# MACROECOLOGY OF BREEDING BIRDS OF NEW YORK STATE. INFLUENCES OF CLIMATE CHANGE, LANDSCAPE MATRIX, AND SPATIAL SCALE.

By

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## A DISSERTATION

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#### ABSTRACT

## MACROECOLOGY OF BREEDING BIRDS OF NEW YORK STATE. INFLUENCES OF CLIMATE CHANGE, LANDSCAPE MATRIX, AND SPATIAL SCALE.

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Climate change has the potential to greatly affect biodiversity and there is convincing evidence that most taxonomic groups are already responding to the recent climate warming. Even though the impacts of climate change on biodiversity are felt across a wide range of ecosystems, the severity and sometimes the direction of these impacts are likely to differ across space because factors other than climate will influence how biodiversity responds to climate change. For example, composition and configuration of land cover may play significant roles in the relative vulnerabilities of biodiversity to changing climate. However, despite some initial investigations, empirical evidence for the influence of land cover is lacking because studies that integrate both land cover and climate are rare. The overarching goal of my dissertation was to assess the relative roles of climate change and land cover in the observed changes in avian biodiversity. Specifically, I was interested in the influences of land-cover composition and configuration on relative vulnerabilities of different avian groups to climate change and spatial scales at which such influences are relevant. Chapter 1 focuses on testing the utility of the spatially-varying coefficients (SVC) model to quantify the influence of non-stationarity on relationships between temporal community change in avian assemblages and environmental covariates. Chapter 2 investigates bioclimatic relationships of grassland and forest breeding birds across varying gradients of grassland and forest habitat. Chapter 3 investigates the relationship between temporal changes in avian assemblages and the interaction of climate change and land-cover fragmentation. Chapter 4 explores scale-dependence of temporal changes in avian communities

and investigates relevant environmental drivers of the community change at different spatial scales.

The collective works in these chapters contribute four primary conclusions for better understanding of the implications of the interaction of land use and climate change to avian diversity. First, relationships between changes in biodiversity and environmental factors are often spatially non-stationary, i.e., the relationship between a response variable and the predictor covariates varies across the spatial extent of the study. Second, the amount of suitable land cover can significantly alter species responses to climate change, but this effect of land cover depends on the type of habitat. Third, impacts of climate change on ecological communities are more pronounced in regions of unfragmented landscapes than in locations with fragmented habitats. Fourth, temporal changes in community composition are scale-dependent and so are the mechanisms driving these changes. Specifically, climate change operates at smaller spatial scales than landscape fragmentation.

The implications of these findings suggest that current conservation strategies may be insufficient to protect biodiversity in the face of climate change. Existing biodiversity conservation generally focuses on conserving large regions with undisturbed and contiguous habitats that generally support high species diversity. My results suggest that ecological communities of such habitats will undergo the most drastic compositional changes as a result of climate change. Thus, it is critical that the existing conservation strategies are placed in the context of climate change. My work suggests that successful biodiversity conservation needs to consider both the individual species' vulnerabilities to climate change based on their habitat association or life-history strategies and relative vulnerabilities of entire communities based on the landscape in which these communities persist.

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#### PROLOGUE

Climate change has potential to greatly affect biodiversity and there is convincing evidence that most taxonomic groups are already responding to the recent climate warming (e.g., Jarzyna et al. 2013). Among those ecological responses most often reported are shifting population sizes and distributions (Jiguet et al. 2010, Zuckerberg et al. 2009), changes in breeding performance (Ahola et al. 2009, Husby et al. 2009), and changes in the timing of breeding (Root et al. 2003, Dunn and Winkler 2010), migration (Jones and Cresswell 2010, Tottrup et al. 2010), and hibernation (Inouye et al. 2000). However, even though the impacts of climate change on biodiversity are felt across a wide range of ecosystems, the severity and sometimes the direction of these impacts are bound to differ across space because factors other than climate will influence how biodiversity responds to climate change. Land cover is among the main factors with the potential to alter biodiversity's responses to climate change.

National Aeronautics and Space Administration (NASA) became interested in assessing the roles of recent climatic and land cover changes in observed landscape-scale shifts in biodiversity and an evaluation of the relative contributions of each as well as their interaction. Indeed, research conducted to date suggests that land cover plays a significant role in the relative vulnerabilities of biodiversity to changing climate. For example, simulation studies have shown that habitat loss reduces species ability to adjust to changing climatic conditions and thus exacerbate the detrimental effects of climate change (Travis 2003). Similarly, an increase in the amount of habitat has been shown to slow down species extinction rates associated with changing climate (Jeltsch et al. 2011). Habitat fragmentation is also thought to influence species responses to climate change by affecting the rate of distributional shifts, allowing species in less fragmented habitats to disperse faster and farther (Opdam and Wascher 2004). However, despite

these initial investigations, empirical evidence is lacking because studies that integrate both land cover and climate are rare.

The overarching goal of my dissertation was to assess the relative roles of climate change and land cover in the observed changes in avian biodiversity. Specifically, I was interested in the influences of land-cover composition and configuration on relative vulnerabilities of different avian groups to climate change and spatial scales at which such influences are relevant. I used the 1980 and 2000 New York State Breeding Bird Atlas. All chapters for this research were conducted with approval of the Michigan State University, Institutional Animal Care and Use Committee for use of digital records (approval date 11-01-2013).

Chapter 1 focuses on testing the utility of the spatially-varying coefficients (SVC) model to quantify the influence of non-stationarity on relationships between temporal community change in avian assemblages and changes in climate and land cover. This chapter has been accepted for the publication in Ecography. Spatial non-stationarity is present when the strength and nature of the relationship between a response variable and the predictor covariates vary across the spatial domain (Fortin and Dale 2009, Miller 2012). This spatial variation might be produced by interactions or feedbacks among covariates or presence of inherently different mechanisms that impact the outcome in different parts of the study region (Miller 2012). Given the ubiquity of space-varying relationships in nature (e.g., Bini et al. 2009), it is often unrealistic to assume that relationships between biodiversity and changes in climate and land cover can be captured by a set of stationary regression coefficients (i.e., coefficients that are constant across space). My objective is to compare inferences drawn from the SVC models to that obtained from space-varying intercept models (i.e., models that account for spatial autocorrelation, but not spatial non-stationarity) and also models that do not acknowledge any spatial structure beyond

what is introduced by the covariates. If the SVC models are superior to the other two tested models, they will be incorporated in the subsequent chapters to account for spatial non-stationarity of ecological relationships.

Chapter 2 builds on Chapter 1 by incorporating SVC models to investigate bioclimatic relationships of grassland and forest breeding birds across varying gradients of grassland and forest habitat. Research suggests that the quantity and quality of available habitat might be important in shaping bioclimatic relationships of species and thus their responses to climate change (Opdam and Wascher 2004, Kampichler et al. 2012). For example, habitat loss has been shown to reduce species ability to adjust to changing climatic conditions and thus exacerbate the detrimental effects of climate change (Travis 2003, Jeltsch et al. 2011). Thus, we can expect the bioclimatic relationships of species to be altered by the amount of habitat within a landscape. Specifically, populations of the same species found in regions with abundant suitable cover should display weaker responses to climatic variability in comparison with populations found in regions characterized by less available habitat. Here, I explore whether an increasing amount of habitat affects avian responses to climatic variability and if the potential effect of more extensive habitat differs for birds inhabiting grassland and forest lands.

Chapter 3 extends the work done in Chapter 2 by focusing on temporal changes of entire communities. Specifically, it investigates the relationship between temporal changes in avian assemblages and the interaction of climate change and land-cover fragmentation. To date, the majority of research regarding the implications of climate change to biodiversity has focused on responses of individual species (e.g., La Sorte and Thompson 2007). Variation in the individual species responses is predicted to lead to disruptions of communities and ecosystems, but the complex nature of ecological interactions makes it difficult to extrapolate from the scales of

individuals and populations to the community or ecosystem level (Walther et al. 2002). Consequently, in order to fully understand consequences of climate change to ecological communities it is imperative that a direct link between changes in community composition and changes in climatic conditions is established. Furthermore, the relationship between community change and climate change will likely be influenced by the landscape matrix surrounding the community; thus, landscape context needs to be considered when quantifying responses of ecological communities to climate change. My objective is to investigate the relationship between temporal change in avian biodiversity and changes in climatic conditions, and to assess the role of landscape fragmentation as a factor affecting this relationship.

Chapter 4 builds on Chapter 3 by investigating temporal changes in avian assemblages across multiple spatial scales. Key biodiversity patterns vary with spatial scale of observation and mechanisms driving these patterns are inherently scale-dependent (e.g., Storch et al. 2004, Keil et al. 2011). Thus far, studies investigating scaling of biodiversity and the mechanisms relevant at each spatial scale have mostly focused on one time step. Measures of temporal changes in biodiversity have been commonly used as indicators of environmental change (e.g., Calvarheiro et al. 2013); thus, it is imperative that we understand how these measures depend on the spatial scale. Furthermore, in the advent of recent global change, a thorough investigation of mechanisms relevant to temporal biodiversity dynamics across spatial scales is perhaps more important than ever. My goal is to evaluate spatial scaling patterns of temporal changes in avian communities and investigate relevant environmental drivers of the community change at each of the investigated spatial scales.

The collective works in these four chapters improve our understanding of the impacts of climate change on avian biodiversity and the role that land-cover composition and configuration

play in the responses of birds to climate change. I believe that by establishing a link between climate change impacts on biodiversity and land cover, I provide a much-needed and major step in global change science.

## ACCOUNTING FOR THE SPACE-VARYING NATURE OF THE RELATIONSHIPS BETWEEN TEMPORAL COMMUNITY TURNOVER AND THE ENVIRONMENT

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## ABSTRACT

Non-spatial regression models are rarely adequate for exploring ecological phenomena, especially in settings where the processes operate at large spatial scales and when model covariates do not explain all variation present in the ecological response. Given the complexity of ecological processes, it is often unrealistic to assume a set of stationary regression coefficients can capture space-varying and scale-dependent relationships between covariates and an outcome variable. Spatially-varying coefficients (SVC) models fit within a Bayesian inferential framework provide a statistically robust method to explore potential space-varying and scaledependent impacts of covariates. My study objective was to assess the utility of SVC models for capturing non-stationary relationships between temporal community dynamics in avian assemblages and variation in environmental factors. I also wanted to compare the inference drawn from SVC models to that obtained from space-varying intercept models and also models that do not acknowledge any spatial structure beyond what is introduced by the covariates. My analysis examines the temporal turnover, expressed as a proportion, of avian communities across New York State, USA. Given the expected outcome is non-Gaussian, I detail a generalized linear model specification of the proposed model structures. My results show the SVC model outperformed the spatially-varying intercept and non-spatial models in terms of model fit and model predictive inference. Further, by fitting these models within a Bayesian inferential framework, I was able to make inferences about the spatial impact of covariates and other

process parameters, as well as obtain full posterior predictive inference about the rate of turnover at new, unobserved locations. I conclude that SVC models provide a flexible framework for exploring and accounting for non-stationary mechanisms driving ecological patterns.

## **1.1 INTRODUCTION**

Ecological relationships are often explored using non-spatial regression models, even though this method is rarely adequate in settings where ecological phenomena exhibit spatial structure that cannot be explained by model covariates (Cressie et al. 2009, Hoeting 2009). This is especially true for data collected and modeled across large-scale spatial domains where locations in close proximity will have similar outcomes, a phenomenon called spatial autocorrelation. Spatial autocorrelation is prevalent in ecology. For example, community composition at any given location is usually influenced by the species assemblage structure at surrounding localities and local environmental factors (Legendre 1993) resulting in species abundances being more similar than expected by chance in locations closer to each other (Lichstein et al. 2002). Ignoring such spatial autocorrelation results in dependence among model residuals, which violates assumptions of most regression models and can lead to erroneous parameter estimates and, ultimately, incorrect ecological inferences and predictions (Dormann et al. 2007, Hoeting 2009, Finley 2011).

Commonly, spatial autocorrelation in ecological phenomena is accommodated by adding a spatial random effect to the model mean. Such random effects are often specified to follow a multivariate normal distribution with a mean of zero and spatially structured covariance matrix. Such specifications provide local adjustment, with spatial structure, to the model intercept (Diggle et al. 1998, Banerjee et al. 2004). When the outcome is Gaussian, such spatially-varying intercept models can partition the residual variance into two components - spatial and non-

spatial. For a non-Gaussian outcome (e.g., binomial, Poisson), the residual error term is omitted from the model equation; thus, spatially-varying intercept models integrate all of the residual variance into the spatial component. Partitioning of residual uncertainty (for a Gaussian outcome) or attributing the residual uncertainty to a spatial process (for a non-Gaussian outcome) can improve inference, increase accuracy and precision of model predictions, and reveal missing covariates.

While adding a space-varying intercept to the model accounts for spatial dependency and often improves inference, it does not explicitly deal with spatial non-stationarity and its associated influence on model covariates. Spatial non-stationarity is present when the strength and nature of the relationship between a response variable and the predictor covariates vary across the spatial domain (Fortin and Dale 2009, Miller 2012). Interactions or feedbacks among unobserved and observed covariates or presence of inherently different mechanisms that impact the outcome in different parts of the study region can produce non-stationarity (Miller 2012). Non-stationary relationships are common in ecology (e.g., Bini et al. 2009). For example, Foody (2004) showed that the relationships between avian species richness and total annual precipitation, mean annual temperature and terrestrial land cover in sub-Saharan Africa were strongly non-stationary. Other large-scale studies support these findings (e.g., Grotan et al. 2009, Martin-Queller et al. 2011, McNew et al. 2013). Thus, given this complexity of ecological phenomena across large spatial scales, it is often unrealistic to assume a set of stationary regression coefficients (i.e., coefficients that are constant across space) can capture spacevarying and scale-dependent relationships between covariates and outcome variables (Finley 2011). In other words, a global ecological relationship is often affected by local processes yielding a heterogeneous pattern, and would be described more accurately by local model

parameter values that differ from the global values (Miller 2012). Ignoring spatial nonstationarity can have similar consequences to those resulting from ignoring spatial autocorrelation. In a strongly non-stationary system, estimates of model parameters and inferences and predictions resulting from models that do not adequately account for spatial heterogeneity are likely to be flawed. Despite the importance of the problem and apparent ubiquity of the space-varying nature of ecological phenomena, few methods provide an opportunity to evaluate and account for potential spatially varying relationships between ecological responses and environmental covariates. Bayesian spatially-varying coefficients (SVC) models are one of the more flexible and robust approaches for accommodating nonstationarity (Gelfand et al. 2003). SVC models use a valid probability model that affords full posterior inferences for model parameters and subsequent prediction of the outcome and covariate processes at any new location. While spatially-varying coefficient models have been developed and tested for data that follow a Gaussian distribution (e.g., Finley 2011), models for non-Gaussian outcomes, e.g., binomial or Poisson distributions, have not yet been widely applied to ecological questions, with a few exceptions that focus on statistical methodology development (i.e., Finley et al. 2009, Finley et al. 2011). Here, I consider a SVC model for evaluating the relationships between the temporal turnover (i.e., changes in community composition across time) in avian biodiversity and a set of environmental covariates.

I chose to focus on temporal turnover in community composition for two reasons. First, patterns and changes in biological diversity are an indication of the underlying mechanisms that control biodiversity and are one of the fundamental fields of investigation in ecology. Consequently, understanding patterns of biodiversity and their environmental determinants have been at the center of recent ecological research (e.g., Buckley and Jetz 2008, Jost 2009, Baselga

2010, Kraft et al. 2011). While traditionally community turnover has been used to describe biodiversity patterns across space rather than time, it can also be viewed in terms of a temporal change in species composition occurring over a specified time period. Indeed, describing temporal changes in communities is of increasing importance because of the global environmental threats such as climate change and land-cover change, both of which have a strong temporal component. Understanding temporal relationships between biodiversity patterns and environmental variability is necessary to accurately forecast the consequences of environmental change and design sound conservation strategies.

Second, the often observed space-varying nature of temporal community turnover and the kinds of inference we seek encourages the use of new, more flexible, tools such as generalized linear SVC models. Further, because biodiversity dynamics are often summarized using indices such as Jaccard, Sorensen, or Diamond-May, there is a need for development of methods appropriate for such non-Gaussian outcomes.

My objective was to test the utility of the SVC model to quantify the influence of nonstationarity on relationships between temporal community dynamics in avian assemblages and changes in environmental factors such as climate variability and patterns of landscape fragmentation. Specifically, I sought to assess the merits of a Bayesian spatially-varying coefficients approach in comparison with non-spatial and spatially-varying intercept models.

#### **1.2 DATA AND METHODS**

#### **1.2.1 Site description**

The study area is the State of New York, USA. New York covers 128,401 km<sup>2</sup>, including 4,240 km<sup>2</sup> of inland water (excluding of the boundary-water areas of Long Island Sound, New York Harbor and lakes Ontario and Erie). Most of the state lies between latitudes 42 and 45°N and

between longitudes 73.5 and 79.75°W. Climate of New York is affected by the state's broad elevation gradient as well as by the proximity to lakes Erie and Ontario, and the Atlantic Ocean. Adirondack and Catskill Mountains in the east are among the highest regions of the state, with elevation varying between 600 and 1,500 m. South-western New York is located in the northern portions of the Allegheny Plateau and its elevation ranges from approximately 300 to 900 m. North-western New York as well as Hudson River valley and New York City are low-elevation regions with elevation ranging from approximately 0 to 200 m.

The state's land-cover is approximately 51.2% forest (deciduous, evergreen, and mixed forests), 13.4% pasture and hay, 8.2% cultivated crops, 2.9% scrub and shrub, 1.0% grassland and herbaceous, 8.0% wetland cover, 8.7% developed land, and 0.2% barren land (Homer et al. 2004). Forested areas dominate the Adirondack, Catskill and Allegany regions, while agriculture is prevalent on historic glacial lake plains south of Lake Ontario.

New York offers a broad gradient of landscape fragmentation. The regions of the Adirondack and Catskill Mountains are the least fragmented. The Hudson River valley runs through the eastern part of the state and is more fragmented in terms of land-cover. The landscapes of western New York are more fragmented and characterized mostly by agricultureforest mosaic. Because of these heterogeneous patterns in landscape fragmentation, elevation gradients, and diversity of ecosystems, we might expect space-varying impacts of covariates to explain variation in ecological outcomes of interest.

#### **1.2.2 Breeding Bird Atlas**

I used the New York State Breeding Bird Atlas (BBA) as our model dataset to characterize changes in avian communities through time. BBA is a statewide survey that documented the distribution of breeding birds in New York. The BBA has been conducted in two time periods,

1980-85 (hereafter, BBA1980; Andrle and Carroll 1988) and 2000-05 (hereafter, BBA2000; McGowan and Corwin 2008). For both BBAs, a grid system was used to define the basic unit for reporting data. The entire State of New York was divided into approximately 1,300 squares, each measuring 10 km x 10 km. The BBA reporting unit (a block) was one quarter of this square and measured 5 km x 5 km and a total of 5,335 blocks covered the entirety of New York State. This data set represents one of the largest and finest resolution atlases in the world (Gibbons et al. 2007).

A total of 242 species were recorded for BBA1980 and 248 species were recorded for BBA2000 (Appendix 1.1). Avian breeding was recorded at three levels of certainty of breeding occurrence based on the behavior of birds observed: *possible, probable,* and *confirmed* (Andrle and Carroll 1988, McGowan and Corwin 2008). Observations were made by skilled birders who spent at least 8 hours in each block, visited all cover types in each block, and included at least one nighttime visit to document nocturnal species. Observer effort was recorded for each BBA and reported as a number of person hours (McGowan and Zuckerberg 2008). A block was considered sufficiently surveyed when at least 76 species were documented (with exceptions of blocks that might be expected to have fewer species). The BBA represents a presence/absence dataset, although absence indicates that species could not be found given search criteria (McGowan and Corwin 2008).

#### **1.2.3 Temporal turnover**

While many different indices for quantifying community turnover has been developed over the years (Gaston et al. 2004, Magurran 2004, Tuomisto 2010a, Tuomisto 2010b), we used Diamond-May (DM) index (Gaston et al. 2004). DM index is calculated as a proportion and designates turnover as high when the proportion of species shared between two sites (or two time

steps) is low (Gaston et al. 2004). From a statistical perspective, DM is a binomial outcome, where the number of species lost and gained across space or time is the number of successes, while the total number of species is the number of trials. DM index has traditionally been used to quantify spatial turnover, but it can be easily adapted to reflect temporal turnover as follows:

$$DM = \frac{E+C}{E+C+P},$$
 Eqn. 1.1

where *E* is the number of species that went extinct in the block between BBA1980 and BBA2000 (i.e., extinction), *C* is the number of species that colonized the block between BBA1980 and BBA2000 (i.e., colonization), and *P* is number of species in the same block common to both BBAs (i.e., persistence). The values of DM are bounded by 0 and 1; values approaching 0 indicate low temporal turnover in a block between BBA1980 and BBA2000, while values approaching 1 indicate high temporal turnover in a block between BBA1980 and BBA2000.

#### **1.2.4 Model covariates**

Environmental factors that I deemed especially important in shaping changes in community composition were trends in climatic variables and landscape fragmentation. I also considered survey effort (number of survey hours) as a variable potentially affecting the observed temporal community turnover.

#### **1.2.4.1 Climatic trends**

The climate data was derived from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate mapping system (Daly and Gibson 2002). PRISM consists of interpolated monthly maximum and minimum temperatures and precipitation at a 2.5-arcmin resolution from 1891-2010 for the entire contiguous United States.

I calculated the magnitude of the 25-year (1980-2005) trend in average monthly maximum and minimum temperatures and in total monthly precipitation using Ordinary Least Squares regression. The slope of the OLS regression indicates the magnitude of the trend and reflects the amount of change in climatic variables that occurred between 1980 and 2005. I then interpolated the trend magnitudes for each BBA block and averaged the monthly values to reflect breeding season (May through September) trend magnitude in maximum and minimum temperatures (TMAX and TMIN, respectively) and in total precipitation (PRECIP). The trend magnitudes of TMAX and TMIN were expressed in °C/25 years, while the units of the trend magnitudes of PRECIP were in mm/25 years.

#### 1.2.4.2 Habitat fragmentation

Even though amount of suitable habitat is often cited as one of the most important factors driving patterns of species occurrence, it is difficult to quantify suitable habitat while dealing with a group of species with vastly different habitat requirements. Habitat fragmentation has been shown to also be a significant driver of songbird community dynamics (e.g., Kennedy et al. 2011). Hence, I chose landscape fragmentation as the primary land-cover factor associated with community turnover.

Habitat fragmentation variables were derived using the 30x30 m National Land Cover Data (NLCD, Homer et al. 2004) product. Because there is no land-cover data readily available for the time period of BBA1980, I used a space-for-time substitution to assess whether temporal turnover is related to landscape fragmentation (Pickett 1989, Zuckerberg and Porter 2010). Space-for-time substitution assumes that spatial variation is equivalent to a temporal variation, and relationships between variables (e.g., species occurrence and land-cover) derived for one time step across a large spatial extent will be equivalent to that derived for two time steps. Thus,

I quantified landscape fragmentation for one time step only and looked for the relationship between the temporal turnover and the observed spatial variation in landscape fragmentation.

I used the 2001 NLCD, because it coincided well with the time of BBA2000. The 2001 NLCD consists of 16 land cover classes. Prior to landscape analysis, I consolidated open space developed, low intensity developed, medium intensity developed, high intensity developed into one class of developed land; cultivated crops and pasture/hay into one class of agriculture; and deciduous forest, evergreen forest, mixed forest, and forested wetland into one class of forest. We decided to consolidate these land-cover types to improve accuracy of classification and to simplify the environment for purposes of our evaluation. Upon consolidation, I examined nine land cover classes: water/ice, developed, barren land, forest, scrub/shrub, grassland/herbaceous, agriculture, and wetlands.

Landscape fragmentation was quantified using FRAGSTATS 4.1 (McGarigal et al. 2002) and the Geospatial Modelling Environment (GME, <u>http://www.spatialecology.com/gme/</u>). I recognize that there are multiple ways to measure fragmentation and that careful characterization of landscape fragmentation for a diverse suite of species often requires multiple metrics. However, my purpose was not comprehensive ecological analyses, but rather evaluation of the space-varying qualities of fragmentation. Therefore, I chose a landscape-scale variable to capture broad-scale variation in habitat fragmentation and best represent requirements of a diverse suite of species with varying habitat requirements. Specifically, I chose Edge Density (ED) as a measure of landscape fragmentation because an increase in habitat edge is a primary outcome of habitat fragmentation (Hargis et al. 1998). ED was also reported as an effective tool for evaluating landscape fragmentation and performed better than other popular landscape fragmentation indices (Hargis et al. 1998). However, in situations when landscape consists

entirely of one cover type, the ED would be 0 regardless of the type of land-cover present. Therefore, in order to differentiate between landscapes that consisted entirely of natural land cover (e.g., forest) and those mostly developed (e.g., urban areas), I also included the proportion of developed land (DEVEL) metric in our models.

## 1.2.4.3 Survey effort

Increasing survey effort often results in a higher number of recorded species (Tobler et al. 2008). Different survey effort between BBA1980 and BBA2000 could decrease the value of the DM indicating high temporal turnover, which could be a result of different number of recorded species rather than actual changes in species identities throughout time. Despite the fact that concerted attention was invested to minimize the effects of survey effort in the BBA surveys, I wanted to recognize the need to control for survey effort bias. To account for potential survey effort bias, I calculated the absolute difference in the number of person hours between BBA1980 and BBA2000 (EFF=|EFF1980-EFF2000|) for each BBA block and included it as a covariate in our models.

### **1.2.5 Statistical analysis**

I evaluated three statistical models, each of which included main effects of all the covariates (TMAX, TMIN, PRECIP, ED, DEVEL, and EFF). I standardized all the covariates to ease the comparison and interpretation of the coefficient estimates. Since the temporal turnover (DM) is a proportion, I used a binomial regression model. I started with a non-spatial regression specification (hereafter, non-spatial model) and then increased the level of model complexity by adding spatially structured random effects first to the intercept to form a spatially-varying intercept (SVI) model, then to the regression parameters associated with the covariates to form the SVC model.

More formally, for a given BBA grid cell the regression outcome variable y(s) is the numerator in Eqn. 1, where *s* represents the grid cell's spatial coordinates. Given the denominator in Eqn. 1, denoted N(s), we assume y(s) follows a binomial distribution. For the given grid cell  $\pi(y(s) \mid \eta(s)) \sim Binomial(N(s), p(\eta(s)))$ , where  $p(\eta(s))$  is the probability of success at location *s* and  $\eta(s)$  is model's regression equation, which for the SVC model is equal to  $\mathbf{x}(s)\mathbf{\beta} + \mathbf{x}(s)\mathbf{w}(s)$  with  $\mathbf{x}(s)$  representing the vector comprising an intercept and location specific covariate values. The parameters to be estimated are the global regression coefficients,  $\mathbf{\beta} = (\beta_0, \beta_{TMAX}, \beta_{TMIN}, \beta_{PRECIP}, \beta_{ED}, \beta_{DEVEL}, \beta_{EFF})^T$ , and associated spatially-varying adjustments,  $\mathbf{w}(s) = (w_0(s), w_{TMAX}(s), w_{TMIN}(s), w_{PRECIP}(s), w_{ED}(s), w_{DEVEL}(s), w_{EFF}(s))^T$ . A logit link function  $\eta(s) = \log[p(s)/\{1-p(s)\}]$  was used for this model.

I assume each element in the spatially-varying coefficients vector, w(s), arises from a spatial Gaussian Process (GP) (see, e.g., Banerjee et al. 2004 or Cressie and Wikle 2011 for more details). Specifically, the *j*-th spatially-varying coefficient at location *s* is  $w_j(s) \sim GP(\theta, C_j(s, s'))$ , where *s* and *s*' are any two locations within the study area, the spatial covariance  $C_j(s, s') = \sigma_{j\rho_j}^2(s, s'; \phi_j)$  with variance parameter  $\sigma_j^2$ , correlation function  $\rho_j(\cdot; \phi_j)$ , and spatial decay parameter  $\phi_j$ . The spatial decay parameter  $\phi_j$  controls the decay in spatial correlation; lower values of the parameter indicate shorter range in spatial correlation. The exponential spatial correlation was assumed for  $\rho_j(\cdot)$ .

Prior distributions on the remaining parameters complete the hierarchical model, see, e.g., Gelman et al. 2004 for detail on Bayesian model specification. Here, I specified uninformative prior distributions. The regression coefficients,  $\beta_j$ 's followed a Normal distribution *N*(0, 100), while the variance components  $\sigma_j^2$ 's were assigned inverse-Gamma IG(2, 1) priors, where 2 and 1 are shape and scale hyper-parameters, respectively. This specification of the IG provides a prior distribution with infinite variance that is centered on 1. The spatial decay parameters,  $\phi_j$  's, followed an informative Uniform prior, with support that ranged from 1 km to the maximum distance between any two grid cells. Exploratory analysis using different hyperparameters suggested prior specification had little influence on parameter and predictive inference. This is not surprising given the large size of the data set and choice of prior distributions. My sensitivity analysis did suggest that given an IG shape hyper-parameter of 2, very large scale parameter values, e.g., greater than 10, resulted in poor MCMC chain convergence by forcing an unreasonable amount variability in the GP. For the SVC model, I ran three MCMC chains for 60,000 iterations each. I ran 10,000 iterations for the non-spatial and SVI models, as those required less time to converge. Convergence was diagnosed using the Gelman-Rubin diagnostic (Gelman and Rubin, 1992).

Given the Bayesian framework, candidate models fit to the observed data were assessed using the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). I computed the expected posterior deviance as  $D(\Omega) = E_{\Omega|Y}\{-2\log L(\text{Data}|\Omega)\}$ , where  $\Omega$  is the set of parameters estimated for each model and  $L(\text{Data}|\Omega)$  is the first stage Gaussian likelihood from the respective models. I computed the effective number of parameters as  $p_D = \overline{D(\Omega)} - D(\overline{\Omega})$ , where  $\overline{\Omega}$  is the posterior mean of the model parameters. The DIC was then computed as  $D(\Omega) + p_D$ . Lower values of DIC indicate improved fit. Model accuracy was compared using Root Mean Square Error (RMSE) that was calculated as the square root of the mean squared deviations between fitted and observed outcomes. Lower values of RMSE indicate improved accuracy.

Candidate model performance for out-of-sample prediction was assessed using a randomly selected 10% holdout dataset. While there is no convention on how much of the original data should be held out for model validation, we believe that 10% of the data is

sufficient as it amounts to approximately 500 observations. Also, while several other approaches to verify model's predictive ability are available, holding-out a set of randomly selected observations is a common model validation technique (e.g., Pearson et al. 2002, Finley 2011). An alternative approach to verifying model's predictive ability would be bootstrapping, where the original dataset is sampled randomly with replacement (e.g., Austin and Tu 2004). Bootstrapping requires building and running multiple models and in each case predictive performance is assessed against the corresponding test data. While bootstrapping is a robust approach, it is computationally costly, particularly in situations when models are complex. Given that fitting a single SVC model is very computationally intensive in itself, repeating this procedure multiple times for bootstrapping would be prohibitive and thus was not feasible in our case. Hold out set predictions were compared to the observed values using Root Mean Square Error (RMSE<sub>pred</sub>) where lower values indicate improved performance.

Prior to statistical analysis, I removed all blocks that did not have continuous land cover coverage; those were mainly blocks at the periphery of the study area, which extended farther than the NLCD layer. Also, blocks with more than 50% open water coverage and those that did not have survey effort data were removed. Ultimately, I used a total of n = 4,271 blocks to fit the models and  $n_{ho} = 473$  holdout blocks to test the models' predictive ability. The non-spatial and SVI models were run in R 2.15.1 statistical package (R Development Core Team 2013, http://www.r-project.org/) using package spBayes (Finley and Banerjee 2013). In close collaboration with Dr. Andrew Finley, I wrote and compiled the SVC model in C++ programming language and R 2.15.1 (R Development Core Team 2013, http://www.r-project.org/). Summaries of parameter estimates were generated using the R CODA package.

## **1.3 RESULTS**

## **1.3.1 Temporal turnover**

The mean grid cell value of the DM index was 0.39, which indicates that on average approximately 39% of species had either colonized or become extinct and 61% of the species were common to both BBAs (Fig. 1.1A). Northern regions of the state (i.e., Adirondack Mountains) experienced the highest temporal community turnover, with values reaching 1.0 (i.e., complete turnover in species assemblage) in several locations (Fig. 1.1A). Western (agricultural) and Eastern (urbanized) parts of the state also showed slightly higher than average temporal turnover, while the central regions of the state generally underwent the lowest temporal turnover (Fig. 1.1A). The lowest values of temporal turnover was approximately 0.11. **Figure 1.1** Observed temporal turnover in communities of breeding birds in New York expressed using Diamond-May index (A) and the fitted temporal turnover values resulting from the non-spatial model (B), spatially-varying intercept (SVI) model (C), and spatially-varying coefficients (SVC) model (D).


#### **1.3.2** Covariates

The north-eastern and south-western parts of the state experienced the largest warming trend, while the southern and central New York generally underwent decreases in average maximum temperatures (Appendix 1.2). Minimum temperatures increased across most of the state, though some small regions have experienced a cooling trend (Appendix 1.2). Northern (i.e., region of the Adirondack Mountains), western and southern New York experienced drier conditions, while the rest of the state experienced wetter conditions (Appendix 1.2).

Regions of Adirondack and Catskill Mountains as well as some locations in the south and south-western parts of the state had the lowest edge density (i.e., lowest habitat fragmentation; Appendix 1.2). The percentage of developed land was low across most of New York, with exception of large urban centers such as New York City, Albany, Syracuse, Rochester, and Buffalo. Survey effort was relatively constant across the study region (Appendix 1.2).

#### **1.3.3 Statistical analysis**

#### **1.3.3.1** Model fit and predictive ability

As suggested by the DIC, RMSE, and RMSE<sub>pred</sub> values provided in Table 1.1, adding spatial random effects to the posited model improves fit to the observed data, model accuracy, and predictive performance for new, unobserved, locations. The improvements to fit and model accuracy suggest there was substantial spatial dependence among the non-spatial models residuals - a generalized linear model assumption violation - and clear indication that a more complex spatial model was warranted. The pD in Table 1.1 is the effective number of parameters and is used in the DIC calculation to penalize more complex models. For example, the non-spatial model has only seven regression coefficients, hence, pD is approximately seven. The increasing number of spatial random effects added to SVI and SVC, respectively, is reflected by

larger penalties. Despite the larger number of effective parameters, the SVC model has lower

DIC than the non-spatial and SVI models.

**Table 1.1** Comparison of the non-spatial, spatially-varying intercept (SVI), and spatially-varying coefficient (SVC) models for four migratory groupings using Deviance Information Criterion (DIC), estimated number of parameters pD, and Relative Mean Square Error (RMSE). Predictive performance of the models was evaluated by calculating RMSE<sub>pred</sub> of the observed values from the hold-out set and the predicted values resulting from all three models.

Model	ΔDIC	pD	RMSE	<b>RMSE</b> <sub>pred</sub>
SVC	0.00	458.90	0.076	0.072
SVI	1,063.84	106.30	0.082	0.079
Non-spatial	2,871.31	7.20	0.090	0.088

All candidate models provide a close visual approximation to the observed data (see Fig. 1.1 for the candidate model fitted value surfaces). For the SVI model (Fig. 1.1C), the addition of the spatial random effect to the model intercept provides a smooth process that captures spatial discrepancies between observed values and those estimated with the additive linear trend involving the covariates. The SVC model fitted surface (Fig. 1.1D) provides the closest approximation to the observed data because the regression coefficients processes are able to estimate the covariates' local and regional impact on temporal turnover. For example, the variation in the temporal turnover in the north-east New York is better represented on the SVC model fitted surface (Fig. 1D) than on surfaces resulting from the other two models (Fig. 1.1B and 1.1C).

In terms of model predictive performance, all models' predicted surfaces approximated the holdout data relatively well (Fig. 1.2). However, by not relying only on the smooth process on the intercept, the SVC model is able to accommodate more local-scale variation than the SVI model (Fig. 1.2D). For example, several locations of high temporal turnover in the western part of the study area were picked up by the SVC predictive model, but not by either the non-spatial or the SVI predictive models (Fig. 1.2D).

**Figure 1.2** Observed temporal turnover of the holdout data set (A) compared with the surfaces of the predicted values resulting from the non-spatial model (B), spatially-varying intercept (SVI) model (C), and spatially-varying coefficients (SVC) model (D).



# **1.3.3.2** Coefficient estimates

All regression coefficients in the non-spatial model were statistically significant (Table 1.2), i.e., the 95% credible intervals did not include zero. For spatially-varying intercept models, all of the regression coefficients remained significant (Table 1.2), but their magnitude and credible intervals changed in comparison with the non-spatial model (the magnitude of the coefficient estimates was assessed by simply comparing the direction and absolute value of the mean estimates resulting from both models). The magnitude of  $\beta_0$ ,  $\beta_{TMAX}$ ,  $\beta_{TMIN}$ ,  $\beta_{PRECIP}$ , and  $\beta_{ED}$  decreased after the residual spatial dependence was accommodated, while  $\beta_{DEVEL}$  and  $\beta_{EFF}$  increased in magnitude.

**Table 1.2** Coefficient estimates resulting from the non-spatial and spatially-varying intercept (SVI) models for all model covariates: intercept ( $\beta_0$ ), magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season ( $\beta_{TMAX}$ ), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season ( $\beta_{TMIN}$ ), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season ( $\beta_{PRECIP}$ ), percent developed land ( $\beta_{DEVEL}$ ), edge density ( $\beta_{ED}$ ), and effort ( $\beta_{EFF}$ ). 50% indicates the mean of the posterior distribution, while 2.5% and 97.5% are the lower and upper quantiles of the posterior distribution.

Model	Coefficient —	Coe	<b>Coefficient Estimates</b>		
Widder		50%	2.5%	97.5%	
	$\beta_0$	-0.492	-0.499	-0.486	
	$\beta_{TMAX}$	0.063	0.055	0.070	
Non Spatial	$\beta_{TMIN}$	0.041	0.034	0.048	
Non-Spatial	$\beta_{PRECIP}$	-0.052	-0.059	-0.045	
	$\beta_{DEVEL}$	0.017	0.010	0.024	
	$\beta_{ED}$	-0.092	-0.099	-0.086	
	$\beta_{EFF}$	-0.010	-0.016	-0.004	
	$\beta_0$	-0.375	-0.435	-0.275	
CVI	$\beta_{TMAX}$	0.018	0.007	0.029	
	$\beta_{TMIN}$	0.026	0.014	0.038	
3 1 1	$\beta_{PRECIP}$	-0.015	-0.031	-0.001	
	$\beta_{DEVEL}$	0.032	0.022	0.042	
	$\beta_{ED}$	-0.047	-0.057	-0.036	
	$\beta_{EFF}$	-0.014	-0.020	-0.008	

For a SVC model, it is typically not instructive to focus on a covariate's regression coefficient mean, i.e.,  $\beta$ , but rather assess the variability of the coefficient over the study area. That is, we draw inference by looking to maps of  $\beta + w(s)$  (see Fig. 1.3 for  $\beta + w(s)$  associated with each covariate). All SVC model coefficient estimates were spatially heterogeneous both in terms of the magnitude of the coefficient estimate as well as the direction of the relationship between the covariate and the outcome variable (Fig. 1.3). Here too, grid cells where the 90% credible intervals of the given  $\beta + w(s)$  include zero are identified with a black point. Or conversely, those regions with no black points differ significantly from zero in the direction indicated by the grid cell color. Some caution needs to be taken when considering the hypothesis tests implied in Fig. 1.3. In a testing situation, where we encounter a very large number of hypotheses, controlling Type-1 errors would be required, hence raising the question of multiple comparisons. However, we do not pursue such a formulation here and simply look to Fig. 1.3 to identify regions of substantial deviations of the spatial coefficients from the global mean (see also Fig. S2 in the Supplementary Material for maps of deviations of the spatially-varying coefficient estimates from the global mean).

**Figure 1.3** Coefficient estimates resulting from the spatially-varying coefficient (SVC) models of (A) the intercept, (B) the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season ( $\beta_{TMAX}$ ), (C) the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season ( $\beta_{TMIN}$ ), (D) the magnitude of the 25-year (1980-2005) trend rates in average total precipitation of the breeding season ( $\beta_{PRECIP}$ ), (E) percent developed land ( $\beta_{DEVEL}$ ), (F) edge density ( $\beta_{ED}$ ), and (G) effort ( $\beta_{EFF}$ ). Black point symbols identify grid cells with posterior 90% credible intervals that include zero. The surface colors identify the direction of the regression coefficients' sign.



#### **1.4 DISCUSSION**

We found that the SVC model outperformed both the non-spatial and SVI models in terms of model fit, despite the large number of parameters it had to estimate, and predictive performance. We feel confident that the increase in model fit is not a result of over parameterization, although, like any highly flexible random effect model, the SVC models can occasionally over fit the observed data. However, compared to models with unstructured random effects, the flexible process imposed by the spatial Gaussian Process reduces the possibility of over fitting. Additionally, the penalizing qualities of the DIC metric account for the potential favoring the parameter rich SVC model. Furthermore, over fitting generally results in reduced predictive performance compared to simpler models; however, we did not find lower predictive performance of the SVC model. Anecdotally, while working with other data sets, we have noticed that the propensity to over fit the observed data is greater when the number of observed locations is small (e.g., n < 100), sparsely sampled, and when the range of spatial dependence is short. In these settings, the interpolating qualities of the Gaussian Processes reduce the predictive power of the SVC model. When the data set is large, however, observations densely cover the domain, and the parameters of the underlying spatial processes associated with the regression coefficients are well estimated, then the risk of over fitting is reduced and prediction does not suffer.

The improvement in model fit suggests the relationship between temporal community turnover and environmental covariates is more spatially-varying in nature than it is stationary. Indeed, by allowing the regression coefficients to vary spatially over the domain and accommodate local impact of the covariates, the SVC model was able to explain more localscale variation in temporal community turnover than the other two models. The assumption that

regression coefficients are stationary results in poor fit and misleading inference about the impact of the covariates on temporal turnover. The assumption of scalar regression coefficients is pervasive in the literature. In the SVC model, any component of model spatial residual pattern due to non-stationarity of the impact of covariates is apportioned to the coefficients. Thus, the SVC model, despite being an intrinsically correlative approach, provides the richer opportunity for ecological interpretation.

We commonly see that once residual spatial dependence is accommodated, e.g., via a spatial random effect, regression coefficients differ from those resulting from a non-spatial model. In the non-spatial model, all covariates were significant predictors of temporal community turnover. Once spatial dependence was taken into account in the SVI model, the covariates remained significant but the magnitude of their coefficient estimates changed. For example, the association of the TMAX, TMIN, PRECIP, and DEVEL with the temporal community turnover was weaker for the SVI model than for the non-spatial model, while that of ED and EFF became stronger. Such results suggest the non-spatial model violated the assumption of independent and identically distributed residuals and imply that ecological inferences drawn from these models will be different. Other research corroborates our findings. For example, Record et al. (2013) found that climatic variables were significant predictors of presence-absence of two tree species in non-spatial models, but in the spatial models the magnitude and sign of some parameter estimates changed. Foody (2004) found the magnitude of relationships between species richness and the explanatory environmental variables changed when spatial dependency and non-stationarity were accounted for, even though statistically significant relationships were established using a conventional global regression analysis.

When the space-varying nature of the regression coefficients is accommodated, different regions within the study area might exhibit conflicting relationships between the outcome and covariate, causing the study-area-wide mean of the associated regression coefficient to be similar to those seen in the SVI models. In our case, spatial heterogeneity of the relationships between covariates and temporal community turnover became apparent after accounting for nonstationarity. Some regions were characterized by negative relationships, other regions displayed positive relationships, yet another showed no significant relationships at all. For example, a positive relationship between temporal community turnover and the magnitude of the trend in minimum temperatures was found in the eastern New York, while this relationship was negative in the central part of the state. Such spatial pattern might indicate that communities in eastern New York are responding stronger or faster to increasing temperatures resulting from climate change than those found in central New York. Similarly, we found that the strongest negative influences of landscape fragmentation were in eastern part of the state, i.e., in regions dominated by the Adirondack Mountains and the Hudson River valley. Perhaps in those historically forested and contiguous habitats, small levels of landscape fragmentation have a much more detrimental effect on community composition than elsewhere within the state. Furthermore, given that the strongest influences of these two covariates were detected in similar geographic regions, it is also plausible that these two ecological factors interact in driving temporal community turnover. The remaining covariates showed similar heterogeneous patterns. These heterogeneous surfaces illustrate the complexity of impact and interplay among the covariates in explaining variability in temporal community turnover.

Other research provides evidence for non-stationarity of ecological relationships (e.g., Bini et al. 2009, Martin-Queller et al. 2011, McNew et al. 2013) and thus corroborates findings

from our study. For example, Grotan et al. (2009) found the proportion of variance in local recruitment of great tit explained by spring temperature differed nearly 10-fold among four Dutch populations. Sæther et al. (2008) showed that population dynamics of eight species of prairie ducks showed pronounced latitudinal gradient; depending on the location, influence of increased spring temperature or winter precipitation on population dynamics was either positive or negative. Anders and Post (2006) found that NAO affected populations of the migrant yellow-billed cuckoo (*Coccyzus americanus*) only in southern and eastern parts of the US, while El Nino Southern Oscillation (ENSO) affected populations in northern and central US. Martin-Queller et al. (2011) found relationships between species richness of woody plants and environmental and biotic factors to also be spatially heterogeneous. Given this apparent ubiquity of space-varying relationships in nature, we suggest that researchers studying large-scale ecological phenomena should be especially cognizant of the need to evaluate and account for potential non-stationarity.

The three models we tested yielded different results despite the fact that the same covariates were included in all of them. By ignoring spatial dependency in model residuals, the non-spatial model produced relationships between the covariates and temporal community turnover. In the SVI model, the relationships between covariate and outcome variable generally weakened as a result of accommodating the spatial autocorrelation in model covariates via spatial random effect. By allowing the coefficient estimates to vary spatially, the SVC model yielded heterogeneous patterns and often conflicting relationships between the outcome and covariate. The heterogeneity of the model covariates themselves (e.g., the magnitude of the climatic trends) might be partly responsible for driving such space-varying relationships. Applying the SVC model enabled us to detect and account for these spatial differences.

It must be noted that other approaches exist to evaluate and account for potential nonstationarity of ecological phenomena. One of the more common options is a frequentist method called geographically-weighted regression (GWR, Fotheringham et al. 2002), which uses spatial weights to estimate spatially adaptive coefficients. GWR has been the leading statistical method to account for spatial non-stationarity (e.g., Ma et al. 2012a, Ma et al. 2012b, Miller 2012), in no small part due to its availability in several popular Geographic Information Systems, e.g., ESRI products, and statistical computing environments, e.g., spgwr package in R statistical program (Bivand and Yu 2013). However, recently it has been shown that GWR is not robust to collinearity among the covariates and the presence of complex spatial correlation structures (Wheeler and Waller 2009, Finley 2011) and it tends to provide less accurate and more correlated regression coefficient estimates than those resulting from SVC models (Wheeler and Cadler 2007). Furthermore, Ma et al. (2012a) used GWR to model species richness derived from the same dataset as ours and concluded that GWR performed poorly the larger the spatial scale of investigation. Another central shortcoming of GWR, from an inferential standpoint, is the lack of a legitimate probability model in the sense that the joint distribution linking the parameters and the data is not a valid probability distribution. This is problematic for inference because the standard errors computed from such models may not be justifiable. Asymptotic arguments may be supplied but are complicated in spatial contexts because of the divergent paradigms of infill and expanding domain asymptotics. Thus, GWR can be a useful tool for exploratory data analysis, but generally should not be used in settings where one seeks inference about the importance of model parameters or in prediction.

Given the growing wealth of space and time indexed ecological data (Kelling et al. 2009, Reichman et al. 2011, Schimel 2011) deeper insight into ecological processes is contingent upon

our ability to specify valid and tractable models able to accommodate often complex spatiotemporal relationships between outcomes and posited environmental drivers. Because the propensity for non-stationary relationships increases over larger spatial domains and time periods, need for more sophisticated models also increase as we begin looking at macro-system questions. This study represents an important case assessing the utility of SVC models for capturing non-stationary relationships between non-Gaussian biodiversity dynamics and environmental changes. We suggest that SVC models are especially appropriate for studying macro-scale (i.e., regional or global) systems where we can expect the ecological processes and environmental drivers to be strongly heterogeneous across the spatial domain. As such, SVC models provide a unique opportunity to explore pressing environmental questions about impact of global environmental change on biodiversity.

#### **1.5 ACKNOWLEDGMENTS**

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# SYNERGISTIC EFFECTS OF CLIMATE AND LAND COVER: ARE GRASSLAND BIRDS MORE VULNERABLE TO CLIMATE CHANGE?

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Jarzyna M.A, Porter W.F, Finley A.O. and Zuckerberg B. In review. Synergistic effects of climate and land cover: Are grassland birds more vulnerable to climate change? *Diversity and Distributions*.

# ABSTRACT

Quantity and quality of available habitat will affect the way species respond to climatic variability. My goal was to investigate bioclimatic relationships of grassland and forest breeding birds along varying gradients of grassland and forest habitat. Specifically, I sought to investigate whether: (i) bioclimatic relationships of birds breeding in grasslands differ from those of forest species, (ii) an increasing amount of habitat affects avian responses to climatic variability, and (iii) the potential effect of more extensive habitat differs for birds inhabiting grassland and forest lands. I used the New York State Breeding Bird Atlas as a model dataset and I chose 11 grassland and 12 forest birds. To evaluate bioclimatic relationships along varying amounts of habitat, I created spatially-varying coefficients models (SVC) by adding spatially-structured random effects to the regression parameters associated with each of the model covariates. The resulting spatially-varying coefficient estimates of all climatic covariates were then regressed against the habitat amount for each individual species. I found that grassland and forest birds exhibited divergent bioclimatic relationships. On average, grassland birds were more likely to occur in regions characterized by higher temperatures and lower precipitation when compared to forest breeding birds. I also found that both groups exhibited heterogeneous bioclimatic relationships across a range of habitat amount, though the influence of land cover differed for grassland and forest birds. I conclude that increasing amount of forest cover likely will buffer the negative consequences of climate change, whereas extensive open grasslands will likely

exacerbate the impacts of climatic variability on bird populations. Thus, grassland birds might be particularly at risk of a changing climate due to the diminished buffering capacity of grassland systems.

#### **2.1 INTRODUCTION**

Global temperature increase resulting from anthropogenic climate change will have far-reaching consequences for biodiversity, and there is growing evidence that most taxonomic groups are already responding to recent climate warming (Walther et al. 2002, Parmesan and Yohe 2003, Jarzyna et al. 2013). However, despite the evidence that climate change is impacting biodiversity, there is still a need to better understand which species and ecosystems are most vulnerable, and under what conditions (Lawler 2009).

Deriving bioclimatic relationships is a critical component of determining the potential impacts of climate change on species and communities (e.g., Guisan and Thuiller 2005, Araújo and Peterson 2012) and remains the most widely used tool for forecasting changes in species distributions (e.g., Miller 2010). However, using bioclimatic relationships as a sole predictor of species' distributional changes is limited (Pearson et al. 2004, Huntley et al. 2010) because factors other than climate will affect the way species respond to climate change (Thomas et al. 2004). For example, research suggests the quantity and quality of available habitat might be important in shaping bioclimatic relationships of species and thus their responses to climate change (Opdam and Wascher 2004, Kampichler et al. 2012). In simulation studies, habitat loss has been shown to reduce species ability to adjust to changing climatic conditions and thus exacerbate the detrimental effects of climate change (Travis 2003), while an increase in the amount of habitat has been shown to slow down species extinction rates (Jeltsch et al. 2011). Empirical evidence, however, is lacking because studies that integrate both kinds of impact (land

cover and climate) are rare (but see Kampichler et al. 2012). Moreover, no studies that explicitly evaluate species bioclimatic relationships across a broad range of habitat amount, to the best of our knowledge, have yet been conducted. Gaining a better understanding of the synergistic effects of climate and habitat will provide a deeper understanding of which species are more or less vulnerable to climate change.

Given that decreasing habitat is likely to alter responses of species to climatic variability and thus potentially exacerbate the negative consequences of climate change (Travis 2003, Jeltsch et al. 2011), we expect the bioclimatic relationships of species to be altered by the amount of habitat within a landscape. Populations of the same species found in regions with abundant suitable cover should display weaker responses to climatic variability in comparison with populations found in regions characterized by less available habitat. Vulnerability to climate change can then be assessed based on the observed strength of bioclimatic associations. Species exhibiting weaker responses to climatic variability and those whose habitats provide modulating capacity against changing climatic conditions (i.e., where increasing amount of habitat weakens species' bioclimatic relationships) would be considered less vulnerable to changing climatic conditions.

The modifying characteristics of habitat amount on bioclimatic relationships are likely to differ depending on the type of land cover. Recent research suggests that forest canopies moderate the impact of climate warming on understory plants by creating cooler microclimatic conditions during the summer months (Bonan 2008, De Frenne et al. 2013). On the other hand, open habitats, such as old fields, agricultural, and pasture land (hereafter called grasslands), generally create warmer, drier, and more variable microclimates than forests (Geiger et al. 2009) and are therefore less likely to provide a similar moderating effect (Villegas et al. 2010). Given

these differences in climatic regimes of both types of cover, and the fact that thermal and habitat niches of species are often correlated (Barnagaud et al. 2012), we might expect that species inhabiting grasslands and forests will display divergent bioclimatic relationships. We can also expect that the presence, absence, and magnitude of the potential mitigating effect of land cover will be different for these two groups of species.

The comparison of grassland and forest species is timely. The velocity of climate change has been shown to be greater along latitudinal than elevational gradients (Dobrowski et al. 2013). Forests are generally found in regions of higher altitudinal gradient than grasslands, which in turn are generally found in low laying and flat areas. Thus, given a similar latitudinal extent, grasslands are likely to experience more rapid changes under future climatic conditions than forested regions. However, how exactly grassland species will respond to this higher rate of climatic variability is largely unknown. Quantifying the range of bioclimatic relationships across a gradient of available habitat would be the first step in determining potential impacts of climate change on these two groups of species.

Here, I used data from the New York State Breeding Bird Atlas to investigate bioclimatic relationships of grassland and forest birds across a range of habitat. I focus on relationships with temperature and precipitation, as the main climatic factors driving distributions and breeding success in bird populations (e.g., Moss et al. 2001). Specifically, I seek to evaluate three interrelated questions: (i) do bioclimatic relationships of birds breeding in grasslands differ from those of forest species? (ii) do increasing amounts of habitat modify responses of grassland- and forest-breeding birds to climatic variability? and (iii) is the effect of increasing habitat amount different for grassland and forest birds? First, I predict that grassland and forest birds will exhibit divergent bioclimatic relationships. Specifically, forest birds will have stronger negative

relationships with temperatures due to their preference for cooler habitats than grassland birds, while grassland birds will be found in warmer and drier regions. Second, I predict that an increasing amount of forest cover will abate the negative responses of forest birds to climatic variability (Cox et al. 2013). Lastly, I predict no change in the magnitude of bioclimatic relationships of grassland birds as the amount of their habitat increases. If my predictions regarding the mitigating qualities of each land cover hold true, we can expect grassland birds to be particularly vulnerable to changing climate due to the diminished modulating capacity provided by their habitat.

# **2.2 METHODS**

## 2.2.1 Breeding Bird Atlas and chosen species

The New York State Breeding Bird Atlas (NYSBBA) is a statewide survey of the distribution of breeding birds in New York that has been conducted to date in two time periods, 1980-85 (Andrle and Carroll 1988) and 2000-05 (McGowan and Corwin 2008). For both atlases, a grid system was used to define the basic unit for reporting data; each unit (a block) measured 5 km x 5 km and a total of 5,335 blocks covered the entirety of New York State. The NYSBBA represents one of the largest and finest resolution atlases in the world (Gibbons et al. 2007) and, in comparison with other datasets of avian distributions, provides a full state coverage in a form of a spatial grid that allows for thorough and systematic evaluation of species' distributional patterns. The NYSBBA is a detection/non-detection dataset, where non-detection indicates that species could not be found given search criteria (McGowan and Corwin 2008).

I used the 2000-05 BBA (hereafter, BBA) to quantify species bioclimatic relationships and to investigate whether birds show spatially-varying (i.e., dependent on the amount of habitat) responses to climatic variability. I chose 11 grassland birds: American kestrel (*Falco sparverius*),

northern harrier (*Circus cyaneus*), eastern bluebird (*Sialia sialis*), eastern kingbird (*Tyrannus tyrannus*), horned lark (*Eremophila alpestris*), grasshopper sparrow (*Ammodramus savannarum*), savannah sparrow (*Passerculus sandwichensis*), vesper sparrow (*Pooecetes gramineus*), bobolink (*Dolichonyx oryzivorus*), brown-headed cowbird (*Molothrus ater*), and eastern meadowlark (*Sturnella magna*). Most of the selected species are grassland generalists and breed in a diversity of different open habitats, including old fields, pastures, hayfields, and cultivated fields (DeGraaf and Yamasaki 2001). In 2000-05, the 11 species occupied the following portion of all BBA blocks: 56% (kestrels), 17% (harriers), 73% (bluebirds), 83% (kingbirds), 13% (larks), 9% (grasshopper sparrows), 58% (savannah sparrows), 11% (vesper sparrows), 60% (bobolinks), 75% (cowbirds), and 49% (meadowlarks).

I chose 12 forest species: blue-gray gnatcatcher (*Polioptila caerulea*), blue-headed vireo (*Vireo solitaries*), golden-crowned kinglet (*Regulus satrapa*), great crested flycatcher (*Myiarchus crinitus*), red-breasted nuthatch (*Sitta canadensis*), tufted titmouse (*Baeolophus bicolor*), veery (*Catharus fuscescens*), black-and-white warbler (*Mniotilta varia*), black-throated blue warbler (*Setophaga caerulescens*), black-throated green warbler (*Setophaga virens*), blackburnian warbler (*Setophaga fusca*), and Canada warbler (*Cardellina canadensis*). Most of these forest birds breed in a variety of forest habitats (deciduous, coniferous, and mixed deciduous-coniferous forests) rather than being restricted to one forest type (DeGraaf and Yamasaki 2001). In 2000-05, the selected forest birds occupied 20% (gnatcatchers), 52% (vireos), 22% (kinglets), 79% (flycatchers), 45% (nuthatches), 59% (titmice), and 80% (veeries), 53% (black-and-white warblers), 38% (black-throated blue warblers), 60% (black-throated green warblers), 40% (blackburnian warblers), and 26% (Canada warblers) of all BBA blocks.

#### 2.2.2 Model covariates

The climatic covariates included in all the models were 5-year (2000-05) average values of maximum and minimum temperatures (TMAX and TMIN, respectively) and average total precipitation (PRECIP) of the breeding season (April-August). The climate data were derived from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate mapping system (Daly and Gibson 2002). Though values of TMAX and TMIN are expected to be correlated with each other (here, Pearson product moment correlation coefficient r = 0.65), both metrics are biologically meaningful and thus often included together in one model (e.g., Stralberg et al. 2009). Correlation between TMAX and PRECIP and TMIN and PRECIP was much lower (r = -0.18 and r = -0.22, respectively). To account for potential survey effort bias, I included survey effort (EFF, number of person hours; McGowan and Zuckerberg 2008) as a variable in all the models.

#### 2.2.3 Habitat amount

Grasslands and forests were identified using the 2001 National Land Cover Data (NLCD) derived from the Landsat Thematic Mapper satellite data (Homer et al. 2004). I used the 2001 NLCD because it coincided well with the time of the BBA. To derive the amount of the grasslands, for nine out of 11 species, I consolidated grassland/herbaceous, cultivated crops, and pasture/hay into one class of grasslands. Due to the more specialized habitat requirements of some grassland species, I implemented further classification rules to the land cover data. For bobolinks, I consolidated grassland/herbaceous and pasture/hay into one class (Martin and Gavin 1995, DeGraaf and Yamasaki 2001), while for harriers, I consolidated grassland/herbaceous, cultivated crops, pasture/hay, and emergent herbaceous wetlands (DeGraaf and Yamasaki 2001, Smith et al. 2011).

To derive the amount of forest within an atlas block, I consolidated deciduous forest, coniferous forest, and mixed forest into one class of forest. I implemented further land-cover classification rules for gnatcatchers and titmice, for which I consolidated deciduous and mixed forest classes (Grubb and Pravasudov 1994, DeGraaf and Yamasaki 2001, Kershner and Ellison 2012), and for kinglets, for which I consolidated coniferous and mixed forest classes (DeGraaf and Yamasaki 2001, Swanson et al. 2012).

The land-cover was quantified using FRAGSTATS 4.2 (McGarigal et al. 2012) and the Geospatial Modelling Environment (GME, <u>http://www.spatialecology.com/gme/</u>). We used Percent Land Cover (PLAND) metric to quantify the amount of grassland (GPLAND) and forested habitats (FPLAND). GPLAND and FPLAND quantify the proportional abundance of each patch type in each BBA block (McGarigal et al. 2012).

#### 2.2.4 Statistical analysis

I evaluated two statistical models for each species, both of which included all climate covariates (TMAX, TMIN, PRECIP) and survey effort (EFF). My first model was a stationary spatial regression, where I added spatially-structured random effects to the intercept to form a spatially-varying intercept (SVI) model. The SVI models accounted for spatial autocorrelation in the residuals, but did not allow slope coefficients to vary across the spatial domain. Second, I created a spatially-varying coefficients model (SVC) by adding spatially-structured random effects to the intercept and slope coefficients associated with each of the climatic covariates and survey effort. By relaxing the assumption that covariates have the same impact across the domain, the SVC models allowed for evaluation of potential changes in bioclimatic relationships across space.

For a given BBA grid cell the regression outcome variable y(s) is the detection or nondetection of a particular species (i.e., 1 or 0), where *s* represents the grid cell's spatial

coordinates. We assumed y(s) follows a Bernoulli distribution. For the more general SVC model,  $\pi(y(s) \mid \eta(s)) \sim Bernoulli(p(\eta(s)))$ , where  $p(\eta(s))$  is the probability of occurrence at *s* and  $\eta(s)$  is  $x(s)\beta + x(s)w(s)$  with x(s) representing the vector comprising an intercept and location specific covariate values. The parameters to be estimated were the global regression coefficients,  $\beta = (\beta_0, \beta_{TMAX}, \beta_{TMIN}, \beta_{PRECIP}, \beta_{EFF})^T$ , and associated spatially-varying adjustments,  $w(s) = (w_0(s), w_{TMAX}(s), w_{TMIN}(s), w_{PRECIP}(s), w_{EFF}(s))^T$ . We used a logit link function  $\eta(s) = \log[p(s)/\{1-p(s)\}]$ for this model.

I assumed each element in the spatially-varying coefficients vector, w(s), arises from a spatial Gaussian Process (GP) (Banerjee et al. 2004, Cressie and Wikle 2011). Specifically the *j*th spatially-varying coefficient at location *s* is  $w_j(s) \sim GP(0, C_j(s, s'))$ , where *s* and *s'* are any two locations within the study area, the spatial covariance  $C_j(s, s') = \sigma_j^2 \rho_j(s, s'; \phi_j)$  with variance parameter  $\sigma_j^2$ , correlation function  $\rho_j(\cdot; \phi_j)$ , and spatial decay parameter  $\phi_j$ . The exponential spatial correlation was assumed for  $\rho_j(\cdot)$ . The SVI sub-model comprises a single GP on the intercept, i.e.,  $\eta(s)$  is  $x(s)\beta + w_0(s)$ .

Prior distributions on the remaining parameters completed the Bayesian formulation of the hierarchical model (e.g., Gelman et al. 2004). The regression coefficients,  $\beta_j$ 's followed a normal distribution *N*(0, 100), while the variance components  $\sigma_j^2$ 's were assigned inverse-gamma IG(2, 1) priors. The spatial decay parameters,  $\phi_j$ 's, followed an informative Uniform prior, with support that ranged from 1 km to the maximum distance between any two grid cells (i.e., approximately 325 km). Parameter estimates were based on post burn-in samples from three MCMC chains of 10,000 iterations each. Burn-in and convergence were diagnosed using the Gelman-Rubin diagnostic (Gelman and Rubin 1992). Candidate model fit to the observed data was assessed using the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). Lower values of DIC indicate improved model fit.

To investigate whether species bioclimatic relationships are related to the amount of habitat, I regressed the resulting spatially-varying coefficient estimates of TMAX, TMIN, and PRECIP against the values of GPLAND and FPLAND (hereafter, TMAX-GPLAND, TMIN-GPLAND, and PRECIP-GPLAND for grassland birds, and TMAX-FPLAND, TMIN-FPLAND, and PRECIP-FPLAND for forest birds).

Prior to statistical analysis, I removed all blocks with more than 50% open water coverage and those that did not have continuous land cover coverage or survey effort data. Ultimately, I used a total of n = 4,490 blocks for birds of open lands and n = 4,492 blocks for forest birds to fit the models. I standardized all the covariates to ease the comparison and interpretation of the coefficient estimates. The SVI models were run in R 2.15.1 statistical program (R Development Core Team, <u>http://www.r-project.org/</u>) using package spBayes (Finley and Banerjee 2013). In close collaboration with Dr. Andrew Finley, I wrote the SVC models in C++ programming language. Summaries of parameter estimates were generated using the R CODA package (Plummer et al. 2012).

#### **2.3 RESULTS**

## 2.3.1 Model comparison

For all species, the SVC model provided improved fit to the data (Appendix 2.1), suggesting that birds are responding to climatic variation in a spatially-dependent manner. This spatial heterogeneity allowed for evaluation of bioclimatic relationships across the changing amount of habitat.

#### 2.3.2 Bioclimatic relationships

For grassland birds, TMAX coefficient estimates resulting from the SVI models were positive for six species (Table 2.1). For five forest birds, TMAX coefficient estimates were negative for black-throated blue warblers, black-throated green warblers, blackburnian warblers, vireos, Canada warblers, and nuthatches (Table 2.1). TMAX estimates were positive for gnatcatchers, kinglets, flycatchers, titmice, and veeries, suggesting that these birds preferred warmer locations. As a group, grassland birds occurred in landscapes of higher maximum temperatures than forest breeding birds (Fig. 2.1).

For most grassland birds, 95% credible intervals of the TMIN coefficient estimates overlapped zero, with exception of kingbirds for which the estimate was positive (Table 2.1). For forest birds, TMIN coefficient estimates were negative for seven species, with exception of kinglets, flycatchers and titmice, for which TMIN was positive. As a group, forest birds in general occurred in landscapes of lower minimum temperature than grassland birds (Fig. 2.1).

PRECIP coefficient estimates were negative for almost all grassland birds (Table 2.1, Fig. 2.1). PRECIP coefficient estimates were positive for seven forest birds and negative for one forest species (Table 1). In general, grassland birds occurred in locations of lower precipitation than forest birds (Fig. 2.1).

**Table 2.1** Coefficient estimates resulting from the spatially-varying intercept (SVI) models for the intercept (INTERCEPT), 2000-05 average maximum temperature of the breeding season (TMAX), 2000-05 average minimum temperature of the breeding season (TMIN), 2000-05 average total precipitation of the breeding season (PRECIP), and 2000-05 survey effort (EFF) for grassland and forest birds. Species occurrence data were retrieved from the 2000-05 New York State Breeding Bird Atlas.

Guild Species Coefficient 50% 2.5% 97   INTERCEPT -0.277 -0.816 0.   American Kestrel TMAX 0.198 -0.044 0.   (Felse memory) TMIN 0.175 -0.098 0.	7.5% 0.353 0.458 0.413 0.386 0.379 .616
INTERCEPT -0.277 -0.816 0.   American Kestrel TMAX 0.198 -0.044 0.   (February manufactor) TMIN 0.175 -0.098 0.	0.353 0.458 0.413 0.386 0.379 .616
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$\begin{array}{c} \text{American Kestrel} \\ (E_{1}) = m m m m m m m m m m m m m m m m m m $	).413 ).386 ).379 .616
	).386 ).379 .616
(Falco sparverius) PRECIP -0.584 -0.827 -0.	0.379 .616
EFF 0.281 0.184 0.	.616
INTERCEPT -2.142 -2.704 -1.	
Northern Herrier TMAX 0.086 -0.205 0.	).364
$(Circus cuspies) \qquad TMIN \qquad 0.001 -0.268  0.$	0.313
PRECIP -0.438 -0.744 -0.	0.163
EFF 0.487 0.387 0.	).596
INTERCEPT 0.205 -0.691 1.	.022
Eastern Plushind TMAX 0.531 0.285 0.	).819
(Siglig siglis) TMIN -0.045 -0.343 0.	0.210
( <i>Statia statis</i> ) PRECIP -0.399 -0.642 -0.	0.126
EFF 0.242 0.152 0.	0.345
INTERCEPT 2.156 1.623 2.	.566
Factor Kinghird TMAX 0.451 0.124 0.	0.801
Crossland (Tyrannus tyrannus) TMIN 0.413 0.094 0.	).734
PRECIP -0.770 -1.049 -0.	0.452
EFF 0.683 0.489 0.	.900
INTERCEPT -2.588 -3.341 -1.	.507
Hornad Lark TMAX -0.008 -0.360 0.	0.322
(Eremonhila alnestric) TMIN 0.354 -0.016 0.	).764
( <i>Eremophila alpesins</i> ) PRECIP -0.617 -0.978 -0.	).222
EFF 0.029 -0.103 0.	0.134
INTERCEPT -3.545 -4.075 -2.	.857
Grasshopper Sparrow TMAX 0.235 -0.133 0.	0.613
( <i>Ammodramus</i> TMIN 0.269 -0.087 0.	0.627
<i>savannarum</i> ) PRECIP -0.291 -0.602 -0.	0.007
EFF 0.206 0.112 0.	0.304
INTERCEPT 0.142 -0.724 0.	0.647
Savannah Sparrow TMAX 0.288 0.009 0.	1.589
( <i>Passerculus</i> TMIN -0.181 -0.491 0.	0.102
<i>sandwichensis</i> ) PRECIP -0.577 -0.879 -0.	.308
EFF 0.178 0.096 0.	.270

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Habitat	Species	Coefficient	Coefficient Estimates		
Guild		coefficient -	50%	2.5%	97.5%
		INTERCEPT	-3.026	-3.768	-2.322
	Vesner Sparrow	TMAX	0.025	-0.336	0.431
	(Poogestas graminaus)	TMIN	0.353	-0.038	0.704
	(Fooeceles grammeus)	PRECIP	-0.277	-0.612	0.035
		EFF	0.067	-0.060	0.165
		INTERCEPT	-0.680	-1.431	-0.202
	Bobolink	TMAX	0.475	0.219	0.833
	(Dolichonyr oryziyorus)	TMIN	-0.334	-0.598	0.056
	(Douchonyx or yzivorus)	PRECIP	-0.614	-0.930	-0.311
Grassland		EFF	0.166	0.065	0.267
Birds		INTERCEPT	1.399	0.264	2.059
	Brown-headed Cowbird	TMAX	0.493	0.229	0.808
	(Molothrus ater)	TMIN	0.219	-0.121	0.538
	(motorninus arer)	PRECIP	-0.544	-0.854	-0.200
		EFF	0.348	0.197	0.507
		INTERCEPT	0.175	-1.018	1.227
	Fastern Meadowlark	TMAX	0.326	0.057	0.611
	( <i>Sturnella magna</i> )	TMIN	0.020	-0.300	0.295
		PRECIP	-0.607	-0.898	-0.289
		EFF	0.155	0.060	0.236
	Blue-gray Gnatcatcher (Polioptila caerulea)	INTERCEPT	-2.402	-2.955	-1.620
		TMAX	0.670	0.406	0.952
		TMIN	0.235	-0.042	0.526
		PRECIP	-0.457	-0.676	-0.198
		EFF	0.248	0.156	0.343
	Blue-headed Vireo (Vireo solitaries)	INTERCEPT	-0.684	-1.927	0.182
		TMAX	-0.367	-0.624	-0.094
		TMIN	-0.746	-1.011	-0.459
		PRECIP	0.602	0.374	0.830
		EFF	0.210	0.120	0.309
Forest Birds		INTERCEPT	-2.254	-2.681	-1.812
	Golden-crowned Kinglet (Regulus satrapa)	TMAX	-0.916	-1.174	-0.678
		TMIN	-0.573	-0.871	-0.249
		PRECIP	0.345	0.091	0.589
		EFF	0.203	0.112	0.296
	Great Crested Flycatcher ( <i>Myiarchus crinitus</i> )	INTERCEPT	0.896	-0.003	2.162
		TMAX	0.422	0.194	0.652
		TMIN	0.257	0.020	0.482
		PRECIP	-0.231	-0.480	0.040
		EFF	0.185	0.079	0.303
			G		

# Table 2.1 (cont'd)

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Habitat	Species	Coefficient	Coefficient Estimates		
Guild		eoemeient -	50%	2.5%	97.5%
		INTERCEPT	-1.089	-1.816	-0.437
	Pod branstad Nutbatab	TMAX	-0.386	-0.634	-0.150
	(Sitta Canadansis)	TMIN	-0.587	-0.842	-0.333
	(sina Canadensis)	PRECIP	0.328	0.108	0.548
		EFF	0.316	0.225	0.404
		INTERCEPT	-0.008	-0.815	0.713
	Tufted Titmouse	TMAX	1.119	0.743	1.451
	(Racelophus bicelor)	TMIN	0.247	-0.092	0.557
	(Baeolophus bicolor)	PRECIP	0.014	-0.311	0.288
		EFF	0.177	0.064	0.299
		INTERCEPT	1.515	0.799	2.247
	Voort	TMAX	0.284	0.024	0.541
	(Cathanus fusacsoons)	TMIN	-1.000	-1.396	-0.736
	(Cainarus Juscescens)	PRECIP	-0.122	-0.403	0.222
		EFF	0.275	0.166	0.389
		INTERCEPT	-0.654	-1.939	0.273
	Black-and-white Warbler ( <i>Mniotilta varia</i> )	TMAX	-0.157	-0.337	0.060
		TMIN	-0.236	-0.544	0.002
		PRECIP	0.128	-0.101	0.339
		EFF	0.301	0.200	0.403
Forest Birds		INTERCEPT	-1.402	-2.097	-0.670
	Black-throated Blue	TMAX	-0.540	-1.010	-0.292
	Warbler	TMIN	-0.799	-1.065	-0.387
	(Setophaga caerulescens)	PRECIP	0.919	0.657	1.215
		EFF	0.232	0.140	0.340
		INTERCEPT	0.192	-0.485	0.806
	Black-throated Green	TMAX	-0.874	-1.173	-0.587
	Warbler	TMIN	-0.884	-1.182	-0.562
	(Dendroica virens)	PRECIP	0.752	0.476	0.993
		EFF	0.188	0.080	0.281
		INTERCEPT	-0.827	-1.308	-0.116
	Blackburnian Warbler ( <i>Dendroica fusca</i> )	TMAX	-0.565	-0.884	-0.250
		TMIN	-0.734	-1.067	-0.397
		PRECIP	0.845	0.581	1.091
		EFF	0.225	0.126	0.325
	Canada Warbler (Cardellina Canadensis)	INTERCEPT	-1.757	-2.247	-1.395
		TMAX	-0.274	-0.553	-0.033
		TMIN	-0.550	-0.849	-0.241
		PRECIP	0.414	0.194	0.607
		EFF	0.143	0.060	0.233

# Table 2.1 (cont'd)

**Figure 2.1** Mean values of the coefficient estimates of 2000-05 average spring maximum temperature (TMAX), 2000-05 average spring minimum temperature (TMIN), and 2000-05 average total spring precipitation (PRECIP) for both avian groups: grassland birds (circles) and forest birds (triangles). 95% confidence intervals indicate whether the mean value of the coefficient estimates is significantly different from zero. On each plot from left to right: American kestrel, northern harrier, eastern bluebird, eastern kingbird, horned lark, grasshopper sparrow, savannah sparrow, vesper sparrow, bobolink, brown-headed cowbird, eastern meadowlark, blue-gray gnatcatcher, blue-headed vireo, golden-crowned kinglet, great crested flycatcher, red-breasted nuthatch, tufted titmouse, veery, black-and-white warbler, black-throated blue warbler, black-throated green warbler, blackburnian warbler, and Canada warbler. Species occurrence data were retrieved from the 2000-05 New York State Breeding Bird Atlas.



#### 2.3.3 Heterogeneity of bioclimatic relationships across habitat amount

After incorporating covariate-specific spatial random effects in the SVC models, coefficient estimates of all variables became strongly spatially varying (Appendix 2.2). There was a clear variation in the values of the TMAX coefficient estimates across the habitat gradient (Table 2.2), but there was no visible pattern that would differentiate responses of grassland birds from those of forest species (Fig. 2.2). The strongest relationship was recorded for black-and-white warblers (posterior mean 0.0089, Table 2.2), followed by larks (posterior mean -0.0082, Table 2.2), Canada warblers (posterior mean 0.0065, Table 2.2), and harriers (posterior mean 0.0052, Table 2.2). The TMAX-GPLAND and TMAX-FPLAND associations were positive for 13 and negative for 9 out of 23 species (Table 2.2).

The strongest TMIN-GPLAND and TMIN-FPLAND associations were recorded for bobolinks (posterior mean -0.0388, Table 2.2), followed by veeries (posterior mean 0.0247, Table 2.2), flycatchers (posterior mean 0.0231, Table 2.2), and savannah sparrows (posterior mean -0.0214, Table 2.2). Most of the associations for grassland birds were negative, with exception of grasshopper sparrows, larks, and vesper sparrows (Table 2.2; Fig. 2.2). The negative TMIN-GPLAND associations suggested that positive values of TMIN coefficient estimates were generally found in localities where grasslands were scarce, and declined steadily towards negative values in regions with abundant grasslands (Appendix 2.2). Thus, only in regions where grassland habitat was limited, birds were more likely to be found when average temperatures were higher, whereas we generally saw the reverse relationship in regions with extensive grasslands.

For forest birds, the TMIN-FPLAND associations were generally positive, with exception of gnatcatchers, kinglets, nuthatches, and black-throated blue warblers (Table 2.2, Fig. 2.2). The

two strongest TMIN-FPLAND associations among forest birds were found for flycatchers and veeries (Table 2.2), both of which were positive. For these two species, the estimates of TMIN coefficients were negative in localities with scarce forests and positive in highly forested regions. Thus, only in regions where forests are scant, flycatchers and veeries are less likely to be found when average temperatures are higher, whereas we will generally see the reverse relationship in extensively forested regions. For the remaining species with the positive TMIN-FPLAND associations, TMIN coefficients were almost exclusively negative (Appendix 2.2). These species are thus least likely to be found when average temperatures are higher, whereas are high, though this relationship is the strongest in scarcely forested habitats and diminishes with increasing amount of forest.

The eight strongest associations between PRECIP coefficient estimates and land cover were recorded for grassland birds (in the order of strength: meadowlarks, harriers, bobolinks, kestrels, kingbirds, vesper sparrows, savannah sparrows, larks; Table 2.2, Fig. 2.2), all of them positive. Positive associations indicate that PRECIP coefficient estimates were negative in locations with low GPLAND, suggesting in those places the likelihood of species occurrence will be low if precipitation is high. With increasing GPLAND, we recorded a weakening of this relationship (Appendix 2.2). The PRECIP-FPLAND associations for forest species were generally weaker than those of grassland birds (Fig. 2.2). **Table 2.2** Relationships between amount of habitat (percent of grassland cover, GPLAND, and percent of forest cover, FPLAND, for grassland and forest birds, respectively) and spatially-varying coefficient estimates for 2000-05 average maximum temperature of the breeding season (TMAX), 2000-05 average minimum temperature of the breeding season (TMIN), and 2000-05 average total precipitation of the breeding season (PRECIP). The "\*" symbol indicates that less than 10% of the spatially-varying coefficient estimates (i.e., TMAX, TMIN, PRECIP coefficient estimates resulting from the SVC models) had the 95% credible intervals not overlapping zero. Species occurrence data were retrieved from the 2000-05 New York State Breeding Bird Atlas.

Habitat	Species	Coefficient	Coef	Coefficient Estimates		
Guild			50%	2.5%	97.5%	
	American Vestral (Eglas	TMAX	-0.0041	-0.0043	-0.0041	
	American Kestrei ( <i>Faico</i>	TMIN	-0.0155	-0.0165	-0.0144	
	sparverius)	PRECIP	0.0158	0.0147	0.0189	
	Northarn Harrian (Cinaus	TMAX	0.0053	0.0048	0.0057	
	Normenn Harner (Circus	TMIN	-0.0188	-0.0198	-0.0178	
	Cyuneus)	PRECIP	0.0281	0.0263	0.0300	
	Eastern Bluebird (Siglig	TMAX	-0.0013	-0.0014	-0.0011	
	sialis)	TMIN	-0.0111	-0.0123	-0.0100	
		PRECIP	0.0033	0.0029	0.0037	
	Fastern Kingbird (Tyrannus	TMAX	0.0015	0.0014	0.0016	
	tyrannus)	TMIN	-0.0133	-0.0144	-0.0123	
	<i>i yrannas)</i>	PRECIP	0.0141	0.0133	0.0149	
	Horned I ark (Fremonhila	TMAX	-0.0082	-0.0085	-0.0079	
	alpostris)	TMIN	0.0051	0.0050	0.0053	
		PRECIP	0.0055	0.0053	0.0057	
Graceland	Grasshopper Sparrow (Ammodramus savannarum)	TMAX	-0.0020	-0.0021	-0.0019	
Birds		TMIN*	0.0025	0.0024	0.0026	
		PRECIP*	-0.00024	-0.00025	-0.00022	
	Savannah Sparrow (Passerculus sandwichensis)	TMAX*	-0.0003	-0.0004	-0.0002	
		TMIN	-0.0214	-0.0223	-0.0205	
		PRECIP	0.0105	0.0093	0.0177	
	Vesper Sparrow ( <i>Pooecetes</i> gramineus)	TMAX*	0.0012	0.0009	0.0015	
		TMIN	0.0023	0.0021	0.0025	
		PRECIP	0.0106	0.0101	0.0111	
	Bobolink (Dolichonyr	TMAX	0.0026	0.0024	0.0029	
	oryzivorus)	TMIN	-0.0576	-0.0616	-0.0534	
		PRECIP	0.0256	0.0234	0.0278	
	Brown-headed Cowbird	TMAX	-0.0041	-0.0044	-0.0037	
	(Molothrus ater)	TMIN	-0.0177	-0.0186	-0.0168	
		PRECIP	-0.0021	-0.0026	-0.0015	
	Fastern Meadowlark	TMAX	0.0048	0.0046	0.0050	
	(Sturnella magna)	TMIN	-0.0099	-0.0106	-0.0093	
	(Surnetta magna)	PRECIP	0.0316	0.0302	0.0328	

Continued on next page

Habitat	Species	Coefficient	Coefficient Estimates		
Guild			50%	2.5%	97.5%
		TMAX	0.00007	0.00001	0.00014
	Blue-gray Ghalcalcher	TMIN	0.0001	-0.0002	0.0004
	(Polioptila caerulea)	PRECIP	-0.00005	-0.00004	0.0003
	Blue-headed Vireo (Vireo solitaries)	TMAX	0.0025	0.0022	0.0029
		TMIN	0.0049	0.0046	0.0051
		PRECIP	-0.0032	-0.0035	-0.0029
	Colden around Kinglet	TMAX	0.0017	0.0013	0.0020
	( <i>Reculus saturana</i> )	TMIN	-0.0013	-0.0019	-0.0008
	(Reguius sairapa)	PRECIP	-0.0017	-0.0033	-0.00009
	Great Created Elwastahar	TMAX	-0.0017	-0.0021	-0.0014
	(Myjarobus origitus)	TMIN	0.0231	0.0221	0.0241
	(Mytarchus crinitus)	PRECIP	0.0048	0.0046	0.0050
	Pad brasstad Nutbatah	TMAX	0.0010	0.0008	0.0012
	(Sitta Canadensis)	TMIN	-0.0013	-0.0015	-0.0011
		PRECIP	0.00075	0.0003	0.0012
	Tufted Titmouse	TMAX	0.00045	0.00009	0.00089
	(Baeolophus bicolor)	TMIN	0.0094	0.0079	0.0108
Equart Dinda		PRECIP	0.00006	-0.00006	0.00018
Forest Birds	Veery (Catharus fuscescens)	TMAX	0.0042	0.0039	0.0045
		TMIN	0.0247	0.0234	0.0261
		PRECIP	-0.0011	-0.0013	-0.0008
	Black-and-white Warbler ( <i>Mniotilta varia</i> )	TMAX	0.0089	0.0084	0.0094
		TMIN	0.0013	0.0011	0.0014
		PRECIP	-0.0008	-0.0011	-0.0005
	Black-throated Blue	TMAX	-0.0020	-0.0021	-0.0019
	Warbler ( <i>Setophaga caerulescens</i> )	TMIN	-0.00011	-0.00014	-0.00009
		PRECIP	0.00164	0.00155	0.00172
	Plack throated Green	TMAX	-0.0004	-0.0008	-0.00001
	Black-throated Green	TMIN	0.0037	0.0033	0.0041
	Warbier (Denaroica virens)	PRECIP	-0.0022	-0.0024	-0.0020
	Plackburnian Warblar	TMAX	0.0037	0.0034	0.0039
	( <i>Dendroica fusca</i> )	TMIN	0.0119	0.0113	0.0125
		PRECIP	-0.0025	-0.0038	-0.0013
	Canada Warbler ( <i>Cardellina Canadensis</i> )	TMAX	0.0065	0.0060	0.0070
		TMIN	0.00603	0.00558	0.00648
		PRECIP	-0.0024	-0.0028	-0.0021

# Table 2.2 (cont'd)

**Figure 2.2** Mean values of the associations between the percent habitat (percent grassland cover, GPLAND, and percent forest cover, FPLAND, for grassland and forest species, respectively) and coefficient estimates of 2000-05 average spring maximum temperature (TMAX), 2000-05 average spring minimum temperature (TMIN), and 2000-05 average total spring precipitation (PRECIP) for both avian groups: grassland birds (circles) and forest birds (triangles). 95% confidence intervals indicate whether the mean value of the associations is significantly different from zero. On each plot from left to right: American kestrel, northern harrier, eastern bluebird, eastern kingbird, horned lark, grasshopper sparrow, savannah sparrow, vesper sparrow, bobolink, brown-headed cowbird, eastern meadowlark, blue-gray gnatcatcher, blue-headed vireo, goldencrowned kinglet, great crested flycatcher, red-breasted nuthatch, tufted titmouse, veery, black-and-white warbler, black-throated blue warbler, black-throated green warbler, blackburnian warbler, and Canada warbler. Species occurrence data were retrieved from the 2000-05 New York State Breeding Bird Atlas.



### **2.4 DISCUSSION**

My findings supported the notion that grassland and forest birds exhibit divergent bioclimatic relationships. Forest breeding birds were more likely to occur in cooler and wetter regions, while grassland birds preferred warmer and drier conditions. I also found support for our second prediction that increasing amounts of forests will mitigate the negative responses of forest breeding birds to climatic variability. Contrary to my prediction that the magnitude of bioclimatic relationships would remain constant for grassland birds, I found that the bioclimatic relationships of grassland birds are highly heterogeneous across the habitat gradient. Notably, the evidence suggests that the negative consequences of climate change are likely to be intensified in regions with extensive grasslands. Taken together, my results support our initial hypothesis that grassland birds will be more vulnerable to a warming climate than birds of forested habitats.

### 2.4.1 Bioclimatic relationships

Space-varying intercept models allowed comparison of the spatially-homogeneous bioclimatic relationships of grassland and forest birds. In general, there were differences in the way grassland and forest birds responded to each of the climatic covariate. Six grassland birds responded positively to maximum temperatures, indicating that in general these birds prefer warmer regions. The likelihood of occurrence of seven forest birds was negatively associated with maximum temperatures, suggesting the higher likelihood of forest birds in cooler locations. Most forest species also had a strong negative response to minimum temperatures, while almost none of the grassland birds responded to this covariate. The spatially-homogeneous bioclimatic relationships suggest that only a portion of grassland birds might benefit from increasing temperatures resulting from climate change. On the other hand, evidence from stationary models suggests that most forest species will be negatively affected as temperatures continue to rise. My

results therefore corroborate other findings, which suggest that forest birds are generally colddwelling species (Clavero and Brotons 2010) and thus, all else being equal, potentially more vulnerable to rising temperatures than grassland birds. However, caution is advised here as the results of the space-varying intercept models do not take into account the potential influences of habitat and thus lead to conclusions that differ from those arising from the models accounting for the spatial heterogeneity of bioclimatic relationships.

I found that grassland birds had a strong negative response to precipitation. This finding fits well with the notion that open habitats generally exhibit drier microclimatic conditions (Geiger et al. 2009), thus supporting fauna more sensitive to high precipitation regimes (Skagen and Adams 2012). On the contrary, the likelihood of occurrence of forest birds was positively affected by precipitation. Thus, my results suggest that precipitation will be an important climatic variable, albeit less predictable than temperature, in shaping responses of breeding birds to climate change. Furthermore, given the disparate relationships of grassland and forest birds with precipitation, we can expect that changing precipitation patterns will likely affect these two avian groups in a contrasting way. In situations when climate change causes precipitation to increase, grassland birds will likely be adversely affected, while forest species will generally benefit from increasing rainfall.

## 2.4.2 Heterogeneity of bioclimatic relationships across habitat amount

Evaluation of spatial variation in bioclimatic relationships using space-varying coefficients models allowed a richer ecological interpretation and painted a different picture of potential vulnerabilities of grassland and forest birds to climate change. My results supported the expectation that bioclimatic relationships of forest birds exhibit strong spatial variation, which was associated with the amount of available forest cover. As I predicted, the relationships

between forest birds and maximum and minimum temperatures showed mostly positive associations with the amount of forest cover. Regions with limited forest cover were characterized by the strongest negative relationships with temperature, and these relationships became weaker or positive as the amount of forest increased. Thus, more extensively forested regions might successfully mitigate the increasing ambient temperatures associated with climate change. Such modulating effect is likely due to the cooler microclimatic conditions created by the forest canopy closure, which decreases summer ground-level temperatures via increased shading (De Frenne et al. 2013). These counteracting effects of forest canopies on climate warming are likely to persist into the future as long as the structure of forest canopies remains undisturbed. My results are also in agreement with studies suggesting that expansion of forests will potentially compensate or reverse responses of communities to climate change (Clavero et al. 2011) by leading to the dominance of cold-dwelling assemblages.

The amount of forest cover in general did not affect the occurrence-precipitation relationships of forest birds. This finding corroborates the results from the spatially-stationary framework, where positive relationships of forest birds with precipitation were recorded. The lack of spatial heterogeneity in the occurrence-forest cover relationship affirms that forest birds will be more likely to occupy wetter regions regardless of the amount of habitat they have available. Thus, the effects of precipitation changes resulting from climate change on forest species will likely be homogenous throughout the species' geographic extent.

I found that bioclimatic relationships of grassland birds were spatially heterogeneous, but the associations between occurrence-climate relationships and habitat were different than the ones found for forest birds. Relationships of grassland species with maximum and minimum temperatures generally showed mostly negative associations with the amount of grassland cover.

Interestingly, responses of grassland birds to maximum temperatures across the increasing amount of their habitat were not consistent across all species within the group, with some species showing negative relationships (kestrels, cowbirds, bluebirds, grasshopper sparrows, and larks) and others having positive associations (bobolinks, kingbirds, meadowlarks, and harriers). For the species exhibiting positive associations, we see an increase in the strength of the relationship between likelihood of species occurrence and maximum temperatures as the amount of grasslands increases. This indicates that birds in localities with abundant grasslands might benefit from climate change-induced temperature increases more than those found in regions with scarce suitable cover. Species exhibiting negative associations will likely benefit from temperature increases in regions with scarce grasslands.

The associations between species responses to minimum temperatures and the amount of grassland cover were more consistent across all grassland species. I found that likelihood of occurrence of grassland birds is greater when minimum temperatures are higher, but only in locations where their habitat is relatively limited. On the other hand, locations characterized by extensive grasslands show decreasing probability of occurrence associated with higher minimum temperatures. Thus, I suggest that extensive grasslands might exacerbate, rather than mitigate, the negative consequences climate change might have on birds of those habitats. One possible explanation may be that smaller patches of grassland habitat are likely to be surrounded by cover types with cooler microclimates, thus creating more benign environmental conditions in the face of increasing temperatures. On the other hand, large and unfragmented grassland patches will be deprived of the potential counteracting effects of surrounding patches on climate warming and thus might be more susceptible to rapid temperature increases. Hence, species found in those habitats will likely experience higher rates of extreme weather events (e.g., heat waves,
flooding), potentially making them more vulnerable to the impacts of climate change. This potential influence of landscape matrix on species bioclimatic relationships is not surprising. Indeed, studies have shown that the quality of the surrounding matrix influences species persistence (e.g., Prugh et al. 2008, Willis and Bhagwat 2009) and has a strong influence on species responses to environmental conditions (Pervedello and Vieira 2010). My results thus reinforce the need to acknowledge the importance of the entire landscape when evaluating bioclimatic relationships and their interactions with land cover, rather than focusing only on the perceived suitable habitat.

Grassland birds also showed strong variation in precipitation relationships across their habitat gradient. For the majority of grassland species, their occurrence was negatively affected by high precipitation regimes in regions with scarce grassland habitat. This relationship weakened with increasing amount of grasslands. Thus, increasing rainfall would be most detrimental to grassland birds in regions with low amounts of their habitat, whereas populations in regions with abundant grasslands should be less affected by increasing precipitation. Given the uncertainty of future precipitation trends (IPCC 2013), forecasting how grassland birds will be affected by changing precipitation patterns is difficult. However, regardless of whether rainfall increases or decreases, my study indicates that the direction and magnitude of responses of these birds will be heavily dependent on the quantity of available habitat.

In summary, I found evidence that grassland and forest birds exhibit divergent bioclimatic relationships. I also found that the responses of both avian groups to climatic variability are affected by the amount of habitat, though the influence of land cover differs for grassland and forest birds. An increasing amount of forest cover might mitigate negative effects of climate change, especially rising temperatures, in populations of forest breeding birds.

However, contrary to my expectations, I found that grasslands will likely exacerbate, rather than mitigate, the negative consequences of increasing temperatures in locations where this habitat is prevalent. Our work thus shows that the interaction of climate and land cover can produce unexpected relationships and needs to be carefully evaluated to make sound forecasts of consequences of climate change to natural communities.

Grassland birds already show almost universal pattern of decline across both North American and European continents (Reif 2013). The decline in area of agricultural lands associated with abandonment of agricultural fields and their conversion to woody successional stages is one of the most important factors responsible for decline of these birds (Fuller et al. 1995, Brennan and Kuvlesky 2005). Recent studies suggest that climate change will likely add to declines of grassland birds (e.g., Kleijn et al. 2010). My work corroborates the results from these studies but also stresses the importance of considering both climate and land cover as synergistic factors shaping avian responses. In terms of grassland birds, the impacts of both climate and land cover are difficult to reconcile. While regions of extensive grasslands generally benefit populations of grassland birds by providing suitable breeding habitat, they are also likely to increase the vulnerability of birds to changing climatic conditions. Thus, climate change will threaten grassland birds mostly in habitats, in which they would otherwise be able to persist. My findings therefore add another dimension to the knowledge of potential vulnerabilities of grassland birds to the environmental change and stress the importance of considering implications of climate change while designing future conservation strategies.

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# LANDSCAPE FRAGMENTATION AFFECTS RESPONSES OF AVIAN COMMUNITIES TO CLIMATE CHANGE

In preparation for publication in *Global Change Biology*:

Jarzyna M.A. (following order of authors TBD, currently alphabetical) Finley A.O., Maurer B.A, Porter W.F. and Zuckerberg B. Landscape fragmentation affects responses of avian communities to climate change. To be submitted to *Global Change Biology*.

# ABSTRACT

Accurate forecasting of the consequences of climate change is contingent upon our understanding of the relationship between biodiversity patterns and climatic variability. While a range of implications of climate change to individual species have been well documented, understanding of the community-level consequences of changing climate is still limited. Additionally, factors other than climate will affect the way communities respond to climate change. My objectives were to investigate the relationship between temporal turnover in avian biodiversity and changes in climatic conditions, and to assess the roles of landscape fragmentation and migratory behavior as factors affecting this relationship. Using data from the 1980 and 2000 New York State Breeding Bird Atlas, I quantified temporal turnover in the entire avian biodiversity and in diversity of different migratory groupings. I applied Bayesian spatiallyvarying intercept models to evaluate the relationship between temporal turnover and covariates of temporal trends in climatic conditions as well as landscape fragmentation. The DIC statistic designated the models including interaction terms between climate change and landscape fragmentation to be superior to the models without the interaction terms, suggesting that the relationship between temporal turnover and changes in climatic conditions was affected by the level of landscape fragmentation. Specifically, I found weaker associations between temporal turnover and climatic change in regions with prevalent habitat fragmentation. I suggest that avian communities in fragmented landscapes are more robust to climate change than communities

found in contiguous habitats because they comprise of species with wider thermal niches and are thus less susceptible to temperature increases. I conclude that highly fragmented regions are like to undergo less pronounced changes in composition and structure of faunal communities as a result of climate change, whereas those changes are likely to be greater in contiguous and unfragmented habitats.

## **3.1 INTRODUCTION**

Accurate forecasting of the consequences of climate change and sound conservation strategies resulting from these forecasts are contingent upon our understanding of the relationship between biodiversity patterns and climatic variability. To date, the majority of research regarding the implications of climate change to biodiversity has evaluated responses of individual species (e.g., Parmesan and Yohe 2003, La Sorte and Thompson 2007, Marini et al. 2009, Zuckerberg et al. 2009). Variation in the individual species responses is predicted to lead to disruptions of communities and ecosystems (Brotons and Jiguet 2010), but the complex nature of ecological interactions makes it difficult to extrapolate from the scales of individuals and populations to the community or ecosystem level (Walther et al. 2002). However, in order to fully understand consequences of climate change to ecological communities it is imperative that a direct link between changes in community composition and changes in climatic conditions is established.

Measuring species turnover has potential to offer a useful and simple way of evaluating the implications of climate change to ecological communities (e.g., Tuomisto 2010a, Tuomisto 2010b, Barton et al. 2013). Species turnover can be quantified in multiple ways but generally is an aggregate of gains and losses of species comprising a community (e.g., Tuomisto 2010b). Traditionally, turnover has been used to describe biodiversity patterns across space rather than time (i.e., spatial turnover), but it can also be viewed in terms of a temporal change in

community composition that has occurred at the same site across a particular time period (i.e., temporal turnover). Given that spatial turnover in species composition is thought to be at least partially related to spatial variation in environmental variables (Gaston et al. 2007, Buckley and Jetz 2008, Gutiérrez-Cánovas et al. 2013, Siefert et al. 2013), it is expected that temporal turnover is related to temporal changes such as climate and thus could be a useful indicator of impacts of climate change on biodiversity.

Even though impacts of climate change on biodiversity will be felt across a wide range of ecosystems, different communities are likely to respond to climate change in a disparate way because a wide range of environmental factors will influence species' vulnerabilities to climate change. For example, past research suggests that the interaction between climate and land cover will affect the way in which biodiversity responds to climate change (Opdam and Wascher 2004; Jeltsch et al. 2011). Specifically, habitat fragmentation is thought to affect the rate of distributional shifts associated with climate change, allowing species in less fragmented habitats to disperse faster and farther (Opdam and Wascher 2004). If species in contiguous (i.e., unfragmented) habitats respond quicker to climate change than species in fragmented habitats, then changes in communities should also follow the same pattern. Thus, higher rates of temporal turnover in contiguous habitats are expected compared to temporal turnover in fragmented habitats is also expected.

Beyond influences of land cover, some behavioral traits are likely to affect species' responses to climate change (e.g., Jones and Cresswell 2010). Migratory strategy is one of such traits (Lehikoinen and Sparks 2010). For example, some resident species of birds are expected to respond relatively fast to changing climate on their breeding and wintering grounds because they

are exposed to year-round climatic conditions of the same site. Similarly, short-distance migrants are likely to adjust the timing of migration to changing temperatures because they are thought to rely more on weather conditions. On the other hand, long-distance migratory birds are cued by photoperiod (Forchhammer et al. 2002, Saino et al. 2009, DeLeon et al. 2011), thus are unlikely to be able to track changing climatic conditions as closely as short-distance migrants or resident species (e.g., Lemoine et al. 2007, Doxa et al. 2012). Indeed, resident birds have undergone increases in occupancy and abundance in recent decades, while migratory birds (long-distance migrants in particular) have experienced population losses (e.g., Lemoine and Böhning-Gaese 2003). However, the consensus what proportion of the decline in migratory bird populations, if any, can be attributed to climate change has not been reached. If migratory traits indeed affect birds' responses to climate change, we can expect different migratory groups to show different associations with changing climate. Specifically, temporal turnover in long-distance migrant communities is expected to show weaker association with changes in climatic conditions than temporal turnover in short-distance migrants or resident birds communities.

Despite some initial investigations into recent temporal changes in community composition (e.g., Kampichler et al. 2012), the relationship between temporal turnover in biodiversity and the interaction of climatic changes, land-cover, and migratory behavior, to the best of my knowledge, has not yet been evaluated. The paucity of research in this arena has likely been caused by the scarcity of long-term, large-scale ecological data. I intend to fill this research gap by investigating the drivers of temporal turnover in avian biodiversity across New York using Breeding Bird Atlas data (Andrle and Carroll 1988, McGowan and Corwin 2008). Specifically, I sought to evaluate two hypotheses: (1) temporal turnover in avian assemblages is related to climate change, but the strength of the relationship between temporal turnover and

changes in climatic conditions varies with the degree of habitat fragmentation, and (2) temporal turnover in communities of long-distance migrants show weaker association with changing climatic conditions than temporal turnover in short-distance migrants and resident birds communities.

## **3.2 METHODS**

#### **3.2.1 Site description**

The study area is the State of New York, USA. New York covers 128,401 km<sup>2</sup>, including 4,240 km<sup>2</sup> of inland water. Climate of New York is affected by the state's broad elevation gradient as well as by the proximity to lakes Erie and Ontario, and the Atlantic Ocean. Adirondack and Catskill Mountains in the east are among the highest regions of the state, with elevation varying between 600 and 1,500 m. The elevation of the south-western New York ranges from approximately 300 to 900 m, while north-western New York as well as Hudson River valley and New York City are low-lying with elevation ranging from approximately 0 to 200 m.

In general, New York state is covered by approximately 51.2% forest (deciduous, evergreen, and mixed forests), 13.4% pasture and hay, 8.2% cultivated crops, 2.9% scrub and shrub, 1.0% grassland and herbaceous, 8.0% wetland cover, 8.7% developed land, and 0.2% barren land (Homer et al. 2004). New York offers a broad gradient of landscape fragmentation. The regions of the Adirondack and Catskill Mountains are the least fragmented, with expansive regions of forest land. The land cover of the Hudson River valley is fragmented by residential and commercial development, whereas the landscapes of western New York are characterized mostly by agriculture-forest mosaic.

### 3.2.2 Breeding Bird Atlas

I used the New York State Breeding Bird Atlas (BBA) to characterize changes in avian communities through time. BBA is a statewide survey that documented the distribution of breeding birds in New York. To date, BBA has been conducted in two time periods, 1980-85 (hereafter, BBA1980; Andrle and Carroll 1988) and 2000-05 (hereafter, BBA2000; McGowan and Corwin 2008). For both BBAs, a grid system was used to define the basic unit for reporting data. The entire State of New York was divided into approximately 1,300 squares, each measuring 10 km x 10 km. The BBA reporting unit (a block) was one quarter of this square and measures 5 km x 5 km and a total of 5,335 blocks covered the entirety of New York State. This data set represents one of the largest and finest resolution atlases in the world (Gibbons et al. 2007).

A total of 242 species were recorded for BBA1980 and 248 species were recorded for BBA2000 (Andrle and Carroll 1988, McGowan and Corwin 2008). Observations were made by skilled birders who spent at least 8 hours in each block, visited all cover types in each block, and included at least one nighttime visit to document nocturnal species. Observer effort was recorded for each BBA and reported as a number of person hours (measured as the sum of the number of hours spent in each block x the number of people surveying each block; McGowan and Zuckerberg 2008). The BBA represents a detection/non-detection dataset, although nondetection indicates that species could not be found given search criteria (McGowan and Corwin 2008).

## **3.2.3 Temporal turnover**

I quantified temporal turnover (TURN) as an aggregate of species gains (hereafter called colonization) and species losses (hereafter called extinction) within a particular site. Specifically, temporal turnover was calculated as follows:

$$TURN = \frac{E+C}{E+C+P},$$
 Eqn. 3.1

where E is the number of species that went extinct in the block between BBA1980 and BBA2000, C is the number of species that colonized the block between BBA1980 and BBA2000, and P is number of species in the same block common to both BBAs (i.e., persistence).

In addition to temporal turnover, I quantified its components: proportion of colonization events (i.e., proportion of species gained a particular site between BBA1980 and BBA2000; COL) and proportion of extinction events (i.e., proportion of species lost a particular site between BBA1980 and BBA2000; EXT) in each block between BBA1980 and BBA2000. COL and EXT were calculated as follows:

$$COL = \frac{C}{E+C+P},$$
 Eqn. 3.2

$$EXT = \frac{E}{E+P},$$
 Eqn. 3.3

For TURN and COL, I used the sum of *E*, *C*, and *P* as the denominator of the Eqns. 3.1 and 3.2. I recognize that species already present in a block in BBA1980 could not have colonized that block and that species other than those included in *E*, *C*, and *P* metrics could have potentially colonized a site. However, I was simply interested in the proportion of species that colonized the site relative to all the species found within the block; thus I deem the sum of *E*, *C*, and *P* as an appropriate choice for the denominator of both equations. For EXT, I used the sum of *E* and *P* as the denominator, because only species present in a block in BBA1980 could have gone extinct. The values of TURN, COL, and EXT are bounded by 0 and 1; values approaching 0 indicate low temporal turnover, colonization, or extinction in a block between BBA1980 and BBA2000, while values approaching 1 indicate high temporal turnover, colonization, or extinction in a block between BBA1980 and BBA2000.

I calculated TURN, EXT, and COL for four groups of birds: all species regardless of their migratory strategy (hereafter, all species), long-distance migrants, short-distance migrants, and resident species. I used The Birds of North America Online to classify birds to migratory groupings (http://bna.birds.cornell.edu/bna/, Appendix 1.1). I considered a species a resident if at least a part of its wintering range is located in New York. I considered a species a long-distance migrant if it crosses a body of water (i.e., either the Gulf of Mexico or both the Gulf of Mexico and the Caribbean Sea) to reach its wintering grounds.

## **3.2.4 Habitat fragmentation**

Habitat fragmentation was identified using the National Land Cover Data (NLCD) derived from the Landsat Thematic Mapper satellite data. Even though the NLCD is available for three time periods (i.e., 1992, 2001, and 2006), there is no land-cover data readily available for the time period of BBA1980. Thus, I used a space-for-time substitution to assess whether temporal turnover is related to landscape fragmentation (e.g., Pickett 1989). Space-for-time substitution assumes that spatial variation is equivalent to a temporal variation, and relationships between variables (e.g., species turnover and land-cover) derived for one time step across a large spatial extent will be equivalent to that derived for two time steps. I used the 2001 NLCD, because it coincided well with the time of BBA2000.

Prior to landscape analysis, I consolidated the following land cover classes: open water and perennial ice and snow classes into one class of water/ice; open space developed, low

intensity developed, medium intensity developed, high intensity developed into one class of developed land; cultivated crops and pasture/hay into one class of agriculture; and deciduous forest, evergreen forest, mixed forest, and forested wetland into one class of forest. Consolidation of these land-cover types improved accuracy of classification and simplified the environment for purposes of our evaluation. Upon consolidation, I examined the following land cover classes: water/ice, developed, barren land, forest, scrub/shrub, grassland/herbaceous, agriculture, and wetlands.

I used FRAGSTATS 4.1 (McGarigal et al. 2012) and the Geospatial Modelling Environment (GME, <u>http://www.spatialecology.com/gme/</u>) to quantify landscape fragmentation. Because I focused my analysis on a diverse suite of species with varying habitat requirements, I chose a landscape-scale variable to capture broad-scale variation in habitat fragmentation. I chose Edge Density (ED) as a measure of landscape fragmentation because an increase in habitat edge is a primary outcome of habitat fragmentation (Hargis et al. 1998). ED was also reported as an effective tool for evaluating landscape fragmentation and performed better than other popular landscape fragmentation indices (Hargis et al. 1998). However, in situations when landscape consists entirely of one cover type, the ED would be 0 regardless of the type of land-cover present. Therefore, in order to differentiate between landscapes that consisted entirely of natural land cover (e.g., forest) and those mostly developed (e.g., cities), I also calculated the proportion of developed land (DEVEL) metric and included it as a covariate in our models.

## 3.2.5 Climatic trends

The climate data was derived from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate mapping system (Daly and Gibson 2002). PRISM consists of interpolated

monthly maximum and minimum temperatures and precipitation at a 2.5-arcmin resolution from 1891-2010 for the entire contiguous United States.

I calculated the magnitude of the 25-year (1980-2005) trend in average monthly maximum and minimum temperatures and in total monthly precipitation using Ordinary Least Squares regression. The slope of the OLS regression indicates the magnitude of the trend and reflects the amount of change in climatic variables that occurred between 1980 and 2005. I then interpolated the trend magnitudes for each BBA block and averaged the monthly values to reflect breeding season (May through September) trend magnitude in maximum and minimum temperatures (TMAX and TMIN, respectively) and in total precipitation (PRECIP). The trend magnitudes of TMAX and TMIN were expressed in °C/25 years, while the units of the trend magnitudes of PRECIP were in mm/25 years.

#### 3.2.6 Survey effort

Increasing survey effort often results in a higher number of recorded species (Tobler et al. 2008). Drastically different survey effort between BBA1980 and BBA2000 could increase the values of TURN, EXT, and COL indices indicating high temporal turnover, which could be a result of different number of recorded species rather than actual changes in species identities throughout time. To account for potential survey effort bias, I calculated the absolute difference in the number of person hours between BBA1980 and BBA2000 (EFF = |EFF1980 - EFF2000|) for each BBA block and included it as a covariate in the models.

## **3.2.7 Statistical analysis**

For each of the four groupings (all species, long-distance migrants, short-distance migrants, and resident species), I evaluated five competing statistical models. All five models included all climatic variables (TMAX, TMIN, and PRECIP) as well as survey effort (EFF), one model

additionally included ED, one included interaction terms between all climatic covariates and ED, one included both ED and DEVEL, and one included interaction terms between all climatic covariates and ED as well as the main effect of DEVEL. I standardized all the covariates to ease the comparison and interpretation of the coefficient estimates.

We used a Bayesian model estimation procedure. Each response variable (temporal turnover TURN, extinction EXT, or colonization COL) at each location (**s**) was modeled as a binomial random variable. Let  $y(\mathbf{s})$  be a response variable, then  $y(\mathbf{s}) \sim B(\rho(s), N(s))$  where N(s) is the total number of species found at least once in a block from the first to the second atlas count (for TURN and COL) or the total number of species found in first atlas count (for EXT). For each BBA block, let p(s) = y(s)/N(s). Also, let  $\mathbf{x}(\mathbf{s})$  be a vector containing the explanatory variables for each model. All models had spatially varying intercepts, which were created by adding spatially structured random effects to the model intercept. A generalized linear model approach was used to relate responses to explanatory variables. Using the logit link  $\eta(s) = \log[p(s)/\{1-p(s)\}]$  the SVI model was

$$\eta(s) = w(\mathbf{s}) + \boldsymbol{\beta} \mathbf{x}(s)$$
Eqn. 3.4

where  $\boldsymbol{\beta}$  is a vector of regression coefficients and w(s) is a random effect representing spatially varying adjustments to the intercept. We assume each element in w(s) arises from a spatial Gaussian Process (GP) (see, e.g., Banerjee et al. 2004 or Cressie and Wikle 2011 for more details). Specifically,  $w(s) \sim GP(\boldsymbol{\theta}, C(s, s'))$ , where *s* and *s*' are any two locations within the study area, the spatial covariance  $C(s, s') = \sigma \rho(s, s'; \phi)$  with variance parameter  $\sigma^2$ , correlation function  $\rho(\cdot; \phi)$ , and spatial decay parameter  $\phi$ . The exponential spatial correlation was assumed for  $\rho(\cdot)$ . Prior distributions on the parameters complete the hierarchical model specification (e.g., Gelman et al. 2004). The global regression coefficients,  $\beta$ 's followed a Normal distribution N(0, 100), while the variance component  $\sigma^2$  was assigned inverse-Gamma IG(2, 1) priors. The spatial decay parameter,  $\phi$ , followed an informative Uniform prior, with support that ranged from 1 km to the maximum distance between any two grid cells (i.e., approximately 350 km). I ran three MCMC chains for 20,000 iterations each. Convergence was diagnosed using the Gelman-Rubin diagnostic (Gelman and Rubin 1992). As appropriate for a Bayesian framework, candidate model fit to the observed data was assessed using the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). Lower values of DIC indicate improved fit.

Prior to statistical analysis, I removed all blocks that did not have continuous land cover coverage, blocks with more than 50% open water coverage, and those that did not have survey effort data. I withheld 10% of the data for model validation. Ultimately, I used a total of N = 4,271 blocks to fit the models and 473 blocks to validate the models. The models were run in R 2.15.1 statistical package (R Development Core Team 2013, http://www.r-project.org/) using package spBayes (Finley and Banerjee 2013). In a Bayesian framework, parameter estimates have valid posterior distributions and inferences are made using mean or median as well as the credible intervals of these posterior distributions. Credible intervals overlapping zero imply that the parameter in question is not different from zero. Summaries of parameter estimates were generated using the R CODA package (Plummer et al. 2012).

## **3.3 RESULTS**

#### **3.3.1 Relationships with climate change and habitat fragmentation**

## **3.3.1.1** Temporal turnover

For all species, the mean value of TURN was 0.384 (95% confidence intervals resulting from 10,000 non-parametric bootstrap samples: LCI 0.381, UCI 0.387). This indicates that on average approximately 62% of the species were common to both BBAs and 38% of species had either colonized or become extinct within the average block (Fig. 3.1). The north-eastern part of the state, which is the location of the Adirondack Mountains, experienced the highest rates of temporal turnover across BBA1980 and BBA2000 (Fig. 3.1). Central and north-western New York underwent lowest temporal turnover (Fig. 3.1).

Model selection indicated that the variation in temporal turnover of all species was best accounted for by the most complex model (Table 3.1). The selection of the most complex model points to the importance of the interactions between landscape fragmentation and change in climatic conditions in explaining temporal turnover in species composition between BBA1980 and BBA2000. Model validation indicated relatively good abilities of the best model to predict temporal turnover in all species, though low values of TURN tended to be over-predicted, while high value tended to be under-predicted (Appendix 3.1). **Figure 3.1** Temporal turnover, extinction, and colonization observed between 1980-85 and 2000-05 for communities of (A) all recorded species regardless of their migratory status, (B) long-distance migrants, (C) short-distance migrants, and (D) resident birds. Temporal turnover was calculated as a proportion of all species gained or lost between 1980-85 and 2000-05 in a particular site (i.e., Breeding Bird Atlas block) relative to all species recorded across both time periods; extinction was calculated as a proportion of species lost between 1980-85 and 2000-05 in a particular site relative to all species present in a block in 1980-85; colonization was calculated as a proportion of species gained between 1980-85 and 2000-05 in a particular site relative to all species recorded across both time periods. High values of all three metrics indicate high temporal turnover, extinction, and colonization.



**Table 3.1** Comparison of five competing models of temporal turnover for all four avian groupings (i.e., all species, long-distance migrants, short-distance migrants, and resident species). Models included the following covariates: magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season and edge density (PRECIP\*ED), and survey effort (EFF). Model comparison was done using Deviance Information Criterion (DIC); pD indicates the effective number of parameters.

Grouping	Model	ΔDIC	pD
All Species	TMAX*ED + TMIN*ED + PRECIP*ED +	0.0	106.7
	TMAX + TMIN + PRECIP + ED + DEVEL +	20.0	104.3
		22.0	106.2
	IMAA*ED + IMIN*ED + PRECIP*ED + EFF	55.9 55.0	106.2
	IMAX + IMIN + PRECIP + ED + EFF	55.9	103.6
	TMAX + TMIN + PRECIP + EFF	109.9	102.6
	TMAX*ED + TMIN*ED + PRECIP*ED +	0.0	96.1
	DEVEL + EFF		
Long-distance	TMAX + TMIN + PRECIP + ED + DEVEL +	10.8	93.6
Migrants	EFF		
wingraints	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	53.9	95.1
	TMAX + TMIN + PRECIP + ED + EFF	69.1	93.3
	TMAX + TMIN + PRECIP + EFF	72.3	92.3
	TMAX + TMIN + PRECIP + ED + DEVEL +	0.0	88.9
	EFF		
~	TMAX*ED + TMIN*ED + PRECIP*ED +	2.3	92.5
Short-distance	DEVEL + EFF		
Migrants	TMAX + TMIN + PRECIP + ED + EFF	22.8	89.3
	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	25.9	92.4
	TMAX + TMIN + PRECIP + EFF	57.1	83.5
Resident Species	TMAX*FD + TMIN*FD + PRFCIP*FD +	0.0	95.0
	DEVEL + FEE	0.0	25.0
	$TM\Delta X = D + TMIN = D + PRECIP = D + EFE$	16	94 5
	TMAX LD + TMIN LD + TRECH LD + LTTMAX + TMIN + DECID + ED + DEVEL +	1.0 7.5	01 /
	$\frac{1}{1} \frac{1}{1} \frac{1}$	1.5	J1. <del>4</del>
	TMAV + TMIN + DDECID + ED + EEE	12.6	01 /
	IWAA + IWIIN + FKEUF + ED + EFF	12.0	91.4 02.6
	IMAX + IMIN + PRECIP + EFF	103.6	93.6

Parameter estimates of the top model indicated that temporal turnover was positively related to TMAX, suggesting that higher temporal turnover was observed in regions where maximum temperatures increased the most (Fig. 3.2; also see Appendix 3.2 for parameter estimates of all models of temporal turnover). Temporal turnover was also positively associated with TMIN, but the effect of minimum temperatures on TURN was affected by the value of ED (Fig. 3.3). In regions of low landscape fragmentation, large increases in minimum temperatures were associated with high temporal turnover, but the effect of TMIN diminished or reversed in locations with high landscape fragmentation. There was a negative association of temporal turnover and ED, but the presence of multiple ED interaction terms in the model makes it difficult to interpret the main effects of ED on temporal turnover. There was a positive relationship between temporal turnover and DEVEL (Fig. 3.2), indicating that highly urbanized regions generally experienced increased temporal turnover.

**Figure 3.2** Coefficient estimates (i.e., mean values of the posterior distribution and associated credible intervals) of the best model for each avian grouping for (A) temporal turnover, (B) extinction, and (C) colonization. Abbreviations for the covariates are as follows: magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX-ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMIN-ED), interaction between magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMIN-ED), interaction between magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMIN-ED), interaction between magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMIN-ED), interaction between magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (PRECIP-ED).



**Figure 3.3** Effects size plots resulting from the best temporal turnover models for (A) the interaction of magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN) and edge density (ED) for all species, (B) the interaction of magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN) and edge density (ED) for long-distance migrants, (C) the interaction of magnitude of the 25-year (1980-2005) trend in total precipitation of the breeding season (PRECIP) and edge density (ED) for long-distance migrants, (D) the interaction of magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX) and edge density (ED) for resident birds, and (E) the interaction of magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN) and edge density (ED) for resident birds. The interaction terms shown here are the ones whose credible intervals did not overlap zero. Green points are the observed data points and are plotted to indicate levels of confidence for the predicted surface.



### 3.3.1.2 Extinction

The mean value of EXT for all species was 0.210 (LCI 0.206, UCI 0.213), which indicates that on average approximately 21% of species of the original assemblage had become extinct within the average block (Fig. 3.1). North-eastern part of the state (i.e., the Adirondack Mountains) and regions surrounding the Finger Lakes displayed higher than average rates extinction (Fig. 3.1). Extinction was lower in remaining parts of New York.

Model selection indicated that the most complex model provided the best fit to the variation in the proportion of extinction events (Table 3.2). Selection of the most complex model indicates that interactions between land cover fragmentation and change in climatic conditions contribute to explaining extinction rates observed in avian communities. Model validation indicated the best model in general under-predicted the low values of extinction and over-predicted high values of extinction (Appendix 3.1).

Parameter estimates of the top model indicated that extinction in communities of all species was positively related to TMIN, though the effect of minimum temperatures on extinction rates was affected by ED (Fig. 3.4; also see Appendix 3.3 for parameter estimates resulting from all models of extinction). In regions of low landscape fragmentation, large increases in minimum temperatures were associated with high proportion of extinction events, but the effect of TMIN diminished or reversed in locations with high landscape fragmentation (Fig. 3.4). Extinction was positively associated with PRECIP (Fig. 3.2), indicating that regions with increasing precipitation experienced higher rates of extinction. This positive relationship between extinction and PRECIP was not influenced by ED. There was a negative association of extinction and ED, but the presence of multiple ED interaction terms in the model makes it difficult to interpret the main effects of ED on extinction in long-distance migrant communities.

There was a positive relationship between extinction and DEVEL (Fig. 3.2), indicating increased proportion of extinction events in highly urbanized regions.

**Table 3.2** Comparison of five competing models of extinction for all four avian groupings (i.e., all species, long-distance migrants, short-distance migrants, and resident species). Models included the following covariates: magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season and edge density (PRECIP\*ED), and survey effort (EFF). Model comparison was done using Deviance Information Criterion (DIC); pD indicates the effective number of parameters.

Grouping	Model	ΔDIC	pD
All Species	TMAX*ED + TMIN*ED + PRECIP*ED + DEVEL + EFF	0.0	118.2
	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	33.4	117.9
	TMAX + TMIN + PRECIP + ED + DEVEL +	45.1	115.3
	EFF		
	TMAX + TMIN + PRECIP + ED + EFF	75.7	114.6
	TMAX + TMIN + PRECIP + EFF	165.8	115.9
	TMAX*ED + TMIN*ED + PRECIP*ED +	0.0	110.6
	DEVEL + EFF		
Long-distance	TMAX + TMIN + PRECIP + ED + DEVEL +	22.8	107.3
Long-distance Migranta	EFF		
wingraints	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	49.3	108.9
	TMAX + TMIN + PRECIP + EFF	78.6	106.7
	TMAX + TMIN + PRECIP + ED + EFF	78.7	106.6
	TMAX*ED + TMIN*ED + PRECIP*ED +	0.0	97.1
	DEVEL + EFF		
Short distance	TMAX + TMIN + PRECIP + ED + DEVEL +	4.7	94.4
Migronto	EFF		
Migrains	TMAX + TMIN + PRECIP + ED + EFF	15.9	93.4
	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	17.4	97.3
	TMAX + TMIN + PRECIP + EFF	77.15	94.8
Resident Species	TMAX*ED + TMIN*ED + PRECIP*ED +	0.0	104.5
	DEVEL + EFF		
	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	2.3	102.5
	TMAX + TMIN + PRECIP + ED + EFF	20.5	99.5
	TMAX + TMIN + PRECIP + ED + DEVEL	20.9	101.5
	+EFF		
	TMAX + TMIN + PRECIP + EFF	93.4	100.7

**Figure 3.4** Effects size plots resulting from the best extinction models for (A) the interaction of magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN) and edge density (ED) for all species, (B) the interaction of magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN) and edge density (ED) for long-distance migrants, (C) the interaction of magnitude of the 25-year (1980-2005) trend in total precipitation of the breeding season (PRECIP) and edge density (ED) for long-distance migrants, (D) the interaction of magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN) and edge density (ED) for short-distance migrants, and (E) the interaction of magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN) and edge density (ED) for resident birds. The interaction terms shown here are the ones whose credible intervals did not overlap zero. Green points are the observed data points and are plotted to indicate levels of confidence for the predicted surface.



### 3.3.1.3 Colonization

For all species, the mean value of COL was 0.214 (LCI 0.211, UCI 0.218), indicating that on average 21% of all the species present in a block across both time periods are the ones that had colonized the site. Colonization was in general higher in eastern and western parts of the state, while central and southern New York underwent lower colonization rates (Fig. 3.1). However, the spatial pattern of colonization rates was less clumped than the one displayed by temporal turnover or extinction.

Model selection procedure selected more than one model as the top model accounting for the variation in the proportion of colonization events. The top two models included the most complex model (i.e., containing all the interaction terms) and the model with main effects of all covariates but without the interaction terms (Table 3.3). However, despite the fact that the most complex model was selected among the top models, none of the interaction terms was associated with COL (see Appendix 3.4 for parameter estimates resulting from all models of colonization). Model validation indicated the top models under-predicted the low values of colonization and over-predicted high values of colonization (Appendix 3.1). Colonization was positively related to TMAX and negatively related to PRECIP, indicating that highest proportions of colonization events were found in regions where maximum temperatures increased the most and precipitation decreased the most (Fig. 3.2). There was a positive relationship between colonization and DEVEL (Fig. 3.2), which indicates that highly urbanized regions experienced highest colonization rates. **Table 3.3** Comparison of five competing models of colonization for all four avian groupings (i.e., all species, long-distance migrants, short-distance migrants, and resident species). Models included the following covariates: magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season and edge density (PRECIP\*ED), and survey effort (EFF). Model comparison was done using Deviance Information Criterion (DIC); pD indicates the effective number of parameters.

Grouping	Model	ΔDIC	pD
All Species	TMAX*ED + TMIN*ED + PRECIP*ED + DEVEL + EFF	0.0	117.0
	TMAX + TMIN + PRECIP + ED + DEVEL + EFF	1.25	114.1
	TMAX + TMIN + PRECIP + EFF	7.5	111.6
	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	8.5	116.7
	TMAX + TMIN + PRECIP + ED + EFF	11.5	114.4
	TMAX*ED + TMIN*ED + PRECIP*ED +	0.0	112.0
	DEVEL + EFF		
Long distance	TMAX + TMIN + PRECIP + ED + DEVEL +	0.19	109.0
Long-distance	EFF		
Migrants	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	10.5	110.8
	TMAX + TMIN + PRECIP + ED + EFF	14.4	108.4
	TMAX + TMIN + PRECIP + EFF	22.1	106.9
	TMAX + TMIN + PRECIP + EFF	0.0	92.3
	TMAX + TMIN + PRECIP + ED + DEVEL +	1.3	95.9
Short distance	EFF		
Migrants	TMAX*ED + TMIN*ED + PRECIP*ED +	4.2	97.8
wingraints	DEVEL + EFF		
	TMAX + TMIN + PRECIP + ED + EFF	5.3	95.8
	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	8.1	98.2
Resident Species	TMAX + TMIN + PRECIP + ED + DEVEL	0.0	104.8
	+EFF		
	TMAX + TMIN + PRECIP + ED + EFF	0.5	104.9
	TMAX*ED + TMIN*ED + PRECIP*ED + EFF	1.3	108.0
	TMAX*ED + TMIN*ED + PRECIP*ED +	5.2	109.8
	DEVEL + EFF		
	TMAX + TMIN + PRECIP + EFF	26.6	103.7

## 3.3.2 Responses of different migratory groupings

#### **3.3.2.1** Temporal turnover

The mean temporal turnover in long-distance migratory communities was 0.381 (LCI 0.377, UCI 0.384). Short-distance migrants displayed lower average temporal turnover than long-distance migrants, with the mean TURN value of 0.349 (LCI 0.345, UCI 0.353). Resident birds underwent higher temporal turnover than other migratory groupings, with the mean value of TURN of 0.423 (LCI 0.419, UCI 0.427). For all three migratory groupings, the Adirondack Mountains underwent the highest temporal turnover across BBA1980 and BBA2000 (Fig. 3.1). Additionally, resident birds also displayed high temporal turnover in the Catskills Mountains, as well as in the western parts of New York. This high-turnover pattern, however, was not found for long- or short-distance migratory birds in these regions (Fig. 3.1). Rather, migratory birds showed higher temporal turnover also in more urbanized areas surrounding New York City; temporal turnover in resident species was low in this region. The remaining regions of the state generally underwent the lower temporal turnover (Fig. 3.1).

The most complex model was selected as the top model for long-distance migrants and resident species (Table 3.1). For resident birds, the second best model (i.e., the model with interaction terms but without main effects of DEVEL) can also be considered viable given the values of  $\Delta$ DIC (Table 3.1). The selection of the most complex model indicates that interactions between landscape fragmentation and some aspects of climatic change are important to explaining the temporal turnover of in communities of long-distance migrant and resident birds. For short-distance migrants, the top selected model was the one with main effects of all covariates, but lacking the interaction terms (Table 3.1), suggesting that interactions between land cover and climate do not contribute importantly to explaining the changes in the

communities of short-distance migrants. Model validation indicated that temporal turnover was best predicted for long-distance migrants and resident birds (Appendix 3.1 for model validation plots), while the top model for short-distance migratory birds performed relatively poorly.

Based on the results from the top model for long-distance migrants, temporal turnover in long-distance migrant communities was positively associated with TMIN (Fig. 3.2), but the effect of minimum temperatures on TURN was affected by the value of ED (Fig. 3.3). Similarly to results for all species, we found that in regions of low landscape fragmentation, large increases in minimum temperatures were associated with high temporal turnover, but the effect of TMIN diminished or reversed in locations with high landscape fragmentation. Temporal turnover was also related to the interaction between PRECIP and ED (Fig. 3.2). In regions of low landscape fragmentation, increasing precipitation is associated with decreasing temporal turnover; on the other hand, in regions of high landscape fragmentation, temporal turnover increases with increasing precipitation. The effect size of the PRECIP-ED interaction on temporal turnover, however, is lower than that of TMIN-ED interaction (Fig. 3.3). There was a positive relationship between temporal turnover and DEVEL (Fig. 3.2), indicating that high temporal turnover is associated with highly urbanized regions.

Parameter estimates of the top model for short-distance migrants indicated that temporal turnover in short-distance migrant communities was positively related to TMAX. Thus, higher temporal turnover was observed in regions where maximum temperatures increased the most (Fig. 3.2). The relationship between temporal turnover in short-distance migratory communities and ED was negative, while the relationship between temporal turnover and DEVEL was positive. These parameter estimates suggest that low temporal turnover was generally found in

regions with high landscape fragmentation, though highly urbanized regions generally experienced increased temporal turnover.

Parameter estimates of the top model for resident species indicated that the effect of both maximum and minimum temperatures on TURN in resident birds was affected by the value of ED (Fig. 3.2, Fig. 3.3). In regions of low landscape fragmentation, large increases in maximum and minimum temperatures were associated with high temporal turnover, but the effect of TMIN diminished or reversed in locations with high landscape fragmentation. Temporal turnover was also negatively associated with PRECIP (Fig. 3.2), indicating that higher temporal turnover was observed in regions where precipitation decreased the most. This relationship between temporal turnover and PRECIP was not affected by the level of landscape fragmentation. There was a negative association of temporal turnover and ED, but the presence of multiple ED interaction terms in the model makes it difficult to interpret the main effects of ED on temporal turnover. TURN in resident birds communities was negatively related to DEVEL, indicating that low temporal turnover in resident birds was generally found in highly developed regions.

#### 3.3.2.2 Extinction

Average extinction in long-distance migrants equaled 0.226 (LCI 0.221, UCI 0.230). Shortdistance migrants displayed slightly lower average extinction than long-distance migrants, with the mean values of EXT of 0.187 (LCI 0.183, UCI 0.190). The mean EXT for resident birds was 0.203 (LCI 0.198, UCI 0.207). For all three migratory groups, higher than average extinction was displayed in the north-eastern part of the state, approximately in the location of the Adirondack Mountains (Fig. 3.1). Long- and short-distance migrants also underwent higher extinction in the Finger Lakes region (Fig. 3.1).

The most complex model was selected as the top model for all three migratory groupings (Table 3.2). Selection of the most complex model suggests that interactions between landscape fragmentation and trends in climatic factors contribute to explaining extinction rates observed in disparate migratory groupings. Similarly to models of temporal turnover, model validation indicated that extinction was best predicted for long-distance migrants and resident birds (see Appendix 3.1 for model validation plots), while the top model for short-distance migratory birds performed relatively poorly.

Based on the results from the top model for long-distance migrants, extinction was negatively associated with TMAX (Fig. 3.2), indicating that higher extinction in long-distance migrant communities was observed in regions where maximum temperatures decreased the most. The relationship between extinction and TMIN was affected by ED (Fig. 3.4). In regions of low landscape fragmentation, large increases in minimum temperatures were associated with high proportion of extinction events, but the effect of TMIN diminished in regions with pervasive landscape fragmentation (Fig. 3.4). PRECIP was positively associated with extinction (Fig. 3.2), though this effect was also affected by the level of landscape fragmentation (Fig. 3.4). In regions of low landscape fragmentation, increasing precipitation was associated with slowly decreasing extinction rates; while in highly-fragmented regions, extinction increased sharply with increasing precipitation (Fig. 3.4). There was a positive association between extinction and DEVEL (Fig. 3.2), suggesting increased extinction in long-distance migrants in highly urbanized regions.

Parameter estimates of the top model for short-distance migrants suggested the importance of the interaction of TMIN and ED (Fig. 3.2). In regions of low landscape fragmentation, large increases in minimum temperatures were associated with high proportion of extinction events in short-distance migratory birds, but the effect of TMIN reversed and

diminished in highly fragmented regions (Fig. 3.4). Extinction was also positively related to DEVEL (Fig. 3.2), suggesting that high rates of extinction were expected in highly urbanized regions.

Based on the results from the top model for resident birds, extinction was positively associated with TMAX (Fig. 3.2), indicating that extinction increased with increasing maximum temperatures. Extinction was related to the interaction of TMIN and ED (Fig. 3.2). Specifically, in regions of low landscape fragmentation, large increases in minimum temperatures were associated with high proportion of extinction events, but the effect of TMIN reversed and diminished in highly fragmented locations (Fig. 3.4). Extinction was also negatively related to DEVEL, indicating that highly developed regions experienced lower rates of extinction in resident birds.

## 3.3.2.3 Colonization

Mean colonization for long-distance migratory birds was 0.192 (LCI 0.188, UCI 0.195), while short-distance migratory birds showed slightly lower rates of colonization, with a mean COL value of 0.155 (LCI 0.152, UCI 0.159). In comparison, resident birds displayed the highest colonization rates, with the mean value of COL of 0.268 (LCI 0.264, UCI 0.272). Resident species underwent high colonization throughout most of the state, with exception of central and southern parts of New York (Fig. 3.1). Long- and short-distance migrants showed relatively low colonization rates throughout New York, with exception of several isolated locations in the Adirondack Mountains (Fig. 3.1).

More than one model was selected as the top model for all three avian groupings (Table 3.3). For long-distance migrants, the most complex model along with the model with main effects of all covariates but without the interaction terms were selected as top models (Table 3.3).

For short-distance migrants, the simplest model along with the model with main effects of all covariates but without the interaction terms were selected as the top models (Table 3.3). For resident birds, the top three models included the model with main effects of all covariates but without the interaction terms (the best model), the model with main effects excluding the DEVEL covariate (second best model), and the model with interaction terms excluding the main effects of DEVEL (third best model). Model validation indicated that colonization was best predicted for resident birds (see Appendix 3.1 for model validation plots), while the top models for long- and short-distance migratory birds performed relatively poorly.

Given that none of the interactions terms from the top model was associated with colonization in long-distance migrants, we make inferences based on the model without the interaction terms. Proportion of colonization events in long-distance migrant communities was positively associated with TMAX and negatively associated with PRECIP (Fig. 3.2), indicating that higher colonization was observed in regions where maximum temperatures increased the most and where precipitation decreased the most. There was a positive relationship between colonization and both ED and DEVEL (Fig. 3.2), suggesting higher colonization rates in regions with high landscape fragmentation and those highly urbanized.

For short-distance migrants, we did not find any relationships between proportion of colonization events and any of the tested covariates in the best model (Fig. 3.2). Based on the results from the top model for resident birds, colonization was negatively associated with PRECIP (Fig. 3.2), indicating higher colonization in regions where precipitation decreased the most. Colonization in resident bird communities was also negatively related to ED (Fig. 3.2), indicating that low colonization in resident birds was generally found in regions with pervasive landscape fragmentation.

## **3.4 DISCUSSION**

My findings supported my first hypothesis that changes in avian community composition are related to changes in climate, but the strength of the relationship between temporal turnover and climate change is affected by the level of landscape fragmentation. Associations were weaker between community change and climatic change in regions with prevalent habitat fragmentation. However, my findings did not support my second hypothesis regarding the differences in responses of long-distance migrants and other migratory groupings to climate change. Associations of temporal turnover and climate change were generally similar among all migratory groupings.

### 3.4.1 Relationships with climate change and habitat fragmentation

There are at least two alternative interpretations for the pattern of associations between community dynamics, climatic change, and landscape fragmentation. One, communities in contiguous landscapes might be able to respond more quickly to changes in temperatures and precipitation, perhaps due to potential for unimpeded movement. Such interpretation would fit well with research suggesting that unfragmented habitats allow higher rates of species distributional shifts associated with climate change (e.g., Opdam and Washer 2004). If that were the case, communities in fragmented habitats would be likely to lag behind changing climatic conditions and, therefore, be less capable of adapting in the face of climate change. This lag would initially be reflected in communities being compositionally similar across time and thus showing no temporal turnover. However, through time, it is likely that species will eventually disappear from locations in which they can no longer find suitable climatic conditions. Such localized species extinctions will ultimately result in higher community temporal turnover and higher extinction rates, perhaps on par with those currently observed in unfragmented landscapes.

How plausible is the unimpeded movement explanation in New York State? Using the same dataset, Zuckerberg et al. (2009) documented shifts in breeding ranges of 129 species of birds. They found that the birds exhibiting shifts in their range boundaries all had different breeding habitat associations, suggesting that land cover was not a factor in the observed range expansion. Specifically, they found no evidence for more pronounced range shifts of forest breeding birds in unfragmented habitats such as those of the Adirondack and Catskill Mountains. Given their findings, it seems unlikely that contiguous habitats facilitating the climate change-driven range shifts may be at the root of the higher rates of temporal turnover, extinction, and colonization I am observing.

An alternative interpretation is that avian communities in fragmented landscapes are more robust to changes in temperatures and precipitation resulting from climate change than communities found in contiguous habitats. If that were the case, we would expect little or no temporal change in community composition and weaker associations with changing climatic conditions in fragmented landscapes. Indeed, heterogeneous and fragmented habitats are often composed of a large proportion of habitat generalists (e.g., Tscharntke et al. 2012, Estavillo et al. 2013). Habitat generalists tend to have wider thermal breadths than habitat specialists (Barnagaud et al. 2012), which potentially allows them to tolerate greater changes in climatic conditions. On the other hand, narrower thermal niches of habitat specialists (Barnagaud et al. 2012) might make them vulnerable to even small increases in temperatures. Thus, in this scenario, we would expect communities in contiguous or less fragmented habitats (i.e., comprised mainly of habitat specialists) to continue to undergo relatively large compositional

changes as a result of climate change, while those found in fragmented regions (i.e., comprised largely of generalists) to show relatively small changes, until perhaps some thermal threshold is reached.

A post hoc analysis revealed that temporal turnover in generalist birds was lower than that of birds with any other habitat associations (mean temporal turnover of 0.238 [LCI 0.234, UCI 0.242] for generalist birds in comparison with 0.384 [LCI 0.381, UCI 0.387] for all breeding birds, 0.444 [LCI 0.440, UCI 0.448] for forest, 0.317 [LCI 0.131, UCI 0.321] for shrubland, 0.439 [LCI 0.432, UCI 0.446] for grassland, and 0.536 [LCI 0.532, UCI 0.541] for wetland breeding birds). Rates of extinction and colonization events were also lower for generalists than for any other habitat grouping (extinction: 0.122 [LCI 0.119, UCI 0.126; generalists], 0.210 [LCI 0.206, UCI 0.213; all breeding birds], 0.233 [LCI 0.228, UCI 0.237; forest], 0.181 [LCI 0.177, UCI 0.186; shrubland], 0.331 [LCI 0.323, UCI 0.339; grassland], 0.307 [LCI 0.301, UCI 0.313; wetland]; colonization: 0.132 [LCI 0.128, UCI 0.135; generalists], 0.214 [LCI 0.211, UCI 0.218; all breeding birds], 0.265 [LCI 0.261, UCI 0.269; forest], 0.159 [LCI 0.156, UCI 0.163; shrubland], 0.148 [LCI 0.143, UCI 0.152; grassland], 0.309 [LCI 0.304, UCI 0.314; wetland]). Lower values of temporal turnover, extinction, and colonization in these communities perhaps suggest that generalist birds are indeed more robust to climatic changes, lending support to the second interpretation of the pattern of stronger associations between community change and climatic change in unfragmented regions.

## 3.4.2 Responses of different migratory groupings

I found differences in the rates of temporal turnover in communities of resident, long-, and shortdistance migratory birds. For example, communities of long-distance migrants showed higher proportion of extinction events than the other two avian groupings. Resident birds displayed
higher temporal turnover and higher proportion of colonization events than long- and shortdistance migratory birds. Despite these differences in community change, I found little evidence to support our second prediction that temporal turnover in communities of long-distance migrants would show weaker associations with changing climatic conditions. In fact, I found that the strength of the associations of temporal turnover with climatic changes was similar across all avian groupings. Thus, it is unlikely that the disparities in the observed rates of community change in this ecological system can be explained by the variation in responses of different migratory groupings to changing climatic conditions.

Similarly, I found few differences in responses of different migratory groupings to landscape fragmentation, though strong interaction between climatic and habitat fragmentation variables might have obscured a potential relationship. Interestingly, however, I found that increasing amount of urban development was associated with high temporal turnover in longand short-distance migratory communities, but resident species underwent lower temporal turnover in highly urbanized regions. It is likely that highly developed and residential areas might be beneficial to some resident birds, especially during the wintering months when supplemental feeding is provided. Thus, it is plausible that the observed higher proportion of colonization events in resident birds is driven by factors other than climatic changes.

Alternatively, higher proportion of colonization events in resident species can be associated with less benign climatic conditions during winter months rather than climatic changes that occurred during the breeding season. Winter temperatures in higher latitudes have shown larger increases than temperatures during spring or summer months and are expected to continue to rise more drastically (IPCC 2013). In contrast, temperatures in lower latitudes have not increased as drastically (IPCC 2013); thus climatic conditions for migratory birds on their

wintering grounds remained relatively stable. Milder winters in higher latitudes combined with increases in supplemental feeding would contribute to higher survival of resident birds, thus potentially increasing chances of colonization of new sites by these birds. It is likely then that future avian communities will become more homogenous by increasing in proportion of resident species and decreasing in proportion of migratory birds.

#### **3.4.3 Conclusions**

My study provides new insights into the drivers of temporal turnover in avian communities. I showed that while changes in avian community composition are closely related to changes in climatic conditions, this association is strongly influenced by the level of landscape fragmentation. Specifically, highly fragmented regions are likely to undergo smaller changes in composition and structure as a result of climate change, whereas those changes are likely to be more pronounced in contiguous and unfragmented habitats. I suggest that relative contributions of habitat generalists and specialists in ecological communities might be one of the leading factors explaining these divergent patterns.

My findings have significant implications for conservation theory and practice. Current conservation strategies commonly focus on conserving large regions with undisturbed and contiguous habitats that generally support high species diversity. My research suggests that faunal communities of such habitats will undergo the most drastic compositional changes as a result of climate change. Thus, my research stresses the importance of putting the existing conservation strategies in the context of climate change.

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# SCALE-DEPENDENCE OF TEMPORAL CHANGES IN AVIAN COMMUNITIES

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# ABSTRACT

It has long been acknowledged that key biodiversity patterns vary with spatial scale and the mechanisms driving these patterns are inherently scale-dependent. Studies investigating scaling of biodiversity and the mechanisms pertinent at each spatial scale have mostly focused on one time step. My goal was to evaluate spatial scaling patterns of avian assemblages through time and to identify environmental drivers of the change. I used temporal turnover, proportion of extinction events, and proportion of colonization events as measures of temporal change in avian communities at 5 spatial resolutions (5x5, 10x10, 20x20, 40x40, and 80x80 km). I applied Bayesian spatially-varying intercept models to evaluate the relationships among community change and change in climatic conditions, landscape fragmentation, and elevation at each of the spatial scales. I found that temporal turnover, extinction, and colonization declined with increasing spatial scale, but this decline was steeper for extinction than for colonization. Specifically, mean temporal turnover decreased from 0.384 at 5x5 km to 0.144 at 80x80 km spatial scale. Mean extinction decreased from 0.210 at 5x5 km to 0.036 at 80x80km scale. Mean colonization decreased from 0.214 at 5x5 km to 0.110 at 80x80 km scale. I also found that the influence of different environmental drivers to changes in avian communities was scaledependent. Specifically, climate change covariates were important at smaller scales (i.e., 5x5 and 10x10 km), while landscape characteristics were relevant across coarser scales. My findings

suggest that climate change will initially affect communities at fine spatial scales, though the magnitude of these changes is likely to be facilitated by landscape fragmentation at larger scales.

### **4.1 INTRODUCTION**

Patterns of biological diversity through space and time are an indication of the underlying mechanisms that control biodiversity and as such are of key interest to ecology. It has long been acknowledged that key biodiversity patterns vary with spatial scale of observation (e.g., Storch et al. 2004, Keil et al. 2011). This scale-dependence is perhaps best demonstrated in patterns of species richness (e.g., Arrhenius 1921, Rahbek 2005), but other attributes of biodiversity have also been shown to be contingent upon the spatial scale of investigation. For example, spatial turnover in species composition (i.e., an aggregate of gains and losses of species comprising a community) has been demonstrated to have scaling properties (Gaston et al. 2007), as have patterns of extinction risk (Hartley and Kunin 2003), immigration and emigration (Englund and Hamback 2007), colonization and biological invasions (Menendez and Thomas 2000, Davies et al. 2005, Powell et al. 2013). Given such pervasive scale-dependence of biodiversity patterns, it is to be expected that mechanisms controlling these patterns are also conditional on the scale of investigation (e.g., Ricklefs 1986, Currie 2004, Storch et al. 2004). For example, many attributes of biological communities at the continental scales are thought to be driven primarily by evolutionary factors (Ricklefs 2004, Keil and Jetz 2014), whereas climate variability and regional land cover dynamics are pertinent across spatial grains of tens or hundreds of kilometers (Willis and Whittaker 2002, Field et al. 2009). At yet finer grains, specific habitat characteristics and intra- and inter-specific interactions are thought to become the primary drivers of biodiversity (Wiens 1989, Tilman 2004, Belmaker and Jetz 2011). However, while research to date has provided insight into scale-dependence of biodiversity patterns, the majority of studies

were limited to one time step and few have looked at spatial scaling of temporal biodiversity change.

Measures of temporal changes in biodiversity have been commonly used as indicators of environmental change (e.g., Calvarheiro et al. 2013, Chapter 3 of this volume); thus, it is important that we understand how these measures depend on the spatial scale. Furthermore, given the widespread use of biodiversity as a measure of ecosystem response to global change, a thorough investigation of mechanisms relevant to temporal biodiversity dynamics across spatial scales is perhaps more important than ever. A few examples of scaling of temporal changes in biodiversity do exist. For example, Keil et al. (2011) found that temporal change in species richness decreased with increasing spatial grain, while Calvarheiro et al. (2013) showed spatial turnover in species composition to be decreasing across time, indicating ongoing homogenization of biological communities. Despite these initial investigations into the scaling properties of temporal biodiversity change, limitations to the understanding of this phenomenon persist. First, studies that explicitly look at scale-dependence of temporal biodiversity change generally focus on species richness as a measure of biodiversity. However, consequences of biodiversity change will extend much beyond changes in species richness (Barbet-Massin and Jetz 2014). Thus, it is important to examine measures that explicitly take species identities into account, such as temporal turnover and the underlying processes contributing to temporal turnover, i.e., extinction and colonization. Second, to the best of my knowledge, none of the studies has yet investigated the relative importance of environmental factors influencing temporal changes in biodiversity at different spatial scales. Indeed, climate and land-cover change are currently considered the two biggest threats to biodiversity (e.g., de Chazal and Rounsevell 2009), but the spatial scales at which these two factors are relevant to biodiversity are not yet fully known.

Here, I used data from the New York State Breeding Bird Atlas to evaluate spatial scaling patterns of temporal changes in avian assemblages. I define temporal change through measures of temporal turnover, proportion of extinction events, and proportion of colonization events. Though spatial scaling often refers to either the resolution (i.e., grain) of the investigation or the geographic extent of the study, I focus on the resolution only and refer to it as *spatial scale* or *spatial grain* interchangeably throughout the paper. I sought to evaluate two interrelated questions: (1) how do patterns of temporal changes in avian assemblages vary across spatial scales? and (2) at what spatial grains do different environmental factors influence temporal turnover, extinction, and colonization?

## **4.2 METHODS**

#### 4.2.1 Breeding Bird Atlas

The New York State Breeding Bird Atlas (BBA) is a statewide survey that documented the distribution of breeding birds in New York. To date, BBA has been conducted in two time periods, 1980-85 (hereafter, BBA1980; Andrle and Carroll 1988) and 2000-05 (hereafter, BBA2000; McGowan and Corwin 2008). For both BBAs, a grid system was used to define the basic unit for reporting data; the BBA reporting unit (a block) measures 5x5 km and a total of 5,335 blocks covered the entirety of New York State. This data set represents one of the largest and finest resolution atlases in the world (Gibbons et al. 2007).

A total of 242 species were recorded for BBA1980 and 248 species were recorded for BBA2000 (Andrle and Carroll 1988, McGowan and Corwin 2008, see Appendix 1.1). Observations were made by skilled birders who spent at least 8 hours in each block, visited all cover types in each block, and included at least one nighttime visit to document nocturnal species. Observer effort was recorded for each BBA and reported as a number of person hours (measured as the sum of the number of hours spent in each block x the number of people surveying each block; McGowan and Zuckerberg 2008). The BBA represents a detection/nondetection dataset and non-detection indicates that species could not be found given search criteria (McGowan and Corwin 2008).

# 4.2.2 Spatial scaling of community change

To quantify temporal change in avian assemblages, I calculated temporal turnover (TURN) as an aggregate of species gains (hereafter called colonization) and species losses (hereafter called extinction):

$$TURN = \frac{E+C}{E+C+P},$$
 Eqn. 4.1

where E is the number of species that went extinct in the block between BBA1980 and BBA2000, C is the number of species that colonized the block between BBA1980 and BBA2000, and P is number of species in the same block common to both BBAs (i.e., persistence).

In addition to temporal turnover, I quantified its components: proportion of extinction events (i.e., proportion of species lost at a particular site between BBA1980 and BBA2000; EXT) and proportion of colonization events (i.e., proportion of species gained at a particular site between BBA1980 and BBA2000; COL) in each block between BBA1980 and BBA2000. Here, I use terms extinction and colonization to refer to the gain or loss of a species from a defined point in space (in this case, a spatial grain of 5x5 km, 10x10 km, 20x20 km, 40x40 km, or 80x80 km; Gaston and Blackburn 2002). EXT and COL were calculated as follows:

$$EXT = \frac{E}{E+P},$$

$$Eqn. 4.2$$

$$COL = \frac{C}{E+C+P},$$
Eqn. 4.3

For TURN and COL, we used the sum of *E*, *C*, and *P* as the denominator of the Eqns. 1 and 2. We recognize that species already present in a block in BBA1980 could not have colonized that block and that species other than those included in *E*, *C*, and *P* metrics could have potentially colonized the site. However, we were simply interested in the proportion of species that colonized the site relative to all the species found within the block; thus we deem the sum of *E*, *C*, and *P* as an appropriate choice for the denominator of both equations. For EXT, we used the sum of *E* and *P* as the denominator, because only species present in a block in BBA1980 could have potentially gone extinct. The values of TURN, EXT, and COL are bounded by 0 and 1; values approaching 0 indicate low temporal turnover, extinction, or colonization while values approaching 1 indicate high temporal turnover, extinction, or colonization in a block between BBA1980 and BBA2000. To account for unequal sampling effort, we followed Chao et al. (2005) and used individual-based probabilistic approach to calculate E, C, and P.

We calculated TURN, EXT, and COL at the following spatial grains: 5x5 km, 10x10 km, 20x20 km, 40x40 km, and 80x 80 km. To estimate the mean of each metric and construct the 95% confidence intervals, we applied a non-parametric bootstrap procedure (10,000 resamplings) at each of the spatial grains.

## 4.2.3 Factors influencing community change across spatial grains

We included temporal trends in climatic conditions across the 1980-2005 time period and landscape fragmentation as potential correlates of temporal turnover, extinction, and colonization. We included elevation in all the models to account for topographical variation of New York State. To quantify trends in climatic conditions, we used the PRISM (Parameterelevation Regressions on Independent Slopes Model) climate mapping system (Daly and Gibson 2002). I calculated the magnitude of the 25-year (1980-2005) trend in average maximum and

minimum temperatures of the breeding season (TMAX and TMIN, respectively; expressed in °C/25 years) and in total monthly precipitation of the breeding season (PRECIP; expressed in mm/25 years) using Ordinary Least Squares regression.

I used the National Land Cover Data (NLCD) derived from the Landsat Thematic Mapper satellite data to quantify landscape fragmentation. There is no NLCD available for the time period of BBA1980; thus, I used a NLCD2001 and space-for-time substitution to assess whether temporal turnover, extinction, and colonization are related to landscape fragmentation (for more information on space-for-time substitution see Pickett 1989). Because I focused our analysis on a diverse suite of species with varying habitat requirements, I chose a landscapescale variable to capture broad-scale variation in habitat fragmentation. Edge Density (ED) is a good measure of landscape fragmentation because an increase in habitat edge is a primary outcome of habitat fragmentation (Hargis et al. 1998). However, in situations when landscape consists entirely of one cover type, the ED would be 0 regardless of the type of land-cover present. Therefore, to differentiate between landscapes that consisted entirely of natural land cover (e.g., forest) and those mostly developed (e.g., cities), I also calculated the proportion of developed land (DEVEL). Landscape analysis was conducted using FRAGSTATS 4.1 (McGarigal et al. 2012) and the Geospatial Modelling Environment (GME, http://www.spatialecology.com/gme/).

I used Digital Elevation Models for New York State to quantify mean elevation in each block and for each spatial grain (ELEV). To account for potential survey effort bias, I calculated the absolute difference in the number of person hours between BBA1980 and BBA2000 (EFF = |EFF1980 - EFF2000|) for each BBA block and included it as a covariate in my

models. I standardized and centered all the covariates to ease the interpretation of the parameter estimates.

To estimate the importance of environmental factors in driving temporal turnover, extinction, and colonization at each of the spatial grains (i.e., 5x5, 10x10, 20x20, and 40x40 km), I built a statistical model that included the main effects of all the covariates (TMAX, TMIN, PRECIP, ED, DEVEL, ELEV, and EFF). I did not run a model for the largest spatial grain (i.e., 80x80 km) because of the insufficient sample size. We used a Bayesian model estimation procedure. Each response variable (temporal turnover TURN, extinction EXT, or colonization COL) at each location (s) was modeled as a binomial random variable. Let y(s) be a response variable, then  $y(s) \sim B(\rho(s), N(s))$  where N(s) is the total number of species found at least once in a block from the first to the second atlas count (for TURN and COL) or the total number of species found in first atlas count (for EXT). For each BBA block, let p(s) = y(s)/N(s). Also, let  $\mathbf{x}(\mathbf{s})$  be a vector containing the explanatory variables for each model. All models had spatially varying intercepts, which were created by adding spatially structured random effects to the model intercept. A generalized linear model approach was used to relate responses to explanatory variables. Using the logit link  $\eta(s) = \log[p(s)/\{1-p(s)\}]$  the SVI model was  $\eta(s) = w(\mathbf{s}) + \boldsymbol{\beta} \mathbf{x}(s)$ Eqn. 4.4

where  $\beta$  is a vector of regression coefficients and w(s) is a random effect representing spatially varying adjustments to the intercept. We assume each element in *w*(*s*) arises from a spatial Gaussian Process (GP) (see, e.g., Banerjee et al. 2004 or Cressie and Wikle 2011 for more details). Specifically, *w*(*s*) ~ *GP*(**0**, *C*(*s*, *s'*)), where *s* and *s'* are any two locations within the study area, the spatial covariance *C*(*s*, *s'*) =  $\sigma \rho(s, s'; \phi)$  with variance parameter  $\sigma^2$ , correlation

function  $\rho(\cdot; \phi)$ , and spatial decay parameter  $\phi$ . The exponential spatial correlation was assumed for  $\rho(\cdot)$ .

Prior distributions on the parameters complete the hierarchical model specification (e.g., Gelman et al. 2004). The global regression coefficients,  $\beta$ 's followed a Normal distribution *N*(0, 100), while the variance component  $\sigma^2$  was assigned inverse-Gamma IG(2, 1) prior. The spatial decay parameter,  $\phi$ , followed an informative Uniform prior, with support that ranged from 1 km to the maximum distance between any two grid cells. I ran three MCMC chains for 20,000 iterations each. Convergence was diagnosed using the Gelman-Rubin diagnostic (Gelman and Rubin 1992).

Prior to statistical analysis, I removed all blocks that did not have continuous land cover coverage, blocks with more than 50% open water coverage, and those that did not have survey effort data. Ultimately, I used a total of  $N_{5x5} = 4,742$  blocks to fit the models for the 5x5 km grain;  $N_{10x10} = 1,186$  blocks to fit the models for the 10x10 km grain;  $N_{20x20} = 226$  blocks to fit the models for the 20x20 km grain; and  $N_{40x40} = 54$  blocks to fit the models for the 40x40 km grain. The 80x80 km spatial grain included only  $N_{80x80} = 7$  blocks. All models were run in R 2.15.1 statistical program (R Development Core Team 2013, http://www.r-project.org/) using package spBayes (Finley and Banerjee 2013). In a Bayesian framework, parameter estimates have valid posterior distributions and inferences are made using mean or median as well as the credible intervals of these posterior distributions. Credible intervals overlapping zero imply that the parameter in question is not different from zero. Summaries of parameter estimates were generated using the R CODA package (Plummer et al. 2012).

## **4.3 RESULTS**

#### **4.3.1** Spatial scaling of community change

Mean TURN decreased with increasing spatial grain (Fig. 4.1A). At 5x5 km spatial grain, mean value of TURN was 0.384, indicating that on average 38% of species had either colonized or become extinct within the average 5x5 km block and approximately 62% of the species persisted across both time periods. At 10x10 km, mean value of TURN decreased to 0.266. At 20x20 km grain, mean TURN further decreased to 0.201; while at 40x40 km it was 0.160. At the largest spatial grain (i.e., 80x80 km), mean value of TURN was 0.144, which indicates that on average only 14% of species had either colonized or become extinct within the average 80x80 km block and approximately 86% of the species persisted over time. In terms of its spatial distribution, the highest temporal turnover at the 5x5 km and 10x10 km spatial grains was in the north-eastern part of the state, where the Adirondack Mountains are (Fig. 4.2). At the 20x20 km grain, the spatial patterns of temporal turnover became more homogenous, with central New York showing lower temporal turnover than eastern or western regions. At the 40x40 km spatial grain, most sites showed temporal turnover between 0.1 and 0.2, with a few exceptions in the north-eastern New York. At the 80x80 km spatial scale, temporal turnover exceeded 0.2 in only one block (Fig. 4.2).

**Figure 4.1** Spatial scaling of temporal turnover, extinction, and colonization observed between 1980-85 and 2000-05 for avian communities in New York State across five different spatial grains (i.e., 5x5 km, 10x10 km, 20x20 km, 40x40 km, and 80x80 km). Temporal turnover was calculated as a proportion of all species gained or lost between 1980-85 and 2000-05 in a particular site (i.e., 5x5 km Breeding Bird Atlas block or a scaled-up version of it) relative to all species recorded across both time periods; extinction was calculated as a proportion of species lost between 1980-85 and 2000-05 in a particular site relative to all species present in a site in 1980-85; colonization was calculated as a proportion of species gained between 1980-85 and 2000-05 in a particular site relative to all species recorded across both time periods. High values of all three metrics indicate high temporal turnover, extinction, and colonization.



**Figure 4.2** Patterns of temporal turnover observed between 1980-85 and 2000-05 for avian communities in New York State across five different spatial grains (i.e., 5x5 km, 10x10 km, 20x20 km, 40x40 km, and 80x80 km). Temporal turnover was calculated as a proportion of all species gained or lost between 1980-85 and 2000-05 in a particular site (i.e., 5x5 km Breeding Bird Atlas block or a scaled-up version of it) relative to all species recorded across both time periods. High values indicate high temporal turnover.



I detected a decrease in mean EXT with increasing spatial grain (Fig. 4.1B). At 5x5 km spatial grain, mean value of EXT was 0.210, indicating that on average 21% of species had become extinct within the average 5x5 km block between 1980 and 2005. At 10x10 km spatial scale, mean value of EXT declined to 0.132. At 20x20 km grain, mean EXT was 0.096; while at 40x40 km, it decreased further and equaled 0.071. At the largest spatial grain (i.e., 80x80 km), mean value of EXT was 0.036, which indicates that on average only 4% of species had become extinct within the average 80x80 km block. Similarly to TURN, the highest proportion of extinction events at the 5x5 km and 10x10 km spatial grains was found in the location of the Adirondack Mountains (Fig. 4.3). At the 20x20 km and 40x40 spatial grains, EXT also was higher in the north-east. At the 80x80 km grain, extinction became more spatially homogeneous and never exceeded 0.1 (Fig. 4.3).

In general, mean COL also decreased with increasing spatial grain (Fig. 4.1C). At 5x5 km, mean COL took a value of 0.214, indicating that approximately 21% of all species found across both time periods in a 5x5 km block were detected only during the second BBA. At the 10x10 km spatial scale, mean COL was 0.152. Starting at the 20x20 km grain, the decline in the mean COL values tapered off and the values stabilized around 0.1. Mean COL was 0.116 at 20x20 km, 0.094 at 40x40 km, and 0.110 at 80x80 km spatial grain. High proportion of colonization events for the 5x5 km and 10x10 km spatial grains were found in the north-eastern and western parts of the state (Fig. 4.4). However, unlike in the case of temporal turnover and extinction, COL values were less spatially clumped and more dispersed (Fig. 4.4). At 20x20 km, colonization rates were homogeneously distributed throughout the state; at the 40x40 km, lower colonization values were found in north-eastern (i.e., Adirondack Mountains) and south-central

(i.e., Allegany Plateau) New York. At the 80x80 km grain, colonization rates were generally low, with the exception of the most northerly block (Fig. 4.4).

**Figure 4.3** Patterns of extinction observed between 1980-85 and 2000-05 for avian communities in New York State across five different spatial grains (i.e., 5x5 km, 10x10 km, 20x20 km, 40x40 km, and 80x80 km). Extinction was calculated as a proportion of species lost between 1980-85 and 2000-05 in a particular site (i.e., 5x5 km Breeding Bird Atlas block or a scaled-up version of it) relative to all species present in a site in 1980-85. High values indicate high proportion of extinction events.



**Figure 4.4** Patterns of colonization observed between 1980-85 and 2000-05 for avian communities in New York State across five different spatial grains (i.e., 5x5 km, 10x10 km, 20x20 km, 40x40 km, and 80x80 km). Colonization was calculated as a proportion of species gained between 1980-85 and 2000-05 in a particular site (i.e., 5x5 km Breeding Bird Atlas block or a scaled-up version of it) relative to all species recorded across both time periods. High values indicate high proportion of colonization events.



### **4.3.2** Factors influencing community change across spatial grains

#### 4.3.2.1 Temporal turnover

At the 5x5 km spatial grain, TMAX was positively associated with TURN, indicating that increasing maximum temperatures were associated with high temporal turnover (Fig. 4.5). There was a negative association of temporal turnover and ED, suggesting that temporal turnover was higher in less fragmented regions. There was a positive relationship between temporal turnover and DEVEL as well as temporal turnover and ELEV (Fig. 4.5), indicating that highly urbanized regions and locations in higher elevations generally experienced increased temporal turnover.

At the 10x10 km spatial grain, TMAX was positively related to TURN (Fig. 4.5). I also found a negative relationship between temporal turnover and ED and a positive relationship between temporal turnover and DEVEL (Fig. 4.5). I detected no relationship between TURN and ELEV at this spatial grain. At the 20x20 km spatial grain, I found no relationships between TURN and any of the climate change covariates. I found a negative relationship between TURN and ED and a positive relationship between TURN and DEVEL (Fig. 4.5). I also detected a negative relationship between TURN and ELEV, suggesting that temporal turnover was higher in lower elevations. At 40x40 km grain, there I found no relationships between temporal turnover and any of the covariates (Fig. 4.5).

### 4.3.2.2 Extinction

At the 5x5 km spatial grain, I found positive relationships between EXT and TMIN (Fig. 4.5), indicating that increasing minimum temperatures were associated with high proportion of extinction events. Extinction was also positively related to PRECIP (Fig. 4.5), suggesting higher extinction in regions where precipitation increased the most. I found a negative association of

extinction and ED and a positive association of extinction and DEVEL, indicating that extinction was highest in contiguous landscapes and in highly urbanized regions. There was a relationship between extinction and ELEV (Fig. 4.5).

At the 10x10 km spatial grain, TMIN was positively associated with EXT, but I no longer found relationships between extinction and TMAX or PRECIP. Extinction was negatively associated with ED and positively related to DEVEL. I found no relationship between extinction and ELEV at this spatial grain. At the 20x20 km spatial grain, none of the climate change variables was associated with EXT. I found a negative relationship between EXT and ED (Fig. 4.5) and a positive relationship between EXT and DEVEL. I found no relationship between extinction and ELEV at this spatial grain. At the 40x40 km spatial grain, I found no relationships between extinction and any of the tested covariates (Fig. 4.5).

### 4.3.2.3 Colonization

At the 5x5 km spatial grain, colonization was positively related to TMAX, indicating that regions where temperatures increased the most experienced highest proportion of colonization events (Fig. 4.5). Colonization was also negatively related to PRECIP (Fig. 4.5), indicating that regions with decreasing precipitation on average experienced higher proportion of colonization events. COL was positively associated with DEVEL (Fig. 4.5), indicating that colonization was generally higher in highly urbanized regions.

At the 10x10 km spatial grain, I found a positive relationship between colonization and DEVEL. However, I did not find associations between COL and climatic change variables, ED, or ELEV at this spatial scale. At the 20x20 km spatial grain, I found a positive relationship between colonization and TMAX and a negative relationship between colonization and TMIN (Fig. 4.5). I also found a positive association of colonization and ED, indicating that highest

colonization occurred in regions of highest fragmentation. I found no relationships between colonization and DEVEL or colonization and ELEV at 20x20 km. At the 40x40 km spatial grain, I found no relationships between colonization and any of the tested covariates (Fig. 4.5).

**Figure 4.5** Coefficient estimates (i.e., mean values of the posterior distribution and associated credible intervals) resulting from the models for (A) temporal turnover, (B) extinction, and (C) colonization. Abbreviations for the covariates are as follows: magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), and elevation (ELEV).



# **4.4 DISCUSSION**

I sought to address the issue of scale-dependence of temporal changes in avian assemblages by evaluating temporal turnover, extinction, and colonization across different spatial grains and investigating potential environmental drivers of these changes in assemblages at each of the scales. I found that temporal turnover, extinction, and colonization declined as the spatial grain increased, indicating that community change is smaller at coarse scales. This decline with increasing spatial grain, however, was faster for temporal turnover and extinction than it was for colonization. I also found that the relevance of different environmental drivers to changes in avian communities was scale-dependent. Specifically, I found that climate change covariates were pertinent at smaller spatial grains than landscape characteristics.

# 4.4.1 Spatial scaling of community change

I found that temporal changes in community composition decreased with increasing spatial scale of investigation. This result is not surprising given that increasing spatial grains will encompass larger areas and higher number of species, thus reducing both the likelihood of individual species extinction or colonization (e.g., Gaston et al. 2004) and the proportion of extinction and colonization events. However, while this decline was relatively steady for temporal turnover and extinction, the decline in the proportion of colonization events tapered off at 20x20 km grain and remained relatively constant across the three coarsest spatial grains (i.e., 20x20 km, 40x40 km, and 80x80 km). While there is little direct evidence that patterns of extinction and colonization exhibit different spatial scaling, there are reasons to suspect that it might be so. For example, Wilson et al. (2004) suggested that processes of range retraction and expansion, and perhaps by extension extinction and colonization, affect species distributional patterns in a disparate way.

either optimal habitats or regions where extinction forces are not operating (Johnson 1998). Thus, it is expected that contracting ranges would result in substantial species loss at fine spatial grains and relatively little loss at coarse grains (Wilson et al. 2004, Keil et al. 2011). The results from my study lend support to this expectation because I showed that there is substantial extinction at fine grains and relatively little species loss at coarser scales.

On the other hand, species expanding their ranges tend to form more aggregated distributions because range expansion is often dispersal-limited (Shigesada and Kawasaki 1997). Therefore, it is expected that expanding range would involve substantial gain at fine scales as coarse-grain areas are slowly colonized (Wilson et al. 2004). My results showing substantial colonization at the finest grain fit well with this expectation. However, I suggest that low colonization at coarse spatial grains proposed by Wilson et al. (2004) is characteristic of species with relatively low mobility and low dispersal abilities, such as investigated in their study butterflies. Birds, as highly mobile and far-dispersing organisms, would likely display a different expansion signature, characterized by relatively high rates of colonization even at coarse grains. Indeed, Gaston and Blackburn (2002) found that birds which exhibited higher colonization rates in the UK tended to disperse farther during both their juvenile and adult life stages. Other examples of a positive relationship between colonization rate and dispersal abilities abound (e.g., Brown and Kodric-Brown 1977, Juliano 1983, Mouquet and Loreau 2003). Consequently, I propose that far-dispersing birds are able to colonize distant coarse-grain areas, resulting in relatively high and constant proportion of colonization events across coarser grains explored in this study (i.e., 20x20, 40x40, and 80x80 km).

## **4.4.2 Factors influencing community change across spatial grains**

I found that the main drivers of avian biodiversity change are not only often specific to the spatial scale of investigation, but also differ in their likely impacts among the different metrics of community change. For example, changes in climatic conditions were relevant to both temporal turnover and extinction only at finer spatial grains of 5x5 and 10x10 km. I detected no impacts of climate change on these two measures of biodiversity change across coarser spatial scales. On the other hand, colonization was associated with changes in climate both at fine grains as well as at the intermediate spatial scales (i.e., 20x20 km). This association of colonization with climate change at coarser grains might further explain why I detected stabilizing of colonization values at coarser spatial grains. Perhaps changing climatic conditions in combination with dispersal abilities are facilitating slightly higher colonization rates at coarser spatial grains in comparison with those of temporal turnover and extinction.

Research to date suggests that while patterns of species richness are associated with climate mostly at coarse spatial grains (>  $500 \text{ km}^2$ ; Field et al. 2009, McGill 2010), species turnover is related to climatic variability at much smaller grains. For example, Gaston et al. (2004) found that the single best environmental predictor of spatial turnover at 10x10 km spatial grain was temperature. In their study, the influence of temperature decreased as the spatial scale increased and became a non-significant predictor of turnover at spatial grains larger than 30x30 km (Gaston et al. 2004). My analysis corroborates their study and extends their results by demonstrating that influences of temporal climate change diminish at spatial scales larger than 20x20 km.

In general, higher rates of temporal turnover, extinction, and colonization were associated with increases in temperatures recorded during the same time period at the two smallest spatial

scales (i.e., 5x5 and 10x10 km). This association indicates that climate change might have partially driven the observed changes in avian communities across New York. As temperatures increased, thermal requirements of some species were no longer met while new thermal niches became available for other species, resulting in higher extinction and colonization, respectively. As temperatures continue to rise in the next decades, we can expect further reshuffling of community composition through processes of extinction and colonization and perhaps even development of novel species assemblages (i.e., assemblages with no modern analogue; Stralberg et al. 2009). My analysis suggests that these novel or close-to-novel communities would initially form at the smallest spatial grains (i.e., up to 100 km<sup>2</sup>), but given enough time coarser spatial scales might also undergo pronounced changes in community composition. Other studies corroborate my results. For example, Stralberg et al. (2009) predicted that up to 57% of California might be occupied by novel bird assemblages by 2070 as a result of individualistic shifts in species distributions driven by changing climate. The percentage of novel assemblages, however, was highly dependent on the spatial scale of investigation and decreased with increasing spatial grain. At the largest spatial scales, novel species assemblages were predicted to occupy only up to 3.5% of California (Stralberg et al. 2009). My results suggest that climate change might induce similar scale-dependent changes in community composition across New York.

Interestingly, I found that colonization was negatively related to minimum temperatures at the 20x20 km spatial grain. This negative association with minimum temperatures indicates, perhaps counterintuitively, that avian communities underwent highest colonization rates in regions where temperatures changed the least, while colonization was lowest in regions that experienced substantial increases in minimum temperatures. I also found a positive association

of maximum temperatures with the proportion of colonization events at this spatial scale. Given that minimum temperatures have shown larger increases than maximum temperatures and are expected to continue to rise more drastically (IPCC 2013), we might expect that changes in minimum temperatures will have stronger impact on avian communities than increasing maximum temperatures. Thus, my results suggest that future changes in temperatures may contribute to lower levels of immigration and colonization from surrounding assemblages, further indicating that climate change-induced temperature increases might reduce colonization rates at the 20x20 km spatial grain. This result might provide further support for the findings from my previous works (Chapters 1 and 2 of this volume). Specifically, I showed that influences of climate change are often spatially non-stationary and depend on other environmental factors, such as land-cover. Thus, while the global coefficient estimate might be indicating a negative association between changing temperatures and colonization, it is likely that this association varies through space and takes both positive and negative values.

My analysis suggests that land-cover is pertinent to changes in avian communities at all spatial grains, with exception of the largest scale (i.e., 40x40 km). These findings indicate that landscape matrix matters over larger spatial scales than changing climatic conditions. Research to date provides conflicting accounts of the relative importance of climate and land-cover as drivers of biodiversity change. Some studies showed that landscape matrix indeed influences species turnover at larger spatial scales (e.g., Krawchuk and Taylor 2003), while other research suggests that landscape structure is a valid predictor at smaller spatial scales than climatic variability (e.g., Rahbek 2005). My results point to the importance of landscape matrix as a potential facilitator of species responses to climate change. While climate change will likely affect ecological communities at smaller spatial grains, landscape matrix might influence the

strength of these responses by facilitating or limiting the dispersal and movement of species through the landscape. Indeed, I showed that responses of avian communities to climate change are influenced by the level of landscape fragmentation (Chapter 3 of this volume). My results add another dimension by showing that these landscape influences are likely to operate at scales larger than climate change.

In general, highly fragmented regions experienced smaller changes in community composition (especially temporal turnover and extinction), while these changes were more pronounced in contiguous landscapes. I suggest that there are at least two alternative interpretations for this pattern. It is plausible that communities in contiguous landscapes might be able to respond quicker to changes in the environment due to potential for unimpeded movement. Indeed, research suggests that unfragmented habitats might allow higher rates of species distributional shifts associated with climate change (Opdam and Washer 2004, Jeltsch et al. 2011), which would ultimately result in more pronounced changes in community composition. Alternatively, avian communities in fragmented landscapes may be more robust to environmental disturbance than communities found in contiguous habitats because they comprise largely of habitat generalists (e.g., Tscharntke et al. 2012, Estavillo et al. 2013), which tend to have wider habitat and thermal breadths than habitat specialists (Barnagaud et al. 2012). These wider niches potentially allow generalist birds to tolerate greater changes in environmental conditions, thus resulting in lower rates of community change. I suggested the latter as more plausible explanation for this ecological system (Chapter 3 of this volume) because communities comprised of generalist species underwent smaller changes than those comprised of habitat specialists.

I found that high levels of development were associated with higher values of temporal turnover, extinction or colonization and this relationship held across most spatial scales. Developed areas generally provide unsuitable conditions for a wide variety of different species due to increasing pressure of human activities on the remaining patches of natural habitat (e.g., Huste and Boulinier 2007). This combination results in high extinction rates. This expectation is supported by my study because I show that development influenced extinction to a higher degree and over larger spatial grains than it did colonization. We can thus expect that increasing human development of natural habitats will result in increased rates of extinction in the future.

I found temporal turnover to be associated with elevation, but this relationship was not found for either extinction or colonization. At the finest spatial grain (i.e., 5x5 km), the association of elevation with temporal turnover was positive, indicating that community change was highest in high elevation regions. Gaston et al. (2007) found a similar relationship for world avifauna. A plausible explanation for this increase in community change with elevation is the relationship between turnover and species richness. Communities that are less species rich tend to undergo higher rates of turnover (e.g., Lennon et al. 2001). In New York, high-elevation regions of the Adirondack or Catskill Mountains generally support lower species richness than low-laying agricultural plains, thus potentially exhibiting higher temporal community change. Perhaps surprisingly, the influence of elevation on temporal turnover either disappeared or became negative with increasing spatial grain. The negative association at coarser grains indicates that high elevation regions experienced smallest changes in composition of avian assemblages. Perhaps the topographical variability at the coarser spatial grains is no longer associated with species richness, thus resulting in the lack of or reverse relationship between elevation and temporal turnover.

## 4.4.3 Conclusions

My study contributes new insights into the patterns of temporal change in avian communities across different spatial grains and drivers relevant to these changes. Changes in community composition are scale-dependent and in general diminish with increasing spatial grain. This decline is steeper for extinction than for colonization, likely due to two factors: (i) differences in spatial patterns of range retraction and expansion and (ii) high mobility and dispersal abilities of birds. The influences of climate change, landscape matrix, and elevation on temporal changes in avian assemblages are scale-dependent. Impacts of climate change are relevant at small spatial grains, whereas influences of landscape matrix remain important also at larger spatial grains. I suggest that, as climate change progresses, avian assemblages will undergo increasing reshuffling at local scales, perhaps resulting in novel species assemblages. The magnitude of these biodiversity changes resulting from climate change, however, is likely to be facilitated by landscape fragmentation at larger scales. By establishing a link between changes in biodiversity and environmental processes controlling these changes across different spatial scales, my study provides a major contribution to the global change science.

### **4.5 ACKNOWLEDGMENTS**

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#### **EPILOGUE**

In my dissertation, I sought to address the need expressed by NASA to assess the relative roles of climate change and land cover in the observed changes in avian biodiversity. Specifically, my goal was to examine influences of land-cover composition and configuration on the way avian biodiversity responds to climate change and to investigate spatial scales relevant to the understanding of the impacts of global change. In Chapter 1, I tested the utility of the spatially-varying coefficients (SVC) models to quantify the influence of spatial non-stationarity on relationships between temporal community change and changes in climate and land cover. In Chapter 2, I evaluated bioclimatic relationships of grassland and forest breeding birds across varying gradients of their habitat. In Chapter 3, I investigated relationships between temporal changes in community composition and the interaction of climate change and land cover fragmentation. In Chapter 4, I investigated temporal community change across different spatial scales and determined factors relevant to changes in avian assemblages at each of the scales.

The collective works in these chapters contribute four primary and novel conclusions for better understanding of the implications of the interaction of land use and climate change to avian diversity. First, relationships between changes in biodiversity and environmental factors are often spatially non-stationary, i.e., the relationship between a response variable and the predictor covariates varies across the spatial extent of the study. Second, the amount of suitable land cover can significantly alter species responses to climate change, but this effect of land cover depends on the type of habitat. Specifically, extensive forest land has potential to mitigate the negative consequences of climate change to forest breeding birds, whereas expansive open lands are likely to exacerbate climate change impacts on populations of grassland birds. Third, impacts of climate change on ecological communities are more pronounced in regions of

unfragmented landscapes than in locations with fragmented habitats. The differences are likely caused by the fact that communities in fragmented habitats generally tend to be comprised of species with wider climatic niches, thus being less vulnerable to changing climatic conditions. Fourth, temporal changes in community composition are scale-dependent and so are the mechanisms driving these changes. Specifically, climate change operates at smaller spatial scales than landscape fragmentation. Consequently, as temperatures continue to rise in the next decades, we can expect reshuffling of community composition and perhaps development of completely novel species assemblages, which will initially form at the smallest spatial grains.

Chapter 1 addressed the issue of spatial non-stationarity in ecological relationships. It is widely recognized that the assumption of stationary regression coefficients results in poor fit and misleading inference about the impact of the covariates on the response variable. However, the current methods for accounting for non-stationarity tend to provide inaccurate and correlated regression coefficient estimates because they are not robust to collinearity among the covariates and the presence of complex spatial correlation structures. I tested the usefulness of spatially-varying coefficient (SVC) models to detect and account for spatial non-stationarity between temporal community changes in avian assemblages and changes in climate and land cover. The SVC method provides an improvement over methods that ignore spatial non-stationarity in terms of model fit and model predictive performance. Further, by fitting these models within a Bayesian inferential framework, I was able to make inferences about the spatial impact of covariates and other process parameters, as well as obtain full posterior predictive inference about the rate of turnover at new, i.e., unobserved locations.

Chapter 2 addressed the issue of variation in bioclimatic relationships of forest and grassland birds across gradients of forest and grassland habitats. Simulation studies suggest that

quantity and quality of available habitat affect the way species respond to climatic variability, but empirical evidence is lacking because studies that integrate both land cover and climate are rare. I identified the spatial variation in bioclimatic relationships of forest and grassland breeding birds and related this variation to changing amount of forest and grassland cover. My analysis indicated that increasing amounts of forests weaken the negative responses of forest breeding birds to climatic variability, while expansive grasslands strengthen these negative relationships. My work suggests that extensive forests will mitigate consequences of climate change to avian populations, but these negative consequences are likely to be intensified in regions with extensive grasslands. It is thus likely that the ongoing field abandonment and reforestation in New York will compensate or reverse the negative consequences of climate change by leading to the dominance of cold-dwelling assemblages (Clavero et al. 2011).

Chapter 3 addressed the lack of understanding in how climate change and landscape fragmentation interact to influence temporal changes in communities. Landscape fragmentation is likely to influence the way communities respond to climate change, for example by affecting the rate of species distributional shifts associated with climate change. My findings suggested that avian communities in regions with prevalent habitat fragmentation were affected by changes in climate to a lesser degree than communities found in unfragmented landscapes. I suggested that avian communities in fragmented landscapes must be more robust to climate change than communities found in contiguous habitats because they comprise of species with wider thermal niches and are thus less susceptible to temperature increases.

Chapter 4 addressed the issue of spatial scaling of temporal community change measured as temporal turnover, extinction, and colonization. It is widely recognized that patterns of biodiversity vary with spatial scale of investigation, but very few studies have investigated such

scaling patterns across more than one time step. My analysis suggested that temporal changes in community composition diminish with increasing spatial scales of investigation. The decline, however, is steeper for extinction than for colonization, likely due to two factors: (i) differences in spatial patterns of range retraction and expansion and (ii) high mobility and dispersal abilities of birds. I showed that processes driving temporal changes in community composition also vary with spatial scale. Impacts of climate change are relevant at small spatial grains, whereas influences of landscape matrix remain important also at larger spatial grains. I suggested that, as climate change progresses, avian assemblages will undergo increasing re-shuffling at local scales, perhaps resulting in novel or close-to-novel species assemblages. The magnitude of these changes associated with climate change, however, is likely to be facilitated by landscape fragmentation at larger scales.

The collective works offer several novel contributions to the understanding of the impacts of the interaction of climate change and land cover on biodiversity. First, I showed that changes in ecological communities will be more severe in open, contiguous and unfragmented habitats than in regions with expansive landscape fragmentation. Second, contrary to the popular belief, I showed that climate change will operate at relatively small spatial scales. The implications of these findings suggest that current conservation strategies may be insufficient to protect biodiversity in the face of climate change. Existing biodiversity conservation generally focuses on conserving large regions with undisturbed and contiguous habitats that generally support high species diversity. My results suggest that ecological communities of such habitats will undergo the most drastic compositional changes as a result of climate change. Thus, it is critical that the existing conservation strategies are placed in the context of climate change. My work suggests that in order to develop successful biodiversity conservation, one needs to consider both the

individual species' vulnerabilities to climate change based on their habitat association or lifehistory strategies and relative vulnerabilities of entire communities based on the landscape in which these communities persist. I believe that my works provide the first step into developing such sound conservation strategies.
APPENDIX

BBA Code	Common Name	Scientific Name
ABDU	American Black Duck	Anas rubripes
ACFL	Acadian Flycatcher	Empidonax virescens
AGWT	Green-winged Teal	Anas crecca
ALFL	Alder Flycatcher	Empidonax alnorum
AMBI	American Bittern	Botaurus lentiginosus
AMCO	American Coot	Fulica americana
AMCR	American Crow	Corvus brachyrhynchos
AMGO	American Goldfinch	Spinus tristis
AMKE	American Kestrel	Falco sparverius
AMOY	American Oystercatcher	Haematopus palliatus
AMRE	American Redstart	Setophaga ruticilla
AMOR	American Robin	Turdus migratorius
AMWI	American Wigeon	Anas americana
AMWO	American Woodcock	Scolopax minor
AWPE	American White Pelican	Pelecanus erythrorhynchos
BAEA	Bald Eagle	Haliaeetus leucocephalus
BANS	Bank Swallow	Riparia riparia
BAOR	Baltimore Oriole	Icterus galbula
BARS	Barn Swallow	Hirundo rustica
BAWW	Black-and-white Warbler	Mniotilta varia
BBCU	Black-billed Cuckoo	Coccyzus erythropthalmus
BBWA	Bay-breasted Warbler	Setophaga castanea
BBWO	Black-backed Woodpecker	Picoides arcticus
BCCH	Black-capped Chickadee	Poecile atricapillus
BCNH	Black-crowned Night-Heron	Nycticorax nycticorax
BDOW	Barred Owl	Strix varia
BEKI	Belted Kingfisher	Megaceryle alcyon
BGGN	Blue-gray Gnatcatcher	Polioptila caerulea
BHCO	Brown-headed Cowbird	Molothrus ater
BHPA	Black-hooded Parakeet	Nandayus nenday
BHVI	Blue-headed Vireo	Vireo solitarius
BITH	Bicknell's Thrush	Catharus bicknelli
BLBW	Blackburnian Warbler	Setophaga fusca
BLGR	Blue Grosbeak	Passerina caerulea
BLJA	Blue Jay	Cyanocitta cristata
BLPW	Blackpoll Warbler	Setophaga striata
BLRA	Black Rail	Laterallus jamaicensis
BLSK	Black Skimmer	Rynchops niger
BLTE	Black Tern	Chlidonias niger

**Table A 1.1** List of all bird species (N = 256) from the New York State Breeding Bird Atlas (BBA) used in the analysis.

BBA Code	Common Name	Scientific Name
BLVU	Black vulture	Coragyps atratus
BNOW	Barn Owl	Tyto alba
BOCH	Boreal Chickadee	Poecile hudsonicus
BRBL	Brewer's Blackbird	Euphagus cyanocephalus
BRCR	Brown Creeper	Certhia Americana
BRTH	Brown Thrasher	Toxostoma rufum
BRWA	Brewster's Warbler	Vermivora chrysoptera x V.
		cyanoptera
BTBW	Black-throated Blue Warbler	Setophaga caerulescens
BTGR	Boat-tailed Grackle	Quiscalus major
BTNW	Black-throated Green Warbler	Setophaga virens
BUFF	Bufflehead	Bucephala albeola
BHWA	Broad-winged Hawk	Buteo platypterus
BWTE	Blue-winged Teal	Anas discors
BWWA	Blue-winged Warbler	Vermivora cyanoptera
CAEG	Cattle Egret	Bubulcus ibis
CAGO	Canada Goose	Branta Canadensis
CANV	Canvasback	Avthva valisineria
CARW	Carolina Wren	Thryothorus ludovicianus
CATE	Caspian Tern	Hydroprogne caspia
CAWA	Canada Warbler	Cardellina Canadensis
CCSP	Clay-colored Sparrow	Spizella pallid
CEDW	Cedar Waxwing	Bombycilla cedrorum
CERW	Cerulean Warbler	Setophaga cerulean
CHSP	Chipping Sparrow	Spizella passerine
CHSW	Chimney Swift	Chaetura pelagic
CLRA	Clapper Rail	Rallus longirostris
CLSW	Cliff Swallow	Petrochelidon pyrrhonota
CMWA	Cape May Warbler	Setophaga tigrina
COEI	Common Eider	Somateria mollissima
COGO	Common Goldeneve	Bucephala clangula
COGR	Common Grackle	Quiscalus quiscula
COHA	Cooper's Hawk	$\widetilde{A}$ ccipiter cooperii
COLO	Common Loon	<i>Gavia immer</i>
COME	Common Merganser	Mergus merganser
COMO	Common Moorhen	Gallinula galeata
CONI	Common Nighthawk	Chordeiles minor
CORA	Common Raven	Corvus corax
COSN	Wilson's Snipe	Gallinago delicate
COTE	Common Tern	Sterna hirundo
COYE	Common Yellowthroat	Geothlypis trichas
CSWA	Chestnut-sided Warbler	Setophaga pensvlvanica

BBA Code	Common Name	Scientific Name
CWWI	Chuck-will's-widow	Antrostomus carolinensis
DCCO	Double-crested Cormorant	Phalacrocorax auritus
DICK	Dickcissel	Spiza Americana
DOWO	Downy Woodpecker	Picoides pubescens
EABL	Eastern Bluebird	Sialia sialis
EAKI	Eastern Kingbird	Tyrannus tyrannus
EAME	Eastern Meadowlark	Sturnella magna
EAPH	Eastern Phoebe	Sayornis phoebe
EASO	Eastern Screech-Owl	Megascops asio
EATO	Eastern Towhee	Pipilo erythrophthalmus
EAWP	Eastern Wood-Pewee	Contopus virens
ECDO	Eurasian Collared-Dove	Streptopelia decaocto
ETTI	Tufted Titmouse	Baeolophus bicolor
EUST	European Starling	Sturnus vulgaris
EVGR	Evening Grosbeak	Coccothraustes vespertinus
FICR	Fish Crow	Corvus ossifragus
FISP	Field Sparrow	Spizella pusilla
FOTE	Forster's Tern	Sterna forsteri
GADW	Gadwall	Anas strepera
GBBG	Great Black-backed Gull	Larus marinus
GBHE	Great Blue Heron	Ardea Herodias
GBTE	Gull-billed Tern	Gelochelidon nilotica
GCFL	Great Crested Flycatcher	Myiarchus crinitus
GCKI	Golden-crowned Kinglet	Regulus satrapa
GHOW	Great Horned Owl	Bubo virginianus
GLIB	Glossy Ibis	Plegadis falcinellus
GOEA	Golden Eagle	Aquila chrysaetos
GRAJ	Gray Jay	Perisoreus Canadensis
GRCA	Gray Catbird	Dumetella carolinensis
GREG	Great Egret	Ardea alba
GRHE	Green Heron	Butorides virescens
GRPA	Gray Partridge	Perdix perdix
GRSC	Greater Scaup	Aythya marila
GRSP	Grasshopper Sparrow	Ammodramus savannarum
GWWA	Golden-winged Warbler	Vermivora chrysoptera
HAWO	Hairy Woodpecker	Picoides villosus
HERG	Herring Gull	Larus argentatus
HESP	Henslow's Sparrow	Ammodramus henslowii
HETH	Hermit Thrush	Catharus guttatus
HOFI	House Finch	Haemorhous mexicanus
HOLA	Horned Lark	Eremophila alpestris
HOME	Hooded Merganser	Lophodytes cucullatus

Table A 1.1 (cont'd)

BBA Code	Common Name	Scientific Name
HOSP	House Sparrow	Passer domesticus
HOWA	Hooded Warbler	Setophaga citrine
HOWR	House Wren	Troglodytes aedon
INBU	Indigo Bunting	Passerina cyanea
KEWA	Kentucky Warbler	Geothlypis Formosa
KILL	Killdeer	Charadrius vociferous
KIRA	King Rail	Rallus elegans
LAGU	Laughing Gull	Leucophaeus atricilla
LAWA	Lawrence's Warbler	Vermivora chrysoptera x V. cvanoptera
LBHE	Little Blue Heron	Egretta caerulea
LEBI	Least Bittern	Ixobrychus exilis
LEFL	Least Flycatcher	Empidonax minimus
LEOW	Long-eared Owl	Asio otus
LESC	Lesser Scaup	Avthya affinis
LETE	Least Tern	Sternula antillarum
LISP	Lincoln's Sparrow	Melospiza lincolnii
LOSH	Loggerhead Shrike	Lanius ludovicianus
LOWA	Louisiana Waterthrush	Parkesia motacilla
MALL	Mallard	Anas platvrhynchos
MAWA	Magnolia Warbler	Setophaga magnolia
MAWR	Marsh Wren	Cistothorus palustris
MBDH	Mallard x American Black Duck Hybrid	Anas platyrhynchos x A.rubripes
MERL	Merlin	Falco columbarius
MODO	Mourning Dove	Zenaida macroura
MOPA	Monk Parakeet	Myiopsitta monachus
MOWA	Mourning Warbler	Geothlypis Philadelphia
MUSW	Mute Swan	Cygnus olor
MYWA	Yellow-rumped Warbler	Setophaga coronate
NAWA	Nashville Warbler	Oreothlypis ruficapilla
NOBO	Northern Bobwhite	Colinus virginianus
NOCA	Northern Cardinal	Cardinalis cardinalis
NOGO	Northern Goshawk	Accipiter gentilis
NOHA	Northern Harrier	Circus cyaneus
NOMO	Northern Mockingbird	Mimus polyglottos
NOPA	Northern Parula	Setophaga Americana
NOPI	Northern Pintail	Anas acuta
NOWA	Northern Waterthrush	Parkesia noveboracensis
NRWS	Northern Rough-winged Swallow	Stelgidopteryx serripennis
NSHO	Northern Shoveler	Anas clypeata
NSTS	Nelson's Sharp-tailed Sparrow	Ammodramus nelson

BBA Code	Common Name	Scientific Name
NSWO	Northern Saw-whet Owl	Aegolius acadicus
OROR	Orchard Oriole	Icterus spurious
OSFL	Olive-sided Flycatcher	Contopus cooperi
OSPR	Osprey	Pandion haliaetus
OVEN	Ovenbird	Seiurus aurocapilla
PBGR	Pied-billed Grebe	Podilymbus podiceps
PEFA	Peregrine Falcon	Falco peregrinus
PHVI	Philadelphia Vireo	Vireo philadelphicus
PIPL	Piping Plover	Charadrius melodus
PISI	Pine Siskin	Spinus pinus
PIWA	Pine Warbler	Setophaga pinus
PIWO	Pileated Woodpecker	Dryocopus pileatus
PRAW	Prairie Warbler	Setophaga discolor
PROW	Prothonotary Warbler	Protonotaria citrea
PUFI	Purple Finch	Haemorhous purpureus
PUMA	Purple Martin	Progne subis
RBGR	Rose-breasted Grosbeak	Pheucticus ludovicianus
RBGU	Ring-billed Gull	Larus delawarensis
RBME	Red-breasted Merganser	Mergus serrator
RBNU	Red-breasted Nuthatch	Sitta Canadensis
RBWO	Red-bellied Woodpecker	Melanerpes carolinus
RCKI	Ruby-crowned Kinglet	Regulus calendula
RECR	Red Crossbill	Loxia curvirostra
REDH	Redhead	Aythya Americana
REVI	Red-eyed Vireo	Vireo olivaceus
RHWO	Red-headed Woodpecker	Melanerpes erythrocephalus
RNDU	Ring-necked duck	Aythya collaris
RODO	Rock Pigeon	Columba livia
ROST	Roseate Tern	Sterna dougallii
RPHE	Ring-necked Pheasant	Phasianus colchicus
RSHA	Red-shouldered Hawk	Buteo lineatus
RTHA	Red-tailed Hawk	Buteo jamaicensis
RTHU	Ruby-throated Hummingbird	Archilochus colubris
RUBL	Rusty Blackbird	Euphagus carolinus
RUDU	Ruddy Duck	Oxyura jamaicensis
RUGR	Ruffed Grouse	Bonasa umbellus
RWBL	Red-winged Blackbird	Agelaius phoeniceus
SACR	Sandhill Crane	Grus Canadensis
SAVS	Savannah Sparrow	Passerculus sandwichensis
SCJU	Dark-eyed Junco	Junco hyemalis
SCTA	Scarlet Tanager	Piranga olivacea
SEOW	Short-eared Owl	Asio flammeus

Tal	ble	Α	1.1	(cont	'd)
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BBA Code	Common Name	Scientific Name
SESP	Seaside Sparrow	Ammodramus maritimus
SEWR	Sedge Wren	Cistothorus platensis
SNEG	Snowy Egret	Egretta thula
SORA	Sora	Porzana Carolina
SOSP	Song Sparrow	Melospiza melodia
SPGR	Spruce Grouse	Falcipennis Canadensis
SPSA	Spotted Sandpiper	Actitis macularius
SSHA	Sharp-shinned Hawk	Accipiter striatus
SSTS	Saltmarsh Sharp-tailed Sparrow	Ammodramus caudacutus
SUTA	Summer Tanager	Piranga rubra
SWSP	Swamp Sparrow	Melospiza Georgiana
SWTH	Swaison's Thrush	Catharus ustulatus
TEWA	Tennessee Warbler	Oreothlypis peregrine
TRES	Tree Swallow	Tachycineta bicolor
TRHE	Tricolored Heron	Egretta tricolor
TRUS	Trumpeter Swan	Cygnus buccinators
TTWO	American Three-toed Woodpecker	Picoides dorsalis
TUVU	Turkey Vulture	Cathartes aura
UPSA	Upland Sandpiper	Bartramia longicauda
VEER	Veerv	Catharus fuscescens
VESP	Vesper Sparrow	Pooecetes gramineus
VIRA	Virginia Rail	Rallus limicola
WAVI	Warbling Vireo	Vireo gilvus
WBNU	White-breasted Nuthatch	Sitta carolinensis
WEKI	Western Kingbird	Tvrannus verticalis
WEME	Western Meadowlark	Sturnella neglecta
WEVI	White-eved Vireo	Vireo griseus
WEWA	Worm-eating Warbler	Helmitheros vermivorum
WFIB	White-faced Ibis	Plegadis chihi
WIFL	Willow Flycatcher	Empidonax traillii
WILL	Willet	Tringa semipalmata
WIPH	Wilson's Phalarope	Phalaropus tricolor
WITU	Wild Turkey	Meleagris gallopavo
WIWA	Wilson's Warbler	Cardellina pusilla
WIWR	Winter Wren	Troglodytes hiemalis
WODU	Wood Duck	Aix sponsa
WOTH	Wood Thrush	Hylocichla mustelina
WPWI	Whip-poor-will	Antrostomus vociferous
WTSP	White-throated Sparrow	Zonotrichia albicollis
WWCR	White-winged Crossbill	Loxia leucoptera
WWTE	White-winged Tern	Chlidonias leucopterus
YBCH	Yellow-breasted Chat	Icteria virens

BBA Code	Common Name	Scientific Name
YBCH	Yellow-breasted Chat	Icteria virens
YBCU	Yellow-billed Cuckoo	Coccyzus americanus
YBFL	Yellow-bellied Flycatcher	Empidonax flaviventris
YBSA	Yellow-bellied Sapsucker	Sphyrapicus varius
YCNH	Yellow-crowned Night Heron	Nyctanassa violacea
YPWA	Palm Warbler	Setophaga palmarum
YSFL	Northern Flicker	Colaptes auratus
YTVI	Yellow-throated Vireo	Vireo flavifrons
YTWA	Yellow-throated Warbler	Setophaga dominica
YWAR	Yellow Warbler	Setophaga petechia

Habitat	Spe	cies	Model	ΔDIC	
Guild	Common Name	Scientific Name	-		
	American	Falco	Spatially-Varying Coefficients	0	
	Kestrel	sparverius	Spatially-Varying Intercept	175.575	
	Northern	Circus manaus	Spatially-Varying Coefficients	0	
	Harrier	Circus cyuneus	Spatially-Varying Intercept	156.97	
	Eastern	Sialia sialis	Spatially-Varying Coefficients	0	
	Bluebird	Statia statis	Spatially-Varying Intercept	132.33	
	Eastern	Sialia sialisSpatially-Varying Coefficients Spatially-Varying InterceptTyrannusSpatially-Varying Coefficients Spatially-Varying InterceptEremophilaSpatially-Varying Coefficients Spatially-Varying InterceptAnmodramusSpatially-Varying Coefficients Spatially-Varying CoefficientssavannarumSpatially-Varying Coefficients 		0	
	Kingbird	tyrannus	Spatially-Varying Intercept	79.087	
	Homod Lonk	Eremophila	Spatially-Varying Coefficients	0	
	Horned Lark	alpestris	ModelADICSpatially-Varying Coefficients0Spatially-Varying Intercept175.573Spatially-Varying Intercept156.97Spatially-Varying Coefficients0Spatially-Varying Intercept132.33Spatially-Varying Intercept132.33Spatially-Varying Coefficients0Spatially-Varying Intercept79.087Spatially-Varying Intercept42.339Spatially-Varying Intercept42.339Spatially-Varying Intercept30.121Spatially-Varying Intercept30.121Spatially-Varying Intercept169.512Spatially-Varying Intercept169.512Spatially-Varying Intercept52.299Spatially-Varying Intercept52.299Spatially-Varying Intercept240.444Spatially-Varying Intercept87.519Spatially-Varying Coefficients0Spatially-Varying Coefficients0Spatially-Varying Coefficients0Spatially-Varying Intercept162.862Spatially-Varying Intercept73.544Spatially-Varying Coefficients0Spatially-Varying Coefficients0Spatially-Varying Intercept112.179Spatially-Varying Intercept112.179Spatially-Varying Intercept112.179Spatially-Varying Intercept112.179Spatially-Varying Coefficients0Spatially-Varying Coefficients0Spatially-Varying Intercept18.148Spatially-Varying Intercept99.505Spatially-Varying Interce		
Grassland	Grasshopper	Ammodramus	Spatially-Varying Coefficients	0	
Birds	Sparrow	savannarum	Spatially-Varying Intercept	30.121	
	Savannah	Passerculus	Spatially-Varying Coefficients	0	
	Sparrow	sandwichensis	Spatially-Varying Intercept	169.515	
	Voor Cromow	Pooecetes	Spatially-Varying Coefficients	0	
	vesper Sparrow	gramineus	Spatially-Varying Intercept	52.299	
	Robolink 1	Dolichonyx	Spatially-Varying Coefficients	0	
	oryzivorus		Spatially-Varying Intercept	240.449	
	Brown-headed	M 1 (1	Spatially-Varying Coefficients	0	
	Cowbird	<i>Molotnrus ater</i>	Spatially-Varying Intercept	87.519	
	Eastern	Sturnella	Spatially-Varying Coefficients	0	
	Meadowlark	magna	Spatially-Varying Intercept	162.862	
	Blue-gray	Polioptila	Spatially-Varying Coefficients	0	
	Gnatcatcher	caerulea	Spatially-Varying Intercept	73.544	
	Blue-headed	Vince gelitaries	Spatially-Varying Coefficients	0	
	Vireo	vireo solitaries	Spatially-Varying Intercept	112.179	
Domost	Golden-	Regulus	Spatially-Varying Coefficients	0	
Forest Birds	crowned	satrapa	Spatially Varying Intercent	10 1 / 0	
	Kinglet		Spanany-varying intercept	16.146	
	Great Crested	Myiarchus	Spatially-Varying Coefficients	0	
	Flycatcher	crinitus	Spatially-Varying Intercept	99.505	
	Red-breasted	Sitta	Spatially-Varying Coefficients	0	
	Nuthatch	canadensis	Spatially-Varying Intercept	114.246	
			Continu	- 1	

**Table A 2.1** Comparison of the spatially-varying intercept (SVI) and spatially-varying coefficients (SVC) models for grassland and forest birds recorded during the 2000-05 New York State Breeding Bird Atlas.

Habitat	Spee	cies	Model	ΔDIC
Guild	Common Name	Scientific Name	-	
	Tufted	Baeolophus	Spatially-Varying Coefficients	0
	Titmouse	bicolor	Spatially-Varying Intercept	138.906
	Vooru	Catharus	Spatially-Varying Coefficients	0
	veery	fuscescens	Spatially-Varying Intercept	133.793
Forest Birds	Black-and-	Mniotilta varia	Spatially-Varying Coefficients	0
	white Warbler		Spatially-Varying Intercept	115.553
	Black-throated Setophaga		Spatially-Varying Coefficients	0
	Blue Warbler caerulescens		Spatially-Varying Intercept	50.915
	Black-throated	Dendroica	Spatially-Varying Coefficients	0
	Green Warbler	virens	Spatially-Varying Intercept	82.678
	Blackburnian	Dendroica	Spatially-Varying Coefficients	0
	Warbler	fusca	Spatially-Varying Intercept	154.844
	Canada Warhler	Cardellina	Spatially-Varying Coefficients 0	
		canadensis	Spatially-Varying Intercept	96.563

**Table A 3.1** Coefficient estimates ( $\beta$ s) of each covariate resulting from all tested models of temporal turnover (starting with the best model as indicated by DIC) for four avian groupings: all species, long-distance migrants, short-distance migrants, and resident species. Covariates included intercept (INT), magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (PRECIP\*ED), and survey effort (EFF). 50% indicates the mean of the posterior distribution, while 2.5% and 97.5% are the lower and upper quantiles of the posterior distribution.

Avian	Model	Coefficient	Coe	Coefficient Estimates	
Grouping	Model	coefficient -	50%	2.5%	97.5%
		$\beta_{INT}$	-0.368	-0.442	-0.294
		$\beta_{TMAX}$	0.018	0.005	0.030
		$\beta_{TMIN}$	0.020	0.008	0.032
	TMAX*ED +	$\beta_{PRECIP}$	-0.014	-0.034	0.005
	TMIN*ED +	$\beta_{ED}$	-0.043	-0.053	-0.032
	PRECIP*ED +	$\beta_{DEVEL}$	0.034	0.023	0.045
	DEVEL + EFF	$\beta_{TMAX-ED}$	-0.003	-0.012	0.006
		$\beta_{TMIN-ED}$	-0.017	-0.025	-0.008
		$\beta_{PRECIP-ED}$	0.070	-0.002	0.018
		$eta_{EFF}$	-0.016	-0.022	-0.009
		$eta_0$	-0.397	-0.466	-0.318
		$\beta_{TMAX}$	0.019	0.008	0.031
A 11 G	I MAA + I MIIN + DECID + ED +	$\beta_{TMIN}$	0.024	0.012	0.037
All Species	DEVEL + EFF	$\beta_{PRECIP}$	-0.019	-0.038	-0.002
		$\beta_{ED}$	-0.041	-0.054	-0.030
		$\beta_{DEVEL}$	0.035	0.024	0.046
		$\beta_{EFF}$	-0.016	-0.022	-0.009
		$\beta_{INT}$	-0.351	-0.433	-0.267
		$\beta_{TMAX}$	0.014	0.002	0.025
		$\beta_{TMIN}$	0.020	0.007	0.032
	TMAX*ED +	$\beta_{PRECIP}$	-0.012	-0.028	0.004
	TMIN*ED +	$\beta_{ED}$	-0.046	-0.056	-0.035
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	-0.001	-0.011	0.008
		$\beta_{TMIN-ED}$	-0.015	-0.025	-0.006
		$\beta_{PRECIP-ED}$	0.012	0.002	0.021
		$\beta_{EFF}$	-0.015	-0.022	-0.008

Grouping 50% 2.5% 9	7.5%
$eta_0$ -0.366 -0.431 -4	).299
$\beta_{TMAX}$ 0.014 0.002	).028
$TMAX + TMIN + \beta_{TMIN} \qquad 0.022 \qquad 0.010$	).034
$PRECIP + ED + EFF  \beta_{PRECIP} \qquad -0.017 \qquad -0.033 \qquad -4$	0.002
$eta_{ED}$ -0.043 -0.054 -0	).031
All Species $\beta_{EFF}$ -0.015 -0.022 -	).009
$\beta_0$ -0.379 -0.451 -0	).327
$TMAX + TMIN + \beta_{TMAX} \qquad 0.019 \qquad 0.007$	).031
$\frac{\beta_{TMIN}}{\beta_{TMIN}} = 0.023 \qquad 0.010$	).034
$\beta_{PRECIP}$ -0.027 -0.041 -0	).009
$\beta_{EFF}$ -0.015 -0.021 -1	).009
$\beta_{INT}$ -0.417 -0.507 -0	).188
$\beta_{TMAX}$ 0.016 -0.003	).034
$\beta_{TMIN}$ 0.033 0.015	).050
TMAX*ED + $\beta_{PRECIP}$ -0.001 -0.028	).026
TMIN*ED + $\beta_{ED}$ 0.008 -0.008	).024
$PRECIP*ED + \beta_{DEVEL} \qquad 0.074 \qquad 0.058$	).092
DEVEL + EFF $\beta_{TMAX-ED}$ 0.002 -0.011	).016
$eta_{TMIN\text{-}ED}$ -0.016 -0.030 -4	).003
$\beta_{PRECIP-ED}$ 0.019 0.003	).030
$\beta_{EFF}$ -0.016 -0.026 -4	).006
$\beta_0$ -0.433 -0.523 -4	).303
$\beta_{TMAX}$ 0.015 -0.003	).032
Long-distance TMAX + TMIN + $\beta_{TMIN}$ 0.035 0.018	).049
Migrants PRECIP + ED + $\beta_{PRECIP}$ -0.012 -0.038	).011
DEVEL + EFF $\beta_{ED}$ 0.011 -0.006	).027
$\beta_{DEVEL}$ 0.074 0.057	).092
$\beta_{EFF}$ -0.016 -0.026 -4	).006
$\beta_{INT}$ -0.370 -0.447 -0	).285
$\beta_{TMAX}$ 0.009 -0.009	).026
$\beta_{TMIN}$ 0.027 0.012	).044
TMAX*ED + $\beta_{PRECIP}$ 0.006 -0.018	0.030
TMIN*ED + $\beta_{ED}$ 0.005 -0.010	).022
$PRECIP*ED + EFF \qquad \beta_{TMAX-ED} \qquad 0.006 \qquad -0.008$	).019
$\beta_{TMIN-FD}$ -0.015 -0.028 -0	0.003
$\beta_{PRECIP-ED}$ 0.024 0.009	0.038
$\beta_{EFF}$ -0.014 -0.024 -0	0.003

Avian	Model	Coefficient	Coe	efficient Estimates	
Grouping	Widder		50%	2.5%	97.5%
		$\beta_0$	-0.277	-0.407	-0.125
		$\beta_{TMAX}$	0.009	-0.008	0.026
	TMAX + TMIN +	$\beta_{TMIN}$	0.032	0.014	0.050
	PRECIP + ED + EFF	$\beta_{PRECIP}$	-0.010	-0.036	0.017
Long distance		$\beta_{ED}$	0.010	-0.006	0.027
Long-uistance Migrants		$\beta_{EFF}$	-0.014	-0.025	-0.005
Wigrains		$\beta_0$	-0.405	-0.493	-0.263
	TMAY   TMIN	$\beta_{TMAX}$	0.007	-0.013	0.023
	$PRECIP \perp EFE$	$\beta_{TMIN}$	0.031	0.014	0.050
		$\beta_{PRECIP}$	-0.008	-0.033	0.014
		$\beta_{EFF}$	-0.014	-0.024	-0.003
		$\beta_0$	-0.598	-0.656	-0.513
		$\beta_{TMAX}$	0.029	0.005	0.051
	TMAX + TMIN +	$\beta_{TMIN}$	0.015	-0.004	0.037
	PRECIP + ED + DEVEL + EFF	$\beta_{PRECIP}$	0.001	-0.028	0.027
		$\beta_{ED}$	-0.068	-0.089	-0.046
		$\beta_{DEVEL}$	0.058	0.039	0.079
		$\beta_{EFF}$	-0.008	-0.022	0.004
		$\beta_{INT}$	-0.584	-0.640	-0.529
		$\beta_{TMAX}$	0.027	0.003	0.050
		$\beta_{TMIN}$	0.016	-0.008	0.035
Chart distance	TMAX*ED +	$\beta_{PRECIP}$	0.000	-0.033	0.032
Short-distance	TMIN*ED +	$\beta_{ED}$	-0.070	-0.093	-0.046
Migrants	PRECIP*ED +	$\beta_{DEVEL}$	0.058	0.037	0.079
	DEVEL + EFF	$\beta_{TMAX-ED}$	0.004	-0.014	0.022
		$\beta_{TMIN-ED}$	-0.014	-0.032	0.004
		$\beta_{PRECIP-ED}$	-0.004	-0.022	0.017
		$\beta_{EFF}$	-0.009	-0.022	0.003
		$\beta_0$	-0.579	-0.656	-0.518
		$\beta_{TMAX}$	0.019	-0.004	0.042
	TMAX + TMIN +	$\beta_{TMIN}$	0.009	-0.015	0.033
	PRECIP + ED + EFF	$\beta_{PRECIP}$	0.002	-0.030	0.033
		$\beta_{ED}$	-0.072	-0.094	-0.046
		$\beta_{EFF}$	-0.007	-0.020	0.006
				~	

Avian	Model	Coefficient	Coeffi	Coefficient Estimates		
Grouping	1110001	coefficient =	50%	2.5%	97.5%	
		$\beta_{INT}$	-0.562	-0.632	-0.456	
		$\beta_{TMAX}$	0.021	-0.002	0.042	
		$\beta_{TMIN}$	0.011	-0.011	0.033	
	TMAX*ED +	$\beta_{PRECIP}$	0.003	-0.029	0.039	
	TMIN*ED +	$\beta_{ED}$	-0.072	-0.094	-0.050	
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	0.008	-0.011	0.026	
Short-distance		$\beta_{TMIN-ED}$	-0.012	-0.031	0.006	
Migrants		$\beta_{PRECIP-ED}$	0.002	-0.019	0.021	
		$\beta_{EFF}$	-0.007	-0.020	0.005	
		$\beta_0$	-0.501	-0.576	-0.385	
		$\beta_{TMAX}$	0.032	0.009	0.053	
	IMAX + IMIN + DDECID + EEE	$\beta_{TMIN}$	0.010	-0.013	0.031	
	PRECIP + EFF	$\beta_{PRECIP}$	-0.008	-0.048	0.024	
		$\beta_{EFF}$	-0.009	-0.024	0.004	
		$\beta_{INT}$	-0.232	-0.331	-0.101	
	TMAX*ED + TMIN*ED + PRECIP*ED +	$\beta_{TMAX}$	0.026	0.005	0.046	
		$\beta_{TMIN}$	0.009	-0.013	0.028	
		$\beta_{PRECIP}$	-0.041	-0.071	-0.016	
		$\beta_{ED}$	-0.105	-0.128	-0.086	
		$\beta_{DEVEL}$	-0.027	-0.047	-0.010	
	DEVEL + EFF	$\beta_{TMAX-ED}$	-0.016	-0.032	-0.002	
		$\beta_{TMIN-ED}$	-0.017	-0.034	-0.002	
		$\beta_{PRECIP-ED}$	0.002	-0.015	0.021	
		$\beta_{EFF}$	-0.024	-0.036	-0.012	
		$\beta_{INT}$	-0.169	-0.349	-0.072	
		$\beta_{TMAX}$	0.024	0.004	0.047	
Resident		$\beta_{TMIN}$	0.009	-0.012	0.033	
Species	TMAX*ED +	$\beta_{PRECIP}$	-0.044	-0.074	-0.014	
	TMIN*ED +	$\beta_{ED}$	-0.104	-0.123	-0.085	
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	-0.018	-0.035	-0.003	
		$\beta_{TMIN-ED}$	-0.018	-0.035	-0.002	
		$\beta_{PRECIP-ED}$	-0.001	-0.018	0.017	
		$\beta_{EFF}$	-0.025	-0.037	-0.014	
		$eta_{0}$	-0.244	-0.350	-0.097	
		$\beta_{TMAX}$	0.028	0.006	0.051	
	TMAX + TMIN +	$\beta_{TMIN}$	0.014	-0.005	0.035	
	PRECIP + ED +	$\beta_{PRECIP}$	-0.045	-0.071	-0.019	
	DEVEL + EFF	$\beta_{ED}$	-0.103	-0.122	-0.083	
		$\beta_{DEVEL}$	-0.027	-0.046	-0.009	
		$\beta_{EFF}$	-0.024	-0.037	-0.012	

Avian	Model	an Model Coefficient —		Coe	<b>Coefficient Estimates</b>		
Grouping	Widder	Coefficient	50%	2.5%	97.5%		
		$\beta_0$	-0.202	-0.337	-0.112		
		$\beta_{TMAX}$	0.032	0.011	0.052		
	TMAX + TMIN +	$\beta_{TMIN}$	0.015	-0.005	0.034		
	PRECIP + ED + EFF	$\beta_{PRECIP}$	-0.041	-0.070	-0.008		
Decident		$\beta_{ED}$	-0.102	-0.121	0.082		
Spacing		$\beta_{EFF}$	-0.025	-0.037	-0.013		
species		$\beta_0$	-0.274	-0.429	-0.201		
	TMAN + TMIN +	$\beta_{TMAX}$	0.042	0.021	0.063		
	$\frac{1}{1} \frac{1}{1} \frac{1}$	$\beta_{TMIN}$	0.012	-0.009	0.036		
	FRECIF + EFF	$\beta_{PRECIP}$	-0.064	-0.093	-0.035		
		$\beta_{EFF}$	-0.025	-0.037	-0.014		

**Table A 3.2** Coefficient estimates ( $\beta$ s) of each covariate resulting from all tested models of extinction (starting with the best model as indicated by DIC) for four avian groupings: all species, long-distance migrants, short-distance migrants, and resident species. Covariates included intercept (INT), magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season and edge density (PRECIP\*ED), and survey effort (EFF). 50% indicates the mean of the posterior distribution, while 2.5% and 97.5% are the lower and upper quantiles of the posterior distribution.

	Avian	Model	Coefficient	Coe	fficient Estimates	
$\begin{tabular}{l c c c c c c c c c c c c c c c c c c c$	Grouping	Model		50%	2.5%	97.5%
$\begin{tabular}{l c c c c c c c c c c c c c c c c c c c$			$\beta_{INT}$	-1.016	-1.088	-0.923
$\begin{tabular}{l l l l l l l l l l l l l l l l l l l $			$\beta_{TMAX}$	0.007	-0.008	0.022
$\begin{tabular}{l l l l l l l l l l l l l l l l l l l $			$\beta_{TMIN}$	0.044	0.027	0.061
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		TMAX*ED +	$\beta_{PRECIP}$	0.036	0.014	0.061
$\label{eq:alpha} \text{All Species} \begin{array}{c ccccccccccccccccccccccccccccccccccc$		TMIN*ED +	$\beta_{ED}$	-0.079	-0.093	-0.063
$\begin{tabular}{ c c c c c c c c c c c c c c c c c c c$		PRECIP*ED +	$\beta_{DEVEL}$	0.043	0.029	0.058
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		DEVEL + EFF	$\beta_{TMAX-ED}$	-0.002	-0.014	0.011
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{TMIN-ED}$	-0.040	-0.052	-0.025
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{PRECIP-ED}$	0.010	-0.003	0.026
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{EFF}$	-0.031	-0.040	-0.022
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{INT}$	-1.039	-1.105	-0.963
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{TMAX}$	0.000	-0.017	0.019
All SpeciesTMAX*ED + TMIN*ED + $\beta_{PRECIP}$ 0.0390.0160.063TMIN*ED + PRECIP*ED + EFF $\beta_{ED}$ -0.082-0.098-0.068PRECIP*ED + EFF $\beta_{TMAX-ED}$ 0.000-0.0130.013 $\beta_{TMIN-ED}$ -0.038-0.052-0.026 $\beta_{PRECIP-ED}$ 0.0140.0010.027 $\beta_{EFF}$ -0.030-0.039-0.020 $\beta_{0}$ -0.948-1.086-0.832 $\beta_{TMAX}$ 0.010-0.0070.026TMAX + TMIN + PRECIP + ED + DEVEL + EFF $\beta_{PRECIP}$ 0.0290.0080.051DEVEL + EFF $\beta_{ED}$ -0.074-0.088-0.059 $\beta_{DEVEL}$ 0.0430.0290.056 $\beta_{EFF}$ -0.030-0.039-0.021	All Spacios		$\beta_{TMIN}$	0.040	0.025	0.055
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	All species	TMAX*ED +	$\beta_{PRECIP}$	0.039	0.016	0.063
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		TMIN*ED +	$\beta_{ED}$	-0.082	-0.098	-0.068
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		PRECIP*ED + EFF	$\beta_{TMAX-ED}$	0.000	-0.013	0.013
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{TMIN-ED}$	-0.038	-0.052	-0.026
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{PRECIP-ED}$	0.014	0.001	0.027
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{EFF}$	-0.030	-0.039	-0.020
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_0$	-0.948	-1.086	-0.832
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{TMAX}$	0.010	-0.007	0.026
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		TMAX + TMIN +	$\beta_{TMIN}$	0.053	0.039	0.070
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		PRECIP + ED +	$\beta_{PRECIP}$	0.029	0.008	0.051
$\begin{array}{c cccc} \beta_{DEVEL} & 0.043 & 0.029 & 0.056 \\ \hline \beta_{EFF} & -0.030 & -0.039 & -0.021 \end{array}$		DEVEL + EFF	$\beta_{ED}$	-0.074	-0.088	-0.059
$\beta_{EFF}$ -0.030 -0.039 -0.021			$\beta_{DEVEL}$	0.043	0.029	0.056
			$eta_{EFF}$	-0.030	-0.039	-0.021

Avian	Model	Coefficient —	Coe	Coefficient Estimates		
Grouping			50%	2.5%	97.5%	
		$\beta_0$	-0.984	-1.079	-0.887	
		$\beta_{TMAX}$	0.004	-0.012	0.021	
	TMAX + TMIN +	$\beta_{TMIN}$	0.052	0.037	0.066	
	PRECIP + ED + EFF	$\beta_{PRECIP}$	0.029	0.007	0.051	
		$\beta_{ED}$	-0.075	-0.091	-0.061	
All Species		$\beta_{EFF}$	-0.030	-0.038	-0.021	
		$\beta_0$	-1.014	-1.114	-0.843	
	TMAX + TMIN +	$\beta_{TMAX}$	0.013	-0.006	0.030	
	$\mathbf{PRECIP} \perp \mathbf{FFE}$	$\beta_{TMIN}$	0.053	0.038	0.070	
		$\beta_{PRECIP}$	0.012	-0.012	0.033	
		$\beta_{EFF}$	-0.031	-0.040	-0.022	
		$\beta_{INT}$	-1.063	-1.176	-0.977	
		$\beta_{TMAX}$	-0.024	-0.049	-0.001	
		$\beta_{TMIN}$	0.056	0.033	0.083	
	TMAX*ED +	$\beta_{PRECIP}$	0.044	0.010	0.080	
	TMIN*ED + PRECIP*ED + DEVEL + EFF	$\beta_{ED}$	-0.029	-0.050	-0.006	
		$\beta_{DEVEL}$	0.087	0.065	0.109	
		$\beta_{TMAX-ED}$	-0.008	-0.026	0.011	
		$\beta_{TMIN-ED}$	-0.032	-0.050	-0.013	
		$\beta_{PRECIP-ED}$	0.026	0.007	0.046	
		$\beta_{EFF}$	-0.024	-0.037	-0.010	
		$\beta_0$	-1.101	-1.171	-1.044	
		$\beta_{TMAX}$	-0.021	-0.047	0.004	
Long-distance	TMAX + TMIN +	$\beta_{TMIN}$	0.069	0.047	0.093	
Migrants	PRECIP + ED +	$\beta_{PRECIP}$	0.030	0.000	0.060	
	DEVEL + EFF	$\beta_{ED}$	-0.023	-0.044	0.001	
		$\beta_{DEVEL}$	0.087	0.066	0.110	
		$\beta_{EFF}$	-0.024	-0.037	-0.011	
		$\beta_{INT}$	-0.985	-1.065	-0.896	
		$\beta_{TMAX}$	-0.031	-0.056	-0.009	
		$\beta_{TMIN}$	0.054	0.030	0.084	
	TMAX*ED +	$\beta_{PRECIP}$	0.051	0.012	0.082	
	TMIN*ED +	$\beta_{ED}$	-0.034	-0.056	-0.012	
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	-0.005	-0.023	0.013	
		$\beta_{TMIN-ED}$	-0.028	-0.046	-0.010	
		$\beta_{PRECIP-ED}$	0.035	0.017	0.054	
		$\beta_{EFF}$	-0.023	-0.035	-0.010	

	Avian	Model	Coefficient	Coe	efficient Estimates	5
	Grouping		eourieiun -	50%	2.5%	97.5%
			$\beta_0$	-1.009	-1.134	-0.850
		TMAX   TMIN	$\beta_{TMAX}$	-0.023	-0.046	-0.004
		$PRECIP \perp EFE$	$\beta_{TMIN}$	0.066	0.042	0.091
			$\beta_{PRECIP}$	0.029	-0.003	0.061
	Long distance		$\beta_{EFF}$	-0.022	-0.035	-0.010
	Long-distance Migrants		$\beta_0$	-1.125	-1.398	-0.962
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	wingraints		$\beta_{TMAX}$	-0.027	-0.051	-0.005
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		TMAX + TMIN +	$\beta_{TMIN}$	0.065	0.042	0.090
		PRECIP + ED + EFF	$\beta_{PRECIP}$	0.031	-0.004	0.061
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			$\beta_{ED}$	-0.024	-0.044	-0.002
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{EFF}$	-0.023	-0.037	-0.010
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{INT}$	-1.302	-1.441	-1.215
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{TMAX}$	0.031	-0.001	0.060
$ \begin{array}{llllllllllllllllllllllllllllllllllll$			$\beta_{TMIN}$	0.024	-0.007	0.059
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		TMAX*ED + TMIN*ED + PRECIP*ED +	$\beta_{PRECIP}$	0.040	-0.005	0.078
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{ED}$	-0.126	-0.153	-0.097
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{DEVEL}$	0.067	0.042	0.096
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		DEVEL + EFF	$\beta_{TMAX-ED}$	0.014	-0.010	0.040
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{TMIN-ED}$	-0.037	-0.062	-0.010
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{PRECIP-ED}$	-0.013	-0.038	0.013
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{EFF}$	-0.032	-0.050	-0.013
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Chart distance		$\beta_0$	-1.307	-1.423	-1.181
MigrantsTMAX + TMIN + PRECIP + ED + DEVEL + EFF $\beta_{TMIN}$ $0.027$ $-0.001$ $0.059$ PRECIPDEVEL + EFF $\beta_{ED}$ $-0.125$ $-0.156$ $-0.094$ $\beta_{DEVEL}$ $\beta_{DEVEL}$ $0.068$ $0.038$ $0.096$ $\beta_{EFF}$ $\beta_0$ $-1.179$ $-1.285$ $-1.108$ $\beta_{TMAX}$ $\beta_{TMAX}$ $0.023$ $-0.010$ $0.053$ TMAX + TMIN + PRECIP + ED + EFF $\beta_{PRECIP}$ $0.039$ $-0.002$ $\beta_{ED}$ $-0.127$ $-0.057$ $-0.099$ $\beta_{EFF}$ $\beta_{EFF}$ $-0.031$ $-0.049$ $-0.012$	Short-distance		$\beta_{TMAX}$	0.031	0.001	0.062
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Migrants	TMAX + TMIN +	$\beta_{TMIN}$	0.027	-0.001	0.059
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		PRECIP + ED +	$\beta_{PRECIP}$	0.039	0.000	0.087
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		DEVEL + EFF	$\beta_{ED}$	-0.125	-0.156	-0.094
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{DEVEL}$	0.068	0.038	0.096
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			$\beta_{EFF}$	-0.032	-0.050	-0.015
$\begin{array}{cccccccc} \beta_{TMAX} & 0.023 & -0.010 & 0.053 \\ TMAX + TMIN + & \beta_{TMIN} & 0.027 & -0.003 & 0.057 \\ PRECIP + ED + EFF & \beta_{PRECIP} & 0.039 & -0.002 & 0.077 \\ & \beta_{ED} & -0.127 & -0.157 & -0.099 \\ & & \beta_{EFF} & -0.031 & -0.049 & -0.012 \end{array}$			$\beta_0$	-1.179	-1.285	-1.108
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			$\beta_{TMAX}$	0.023	-0.010	0.053
PRECIP + ED + EFF $\beta_{PRECIP}$ 0.039-0.0020.077 $\beta_{ED}$ -0.127-0.157-0.099 $\beta_{EFF}$ -0.031-0.049-0.012		TMAX + TMIN +	$\beta_{TMIN}$	0.027	-0.003	0.057
$ \begin{array}{cccc} \beta_{ED} & -0.127 & -0.157 & -0.099 \\ \beta_{EFF} & -0.031 & -0.049 & -0.012 \end{array} $		PRECIP + ED + EFF	$\beta_{PRECIP}$	0.039	-0.002	0.077
$\beta_{EFF}$ -0.031 -0.049 -0.012			$\beta_{ED}$	-0.127	-0.157	-0.099
			$\beta_{EFF}$	-0.031	-0.049	-0.012

Avian	Model	Coefficient	Coef	Coefficient Estimates		
Grouping			50%	2.5%	97.5%	
		$\beta_{INT}$	-1.300	-1.389	-0.981	
		$\beta_{TMAX}$	0.022	-0.009	0.059	
		$\beta_{TMIN}$	0.021	-0.015	0.054	
	TMAX*ED +	$\beta_{PRECIP}$	0.035	-0.007	0.073	
	TMIN*ED +	$\beta_{ED}$	-0.129	-0.159	-0.101	
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	0.016	-0.010	0.042	
Short-distance		$\beta_{TMIN-ED}$	-0.034	-0.060	-0.008	
Migrants		$\beta_{PRECIP-ED}$	-0.007	-0.034	0.019	
		$\beta_{EFF}$	-0.030	-0.050	-0.011	
		$\beta_0$	-1.223	-1.397	-1.014	
		$\beta_{TMAX}$	0.035	0.005	0.065	
	IMAA + IMIN + DDECID + EEE	$\beta_{TMIN}$	0.029	-0.006	0.062	
	PKECIP + EFF	$\beta_{PRECIP}$	0.008	-0.031	0.056	
		$\beta_{EFF}$	-0.032	-0.050	-0.014	
		$\beta_{INT}$	-1.209	-1.351	-1.015	
	TMAX*ED + TMIN*ED + PRECIP*ED +	$\beta_{TMAX}$	0.035	0.003	0.068	
		$\beta_{TMIN}$	0.019	-0.011	0.052	
		$\beta_{PRECIP}$	0.035	-0.009	0.071	
		$\beta_{ED}$	-0.144	-0.174	-0.133	
		$\beta_{DEVEL}$	-0.032	-0.058	-0.005	
	DEVEL + EFF	$\beta_{TMAX-ED}$	-0.010	-0.033	0.014	
		$\beta_{TMIN-ED}$	-0.047	-0.073	-0.019	
		$\beta_{PRECIP-ED}$	0.010	-0.019	0.034	
		$\beta_{EFF}$	-0.041	-0.058	-0.024	
		$\beta_{INT}$	-1.210	-1.347	-1.055	
Resident		$\beta_{TMAX}$	0.039	0.011	0.068	
Species		$\beta_{TMIN}$	0.023	-0.010	0.054	
Species	TMAX*ED +	$\beta_{PRECIP}$	0.036	-0.010	0.082	
	TMIN*ED +	$\beta_{ED}$	-0.143	-0.172	-0.115	
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	-0.010	-0.033	0.011	
		$\beta_{TMIN-ED}$	-0.048	-0.071	-0.024	
		$\beta_{PRECIP-ED}$	0.008	-0.018	0.034	
		$\beta_{EFF}$	-0.042	-0.061	-0.025	
		$eta_0$	-1.206	-1.300	-1.034	
		$\beta_{TMAX}$	0.046	0.012	0.079	
	TMAX + TMIN +	$\beta_{TMIN}$	0.034	0.005	0.061	
	PRECIP + ED + EFF	$\beta_{PRECIP}$	0.021	-0.016	0.064	
		$\beta_{ED}$	-0.131	-0.160	-0.104	
		$\beta_{EFF}$	-0.041	-0.059	-0.024	

Avian	vian Model Coefficient ——		Coet	Coefficient Estimates		
Grouping		eoemeient =	50%	2.5%	97.5%	
		$\beta_0$	-1.194	-1.308	-1.044	
		$\beta_{TMAX}$	0.040	0.007	-0.074	
	TMAX + TMIN +	$\beta_{TMIN}$	0.033	0.000	0.065	
PRECIP + ED +	PRECIP + ED +	$\beta_{PRECIP}$	0.026	-0.017	0.069	
	DEVEL + EFF	$\beta_{ED}$	-0.136	-0.165	-0.110	
Resident		$\beta_{DEVEL}$	-0.034	-0.063	-0.007	
Species		$\beta_{EFF}$	-0.041	-0.059	-0.025	
		$\beta_0$	-1.253	-1.394	-1.135	
	TMAX   TMIN	$\beta_{TMAX}$	0.059	0.029	0.092	
PRECIP + EFF	DECID + EEE	$\beta_{TMIN}$	0.035	0.005	0.064	
	$\Gamma \mathbf{N} \mathbf{L} \mathbf{C} \mathbf{I} \mathbf{\Gamma} + \mathbf{L} \Gamma \Gamma$	$\beta_{PRECIP}$	-0.009	-0.045	0.033	
	$\beta_{EFF}$	-0.044	-0.061	-0.027		

**Table A 3.3** Coefficient estimates ( $\beta$ s) of each covariate resulting from all tested models of colonization (starting with the best model as indicated by DIC) for four avian groupings: all species, long-distance migrants, short-distance migrants, and resident species. Covariates included intercept (INT), magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season (TMAX), magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season (TMIN), magnitude of the 25-year (1980-2005) trend in average total precipitation of the breeding season (PRECIP), edge density (ED), percent developed land (DEVEL), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the 25-year (1980-2005) trend in average maximum temperature of the breeding season and edge density (TMAX\*ED), interaction between the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (TMIN\*ED), interaction between magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season and edge density (PRECIP\*ED), and survey effort (EFF). 50% indicates the mean of the posterior distribution, while 2.5% and 97.5% are the lower and upper quantiles of the posterior distribution.

Avian	Model	Coefficient	Coef	Coefficient Estimates		
Grouping	1110401		50%	2.5%	97.5%	
		$\beta_{INT}$	-1.337	-1.408	-1.276	
		$\beta_{TMAX}$	0.020	0.006	0.035	
		$\beta_{TMIN}$	-0.011	-0.025	0.003	
	TMAX*ED +	$\beta_{PRECIP}$	-0.058	-0.076	-0.038	
	TMIN*ED +	$\beta_{ED}$	-0.005	-0.017	0.009	
	PRECIP*ED +	$\beta_{DEVEL}$	0.021	0.007	0.033	
	DEVEL + EFF	$\beta_{TMAX\text{-}ED}$	0.000	-0.011	0.011	
		$\beta_{TMIN-ED}$	0.011	0.000	0.022	
		$\beta_{PRECIP-ED}$	0.011	-0.001	0.023	
		$eta_{EFF}$	0.002	-0.006	0.010	
A 11 C		$eta_0$	-1.323	-1.422	-1.269	
All Species		$\beta_{TMAX}$	0.017	0.003	0.032	
	TMAX + TMIN +	$\beta_{TMIN}$	-0.011	-0.025	0.002	
	PRECIP + ED +	$\beta_{PRECIP}$	-0.059	-0.077	-0.040	
	DEVEL + EFF	$\beta_{ED}$	-0.004	-0.019	0.012	
		$\beta_{DEVEL}$	0.022	0.009	0.035	
		$\beta_{EFF}$	0.002	-0.006	0.010	
		$\beta_0$	-1.320	-1.401	-1.260	
		$\beta_{TMAX}$	0.017	0.000	0.031	
	IMAA + IMIN + DECID + EEE	$\beta_{TMIN}$	-0.013	-0.026	0.001	
	ΓΝΈυΙΡ + ΕΓΓ	$\beta_{PRECIP}$	-0.061	-0.077	-0.042	
		$\beta_{EFF}$	0.003	-0.005	0.010	
				<u>a</u> .: 1		

Avian	Model	Coefficient	Coe	efficient Estimate	s
Grouping	Widder		50%	2.5%	97.5%
		$\beta_{INT}$	-1.355	-1.412	-1.247
		$\beta_{TMAX}$	0.016	0.000	0.030
		$\beta_{TMIN}$	-0.013	-0.028	0.003
	TMAX*ED +	$\beta_{PRECIP}$	-0.056	-0.075	-0.037
	TMIN*ED +	$\beta_{ED}$	-0.005	-0.019	0.010
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	0.001	-0.011	0.012
		$\beta_{TMIN-ED}$	0.011	0.000	0.022
All Species		$\beta_{PRECIP-ED}$	0.013	0.002	0.026
		$\beta_{EFF}$	0.003	-0.006	0.011
		$eta_0$	-1.317	-1.364	-1.254
		$\beta_{TMAX}$	0.015	0.001	0.031
	TMAX + TMIN +	$\beta_{TMIN}$	-0.012	-0.025	0.002
	PRECIP + ED + EFF	$\beta_{PRECIP}$	-0.060	-0.079	-0.041
		$\beta_{ED}$	-0.006	-0.019	0.007
		$\beta_{EFF}$	0.002	-0.006	0.010
		$\beta_{INT}$	-1.410	-1.471	-1.296
		$\beta_{TMAX}$	0.046	0.026	0.068
		$\beta_{TMIN}$	-0.006	-0.027	0.016
	TMAX*ED +	$\beta_{PRECIP}$	-0.045	-0.078	-0.013
	TMIN*ED +	$\beta_{ED}$	0.043	0.018	0.063
	PRECIP*ED +	$\beta_{DEVEL}$	0.041	0.020	0.062
	DEVEL + EFF	$\beta_{TMAX-ED}$	0.015	-0.002	0.034
I and distance		$\beta_{TMIN-ED}$	0.008	-0.009	0.026
Long-distance		$\beta_{PRECIP-ED}$	0.015	-0.004	0.034
Migrants		$\beta_{EFF}$	-0.002	-0.016	0.011
		$\beta_0$	-1.423	-1.503	-1.358
		$\beta_{TMAX}$	0.043	0.017	0.066
	TMAX + TMIN +	$\beta_{TMIN}$	-0.007	-0.029	0.014
	PRECIP + ED +	$\beta_{PRECIP}$	-0.056	-0.083	-0.023
	DEVEL + EFF	$\beta_{ED}$	0.042	0.022	0.065
		$\beta_{DEVEL}$	0.042	0.020	0.064
		$\beta_{EFF}$	-0.003	-0.016	0.011
		,		~	

Avian	Model	Coefficient	Coe	efficient Estimates	
Grouping	WIGHEI	coefficient -	50%	2.5%	97.5%
		$\beta_{INT}$	-1.432	-1.518	-1.369
		$\beta_{TMAX}$	0.042	0.019	0.067
		$\beta_{TMIN}$	-0.008	-0.028	0.012
	TMAX*ED +	$\beta_{PRECIP}$	-0.047	-0.078	-0.016
	TMIN*ED +	$\beta_{ED}$	0.041	0.022	0.060
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	0.019	0.000	0.036
		$\beta_{TMIN-ED}$	0.008	-0.008	0.026
		$\beta_{PRECIP-ED}$	0.018	-0.003	0.036
		$\beta_{EFF}$	0.000	-0.013	0.011
Long-distance		$\beta_0$	-1.421	-1.491	-1.361
Migrants		$\beta_{TMAX}$	0.037	0.012	0.059
	TMAX + TMIN +	$\beta_{TMIN}$	-0.010	-0.031	0.013
	PRECIP + ED + EFF	$\beta_{PRECIP}$	-0.057	-0.083	-0.028
		$\beta_{ED}$	0.040	0.018	0.064
		$\beta_{EFF}$	-0.001	-0.014	0.011
		$\beta_0$	-1.418	-1.484	-1.355
	TMAX + TMINI +	$\beta_{TMAX}$	0.033	0.012	0.056
	IMAA + IMIN + DDECID + EEE	$\beta_{TMIN}$	-0.010	-0.030	0.012
	FRECIF + EFT	$\beta_{PRECIP}$	-0.047	-0.077	-0.019
		$\beta_{EFF}$	-0.001	-0.015	0.012
		$\beta_0$	-1.436	-1.507	-1.362
		$\beta_{TMAX}$	0.009	-0.019	0.040
	$PRECIP \perp EFE$	$\beta_{TMIN}$	-0.006	-0.034	0.019
		$\beta_{PRECIP}$	-0.029	-0.066	0.009
		$\beta_{EFF}$	0.014	-0.003	0.029
Short-distance		$\beta_0$	-1.429	-1.530	-1.361
Migrants		$\beta_{TMAX}$	0.014	-0.014	0.040
-	TMAX + TMIN +	$\beta_{TMIN}$	-0.006	-0.036	0.021
	PRECIP + ED +	$\beta_{PRECIP}$	-0.028	-0.063	0.015
	DEVEL + EFF	$\beta_{ED}$	-0.003	-0.028	0.023
		$\beta_{DEVEL}$	0.027	0.000	0.052
		$eta_{EFF}$	0.013	-0.003	0.028

Avian	Model	Coefficient	Coe	efficient Estimates	
Grouping	Widder	coefficient	50%	2.5%	97.5%
		$\beta_{INT}$	-1.457	-1.564	-1.383
		$\beta_{TMAX}$	0.016	-0.016	0.043
		$\beta_{TMIN}$	-0.006	-0.033	0.022
	TMAX*ED +	$\beta_{PRECIP}$	-0.027	-0.066	0.009
	TMIN*ED +	$\beta_{ED}$	-0.003	-0.029	0.026
	PRECIP*ED +	$\beta_{DEVEL}$	0.026	-0.004	0.052
	DEVEL + EFF	$\beta_{TMAX-ED}$	0.000	-0.021	0.020
		$\beta_{TMIN-ED}$	0.009	-0.012	0.031
		$\beta_{PRECIP-ED}$	0.007	-0.016	0.030
		$\beta_{EFF}$	0.013	-0.002	0.028
		$\beta_0$	-1.448	-1.583	-1.371
Chart distance		$\beta_{TMAX}$	0.011	-0.018	0.045
Migranta	TMAX + TMIN +	$\beta_{TMIN}$	-0.011	-0.036	0.015
wingraints	PRECIP + ED + EFF	$\beta_{PRECIP}$	-0.026	-0.064	0.009
		$\beta_{ED}$	-0.006	-0.031	0.019
		$\beta_{EFF}$	0.014	-0.002	0.028
	TMAX*ED +	$\beta_{INT}$	-1.475	-1.552	-1.396
		$\beta_{TMAX}$	0.013	-0.018	0.044
		$\beta_{TMIN}$	-0.010	-0.036	0.021
		$\beta_{PRECIP}$	-0.028	-0.071	0.015
	TMIN*ED +	$\beta_{ED}$	-0.002	-0.028	0.022
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	0.001	-0.021	0.023
		$\beta_{TMIN-ED}$	0.013	-0.010	0.035
		$\beta_{PRECIP-ED}$	0.012	-0.011	0.034
		$\beta_{EFF}$	0.014	-0.001	0.030
		$\beta_0$	-0.989	-1.137	-0.829
		$\beta_{TMAX}$	0.000	-0.025	0.026
	TMAX + TMIN +	$\beta_{TMIN}$	-0.014	-0.038	0.011
	PRECIP + ED +	$\beta_{PRECIP}$	-0.090	-0.126	-0.050
	DEVEL + EFF	$\beta_{ED}$	-0.062	-0.085	-0.040
Pasidant		$\beta_{DEVEL}$	-0.016	-0.039	0.006
Species		$\beta_{EFF}$	-0.006	-0.019	0.006
species		$\beta_0$	-0.976	-1.113	-0.864
		$\beta_{TMAX}$	0.000	-0.024	0.025
	TMAX + TMIN +	$\beta_{TMIN}$	-0.012	-0.037	0.012
	PRECIP + ED + EFF	$\beta_{PRECIP}$	-0.091	-0.122	-0.057
		$\beta_{ED}$	-0.061	-0.084	-0.037
		$\beta_{EFF}$	-0.007	-0.019	0.007

Avian	Model	Coefficient —	Coe	Coefficient Estimates		
Grouping			50%	2.5%	97.5%	
Resident Species T P C C T P P		$\beta_{INT}$	-1.072	-1.200	-0.950	
		$\beta_{TMAX}$	-0.002	-0.025	0.025	
		$\beta_{TMIN}$	-0.012	-0.035	0.012	
	TMAX*ED +	$\beta_{PRECIP}$	-0.090	-0.127	-0.060	
	TMIN*ED +	$\beta_{ED}$	-0.060	-0.086	-0.036	
	PRECIP*ED +	$\beta_{DEVEL}$	-0.015	-0.038	0.007	
	DEVEL + EFF	$\beta_{TMAX-ED}$	-0.014	-0.033	0.006	
		$\beta_{TMIN-ED}$	0.013	-0.007	0.031	
		$\beta_{PRECIP-ED}$	0.004	-0.014	0.025	
		$\beta_{EFF}$	-0.006	-0.020	0.008	
		$\beta_{INT}$	-0.974	-1.079	-0.819	
		$\beta_{TMAX}$	-0.001	-0.024	0.023	
		$\beta_{TMIN}$	-0.011	-0.033	0.012	
	TMAX*ED +	$\beta_{PRECIP}$	-0.090	-0.121	-0.055	
	TMIN*ED +	$\beta_{ED}$	-0.058	-0.080	-0.035	
	PRECIP*ED + EFF	$\beta_{TMAX-ED}$	-0.015	-0.034	0.005	
		$\beta_{TMIN-ED}$	0.013	-0.007	0.031	
		$\beta_{PRECIP-ED}$	0.003	-0.017	0.022	
		$\beta_{EFF}$	-0.006	-0.021	0.007	
	TMAX + TMIN + PRECIP + EFF	$\beta_0$	-0.951	-1.170	-0.681	
		$\beta_{TMAX}$	0.006	-0.016	0.031	
		$\beta_{TMIN}$	-0.011	-0.034	0.013	
		$\beta_{PRECIP}$	-0.099	-0.128	-0.070	
		$\beta_{EFF}$	-0.007	-0.022	0.007	

**Figure A 1.1** Spatial distribution of (A) magnitude of the 25-year (1980-2005) trend in average maximum temperatures [°C], (B) magnitude of the 25-year (1980-2005) trend in average minimum temperatures [°C], (C) magnitude of the 25-year (1980-2005) trend in total precipitation [mm], (D) percent developed land [%], (E) edge density [m/ha], and (F) survey effort [h].



**Figure A 1.2** Deviations of the spatially-varying coefficient estimates from the global mean for (A) the intercept, (B) the magnitude of the 25-year (1980-2005) trend in average maximum temperature of the breeding season ( $\beta_{TMAX}$ ), (C) the magnitude of the 25-year (1980-2005) trend in average minimum temperature of the breeding season ( $\beta_{TMIN}$ ), (D) the magnitude of the 25-year (1980-2005) trend rates in average total precipitation of the breeding season ( $\beta_{PRECIP}$ ), (E) percent developed land ( $\beta_{DEVEL}$ ), (F) edge density ( $\beta_{ED}$ ), and (G) effort ( $\beta_{EFF}$ ).



Figure A 2.1 The relationships between the amount of habitat (GPLAND and FPLAND for grassland and forest birds, respectively; left-hand panel of each column) and spatially-varying coefficient estimates (right-hand panel of each column) of 2000-05 average spring maximum temperature (TMAX, left column), 2000-05 average spring minimum temperature (TMIN, middle column), and 2000-05 average total spring precipitation (PRECIP, right column) for [from top to bottom] American kestrel (AMKE), northern harrier (NOHA), eastern bluebird (EABL), eastern kingbird (EAKI), horned lark (HOLA), grasshopper sparrow (GRSP), savannah sparrow (SAVS), vesper sparrow (VESP), bobolink (BOBO), brown-headed cowbird (BHCO), eastern meadowlark (EAME)], blue-gray gnatcatcher (BGGN), blue-headed vireo (BHVI), golden-crowned kinglet (GCKI), great crested flycatcher (GCFL), red-breasted nuthatch (RBNU), tufted titmouse (ETTI), veery (VEER), black-and-white warbler (BAWW), blackthroated blue warbler (BTBW), black-throated green warbler (BTNW), blackburnian warbler (BLBW), and Canada warbler (CAWA). Dark blue symbols represent coefficient estimates with 95% credible intervals not overlapping zero in locations where species was detected; black symbols represent coefficient estimates with 95% credible intervals not overlapping zero in locations where species was not detected; light blue points represent with 95% credible intervals overlapping zero coefficient estimates in locations where species was not detected; grey points represent coefficient estimates with 95% credible intervals overlapping zero in locations where the species was not detected. Black dashed line represents the slope of the relationship between the coefficient estimates and GPLAND and FPLAND. The right-hand panel shows coefficient estimates of TMAX, TMIN, and PRECIP resulting from the spatially-varying coefficients models. Grayed-out locations indicate coefficient estimates with 95% credible intervals overlapping zero. Species occurrence data were retrieved from the 2000-05 New York State Breeding Bird Atlas.



Continued on next page

Figure A 2.1 (cont'd)



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Figure A 2.1 (cont'd)



Continued on next page

Figure A 2.1 (cont'd)



**Figure A 3.1** Model validation using plots of predicted vs observed values for temporal turnover, extinction, and colonization observed between 1980-85 and 2000-05 for communities of (A) all recorded species regardless of their migratory status, (B) long-distance migrants, (C) short-distance migrants, and (D) resident birds. Model validation was done for the best model only.



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