreased	0
5940	EXTRE	-0.33849	Pyrrhuloxia	TRUE	FALSE	FALSE	TRUE	Decreased	0
5940	LC_CEN	0.165356	Pyrrhuloxia	TRUE	FALSE	FALSE	TRUE	Decreased	0.165356
5940	PREC	-0.18941	Pyrrhuloxia	TRUE	FALSE	FALSE	TRUE	Decreased	0
5940	TEMP	-0.47723	Pyrrhuloxia	TRUE	FALSE	FALSE	TRUE	Decreased	0
7030	BIOCLIM	0.110471	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.110471
7030	EXTRE	0.068686	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.068686
7030	LC_CEN	0.047739	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.047739

			rd						
7030	PREC	0.11801	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.11801
7030	TEMP	0.065842	Northern Mockingbird	TRUE	FALSE	FALSE	FALSE	Decreased	0.065842
7180	BIOCLIM	0.319344	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.319344
7180	EXTRE	0.191658	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.191658
7180	LC_CEN	0.314354	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.314354
7180	PREC	0.207495	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.207495
7180	TEMP	0.236358	Carolina Wren	TRUE	FALSE	FALSE	TRUE	Increased	0.236358
7270	BIOCLIM	0.05851	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.05851
7270	EXTRE	0.001334	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.001334
7270	LC_CEN	0.19966	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.19966
7270	PREC	0.003442	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0.003442
7270	TEMP	-0.03547	White-breasted Nuthatch	FALSE	FALSE	TRUE	FALSE	Increased	0
7290	BIOCLIM	-0.02599	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	0
7290	EXTRE	-0.01815	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	0
7290	LC_CEN	0.179951	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	0.179951
7290	PREC	0.012687	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	0.012687
7290	TEMP	0.015514	Brown-headed Nuthatch	TRUE	FALSE	TRUE	FALSE	Stable	0.015514
7310	BIOCLIM	0.512956	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.512956
7310	EXTRE	0.372111	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.372111

7310	LC_CEN	0.123002	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.123002
7310	PREC	0.320478	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.320478
7310	TEMP	0.468715	Tufted Titmouse	TRUE	FALSE	TRUE	FALSE	Increased	0.468715
7350	BIOCLIM	0.009592	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	0.009592
7350	EXTRE	0.15581	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	0.15581
7350	LC_CEN	-0.14533	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	0
7350	PREC	0.045464	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	0.045464
7350	TEMP	0.093305	Black-capped Chickadee	FALSE	FALSE	TRUE	FALSE	Increased	0.093305
7360	BIOCLIM	0.050474	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0.050474
7360	EXTRE	-0.01219	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0
7360	LC_CEN	-0.01159	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0
7360	PREC	0.0773	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0.0773
7360	TEMP	0.079112	Carolina Chickadee	TRUE	FALSE	FALSE	FALSE	Decreased	0.079112
7410	BIOCLIM	-0.23526	Chestnut-backed Chickadee	FALSE	FALSE	TRUE	FALSE	Decreased	0
7410	EXTRE	-0.24129	Chestnut-backed Chickadee	FALSE	FALSE	TRUE	FALSE	Decreased	0
7410	LC_CEN	0.093445	Chestnut-backed Chickadee	FALSE	FALSE	TRUE	FALSE	Decreased	0.093445
7410	PREC	-0.47722	Chestnut-backed Chickadee	FALSE	FALSE	TRUE	FALSE	Decreased	0
7410	TEMP	-0.16779	Chestnut-backed Chickadee	FALSE	FALSE	TRUE	FALSE	Decreased	0
7430	BIOCLIM	0.010771	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	0.010771
7430	EXTRE	-0.06831	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	0
7430	LC_CEN	0.041112	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	0.041112
7430	PREC	-0.0937	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	0

7430	TEMP	-0.02483	Bushtit	FALSE	FALSE	TRUE	FALSE	Stable	0

Bibliography

- Alexander, L. V. et al. 2006. Global observed changes in daily climate extremes of temperature and precipitation. - *J. Geophys. Res. Atmospheres* 111: D05109.
- Anderson, T. W. 1994. *The Statistical Analysis of Time Series*. - Wiley-Interscience.
- Andrle, R. F. and Carroll, J. R. 1988. *The atlas of breeding birds in New York State*. - Cornell University Press.
- Araújo, M. B. and Pearson, R. G. 2005. Equilibrium of species' distributions with climate. - *Ecography* 28: 693–695.
- Baatz, M. et al. 2003. *eCognition user guide*. - Defini. Imaging GmbH in press.
- Baccini, A. et al. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. - *Nat. Clim. Change* 2: 182–185.
- Bailey, R. G. 1995. *Description of the Ecoregions of the United States: Miscellaneous Publication*.
- Barbet-Massin, M. and Jetz, W. 2014. A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. - *Divers. Distrib.* 20: 1285–1295.
- Barker, R. J. and Sauer, J. R. 1992. Modelling Population Change From Time Series Data. - In: McCullough, D. R. and Barrett, R. H. (eds), *Wildlife 2001: Populations*. Springer Netherlands, pp. 182–194.
- Batschelet, E. 1981. *Circular statistics in biology*. - Academic Press.
- Beever, E. A. et al. 2003. Patterns of Apparent Extirpation among Isolated Populations of Pikas (*Ochotona princeps*) in the Great Basin. - *J. Mammal.* 84: 37–54.
- Bergen, K. M. et al. 2007. Multi-dimensional vegetation structure in modeling avian habitat. - *Ecol. Inform.* 2: 9–22.
- Bergen, K. M. et al. 2009. Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for lidar and radar spaceborne missions. - *J. Geophys. Res.* in press.
- Biau, G. 2012. Analysis of a Random Forests Model. - *J Mach Learn Res* 98888: 1063–1095.
- Bled, F. et al. 2011. Hierarchical modeling of an invasive spread: the Eurasian Collared-Dove *Streptopelia decaocto* in the United States. - *Ecol. Appl. Publ. Ecol. Soc. Am.* 21: 290–302.
- Bled, F. et al. 2013. Modeling Trends from North American Breeding Bird Survey Data: A Spatially Explicit Approach. - *PLoS ONE* 8: e81867.

- Boulinier, T. et al. 1998. Higher temporal variability of forest breeding bird communities in fragmented landscapes. - *Proc. Natl. Acad. Sci. U. S. A.* 95: 7497–7501.
- Brauning, D. W. et al. 1992. Atlas of breeding birds in Pennsylvania. - University of Pittsburgh Press.
- Braunisch, V. et al. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. - *Ecography* 36: 971–983.
- Breiman, L. 1996. Bagging predictors. - *Mach. Learn.* 24: 123–140.
- Breiman, L. 2001. Random Forests. - *Mach. Learn.* 45: 5–23.
- Brennan, L. A. et al. 2005. Invited paper: north american grassland birds: an unfolding conservation crisis? - *J. Wildl. Manag.* 69: 1–13.
- Brewer, R. et al. 1991. The atlas of breeding birds of Michigan. - Mich. State Univ. Press East Lansing Miusa 1991 in press.
- Brooks, T. M. et al. 2002. Habitat Loss and Extinction in the Hotspots of Biodiversity. - *Conserv. Biol.* 16: 909–923.
- Broughton, R. K. et al. 2006. Marsh Tit *Poecile palustris* territories in a British broad-leaved wood. - *Ibis* 148: 744–752.
- Brown, J. H. et al. 1996. The Geographic Range: Size, Shape, Boundaries, and Internal Structure. - *Annu. Rev. Ecol. Syst.* 27: 597–623.
- Burnham, K. P. and Overton, W. S. 1978. Estimation of the Size of a Closed Population When Capture Probabilities Vary Among Animals. - *Biometrika* 65: 625–633.
- Burnham, K. P. and Overton, W. S. 1979. Robust Estimation of Population Size When Capture Probabilities Vary Among Animals. - *Ecology* 60: 927–936.
- Cavanaugh, K. C. et al. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. - *Proc. Natl. Acad. Sci.* 111: 723–727.
- Chen, I.-C. et al. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. - *Science* 333: 1024–1026.
- Coburn, C. A. and Roberts, A. C. B. 2004. A multiscale texture analysis procedure for improved forest stand classification. - *Int. J. Remote Sens.* 25: 4287–4308.
- Cody, M. L. 1974. Competition and the Structure of Bird Communities. - Princeton University Press.
- Colwell, R. K. et al. 2004. The mid-domain effect and species richness patterns: what have we learned so far? - *Am. Nat.* 163: E1–23.

- Crozier, L. 2003. Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. - *Oecologia* 135: 648–656.
- Culbert, P. D. et al. 2012. Modeling broad-scale patterns of avian species richness across the Midwestern United States with measures of satellite image texture. - *Remote Sens. Environ.* 118: 140–150.
- Culbert, P. D. et al. 2013. The Influence of Vertical and Horizontal Habitat Structure on Nationwide Patterns of Avian Biodiversity. - *The Auk* 130: 656–665.
- Currie, D. J. et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. - *Ecol. Lett.* 7: 1121–1134.
- Darwish, A. et al. 2003. Image segmentation for the purpose of object-based classification. - *Geosci. Remote Sens. Symp. 2003 IGARSS 03 Proc. 2003 IEEE Int.* 3: 2039–2041.
- Davies, R. G. et al. 2007. Topography, energy and the global distribution of bird species richness. - *Proc. R. Soc. B Biol. Sci.* 274: 1189–1197.
- Dhondt, A. A. et al. 1998. Epidemic mycoplasmal conjunctivitis in house finches from eastern North America. - *J. Wildl. Dis.* 34: 265–280.
- Donald, P. F. et al. 2007. International Conservation Policy Delivers Benefits for Birds in Europe. - *Science* 317: 810–813.
- Donovan, T. M. and Flather, C. H. 2002. Relationships among North American Songbird Trends, Habitat Fragmentation, and Landscape Occupancy. - *Ecol. Appl.* 12: 364–374.
- Duro, D. C. et al. 2007. Development of a large area biodiversity monitoring system driven by remote sensing. - *Prog. Phys. Geogr.* 31: 235–260.
- Easterling, T. et al. 1999. United States Historical Climatology Network Daily Temperature, Precipitation, and Snow Data for 1871–1997.
- Easterling, D. R. et al. 2000. Climate Extremes: Observations, Modeling, and Impacts. - *Science* 289: 2068–2074.
- Efron, B. 1987. Better Bootstrap Confidence Intervals. - *J. Am. Stat. Assoc.* 82: 171–185.
- Elliott, J. J. and Arbib, R. S., Jr. 1953. Origin and Status of the House Finch in the Eastern United States. - *The Auk* 70: 31–37.
- Environmental Systems Research Institute 1999. Arc GIS.
- Evans, K. L. et al. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. - *Biol. Rev. Camb. Philos. Soc.* 80: 1–25.
- Exelis Visual Information Solutions Boulder, Colorado. ENVI. - Exelis Visual Information Solutions.

- Fagan, W. E. et al. 1999. How habitat edges change species interactions. - *Am. Nat.* 153: 165–182.
- Franklin, S. E. et al. 2000. Incorporating texture into classification of forest species composition from airborne multispectral images. - *Int. J. Remote Sens.* 21: 61–79.
- Fry, J. A. et al. 2009. Completion of the National Land Cover Database (NLCD) 1992-2001 land cover change retrofit product.
- Gaston, K. J. 2000. Global patterns in biodiversity. - *Nature* 405: 220–227.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges.* - Oxford University Press.
- Gaston, K. J. and Spicer, J. I. 2004. *Biodiversity: An Introduction.* - Wiley-Blackwell.
- Gaston, K. J. et al. 2003. Habitat conversion and global avian biodiversity loss. - *Proc. R. Soc. Lond. B Biol. Sci.* 270: 1293–1300.
- Gear, A. J. and Huntley, B. 1991. Rapid changes in the range limits of scots pine 4000 years ago. - *Science* 251: 544–547.
- Gillings, S. et al. 2015. Directionality of recent bird distribution shifts and climate change in Great Britain. - *Glob. Change Biol.* 21: 2155–2168.
- Girvetz, E. H. and Greco, S. E. 2007. How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. - *Landsc. Ecol.* 22: 1131–1142.
- Goetz, S. et al. 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. - *Remote Sens. Environ.* 108: 254–263.
- Goetz, S. J. et al. 2010. Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. - *Ecology* 91: 1569–1576.
- Goetz, S. J. et al. 2014. The relative importance of climate and vegetation properties on patterns of North American breeding bird species richness. - *Environ. Res. Lett.* 9: 034013.
- Good, R. D. 1931. *A Theory of Plant Geography.* - *New Phytol.* 30: 149–149.
- Gould, W. 2000. Remote Sensing of Vegetation, Plant Species Richness, and Regional Biodiversity Hotspots. - *Ecol. Appl.* 10: 1861–1870.
- Griffith, E. H. et al. 2010. Traffic Effects on Bird Counts on North American Breeding Bird Survey Routes. - *The Auk* 127: 387–393.
- Griffiths, G. H. and Lee, J. 2000. Landscape pattern and species richness; regional scale analysis from remote sensing. - *Int. J. Remote Sens.* 21: 2685–2704.
- Guégan, J.-F. et al. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. - *Nature* 391: 382–384.

- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. - *Ecol. Model.* 135: 147–186.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. - *Ecol. Lett.* 8: 993–1009.
- Hagan, J. M. et al. 1996. The Early Development of Forest Fragmentation Effects on Birds. - *Conserv. Biol.* 10: 188–202.
- Halaj, J. et al. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. - *Oikos* 90: 139–152.
- Hamza, M. and Larocque, D. 2005. An empirical comparison of ensemble methods based on classification trees. - *J. Stat. Comput. Simul.* 75: 629–643.
- Haralick, R. M. et al. 1973. Textural Features for Image Classification. - *Syst. Man Cybern. IEEE Trans. On* 3: 610–621.
- Harding, B. D. 1979. Bedfordshire bird atlas. - *Beds. Nat. Hist. Soc.* Kettering in press.
- Hawkins, B. A. et al. 2003. Energy, Water, and Broad-Scale Geographic Patterns of Species Richness. - *Ecology* 84: 3105–3117.
- Hawkins, B. A. et al. 2007. Climate, niche conservatism, and the global bird diversity gradient. - *Am. Nat.* 170: S16–S27.
- Helzer, C. J. and Jelinski, D. E. 1999. The Relative Importance of Patch Area and Perimeter–Area Ratio to Grassland Breeding Birds. - *Ecol. Appl.* 9: 1448–1458.
- Hickling, R. et al. 2005. A northward shift of range margins in British Odonata. - *Glob. Change Biol.* 11: 502–506.
- Hickling, R. et al. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. - *Glob. Change Biol.* 12: 450–455.
- Hijmans, R. J. and Graham, C. H. 2006. The Ability of Climate Envelope Models to Predict the effect of Climate Change on Species Distributions. - *Glob. Change Biol.* 12: 2272–2281.
- Hijmans, R. J. et al. 2015. *dismo: Species Distribution Modeling.*
- Hill, J. K. et al. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. - *Proc. R. Soc. Lond. B Biol. Sci.* 266: 1197–1206.
- Hill, R. A. et al. 2004. Predicting habitat quality for Great Tits (*Parus major*) with airborne laser scanning data. - *Int. J. Remote Sens.* 25: 4851–4855.
- Hines, J. E. et al. 1999. COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. - *Bird Study* 46: 209–217.
- Hinsley, S. A. et al. 2009. Bird species distributions across woodland canopy structure gradients. - *Community Ecol.* 10: 99–110.

- Hitch, A. T. and Leberg, P. L. 2007. Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change. - *Conserv. Biol.* 21: 534–539.
- Hochachka, W. M. and Dhondt, A. A. 2000. Density-dependent decline of host abundance resulting from a new infectious disease. - *Proc. Natl. Acad. Sci.* 97: 5303–5306.
- Holmes, R. T. 2007. Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. - *Ibis* 149: 2–13.
- Holmes, R. T. and Sherry, T. W. 2001. Thirty-Year Bird Population Trends in an Unfragmented Temperate Deciduous Forest: Importance of Habitat Change. - *The Auk* 118: 589.
- Homer, C. et al. 2015. Completion of the 2011 National Land Cover Database for the Conterminous United States - Representing a Decade of Land Cover Change Information. - *Photogramm. Eng. Remote Sens.* 81: 345–354.
- Huang, Q. et al. 2014. The Influence of Vegetation Height Heterogeneity on Forest and Woodland Bird Species Richness across the United States. - *PLoS ONE* 9: e103236.
- Huang, Q. et al. 2015. A centroid model of species distribution with applications to the Carolina wren *Thryothorus ludovicianus* and house finch *Haemorhous mexicanus* in the United States. - *Ecography*: n/a–n/a.
- Hurlbert, A. H. and Haskell, J. P. 2003. The Effect of Energy and Seasonality on Avian Species Richness and Community Composition. - *Am. Nat.* 161: 83–97.
- Imhoff, M. L. et al. 1997. Remotely sensed indicators of habitat heterogeneity: Use of synthetic aperture radar in mapping vegetation structure and bird habitat. - *Remote Sens. Environ.* 60: 217–227.
2014. Climate Change 2013 - The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, Ed.). - Cambridge University Press.
- Jeffree, E. P. and Jeffree, C. E. 1994. Temperature and the Biogeographical Distributions of Species. - *Funct. Ecol.* 8: 640–650.
- Karl, T. R. et al. 1999. CLIVAR/GCOS/WMO Workshop on Indices and Indicators for Climate Extremes Workshop Summary. - In: Karl, T. R. et al. (eds), *Weather and Climate Extremes*. Springer Netherlands, pp. 3–7.
- Keller, C. M. E. and Scallan, J. T. 1999. Potential Roadside Biases Due to Habitat Changes along Breeding Bird Survey Routes. - *The Condor* 101: 50–57.
- Kellndorfer, J. M. et al. 2010. Statistical fusion of lidar, InSAR, and optical remote sensing data for forest stand height characterization: A regional-scale method based on LVIS, SRTM, Landsat ETM+, and ancillary data sets. - *J. Geophys. Res.* in press.
- Kellndorfer, J. et al. 2011. National Biomass and Carbon Dataset for the Year 2000.

- Kelly, J. 1993. The Effect of Nest Predation on Habitat Selection by Dusky Flycatchers. - *Condor* 95: 83–93.
- Kendall, W. L. et al. 1996. First-Time Observer Effects in the North American Breeding Bird Survey. - *The Auk* 113: 823–829.
- Kerr, J. T. and Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. - *Nature* 385: 252–254.
- Kerr, J. T. et al. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. - *Proc. Natl. Acad. Sci.* 98: 11365–11370.
- Kéry, M. 2010. Introduction to WinBUGS for ecologists Bayesian approach to regression, ANOVA, mixed models and related analyses. - Elsevier.
- Kéry, M. and Schmid, H. 2004. Monitoring programs need to take into account imperfect species detectability. - *Basic Appl. Ecol.* 5: 65–73.
- Koh, C.-N. et al. 2006. Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. - *Divers. Distrib.* 12: 546–554.
- La Sorte, F. A. and Thompson, F. R. I. 2007. Poleward Shifts in Winter Ranges of North American Birds. - *Ecology* 88: 1803–1812.
- La Sorte, F. A. and Jetz, W. 2012. Tracking of climatic niche boundaries under recent climate change. - *J. Anim. Ecol.* 81: 914–925.
- La Sorte, F. A. et al. 2013. Population-level scaling of avian migration speed with body size and migration distance for powered fliers. - *Ecology* 94: 1839–1847.
- Lawler, J. J. et al. 2006. Predicting climate-induced range shifts: model differences and model reliability. - *Glob. Change Biol.* 12: 1568–1584.
- Lefsky, M. A. et al. 2002. Lidar Remote Sensing for Ecosystem Studies. - *BioScience* 52: 19.
- Lenoir, J. et al. 2008. A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. - *Science* 320: 1768–1771.
- Liaw, A. and Wiener, M. 2002. Classification and Regression by randomForest. - *R News* 2: 18–22.
- Link, W. A. and Sauer, J. R. 1998. Estimating Population Change from Count Data: Application to the North American Breeding Bird Survey. - *Ecol. Appl.* 8: 258–268.
- Link, W. A. and Sauer, J. R. 2002. A Hierarchical Analysis of Population Change with Application to Cerulean Warblers. - *Ecology* 83: 2832–2840.
- Link, W. A. and Sauer, J. R. 2007. Seasonal Components of Avian Population Change: Joint Analysis of Two Large-Scale Monitoring Programs. - *Ecology* 88: 49–55.
- Loarie, S. R. et al. 2009. The velocity of climate change. - *Nature* 462: 1052–1055.

- Lunn, D. J. et al. 2000. WinBUGS- A Bayesian Modelling Framework: Concepts, Structure, and Extensibility. - *Stat. Comput.* 10: 325–337.
- Luoto, M. et al. 2004. Predicting Bird Species Richness Using Remote Sensing in Boreal Agricultural-Forest Mosaics. - *Ecol. Appl.* 14: 1946–1962.
- MacArthur, R. H. and MacArthur, J. W. 1961. On Bird Species Diversity. - *Ecology* 42: 594–598.
- Maclean, I. M. D. et al. 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. - *Glob. Change Biol.* 14: 2489–2500.
- Martínez-Meyer, E. et al. 2004. Ecological Niches as Stable Distributional Constraints on Mammal Species, with Implications for Pleistocene Extinctions and Climate Change Projections for Biodiversity. - *Glob. Ecol. Biogeogr.* 13: 305–314.
- McGarigal, K. et al. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. - University of Massachusetts.
- Mehlman, D. W. 1997. Change in Avian Abundance Across the Geographic Range in Response to Environmental Change. - *Ecol. Appl.* 7: 614–624.
- Menne, M. J. et al. 2009. The U.S. Historical Climatology Network Monthly Temperature Data, Version 2. - *Bull. Am. Meteorol. Soc.* 90: 993–1007.
- Midgley, G. F. et al. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. - *Divers. Distrib.* 12: 555–562.
- Minnesota Population Center 2011. National historical geographic information system: Version 2.0. - Minneap. MN Univ. Minn. in press.
- Morgan, K. and Freedman, B. 1985. Breeding Bird Communities in a Hardwood Forest Succession in Nova Scotia Canada. - *Can. Field Nat.* 100: 506–519.
- Nakicenovic, N. and Swart, R. 2000. Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change. - Cambridge University Press.
- Namias, J. 1978. Multiple Causes of the North American Abnormal Winter 1976–77. - *Mon. Weather Rev.* 106: 279–295.
- Niven, D. K. and Butcher, G. S. 2009. Northward Shifts in the Abundance of North American Birds in Early Winter: A Response to Warmer Winter Temperatures?
- North, M. P. et al. 1999. Forest Stand Structure of the Northern Spotted Owl's Foraging Habitat. - *For. Sci.* 45: 520–527.
- Oindo, B. O. and Skidmore, A. K. 2002. Interannual variability of NDVI and species richness in Kenya. - *Int. J. Remote Sens.* 23: 285–298.

- Palmer, M. W. 1994. Variation in species richness: Towards a unification of hypotheses. - *Folia Geobot. Phytotaxon.* 29: 511–530.
- Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. - *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Parmesan, C. and Yohe, G. 2003. A Globally Coherent Fingerprint of Climate Change Impacts Across Natural Systems. - *Nature* 421: 37–42.
- Parmesan, C. et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. - *Nature* 399: 579–583.
- Parmesan, C. et al. 2000. Impacts of Extreme Weather and Climate on Terrestrial Biota*. - *Bull. Am. Meteorol. Soc.* 81: 443–450.
- Pau, G. et al. 2010. EBImage—an R package for image processing with applications to cellular phenotypes. - *Bioinformatics* 26: 979–981.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the Impacts of Climate Change on the Distribution of Species: Are Bioclimate Envelope Models Useful? - *Glob. Ecol. Biogeogr.* 12: 361–371.
- Pereira, H. M. et al. 2010. Scenarios for Global Biodiversity in the 21st Century. - *Science* 330: 1496–1501.
- Peterjohn, B. and Sauer, J. R. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey.: 27–44.
- Phillips, L. B. et al. 2008. Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production. - *Remote Sens. Environ.* 112: 4381–4392.
- Pidgeon, A. M. et al. 2007. Associations of Forest Bird Species Richness with Housing and Landscape Patterns across the USA. - *Ecol. Appl.* 17: 1989–2010.
- Pollard, E. 1979. Population ecology and change in range of the white admiral butterfly *Ladoga Camilla L.* in England. - *Ecol. Entomol.* 4: 61–74.
- Pounds, J. A. et al. 1999. Biological response to climate change on a tropical mountain. - *Nature* 398: 611–615.
- Rahbek, C. and Graves, G. R. 2001. Multiscale assessment of patterns of avian species richness. - *Proc. Natl. Acad. Sci.* 98: 4534–4539.
- Rahbek, C. et al. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. - *Proc. R. Soc. B Biol. Sci.* 274: 165–174.
- R Development Core Team 2011. R: A Language and Environment for Statistical Computing. - R Foundation for Statistical Computing.

- Reilly, J. et al. 2001. Climate Change. Uncertainty and Climate Change Assessments. - *Science* 293: 430–433.
- Richerson, P. J. and Lum, K. 1980. Patterns of plant species diversity in California: relation to weather and topography. - *Am. Nat.*: 504–536.
- Rittenhouse, C. D. et al. 2010. Avifauna response to hurricanes: regional changes in community similarity. - *Glob. Change Biol.* 16: 905–917.
- Rittenhouse, C. D. et al. 2012. Land-cover change and avian diversity in the conterminous United States. - *Conserv. Biol. J. Soc. Conserv. Biol.* 26: 821–829.
- Robbins, C. S. ;Bystrak 1986. The breeding bird survey: its first fifteen years, 1965-1979. - *Resour. Publ. US Fish Wildl. Serv.* in press.
- Robbins, C. S. et al. 1986. The breeding bird survey: its first fifteen years, 1965-1979. - U.S. Dept. of the Interior, Fish and Wildlife Service.
- Robbins, C. S. et al. 1989a. Habitat Area Requirements of Breeding Forest Birds of the Middle Atlantic States. - *Wildl. Monogr.*: 3–34.
- Robbins, C. S. et al. 1989b. Population declines in North American birds that migrate to the neotropics. - *Proc. Natl. Acad. Sci.* 86: 7658 –7662.
- Robinson, S. K. and Holmes, R. T. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. - *The Auk* 101: 672–684.
- Root, T. 1988. Environmental Factors Associated with Avian Distributional Boundaries. - *J. Biogeogr.* 15: 489–505.
- Root, T. L. et al. 2003. Fingerprints of global warming on wild animals and plants. - *Nature* 421: 57–60.
- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time.* - Cambridge University Press.
- Royle, J. A. and Link, W. A. 2006. Generalized site occupancy models allowing for false positive and false negative errors. - *Ecology* 87: 835–841.
- Royle, J. A. and Kéry, M. 2007. A bayesian state-space formulation of dynamic occupancy models. - *Ecology* 88: 1813–1823.
- Saatchi, S. S. et al. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. - *Proc. Natl. Acad. Sci.* 108: 9899–9904.
- Sagarin, R. D. et al. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. - *Trends Ecol. Evol.* 21: 524–530.
- Santelmann, M. V. 1991. Influences on the Distribution of *Carex Exilis*: An Experimental Approach. - *Ecology* 72: 2025–2037.

- Sauer, J. R. et al. 1994. Observer Differences in the North American Breeding Bird Survey. - *The Auk* 111: 50–62.
- Sauer, J. R. et al. 1995. Mapping of bird distributions from point count surveys.: 151–160.
- Sauer, J. R. et al. 1996. Evaluating Causes of Population Change in North American Insectivorous Songbirds. - *Conserv. Biol.* 10: 465–478.
- Sauer, J. R. et al. 2003. Use of North American Breeding Bird Survey Data to Estimate Population Change for Bird Conservation Regions. - *J. Wildl. Manag.* 67: 372–389.
- Sauer, J. R. et al. 2011. The North American Breeding Bird Survey, Results and Analysis 1966 - 2010.
- Sauer, J. R. et al. 2014. The North American breeding bird survey, results and analysis 1966-2013. - Version 5: 2008.
- Schiewe, J. 2002. Segmentation of high-resolution remotely sensed data – concepts, applications and problems. - *Symp. Geospatial Theory Process. Appl.*
- Seto, K. C. et al. 2004. Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI. - *Int. J. Remote Sens.* 25: 4309–4324.
- Sharrock, J. T. R. 2010. The atlas of breeding birds in Britain and Ireland. - A&C Black.
- Sillmann, J. and Roeckner, E. 2007. Indices for extreme events in projections of anthropogenic climate change. - *Clim. Change* 86: 83–104.
- Sillmann, J. et al. 2013. Climate extremes indices in the CMIP5 multimodel ensemble: Part 1. Model evaluation in the present climate. - *J. Geophys. Res. Atmospheres* 118: 1716–1733.
- Songer, M. et al. 2012. Modeling Impacts of Climate Change on Giant Panda Habitat. - *Int. J. Ecol.* 2012: 1–12.
- Spiegelhalter, D. et al. 2003. WinBUGS user manual. - MRC Biostat. Unit in press.
- St-Louis, V. et al. 2006. High-resolution image texture as a predictor of bird species richness. - *Remote Sens. Environ.* 105: 299–312.
- St-Louis, V. et al. 2009. Satellite image texture and a vegetation index predict avian biodiversity in the Chihuahuan Desert of New Mexico. - *Ecography* 32: 468–480.
- Strelke, W. K. and Dickson, J. G. 1980. Effect of Forest Clear-Cut Edge on Breeding Birds in East Texas. - *J. Wildl. Manag.* 44: 559–567.
- Sturtz, S. et al. 2005. R2WinBUGS: A Package for Running WinBUGS from R. - *J. Stat. Softw.*: 1–16.
- Swatantran, A. et al. 2012. Mapping Migratory Bird Prevalence Using Remote Sensing Data Fusion. - *PLoS ONE* 7: e28922.

- Thomas, C. D. and Lennon, J. J. 1999. Birds extend their ranges northwards. - *Nature* 399: 213–213.
- Thompson, K. R. and Page, F. H. 1989. Detecting Synchrony of Recruitment using Short, Autocorrelated Time Series. - *Can. J. Fish. Aquat. Sci.* 46: 1831–1838.
- Thuiller, W. et al. 2006. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. - *Glob. Change Biol.* 12: 424–440.
- Tingley, M. W. et al. 2009. Birds track their Grinnellian niche through a century of climate change. - *Proc. Natl. Acad. Sci.* 106: 19637–19643.
- Turner, J. R. G. et al. 1988. British bird species distributions and the energy theory. - *Nature* 335: 539–541.
- United States Forest Service 2001. U.S. forest facts and historical trends. - U.S. Dept. of Agriculture, Forest Service.
- US Census Bureau 2010. Center of Population, US Census Bureau 2010 Census.
- U.S. Geological Survey 2012. List of Species Groupings.
- VanDerWal, J. et al. 2011. SDMTTools: Species distribution modelling tools: Tools for processing data associated with species distribution modelling exercises. - R Package Version in press.
- VanDerWal, J. et al. 2013. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. - *Nat. Clim. Change* 3: 239–243.
- Van Rossum, F. et al. 1997. Allozyme variation in relation to ecotypic differentiation and population size in marginal populations of *Silene nutans*. - *Heredity* 78: 552.
- Vavrek, M. J. 2011. fossil: palaeoecological and palaeogeographical analysis tools. - *Palaeontol. Electron.* 14: 1T.
- Veit, R. R. and Lewis, M. A. 1996. Dispersal, Population Growth, and the Allee Effect: Dynamics of the House Finch Invasion of Eastern North America. - *Am. Nat.* 148: 255–274.
- Vitousek, P. M. et al. 1997. Human Domination of Earth's Ecosystems. - *Science* 277: 494–499.
- Waide, R. B. et al. 1999. The Relationship Between Productivity and Species Richness. - *Annu. Rev. Ecol. Syst.* 30: 257–300.
- Walker, W. S. et al. 2007. An empirical InSAR-optical fusion approach to mapping vegetation canopy height. - *Remote Sens. Environ.* 109: 482–499.
- Walther, G.-R. et al. 2002. Ecological responses to recent climate change. - *Nature* 416: 389–395.
- Wei, C.-L. et al. 2010. Global Patterns and Predictions of Seafloor Biomass Using Random Forests. - *PLoS ONE* 5: e15323.

- Whitehurst, A. S. et al. 2013. Characterization of Canopy Layering in Forested Ecosystems Using Full Waveform Lidar. - *Remote Sens.* 5: 2014–2036.
- Whittaker, R. J. et al. 2001. Scale and Species Richness: Towards a General, Hierarchical Theory of Species Diversity. - *J. Biogeogr.* 28: 453–470.
- Williams, Jr., C. N. et al. 2006. U.S. HISTORICAL CLIMATOLOGY NETWORK (USHCN): Daily Temperature, Precipitation, and Snow Data.
- Williamson, K. 1975. Birds and climatic change. - *Bird Study* 22: 143–164.
- Willig, M. R. et al. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. - *Annu. Rev. Ecol. Evol. Syst.*: 273–309.
- Zellweger, F. et al. 2013. Remotely sensed forest structural complexity predicts multi species occurrence at the landscape scale. - *For. Ecol. Manag.* 307: 303–312.