EVALUATING THE ROLE OF PROTECTED AREAS IN MITIGATING AVIAN RESPONSES TO CLIMATE AND LAND USE CHANGE

By

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ABSTRACT

M.A. Peach. Evaluating the Role of Protected Areas in Mitigating Species' Responses to Climate and Land Use Change, 157 pages, 4 tables, 12 figures, 2017.

Billions of dollars have been invested in land protection as a strategy to conserve biodiversity based on the assumption that protected areas buffer species from processes that drive extinction. Increasingly, protected area expansion and connectivity are being incorporated into climate change adaptation strategies to facilitate anticipated shifts in species ranges in response to predicted changes in temperature and precipitation. However, the effectiveness of protected areas at maintaining biodiversity, either by reducing the risk of extinction or facilitating colonization into new areas, has not been well established. In addition, the growing reliance on multiple-use protected areas that allow resource extraction, such as timber harvest and mineral mining, has raised questions about whether multiple-use protected areas are equally beneficial for long-term biodiversity conservation as more strictly protected areas that limit active resource management. In order to address these questions using repeated Breeding Bird Atlas data, I first had to confront the limitations of existing approaches to account for imperfect detection by developing a novel modelling approach to addresses the gap between requirements of other multi-season occupancy models (i.e. repeated sampling) and existing datasets. I then applied that single-visit dynamic occupancy modelling approach to Atlas data in New York and Pennsylvania for 97 species to quantify drivers of colonization and extinction while accounting for imperfect detection in landscapes that varied by type and amount of land cover and area under protection. In general, protected areas increased colonization and lowered extinction probabilities to an increasing degree as both forest cover and neighborhood protection decreased, with particular benefits for forest breeding birds. Both strict and multiple-use protected areas increased colonization and reduced extinction more for mature forest species than early forest species, with the greatest benefits accruing when forest cover was relatively low. These results provided the most comprehensive evidence to date that protected areas can facilitate species persistence by both reducing the risk of extinction and providing attractive colonization sites as species' ranges shift and that biodiversity conservation can be compatible with renewable resource extraction.

areas, stepping stones, urban/generalist

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CHAPTER 1: BACKGROUND AND INTRODUCTION

PROTECTED AREA EFFECTIVENESS

Billions of dollars have been invested globally in land protection as a strategy to conserve biodiversity in the face of threats such as land use change, habitat degradation, fragmentation, and invasive species introductions (Margules and Pressey 2002, Gaston et al. 2008). Although not designed specifically to address the threat of climate change, the existing protected area network may be essential for biodiversity conservation in the face of a changing climate. Increasing the amount of protected land and improving connectivity among existing reserves figure prominently in recommendations for climate change adaptation (Heller and Zavaleta 2009).

In order to be an effective conservation strategy, land protection must 1) provide adequate representation of existing biodiversity and 2) ensure its persistence into the future (Margules and Presey 2002). Empirical studies of land protection effectiveness have primarily focused on the question of representation by considering the spatial overlap between protected lands and species distributions (e.g. species richness) at a single point in time (Kerr and Burkey 2002, Evans et al. 2006, Jackson et al. 2009). Such analyses indicate that protected lands do not adequately represent existing biodiversity (Brooks et al. 2004, Rodrigues et al. 2004) as a result of underlying biodiversity gradients, human population density patterns, and reserve establishment bias (Hunter and Yonzon 1993, Lan and Dunbar 2000, Pautasso and Dinetti 2009). An accurate test of the second aspect of protected land effectiveness—sustaining biodiversity over time—requires comparing biodiversity measures on protected and unprotected lands within the same region over time. The assumption has been that protected areas buffer species from processes that drive extinctions, but the effectiveness of protected areas at reducing the risk of extinction and maintaining biodiversity has been insufficiently established (Gaston et al. 2006). Longitudinal analyses of protected areas are rare and indicate that while protected areas are generally effective at maintaining forest cover (Joppa et al. 2008, Geldmann et al. 2013) they provide less consistent results for sustaining plant and animal populations (Greve et al. 2001, Geldmann et al. 2013, Rayner et al 2014, Tóth et al. 2014). Even when protected areas perform better than

unprotected areas in terms of overall biodiversity over time, there can still be significant declines in species abundance and richness within protected areas (Thiollay 2006, Stoner et al. 2007).

As species shift their ranges in response to climatic changes, protected areas could also become important as early colonization sites for species moving into new areas. At a broad scale, species' distributions are expected to shift poleward in latitude and upward in elevation in response to warming temperatures (Peters and Darling 1985, Parmesan 1996). Empirical studies have documented such shifts for many species worldwide, including birds, butterflies and plants (Thomas and Lennon 1999, Parmesan et al. 1999, Parmesan and Yohe 2003, Zuckerberg et al. 2009). Observed changes in climate variables, however, have not been uniform over space and time, which suggests that the response of individual species and assemblages might be more spatially complex than a simple unidirectional range shift (Huntington et al. 2009). Analysis of mammalian responses to the Pleistocene warming revealed that species' ranges shifted in all cardinal directions, with peak movements towards the northwest and southwest (Lyons 2003), a complex pattern that would be obscured by a focus on unidirectional poleward movement. An increasing number of studies on distributional shifts as a result of recent climatic changes have also documented more varied responses than expected (Lenoir et al. 2010, Crimmins et al. 2011, Tingley et al. 2012). Multi-directional shifts in species' distributions may be the result of interactions between multiple climatic aspects of a species' niche, such as temperature and precipitation (Tingley et al. 2009, vanDerWal 2013). Existing protected areas may provide stepping stones for species as their ranges shift in response to the multi-faceted aspects of climate change by providing desirable colonization sites.

There is evidence that birds and butterflies preferentially colonized protected areas during recent range boundary expansions in Great Britain (Thomas et al. 2012, Hiley et al. 2013), which provides preliminary support for the role of protected areas in facilitating range boundary shifts in response to climate change. Virkkala et al. (2014) found that protected areas maintained higher levels of richness for 90 species of Finnish birds of conservation concern during recent distributional shifts that were consistent with climate change predictions, primarily as a result of increased colonization at the leading range boundary. While not explicitly examining the effects of climate change, Butchart et al. (2012) found that species occurring in sites with a greater proportion of protected areas had lower extinction rates. No studies to date have explicitly quantified the effect of protected areas simultaneously on both on colonization and extinction probabilities.

An explicit test of the effect of protected areas on both colonization and extinction rates as a result of fine scale changes in climate and habitat variables over a broader spatial extent and more heterogeneous landscape than previous studies should make it possible to determine whether protected areas consistently serve as refugia, colonization sites or neither throughout a species' range. Further research into the generality of land protection as an effective conservation strategy is warranted, particularly efforts to identify characteristics of protected lands (e.g. amount, spatial configuration, and level of protection) that exert the strongest influence on biodiversity outcomes (Margules and Pressey 2000, Bonn and Gaston 2005, Geldmann et al. 2013, Virkkala et al. 2014).

CHARACTERISTICS OF PROTECTED AREAS

Legally protected areas typically restrict permanent and extensive conversion of forest and other perennially vegetated cover to human modified cover types or land uses (e.g. developed areas) in order to conserve biodiversity. However, protected areas vary in the amount of allowed human activities. Multiple-use protected areas allow resource extraction, such as timber harvest, gas drilling and mineral mining, whereas strictly protected areas limit active management of any type (Dudley 2013). Acquisition of protected areas has accelerated in recent decades, and, concurrently, the proportion of multiple-use protected areas that combine resource extraction with conservation objectives has increased (Locke and Dearden 2005). Unsurprisingly, the growing reliance on protected areas that allow resource extraction activities that might contribute to species declines over time has raised concerns about their ability to effectively maintain biodiversity (Locke and Dearden 2005, Szabo et al. 2012). However, limiting resource extraction on protected lands does not diminish demands for products and can lead to increased extraction in unprotected areas, which may reduce the overall conservation benefit of strict land protection (Sohngen et al. 1999). In addition, active management may be required to sustain the habitats and species protected areas were established to conserve (Bernes et al. 2014). Understanding the effect of different types of protected areas on biodiversity persistence over time is essential for determining the effectiveness of each approach at achieving conservation outcomes.

Long-term comparisons of the effect of different types of protected areas are rare. In tropical forests, multiple-use protected areas have been equally or more effective than strict protected areas at reducing

deforestation (Nelson and Chomitz 2011, Nolte et al. 2013), whereas only strict protection reduced the rate of deforestation in Russia (Wendland et al. 2015). Rates of deforestation, however, are an indirect measure of biodiversity conservation. Glennon and Porter (2005) found that bird communities did not differ across areas having different intensities of forest use and management (ranging from no management to extractive uses) but differed considerably between forest- and human- dominated landscapes. This finding indicates that resource extraction and wildlife conservation through land protection need not be viewed as competing goals. However, their study location, the Adirondack Park in New York State, has exceptionally large amounts of protected land relative to developed areas as well as restrictive policies on timber harvest management. Whether the Glennon and Porter (2005) findings hold over a broader landscape given greater variability in protection levels and management constraints, and a broader array of landscape contexts within which protected areas are embedded, remains in question. Moreover, Glennon and Porter (2005) conducted a "space-for-time" substitution by comparing bird communities across different landscape contexts within the same time frame as a means of evaluating potential changes in bird communities in response to changes in landscape contexts over time. Importantly, bird communities may change over time in response to climate and other pressures unrelated to local forest management. Any study designed to evaluate the effects of protected areas on biodiversity protection must necessarily study changes in bird communities over time and over a large, heterogeneous landscape.

ACCOUNTING FOR IMPERFECT DETECTION WITH BREEDING BIRD ATLAS DATA

Linking biodiversity changes to landscape-level effects such as habitat, climate, and protection status requires both biodiversity and landscape data collected at a relatively fine resolution over a large spatial scale at multiple points in time. Whereas landscape-level environmental data have been available and periodically updated for decades (e.g. National Land Cover Dataset 1992, Vogelmann *et al*. 2001), comparable and repeated surveys of species' occurrences are less common. Coordinated citizen science efforts that incorporate long-term monitoring of permanent survey locations, such as breeding bird atlases (BBA) and breeding bird surveys (BBS), provide substantial biodiversity data (Donald and Fuller 1998, Tulloch *et al*. 2013). BBAs provide information on avian distributions by subdividing a geographic area into smaller units that are typically surveyed by volunteers. The NY BBA, for example, consists of 5,332 25-km^2 blocks that

cover the entire state. BBAs were first established in the 1950s and have been completed for over 50 countries on 6 continents (Gibbons et al. 2007, Dunn and Weston 2008).

Data from BBAs at a single point in time have been used to analyse patterns of species richness and beta diversity (Desrochers, Kerr & Currie 2011; Fitterer *et al.* 2013), describe species-habitat relationships (Glennon & Porter 2005, Ferenc *et al.* 2014) and predict species' sensitivity to climate change (Virkkala *et al*. 2008; DesGranges & Morneau 2010). Although still rare, repeated BBAs that provide data for the same locations at multiple points in time are in progress or completed in at least 9 US states (U.S. Geological Survey 2014). Repeated BBAs enable dynamic analyses of how species' ranges have shifted over time in response to changing habitat amount and fragmentation (Zuckerberg & Porter 2009; van der Hoek, Renfrew & Manne 2013), climate (Thomas & Lennon 1999; Zuckerberg, Woods & Porter 2009; Virkkala *et al*. 2014) and interacting biotic and abiotic factors (Melles *et al*. 2011; Bradshaw *et al*. 2014). Although repeated BBAs enable broader exploration of changing species' distributions, imperfect species detection during the surveys poses a non-trivial challenge to accurate inference.

The inception of many BBAs predates the introduction of occupancy modelling and sampling designs that account for imperfect detection (MacKenzie et al. 2006). When presence data with imperfect detection (i.e. $p < 1$) are used, model parameter estimates are biased and can result in inaccurate conclusions about the ecological and biophysical relationships in question (MacKenzie et al 2002, Gu and Swihart 2004). Parameter estimates will generally be biased toward zero, but the direction and magnitude of the bias in each particular case will vary depending on the relationship between detection probability and occupancy (Gu and Swihart 2004, Kéry et al. 2010).

Most proposed methods for overcoming the bias introduced by assuming perfect detection require repeated sampling to estimate and account for detection probability (MacKenzie and Royle 2005). In general, these approaches rely on repeat visits over a relatively short timeframe to ensure that assumptions about population closure (i.e. no change in occupancy) are met (MacKenzie and Royal 2005). Models based on detection histories for each site can then be evaluated using a variety of likelihood and Bayesian approaches (MacKenzie et al. 2002, Royle and Kéry 2007). Multi-season occupancy models that include terms describing extinction and colonization in subsequent time periods have been developed to enable analyses of change over time in population dynamics and patterns, but these models also rely on repeat visits during each

sampling period to account for imperfect detection (Royle and Kéry 2007, MacKenzie et al. 2003, Kéry et al. 2013). Further extensions of the occupancy model include multi-species approaches that link species-specific models in a hierarchical framework to increase precision of parameter estimates, particularly for less common species (Kéry and Royle 2008). Unfortunately, records of repeated sampling within a single study time period are often unavailable for historical data sets, including the majority of BBAs.

An alternative approach is to rely on spatial rather than temporal replicates (MacKenzie and Royle 2005). Sadoti et al. (2013) successfully developed a multi-season occupancy model for Canada Warbler (*Cardellina canadensis*) using NY BBA data. After excluding BBA blocks where the majority of survey effort did not occur in a single year, effort data were not recorded, or appropriate habitat was not available, they analyzed the data in groups of four 5 x 5-km blocks (except where blocks had been excluded), wherein each block was considered a spatial replicate for estimating detection probability over the entire 10 x 10-km area. A critical assumption of this approach, as with all occupancy models, is that the replicate samples have the same true state of occupancy (i.e. there is population closure across space). The primary limitation of this approach is that it drastically reduces sample size, which may be particularly problematic for rare species (Sadoti et al. 2013).

Lele et al. (2012) developed another approach to model both occupancy and detection probability that relies on covariates that are strong predictors of each, to statistically separate the two processes. Their model requires at least one unique, continuous variable that predicts the probability of occupancy and another that predicts detection probability. Other continuous and categorical variables can be included to model occupancy, detection or both. Following the examples of Kéry and Schaub (2011), Royle and Kéry (2007), and MacKenzie et al. (2003), Lele et al.'s (2012) approach could be expanded to a single visit, multi-season occupancy model that makes it possible to estimate and correct for imperfect detection in BBA data without reducing sample size. Those models could then be integrated into multi-species occupancy models to draw inferences about community patterns.

DISSERTATION COMPONENTS

This dissertation evaluates the effectiveness of land protection as a strategy for avian conservation in the face of changing climate and land use. In particular, I test whether protected areas can influence avian

persistence by both lowering the risk of extinction and facilitating movement into new areas by increasing colonization. Finally, I explore whether the type of protection, strict or multiple-use, affects the relationship between protected areas and avian colonization and extinction. lIn Chapter 2, "Single-visit dynamic occupancy models: An approach to account for imperfect detection with Atlas data", I propose a novel occupancy model for use with Atlas data that relies on effort, or the amount of hours spent surveying a block, to estimate detection probability. I explain the formulation and rationale for the model, validate that it produces accurate parameter estimates using simulation, and, finally, apply it to Canada warbler distributions in NY using BBA data. I conclude that the single-visit dynamic occupancy model provides unbiased estimates of occupancy, colonization, extinction and detection parameters in most cases. Bias may be introduced, however, when initial occupancy is either very high (> 0.9) or low (< 0.1). In addition, the single-visit dynamic occupancy model has several advantages over alternative approaches. Applying the approach to Canada warbler data identified widespread declines in occupancy, and highlighted that declines in occupancy probability were particularly high in areas where Canada warblers were initially more likely to occur. The chapter is formatted following the guidelines for the *Journal of Applied Ecology*, in which it is currently in press.

In chapter 3, "Protected areas facilitate avian persistence by reducing extinction and improving colonization", I apply the methodology developed in Chapter 2 to 96 species in New York and Pennsylvania to identify whether protected areas effectively reduce the risk of extinction and provide attractive colonization sites as species move into new locations. I found that protected areas facilitated species persistence over time by both reducing the risk of extinction in situ and providing attractive colonization sites, but that the benefits for individual species depended on landscape context and species characteristics. This chapter will be submitted to *Conservation Biology* for consideration and is formatted in that style.

In Chapter 4, "The effect of strict and multiple-use land protection on forest bird species that prefer early and mature habitat conditions", I incorporate the single-visit dynamic occupancy model from Chapter 2 into multi-species dynamic occupancy models that link species-specific models in a hierarchical framework and increase the precision of parameter estimates, particularly for less common species. I compared the effect of strict and multiple-use protected areas on colonization and extinction probabilities for 5 birds that prefer mature forest habitat and 5 species that prefer early forest conditions. While both types of protected areas

typically improved colonization and extinction for all species considered, contrary to expectations, mature forest species received the greatest benefit from both types of protection. This chapter is also in the style of *Conservation Biology* but may be submitted elsewhere.

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CHAPTER 2: SINGLE-VISIT DYNAMIC OCCUPANCY MODELS: AN APPROACH TO ACCOUNT FOR IMPERFECT DETECTION WITH ATLAS DATA

ABSTRACT

1. Atlas data provide biodiversity information at a relatively fine spatial grain over a broad spatial extent and, increasingly, at multiple points in time, which make them invaluable for understanding processes that affect species distributions over time. The effect of survey effort on species detection has long been appreciated and Atlases typically include survey standards and records of effort, but challenges remain in analysing Atlas data that has not been collected using a repeated sampling protocol designed to correct for imperfect detection.

2. We developed a single-visit dynamic occupancy model to quantify the effects of climatic and land-use drivers on local species extinction and colonization while accounting for imperfect detection using repeat Atlas data. We evaluated model stability using data simulated under alternative scenarios and, ultimately, applied the model to empirical data for Canada warbler *Cardellina canadensis*, a wide-spread species exhibiting a long-term population decline.

3. At sample sizes that are realistic for many Atlases (n=1000–10 000 independent survey blocks), our models produced unbiased estimates of detection, occupancy, colonization and extinction parameters. Slope estimates for explanatory covariates were somewhat less stable than overall occupancy, colonization and extinction rates, with covariate effects being sensitive to the total number of, and relationships among, explanatory variables.

4. In comparison to other analyses of Canada warbler distributions that indicated minor changes over time, our approach identified a widespread decline in occupancy probability across New York, consistent with the broader population trend, particularly in the areas where it was initially more likely to occur.

5. *Synthesis and applications.* A single-visit dynamic occupancy model is a novel method for analysing common, ecologically valuable datasets, such as Atlases, that lack repeated sampling necessary to correct for imperfect detection using alternative multi-season occupancy modelling approaches. As a result, using this

method can improve understanding of species distributions and factors that shape them over time, thereby providing more accurate information to guide conservation and management.

INTRODUCTION

To understand drivers of change in biodiversity over time, comparable data are required on species' occurrence and environmental conditions. Given the multi-scale nature of species habitat selection and broad species ranges, such data must be collected at a relatively fine-grain over broad spatial extents. Moreover, because the goal is to make inferences about changes in species distribution over time, both sets of data ideally should reference multiple points in time rather than different locations at a single point in time (i.e., a space-for-time substitution). Whereas landscape-level environmental data have been available and periodically updated for decades (e.g. National Land Cover Dataset 1992, Vogelmann *et al*. 2001), comparable and repeated surveys of species' occurrences are more recent. As a result, researchers have only recently begun exploring how to best utilize large-scale, repeat surveys to evaluate spatio-temporal drivers of biodiversity change.

Coordinated citizen science efforts that incorporate long-term monitoring of permanent survey locations, such as Atlases and breeding bird surveys, provide substantial biodiversity data (Donald and Fuller 1998, Tulloch *et al*. 2013). Atlases record species' occurrences from surveys that are conducted in relatively small sampling blocks (on the order of 25 km^2) that often cover entire states or countries. First established in the 1950s, Atlas data are currently available for avian, mammalian, reptilian, amphibian, and fish species worldwide. Breeding bird atlas data in particular are available in over 50 countries on 6 continents (Gibbons et al. 2007, Dunn and Weston 2008). Data from single Atlases have been used to analyse patterns of species richness and beta diversity (Desrochers, Kerr & Currie 2011; Fitterer *et al.* 2013), describe species-habitat relationships (Glennon & Porter 2005, Ferenc *et al.* 2014) and predict species' sensitivity to climate change (Virkkala *et al*. 2008; DesGranges & Morneau 2010). Although still rare, repeated Atlases that provide data for the same locations at multiple points in time are in progress or completed in at least 9 US states (U.S. Geological Survey 2014). Repeated Atlases enable dynamic analyses of how species' ranges have shifted over time in response to changing habitat amount and fragmentation (Zuckerberg & Porter 2009; van der Hoek, Renfrew & Manne 2013), climate (Thomas & Lennon 1999; Zuckerberg, Woods & Porter 2009; Virkkala *et al*.

2014) and interacting biotic and abiotic factors (Melles *et al*. 2011; Bradshaw *et al*. 2014). Although repeated Atlases enable broader exploration of changing species' distributions, imperfect species detection during the surveys poses a non-trivial challenge to accurate inference.

The sampling design leading to many Atlas-based products predates modern occupancy methods that formally estimate detection probability as part of the survey process (MacKenzie *et al*. 2006), instead adopting survey standards, such as minimum number of hours spent surveying a block, to favor higher species detection probabilities. Failure to account for imperfect detection, even when detection probability is high, consistently underestimates the probability of site occupancy and yields biased inference about drivers of population change (Gu & Swihart 2004). Estimates tend toward zero when detection is not accounted for, but the direction and magnitude of bias depends on the relationship between detection probability and occupancy (Kéry, Gardner & Monnerat 2010). In an occupancy framework, quantifying detection probability typically relies on repeated sampling over a limited time at a given location. In a novel dynamic (or multi-season) modelling effort using Atlas data, Sadoti et al. (2013) used spatial rather than temporal replicates by aggregating 2-4 survey blocks into "sites" enabling an estimate of detection probability for Canada Warbler *Cardellina canadensis* (CAWA hereafter) at the site level and occupancy probability at the block level. A critical assumption of this approach, as with all occupancy models, is that replicate samples (here adjacent BBA blocks) have the same true state of occupancy (i.e. population closure). With spatial replication, differences between blocks in sampling and environmental characteristics can lead to inaccurate estimates of detection probability (Kéry & Royle 2015). Moreover, the spatial-replicate approach reduces the effective sample size and consequent statistical power, which will be particularly problematic for rare species that are already data-limited (Sadoti *et al*. 2013).

A promising alternative when repeat visits are lacking involves environmental covariates that are strong predictors of detectability and occupancy to help statistically separate these two processes in an occupancy modelling framework (Lele, Moreno & Bayne 2012). Formulated as a single-visit static (or single-season) occupancy model, the approach requires one unique continuous variable informing occupancy probability and another for detection probability. Other variables (continuous or categorical) can be included and shared between detection and occupancy. The Lele, Moreno & Bayne (2012) model improved analyses of Atlas-style data by removing a source of bias (imperfect detection) without the attendant assumptions and

reductions in sample size associated with spatial replicates. Importantly, Atlas data typically include a record of effort, or the amount of time spent surveying, which provides the unique, continuous variable needed to inform detection probability. Effort has regularly been included as the best available surrogate for detection probability in a non-occupancy modelling framework (e.g. Gaston *et al*. 2008), although always as a linear predictor. The probability of detection might be expected to increase linearly with low levels of effort, but eventually approaches unity where additional effort has negligible impact. As a result, including effort as a power term would more accurately describe the expected relationship with detection probability.

Herein, our goal was to extend the Lele, Moreno & Bayne (2012) approach to a multi-season, or dynamic, model for use with repeated Atlas-style data. Our specific objectives were to: 1) evaluate the ability of a dynamic occupancy model to produce unbiased estimates of site occupancy, extinction and colonization, and their drivers, under sample sizes typical for Atlas data, 2) improve how effort informs the detection process by incorporating a power function, and 3) compare occupancy, extinction and colonization estimates for CAWA in New York State using our dynamic occupancy model versus the spatial-replicate approach applied by Sadoti et al. (2013). Ultimately, we provide guidance on applying our single-visit dynamic occupancy model to data for other systems to enable accurate estimation of population change and the drivers of change when replicate samples are lacking.

MATERIALS AND METHODS

OCCUPANCY MODEL

Expanding the single-visit static model (Lele, Moreno & Bayne 2012) to a dynamic occupancy approach still requires detection to be modelled with at least one unique continuous covariate. Occupancy, colonization and extinction models can be identical, but each needs to include a continuous covariate not in the detection model. Following the Bayesian dynamic occupancy approach of Royle & Kéry (2007), we modelled occupancy probability in time one using the equation

$$\text{logit}(\psi_{1,j}) = \beta_{0o} + \beta_{1o}x_{1,j} + \ldots + \beta_{Uo}x_{U,j} \qquad \text{eqn 1}$$

where $\psi_{1,j}$ is the probability of occupancy at site *j* in time one as a function of *U* covariates. We modelled the probability of colonization and extinction using the equations

$$\text{logit}(\gamma_j) = \beta_{0c} + \beta_{1c}x_{1,j} + \ldots + \beta_{Uc}x_{U,j} \qquad \text{eqn 2}$$

$$\text{logit}(\varepsilon_j) = \beta_{0e} + \beta_{1e}x_{1,j} + \ldots + \beta_{Ue}x_{U,j} \qquad \text{eqn 3}$$

where γ_j and ε_j are probabilities of colonization and extinction respectively, each of which is a function of *U* covariates. Detection is usually modeled as a continuous function of effort (e.g. Sadoti *et al*. 2013), but such an approach does not account for the nonlinear relationship between time spent in an area and the probability of detecting a species. Thus, we took a novel approach incorporating effort as a power term using the equation

$$p_{*i,j} = 1 - (1 - \text{logit}^{-1}(y))^{E_{i,j}} \qquad \text{eqn 4}$$

where $p_{*i,j}$ is the probability of detection at site *j* in time *i* and $\text{logit}^{-1}(y)$ describes the detection rate for one unit of effort. Here, *y* could be modeled as intercept-only or using linear covariates. Equation 4 is similar to the model describing the probability of detecting a species at least once during repeat surveys (MacKenzie & Royle 2005), but units of effort ($E_{i,j}$) replace the number of surveys (*K*).

SIMULATION

Using equations 1-4 we simulated one dataset for each of 69 scenarios to explore the effect of sample size, detection probability, occupancy probability and covariate relationships on parameter estimation in a single-visit dynamic occupancy framework. In each scenario we evaluated the estimates of population parameters (occupancy, colonization, extinction, and detection) as well as estimates of regression coefficients for predictor variables.

Our simplest scenarios included a single covariate in each of the occupancy, colonization, extinction and detection models. The occupancy covariate (equation 1) was simulated from

$$x_{1,j} \sim \text{Uniform}(\text{min},\text{max}) \qquad \text{eqn 5}$$

We assumed colonization and extinction models (equations 2 and 3) were identical and a function of the same covariate as occupancy, with new values to reflect random fluctuations over time. The colonization and extinction covariate was simulated from

$$x_{2,j} \sim \text{Normal}(x_{1,j}, \sigma) \qquad \text{eqn 6}$$

In our simplest scenarios, we assumed y in equation 4 was a constant (i.e., an intercept-only linear model). The number of hours spent surveying, $E_{i,j}$, was simulated at time i in site j as

$$E_{i,j} \sim \text{TruncatedNormal}(\mu,\sigma,a,b) \qquad \text{eqn 7}$$

where μ represents the mean value, σ is the standard deviation, and a and b set upper and lower truncation values. For simplicity, we assumed that y, and therefore the probability of detection, remained constant over both time periods in all scenarios.

We used equations 1 – 7 as the basis for our simulations (simulation values in Table S1 in Supporting Information). We generated more complex occupancy scenarios by incorporating additional covariates into equation 1 and replacing β_{0o} with a random effect $\alpha_{j(i)}$ modeled as

$$\alpha_j \sim \text{Normal}(\mu,\sigma) \qquad \text{eqn 8}$$

We assumed sites were evenly distributed among $j = 1 \ldots J$ groups. We generated 10 groups for each scenario except the smallest sample sizes (n = 1000), which had five groups. In scenarios where we added covariates to $\psi_{1,j}$ (equation 1), the same covariates were added to γ_j and ε_j (equations 2 and 3) and assumed to remain constant over time or to deviate based on a normal distribution (equation 6). We created more complex detection probability scenarios by modelling y in equation 4 as a linear function of one or two variables that were either unique or shared with the occupancy, colonization and extinction models.

We generated sample sizes roughly equivalent to those of an Atlas in a small state (1000), a large state (5000) and multiple states (10 000). To vary occupancy probability, we altered the slope of a linear covariate to establish low (ψ = 0.11 on average), medium (ψ = 0.40), high (ψ = 0.71) and very high (ψ = 0.90)

initial occupancy states. In order to more systematically explore the limitations of our approach, we also simulated data with fixed occupancy probabilities ranging from 0.1 – 0.9 using our simplest models and largest sample size. We varied detection probabilities by changing the intercept or one of the slopes in y to represent species with low ($p_* = 0.01$ on average), intermediate ($p_* = 0.05$) and high ($p_* = 0.30$) detection probabilities per unit effort (hours in the case of atlas data).

We modelled latent occupancy (i.e. true occupancy) using the equations

$$Z_{i,j} \sim \text{dbern}(\psi_{i,j}) \qquad \text{eqn 9}$$

$$\psi_{1,j} = 1/(1 + \exp(\text{logit}^{-1}(\psi_{1,j})) \qquad \text{eqn 10}$$

$$\psi_{2,j} = Z_{1,j} * (1 - 1/(1 + \exp(\text{logit}^{-1}(\varepsilon_j)) + (1 - z_{1,j}) * 1/(1 + \exp(\text{logit}^{-1}(\gamma_j)) \qquad \text{eqn 11}$$

where $Z_{i,j}$ represents occupancy in time i at site j (MacKenzie *et al*. 2006). We then used latent occupancy estimates to derive occupancy probability (mean of $Z_{i,j}$) and colonization and extinction probabilities (differences between $Z_{1,j}$ and $Z_{2,j}$).

All simulations were completed using R 3.2.0 and Bayesian model fitting was performed using the R package rjags which calls the JAGS software (Plummer 2002; R Core Team 2015; Plummer 2015), using uninformative priors, 3 chains, 50,000 iterations and a burn-in of 500 iterations (see R code in Appendix S1).

Application to New York Breeding Bird Atlas Data

We reanalysed BBA CAWA data used by Sadoti *et al*. (2013) with input from the authors and data from the New York Department of Environmental Conservation (2007a and 2007b). CAWA is considered a High Priority Species of Greatest Conservation Need in NY (New York State Department of Environmental Conservation 2015) and has experienced an overall decline in the US over the past 40 years (Sauer *et al*. 2011). It is associated with a variety of forested habitats and was observed in 32% of blocks in the first BBA. For the BBA, New York was divided into 5,332 25-km^2 blocks, each of which was surveyed by volunteers during the periods 1980-85 and 2000-05 (Anderle & Carroll 1988; McGowan & Corwin 2008). Sadoti *et al*. (2013) aggregated blocks into sites containing 2-4 contiguous blocks, with each block serving as a spatial

replicate for site level detection. In order to reduce violations to the population closure assumption, they excluded all blocks with <50% forest cover to ensure adequate habitat availability and <90% of species detected in a single sampling year for each BBA period. They also excluded blocks lacking effort data in both BBA periods but retained blocks with effort for a single period. Finally, they excluded all sites containing <2 blocks, leaving a total of 1458 blocks and 504 sites.

We replicated the Sadoti *et al*. (2013) covariates and block selection to the extent possible (G. Sadoti provided a list of blocks and covariate values to ensure accurate replication). While they could retain blocks for analysis in a single BBA period even if they were excluded from the other period, our approach required all blocks be included in both periods. When effort was unavailable for a single BBA period, we substituted the average effort for that period and coded the observed occupancy as NA. This allowed us to retain the block for information on detection probability for the BBA period during which effort data were available without including occupancy information when they were not. We again estimated latent occupancy to derive population level estimates of occupancy, colonization and extinction (equations 9-11).

In order to make direct comparisons with the spatial-replicate analyses we aggregated blocks to the site level and considered a site to be occupied if any of the blocks within it was predicted to be occupied ($Z_{i,j} = 1$). We estimated block-level occupancy probabilities based on block-level covariates and estimated model coefficients derived from the single-visit dynamic occupancy model. We did the same for site-level occupancy probabilities using coefficients estimated from Sadoti *et al.*'s (2013) model. Block- and site-level occupancy probabilities in the second BBA were calculated using the equation

$$\psi_{1,j} * (1 - \varepsilon_j) + (1 - \psi_{1,j}) * \gamma_j$$

We conducted a second analysis of the BBA CAWA data with an expanded sample size because we did not need to exclude as many blocks to meet our model assumptions. For the expanded analysis, we focused on block-level results and only excluded blocks with no observation data in either BBA period (n=5,007)

When analysing both BBA data subsets, we estimated occupancy in the first BBA ($\psi_{1,j}$), as well as colonization (γ_j) and extinction (ε_j) in the second BBA at the block level using the equations

$$\text{logit}(\psi_{1,j}) = \beta_{0o} + \beta_{1o} * \text{ELEV}_j + \beta_{2o} * \text{ELEV2}_j + \beta_{3o} * \text{FOREST}_j + \beta_{4o} * \text{ACOV}_{1,j}$$

$$\text{logit}(\gamma_j) = \beta_{0c}$$

$$\text{logit}(\varepsilon_j) = \beta_{0e} + \beta_{1e} * \text{EDGEj} + \beta_{2e} * \text{NEIGHBORS}_j$$

where the variables included were identified in the most competitive model of Sadoti *et al*. (2013) and β_i are the regression coefficients for the variables indicated (See Appendix S3 for a description of covariates).

We modified Sadoti *et al.*'s (2013) detection equation to reflect our approach to account for the non-linear relationship between effort in block *j* during BBA survey *i* and detection using equation 6 where

$$\text{Logit}\ (y) = \beta_{0d} + \beta_{1d} * \text{FOREST}_i + \beta_{2d} * \text{DETECT80}_{i,j} + \beta_{3d} * \text{NEIGH3}_{i,j} + \beta_{4d} * \text{Y1980}_j + \beta_{5d} * \text{Y1981}_j + \beta_{6d} * \text{Y1982}_j + \beta_{7d} * \text{Y1983}_j + \beta_{8d} * \text{Y1985}_j + \beta_{9d} * \text{Y2000}_j + \beta_{10d} * \text{Y2001}_j + \beta_{11d} * \text{Y2002}_j + \beta_{12d} * \text{Y2003}_j + \beta_{13d} * \text{Y2004}_j + \beta_{14d} * \text{Y2005}_j$$

and $E_{i,j}$ is the effort in block *j* during BBA survey *i* in hours.

Ultimately, we had to remove NEIGH3, a spatial autocovariate, and Y1980 through Y2005, which were dummy variables indicating the primary year (Y) of sampling using 1984 as a reference, due to a lack of convergence in estimates of coefficients for those and other variables when they were included in the model. We expect these modifications to have a relatively minor effect on predictions. Five of eleven year parameters included 0 in the 95% confidence interval. The remaining year parameters, primarily from the second BBA period, were negative, which implies that later years contributed less to detection probability than the 1984 baseline. Given that average effort increased in the second BBA, we suspect the negative year effects in the second BBA period were an artifact of confounding true site-level occupancy probability declines with false reductions in block-level detection probability. NEIGH3 was strongly correlated with other spatial covariates remaining in the model.

All analyses were completed using R 3.2.0 (R Core Team 2015). Spatial covariates were calculated using the packages maptools, rgdal and spdep (Bivand, Hauke & Kossowski 2013; Bivand and Lewin-Koh

2015; Bivand, Keitt & Rowlingson 2015). We used JAGS and the R package rjags to conduct Bayesian analyses (Plummer 2002; Plummer 2015). As with the simulated data, we used uninformative priors.

RESULTS

SIMULATION

In general, results for the most complex scenarios followed the same patterns as those for the simplest scenarios. For ease of interpretation, we present the results for the simplest scenarios (where occupancy, colonization and extinction are predicted by a single linear covariate and detection has a constant hourly rate with effort included as a power term) except where more complex scenarios produced different outcomes.

Our simulations revealed that extremes in initial occupancy probability challenge inference regarding colonization and extinction probabilities. Colonization probability estimates exhibited a slight negative bias when initial occupancy probability was very high and true detection probability low (Figures 1-1 and Appendix 2-2), whereas extinction probability estimates exhibited a slight positive bias when initial occupancy probability was low regardless of detection probability (Figure 2-1, Appendix 2-2). Aside from these exceptions, and consistent with expectations, estimates of population parameters (i.e., occupancy, colonization, and extinction probability) generally became more precise given increasing sample size, higher initial occupancy probability and higher detection probability (Appendix 2-1). Similar patterns were observed for estimates of covariate effects on occupancy, colonization and extinction probabilities. Parameter estimates for the occupancy covariate when associated with high occupancy and low detection probability exhibited a slight negative bias (Figure 2-2a). The colonization covariate was biased at very high occupancy levels and became increasingly imprecise as detection probability decreased (Figure 2-2b). In contrast, the covariate associated with extinction probability showed a negative bias given extremely low occupancy combined with low detection probability (Figure 2-2c). Population parameters were considered more robust than covariate coefficient estimates because the latter indicated bias at less extreme initial occupancy levels.

True detection probability exhibited a strong influence on precision of population parameters (Figure 2-1) and covariate effects (Figure 2-2). The only exception was for estimates of detection parameters

themselves, which, consistent with expectations as a proportion increases from near 0 to 0.5, became less precise as detection probability increased (Figures 1-2d and Appendix 2-4). Moreover, estimates of regression coefficient effects on detection were more robust to variation in sample size, occupancy level, and detection probability than other covariates except at the highest detection levels (Appendix 2-4).

Estimates of population parameters remained unbiased under more complex scenarios in which we added an additional covariate to occupancy, colonization and extinction models as well as a unique linear covariate to detection (Figure 2-3a), a linear covariate to detection that was also shared with occupancy, colonization and extinction models (Figure 2-3b), and two additional linear covariates – one unique to detection and the other shared with occupancy, colonization and extinction (Figure 2-3c). Estimates of covariate effects were less robust, showing a slight and inconsistent bias across multiple levels of true occupancy probability given a detection model based on a single unique linear covariate (Figure 2-4a and Appendix 2-5), a linear covariate shared with occupancy, colonization and extinction models (Figure 2-4b and Appendix 2-5), or one linear covariate unique to detection as well as one shared with the occupancy, colonization and extinction models (Figure 2-4c and Appendix 2-5).

Application to New York Breeding Bird Atlas Data

Our estimates of occupancy probability for CAWA (ψ_1 = 0.73 and ψ_2 = 0.66) were intermediate between those assuming perfect detection (ψ_1 = 0.71 and ψ_2 = 0.6) and those based on a space-for-time substitution to correct for imperfect detection (ψ_1 = 0.81 and ψ_2 = 0.71). When mapping occupancy probability for CAWA across the state, our model produced more heterogeneous predictions (compare the a panels to the b panels in Figure 2-5). This pattern was driven by the larger grain used to determine detection in the spatial-replicate approach (100 km^2 sites versus 25 km^2 blocks) and the tendency of spatial replicates to underestimate detection and, by extension, overestimate occupancy. Differences between the two approaches were most pronounced during the second BBA period (a2 versus b2 in Figure 2-5), where the spatial-replicate approach indicated the majority of landscape to have an occupancy probability >0.8 for CAWA whereas our single-visit dynamic occupancy model estimated probability of occupancy to be no higher than 0.8 anywhere in the state, consistent with the long-term decline observed for this species. Although overall patterns in block level occupancy probabilities were similar for our model whether based on the full

dataset or the restricted subset applicable to the spatial-replicate approach (c1versus b1 in Figure 2-5), being able to fit models using the full set of survey blocks is a clear advantage of our modelling approach. Importantly, to make a fair comparison of these two approaches, occupancy estimates for the second BBA period using our model were restricted to an intercept-only colonization model, which may have been reasonable for the Sadoti *et al*. (2013) model that focused only on areas having a threshold level of suitable habitat, but would be inappropriate when including blocks encompassing a greater range of suitable habitat. Moreover, our estimates of regression parameters were not directly comparable to Sadoti *et al*.'s (2013) because we included effort as a power term in the detection model and had to remove other variables due to convergence issues.

DISCUSSION

We extended the single-visit single-season occupancy model of Lele, Moreno & Bayne (2012) to the multi-season case, providing a substantively improved set of analytical tools for ecologists working with repeated instances of single-visit monitoring data to understand the drivers of change in species distributions over time. Several advantages were apparent when comparing our single-visit dynamic occupancy model to a spatial-replicate dynamic occupancy model (sensu Sadoti et al. 2013) in the case of a declining songbird (CAWA) in New York State. Foremost, our approach maintained a larger sample size. Rather than aggregating blocks to effectively yield spatial replicates at a larger site-level, our approach retained the original data resolution enabling finer-scale inference, greater coverage of potential environmental or land use drivers affecting the distributional shifts of species, and greater statistical power. Importantly, our single-visit dynamic occupancy model was proven to provide unbiased and precise estimates of population parameters and covariate effect sizes given the sample size, detection probability and occupancy levels observed for CAWA in NY. In light of this, and given the greater number of assumptions and data manipulations required by the spatial-replicate approach, we believe our approach provides a more robust picture of CAWA status in NY. Given a more explicit treatment of the detection process, our model estimated a higher probability of local CAWA extinction and lower probability of persistence between 1980 and 2005 than the spatial-replicate approach. We documented that declines in occupancy probability were particularly high in areas where CAWA were initially more likely to occur which, in combination with the lower

probability of colonization estimated by our model, points to species decline rather than distributional shift. Such a case warrants more attention to local habitat characteristics in population strongholds to better understand local drivers of decline, e.g. changes in understory habitat quality. In contrast, maps from the spatial-replicate approach indicated relatively small changes in CAWA patterns of occupancy over time, providing little justification or guidance for conservation efforts.

Importantly, using spatial replicates confounds species detection with site occupancy processes. Under the spatial-replicate design, when one block in a site was occupied all others were assumed to be occupied as well, which tended to underestimate detection probability because in reality some blocks could be unoccupied (Kéry & Royle 2015). This resulted in an inflated estimate of occupancy probability as we observed in our application for CAWA – a problem circumvented when applying our single-visit dynamic occupancy model. Although we limited our consideration of covariates to those identified by Sadoti et al. (2013), our approach enables greater resolution of potential forest cover effects (no need for a priori exclusion of blocks of low habitat amount), as well as additional covariates given the increased statistical power associated with retaining the original sample size of survey blocks.

In addition to Lele, Moreno & Bayne's (2012) requirement that detection and occupancy models each have a unique, continuous covariate, our simulations indicated that three other guidelines apply to single-visit occupancy models whether static or dynamic in order to achieve unbiased and precise estimates: 1) ensure adequate numbers of occurrence, colonization and extinction events, 2) include a continuous predictor of detection probability as a power term, and 3) consider the value of including covariates shared by the detection and occupancy models. We address each of these in the paragraphs to follow.

First, our results highlighted the importance of considering not only sample size but also the number of occurrence, colonization and extinction events when determining whether a single visit approach will provide accurate parameter estimates. In particular, estimates of occupancy probability remained unbiased across our scenarios whereas colonization and extinction estimates became biased as occupancy probability approached extremes (i.e., 0.1 or 0.9). Although we did not explicitly vary colonization and extinction rates or set initial occupancy probabilities <0.1 or >0.9, it is logical to conclude that this bias applies generally to species with low numbers of absolute colonization, extinction or occupancy events. Moreover with ubiquitous species, i.e. when baseline occupancy probability is high, parameter estimates are consistently

biased regardless of sample size (Field, Tyre & Possingham 2005; MacKenzie & Royle 2005). Our estimates for CAWA remain robust despite these restrictions given its intermediate level of occupancy, colonization and extinction, However, ubiquitous species such as red-winged blackbird (*Agelaius phoeniceus*), rare species such as spruce grouse (*Falcipennis canadensis*), and species with little change in distribution in NY might generate inaccurate estimates using our approach.

Second, a non-linear detection model provides accurate parameter estimates and assumes a more realistic relationship between detection and effort. A non-linear relationship also eliminates the parameter non-identifiability problem described by Knape & Korner-Nievetgelt (2015) for single-visit occupancy models. When detection is fitted as a linear process, more than one set of parameter values could produce the same predictions for certain link functions. In our model, detection and occupancy regression parameters are uniquely identifiable regardless of the link functions chosen because our method models detection similarly to a repeat-visit framework. Each unit of time is treated as a repeat visit with the assumption that there is a detection rate associated with a base unit of effort (i.e., one hour). Given adequate variability in effort, only a single combination of parameters values could produce the given set of observations. Our assumption that hours can be considered discrete units of effort is testable in the field.

Third, shared covariates can result in biased estimates for regression coefficients, although estimates of occupancy, colonization and extinction probabilities remain robust. We suspect that the relationship between covariates within and between occupancy, colonization, extinction and detection models will influence the accuracy of parameter estimates, particularly the magnitude of unique covariates relative to shared ones, and future studies could improve understanding of these relationships. Our CAWA analyses are unaffected by this caveat because the occupancy, colonization and extinction probabilities we examined are robust to these challenges. Interpretation of regression coefficients would have been subject to potential bias because percent forest cover was used to model both occupancy and detection, but, based on our simulation results, that bias would have been slight.

One non-trivial consideration in the use of our approach is the time required because working with large sample sizes in a Bayesian framework can be processing intensive and thus time-limiting, particularly as the number of covariates or sample size increases. However, it is possible to apply a single-visit dynamic occupancy approach in a maximum likelihood framework for which we provide sample code in Appendix S2.

We preferred the Bayesian framework for this application due to the ease of incorporating a random effect and estimating latent occupancy, which makes it easy to derive population level occupancy, colonization and extinction probabilities. With different analysis questions or larger datasets, those benefits may not be worth the trade-offs in processing time.

Our modelling approach addresses a gap between the requirements of other multi-season occupancy models (i.e. repeated sampling) and many existing datasets. Although we applied it specifically to Atlas data, this method may be relevant to other types of data that lack repeated sampling. For example, Hostetler & Chandler (2015) compared a variety of state-space models describing abundance that relied on covariates to predict detection. While they concluded that direct information about detection probability is preferable to using covariates, such information is not always available. In these cases, the single-visit dynamic approach is a useful method for more accurately describing population parameters and environmental relationships than ignoring the effects of imperfect detection. An accurate understanding of species distribution and the factors that shape them at meaningful spatial scales are essential for effective conservation and management. Our CAWA results highlight the necessity of properly accounting for imperfect detection to identify species in decline and guide conservation efforts.

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FIGURES

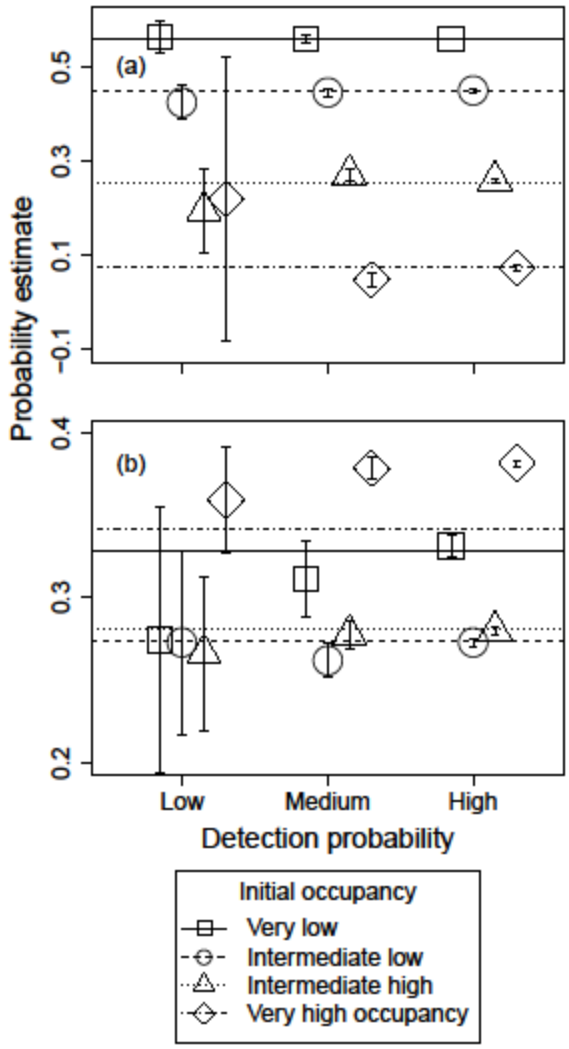

Figure 2-1. Estimates of (a) colonization and (b) extinction probability across 3 levels of detection probability and 4 levels of initial occupancy probability (n = 1000). Estimates are based on a single linear covariate predicting colonization and extinction and a constant describing detection. Actual values are indicated by horizontal dashed lines. Standard deviation bars are shown but may be smaller than symbols.

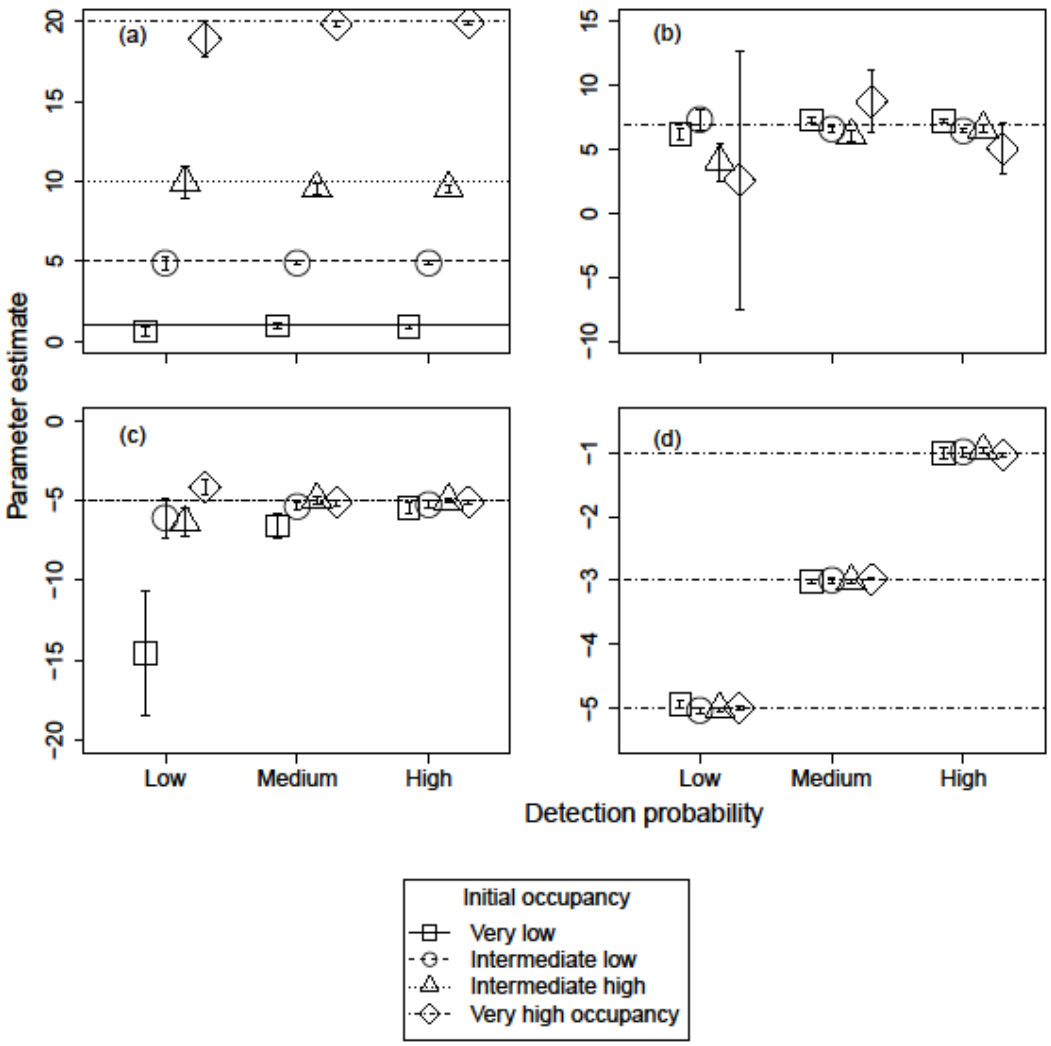

Figure 2-2. Estimates of a regression coefficient for the effect of a random uniform covariate on (a) occupancy, (b) colonization, and (c) extinction probabilities and (d) a constant that when inverse-logit transformed represents the hourly detection across 3 levels of detection probability and 4 levels of occupancy probability (n = 10 000). Actual values are indicated by horizontal dashed lines. Standard deviation bars are shown but may be smaller than symbols.

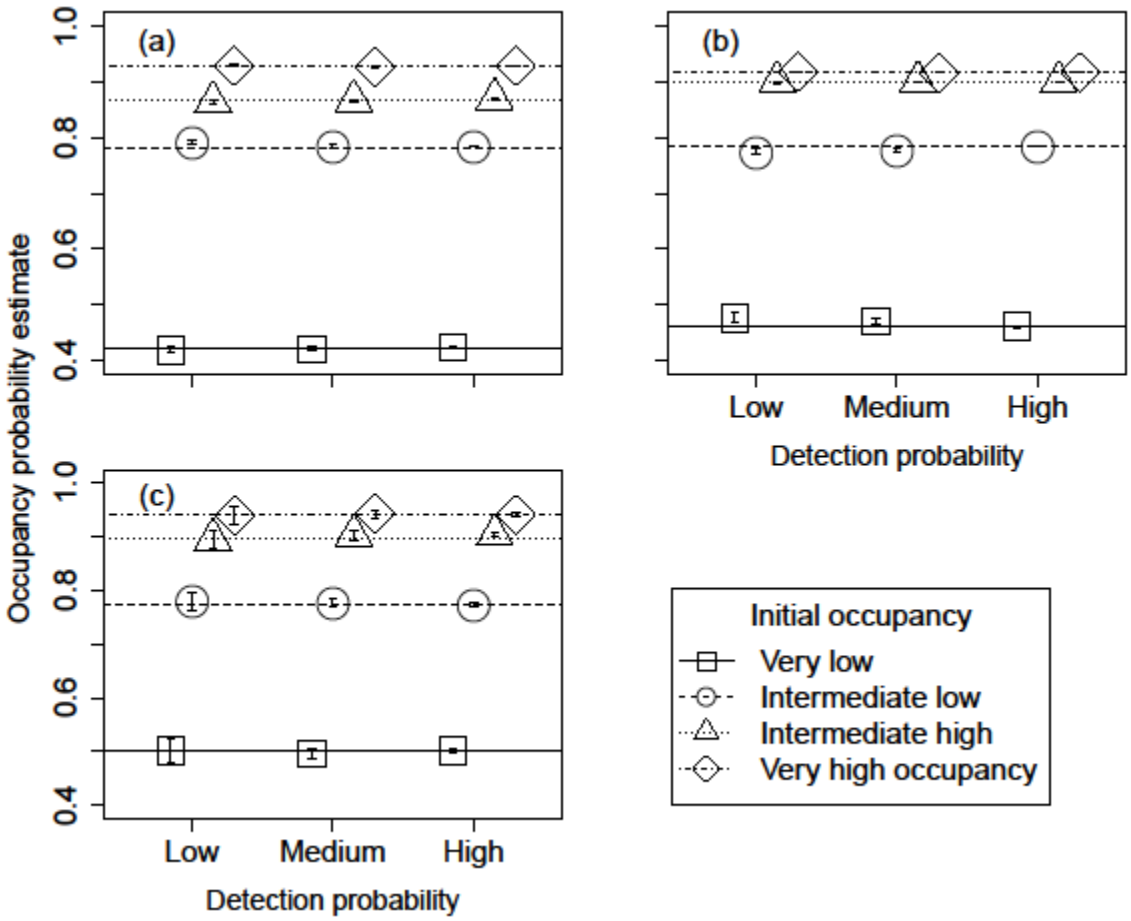

Figure 2-3. Estimates of the occupancy probability in time one when the linear part of detection model contained (a) a single, unique covariate, (b) a single covariate that was also shared with the occupancy model and (c) one unique covariate and one covariate that was shared with the occupancy model. Actual values are indicated by horizontal dashed lines. Standard deviation bars are shown but may be smaller than symbols.

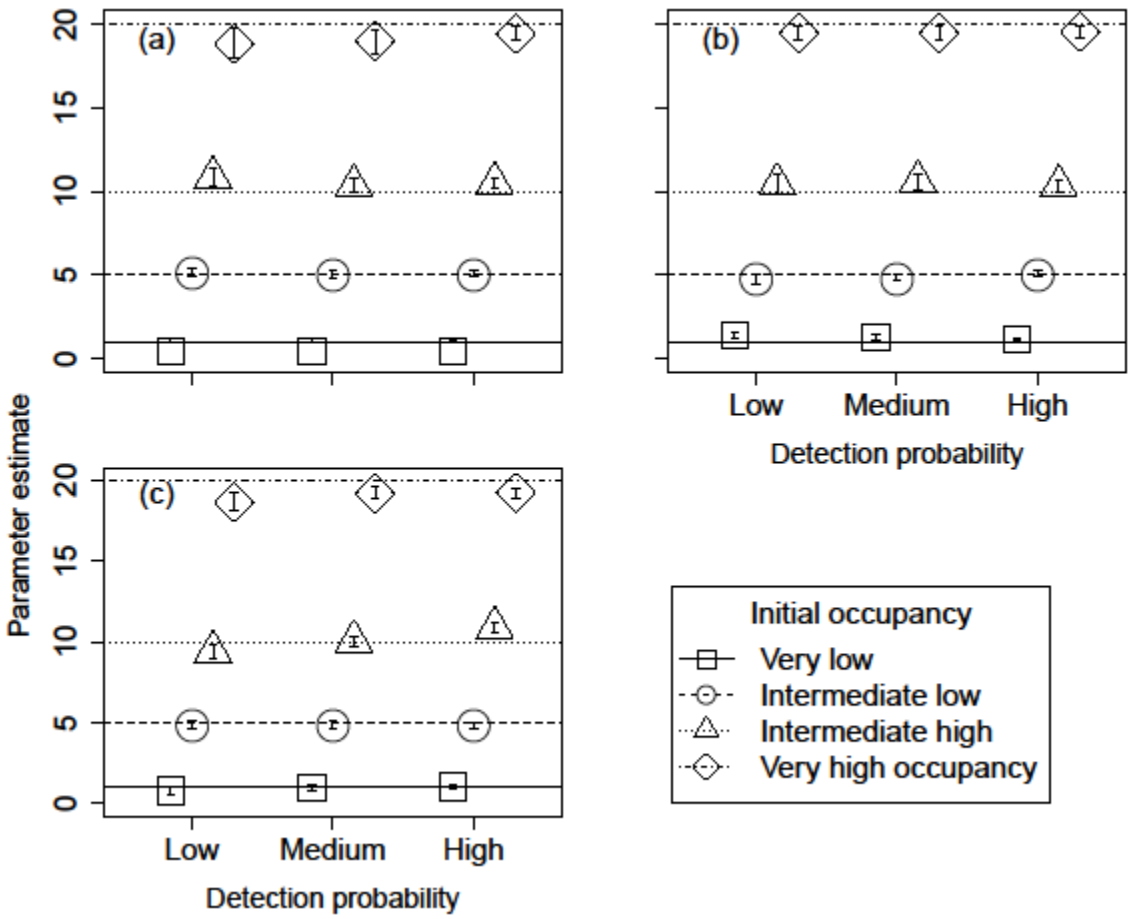

Figure 2-4. Estimates of an occupancy regression coefficient for the effects of one of two random uniform covariates when the linear part of detection mode (equation 6) contained (a) a single, unique covariate, (b) a single covariate that was also shared with the occupancy model and (c) one unique covariate and one covariate that was shared with the occupancy model. Actual values are indicated by horizontal dashed lines. Standard deviation bars are shown but may be smaller than symbols.

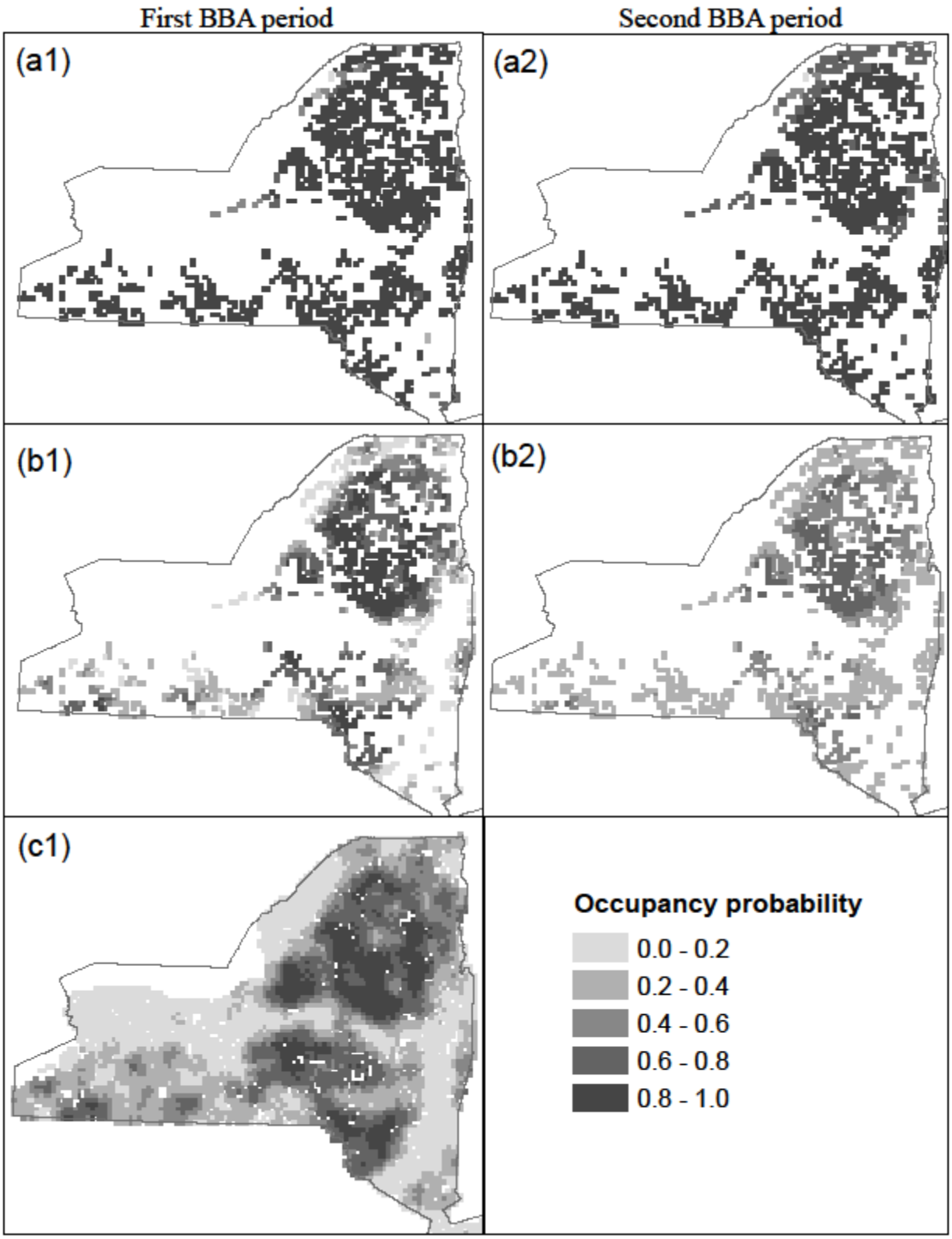

Figure 2-5. Estimated occupancy probabilities for Cardellina canadensis in New York State BBA blocks based on (a) spatial-replicate model, (b) a single-visit dynamic occupancy model using an identical subset of

BBA blocks as the spatial-replicate model (Sadoti et al. 2013) and (c) a single-visit dynamic occupancy model using a larger subset of BBA blocks for the (1) first and (2) second Atlas periods. A single-visit dynamic occupancy model using a larger subset of BBA blocks was not possible for the second Atlas period given the Sadoti et al. 2013 variables and models. Occupancy probabilities in the first Atlas period were estimated based on the occupancy equations in each model.

CHAPTER 3: PROTECTED AREAS FACILITATE AVIAN PERSISTENCE THROUGH 20 YEARS OF CLIMATE AND LAND USE CHANGE

ABSTRACT

Billions of dollars have been invested in land protection as a strategy to conserve biodiversity based on the assumption that protected areas buffer species from processes that drive extinction. Increasingly, protected area expansion and connectivity are being incorporated into climate change adaptation strategies to facilitate anticipated shifts in species ranges in response to predicted changes in temperature and precipitation. However, the effectiveness of protected areas at maintaining biodiversity, either by reducing the risk of extinction or facilitating colonization into new areas, has not been well established. Our goal was to evaluate the degree to which protected areas influenced colonization and extinction patterns for 96 avian species over 20 years in the northeastern US. Using breeding bird atlas data, we fit single-visit, dynamic occupancy models to quantify drivers of colonization and extinction while accounting for imperfect detection in landscapes that varied by type and amount of land cover and area under protection. In general, protected areas increased colonization and lowered extinction to an increasing degree as both forest cover and amount of regional land protection decreased. Both habitat affinity and range boundary location influenced the effect of protected areas on colonization and extinction, with forest species benefitting most from protected areas. Moreover, protected areas reduced extinction and increased colonization for northern species (with a southern range boundary within 100 km of the study area), which coincided with greater range boundary fluctuation for those species, but not southern or core-range species. Neither migratory habit nor conservation status influenced the effect of protected areas on colonization and extinction. Encouragingly, our results indicate that land protection remains a viable conservation strategy for many species in the face of changing habitat and climate. The benefits for individual species, however, depend on landscape context and species characteristics.

INTRODUCTION

Rates of global biodiversity loss have risen to up to 1,000 times greater than background levels following expansion of human civilization (Pimm et al. 1995). Billions of dollars have been invested globally in land protection as a strategy to conserve biodiversity based on the assumption that protected areas buffer species from processes such as land use change, habitat degradation, fragmentation, and invasive species that drive extinctions elsewhere in the landscape (Margules and Pressey 2002, Gaston et al. 2008). Although the existing reserve network was not designed specifically to address the threat of climate change, increasing the amount of protected land and improving connectivity among existing reserves figures prominently in recommendations for climate change adaptation (Heller and Zavaleta 2009, Mawdsley et al. 2009).

The effectiveness of protected areas at reducing the risk of extinction and maintaining biodiversity has been insufficiently established (Gaston et al. 2006). Such a test requires simultaneously comparing biodiversity measures on protected and unprotected lands within the same geographic region over a time scale that allows for environmental change and demographic responses. Longitudinal studies indicate that although protected areas are generally effective at maintaining forest cover (Joppa et al. 2008, Geldmann et al. 2013) they are inconsistent in their effects on specific plant and animal populations (Greve et al. 2011, Rayner et al 2014, Tóth et al. 2014, Barnes et al 2016). Even where protected areas perform better than unprotected areas, overall declines in species abundance and richness may still be observed (Thiollay 2006, Stoner et al. 2007).

Moreover, distributional shifts in response to warming temperatures have been observed for many species around the world, including birds, butterflies and plants (Parmesan et al. 1999, Parmesan and Yohe 2003, Lenoir et al. 2010, Crimmins et al. 2011, Tingley et al. 2012). Increasingly, protected areas may be viewed as potential stepping stone locales for species that shift their geographic ranges to track the changing climate, with the caveat that appropriate habitat must be available in the new areas (Thomas et al. 2012, Hiley et al. 2013, Virkkala et al. 2014). As a result, a focus on local site extinction, or retention, may be too simple to capture dynamic population responses to climate change.

Importantly, species natural history is likely to influence the role protected areas play in colonization and extinction patterns. For example, population status (increasing or declining), whether the protected area occurs at a population edge or established core (Hiley et al. 2014), whether the species is a year-round

resident or seasonal migrant (Virkkala and Rajasärkkä 2010), and the overlap between preferred habitat and protected areas (Virkkala et al. 1994) might affect the degree to which protected areas influence species occurrence over time.

Previous studies of protected area effectiveness have focused primarily on biodiversity at a single point in time or case studies having a relatively narrow geographic scope or involving a limited number of species (Gaston et al. 2008). Comparisons of colonization and extinction dynamics for a large number of species on protected and unprotected areas are lacking. In addition, previous studies have used observational data without accounting for imperfect species detection. Failure to account for imperfect detection hinders inference about both occupancy patterns and drivers of change because model estimates will be biased (MacKenzie et al. 2006). Applying a dynamic occupancy modelling approach to account for imperfect detection and explicitly estimate colonization and extinction probabilities as a function of protected areas would overcome the limitations of previous studies (MacKenzie et al. 2003).

Our goal was to evaluate the degree to which protected areas influenced colonization and extinction patterns for a large suite of avian species over a 20-year period in the northeastern United States. This region is experiencing some of the most rapidly rising temperatures in the U.S. along with predicted increases in precipitation (Karmalkar and Bradley 2017), making it ideal for assessing demographic responses. Moreover our study covered two states—New York and Pennsylvania—providing regional variation in the amount of forest cover as well as amount of land protection. Our specific objectives were to 1) determine if species use protected areas as stepping stones when shifting distribution, which would be indicated by landscapes containing protected areas showing higher colonization probability than surrounding areas, our expectation should species use protected areas as stepping stones when shifting their distribution; 2) to determine whether protected areas buffer populations against deterministic stressors in the larger landscape, which would be evident should landscapes containing protected areas have lower extinction probabilities relative to surrounding areas, our expectation; and 3) identify characteristics of species most and least likely to benefit from protected areas. Our results provide insights into the long-term benefits of protected areas for biodiversity conservation in an era of rapid environmental change.

METHODS

Our study area covered an approximately 260,000-km^2 region of the northeastern United States that encompassed the states of New York (NY) and Pennsylvania (PA). This region is predicted to experience continued increases in temperature and precipitation with consequent lengthening of the growing season and rising productivity, evapotranspiration, and frequency of drought in the 21st century (Huntington et al. 2009). Forests cover the majority of the region with oak-hickory predominant in the south then transitioning to northern hardwoods (characterized by a mixture of *Acer saccharum*, *Fagus grandifolia*, and *Betula alleghaniensis*) and conifers at higher latitudes (NYS DEC 2010, USDA 2013).

Records of avian species occurrence and survey effort in hours were acquired from repeated Breeding Bird Atlases (BBA) completed between 1980-1985 and 2000-2005 in NY and 1983-1989 and 2004-2009 in PA (Anderle and Carroll 1988, McGowan and Corwin 2008, Wilson et al 2012). Each BBA involved uniform sampling blocks (approximately 25 km^2) that volunteers surveyed to record all avian species detected by sight and sound, the breeding status of each species, and the number of hours spent surveying. We selected records for all species having "possible", "probable" and "confirmed" breeding observations. Then, to ensure adequate sample size for accurate parameter estimates, we limited our analyses to species having naïve colonization or extinction probabilities ≥ 0.1 (Peach et al. in press), yielding 96 species for our analysis (Supporting Information Table 3-1). We further excluded individual survey blocks that had zero effort in either time period (n=773), overlapped between the two states (n=116 PA blocks), or lacked environmental data (n=3), leaving 9,394 blocks for our analyses.

To understand drivers of site occupancy, colonization and extinction over time, we quantified the landscape and climate context of each survey block in each time period (Table 3-1). All spatial data and analyses were managed in ArcGIS 10.1 (ESRI, Redlands, CA). To represent climate in each of the two BBA time periods (t), we calculated average annual precipitation (hereafter, $TOTP_t$), average annual temperature ($BSAT_t$) during the breeding season (June/July/August), and average annual minimum temperature ($MINT_t$). Climate values were calculated at the centroid of each BBA survey block using the Parameter-elevation Regression on Independent Slopes Model Climate Group monthly data (PRISM Climate Group 2004). Although there are many ways to characterize climate and its impact on birds, we selected TOTP, BSAT, and MINT because they are relatively easy to derive and have been shown to influence avian abundance and

distributions in previous studies (Root 1988, Tingley et al. 2009. Gutiérrez Ilán et al. 2014). We characterized land cover within each BBA block using the 1992/2001 retrofit land cover change product from the National Land Cover Database (NLCD; Fry et al. 2009; Figure 3-1). We calculated the proportion of each BBA block in two broad land cover classes ($FOREST_t$ versus $OPEN_t$) in 1992 (t = 1) and 2001 (t = 2). Using the Anderson Level I classes (Anderson et al. 1976), FOREST included the NLCD cover class "Forest" whereas OPEN included the classes "Grassland/Shrub", "Agriculture" and "Wetlands". Because available land cover data do not align perfectly with BBA periods, these data were considered to represent the minimum land cover change between our two survey periods.

To represent protected areas, we relied on the Protected Areas Database of the United States (PAD-US, USGS 2012), which includes all publically-owned protected areas as well as private protected areas whose data were voluntarily provided from organizations such as The Nature Conservancy and local land trusts. We excluded all protected areas that were acquired after the first BBA survey, assuming these newly protected areas were not effectively protected at the time of the first survey period. We retained areas classified as "fee ownership" that lacked acquisition dates because these were likely old protected areas for which digital information is commonly not available. However, we excluded "easement" records that lacked an establishment date because easements did not become widely used as a land conservation tool until the late 1990's (Meyer et al. 2014). The remaining protected areas covered 16% of the study area and were primarily forested (83% in 1992 and 82% in 2001). For each BBA block, we calculated the proportion of the block under protection (B_PA). Each block was further categorized as belonging to a high (R_PA = 1) or low (R_PA = 0) neighborhood protection context based on whether >50% of the area in its contiguous neighbors was protected (Figure 3-1).

Occupancy Model

For each species, we fit a single-visit, dynamic occupancy model (Peach et al. 2017), which accounts for imperfect species detection and enables assessment of factors affecting the colonization and extinction processes, including land protection. To quantify occupancy probability in the first survey period, we fit our global model as:

$$\text{logit}(\psi_{i,1}) = \beta_{0o} + \beta_{1o} * TOTP_{i,1} + \beta_{2o} * BSAT_{i,1} + \beta_{3o} * MINT_{i,1} + \beta_{4o} * FOREST_{i,1} + \beta_{5o} * OPEN_{i,1} + \beta_{6o} * B\_PA_i + \beta_{7o} * R\_PA_i + \beta_{8o} * B\_PA_i * FOREST_{i,1} + \beta_{9o} * B\_PA_i * R\_PA_i + \beta_{10o} * R\_PA_i * FOREST_{i,1} + \beta_{11o} * B\_PA_i * R\_PA_i * FOREST_{i,1} \quad \text{(eqn 1)}$$

where ψ_{i1} is the occupancy probability at site *i* during BBA period 1. For alternative candidate models we retained all climate variables while removing subsets of habitat and protection variables and, (Appendix 3-2). Assuming that land protection in the absence of habitat is not beneficial to a species, we only considered models with interactions between $FOREST_{i,1}$ and land protection (Table 3-2). We did not include interactions with $OPEN_{i,1}$ to minimize model complexity and because the proportion of forest and open cover were inversely correlated. Candidate colonization ($\gamma_{i,2}$) and extinction ($\varepsilon_{i,2}$) models were identical to occupancy models with one additional variable, $NEIGH_{i,1}$,the proportion of the contiguous neighbors in which the species was observed in time t = 1, to account for spatial autocorrelation in colonization and extinction processes.

Detection probability at time t was modeled as:

$$p_{*i,j,t} = 1 - (1 - logit^{-1}(y_{i,j,t}))^{E_{i,}} \quad \text{(eqn 2)}$$

where $p_{*i,t}$ is the probability of detection at site *i* during BBA period *t*, $\text{logit}^{-1}(y)$ is a constant describing the hourly rate of detection, and $E_{i,t}$ is the amount of effort (i.e. number of hours) spent surveying site *i* during BBA period *t*. In models where effort is modeled linearly, identifiability in single-visit models depends on the link functions chosen for the models (Knape and Korner-Nievergelt 2015). The parameterization of effort as a power term avoids problems with identifiability inherent in other single-visit models and is a more accurate representation of our assumptions about the relationship between detection probability and time spent surveying (Peach et al. 2017).

For each species, we fit 216 plausible combinations of occupancy, colonization and extinction candidate models using maximum likelihood with optim() function and a Newton-Raphson algorithm in R (R Core Team 2015). Due to model fitting errors for all candidate models describing *Dolichonyx oryxivorus* we eliminated that species from further analyses. For some species, detection probability was close to 1, which made it impossible to estimate the standard error of *y* (equation 2) or, in extreme cases, of all parameter

values, because $p^*_{i,t}$ was approaching the maximum (n = 19 species). We successfully estimated standard errors in all cases after fixing $p^*_{i,t} = 1$, and used parameter estimates from those models for subsequent analyses.

We identified the most parsimonious models for each species using the difference in Akaike's Information Criterion (ΔAIC; Burnham and Anderson 2002). For models with $p^*_{i,t}$ fixed at 1, we still included detection rate as an estimated parameter when calculating AIC because we did not know *a priori* to fix the value. For each model having ΔAIC < 2 we estimated the main effect of block-level protected areas (B_PA) on colonization and extinction probabilities by taking the partial derivative given a categorical value representing neighborhood protection level (1: >0.5 of neighborhood is protected, 0: <0.5 of neighborhood is protected) and partitioning forest cover into categories of low (25th percentile = 0.36), intermediate (average = 0.56) and high (75th percentile = 0.77) amounts (Wooldridge 2013). For example, the main effect of B_PA on occupancy in time 1, given the most complex occupancy model (equation 1) and using the average value of $FOREST_t$ and an index of 1 for the high category of neighborhood protection (R_PA) was calculated as:

$$d\psi/dB\_PA = \beta_{6o} + \beta_{8o} * mean(FOREST_1) + \beta_{9o} * high(R\_PA) + \beta_{10o} * high(R\_PA) * mean(FOREST_1)$$

Standard errors for each main effect were calculated using the delta method (Powell 2007). We then tallied species' relationships to protected areas as being positive or negative under each combination of forest cover and neighborhood protection. For species demonstrating equivocal responses, i.e., when the direction of the relationship differed among competing models for either colonization or extinction, we excluded that species-parameter combination from subsequent analyses (e.g. *Setophaga citrina* was excluded from colonization analyses because parsimonious models included positive, negative and zero main effects of B_PA, but it was not excluded from extinction analyses for which a consistent negative relationship was estimated). We also excluded estimates having a 95% confidence interval that included zero. Using data visualization, we identified potential outliers then applied Grubbs test to determine if individual values should be excluded from further analyses (Grubbs 1950).

We conducted post-hoc analyses on the main effects to examine the influence of protected areas on colonization and extinction across species. First, we plotted the estimated B_PA main effect from the top-

ranked model for each species (or model-averaged estimates of the main effects when multiple models were supported), with the extinction-specific parameter on the x-axis and colonization-specific parameter on the y-axis, and calculated the correlation between them to determine whether protected area main effects on colonization and extinction negatively correlated. We then grouped species based on habitat, range boundary, conservation status, and residency status (Appendix 3-1). We assigned each species to a habitat, specifically, as either forest (n=50), open (n=32) or generalist/urban (n=15) based primarily on Breeding Bird Survey (BBS) breeding habitat classifications (Sauer at al. 2017) with supplements as needed (DeGraaf and Yamasaki 2001, Rodewald 2014). For consistency with our land cover category, we grouped grassland, shrubland, agriculture and wetland/aquatic species together in the open habitat group. We further classified species based on whether their range boundary was within 100 m of either the northern (southern species, n=29) or southern (northern species, n = 18) boundary of the study area using BirdLife International range maps (BirdLife International 2016). Species whose ranges extended beyond 100 m of the northern and southern boundaries of the study area were classified as "core" (n = 50). We classified 27 species of "conservation concern" based on identification in NY and PA state lists or inclusion in the Partners in Flight Land Bird Conservation Plan (Rosenberg et al. 2016). Lastly, we classified residency status as resident (n=22), short-distance migrant (n=31), and neo-tropical migrant (n=44) following BBS migration form groups (Sauer at al. 2017) supplemented as necessary (Rodewald 2014). We tested for differences among categories using ANOVA, with t-tests used to make pairwise comparisons among levels within categories and a Bonferroni correction to adjust *p*-values for the multiple comparisons. Given the time required for a multi-species occupancy modelling approach that simultaneously estimated parameters and made comparison between groups for 97 species for 9,394 blocks, a Bayesian approach was impractical.

RESULTS

The number of competing models (those where $\Delta AIC < 2$) ranged from 1 – 19 per species. For most species (78-89%), competing models estimated a consistent sign for the main effect of B_PA on colonization and extinction in all scenarios (Table 3-2). Due to limitations of model averaging for estimating individual model coefficients (Cade 2015) and our focus on broad patterns rather than species specific responses, we

present results based on the most parsimonious model for each species. Maps of occupancy probabilities in both Atlas periods based on the best fitting model for each species are available in Appendix 3-5.

In general, block-level protection was less beneficial for increasing colonization or lowering extinction probabilities as forest cover increased and when neighborhood protection was high (Table 3-2, Figure 3-2). In fact, extinction became more likely and colonization less likely for with increasing block-level protected area for the most species when both forest cover and the amount of neighborhood protection were high (Figure 3-2f). The opposite was true, and the most benefits accrued by species, when forest cover and the amount of neighborhood protection were low (Figure 3-2a). Under low neighborhood protection, the main effect of block-level protected area on colonization was significantly inversely correlated with the main effect on extinction, indicating that protected areas tend to consistently either improve or worsen both colonization and extinction probabilities for individual species. In contrast, under high neighborhood protection, individual species responses were more variable and the correlation between the main effect of protected area on colonization and extinction disappeared. Results based on combinations of high neighborhood protection with low or intermediate forest cover should be interpreted with caution since they represent extrapolation beyond landscapes present in the study area (Figure 3-1).

Post-hoc analyses revealed that the main effects of B_PA on colonization and extinction differed among groups of bird species based on habitat affinity, range boundary location, and migratory habit. There were significant differences between groups based on habitat affinity for colonization when neighborhood protected was low (all $p < 0.001$). When neighborhood protection was high, there was only a significant difference between groups at high forest cover. Colonization consistently increased with increasing proportion of block level protection, with a main effect that was twice as high for forest species than generalist species, and pairwise comparisons indicated significant differences when neighborhood protection was low ($p < 0.001$ at Bonferroni-corrected $\alpha = 0.006$; Figure 3-3 a and b). Pairwise comparisons only indicated a significant difference in the main effect of protected area on colonization between forest and open when neighborhood protection was low and forest cover was high. Notably, when neighborhood protection was high, colonization values were negative or zero for all groups. Under low neighborhood protection, there were also significant differences between species based on habitat affinity for the main effect of protection on extinction (all $p < 0.001$). Under high neighborhood protection, there were only significant differences

between groups when forest cover was low. In all cases, the greatest reductions in extinction probabilities were observed for forest birds, but pairwise comparisons only indicated a significant difference between forest and generalist species (all $p < 0.003$ at Bonferroni-corrected $\alpha = 0.006$; Figure 3-3 c and d). There were no significant differences for extinction among groups when neighborhood protection was high.

Range boundary location was also associated with significant differences in the effect of block level protection on both colonization and extinction when neighborhood protection was low (all $p < 0.001$). Northern species (i.e. those with a southern range boundary within 100 m of the study area) consistently exhibited the greatest improvements to colonization from increasing block-level protection followed by core-range species then southern species (i.e. a northern range boundary within 100 m of the study area; all $p < 0.005$ at Bonferroni corrected $\alpha = 0.006$; Figure 3-4 a and b). Pairwise differences between northern and southern species were significant (all $p < 0.005$ at Bonferroni corrected $\alpha = 0.006$) only when forest was average-high whereas core-range species were different from northern species when forest cover was low-average ($p < 0.007$ at Bonferroni corrected $\alpha = 0.008$). There were no significant pairwise differences in the main effect of block level protection on colonization at high neighborhood protection or on extinction in any scenario (Figure 3-4 c and d).

We found differences in the size of the main effect of B_PA between groups of birds based on migratory status for colonization (all $p < 0.02$) for the combinations of low and average forest cover with low neighborhood protection as well as high forest cover and high neighborhood protection (Appendix 4-3). There was a significant difference in the main effect of B_PA on extinction based on migratory habit when neighborhood protection was low (all $p < 0.001$) but not when neighborhood protection was high. Pairwise comparisons, however, did not identify significant differences in any scenario. Species of conservation concern did not benefit more than other species from either reduced extinction or increased colonization as a result of increasing block-level protected area (Appendix 4-4). Even after repeating analyses with only the most threatened species we still did not find significant differences in the effect of block-level protected area on colonization or extinction.

DISCUSSION

We documented that protected areas facilitated avian persistence over time by both reducing the risk of extinction in situ and providing attractive colonization sites. In general, we observed that reductions in extinction were strongly correlated with increases in colonization at low neighborhood protection, and protected areas overall had a greater impact on stemming extinctions than promoting colonizations. The benefits for individual species depended on both landscape context and species characteristics, with some diminishing returns evident for increasing block level protection when forest cover or neighborhood protection was high.

Reserve design theory initially drew insights from island biogeography and described protected areas as islands of suitable habitat surrounded by seas of human modified landscapes (MacArthur and Wilson 1967, Diamond 1975). As a result, larger protected areas in close proximity to other protected areas were presumed to support higher species richness and lower rates of extinction. This assumption was quickly challenged based on theoretical, empirical, and practical grounds (Simberloff and Abele 1976, Simberloff and Abele 1982), but expanding existing reserves still figures prominently in conservation planning and climate change mitigation recommendations (Heller and Zavaleta 2009). Although colonization and extinction probabilities may be most favorable for long-term persistence in highly protected landscapes, particularly in conjunction with favorable environmental conditions, our study emphasizes that the relative contribution of block-level protected area to extinction and colonization is actually greatest when neighborhood protection is low. Thus, the marginal benefits of adding new protected areas will be maximized in regions currently lacking significant investment in land protection with the caveat that suitable habitat must be available and in an amount sufficient to support a viable population.

Many protected areas were not explicitly established with the goal of conserving biodiversity, and, as a result, there can be a spatial mismatch between species' distributions and protected areas (Margules and Pressey 2002, Deguise and Kerr 2006). Globally, threatened species are disproportionately underrepresented on protected areas, which limits the ability of protected areas to conserve species at risk (Rodrigues et al. 2004). Similarly, we found that protected areas did not differentially affect either extinction or colonization rates for species of conservation. Species of concern in in the northeastern US are predominantly open habitat species, and, thus, less likely to benefit from forest protection than forest species in the northeast (Valiela and

Martinetto 2007). Efforts to increase representation of open habitats on protected areas in the region, through acquisition or active management, may be critical for retaining species that depend on them.

Habitat availability is an important factor in protected area effectiveness, even for widespread species. In this forest dominated landscape, protected areas consistently reduced extinction and improved colonization for forest birds, but they were particularly valuable when forest habitat was relatively rare. In contrast, protected areas had a negative effect on open-land species' ability to persist in landscapes with little open habitat (i.e. high forest cover with an average of 8% open), which likely reflects poor representation of open habitat on protected areas in the northeastern US. When open habitat was common (i.e. low forest cover with an average of 50% open) protected areas improved both colonization and extinction for open species. We hypothesize that protected areas generally provide the greatest marginal benefits at low to intermediate levels of habitat availability. Species cannot persist in the absence of suitable habitat regardless of the amount of protected area, and protected areas become less necessary for persistence when habitat is widespread.

Globally, habitat generalists have been expanding their ranges. Concurrent declines in other species have led to increased biotic homogenization, or a growing similarity between avian communities in different locations (McKinney and Lockwood 1999). Climate change is predicted to accelerate this process (Davey et al. 2011), but, consistent with Thomas et al.'s (2010) findings, protected areas in our study inhibited the persistence and spread of generalist species while leading to better outcomes for habitat specialists. Protected areas may, therefore, help counteract broad-scale trends of increasing biotic homogenization.

Although migratory species have experienced long-term population declines as a result of changing climate and habitat conditions throughout their annual range (Robbins et al. 1989), in the northeastern US the expansion of forest in the 20th-century corresponds to increases in both resident and migratory forest bird abundance (Valiela and Martinetto 2007). In our landscape, protected areas benefitted both migratory and resident species by reducing extinction and increasing colonization during the breeding season, but any advantage to migratory species over resident species was ambiguous. Migratory species typically do not have access to protected areas throughout all stages of their annual cycle (Runge et al. 2015). Focusing land protection efforts in in areas occupied by migratory species during phases of their annual life cycles that currently have the lowest levels of land protection may be more constructive for migratory species

conservation than promoting additional land protection in North American breeding grounds. Our results indicate that resident species in those areas would likely benefit from increased protected area as well.

We expected range boundaries to experience increased colonization and extinction relative to range centers (La Sorte and Thompson 2007). Moreover, given general trends of northward range shifts, we hypothesized that northern species (whose southern range margin occurred within 100 m of our study area) would exhibit reduced extinction at the southern range boundary while southern species, which are expected to expand their ranges northward under climate change, would exhibit improved colonization of protected areas at the northern range boundary (Hiley et al. 2014). Whereas we found no evidence that protected areas improved colonization outcomes for southern species, northern species exhibited higher colonization and lower, although not statistically significant, extinction in association with protected areas. Using a slightly different subset of species from the same NY BBA data, Zuckerberg et al. (2009) documented northward range boundary shifts for northern species with less evidence of shifts for southern species, which parallels our findings. We clarified the value of protected areas in this study for northern species via providing colonization sites as ranges shift and, to a lesser degree, buffering against local extinction. In conjunction, these results suggest that species experiencing the greatest range boundary fluctuations also rely most heavily on protected areas.

Empirical studies have documented poleward range shifts for many species across the globe, (Thomas and Lennon 1999, Parmesan et al. 1999, Parmesan and Yohe 2003, Zuckerberg et al. 2009), but observed changes in climate variables have not been uniform over space and time. The response of individual species and assemblages might, thus, be more spatially complex than a simple unidirectional range shift (Huntington et al. 2009, Lenoir et al. 2010, Crimmins et al. 2011, Tingley et al. 2012, vanDerWal 2013). Species responses to climatic changes may also be mitigated by factors including habitat availability and condition as well as biotic interactions. Jarzyna (2014), for example, found increasing amounts of forest cover reduced the effects of climatic changes on forest breeding bird distributions. A combination of these factors could explain why southern species do not appear to be advancing northward and, in our study, did not preferentially rely on protected areas to colonize new blocks (Zuckerberg et al. 2009).

Our findings contradict those of Kharoub and Kerr (2010) who concluded that protected areas did not improve outcomes any more than unprotected areas for butterfly species facing changing climatic

conditions in Canada during the 20th-century. Several factors could have contributed to these inconsistencies including the species under consideration, landscape context and methodological differences. Protected areas may be more effective at mitigating indirect (e.g. habitat change) rather than direct (e.g. temperature and precipitation) impacts of climate change. As a consequence, ectotherms, including butterflies, whose distributions are directly influenced by climate, may not benefit as much from protected areas as endotherms such as birds (Deutsh et al. 2008). Notably, Canada retains extensive areas of high forest cover. Based on our results, those landscape conditions reduce the ability of protected areas to affect colonization and extinction relative to unprotected areas. Finally, Kharoub and Kerr (2010) relied on species distribution models rather than direct observations as in our study. In addition, they did not correct for imperfect detection in the occurrence records from which the distribution models were constructed, which we were able to do in an occupancy modelling framework.

We conclude that protected areas remain a useful conservation strategy despite anticipated shifts in species distributions because, in addition to reducing the risk of extinction, they can facilitate movement to new locations, at least for vagile species such as birds. However, existing protected areas cannot ensure long-term persistence of all species. They do not adequately encompass global biodiversity (Brooks et al. 2004, Rodrigues et al. 2004) as a result of underlying biodiversity gradients, human population density patterns, and reserve establishment bias (Hunter and Yonzon 1993, Lan and Dunbar 2000, Pautasso and Dinetti 2009). Species missing from protected areas, including many species of conservation concern, will not benefit from protected areas if suitable habitat conditions are lacking. In addition, amount of protected area is only one determinant of colonization and extinction probabilities. Changes in other factors that shape species distributions, such as climate or habitat, can produce low colonization and high extinction despite the presence of protected areas. For example, temperature and precipitation are predicted to change more dramatically in the future than during the 20 year period of this study (Huntington et al. 2009).

An alternative approach to conservation planning given anticipated changes in climate is to shift the focus from protecting species to protecting the underlying geophysical drivers of biodiversity at evolutionary scales thereby protecting the "stage" while recognizing that the cast of species will change over time (Anderson and Ferree 2010). In practice this approach has been used to identify priority conservation sites based on the number of unique topography and elevation microclimates in combination with natural cover

connectivity that are presumed to represent sites with the greatest resilience to climate change driven changes in species richness. These sites have significant overlap with species-based conservation priority sites to protect high-quality rare species and natural communities, meaning they may both capture existing biodiversity and provide the greatest resilience to changes in climate (Anderson et al. 2014). Regardless of the approach to identifying future priorities for protected area acquisition, our results indicated that protected areas can be an effective biodiversity conservation tool by both reducing the risk of extinction and facilitating movement in to new areas.

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TABLES

Table 3-1. Summary values for all covariates included in models describing occupancy, colonization, extinction and detection of breeding birds in New York and Pennsylvania, 1980-89 and 2000-09.

Covariate	Minimum	Average	Maximum
E_1[a]	0.2	21.58	562
E_2[a]	0.5	26.07	1352
B_PA[b]	0	0.15	1
R_PA[c]	0	0.09	1
$FOREST_1$[d]	0	0.56	1
$FOREST_2$[d]	0	0.55	1
$OPEN_1$[d]	0	0.31	0.95
$OPEN_2$[d]	0	0.31	0.95
$MINT_1$[e]	-19.82	-11.99	-4.45
$MINT_2$[e]	-17.98	010.78	-3.26
$BSAT_1$[f]	14.08	18.79	23.82
$BSAT_2$[f]	14.77	19.39	24.16
$TOTP_1$[g]	756.6	1084.0	1725.0
$TOTP_2$[g]	797.0	1145.0	1714.0

[a]Number of hours spent surveying each block during first (1) and second (2) survey.

[b]Proportion of block covered by protected area

[c]Binary, ascribed 1 when >50% of the area of contiguous blocks was protected, else 0.

[d]Proportion of block covered by forest and open land cover types

[e]Annual average minimum temperature in degrees C in first (1) versus second (2) survey

[f]Average June/July/August average temperature in degrees C in first (1) versus second (2) survey

[g]Average total precipitation in mm in first (1) versus second (2) survey

Table 3-2. Number of species showing positive, negative and zero main effects of protected areas on logit scale colonization or extinction probabilities.

Forest Cover[a]	Neighborhood Protection[b]	Parameter	Sign Consistency	Sign Direction: Positive	Negative	Zero	NA[e]	Total
Low	*Low*	*Colonization*	Consistent[c]	56	14	15		86
			Inconsistent[c]	4	0	6		10
		Extinction	Consistent	10	65	10		85
			Inconsistent	2	5	3	1	11
Low	*High*	*Colonization*	Consistent	33	27	15		75
			Inconsistent	8	0	6	7	21
		Extinction	Consistent	20	49	10		79
			Inconsistent	0	8	8	6	17
Average	*Low*	*Colonization*	Consistent	37	33	15		81
			Inconsistent	4	0	6	1	15
		Extinction	Consistent	15	57	10		84
			Inconsistent	1	5	3	3	12
Average	*High*	*Colonization*	Consistent	21	42	10		80
			Inconsistent	4	5	3	4	16
		Extinction	Consistent	28	42	10		80

			Inconsistent	4	5	3	4	16
High	*Low*	*Colonization*	Consistent	33	27	15		75
			Inconsistent	8	0	6	7	21
		Extinction	Consistent	20	49	10		79
			Inconsistent	0	8	3	6	17
High	*High*	*Colonization*	Consistent	20	47	15		82
			Inconsistent	3	3	6	2	14
		Extinction	Consistent	41	28	10		79
			Inconsistent	8	2	3	4	17

[a]Results for main effects estimated when forest cover was low (25% percentile = 0.36), average (0.56) and high (75% percentile = 0.77)

[b]Results for main effect estimated when neighborhood protection was low (<50% of the area of contiguous blocks protected) and high (>50% of the area of contiguous blocks protected).

[c]Consistent signs indicates that all of the best fitting models for a species exhibited either a positive, negative or no relationship. Species were categorized as inconsistent if the best fitting models exhibited variable signs for the relationship.

[d]When the best fitting models showed an inconsistent relationship, the relationship describing a majority of the models is indicated.

[e]When no consistent relationship was observed for at least 50% of the models, the relationship was categorized as NA.

FIGURES

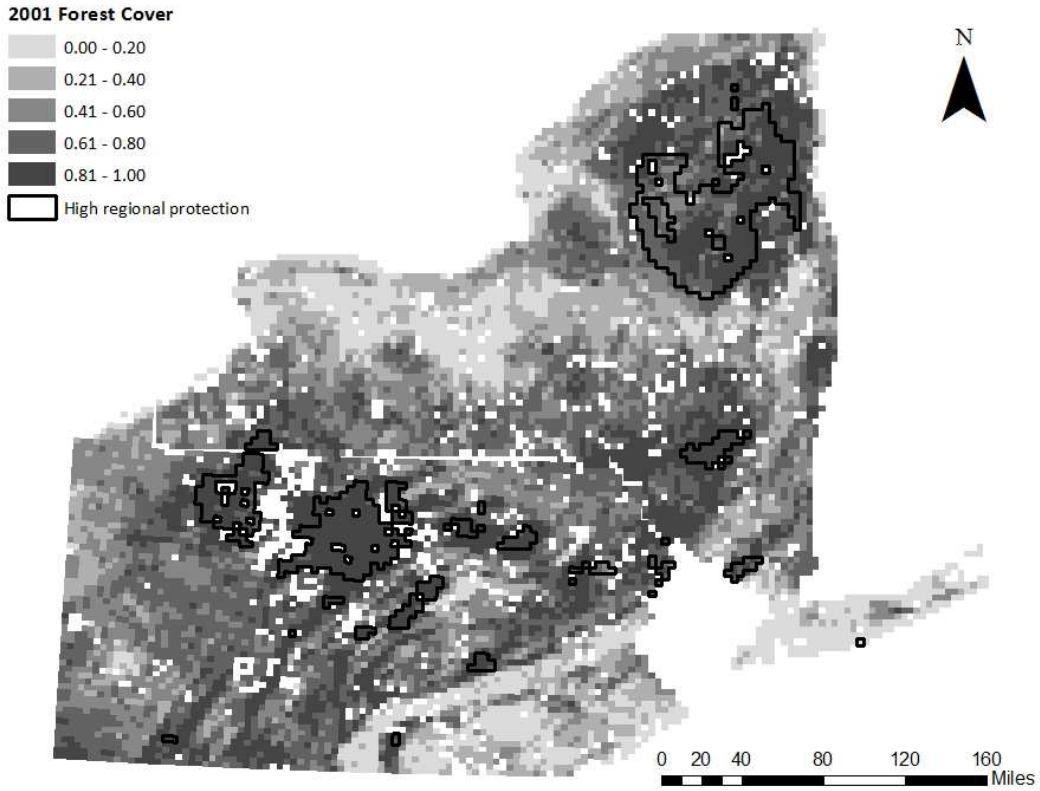

Figure 3-1. Distribution of forest cover and areas of high neighborhood protection across Breeding Bird Atlas blocks in New York and Pennsylvania, 2001. Gaps represent blocks that were excluded from the study due to missing covariate values or spatial overlap between NY and PA Atlas blocks.

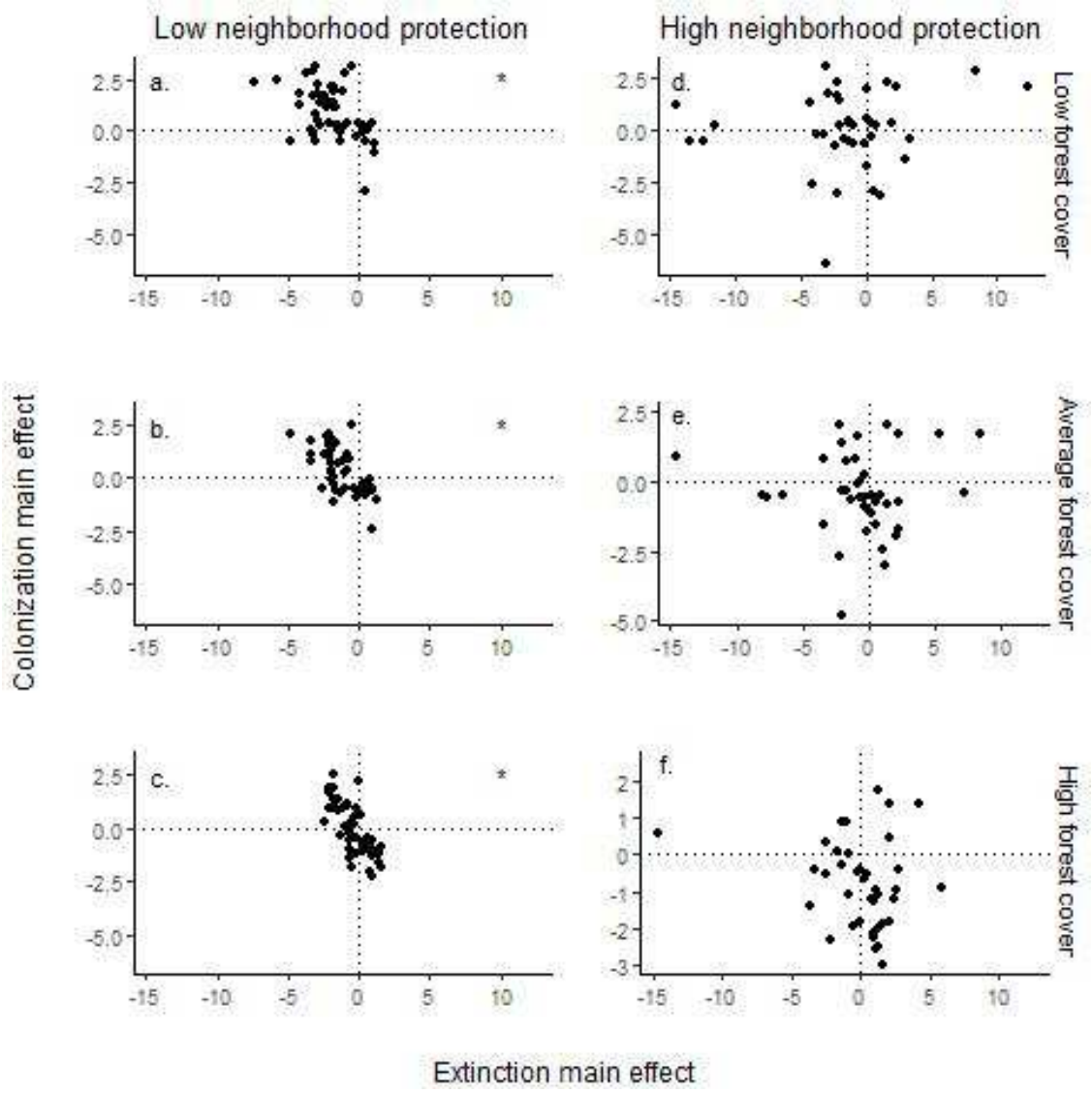

Figure 3-2. Relationship between the average main effect of block level protection on colonization and extinction given (a) low forest cover (0.36) and low neighborhood protection (< 0.5 of area of surrounding blocks protected), (b) average forest cover (0.56) and low neighborhood protection, (c) high forest cover (0.77) and low neighborhood protection, (d) low forest cover and high neighborhood protection (> 0.5 of area of surrounding blocks protected), (e) average forest cover and high neighborhood protection, and (f) high forest cover and high neighborhood protection for breeding bird atlas blocks in NY and PA 1980-89 and 2001-09. The greatest benefits are accrued by species in the upper left quadrant of each plot, coinciding with increased colonization and reduced extinction. An asterisk indicates a significant correlation between the main effect of protected areas on colonization and extinction.

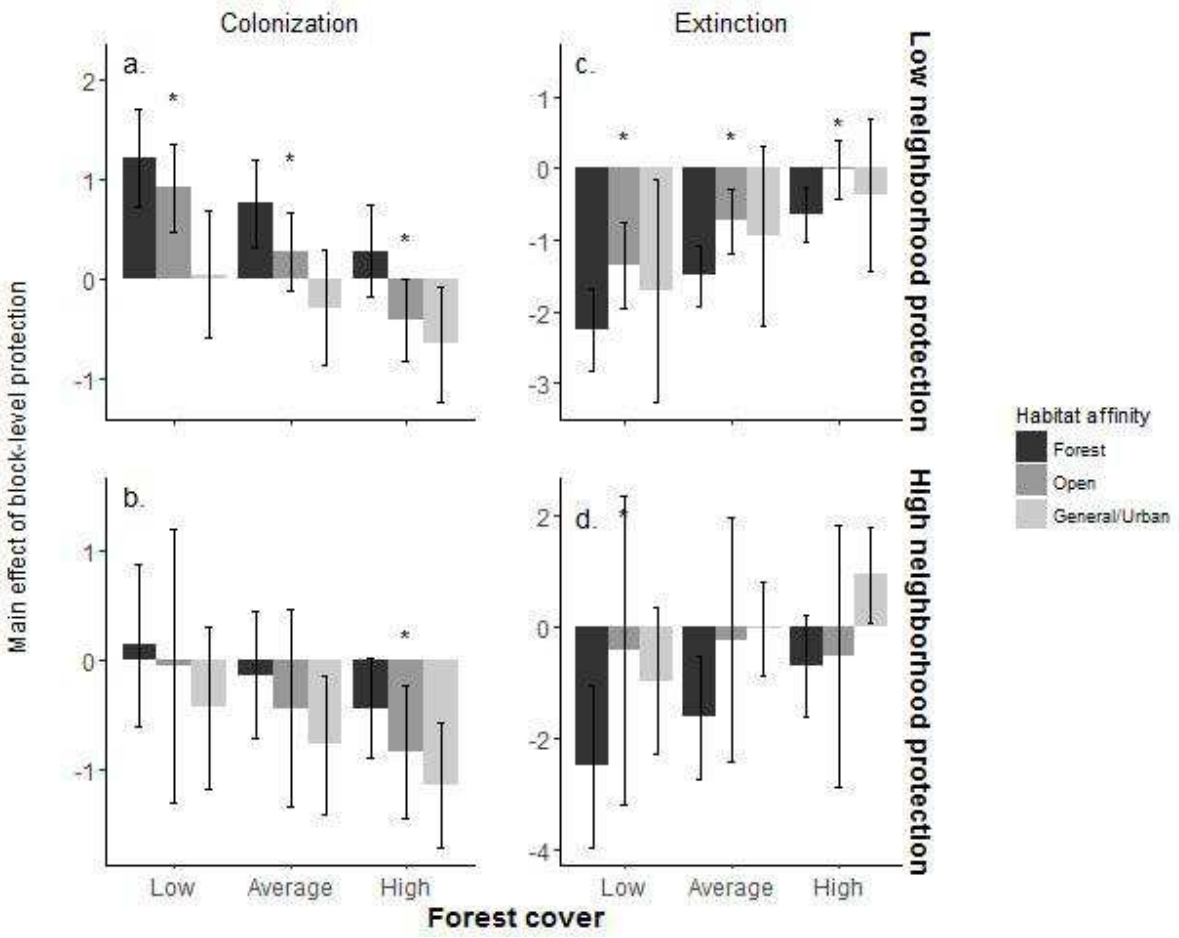

Figure 3-3. The average main effect of block level protection on colonization at (a) low neighborhood protection (< 0.5 of area of surrounding blocks protected) and (b) high neighborhood protection (> 0.5 of area of surrounding blocks protected) and on extinction at (c) low neighborhood protection and (d) high neighborhood protection given low (0.36), average (0.56) and high (0.77) amounts of block-level forest cover in NY and PA 1980-89 and 2001-09. Effects are shown separated for forest, open habitat and generalist avian species, with an asterisk indicating a significant difference between groups.

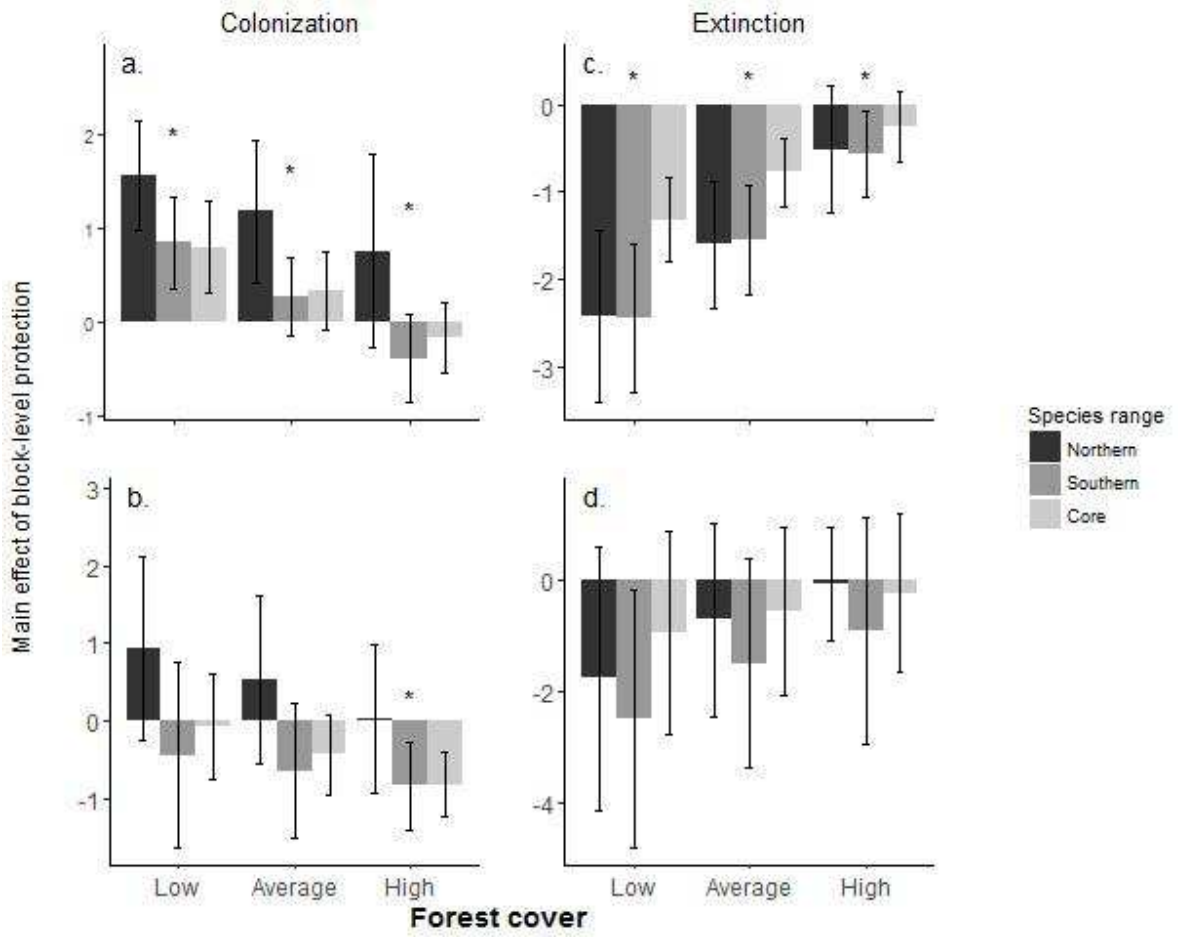

Figure 3-4. The average main effect of block level protection on colonization at (a) low neighborhood protection (< 0.5 of area of surrounding blocks protected) and (b) high neighborhood protection (> 0.5 of area of surrounding blocks protected) and on extinction at (c) low neighborhood protection and (d) high neighborhood protection given low (0.36), average (0.56) and high (0.77) amounts of block-level forest cover in NY and PA 1980-89 and 2001-09. Effects are shown separated for northern, southern and core range avian species, with an astersik indicating a significant difference between groups.

Chapter 4: A Comparison of the effects of strict and multiple-use protected areas on forest bird conservation

Abstract

Multiple-use protected areas that allow resource extraction are an increasingly important component of the global protected areas network. The growing reliance on protected areas that allow activities, such as timber harvest and mineral mining, has raised concerns about their ability to conserve biodiversity over time while also providing renewable resources for human consumption. However, active management may be required to retain certain species, such as those that prefer early successional habitats. Our goal was to assess the differential impact of strict versus multiple-use protected areas on avian persistence over a 20-year period in the northeastern United States. Specifically, we tested the hypotheses that strictly protected areas that limited anthropogenic disturbance would improve outcomes for mature forest species while multiple-use protected areas that allowed timber harvest would be more beneficial for species that prefer young forest or edge habitat. Using breeding bird atlas data, we fit multi-species dynamic occupancy models to quantify drivers of colonization and extinction while accounting for imperfect detection. Because breeding bird atlas data do not include repeated surveys from which to derive detection histories, we incorporated single-visit dynamic occupancy models into a multi-species framework relying on environmental covariates to statistically separate occupancy and detection processes. Both strict and multiple-use protected areas improved colonization and reduced extinction more for mature forest species than early forest species, with the greatest benefits accruing when forest cover was relatively low. In our study region, where timber harvests are primarily low intensity partial cuts, a continued focus on multiple-use protected areas will facilitate persistence of mature forest species. However, increased harvest patch size, or frequency on multiple-use protected areas may be required to achieve conservation objectives related to early successional species and habitats in this forest-dominated region.

INTRODUCTION

Legally protected areas typically restrict permanent and extensive conversion of forest and other perennially vegetated cover to human modified cover types or land uses (e.g. developed areas) in order to conserve biodiversity. However, protected areas vary in the amount of allowed human activities. Multiple-use protected areas allow resource extraction, such as timber harvest, gas drilling and mineral mining, whereas strictly protected areas limit active management of any type (Dudley 2013). Acquisition of protected areas has accelerated in recent decades, particularly multiple-use protected areas that combine resource extraction with conservation objectives (Locke and Dearden 2005). The growing reliance on multiple-use protected areas has raised questions about their ability to effectively conserve biodiversity while also providing renewable resources for human consumption (Locke and Dearden 2005).

Protected areas are assumed to maintain species by reducing the risk of extinction from processes such as such as habitat degradation, fragmentation, and invasive species (Gaston et al. 2008), all of which can result from resource extraction (e.g. Sakai et al. 2001, Gerwig 2002, Broadbent et al. 2008). However, limiting resource extraction on protected lands does not diminish demands for products and can lead to increased extraction in unprotected areas, which reduces the overall conservation benefit of strict protection (Sohngen et al. 1999). In addition, active management may be required to sustain the species and habitats for which protected areas were established (Bernes et al. 2014). Logging, for example, has caused avian extinctions and is a continuing threat to the persistence of extant species (Szabo 2012), but can be a useful tool to create habitat for declining species, restore ecological process by replicating past disturbance regimes, or accelerate forest regeneration after extensive harvesting (Brawn et al. 2001, Quine et al. 2007, Bernes et al. 2014). Active management to set back forest succession may also be required to create or maintain habitat for species of conservation concern (Bernes et al. 2014, Brodie et al. 2015), such as in the northeastern United States where widespread forest maturation has led to declining populations of open and edge-dependent species (Valiela and Martinetto 2007). Without ongoing timber harvest in the region early successional habitats and species will become increasingly rare (DeGraaf and Yamasaki 2003). In contrast, disturbance-sensitive species may require limited or low-intensity timber harvest in order to persist (Annand and Thompson 1997, Brodie et al. 2015)

In tropical forests, multiple-use protected areas have been equally or more effective than strict protected areas at reducing deforestation (Nelson and Chomitz 2011, Nolte et al. 2013), whereas only strict protection reduced the rate of deforestation in Russia (Wendland et al. 2015). Rates of deforestation, however, are an indirect measure of biodiversity conservation. Preventing forest conversion was found to be more important than restricting production forestry for achieving wildlife conservation objectives in a highly protected region of the northeastern U.S. (Glennon and Porter 2005). Like Glennon and Porter (2005) the majority of studies relating to forest condition and protection to biodiversity have involved space-for-time substitutions, with longitudinal studies being exceedingly rare. Longitudinal comparisons have shown that while protected areas retain forest cover their impacts on pland and animal conservation are less certain. Wildlife communities may change in response to climate and other processes unrelated to local forest management (Sallabanks et al. 2000). Longitudinal analyses that directly examine the effect of different types of protected areas on species persistence over time in a heterogeneous landscape are thus required to determine the effectiveness of each approach at achieving conservation outcomes.

Repeat Breeding Bird Atlas data provide a unique opportunity to compare species occurrence patterns across decades over large-scale regions—a spatio-temporal extent that has proven sufficient to detect shifts in species distributions in response to land use, climate, and amount of protected area (Zuckerberg et al. 2009, Virkkala et al. 2014, Peach 2017b). When coupled with dynamic occupancy models, Atlas data can be used to identify drivers of change in species distributions as a result of underlying colonization and extinction dynamics while accounting for imperfect detection of species (MacKenzie et al. 2003, Peach et al. 2017a). Our goal was to assess the differential impact of strict versus multiple-use protected areas on avian persistence over a 20 year period in the northeastern United States. In particular, we wanted to test the hypotheses that strictly protected areas with limited anthropogenic disturbance would improve outcomes for mature forest species while multiple-use protected areas that allowed timber harvest would be more beneficial for species that prefer young forest or edge habitat. We assessed the ability of each type of protected area to reduce extinction and increase colonization probabilities for both early and mature forest species. An accurate understanding of the relative benefits of different types of land protection is essential for effective conservation and management, particularly when balancing dual objectives of wildlife conservation and provision of renewable resources for human consumption (Wells et al. 2004).

METHODS

We examined changes in avian distribution over time in the 120,000-km^2 state of Pennsylvania (PA), which is primarily forested and contains a mix of strict and multiple-use protected areas (Figure 4-1). Forest cover in the region increased following agricultural abandonment and, as a result, increases in the abundance of forest dependent birds have been recorded along with declines of birds that require open and edge habitats (Valiela and Martinetto 2007). Our study area followed global patterns of accelerating rates of land protection and increasing proportions of protected areas that allow resource extraction (Meyer et al. 2014), with ~15% of the study area under some form of protection at the time of the study.

We obtained data on species distributions from the PA Breeding Bird Atlas (BBA hereafter), which was initially completed 1983-89 and repeated 2004-09 (Wilson et al. 2012). Volunteers surveyed 4,937 blocks covering 1/6 of a standard USGS 7.5 minute topographic map (approximately 24.8 km^2) and recorded the breeding status for all species observed as well as the number of hours spent surveying. We included all possible, probable and confirmed breeding observations in our analyses. We excluded blocks with no effort in either time period (n = 448) and blocks missing data on other variables data (n = 1) leaving 4,488 blocks for our analyses. We identified all forest breeding passerines in the BBA that preferred either mature or young/edge forest habitat (Rodewald 2014, Table 4-1). We counted canopy gap specialists, such as hooded warbler (*Setophaga citrina*) and black-throated blue warbler (*Setophaga caerulescens*), as early successional forest species because they prefer early seral stages found in small forest gaps within a matrix of mature forest (Annand and Thompson 1997). We then excluded species having a naïve colonization or extinction probability < 0.1 to ensure adequate sample sizes for accurate parameter estimates (Peach et al. in 2017a). Finally, we randomly selected 5 species from each group to compare the effect of different types of protection on colonization and extinction probabilities between mature and early successional forest bird species (Table 4-1).

In order to account for broad-scale factors that drive occupancy, colonization and extinction patterns, we quantified habitat and climate characteristics of each survey block in both BBA periods. All spatial data and analyses were managed in ArcGIS 10.1 (ESRI, Redlands, CA). We calculated average values for three climate variables within each BBA period: average annual precipitation $TOTP_t$), average annual minimum temperature ($MINT_t$), and average annual temperature during the breeding season of Jun-Aug ($BSAT_t$). The

subscript *t* references the first (*t* = 1) or second (*t* = 2) BBA period. Climate values were calculated at the centroid of each block based on Parameter-elevation Regression on Independent Slopes Model (PRISM) Climate Group monthly data (PRISM Climate Group 2004). Although there are many ways to characterize climate and its impact on birds, we selected TOTP, BSAT, and MINT Although there are many ways to characterize climate and its impact on birds, we selected TOTP, BSAT, and MINT because they are relatively easy to derive and have been shown to influence avian abundance and distributions in previous studies (Root 1988, Tingley et al. 2009. Gutiérrez Ilán et al. 2014)..

We characterized land cover within each block using the 1992 and 2001 retrofit land cover change product from the National Land Cover Database (NLCD; Fry et al. 2009). We calculated the proportion of each block in two broad land cover classes: $FOREST_t$ and $OPEN_t$. FOREST included the NLCD cover class "Forest" whereas OPEN included the classes "Grassland/Shrub", "Agriculture" and "Wetlands". We used broad land cover classes to minimize model complexity and to minimize classification errors inherent in the NLCD dataset (Wickham et a.l 2010). For these data *t* = 1 corresponds to 1992 and *t* = 2 corresponds to 2001. Because available land cover data do not align perfectly with BBA periods, we considered these data to represent the minimum land cover change between our two survey periods.

We identified protected areas using the Protected Areas Database of the United States (PAD_US; USGS 2012; Figure 4-1), which includes all publically protected areas as well as privately protected areas based on voluntarily provided data from large (e.g. The Nature Conservancy) and small (local land trusts) conservation organizations. We excluded individual protected areas that were acquired after the first BBA period, assuming these areas were not effectively protected at the beginning of the BBA. We included areas classified as "fee ownership" that lacked acquisition dates because these were likely older protected areas for which digital information is commonly unavailable. However, we excluded "easement" records that lacked an establishment date because easements did not become widely employed as a land conservation tool until the late 1990's (Meyer et al. 2014), so were not likely to be established over the duration of our study. In addition to delineating the boundary of protected areas, PAD_US provides information regarding the level of protection and allowable activities using GAP codes of 1) permanent protection from conversion of natural land cover and natural disturbances are allowed to proceed without interference or are mimicked through management, 2) permanent protection from conversion of natural land cover but uses that degrade the

quality of existing natural communities, including suppression of natural disturbances, are allowed, 3) permanent protection from conversion of natural land cover for the majority of the area but extractive uses are permitted, and 4) no permanent protection from conversion of natural habitat types. For our analyses, we combined GAP 1 and 2 (hereafter GAP12) to represent strict protection and GAP 3 as multiple-use protection.

Occupancy Model

We fit multi-species hierarchical occupancy models to increase the precision of parameter estimates over species-specific models (Kéry and Royle 2008). Multi-species models assume that the parameters describing individual species' responses are not independent but instead are based on a community-level distribution of values. As a result, species-specific parameters are modeled using random effects defined by hyper-parameters representing the community-level distribution. One tangible benefit of this approach is effective parameter estimateion even for species where sparse occupancy records might limit inference in a single species model. We included all species-level parameters (intercepts and slopes for occupancy, colonization, extinction and detection) as independent random effects (Kéry and Royle 2009, Zipkin et al. 2009). We further used multi-season, or dynamic, occupancy models that enable direct estimation of the effects of factors that drive colonization and extinction processes over time (Royle and Kéry 2007). Previous applications of multi-species occupancy models have estimated species-specific and community level detection probability based on replicate surveys that produce a detection history (e.g. Dorazio et al. 2010, Giojman et al. 2015). Because BBA data used in this study do not include repeated surveys from which to derive detection histories, we modeled occupancy, colonization, extinction and detection using single-visit dynamic occupancy models that rely on environmental covariates that are strong predictors of detectability and occupancy dynamics to help statistically separate these processes (Lele et al. 2012, Peach et al. 2017a).

We estimated occupancy probability ($\psi_{i,j,1}$) at site *i* for species *j* in the first BBA period (*t*=1) based on the previously described climate, habitat and protection variables as:

$$\text{logit}(\psi_{i,j,1}) = \beta_{o1,j} + \beta_{o2,j} * MINT_{i,1} + \beta_{o3,j} * BSAT_{i,1} + \beta_{o4,j} * TOTP_{i,1} + \beta_{o5,j} * FOREST_{i,1} + \beta_{o6,j} * OPEN_{i,1} + \beta_{o7,j} * GAP12_i + \beta_{o8,j} * GAP3_i + \beta_{o9,j} * GAP12_i * GAP3_i + \beta_{o10,j} * GAP12_i * FOREST_{i,1} + \beta_{o11,j} * GAP3_i * FOREST_{i,1}$$

(Eqn 1)

This model differs from Peach et al. (2017 b) specifically in the expansion of protected areas into two types and the inclusion of interaction terms between both types of protection and forest cover in addition to the hierarchical model structure. We assumed parameter estimates for individual species followed a normal distribution, with hyperparameters describing the mean and variance of each distribution.

Following Peach et al. (2017a and b) the probability of detection for species *i* in block *j* during BBA period *t*, was modeled as:

$$p_{*i,j,t} = 1 - (1 - logit^{-1}(y_{i,j,t}))^{E_{i,t}} \qquad \text{(Eqn 2)}$$

where $\text{logit}^{-1}(y_{i,j,t})$ is the probability of detection during 1 survey hour for species *j* at site *i* during period *t*, and $E_{i,t}$ is the amount of effort (i.e. number of hours) spent surveying site *i* during BBA period *t*. Models for colonization ($\gamma_{i,j,2}$) and extinction ($\varepsilon_{i,j,2}$) probabilities and their hyperparameters were fit identical to those for occupancy except that $t = 2$ in all cases.

To estimate the main effect of GAP12 and GPA3 on colonization and extinction probabilities we took the partial derivative after model fitting, which provides an estimate of the overall effect of the covariate of interest, including interactions, for each species (Woolridge 2013; see Peach et al. 2017b). For example, assuming average values for interacting covariates, the main effect of GAP12 on occupancy for species *j* would be expressed as:

$$\frac{d\Psi}{dGAP12} = \text{GAP12}\Psi = \beta_{o7,j} + \beta_{o9,j} * \text{mean(GAP3)} + \beta_{o10,j} * \text{mean(FOREST}_1\text{)} \qquad \text{(Eqn 3)}$$

We thus estimated the main effect of each type of protection (GAP12 and GAP3) on both colonization and extinction under 3 scenarios using combinations of low (25th percentile), average and high (75th percentile) values of each interacting variable. We used this approach to further isolate the main effect of each type of protection on colonization and extinction in the absence of the other type of protection at low, average and high forest cover. To determine whether the level of protection differentially influenced colonization or

extinction for mature (e.g., $\overline{GAP12\gamma}_{Mature}$) and early (e.g., $\overline{GAP12\gamma}_{Early}$) forest species, we took the difference between the averaged main effects for each group of species and assessed whether 95% credible intervals for that difference (e.g., $\overline{GAP12\gamma}_{Mature} -$ (e.g., $\overline{GAP12\gamma}_{Early}$) included zero.

Models were fit using a Bayesian framework in R 3.2.0 with package rjags (Plummer 2003; R Core Team 2015; Plummer 2015). We specified uninformative priors, 3 chains, 150,000 iterations and a burn-in of 100,000 iterations. We assessed convergence using the Brooks-Gelman-Rubin ($\hat{R}$) statistic with a threshold of 1.1 indicating acceptable convergence and visual inspection of traceplots (Brooks and Gelman 1998).

RESULTS

In general, increasing the amount of either strict or multiple-use land protection increased probabilities of colonization for mature forest species and decreased probabilities of extinction for both mature and early forest species (Figure 4-2 and 4-3). Two key trends were apparent. First, the proportion of protected area (regardless of type of protection) had a greater overall effect on species dependent on mature rather than early successional forest. Second, apparent benefits of protection declined with the overall proportion of available forest cover and in the extreme (at high forest cover) led to reduced colonization probability for young forest species in multiple-use protected areas.

Colonization and extinction probabilities at the community level were further influenced by climate and habitat, based on 95% credible intervals for hyper-parameters (Tables 4-2 and 4-3). Overall, colonization increased (positive coefficients) and extinction decreased (negative coefficients) with increasing precipitation (TOTP), forest cover (FOREST) and multiple-use protection (GAP3). In addition, colonization decreased with increasing minimum temperatures (MINT) and an interaction between GAP3 and FOREST whereas extinction decreased with increasing proportions of open cover (OPEN) and strictly protected areas (GAP12). Colonization and extinction probabilities for individual species were influenced by additional covariates, but strict protection was never an important driver of colonization based on 95% credible intervals for species-specific parameters (Tables 4-2 and 4-3).

Although we evaluated the effect of each type of protected area on colonization and extinction under a variety of scenarios, the patterns were identical regardless of the proportion of area covered by the other type of protection. For simplicity, we present the results assuming a single type of protection was present

only (i.e. GAP3 in the absence of GAP12 and GAP12 in the absence of GAP3). The magnitude of the main effects of protected areas decreased consistently as the proportion of forest increased (Figures 2 and 3) except for the relatively constant main effect of strict protection on colonization (Figure 4-2). Moreover, the main effect of both strict and multiple-use protected areas on colonization was always positive for mature forest species; the 95% credible interval never included zero. In this study region, neither type of protection significantly improved colonization for early forest species (Figure 4-2). Surprisingly, multiple-use protection apparently reduced colonization probability for early forest species under a high forest cover context. In contrast to our expectations, multiple-use protected area, rather than strict protected area, always increased colonization probability significantly more for mature forest species than early forest species (Figure 4-3).

Both types of protection consistently reduced extinction probabilities regardless of species habitat-affinity, except for early forest species under the high forest context (Figure 4-3). Mature forest species, however, exhibited significantly greater reductions in extinction probability than early forest species except when forest cover was low; in that case the effects of protection on extinction probabilities for the two groups were indistinguishable. Although we did not explicitly test for differences in the magnitude of the main effect of strict versus multiple-use protection, the trend was for multiple-use protection to have a greater positive main effect on colonization than strict protection for mature forest species with no consistent pattern for early forest species (Figure 4-2). Moreover, strict and multiple-use protected areas yielded effectively equivalent reductions in extinction probabilities, with mature forest species again showing greater overall benefits than young forest species (Figure 4-3).

DISCUSSION

Given current tree harvest frequency and intensity in the study region, our results support the conclusion that multiple-use protected areas and resource extraction are compatible with avian conservation. Our unexpected finding that multiple-use protected areas benefitted mature forest species moreso than early forest species may be a function of the predominant timber harvesting techniques in this region. Forest management in the northeastern US primarily relies on partial cuts (USDA Forest Service 2001). Single-tree selection, where individual trees are removed throughout the stand, and group selection, in which multiple small-scale clearcuts are created, are examples of partial cuts. These silvicultural practices mimic the

relatively frequent small-scale natural disturbance events that historically structured forest habitats across the landscape (Bengtsson et al. 2000, Seymour et al. 2002). In contrast to large-scale clearcuts, partial cuts retain structural elements in forest stands post-harvest, including living trees, standing dead trees (i.e. snags), and logs, that may continue to provide habitat for mature forest dependent birds, mammals, and amphibians (Fisher and Wilkinson 2005, McKenney et al. 2006, Campbell et al. 2007, Holmes and Pitt 2007). Although many forest interior species may not use the openings, they remain present in unharvested portions of the stand and readily colonize regrowth as it becomes suitable (Costello et al. 2000). Over the long term, these forest management strategies can effectively attract and retain mature forest species (Campbell et al. 2007), which was evident in our study given that protection of any type consistently lowerd extinction probability and increased colonization probability for mature forest species.

While partial cuts do create early successional habitat, the patches are small and the effects ephemeral (≤8 years; Robinson and Robinson 1999, Campbell et al. 2007). Single-tree and group selection harvest techniques may create openings that are to support area-sensitive young forest species and rarely do they provide suitable habitat for the full suite of forest birds that require early successional habitat (Annand and Thompson 1997). Ultimately, the response of both mature and early forest birds to partial cuts is primarily determined by the size of the openings, frequency of harvest, and availability of suitable forest structure for nesting and foraging (Annand and Thompson 1997, Robinson and Robinson 1999, Holmes and Pitt 2007). Relative to larger clearcuts, partial cuts may not substantially alter avian communities because the magnitude and duration of habitat alteration are not as great (Tozer et al. 2013). As a result, early forest species in our study responded similarly to strict and multiple-used protected areas despite the potential for resource extraction on multiple-use protected areas to create more of the early successional habitat on which those species rely. That said, our results corroborate the purported success of partial cutting practices at mimicking natural disturbances and maintaining 'natural' forest condition in the region.

It is important to also consider landscape context when evaluating or predicting the effect of protected areas (Peach et al. 2017b). In particular, the amount of available habitat can influence species responses to habitat as well as other environmental variables (Mysterud and Ims 1998, Aarts et al. 2013). Functional responses, whereby species exhibit a non-linear response to changes in habitat availability are common and make it difficult to generalize from one study to other places and times (Matthiopoulos et al.

2001). We focused on forest-dependent species in a heavily forested landscape. In this context, we considered "low" forest cover to occur where forest comprised 43% of a block. Even so, we observed that the effect of protected areas was context-sensitive, given the overall amount of forest available. Birds were undoubtedly responding to forest management and conditions outside of protected areas, and, as forest availability decreased, protected areas became more important for conserving forest-dependent birds in our study. However, multiple-use protected areas reduced colonization probability (with a negligible impact on extinction probability) for early forest species when forest cover was high, covering 80% of a block. Perhaps a greater frequency or intensity of timber harvest on unprotected areas, or alternative land uses such as the agricultural-forest matrix, resulted in more suitable early successional habitat conditions for early forest species outside of protected areas.

One limitation of our analyses is that we relied on type of protection as a surrogate for direct information about forest condition and management. As a result, we were unable to explicitly relate timber harvests, or lack thereof, on protected areas to colonization and extinction dynamics. For example, strict protection indicates limitations on future management but does not preclude timber harvesting by previous owners. Thus, strictly protected areas may not have contained mature forest conditions for the duration of the study if they were acquired post-harvest near the beginning of the BBA. Similarly, multiple-use protected areas may not have included early successional habitat if no harvest occurred. As records of forest management on protected areas become more available, assessment of the direct effects of management activities will be possible along with comparisons of the types of silviculture that typically occur on protected and unprotected areas in this region. Future research could also explore whether functional groups that rely on specific features altered by forest management, such as vertical structure required for nesting or foraging, exhibit differential responses to multiple-use and strict protection. For example, cavity nesting birds frequently become less abundant after timber harvesting, including partial cuts, (Chadwick et al. 1986, Virkkala 2004, Quine et al. 2007) and might, therefore, be expected to benefit more from strict protection which should support a greater abundance of over-mature and decaying trees compared to managed forests.

In order to evaluate the effectiveness of different conservation strategies, such as type of protection, it is essential to identify clear targets against which outcomes can be measured. Every conservation and management decision involves trade-offs with some species benefitting to the detriment of others (Quine et

al. 2007). In our study region, a continued focus on multiple-use protected areas under current forest management practices may facilitate persistence of mature forest species to the detriment of early successional specialists. However, increased harvest intensity (i.e. size of harvest patch or amount of timber removed) or frequency on multiple-use protected areas may be required to improve conservation outcomes for early successional species and habitats (Costello et al. 2000). Therefore, multiple-use protected areas may not only provide natural resources for human consumption but also be the best approach in many situations for addressing conservation objectives. However, guiding principles are difficult to formulate given the variety of conservation targets, threats, and landscape contexts (Quine et al. 2007). In general, the intensity of forest management is correlated with the magnitude of change in species richness and community composition, but that relationship operates at different scales for different species (Annand and Thompson 1997, Burivalova et al. 2014). Amphibians, for example, appear particularly sensitive to increasing logging intensities and the subsequent changes in light, temperature, moisture and litter (Semlitsch et al. 2009, Burivalova et al. 2014), as are lichen, fungi and saproxylic beetles that depend on forest structures associated with mature conditions (Paillet et al. 2010). Birds are vagile species that can follow the shifting mosaic of preferred forest habitat features created by timber harvest, but other species may benefit more from strict protection or less intense timber harvest that retains suitable habitat conditions (Paillet et al. 2010). As a result, we suggest repeating out analyses as data becomes available for other subsets of species so as to vie a more complete understanding of the biodiversity considerations in managed forests.

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TABLES

Table 4-1. Breeding Bird Atlas block-level colonization and extinction probabilities of early and mature forest passerines included in our study that were observed during the Pennsylvania breeding bird atlas with naïve colonization and/or extinction probabilities ≥ 0.1,1983-89 and 2004-09.

Common name	Scientific name	Colonization	Extinction	Habitat
Blue-gray Gnatcatcher	*Polioptila caerulea*	0.16	0.11	EF
Blue-headed Vireo	*Vireo solitarius*	0.22	0.06	MF
Blackburnian Warbler	*Setophaga fusca*	0.15	0.06	MF
Black-throated Green Warbler	*Setophaga virens*	0.20	0.05	MF
Eastern Wood-Pewee	*Contopus virens*	0.08	0.10	EF
Great Crested Flycatcher	*Myiarchus crinitus*	0.13	0.14	EF
Northern Parula	*Setophaga americana*	0.11	0.03	MF
Purple Finch	*Haemorhous purpureus*	0.17	0.14	EF
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	0.13	0.12	EF
Red-breasted Nuthatch	*Sitta canadensis*	0.15	0.06	MF

Table 4-2. Point estimates for species-level coefficients and community-level hyperparameters in colonization models. An asterisk indicates that the 95% confidence interval did not include 0.

	Early forest species[a]					Mature forest species[b]					
Variable	BGGN	EAWP	GCFL	PUFI	RBGR	BHVI	BLBW	BTNW	NOPA	RBNU	μ[c]
Intercept	-1.81*	0.27	-1.15*	0.49	2.32*	-3.52*	-4.59*	-3.57*	-4.15*	-2.34*	-1.68
MINT	0.13	-0.47	-0.71*	-0.91*	-1.04*	-0.98*	-1.18*	-1.28*	0.38*	-0.89*	-0.69*
BSAT	0.97*	0.64	1.04*	-1.21*	-0.72*	-0.57*	-0.40*	-0.21	0.48*	-0.22	-0.02
TOTP	0.16*	0.17*	0.19*	0.14*	0.15*	0.20*	0.13*	0.27*	0.14*	0.16*	0.17*
FOREST	3.08*	2.41	1.93*	-1.56*	-0.06	4.39*	4.15*	4.84*	4.41*	0.17	2.21*
OPEN	0.00	0.138	2.72*	-1.71*	-2.16*	0.25	-0.43	0.59	0.57	-0.53	-0.06
GAP12	0.69	0.78	1.27	1.07	0.96	1.25	1.35	0.94	0.85	1.35	1.04
GAP3	3.49*	1.54	2.37	1.54	2.24	3.73*	4.66*	4.48*	2.89*	2.86*	2.89*
GAP12*GAP3	2.22	1.29	3.26	0.86	1.25	1.06	3.22	-0.59	2.92	3.01	1.72
GAP12*FOREST	-1.83	-1.04	-0.17	-1.62	-1.22	0.50	-0.23	0.49	-1.12	-0.85	-0.70
GAP3*FOREST	-4.81*	-3.90*	-3.53*	-3.28*	-4.08*	-1.37	-2.73*	-2.05	-3.93*	-2.61*	-3.12*

[a]Early forest species included *Polioptila caerulea* (BGGN), *Contopus virens* (EAWP), *Myiarchus crinitus* (GCFL), *Haemorhous purpureus* (PUFI), and *Pheucticus ludovicianus* (RBGR).

[b]Mature forest species included *Vireo solitarius* (BHVI), *Setophaga fusca* (BLBW), *Setophaga virens* (BTNW), *Setophaga americana* (NOPA), and *Sitta canadensis* (RBNU).

[c]μ is the hyperparameter for the mean of the normal distribution describing the community-level response.

Table 4-2. Point estimates for species-level coefficients and community-level hyperparameters in extinction models. An asterisk indicates that the 95% confidence interval did not include 0.

	Early forest species[a]					Mature forest species[b]					
Variable	BGGN	EAWP	GCFL	PUFI	RBGR	BHVI	BLBW	BTNW	NOPA	RBNU	μ[c]
Intercept	1.98*	-0.07	0.35	0.63	-0.54	2.47*	3.37*	2.01*	3.02*	1.51	1.42*
MINT	-0.03	0.15	0.22	0.57*	0.63*	0.55*	0.95*	0.35	-0.62*	0.45	0.32
BSAT	-1.06*	-0.87*	-1.12*	0.94*	0.09	0.64*	0.23	0.64*	-0.24	0.45	-0.03
TOTP	-0.06	-0.20*	-0.24*	-0.23*	0.11*	-0.16*	-0.14	-0.10	-0.15	-0.37*	-0.15*
FOREST	-3.96*	-3.34*	-2.65*	-0.10	-1.75*	-3.56*	-4.31*	-4.58*	-5.07*	-0.50	-2.83*
OPEN	-1.72*	-1.59*	-1.92*	-1.28*	-0.48	-1.48*	-0.65	-0.92	-1.45	-1.51	-1.28*
GAP12	-2.34	-3.27*	-3.05*	-2.25	-2.84*	-3.50*	-3.20*	-3.15*	-2.86*	-2.90	-2.82*
GAP3	-2.92*	-2.03	-2.53*	-2.10	-1.77	-3.278	-2.65*	-3.37*	-2.00	-2.34	-2.41*
GAP12*GAP3	1.03	-0.81	1.01	1.12	2.17	-0.08	0.42	0.55	-1.29	2.79	0.67
GAP12*FOREST	3.35*	1.03	2.87	3.32*	2.91	1.01	1.14	1.67	1.82	2.21	1.97
GAP3*FOREST	3.41*	2.40	3.28*	1.60	2.81*	0.02	1.08	0.60	3.83*	2.11	1.98

[a]Early forest species included *Polioptila caerulea* (BGGN), *Contopus virens* (EAWP), *Myiarchus crinitus* (GCFL), *Haemorhous purpureus* (PUFI), and *Pheucticus ludovicianus* (RBGR).

[b]Mature forest species included *Vireo solitarius* (BHVI), *Setophaga fusca* (BLBW), *Setophaga virens* (BTNW), *Setophaga americana* (NOPA), and *Sitta canadensis* (RBNU).

[c]μ is the hyperparameter for the mean of the normal distribution describing the community-level response.

FIGURES

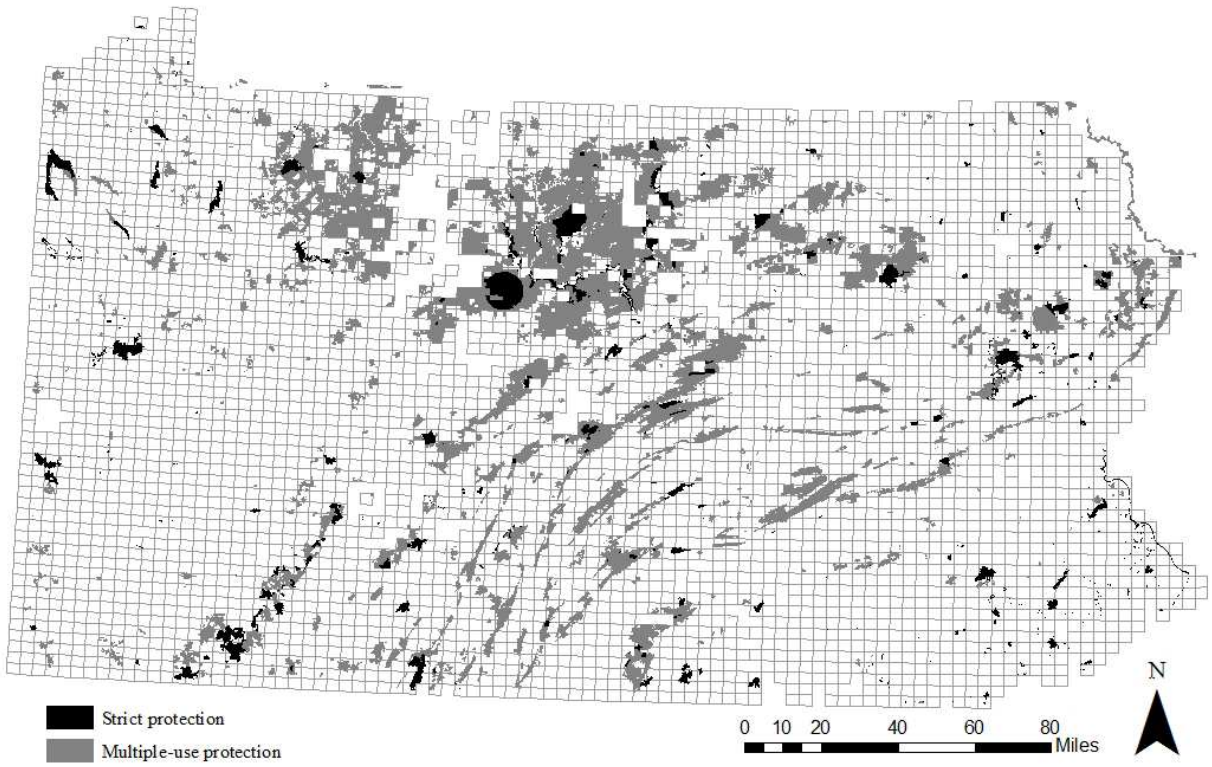


Figure 4-1. Distribution of strict and multiple-use protected areas across Pennsylvania breeding bird atlas blocks. Gaps indicate blocks that were removed due to data gaps.

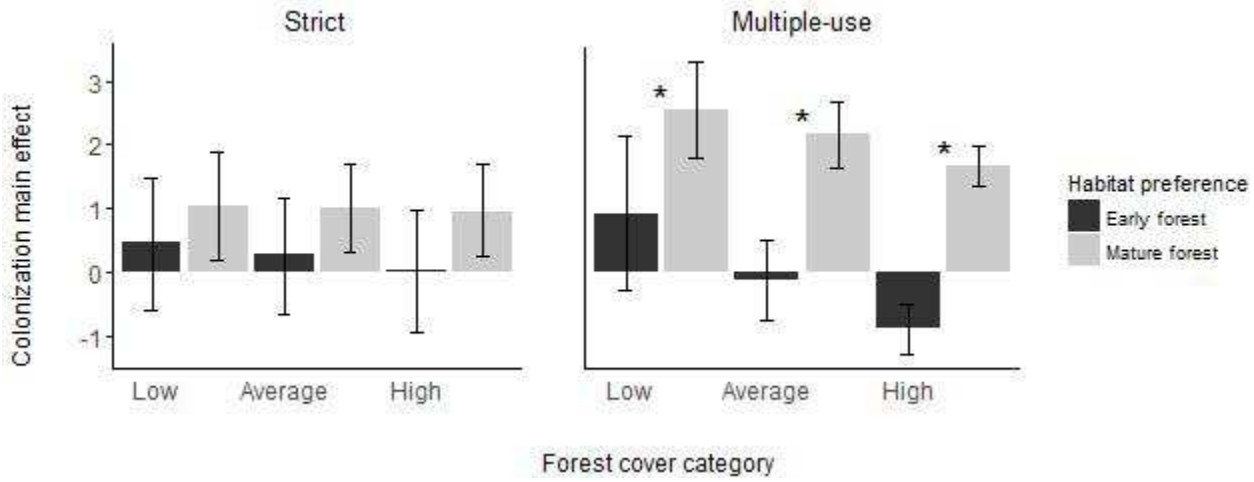


Figure 4-2. The main effect of strict and multiple-use protection on colonization for early and mature forest birds at low, average and high forest cover in the absence of the other type of protection in Pennsylvania, 1983-89 to 2001-2005. An asterisk indicates the 95% credible interval for the difference between estimates for early and mature forest species did not include zero.

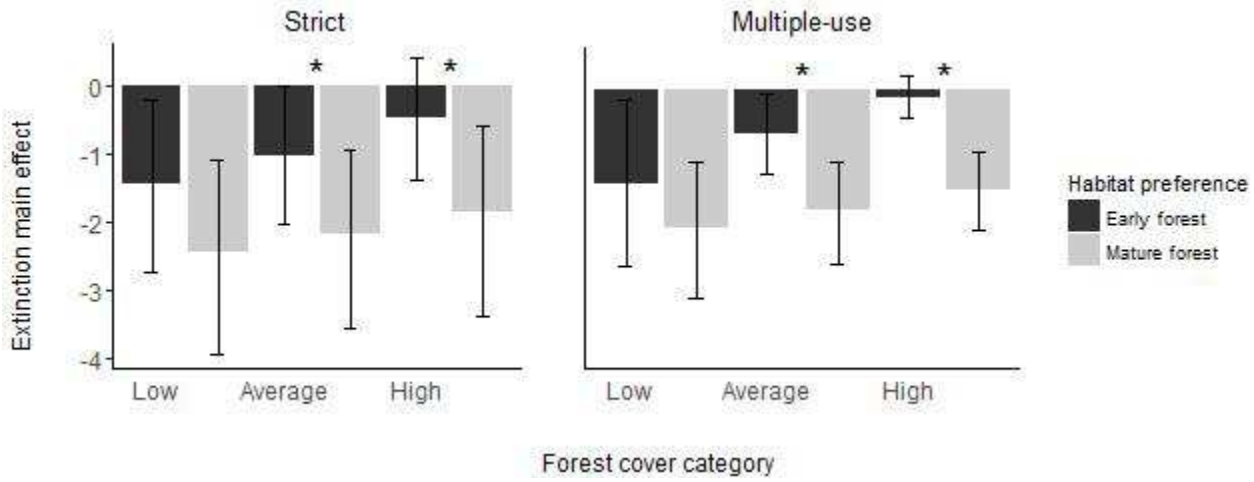


Figure 4-3. The main effect of strict and multiple-use protection on extinction for early and mature forest birds at low, average and high forest cover in the absence of the other type of protection in Pennsylvania, 1983-89 to 2001-2005. An asterisk indicates the 95% credible interval for the difference between estimates for early and mature forest species did5 not include zero.

CHAPTER 5: CONCLUSIONS

The primary goal of this dissertation was to evaluate the effectiveness of land protection as a tool for biodiversity conservation in the face of increasing climate and land use changes. Before addressing that goal, however, I first had to confront the limitations of existing approaches to account for imperfect detection (Lele et al. 2012). I developed a novel modelling approach to addresses the gap between requirements of other multi-season occupancy models (i.e. repeated sampling) and existing datasets, such as breeding bird atlases. Atlases combine fine-scale observations of species distributions with a relatively broad spatial extent, making them ideal datasets for evaluating how environmental variables shape species distributions over space and time. Analyzing Atlas datasets without accounting for imperfect detection during surveys, however, can lead to inaccurate conclusions about changes in distributions over time as well as the underlying drivers of those changes (Gu & Swihart 2004). The single-visit dynamic occupancy model presented in this dissertation overcomes these limitations by relying on effort to predict occupancy probability and other covariates to predict occupancy, colonization and extinction. In addition, our formulation of the detection model as a power relationship more accurately represents our assumptions about how detection increases as a function of effort while overcoming problems with non-identifiability (Knape & Korner-Nievetgelt 2015)

The single-visit dynamic occupancy model is based on assumptions that could be verified with further study. First, the assumption that survey effort can treated as repeat visits with a constant detection rate associated with a base unit of effort (i.e., one hour) can be tested using field surveys. Similarly, the non-linear relationship between detection and effort could be validated. Direct comparisons between single-visit and repeat-visit occupancy models using species occurrence data that were collected with both repeat visits and records of effort would provide additional validation of the single-visit approach. Further exploration of how shared covariates affect the accuracy and precision of coefficient estimates is also warranted. We suspect that the relationship between covariates within and between occupancy, colonization, extinction and detection models will influence the accuracy of parameter estimates, particularly the magnitude of unique covariates relative to shared ones, and future studies could improve understanding of these relationships.

Application of the single-visit dynamic occupancy modelling approach to assess the effectiveness of protected areas for avian conservation in this dissertation provided the most comprehensive evidence to date

that protected areas facilitate species persistence by both reducing the risk of extinction and providing attractive colonization sites as species' ranges shift. Thus, these results support continued reliance on protected areas as a conservation tool despite uncertainty about future species distributions under changing climate and land use (Heller and Zavaleta 2009, Mawdsley et al. 2009). Our results also demonstrated that multiple-use protected areas can be more beneficial than strict protected areas, at least for some species. In our study area, where the frequency and intensity of timber harvest are relatively low, multiple-use protected areas actually reduced extinction and increased colonization more than strict protected areas. Low intensity timber harvest can, therefore, be compatible with avian conservation. Protected areas did not benefit all species equally, however, and landscape context affects the outcomes.

Species that preferred less common habitats (i.e. open cover in this study area) were less likely to exhibit improved outcomes with increasing protected area, likely as a result of poor representation of open habitat on protected areas in the northeastern U.S. As a result, conservation planning efforts that focus on increasing protected area coverage of under-represented species and habitats should continue to be a priority. I hypothesize that the relationship between protected areas and colonization and extinction has a peak at intermediate amounts of habitat as a result of limited protected area effects when habitat availability is either too low or relatively high. Future research could quantify this pattern and enable identification of regions where new protected areas would produce maximum benefits for the most species. In addition, characteristics of protected areas, such as

Protected areas also did not confer particular benefits on species of conservation concern in the northeastern U.S. While species of conservation concern may be underrepresented in protected areas, they may also require active management to create or maintain appropriate habitat (Margules and Pressey 2002, Deguise and Kerr 2006, Bernes et al. 2014). Silvicultural practices in multiple-use protected areas may be appropriate in many situations to address conservation objectives in addition to providing renewable resources, but field-based comparison of the long-terms effects of specific management techniques are necessary to ensure desired conservation outcomes. Guiding principles for active management of protected areas are difficult to formulate given the variety of conservation targets, threats, and landscape contexts (Quine et al. 2007). Ultimately, all decisions about location and management of protected areas must be informed by the desired conservation outcomes.

Although our findings demonstrate that protected areas can facilitate species persistence, both habitat and climate likely play a more significant role in shaping overall species distributions. For long term biodiversity conservation, it will be critical to understand how much climate and land use change can be offset by the reductions to extinction and increases to colonization protected areas provide, particularly since previous studies have shown that protected areas can reduce the risk of extinction without preventing it entirely (Thiollay 2006, Stoner et al. 2007). Over the 20-year period between Atlas periods, changes in both climate and habitat were fairly minimal compared to projected climate changes over the next 100 years (Campbell et al. 2009, Huntington et al. 2009). These limitations may be of particular concern for less vagile species that rely more on protected areas for reducing extinction *in situ* than providing stepping stones for range shifts. Thus, understanding how protected areas interact with broad scale drivers to shape local species distributions is an essential component of effective conservation planning and management.

Our results highlight the importance of protected areas for species experiencing range boundary fluctuations and in landscapes with minimal existing land protection or habitat availability. Focusing protected area acquisition in areas that meet those criteria will provide the greatest marginal improvements to colonization and extinction probabilities for target species. In addition, our findings document the conservation benefits multiple-use protected areas can provide, even for species that are not disturbance-dependent.

APPENDICES

Appendix 2-1. Values used to generate simulated datasets for analysis. The covariate for equation 2 was simulated to represent proportion (e.g., land cover). Equation 5 was used to simulated minor changes over time to the covariate from equation 2 and was modeled as a random normal variable. Effort values were simulated using a random normal distribution with upper and lower truncation values as well as mean and error parameters based on Breeding Bird Atlas data from New York. The random intercept for occupancy models was simulated using a random normal distribution with parameters chosen to generate baseline occupancy at a relatively low level (logit-1(-3) = 0.047).

Equation	Variable	Parameter	Value
2	Environmental (T1)	Min	0
		Max	1
5	Environmental (T2)	μ	Environmental (T1)
		σ	0.001
7	Effort	μ	22
		σ	33
		a	0
		b	500
8	Random effect	μ	-3
		σ	1

Appendix 2-2. R code used to simulate and analyze data in a Bayesian framework

```
n = 1000# NUMBER OF SAMPLE UNITS


#INITIALIZE X-VARIABLES

x1 <- runif(n,0,1)

x2 <- rep(NA,length(for1))

for(i in 1:n){

  x2[i] <- max(rnorm(n,mean=for1[i],sd=0.001),0)

}


library(truncnorm)

eff1 <- rtruncnorm(n,0,500,22,33)

eff2 <- rtruncnorm(n,0,1000,29,35)

effort <- data.frame(eff1,eff2)


#ADD TO DATAFRAME

occdata <- data.frame(x1)

occdata$x2 <- x2

occdata$eff1 <- eff1

occdata$eff2 <- eff2


# GENERATE RANDOM INTERCEPT FOR OCCUPANCY

n.groups = 5                    #NUNBER OF GROUPS FOR RANDOM EFFECT

occdata$RV <- rep(1:n.groups,each=n.groups)

alpha <- rnorm(n.groups,-3,1)


#CALCULATE PROBABILITIES FOR OCCUPANCY IN YEAR 1 AS A FUNCTION OF X1

occdata$pocc <- plogis(alpha[occdata$RV] + 1*occdata$x1)
```

```
#CALCULATE PROBABILITIES OF COLONIZATION AND EXTINCTION AS A FUNCTION OF X2
occdata$pcol = plogis(-3 + 7*occdata$for2)
occdata$pext = plogis(2 - 5*occdata$for2)

#PROBABILITY OF NOT GOING EXTINCT
occdata$pextant = 1-occdata$pext

#INITIALIZE TRUE AND NAÏVE OCCUPANCY IN TIME 1 AND TIME 2
occdata$occ1 <- 0
occdata$occ2 <- 0
occdata$obs1 <- 0
occdata$obs2 <- 0

#CALCULATE TRUE OCCUPANCY IN TIMES 1 AND 2
for(i in 1:n){
  occdata$occ1[i] <- rbinom(1,1,occdata$pocc[i])
  if (occdata$occ1[i]==0) {occdata$occ2[i] =rbinom(1,1,occdata$pcol[i])}
  if (occdata$occ1[i]==1) {occdata$occ2[i] =rbinom(1,1,occdata$pextant[i])}
}

 # CALCULATE DETECTION PROBABILITIES IN TIME 1
  occdata$pp <- plogis(-5) #ASSUMING CONSTANT DETECTION PROBABILITY
  occdata$pstar1 <- 1-(1-occdata$pp)^eff1

 # CALCULATE DETETCTION PROBABILITIES IN TIME 2
  occdata$pp2 <- plogis(-5)
  occdata$pstar2 <- 1-(1-occdata$pp2)^eff2
```

```
# CALCULATE OBSERVATIONS IN TIMES 1 AND 2
  for (i in 1:n){
    occdata$obs1[i] <- rbinom(1,occdata$occ1[i],occdata$pstar1[i])
    occdata$obs2[i] <- rbinom(1,occdata$occ2[i],occdata$pstar2[i])
  }

#CREATE DATAFRAME FOR ANALYSIS
  y = data.frame(occdata$obs1,occdata$obs2)

  #TWO SEASON ONE VISIT
  library(rjags)

 # SPECIFY MODEL IN BUGS LANGUAGE
  sink("Dynoccre.txt")
  cat("
      model {

     # SPECIFY PRIORS

      # BETA PARAMETERS FOR EXPLANATORY VARIABLES
      for (k in 1:5){
      beta[k] ~ dunif(-20,20)
      }

      # ALPHA PARAMETERS FOR OCCUPANCY INTERCEPT
      for (l in 1:n.groups){
      alpha[l] ~ dnorm(mu.int,tau.int)
      }
```

```
mu.int~dnorm(0,0.1)

tau.int <- 1/(sigma.int*sigma.int)

sigma.int~dunif(0,100)


# CONSTANT FOR HOURLY DETECTION RATE

gamma~dunif(-20,20)


# ECOLOGICAL SUBMODEL

for (i in 1:nsite){

z[i,2] ~ dbern(psi2[i])

psi2[i] <- z[i,1]*extant[i] + (1-z[i,1])*col[i]

z[i,1] ~ dbern(psi1[i])

psi1[i] <- 1/(1+exp(-logitpsi[i]))

logitpsi[i] <- alpha[group[i]] + beta[1]*x1[i]

extant[i] <- 1-ext[i]

col[i] <- 1/(1+exp(-logitcol[i]))

ext[i] <- 1/(1+exp(-logitexp[i]))

logitcol[i] <- beta[2] + beta[3]*x2[i]

logitexp[i] <- beta[4] + beta[5]*x2[i]


# OBSERVATION SUBMODEL

for (j in 1:nyear){

y[i,j] ~ dbern(muy[i,j])

muy[i,j] <- z[i,j]*pstar[i,j]

pstar[i,j] <- 1-(1-logitp[i,j])^effort[i,j]

logitp[i,j] <- 1/(1+exp(-gamma))

} #j

} #i
```

```
    # DERIVED PARAMETERS
    meanpsi[1] <- mean(psi1[])
    meanpsi[2] <- mean(psi2[])
    n.occ[1]<-sum(z[1:nsite,1])
    pocc[1] <- n.occ[1]/nsite
    n.occ[2]<-sum(z[1:nsite,2])
    pocc[2] <- n.occ[2]/nsite
   for(i in 1:nsite){
    colyn[i] <- step(z[i,2]-z[i,1]-1)
    extyn[i] <- step(z[i,1]-z[i,2]-1)
    }
    scol <- sum(colyn[])
    sext <- sum(extyn[])
    }
    ",fill = TRUE)
  sink()

  # BUNDLE DATA
  win.data <- list(y = y, nsite = dim(y)[1], nyear = dim(y)[2],
                effort=effort,x1=x1,x2=x2,n.groups=n.groups,
                group=occdata$RV)

  # INITIAL VALUES
  inits <- function(){list(z = matrix(1,dim(y)[1],dim(y)[2]),alpha=runif(n.groups,-10,-
3),beta=rnorm(5,0,0.001),gamma=runif(1,-10,-3))}
  # PARAMETERS MONITORED
  params <- c("alpha","beta","gamma","meanpsi","pocc","scol","sext","sigma.int")
```

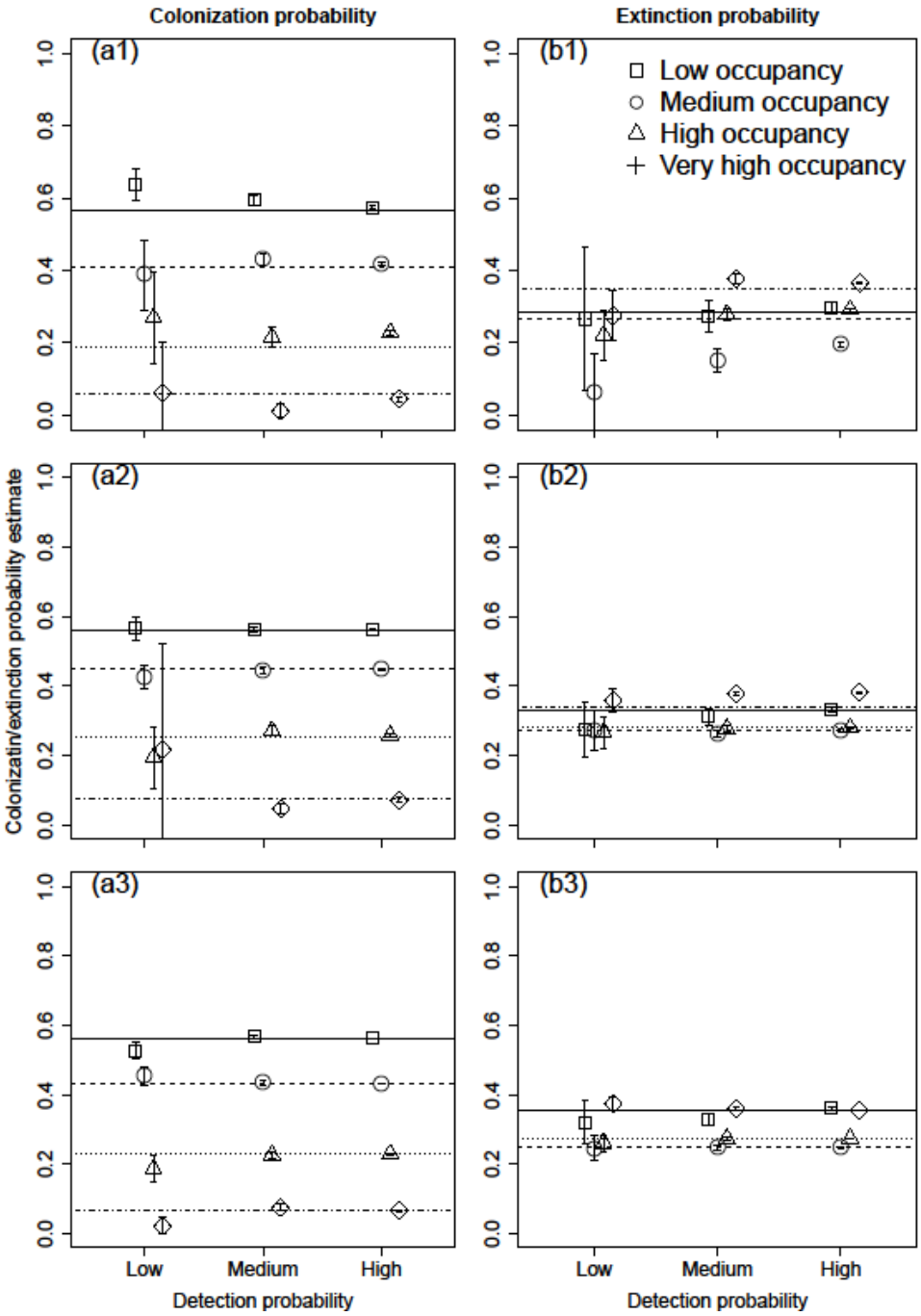
```
# MCMC SETTINGS

ni <- 5000;  nt <- 4;  nb <- 500;  nc <- 3

out.glmm <- jags.model('Dynoccre.txt', win.data, inits, n.chain=nc, n.adapt=100)


res.glmm <- coda.samples(test1.glmm, params, n.iter=ni, thin=nt,n.burnin=nb)
```

Appendix 2-3. Sample R code to conduct single visit dynamic occupancy analyses in a maximum likelihood framework using data simulated with one covariate related to occupancy, colonization, and extinction and a constant describing the hourly detection rate.

```
#CREATE FUNCTION FOR OCCUPANCY MODEL
onevisit.dyn.occ. <-function(b,y,x){
#FORMULAS FOR OCCUPANCY, COLONIZATION, EXTINCTION AND DETECTION
  psi = plogis(b[1] + b[2]*occdata$x1)
  col = plogis(b[3] + b[4]*occdata$x2)
  ext = plogis(b[5] + b[6]*occdata$x2)
  p1 <- p2 <- plogis(b[7])
  pstar1 = 1-(1-p1)^occdata$eff1
  pstar2 = 1-(1-p2)^occdata$eff2

#DEFINE PROBABILITIES FOR EACH OUTCOME
 prob01 <- psi*(1-pstar1)*(1-ext)*pstar2 + (1-psi)*col*pstar2
prob10 <- psi*pstar1*(1-ext)*(1-pstar2) + psi*pstar1*ext
prob11 <-  psi*pstar1*(1-ext)*pstar2
prob00 <- (1-psi)*(1-col) + (1-psi)*col*(1-pstar2) + psi*(1-pstar1)*(1-ext)*(1-pstar2) + psi*(1-pstar1)*ext
 pvec = cbind(prob01,prob10,prob11,prob00)

#CREATE LIKELIHOOD
likelihood <- apply(y*pvec,1,max)
return(-sum(log(likelihood)))
}

#SET INITIAL VALUES FOR BETA PARAMETERS
starting.values <- c(b1=1,b2=1,b3=1,b4=1,b5=1,b6=1,b7=1)
```

```
#RUN ANALYSIS USING OPTIM()

opt.out <- optim(starting.values, onevisit.dyn.occ.2, y=y, occdata=occdata,method="BFGS",hessian=T)

opt.out$par
```

Appendix 2-4. Colonization (a) and extinction (b) probability estimates for sample sizes of (1) 1000, (2) 5000 and (3) 10000 across 3 levels of detection probability and 4 levels of occupancy probability. Estimates are based on a single linear covariate predicting occupancy and a constant describing detection with effort as a power term. Actual values are indicated by horizontal dashed lines and standard deviation bars are shown.

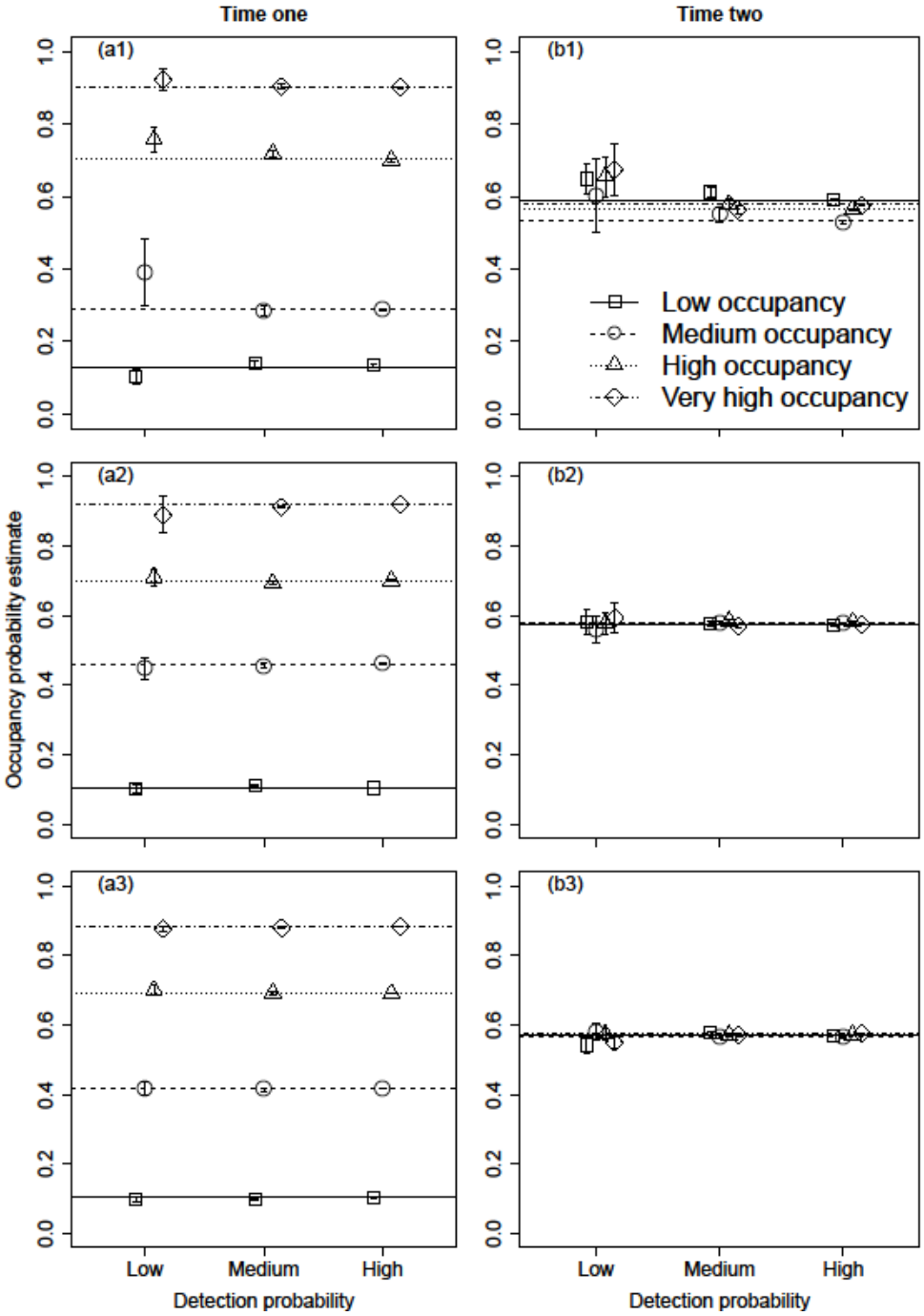


Appendix 2-5. Accuracy of population parameter estimates for varying occupancy and detection probabilities when all models contained one unique, continuous covariate and one shared covariate. "In" indicates that the estimated credible interval contained the true value while "Out" indicates that it did not. N = 1000.

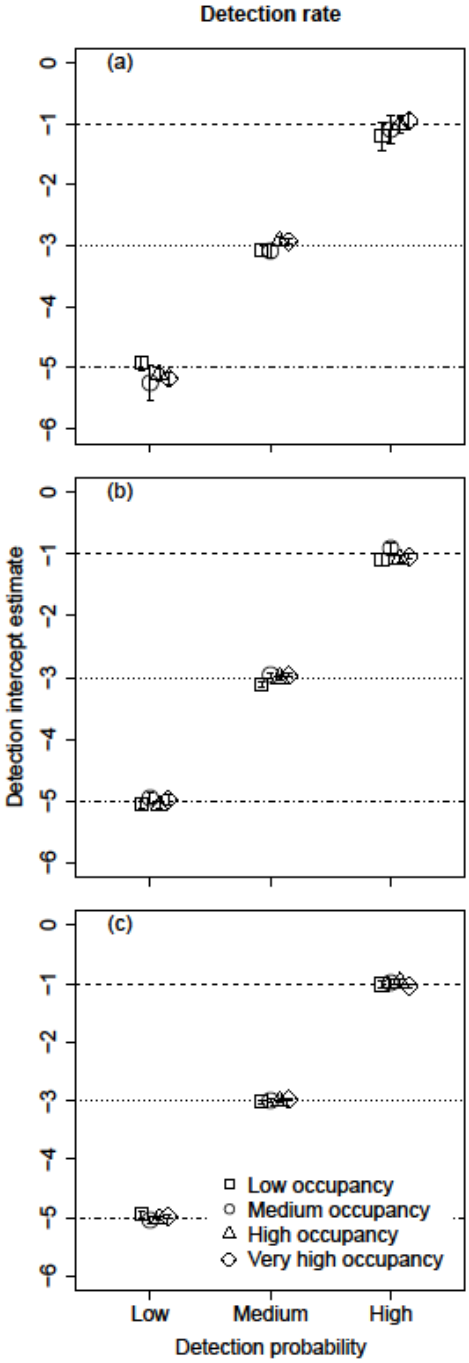
	True occupancy probability	Observed occupancy probability	Estimated occupancy probability	Estimated colonization probability	Estimated extinction probability
	0.1	0.01	In	In	*Out*
	0.2	0.03	In	In	In
	0.3	0.02	In	In	In
Low	0.4	0.03	In	In	In
detection	0.5	0.03	In	In	In
(0.01/hour)	0.6	0.06	In	In	In
	0.7	0.06	In	In	In
	0.8	0.08	In	In	In
	0.9	0.09	In	In	In
	0.1	0.05	In	In	In
	0.2	0.10	In	In	In
	0.3	0.13	In	In	In
Medium	0.4	0.18	In	In	In
detection	0.5	0.20	In	In	In
(0.05/hour)	0.6	0.28	In	In	In
	0.7	0.33	In	In	In
	0.8	0.41	In	In	In
	0.9	0.46	In	*Out*	In

	0.1	0.08	In	In	*Out*
	0.2	0.18	In	In	In
	0.3	0.20	In	In	In
High	0.4	0.18	In	In	In
detection	0.5	0.20	In	In	In
(0.10/hour)	0.6	0.28	In	In	In
	0.7	0.33	In	In	In
	0.8	0.41	In	In	In
	0.9	0.46	In	*Out*	In

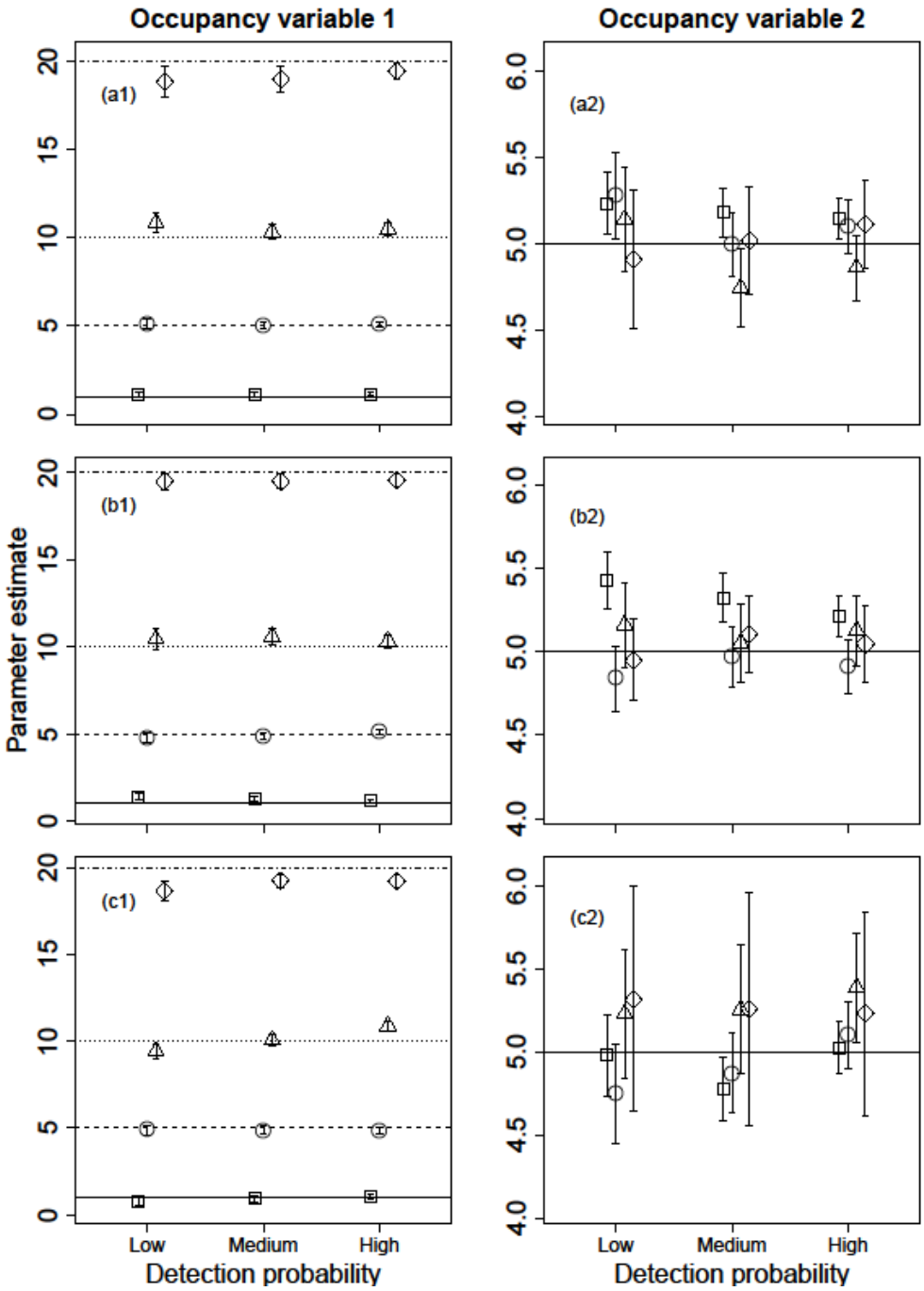
Appendix 2-6. Occupancy probability estimates in time one (a) and time two (b) for sample sizes of (1) 1000, (2) 5000 and (3) 10000 across 3 levels of detection probability and 4 levels of occupancy probability. Estimates are based on a single linear covariate predicting occupancy and a constant describing detection with effort as a power term. Actual values are indicated by horizontal dashed lines and standard deviation bars are shown.

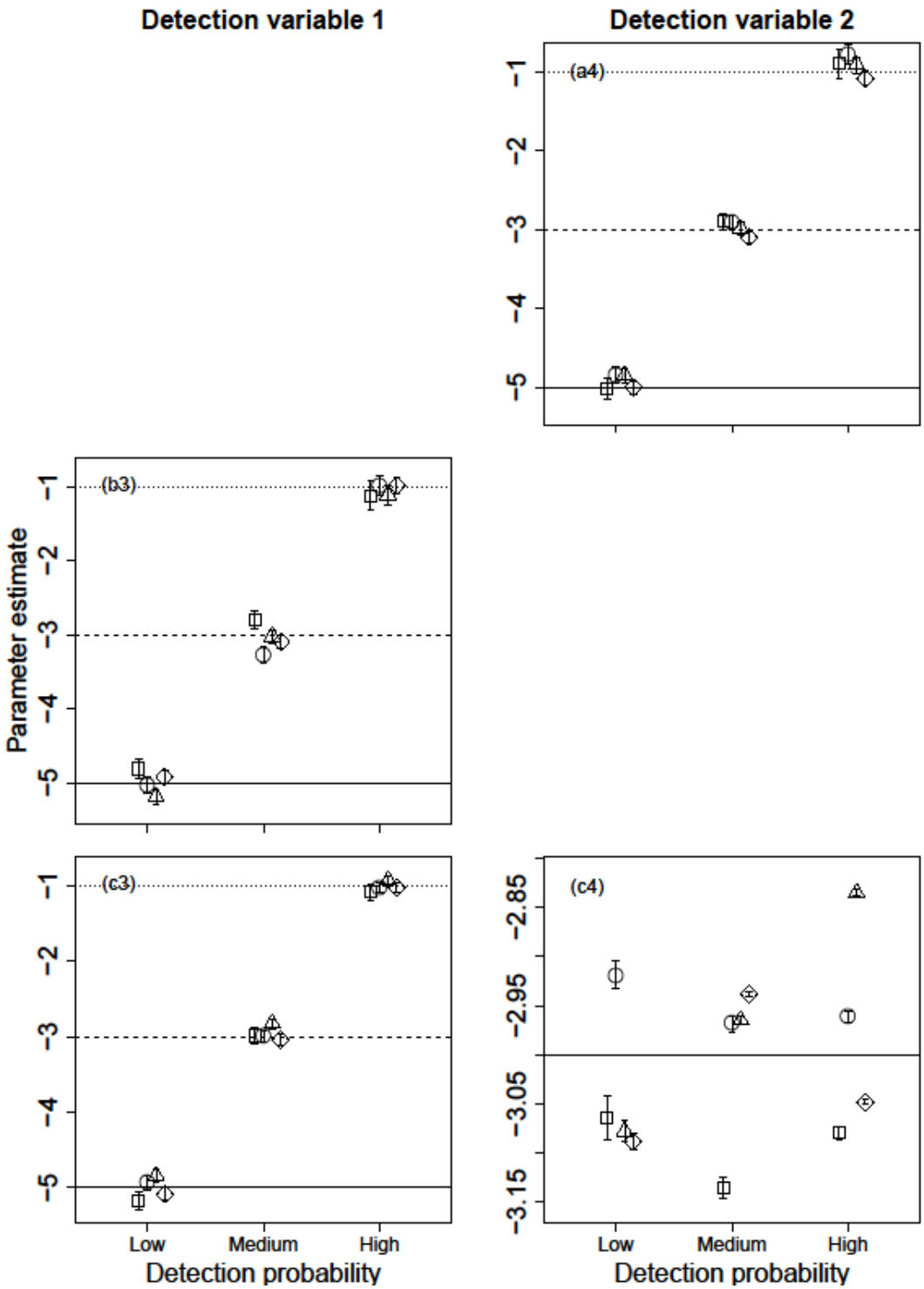


Appendix 2-7. Estimates of the detection constant across 3 levels of detection probability and 4 levels of occupancy probability based on a sample size of (a) 1000, (b) 5000 and (c) 10000. Estimates are based on a single linear covariate predicting colonization and extinction and a constant describing detection. Actual values are indicated by horizontal dashed lines, and standard deviation bars are shown.



Appendix 2-8. Estimates of beta parameters for the linear effects of random uniform covariates describing occupancy (1 and 2) and detection (3 and 4) when when (a) all variables are unique, (b) the first occupancy covariate is also the sole linear predictor of detection and (c) the occupancy and detection models contain one unique and one shared covariate. Shared covariates are always the first variable in each model. Actual values are indicated by horizontal dashed lines, and standard deviation bars are shown.




Detection variable 1
Detection variable 2
(a4)
(b3)
(c3)
(c4)
Parameter estimate
−1
−2
−3
−4
−5
−2.85
−2.95
−3.05
−3.15
Low
Medium
High
Detection probability

Appendix 2-9. Description of variables used in CAWA analysis

Using ArcGIS 10.2.2 (ESRI, Redlands, CA) we derived spatial covariates following Sadoti *et al*. (2013). ELEV was derived by averaging values from the National Elevation Dataset within each block (Gesch *et al*. 2002) then standardizing by subtracting the mean and dividing by the standard deviation. ELEV2 is a quadratic term allowing nonlinear response to elevation. FOREST was calculated using the 2001 National Land Cover Data (Homer *et al*. 2007) as the percent of each block covered by deciduous, mixed or evergreen forest or woody wetlands. Two spatial autocovariates (ACOV and NEIGHBORS) were included to account for landscape-level species aggregations that might influence local occupancy patterns, such as proximity to local populations for ease of colonization. Spatial autocovariates described naïve occupancy (i.e. observation data uncorrected for imperfect detection) of blocks in the 1980 BBA using inverse distance weighting of observed occupancy within 15-km (ACOV) or 50-km (NEIGHBORS) of the focal block. EDGE was determined by calculating the residuals of a simple linear regression of the length of forest-non-forest edge on the amount of forest cover in each block. DETECT80 indicates whether CAWA was observed in a block during an earlier BBA period. NEIGH3 indicates the proportion of neighboring blocks in which CAWA was found during an earlier survey year than the focal block for a given BBA period. Y1980 through Y2005 are categorical variables that indicate the primary year of sampling in each BBA period. $EFFORT_{i,j}$ represents the number of person hours spent surveying block j in BBA period i.

References

Gesch, D., Oimoen, M., Greenlee, S., Nelson, C., Steuck, M. & Tyler, D. (2002) The National Elevation Dataset. *Photogrammetric Engineering and Remote Sensing*, **68**, 5–11.

Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., Van Driel, J.N. & Wickham, J. (2007) Completion of the 2001 Nation Land Cover Database for the coterminous United States. *Photogrammetric Engineering and Remote Sensing*, **4**, 337-341.

Sadoti, G., Zuckerberg, B., Jarzyna, M.A. & Porter, W.F. (2013) Applying occupancy estimation and modelling to the analysis of atlas data. *Diversity and Distributions*, **19**, 804–814.

Appendix 3-1. Species classification into habitat, range boundary, conservation concern, and migratory status categories.

Code	Scientific name	Common name	Habitat[a]	Range boundary[b]	Conser-vation[c]	Migratory habit[d]
ABDU	*Anas rubripes*	American Black Duck	O	N		Res
ACFL	*Empidonax virescens*	Acadian Flycatcher	F	S		Neo
ALFL	*Empidonax alnorum*	Alder Flycatcher	O	N		Neo
AMKE	*Falco sparverius*	American Kestrel	O	C		Short
AMRE	*Setophaga ruticilla*	American Redstart	F	C		Neo
AMWO	*Scolopax minor*	American Woodcock	F	C	CC	Short
BADO	*Strix varia*	Barred Owl	F	C		Res
BANS	*Riparia riparia*	Bank Swallow	O	N	CC	Neo
BAWW	*Mniotilta varia*	Black-and-white Warbler	F	C		Neo
BBCU	*Coccyzus erythropthalmus*	Black-billed Cuckoo	F	C	CC	Neo
BEKI	*Megaceryle alcyon*	Belted Kingfisher	O	C	CC	Res
BGGN	*Polioptila caerulea*	Blue-gray Gnatcatcher	F	S		Neo
BHVI	*Vireo solitarius*	Blue-headed Vireo	F	N		Neo

BLBW	*Setophaga fusca*	Blackburnian Warbler	F	N		Neo
BOBO		Bobolink	O			Neo
BRCR	*Certhia americana*	Brown Creeper	F	N		Short
BRTH	*Toxostoma rufum*	Brown Thrasher	O	C		Short
BTBW	*Setophaga caerulescens*	Black-throated Blue Warbler	F	N	CC	Neo
BTNW	*Setophaga virens*	Black-throated Green Warbler	F	N		Neo
BWHA	*Buteo platypterus*	Broad-winged Hawk	F	C		Neo
BWWA	*Vermivora cyanoptera*	Blue-winged Warbler	O	S	CC	Neo
CANG	*Branta canadensis*	Canada Goose	G	C		Res
CARW	*Thryothorus ludovicianus*	Carolina Wren	O	S		Res
CAWA	*Cardellina canadensis*	Canada Warbler	F	N	CC	Neo
CHSW	*Chaetura pelagica*	Chimney Swift	G	C	CC	Neo
CLSW	*Petrochelidon pyrrhonota*	Cliff Swallow	O	N		Neo
COHA	*Accipiter cooperii*	Cooper's Hawk	F	C	CC	Short
COME	*Mergus merganser*	Common Merganser	O	N		Res
CONI	*Chordeiles minor*	Common Nighthawk	O	C	CC	Neo
CORA	*Corvus corax*	Common Raven	G	N		Res

CSWA	*Setophaga pensylvanica*	Chestnut-sided Warbler	O	N		Neo
DEJU	*Junco hyemalis*	Dark-eyed Junco	F	N		Short
DOWO	*Picoides pubescens*	Downy Woodpecker	F	C		Res
EABL	*Sialia sialis*	Eastern Bluebird	G	C		Short
EAKI	*Tyrannus tyrannus*	Eastern Kingbird	O	C		Neo
EAME	*Sturnella magna*	Eastern Meadowlark	O	C	CC	Short
EAPH	*Sayornis phoebe*	Eastern Phoebe	G	S		Short
EASO	*Megascops asio*	Eastern Screech-Owl	F	S		Res
EATO	*Pipilo erythrophthalmus*	Eastern Towhee	O	S		Short
EAWP	*Contopus virens*	Eastern Wood-Pewee	F	S		Neo
EWPW	*Antrostomus vociferus*	Eastern Whip-poor-will	F	C	CC	Neo
FISP	*Spizella pusilla*	Field Sparrow	O	S	CC	Short
GBHE	*Ardea herodias*	Great Blue Heron	O	C	CC	Short
GCFL	*Myiarchus crinitus*	Great Crested Flycatcher	F	C		Neo
GHOW	*Bubo virginianus*	Great Horned Owl	G	C		Res
GRHE	*Butorides virescens*	Green Heron	O	C		Neo
GRSP	*Ammodramus savannarum*	Grasshopper Sparrow	O	S	CC	Neo
HAWO	*Picoides villosus*	Hairy	F	C		Res

		Woodpecker				
HETH	*Catharus guttatus*	Hermit Thrush	F	N		Short
HOFI	*Haemorhous mexicanus*	House Finch	G	C		Short
HOLA	*Eremophila alpestris*	Horned Lark	O	C	CC	Short
HOWA	*Setophaga citrina*	Hooded Warbler	F	S		Neo
KILL	*Charadrius vociferus*	Killdeer	O	C		Short
LEFL	*Empidonax minimus*	Least Flycatcher	F	N		Neo
LOWA	*Parkesia motacilla*	Louisiana Waterthrush	F	S	CC	Neo
MALL	*Anas platyrhynchos*	Mallard	G	C		Res
MAWA	*Setophaga magnolia*	Magnolia Warbler	F	N		Neo
NOMO	*Mimus polyglottos*	Northern Mockingbird	G	S		Res
NOPA	*Setophaga americana*	Northern Parula	F	C		Neo
NRWS	*Stelgidopteryx serripennis*	Northern Rough-winged Swallow	O	C		Neo
OROR	*Icterus spurius*	Orchard Oriole	G	S		Neo
OVEN	*Seiurus aurocapilla*	Ovenbird	F	C		Neo
PIWA	*Setophaga pinus*	Pine Warbler	F	C		Short
PIWO	*Dryocopus pileatus*	Pileated Woodpecker	F	C		Res
PRAW	*Setophaga discolor*	Prairie Warbler	O	S	CC	Neo
PUFI	*Haemorhous purpureus*	Purple Finch	F	N		Short
PUMA	*Progne subis*	Purple Martin	G	C		Neo
RBGR	*Pheucticus ludovicianus*	Rose-breasted Grosbeak	F	S		Neo

RBNU	*Sitta canadensis*	Red-breasted Nuthatch	F	N		Short
RBWO	*Melanerpes carolinus*	Red-bellied Woodpecker	F	S		Res
RHWO	*Melanerpes erythrocephalus*	Red-headed Woodpecker	G	S	CC	Short
RNEP	*Phasianus colchicus*	Ring-necked Pheasant	O	S		Res
ROPI	*Columba livia*	Rock Pigeon	G	C		Res
RSHA	*Buteo lineatus*	Red-shouldered Hawk	F	S	CC	Short
RTHA	*Buteo jamaicensis*	Red-tailed Hawk	G	C		Short
RTHU	*Archilochus colubris*	Ruby-throated Hummingbird	F	C		Neo
RUGR	*Bonasa umbellus*	Ruffed Grouse	F	N	CC	Res
SAVS	*Passerculus sandwichensis*	Savannah Sparrow	O	N		Short
SCTA	*Piranga olivacea*	Scarlet Tanager	F	S	CC	Neo
SPSA	*Actitis macularius*	Spotted Sandpiper	O	C		Neo
SSHA	*Accipiter striatus*	Sharp-shinned Hawk	F	C	CC	Short
SWSP	*Melospiza georgiana*	Swamp Sparrow	O	N		Short
TRES	*Tachycineta bicolor*	Tree Swallow	O	C		Short
TUTI	*Baeolophus bicolor*	Tufted Titmouse	F	S		Res
TUVU	*Cathartes aura*	Turkey Vulture	G	S		Short

VEER	*Catharus fuscescens*	Veery	F	N		Neo
VESP	*Pooecetes gramineus*	Vesper Sparrow	O	N	CC	Short
WAVI	*Vireo gilvus*	Warbling Vireo	F	S		Neo
WBNU	*Sitta carolinensis*	White-breasted Nuthatch	F	S		Res
WIFL	*Empidonax traillii*	Willow Flycatcher	O	C	CC	Neo
WITU	*Meleagris gallopavo*	Wild Turkey	F	S		Res
WIWR	*Troglodytes hiemalis*	Winter Wren	F	N		Short
WODU	*Aix sponsa*	Wood Duck	O	C		Res
YBCU	*Coccyzus americanus*	Yellow-billed Cuckoo	F	S	CC	Neo
YBSA	*Sphyrapicus varius*	Yellow-bellied Sapsucker	F	N		Short
YRWA	*Setophaga coronata*	Yellow-rumped Warbler	F	N		Short
YTVI	*Vireo flavifrons*	Yellow-throated Vireo	F	C	CC	Neo

[a]Habitat groups include Forest (F), Open (O) and Generalist/Urban (G)

[b]Range boundary indicates whether the species is northern (N; the southern boundary is within 100 m of the study area), southern (S; the northern boundary is within 100 m of the study area) or core (C; no range boundaries within 100 m of the study area).

[c]Conservation concern species have been identified by NY, PA, US or Partners in Flight as a species of conservation or management concern.

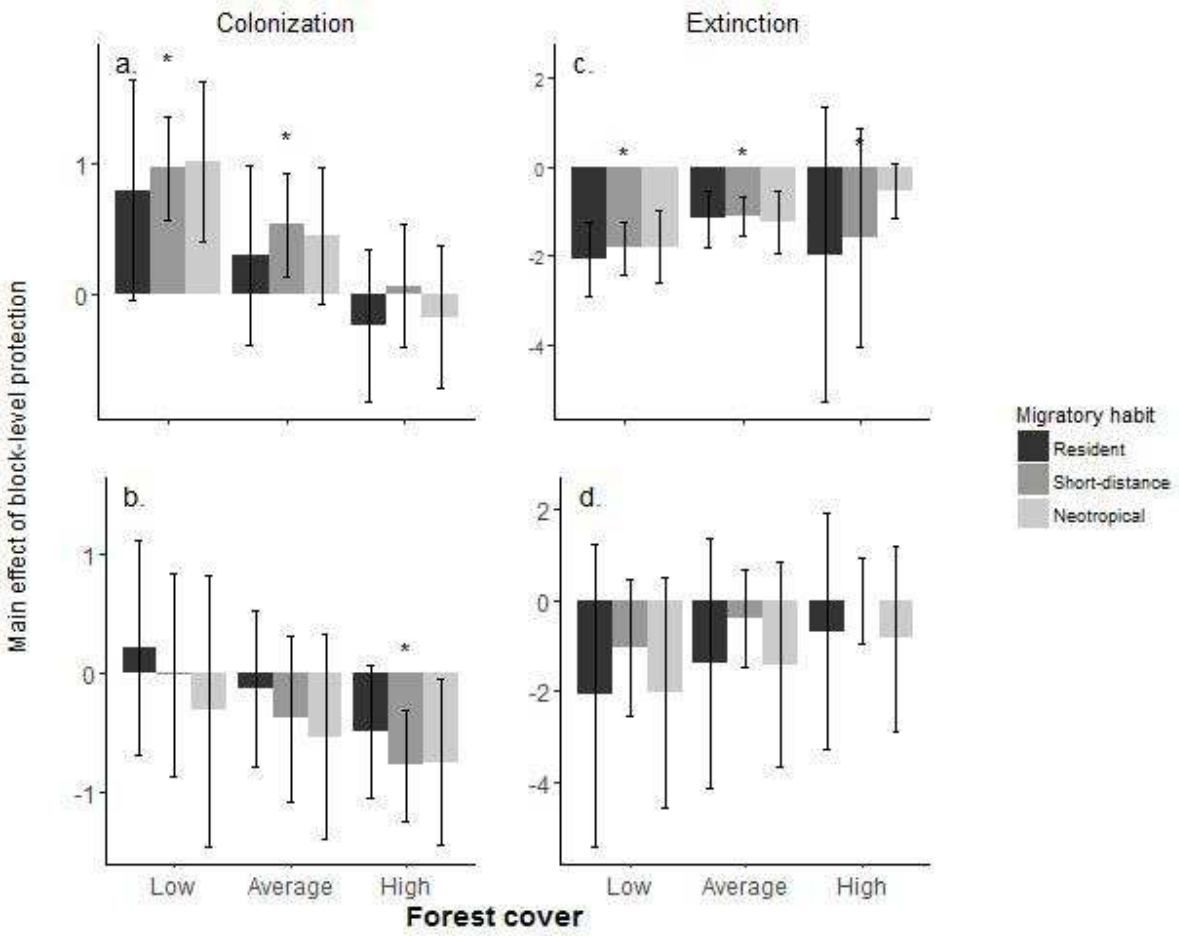
[d]Migratory habit indications whether the species is a resident, short-distance migrant or neotropical migrant.

Appendix 3-2. Variables included in candidate models describing occupancy (ψ_i), colonization(γ_i) and extinction (ε_i). MinT represents average annual minimum temperature, BSAveT is the average of June, July and August temperatures, TotP is the average annual precipitation, Forest and Open represent the proportion of each habitat type, B_PA is the proportion of protected area, and R_PA is a categorical variable identifying whether > or < 50% of contiguous blocks are protected.

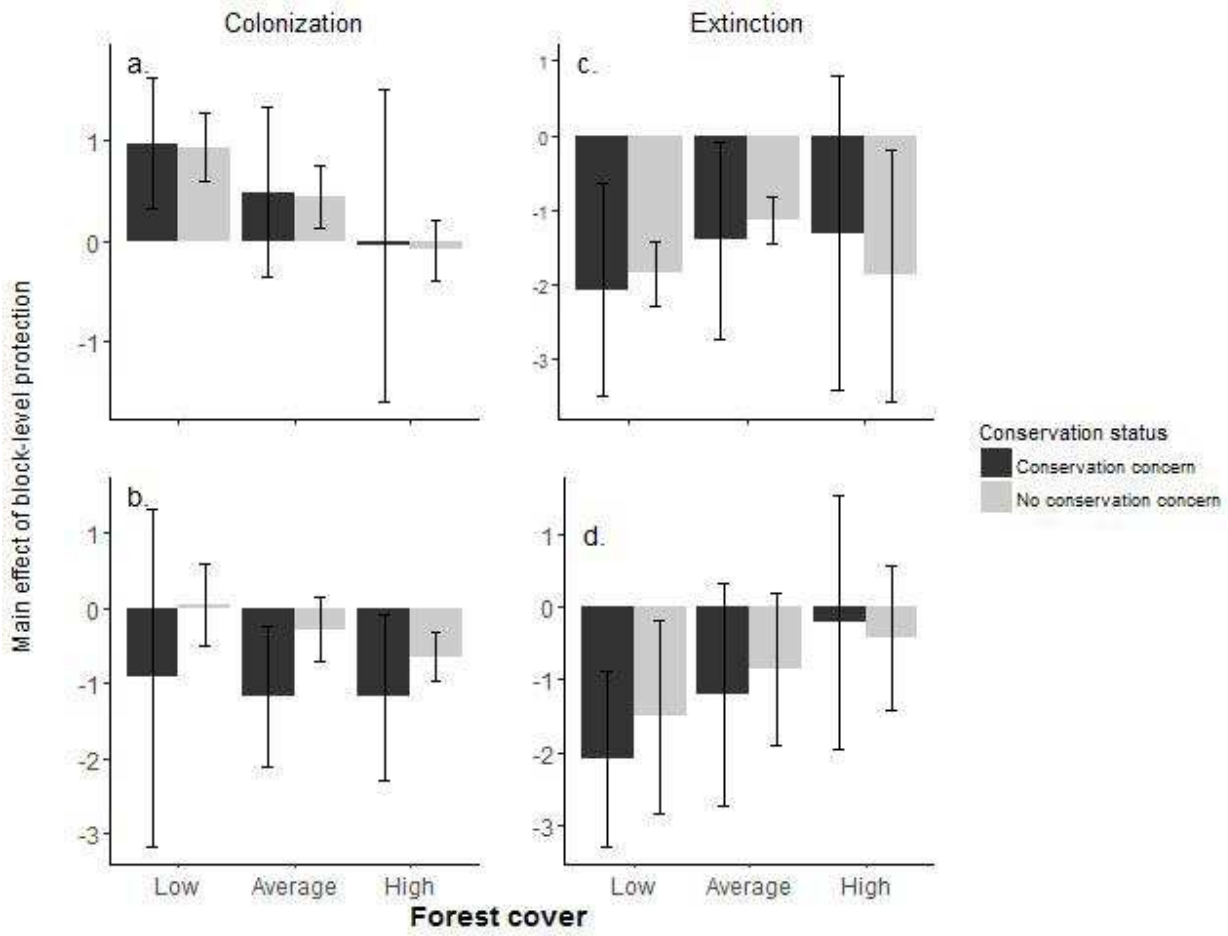
	Global		2-way interactions		Block PA * Forest		Block PA		Regional PA		No PA	
Variables	ψ_i	γ_i/ε_i	ψ_i	γ_i/ε_i	ψ_i	γ_i/ε_i	ψ_i	γ_i/ε_i	ψ_i	γ_i/ε_i	ψ_i	γ_i/ε_i
Intercept	X	X	X	X	X	X	X	X	X	X	X	X
MinT	X	X	X	X	X	X	X	X	X	X	X	X
BSAveT	X	X	X	X	X	X	X	X	X	X	X	X
TotP	X	X	X	X	X	X	X	X	X	X	X	X
Forest	X	X	X	X	X	X	X	X	X	X	X	X
Open	X	X	X	X	X	X	X	X	X	X	X	X
B_PA	X	X	X	X	X	X	X	X				
R_PA	X	X	X	X	X	X			X	X		
*B_PA**	X	X	X	X	X	X						

Forest								
*B_PA**	X	X	X	X				
R_PA								
*R_PA**	X						X	X
Forest								
*B_PA*R_PA**	X	X						
Forest								
Neigh		X		X	X	X	X	X

Appendix 3-3. The average main effect of block level protection on colonization at (a) low neighborhood protection (< 0.5 of area of surrounding blocks protected) and (b) high neighborhood protection (> 0.5 of area of surrounding blocks protected) and on extinction at (c) low neighborhood protection and (d) high neighborhood protection given low (0.36), average (0.56) and high (0.77) amounts of block-level forest cover in NY and PA 1980-89 and 2001-09. Effects are shown separated for northern, southern and core range avian species, with * indicating a significant difference between groups.

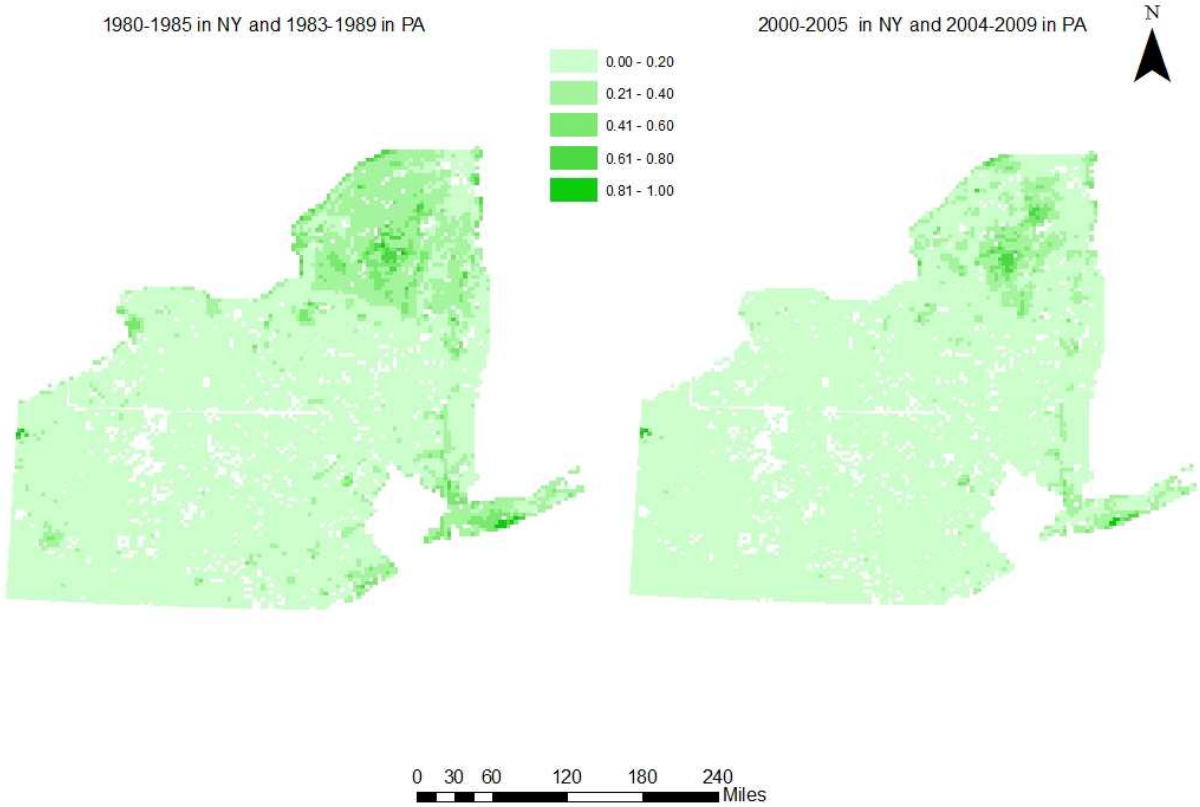


Appendix 3-4. The average main effect of block level protection on colonization at (a) low neighborhood protection (< 0.5 of area of surrounding blocks protected) and (b) high neighborhood protection (> 0.5 of area of surrounding blocks protected) and on extinction at (c) low neighborhood protection and (d) high neighborhood protection given low (0.36), average (0.56) and high (0.77) amounts of block-level forest cover in NY and PA 1980-89 and 2001-09. Effects are shown separated for avian species of conservation concern, with * indicating a significant difference between groups.

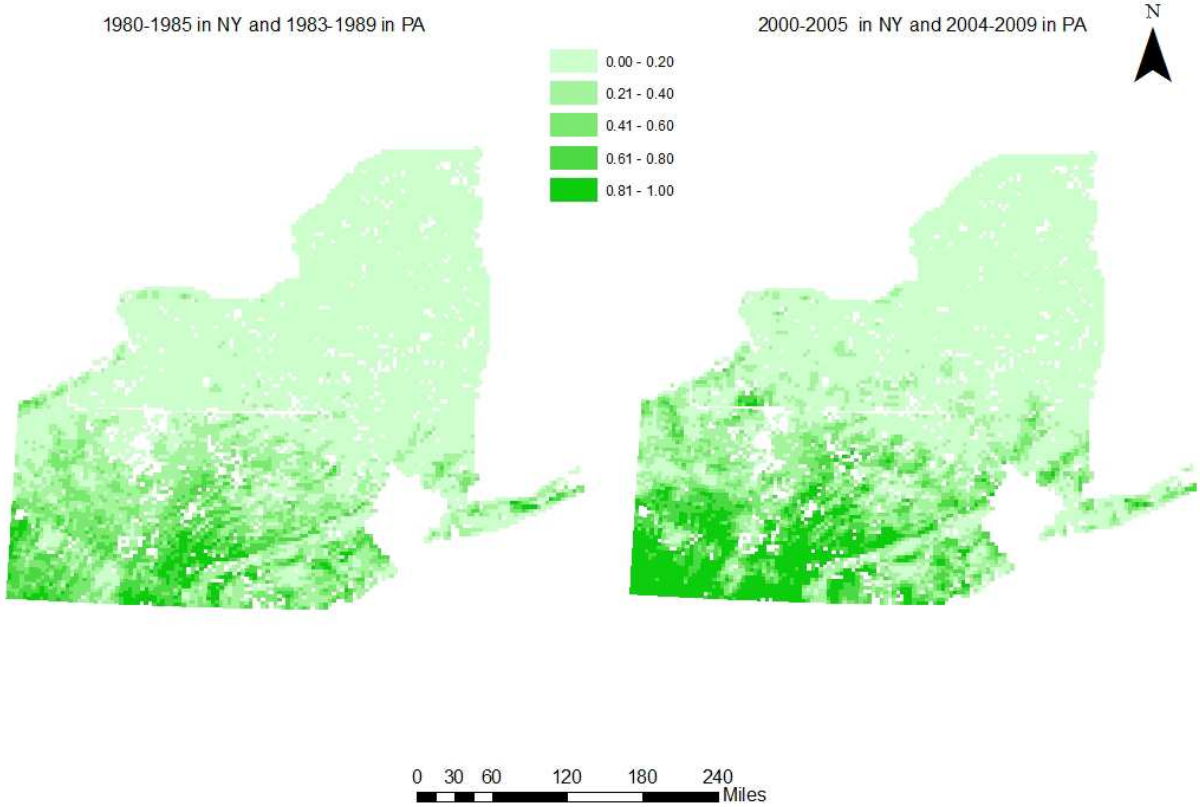


Appendix 3-5. Occupancy probability maps based on the best fitting model for each species.

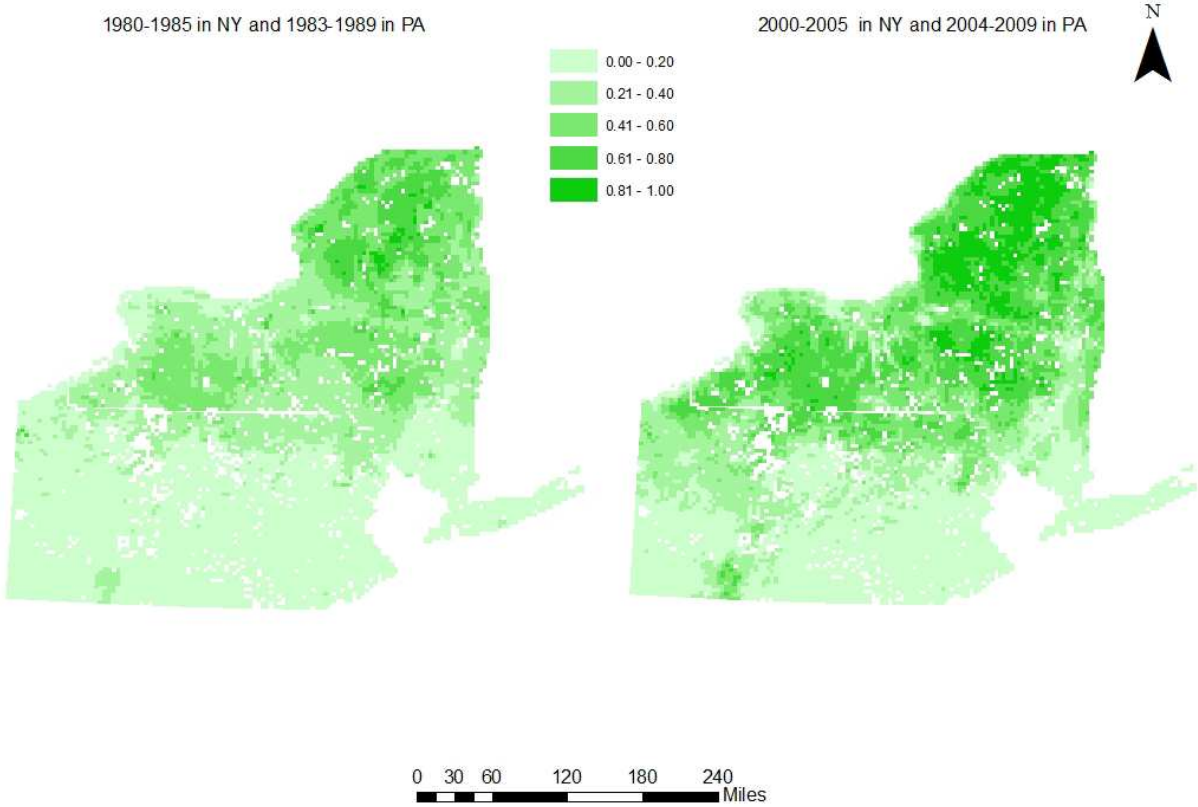
American black duck (Anas rubripes) occupancy probability



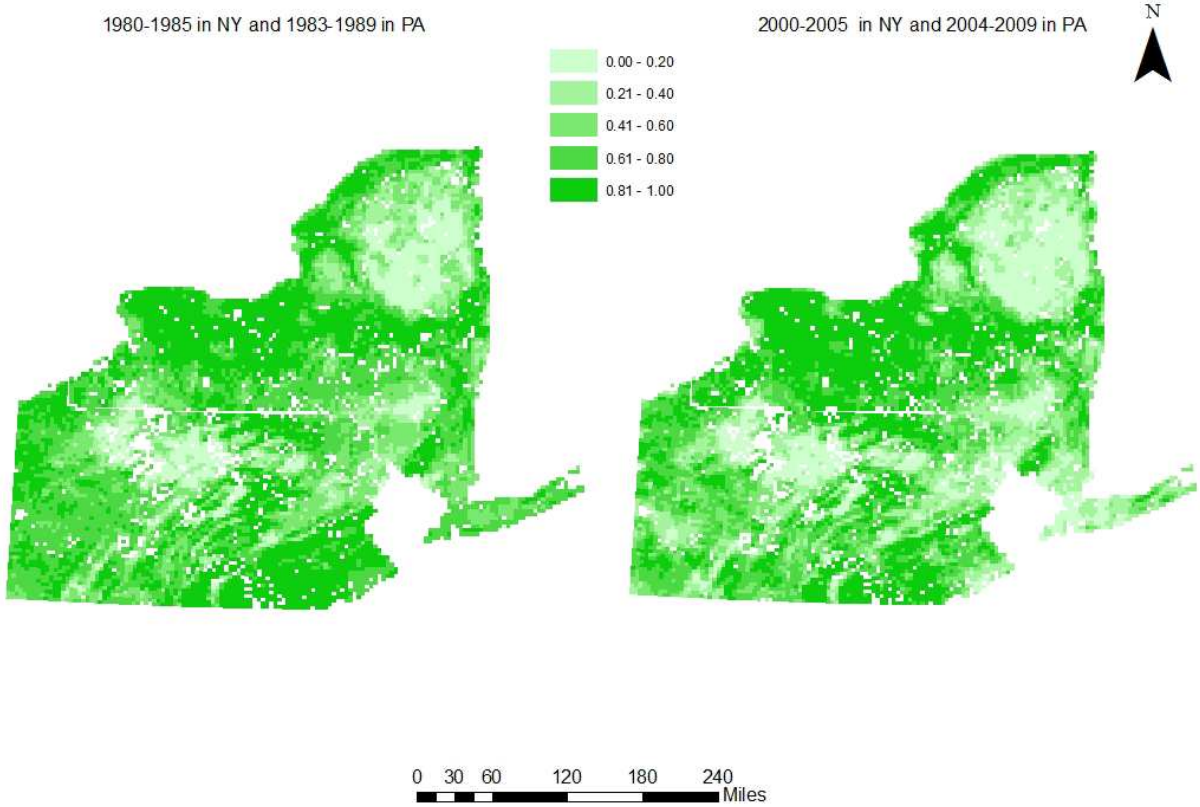
Acadian flycatcher (Empidonax virescens) occupancy probability



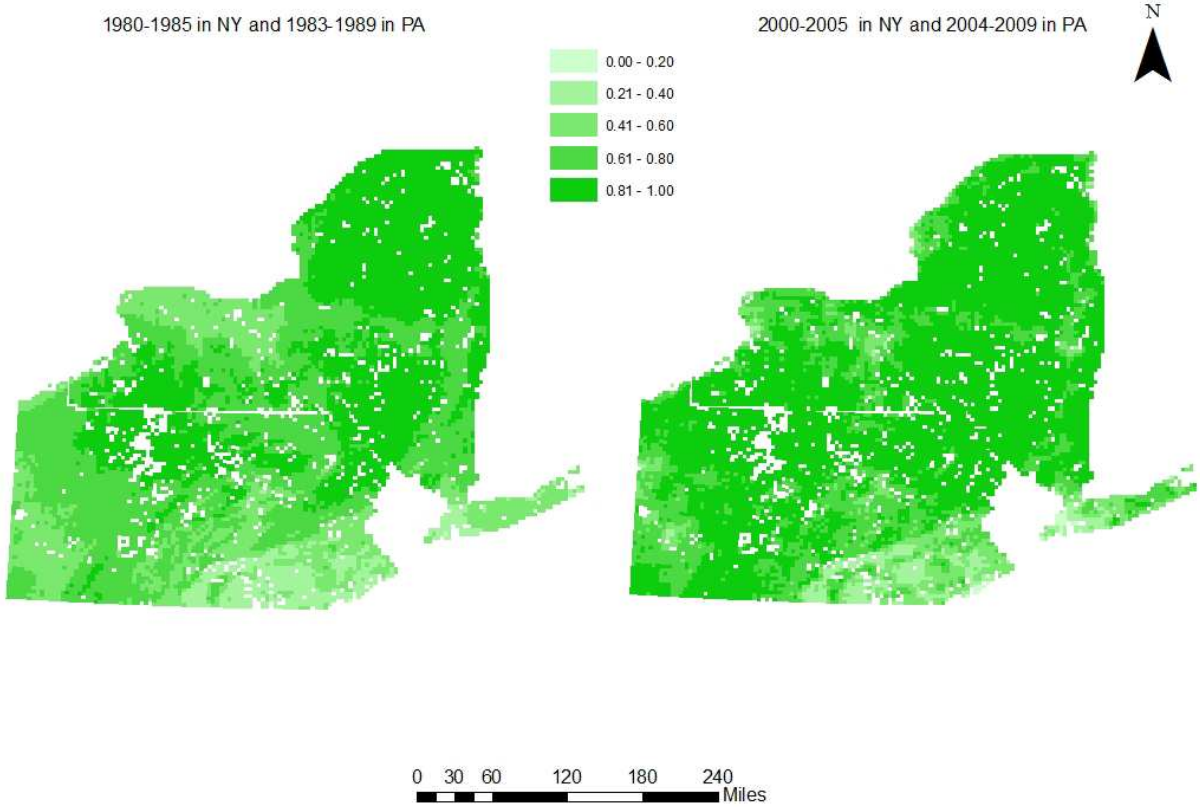
Alder flycatcher (Empidonax alnorum) occupancy probability



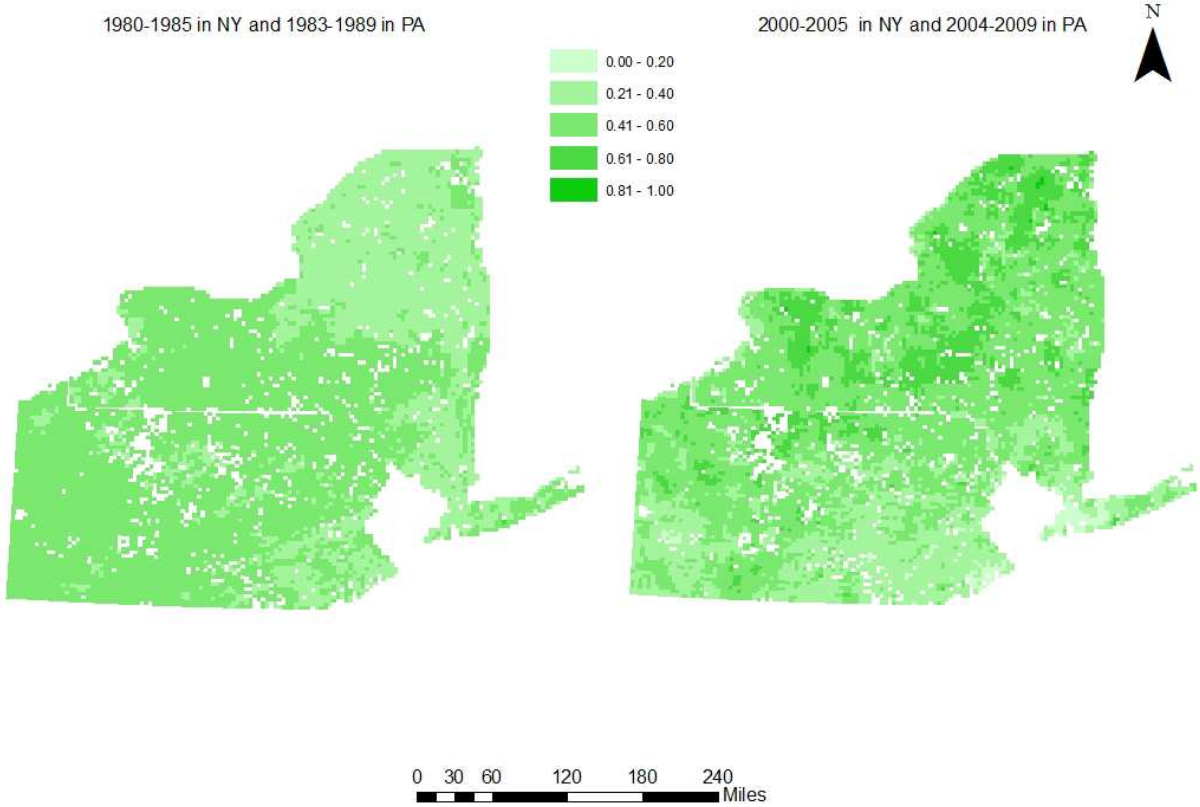
American kestrel (Falco sparverius) occupancy probability



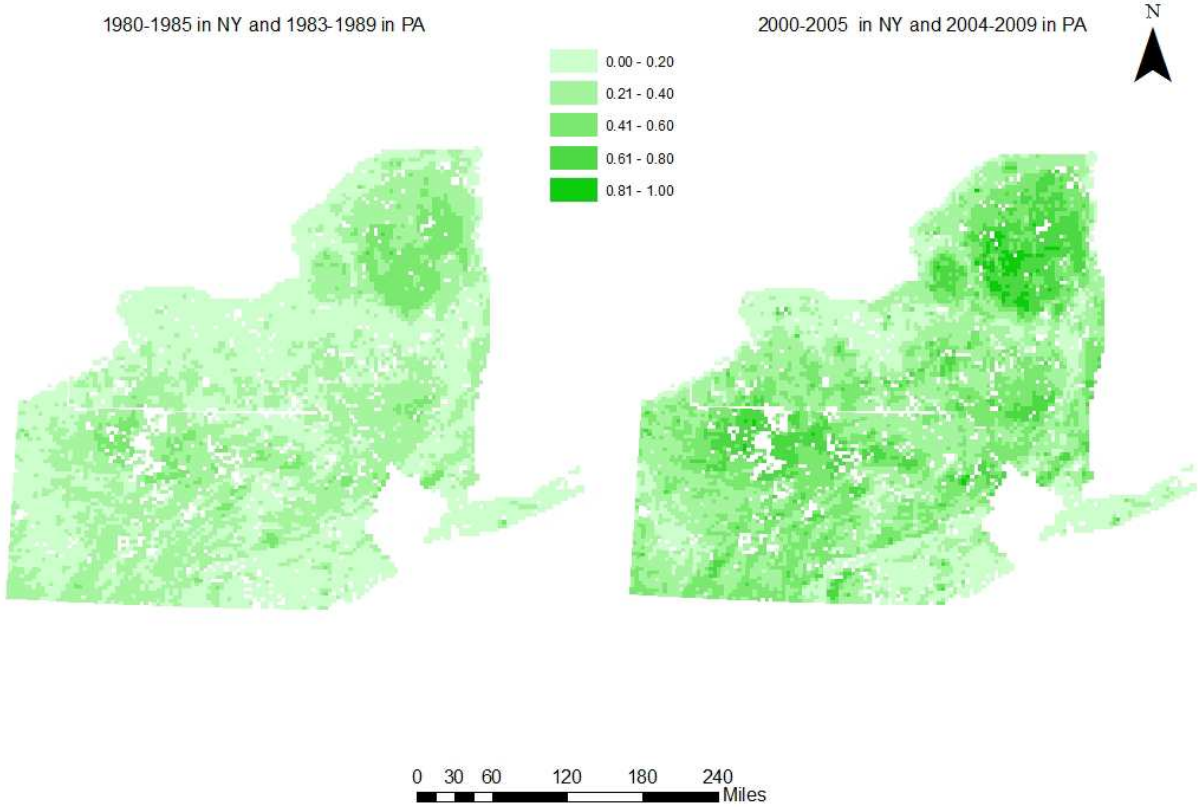
American redstart (Setophaga ruticilla) occupancy probability



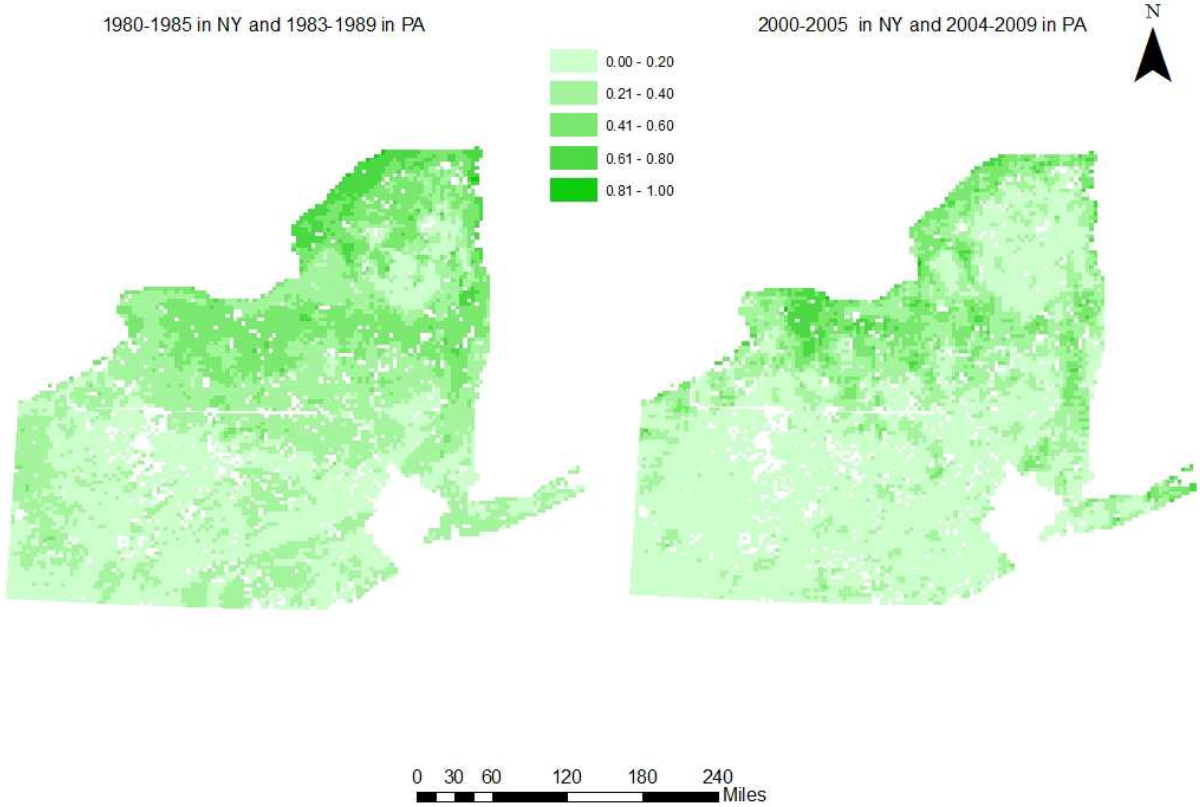
American woodcock (Scolopax minor) occupancy probability



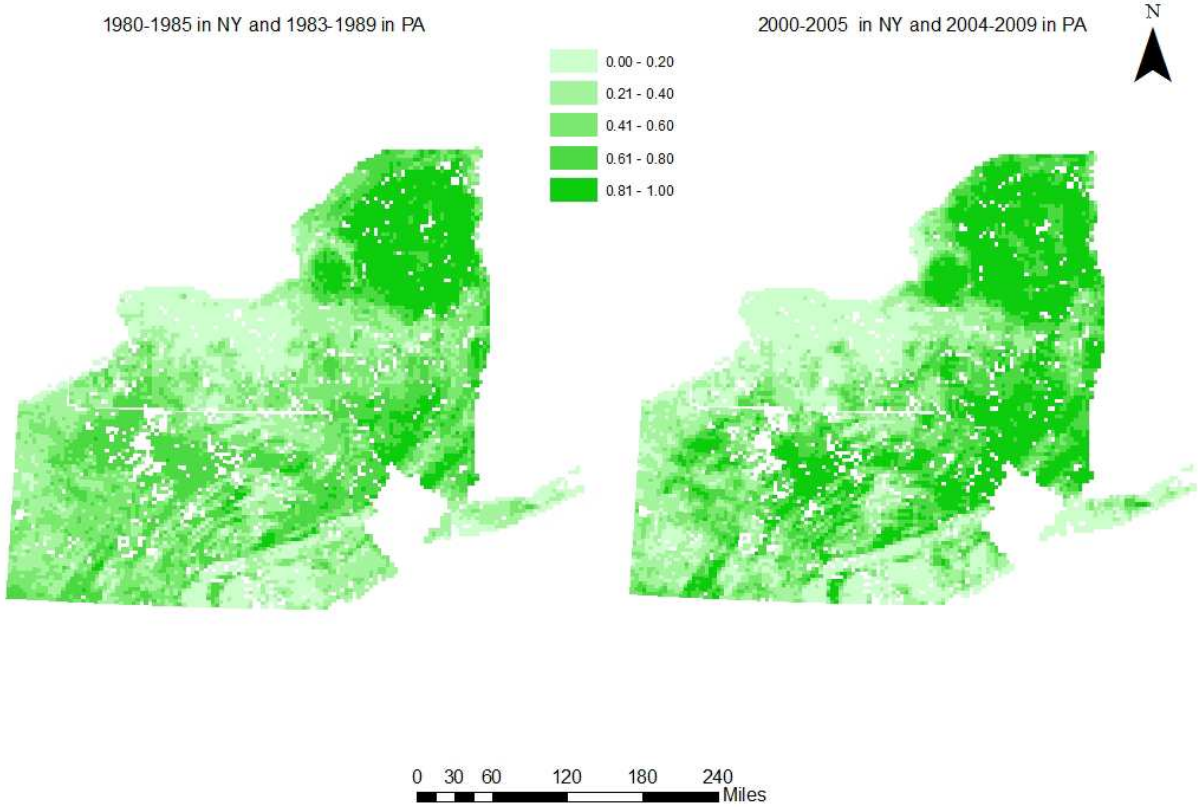
Barred owl (Strix varia) occupancy probability



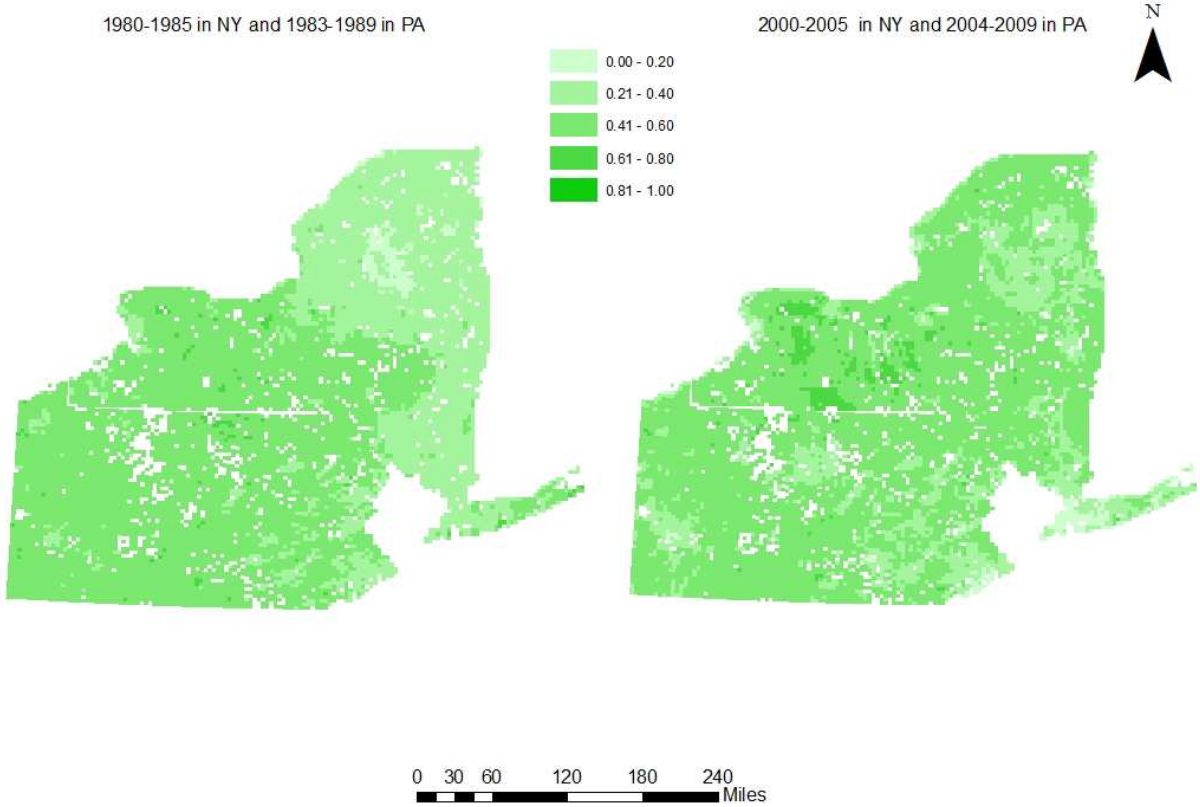
Bank swallow (Riparia riparia) occupancy probability



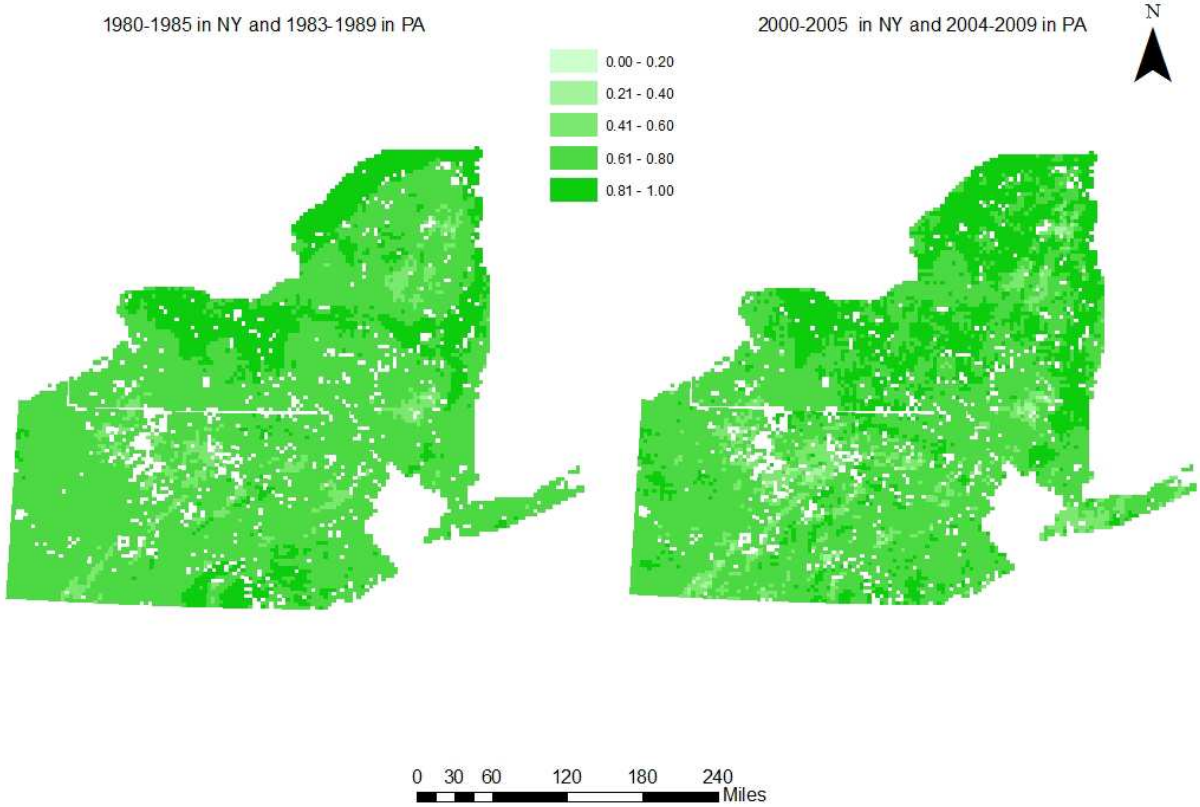
Black-and-white warbler (Mniotilta varia) occupancy probability



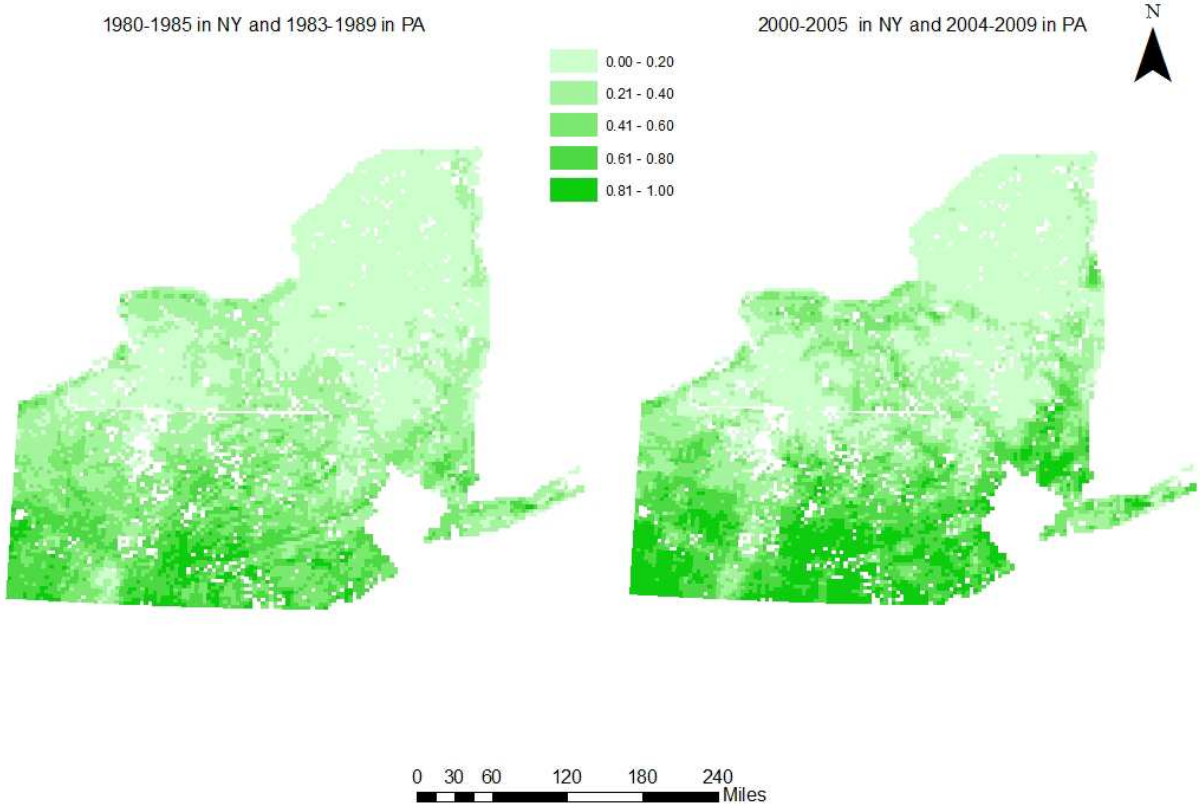
Black-billed cuckoo (Coccyzus erythropthalmus) occupancy probability



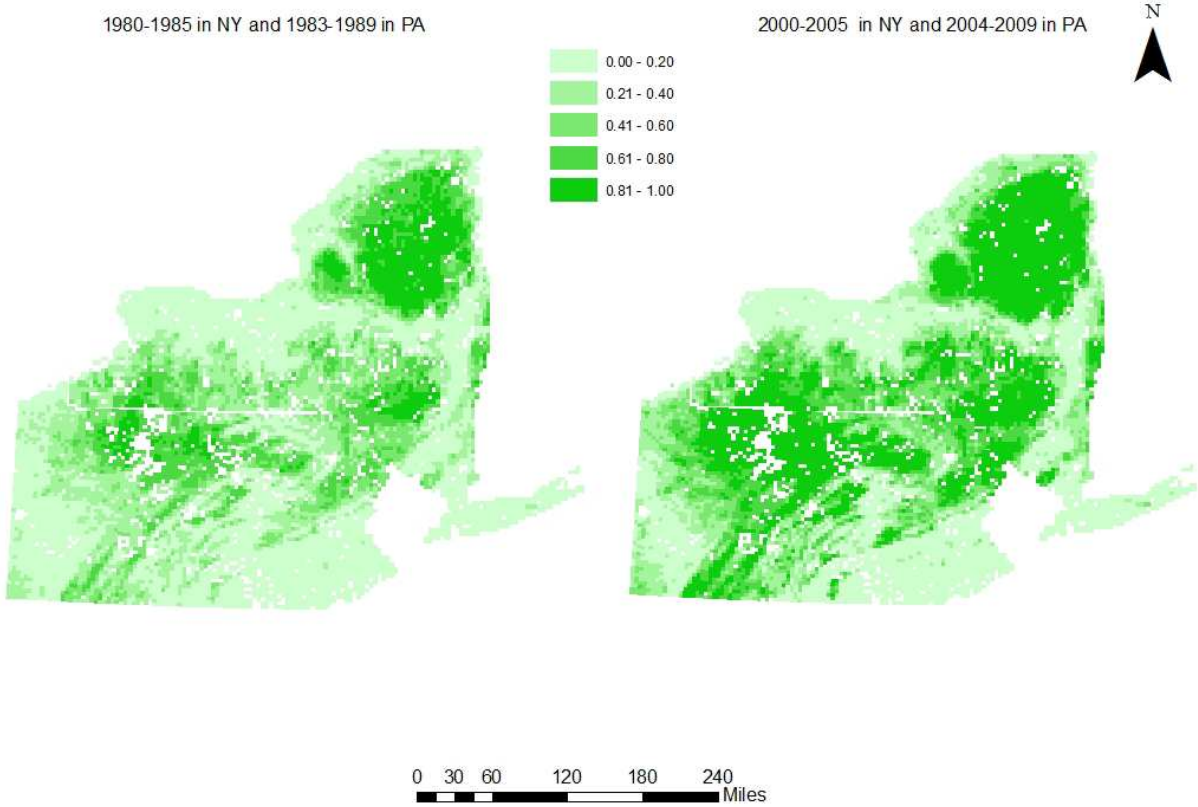
Belted kingfisher (Megaceryle alcyon) occupancy probability



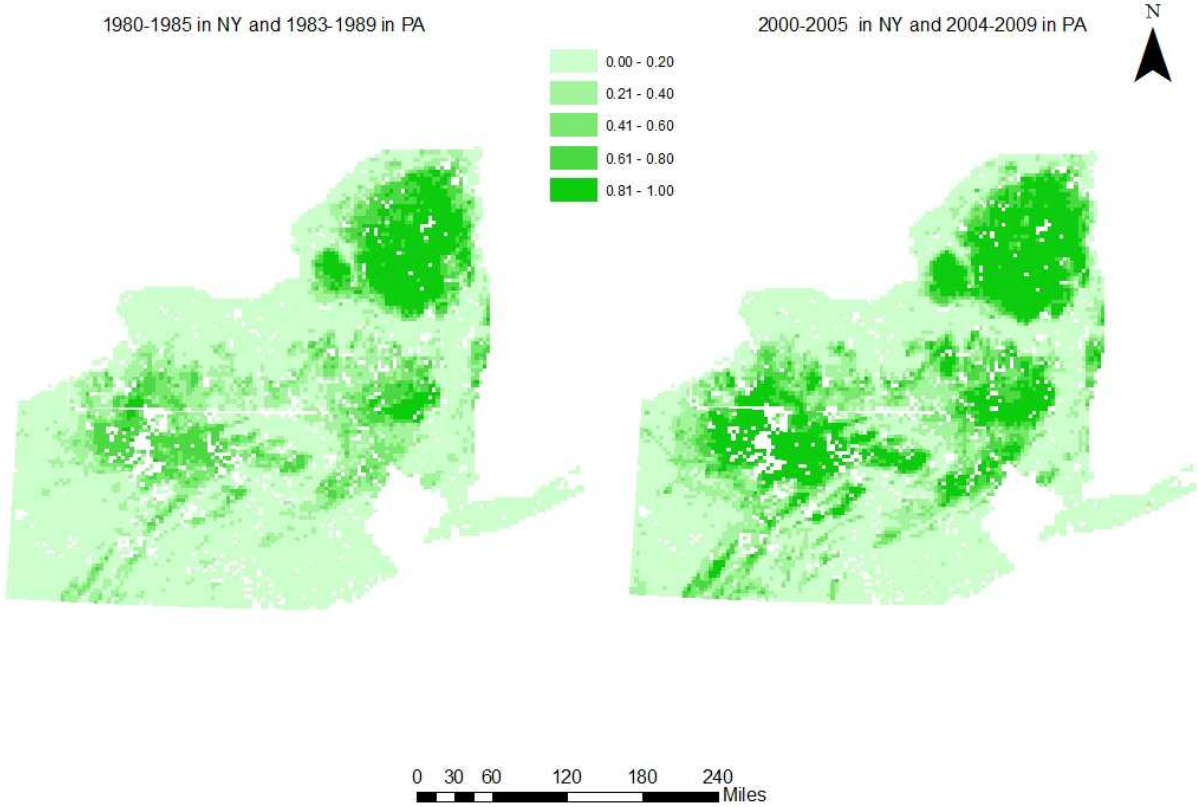
Blue-gray gnatcatcher (Polioptila caerulea) occupancy probability



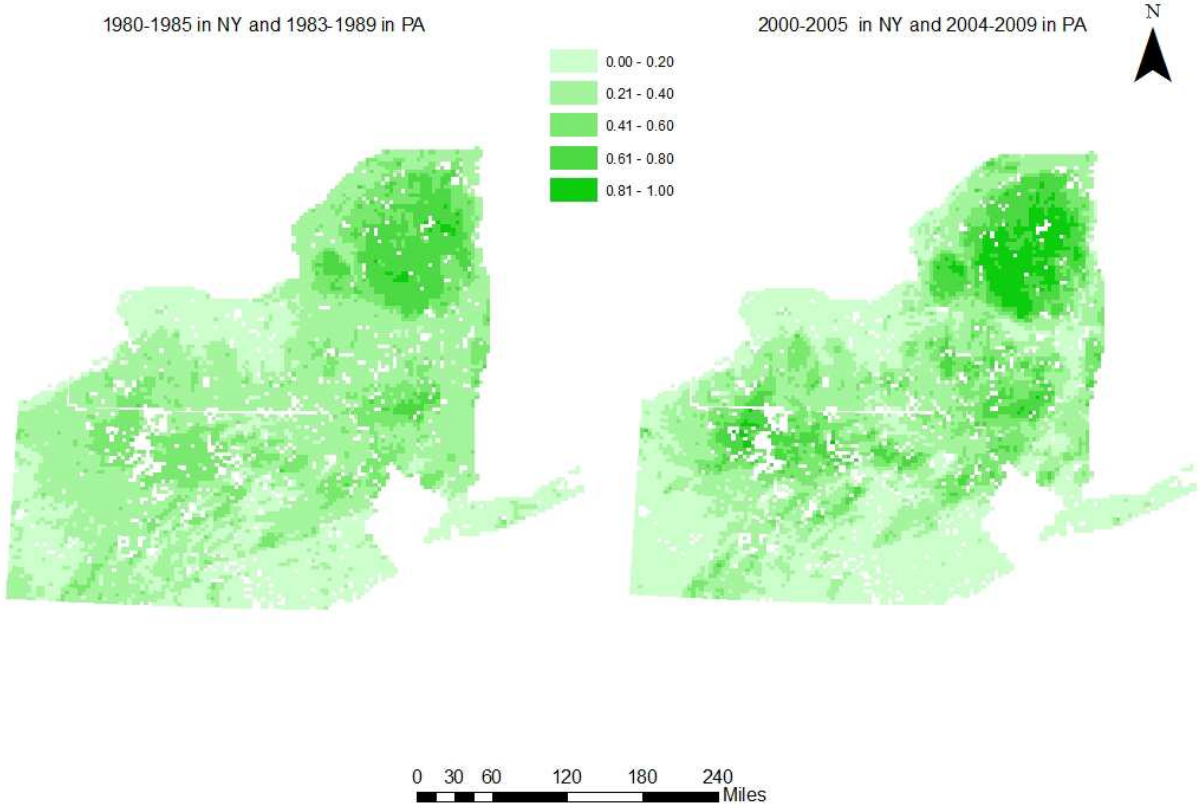
Blue-headed vireo (Vireo solitarius) occupancy probability



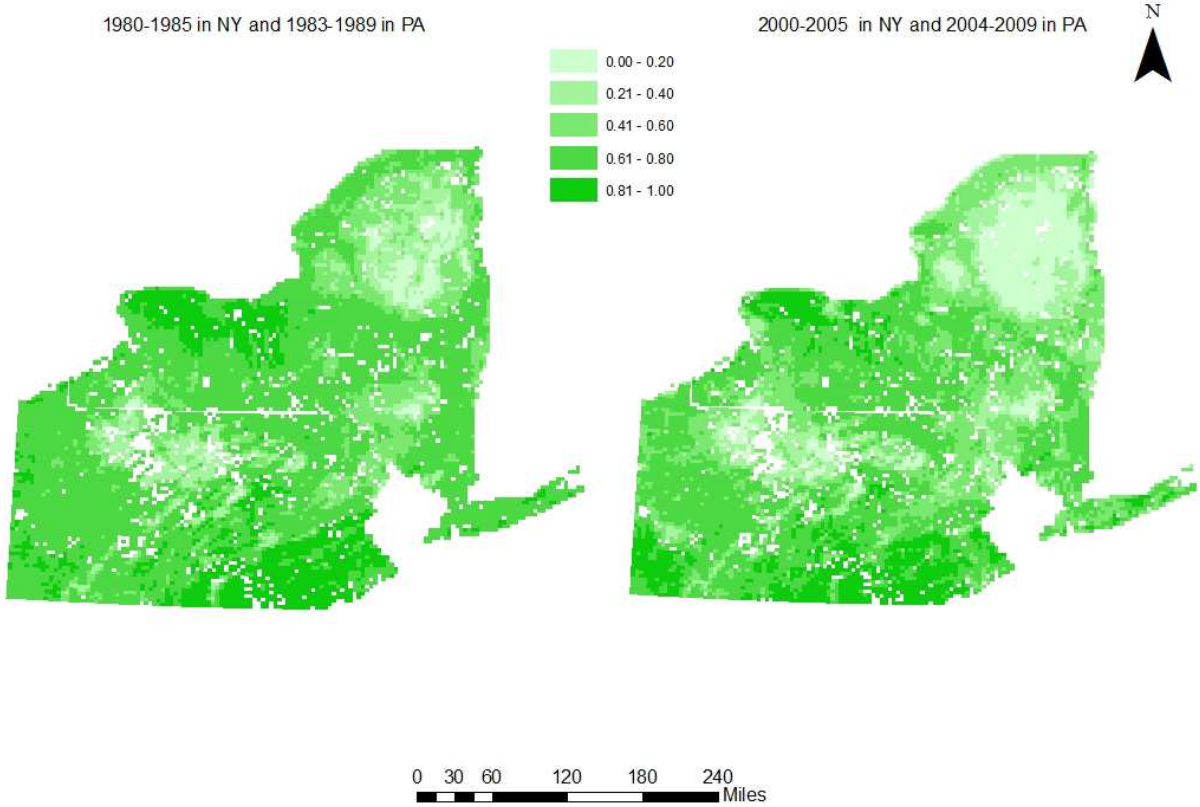
Blackburnian warbler (Setophaga fusca) occupancy probability



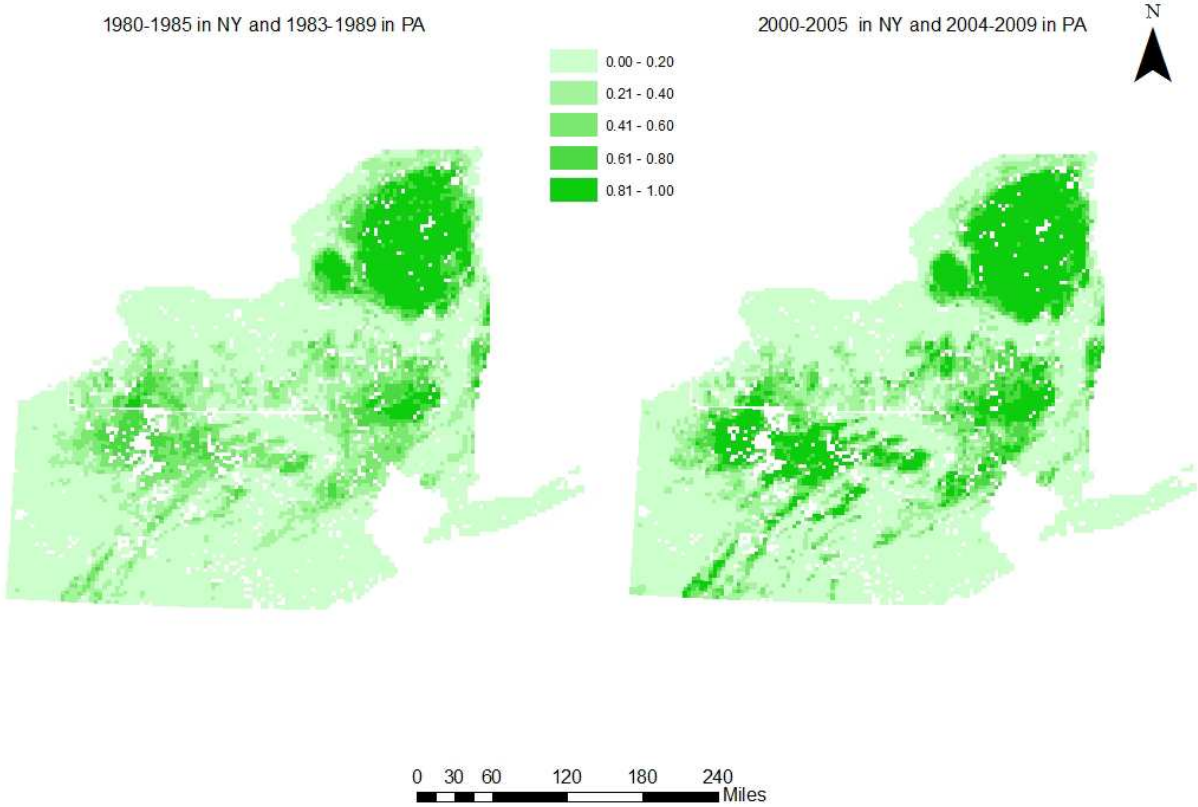
Brown creeper (Certhia americana) occupancy probability



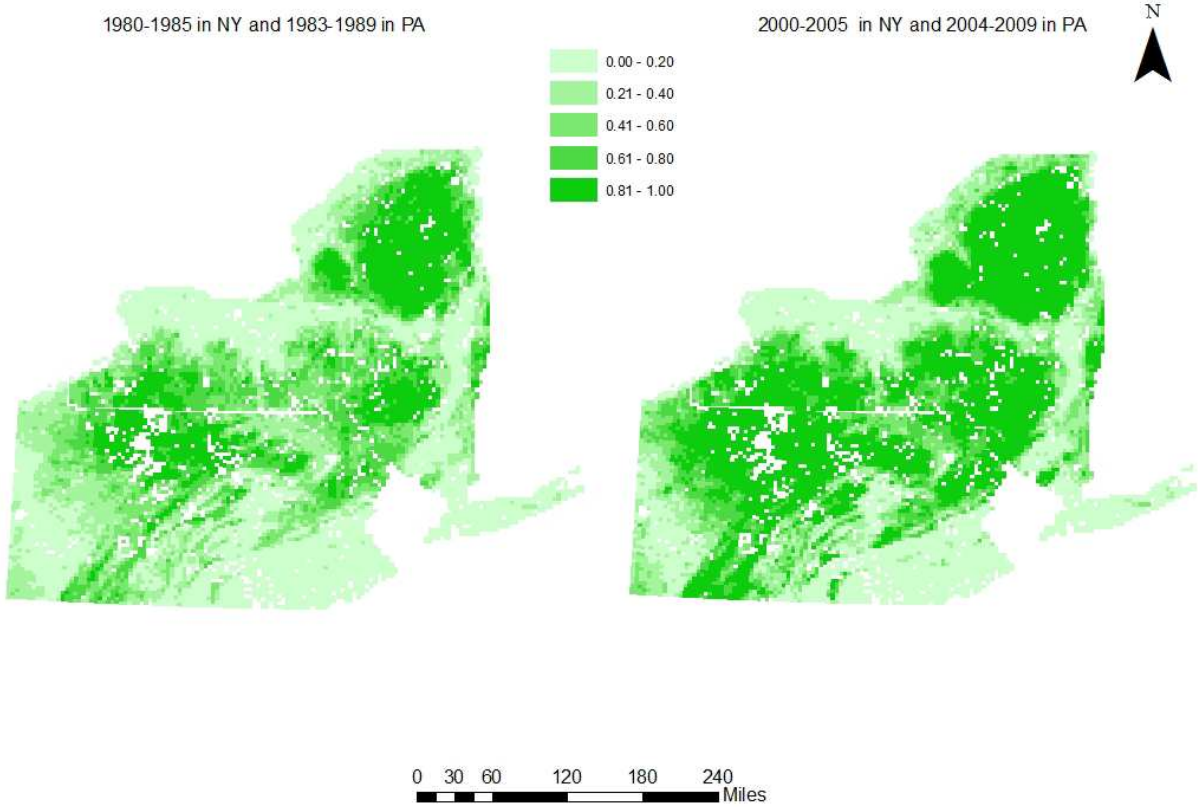
Brown thrasher (Toxostoma rufum) occupancy probability



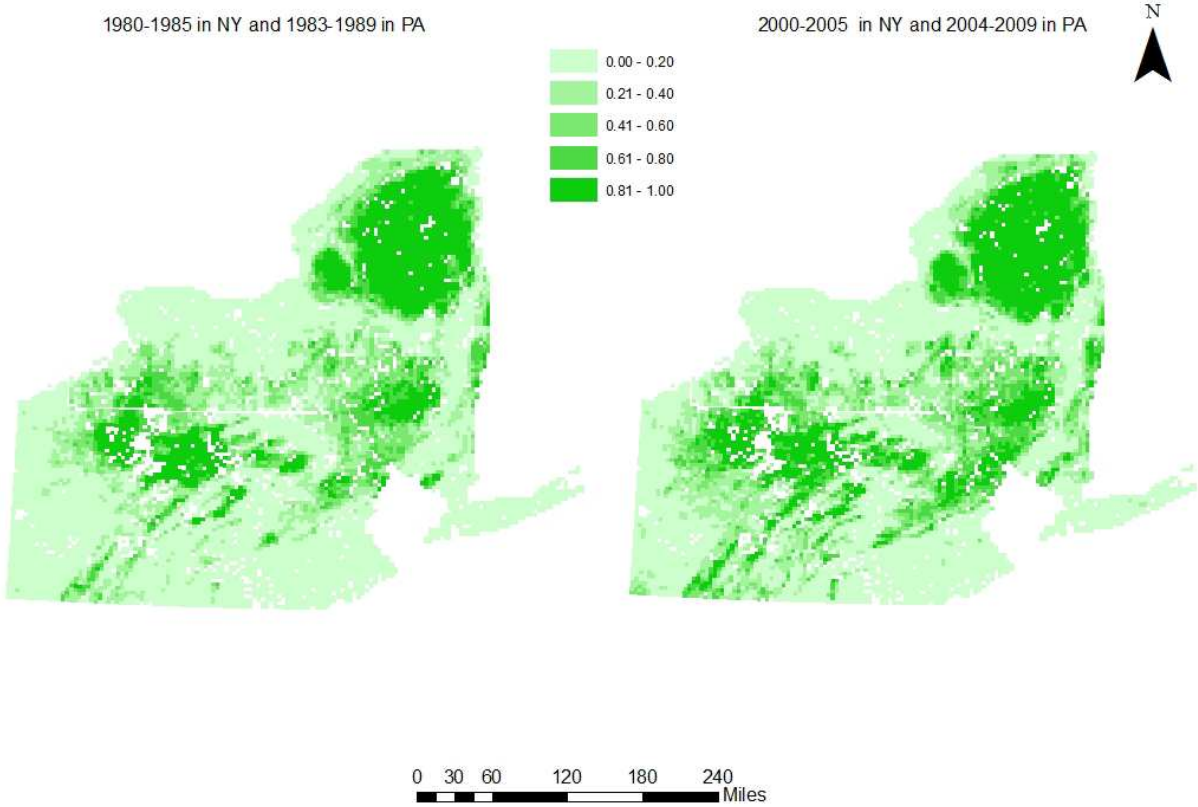
Black-throated blue warbler (Setophaga caerulescens) occupancy probability



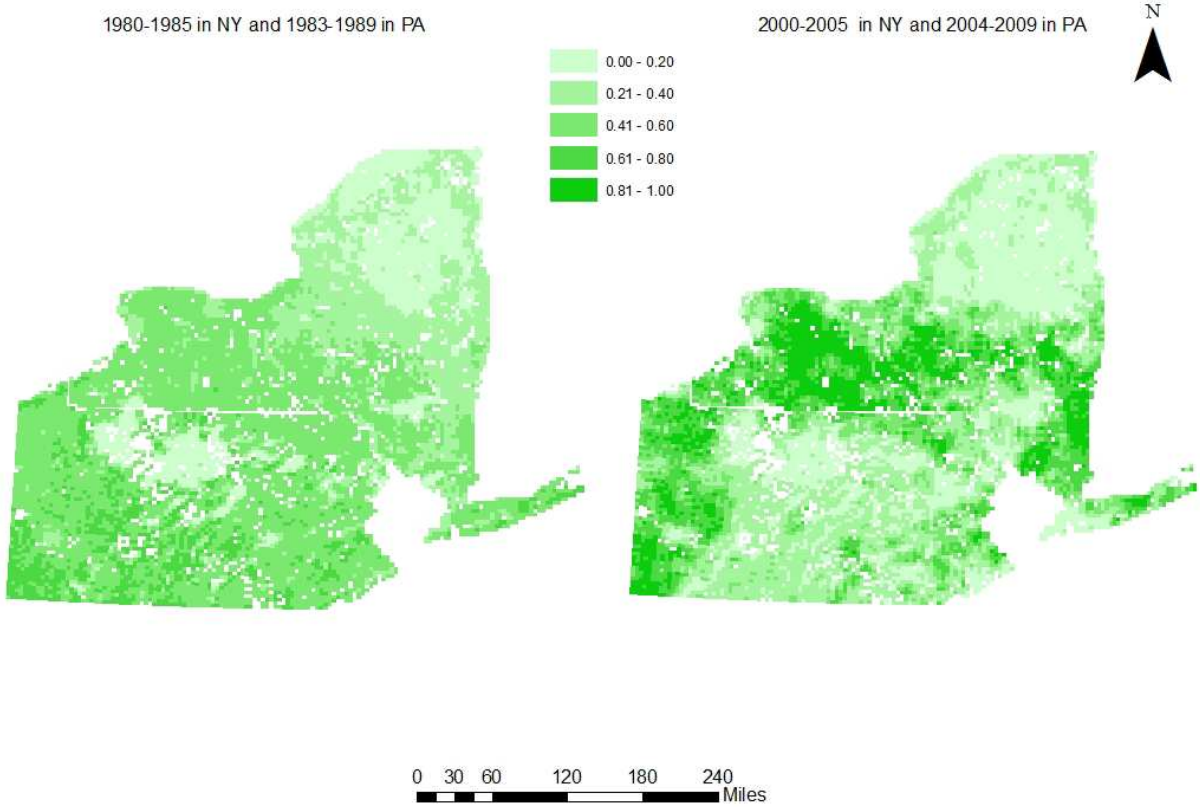
Black-throated green warbler (Setophaga virens) occupancy probability



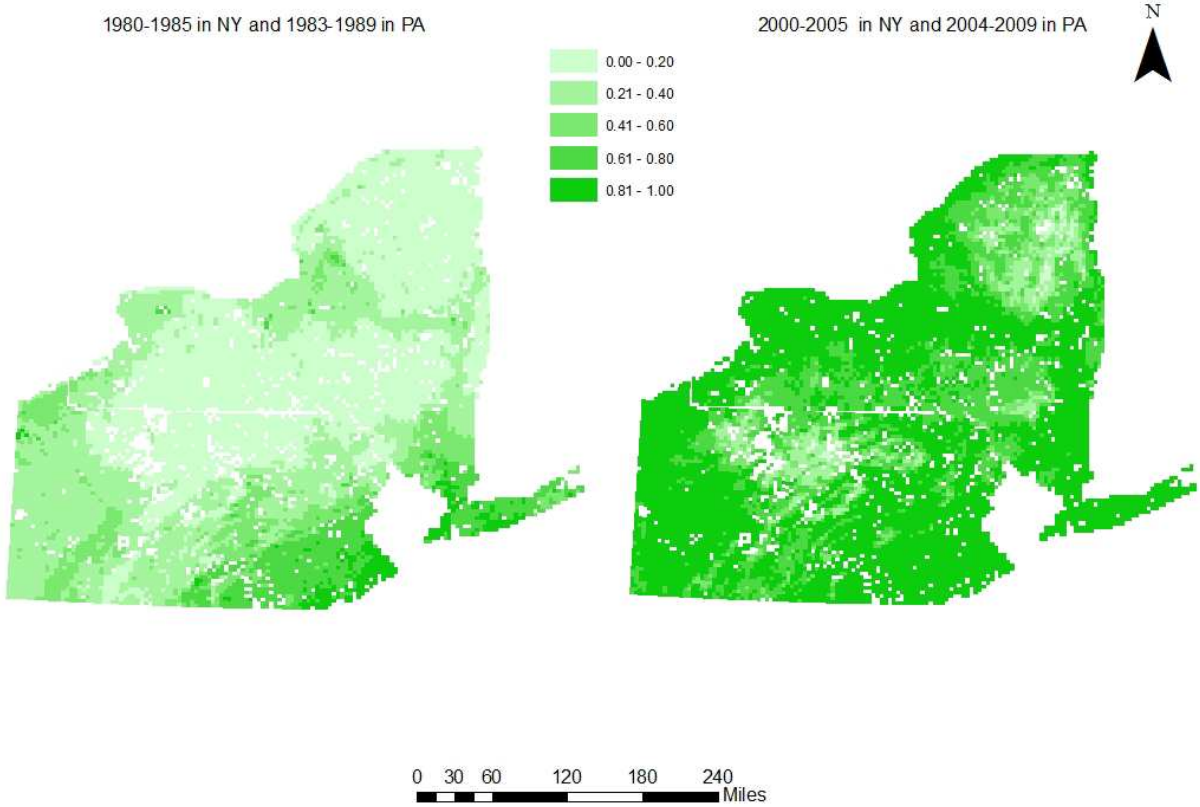
Broad-winged hawk (Buteo platypterus) occupancy probability



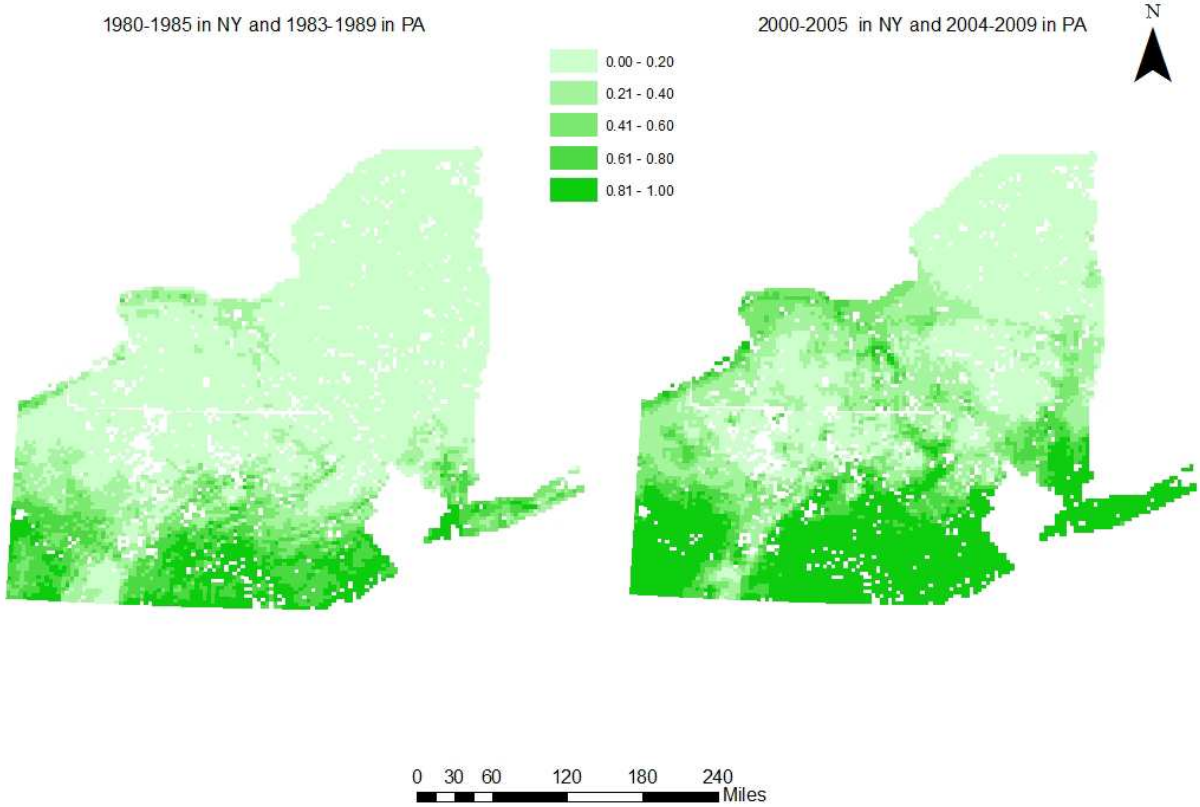
Blue-winged warbler (Vermivora cyanoptera) occupancy probability



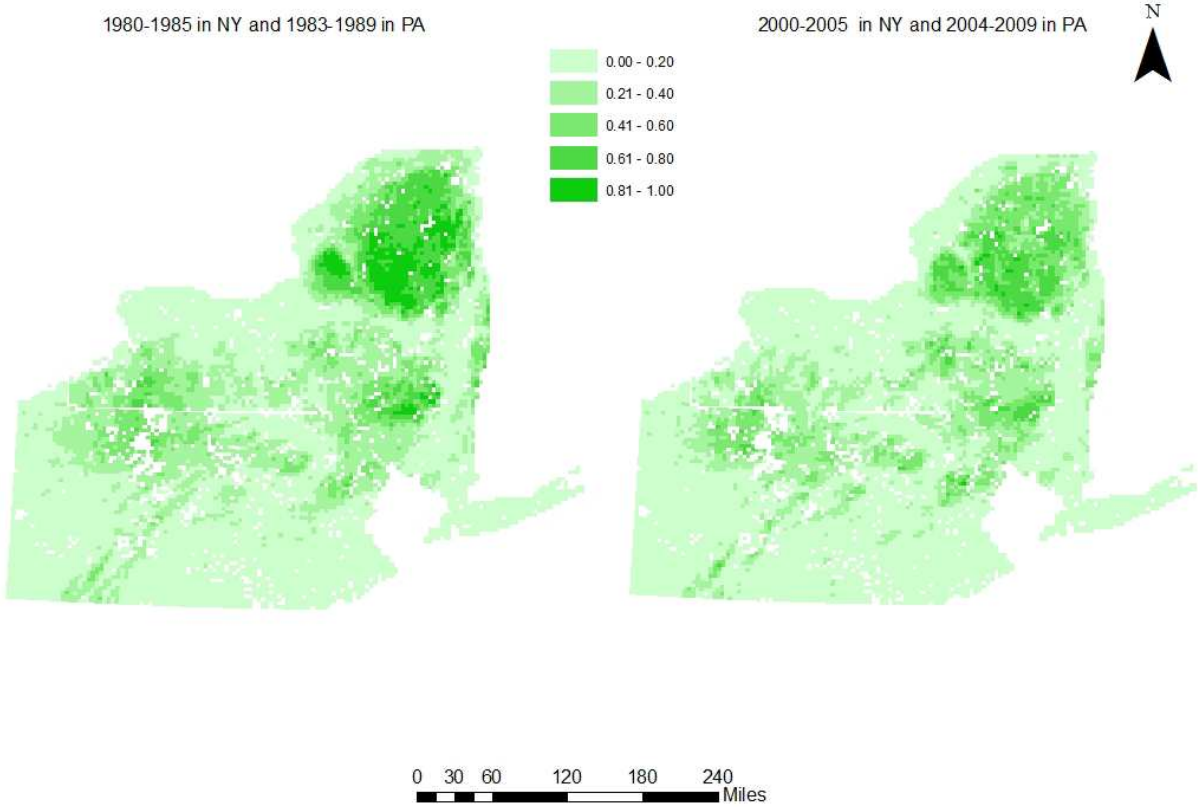
Canada goose (Branta canadensis) occupancy probability



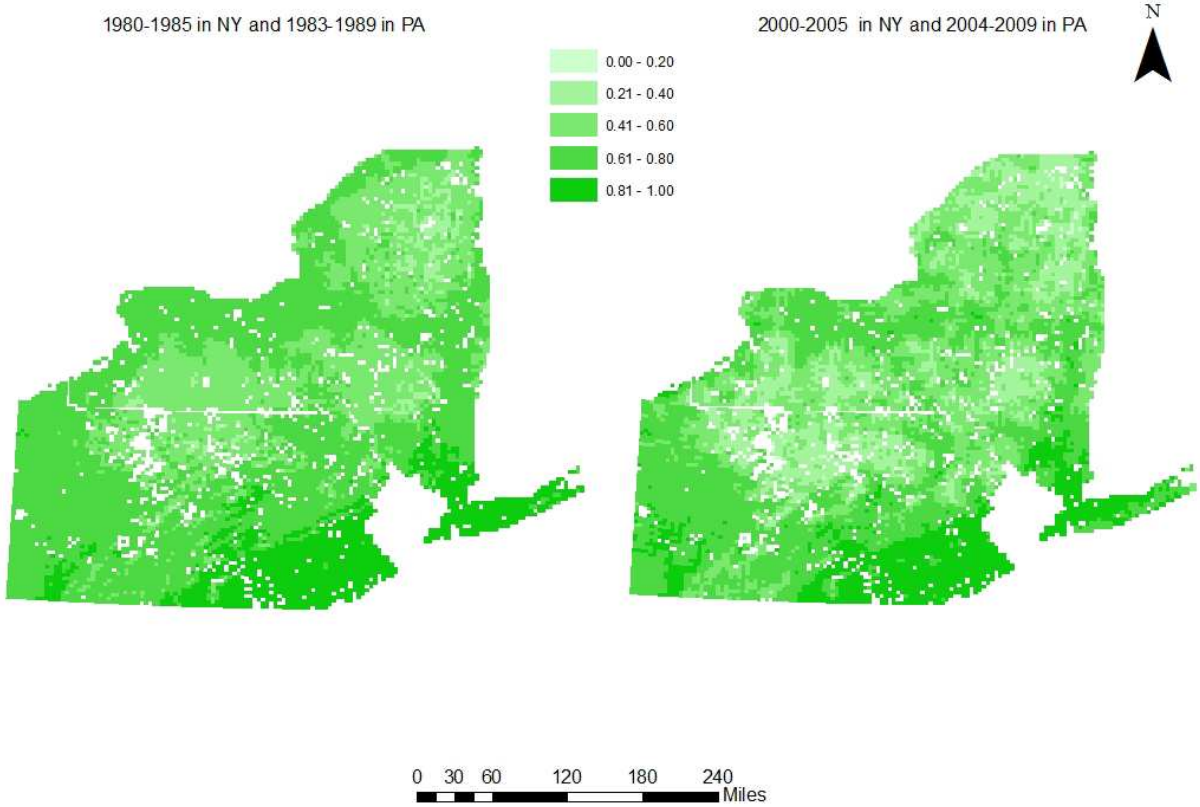
Carolina wren (Thryothorus ludovicianus) occupancy probability



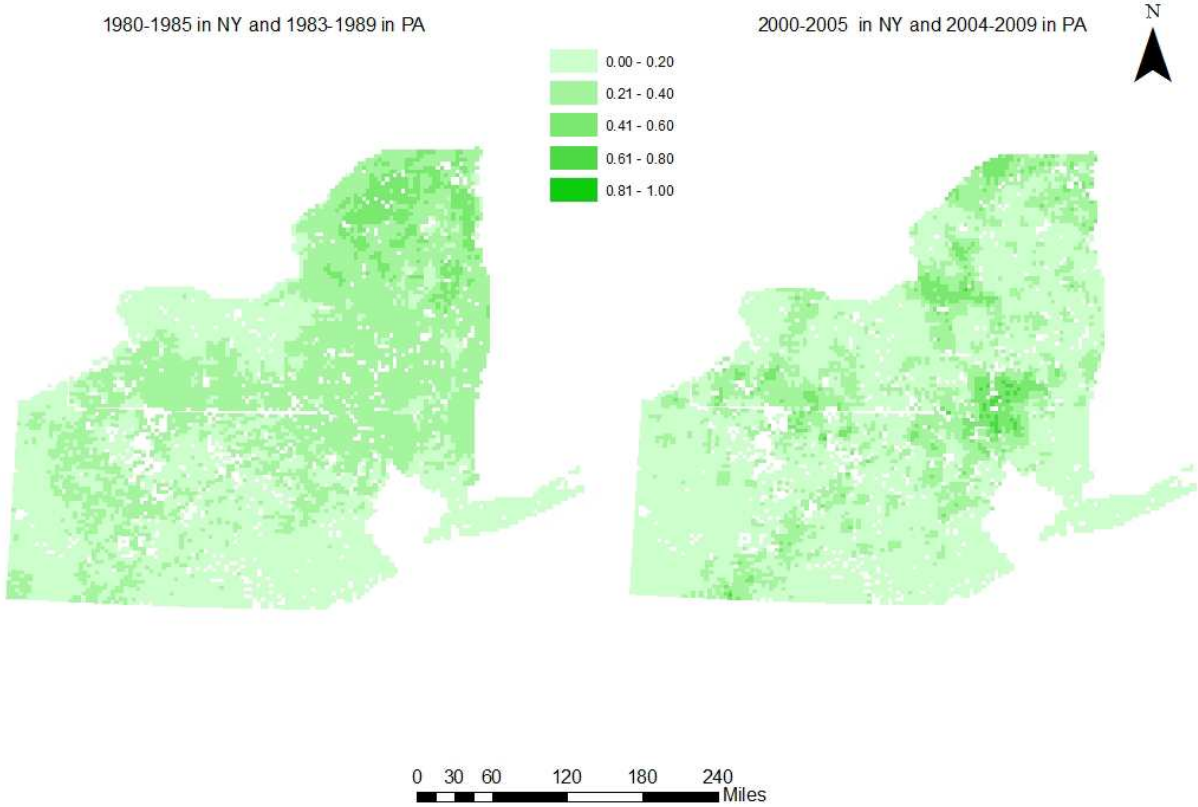
Canada warbler (Cardellina canadensis) occupancy probability



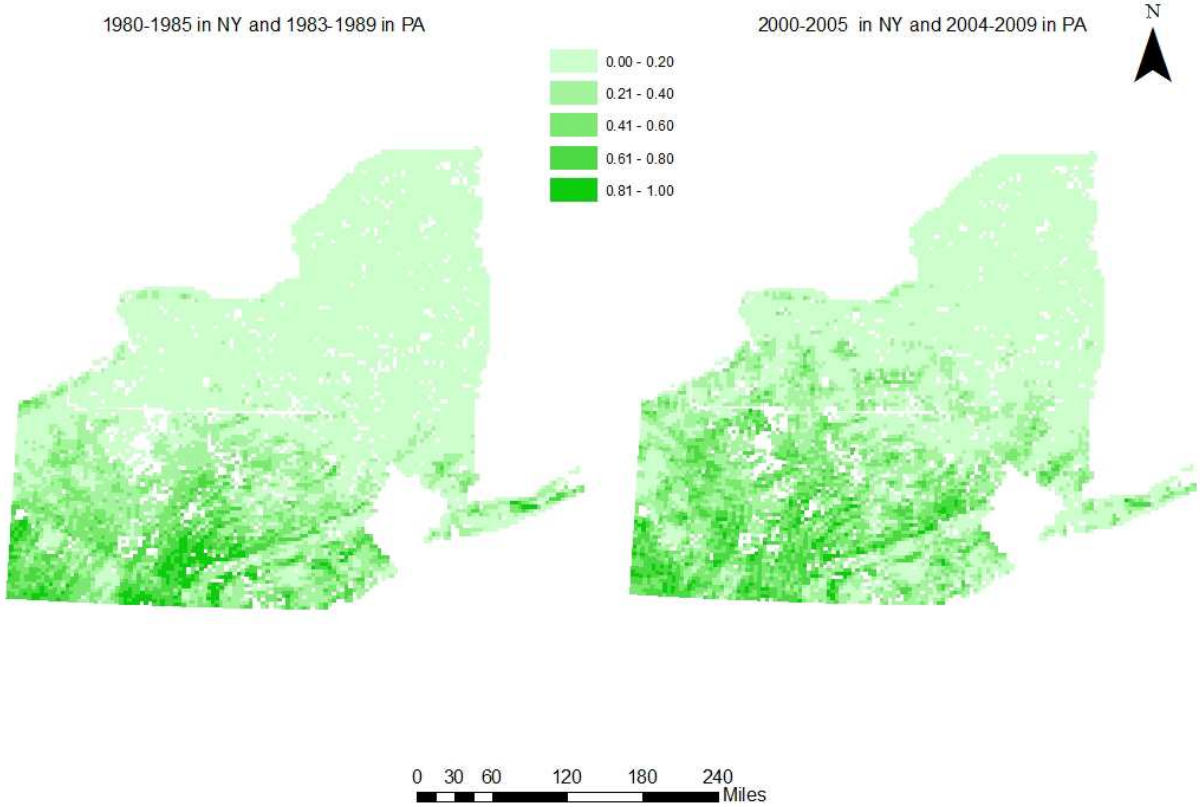
Chimney swift (Chaetura pelagica) occupancy probability



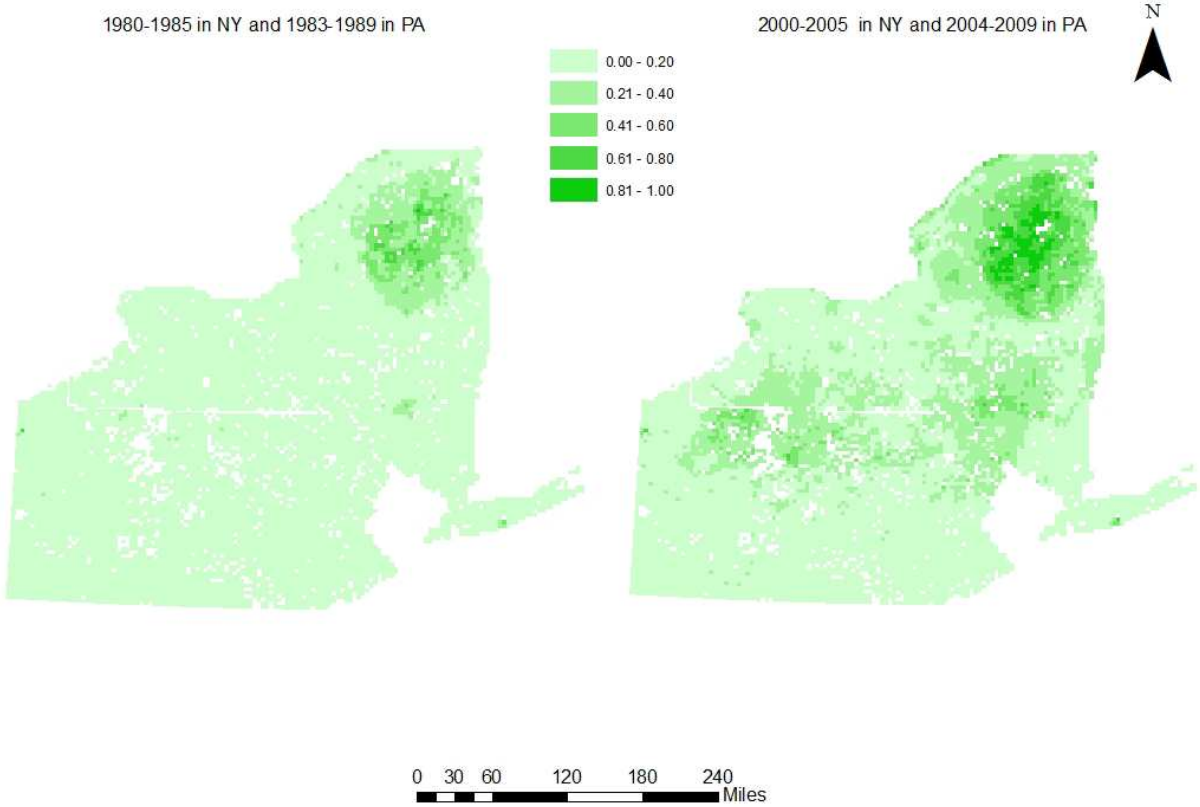
Cliff swallow (Petrochelidon pyrrhonota) occupancy probability



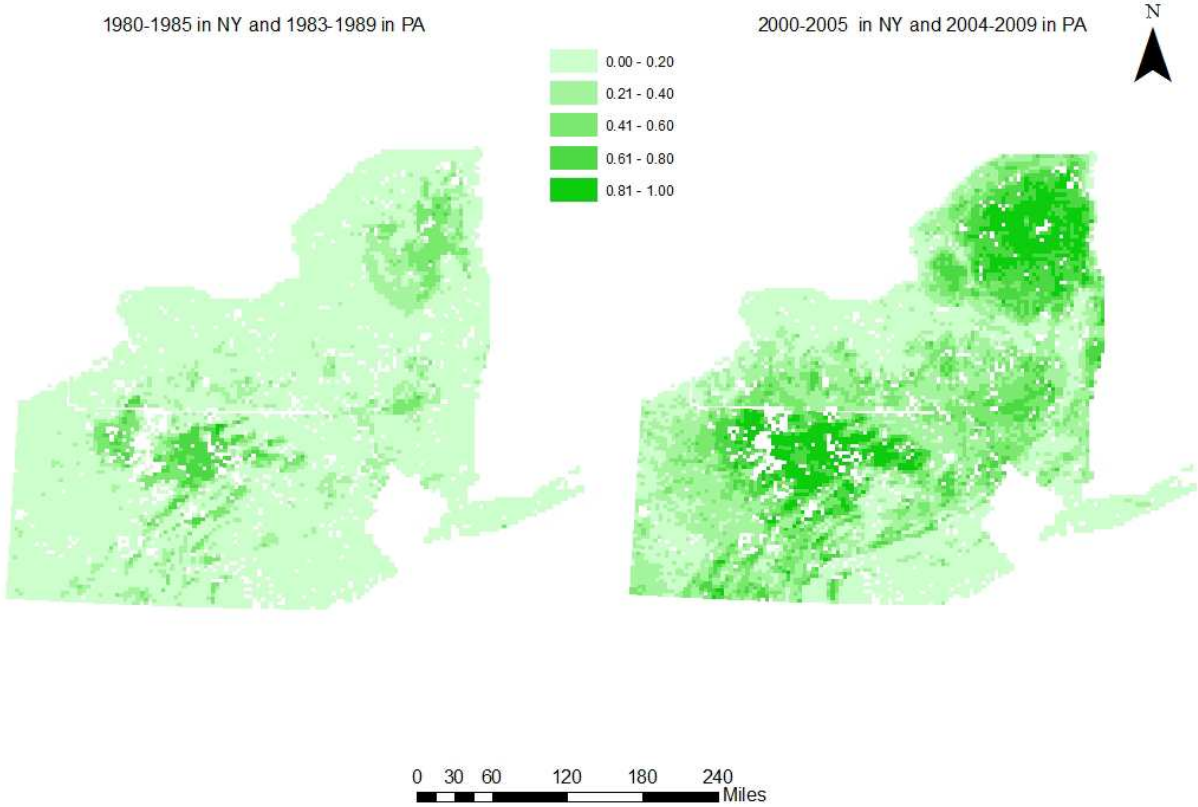
Cooper's hawk (Accipiter cooperii) occupancy probability



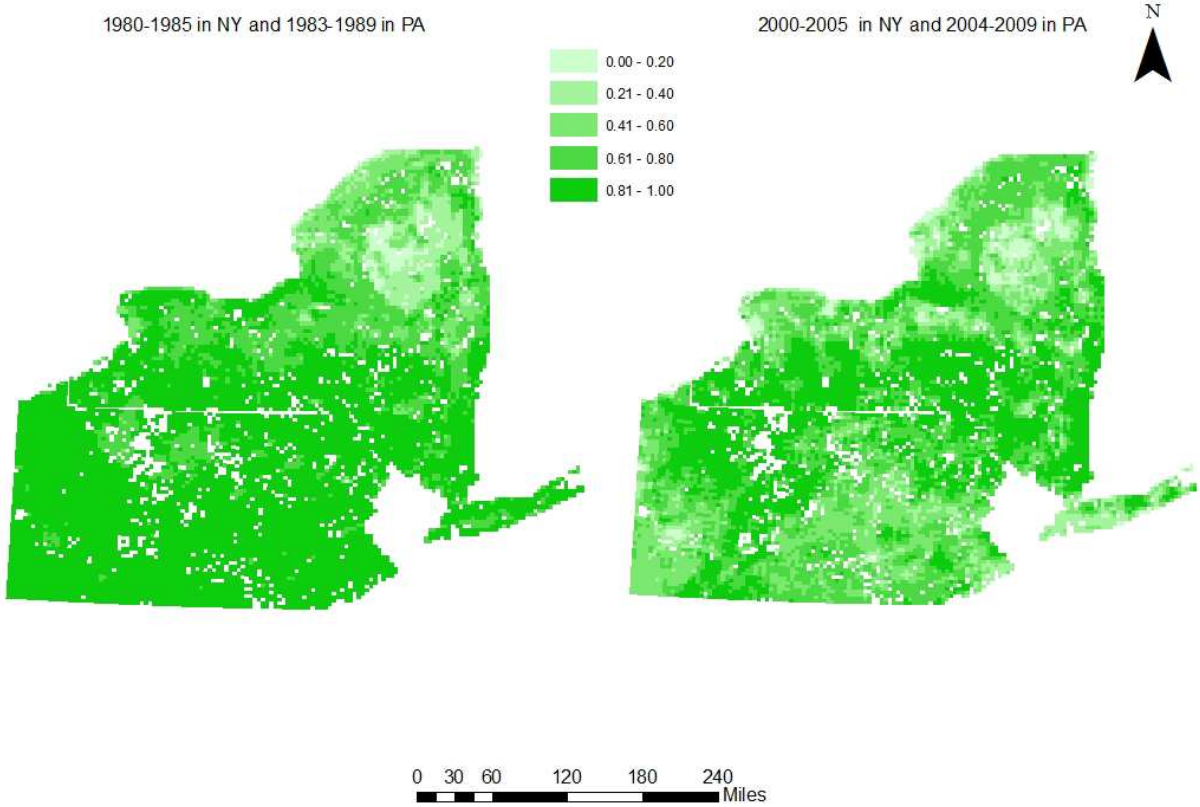
Common merganser (Mergus merganser) occupancy probability



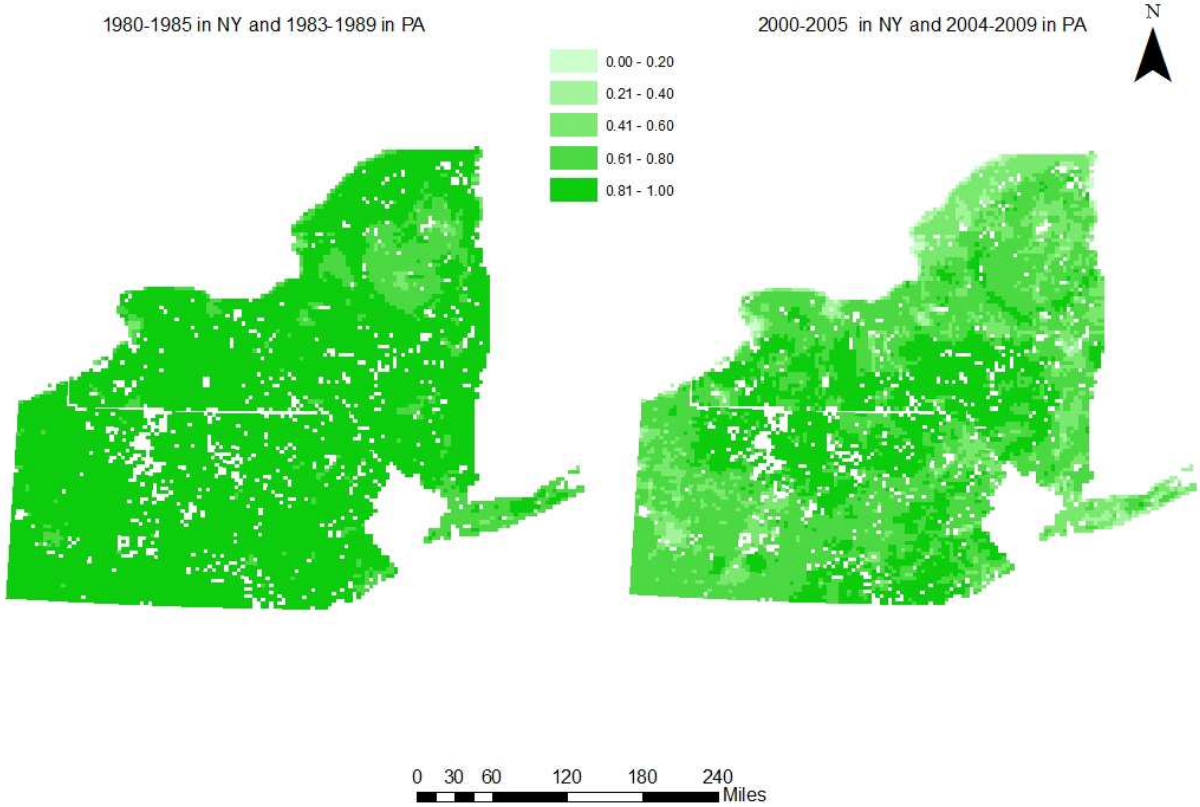
Common raven (Corvus corax) occupancy probability



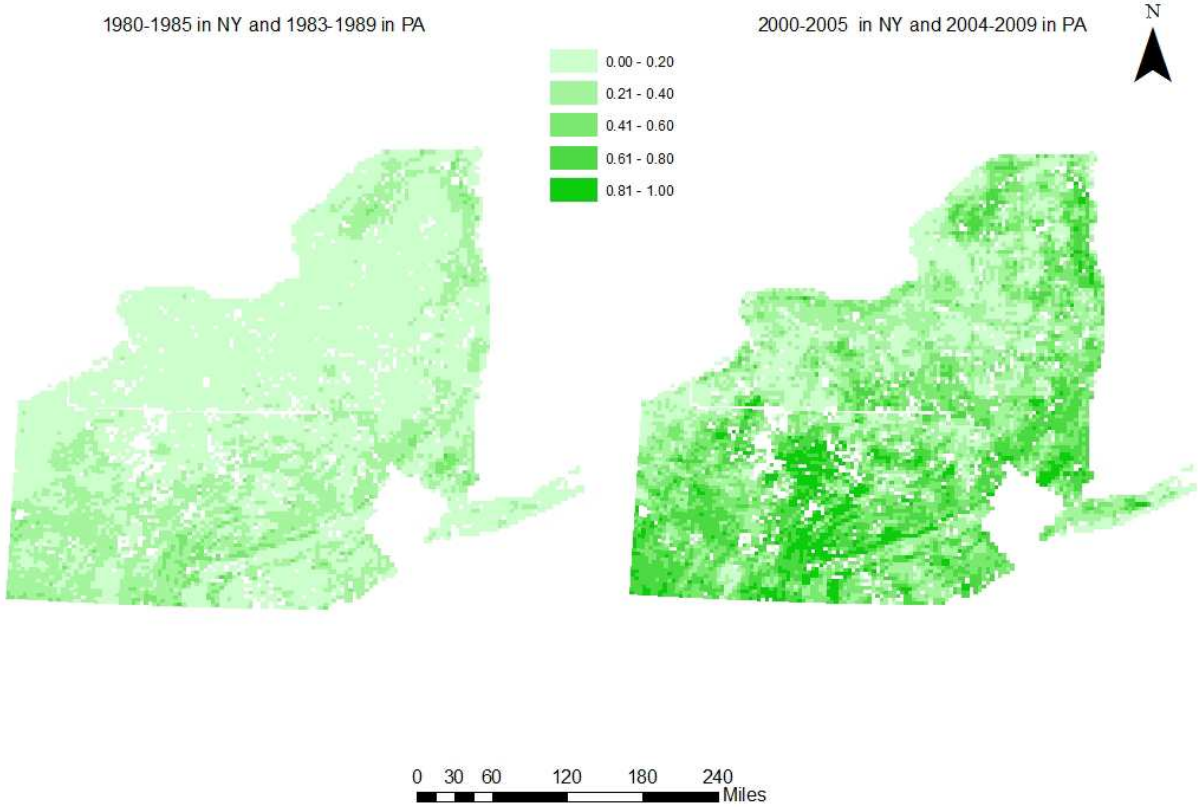
Chestnut-sided warbler (Setophaga pensylvanica) occupancy probability



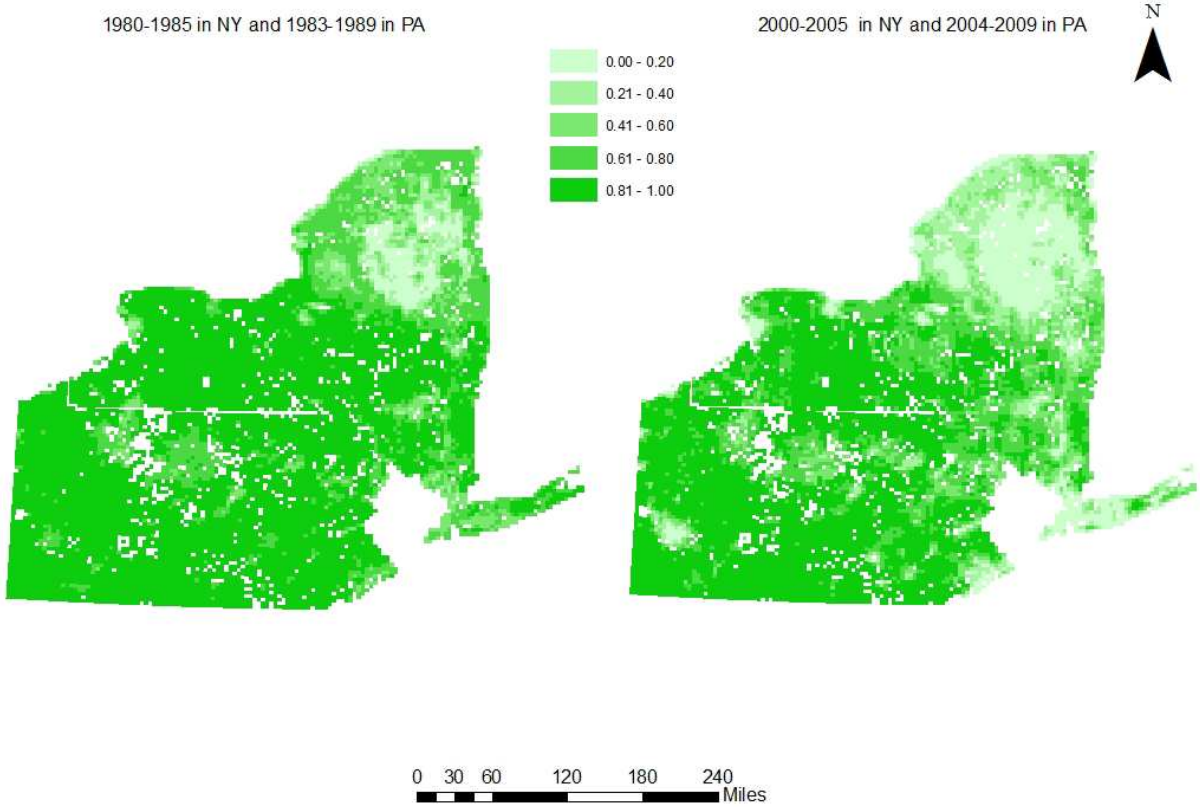
Dark-eyed junco (Junco hyemalis) occupancy probability



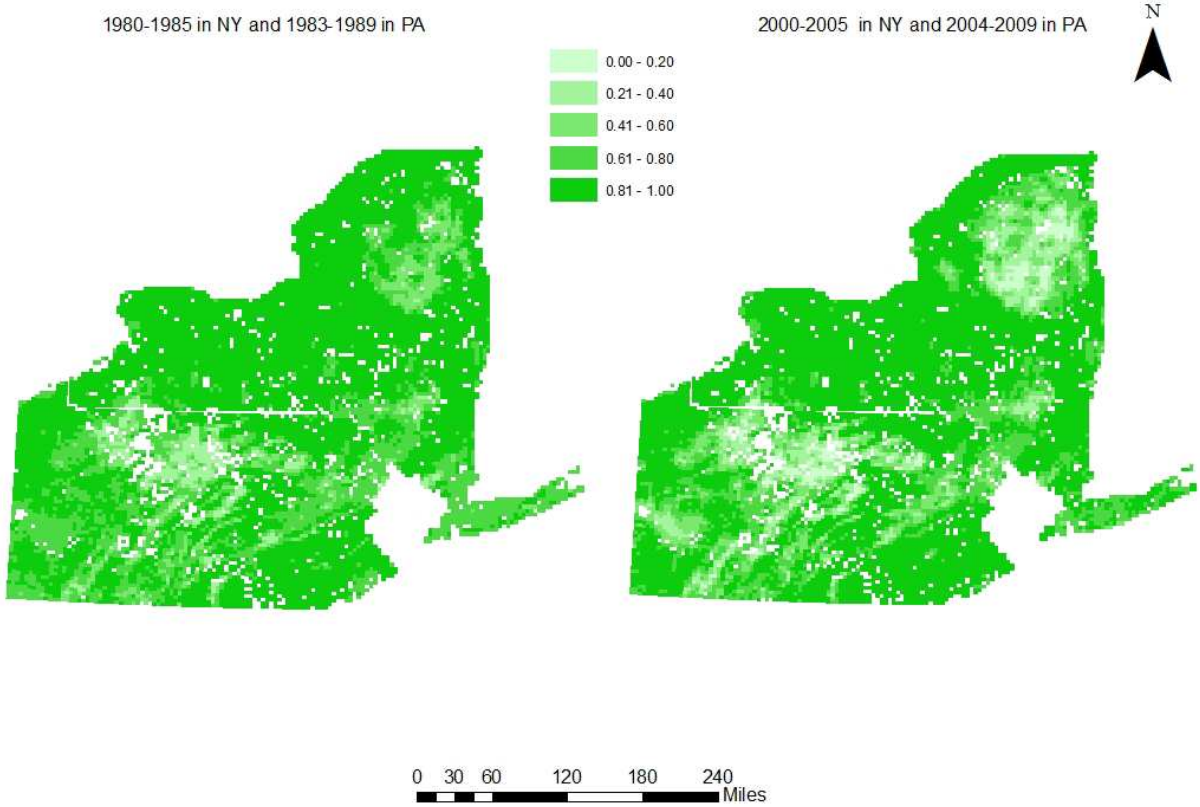
Downy woodpecker (Picoides pubescens) occupancy probability



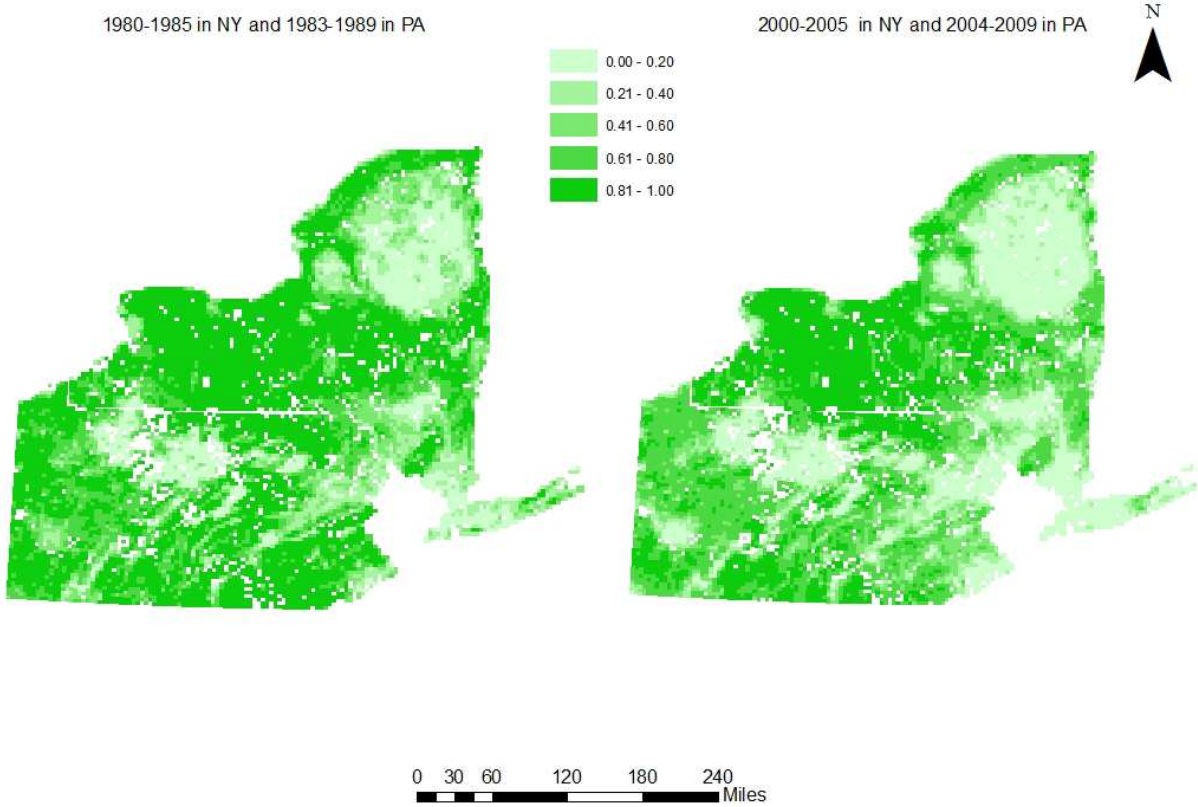
Eastern bluebird (Sialia sialis) occupancy probability



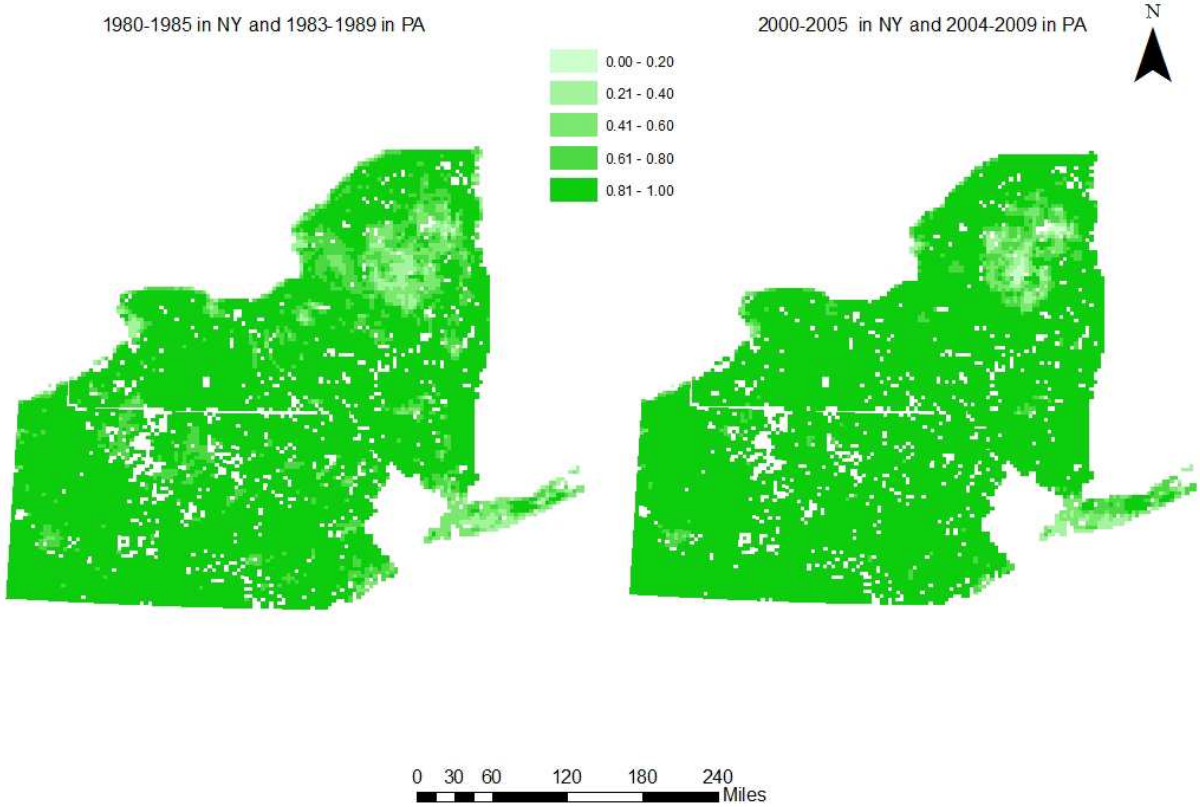
Eastern kingbird (Tyrannus tyrannus) occupancy probability



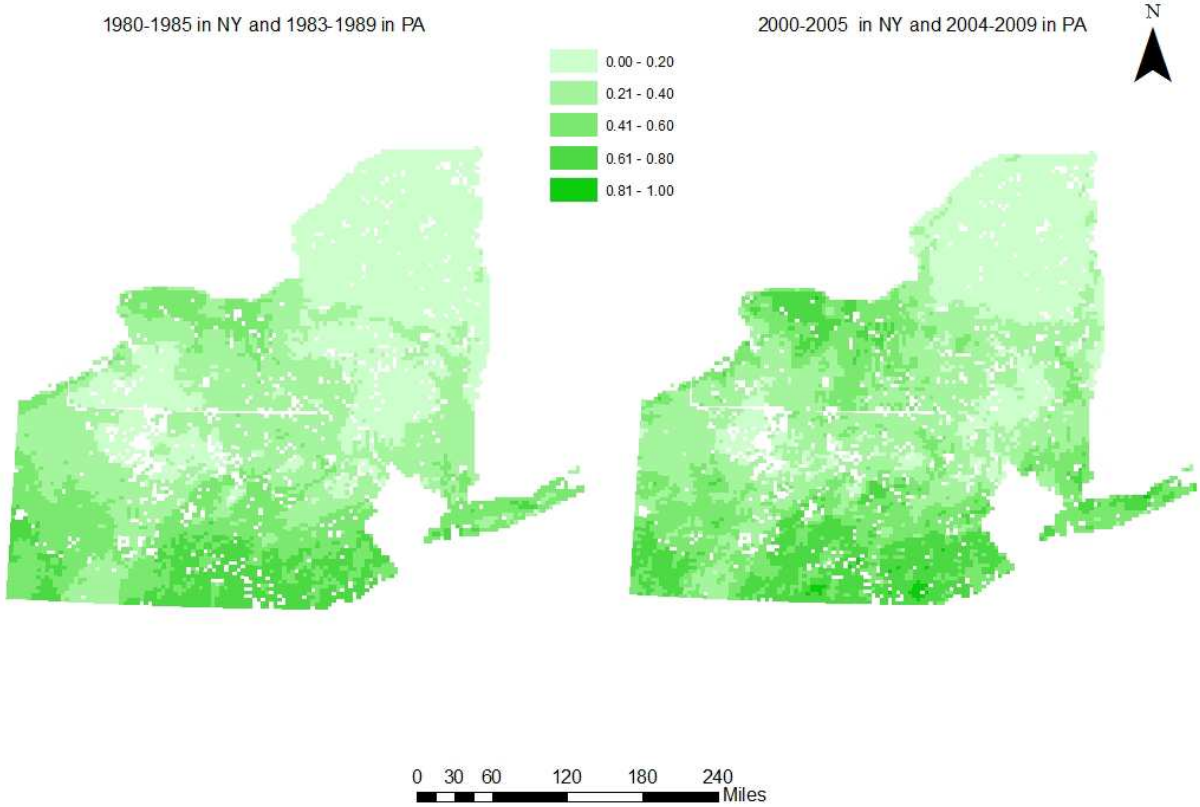
Eastern meadowlark (Sturnella magna) occupancy probability



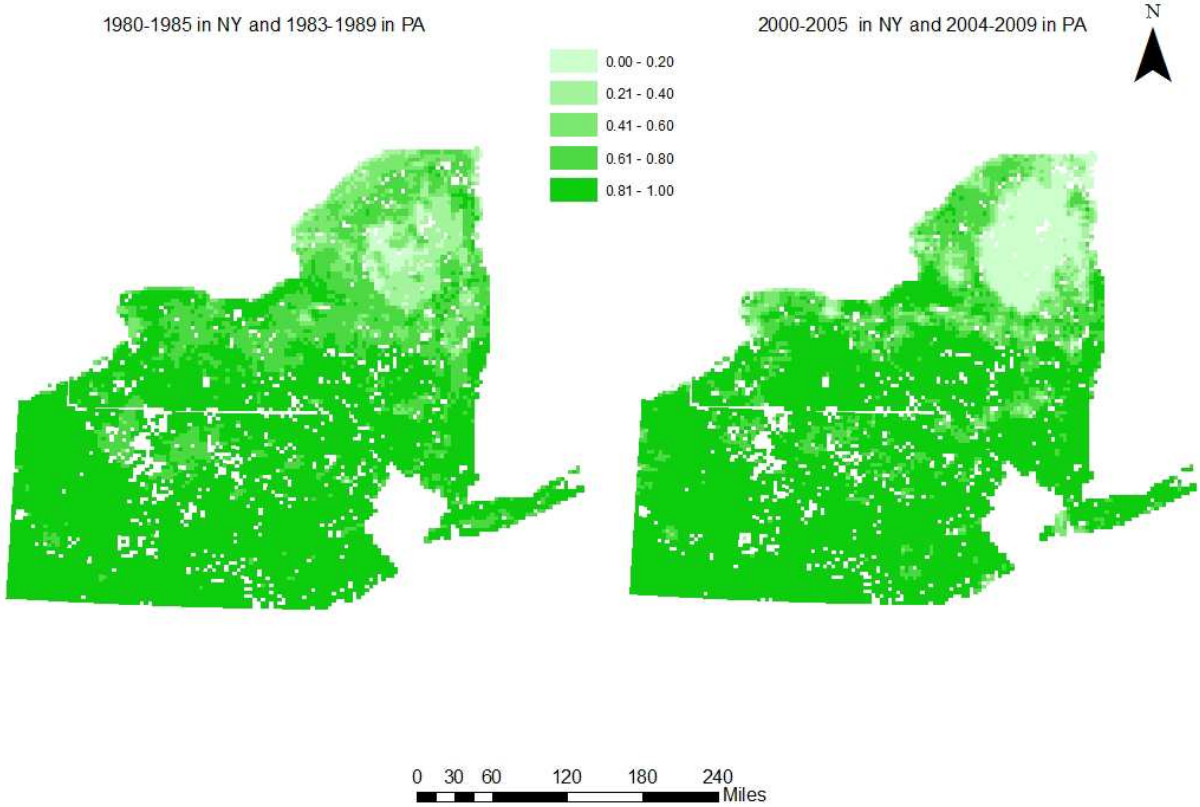
Eastern phoebe (Sayornis phoebe) occupancy probability



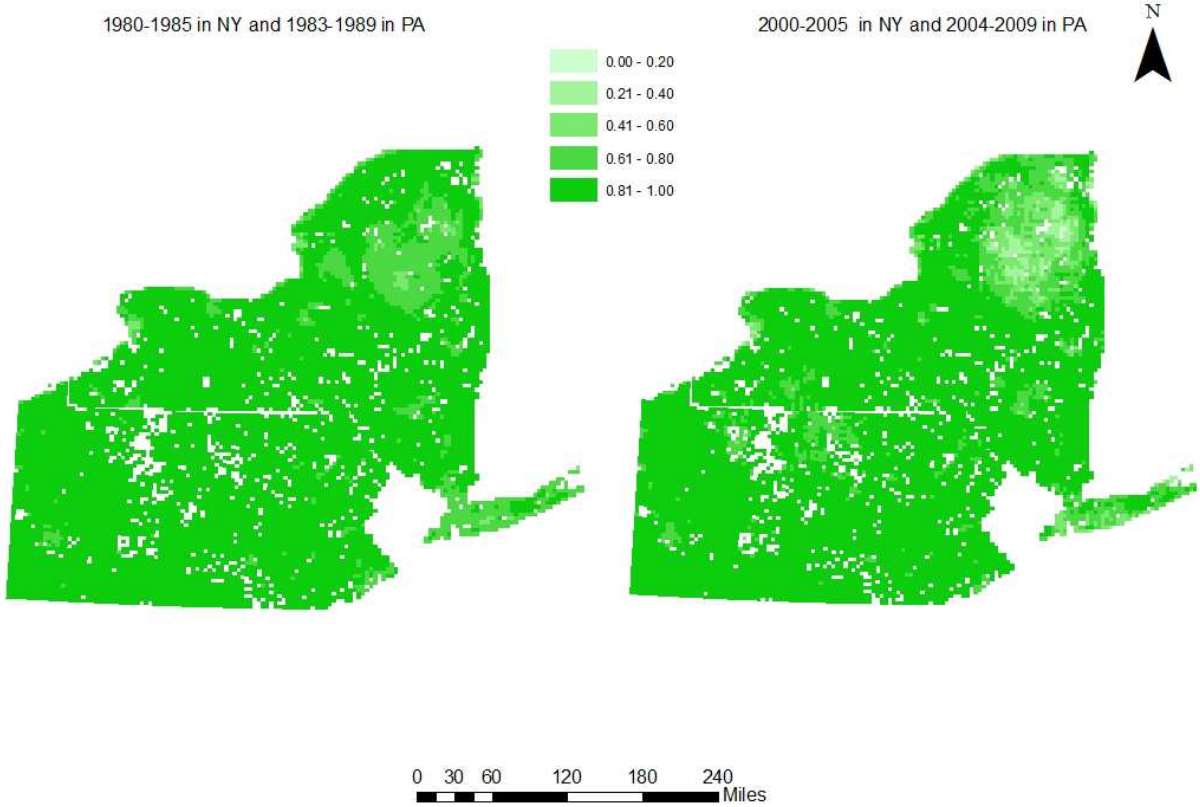
Eastern screech-owl (Megascops asio) occupancy probability



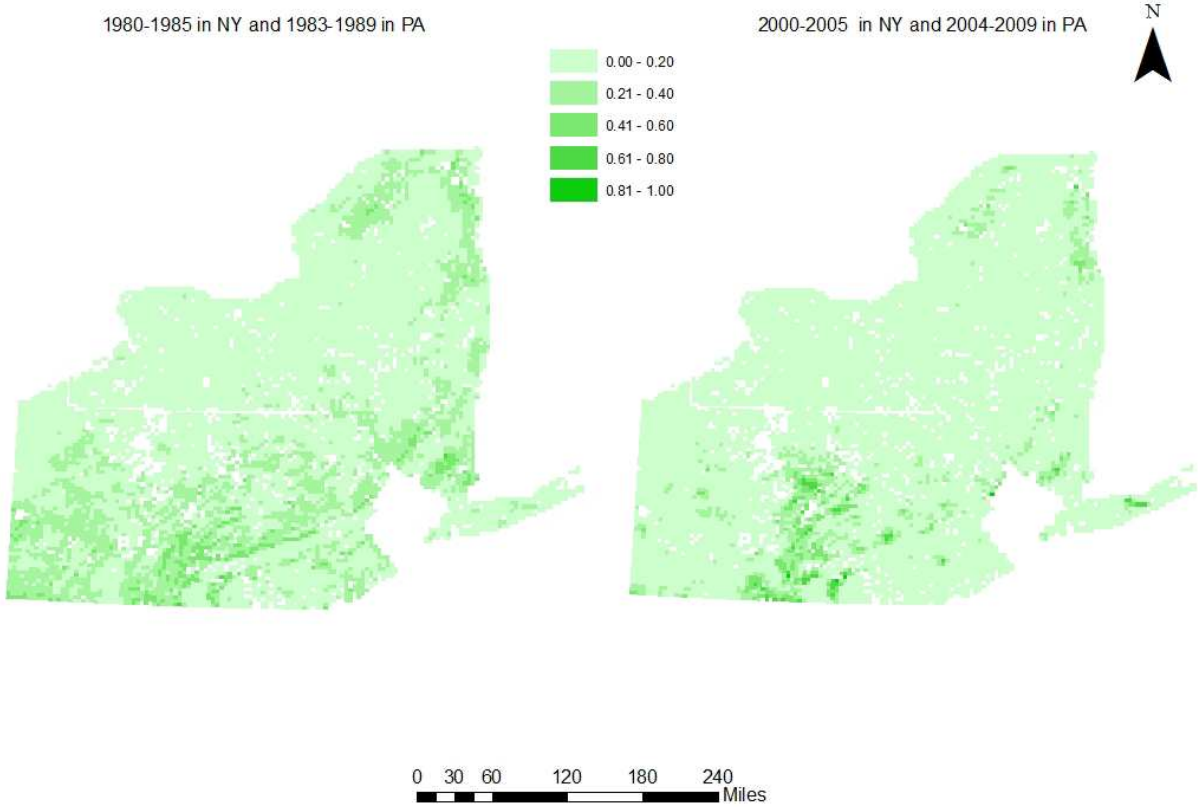
Eastern towhee (Pipilo erythrophthalmus) occupancy probability



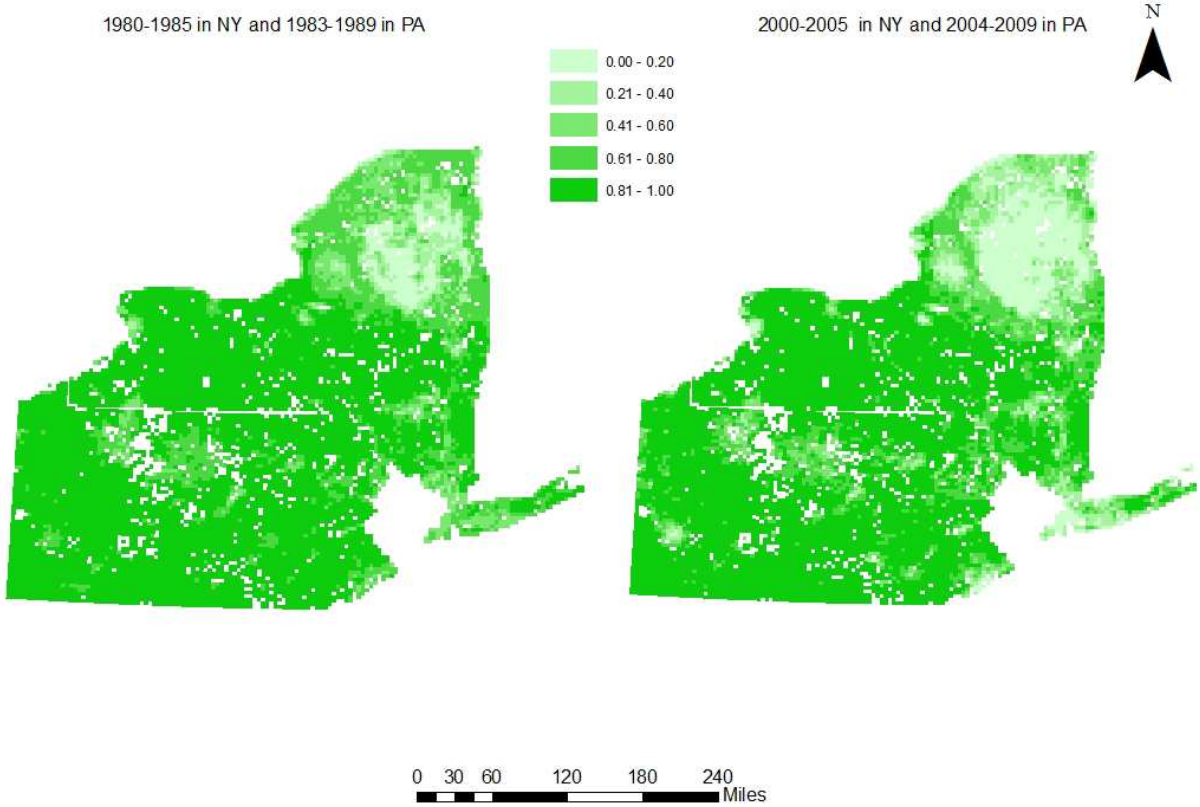
Eastern wood-pewee (Contopus virens) occupancy probability



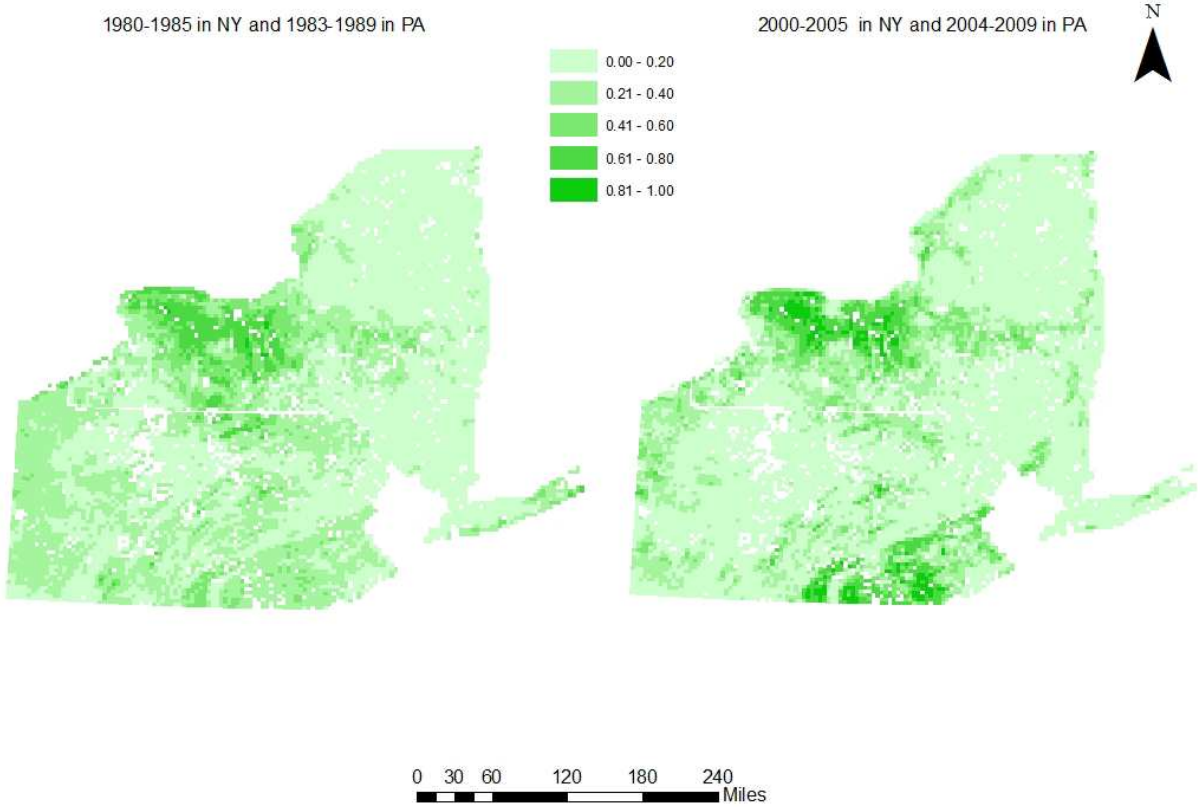
Eastern whip-poor-will (Antrostomus vociferus) occupancy probability



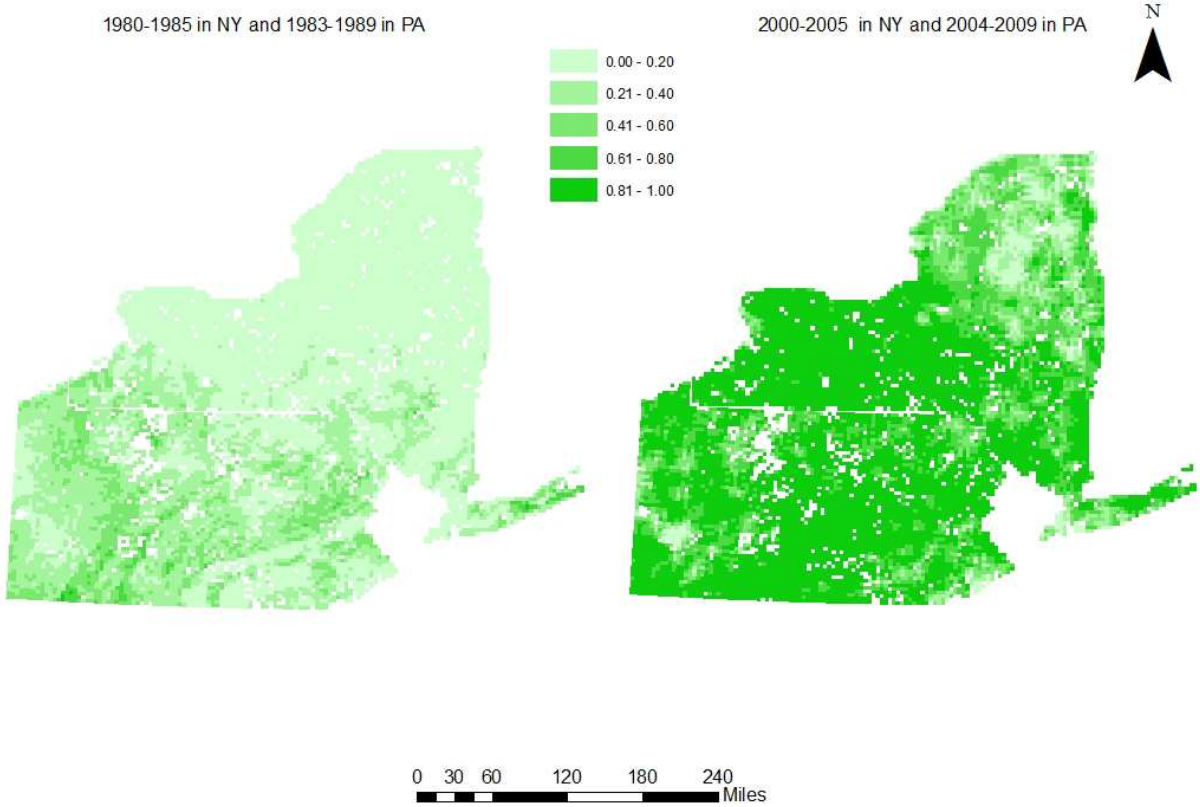
Field sparrow (Spizella pusilla) occupancy probability



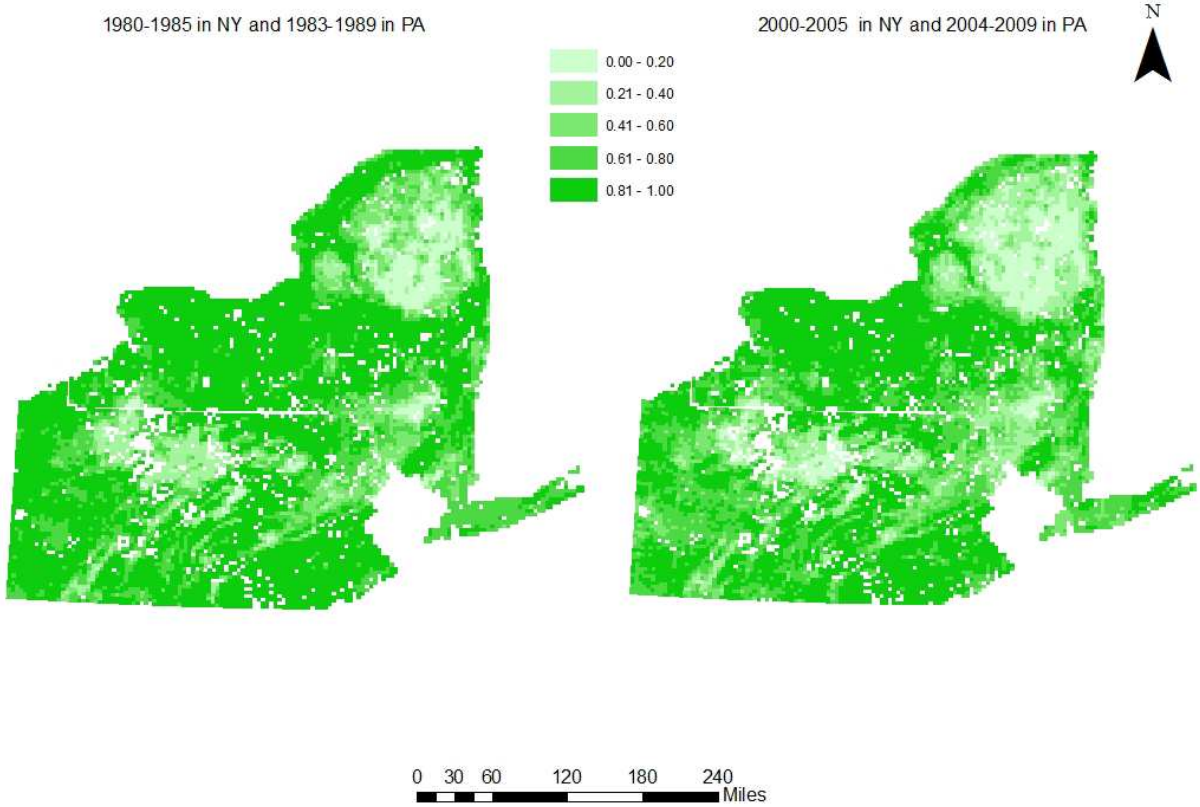
Great blue heron (Ardea herodias) occupancy probability



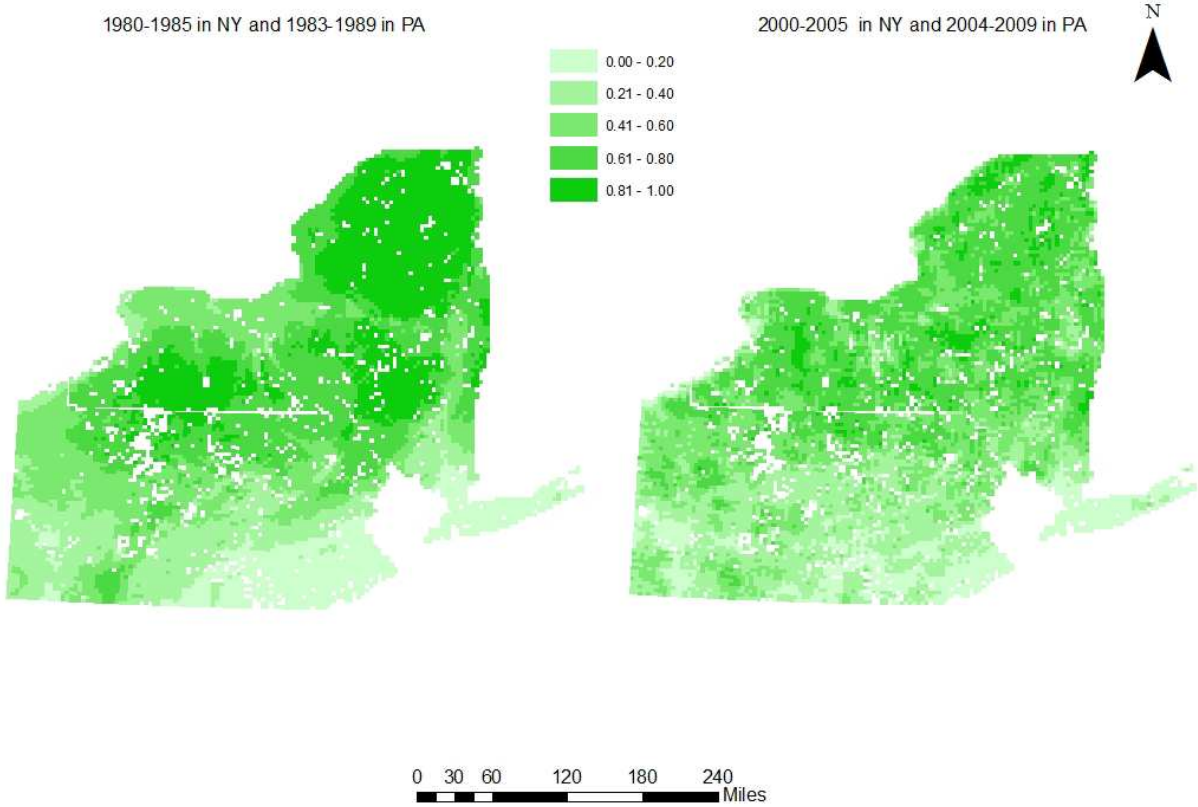
Great crested flycatcher (Myiarchus crinitus) occupancy probability



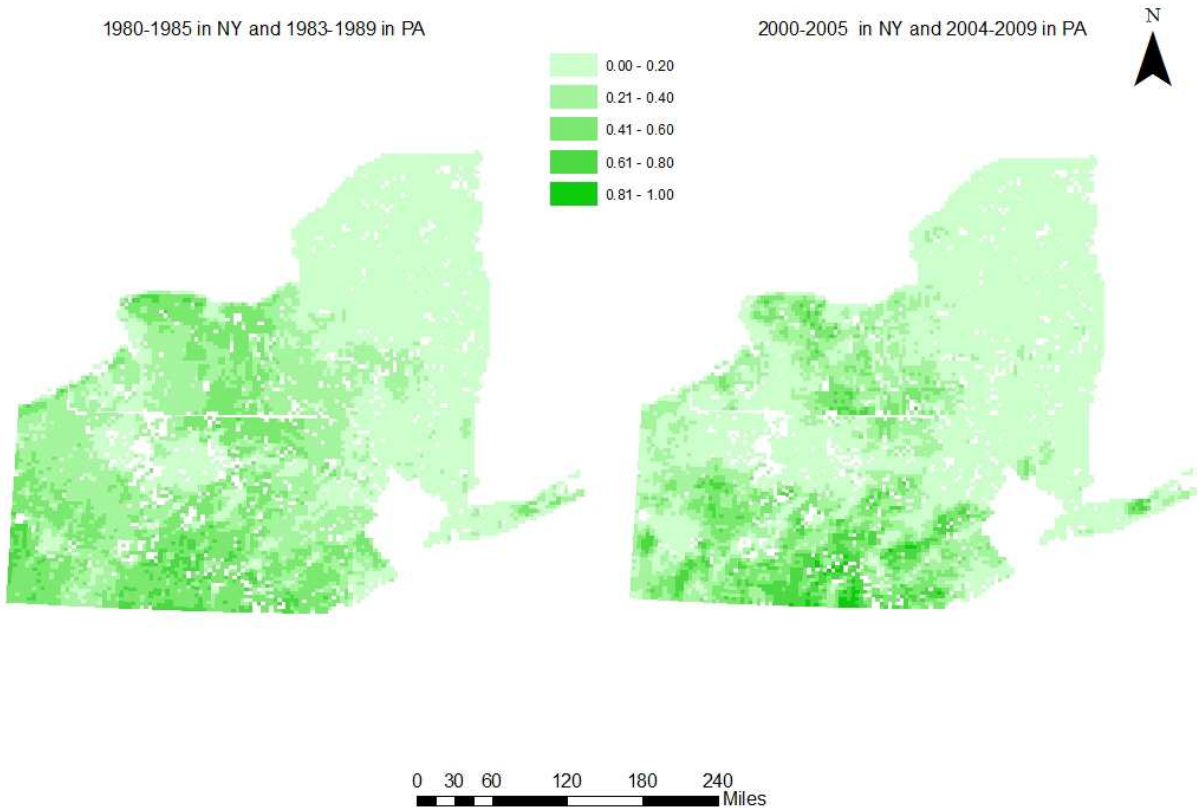
Great horned owl (Bubo virginianus) occupancy probability



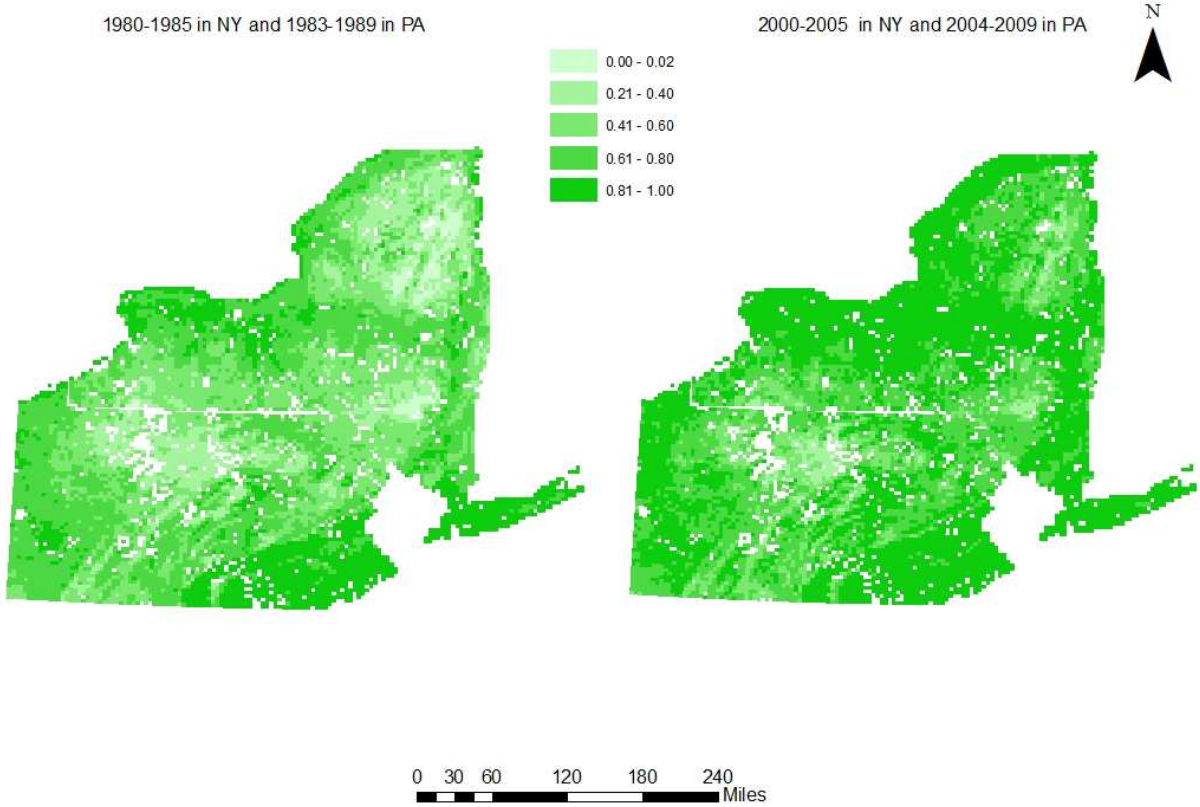
Green heron (Butorides virescens) occupancy probability



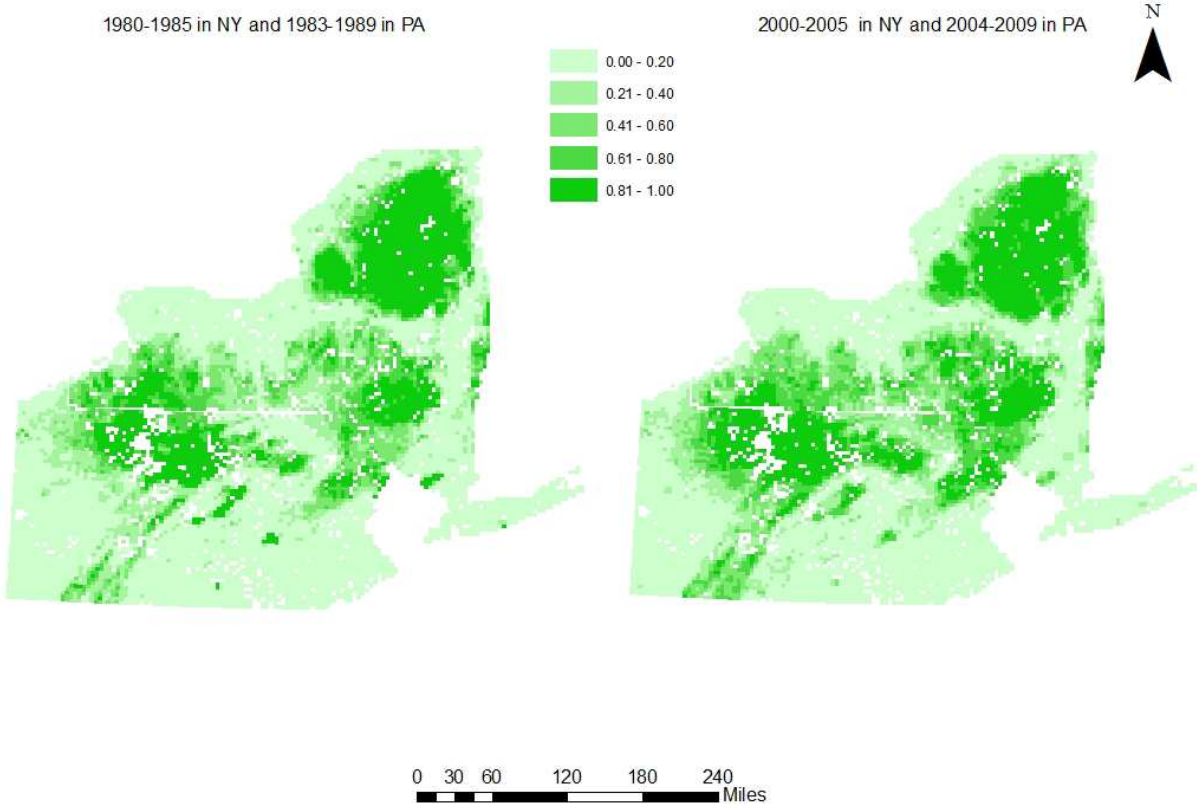
Grasshopper sparrow (Ammodramus savannarum) occupancy probability



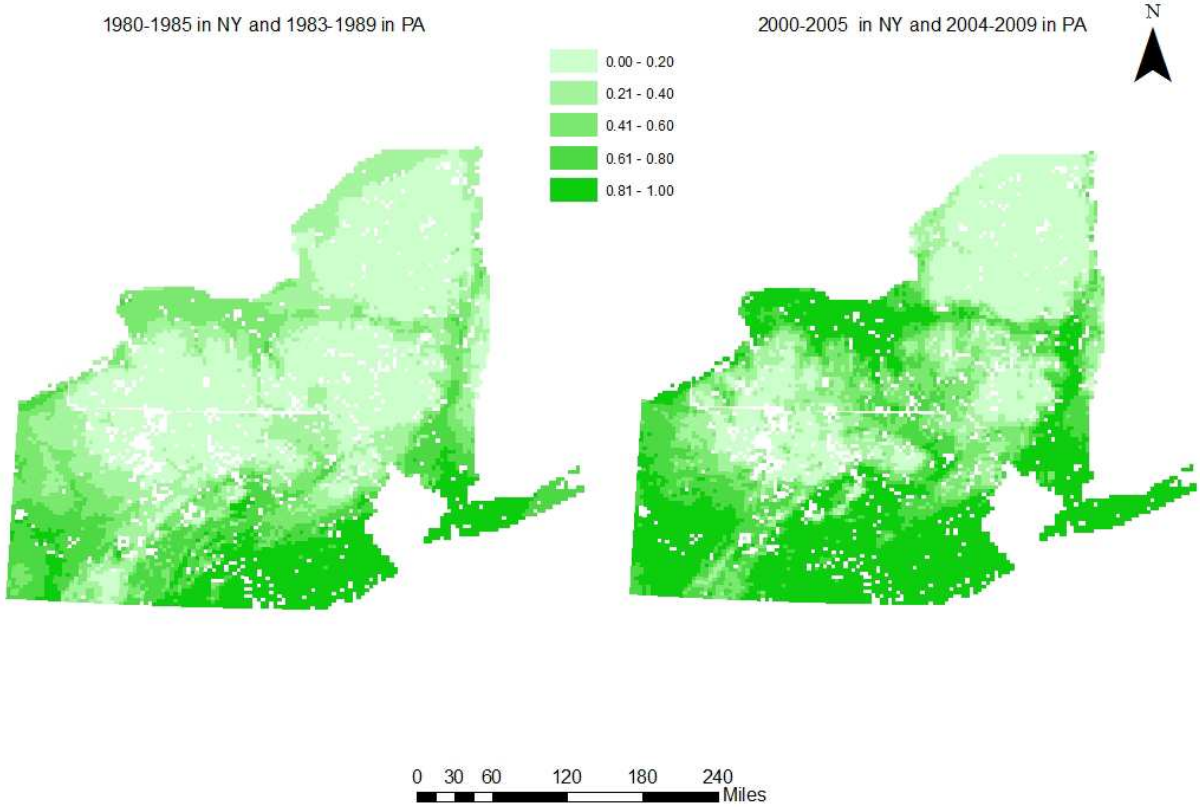
Hairy woodpecker (Picoides villosus) occupancy probability



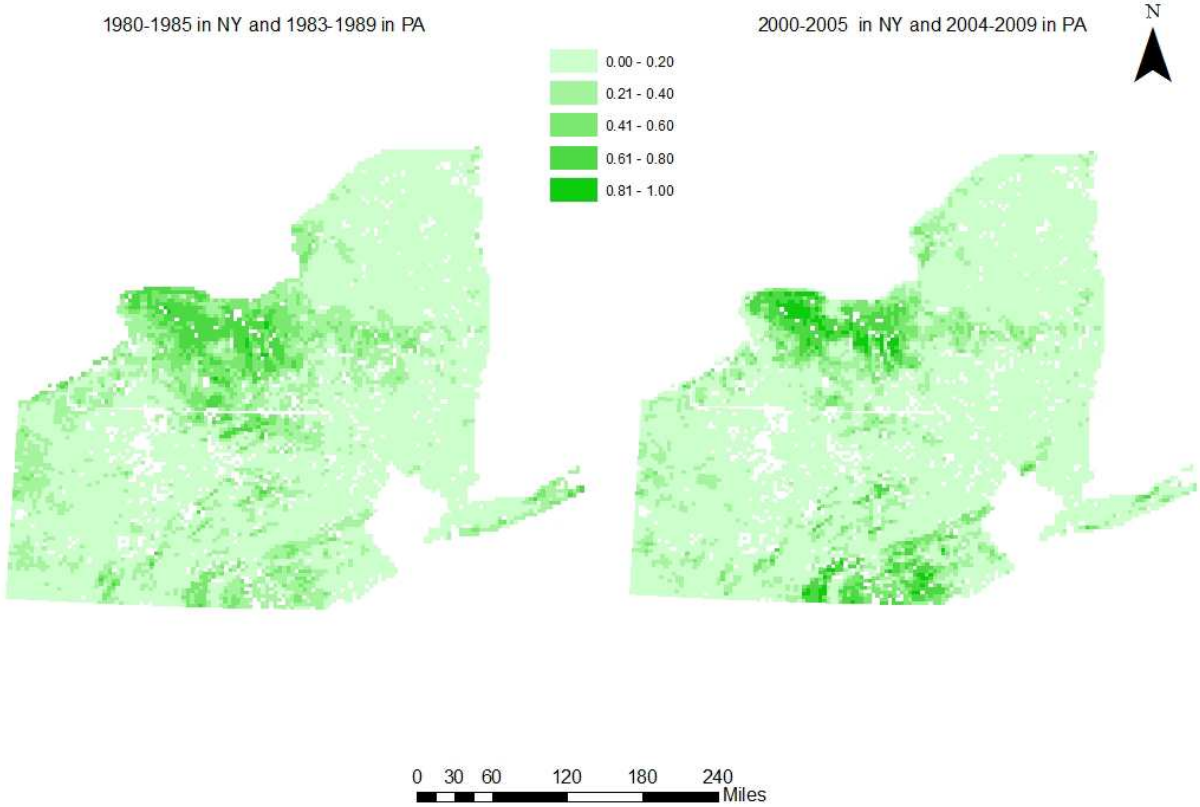
Hermit thrush (Catharus guttatus) occupancy probability



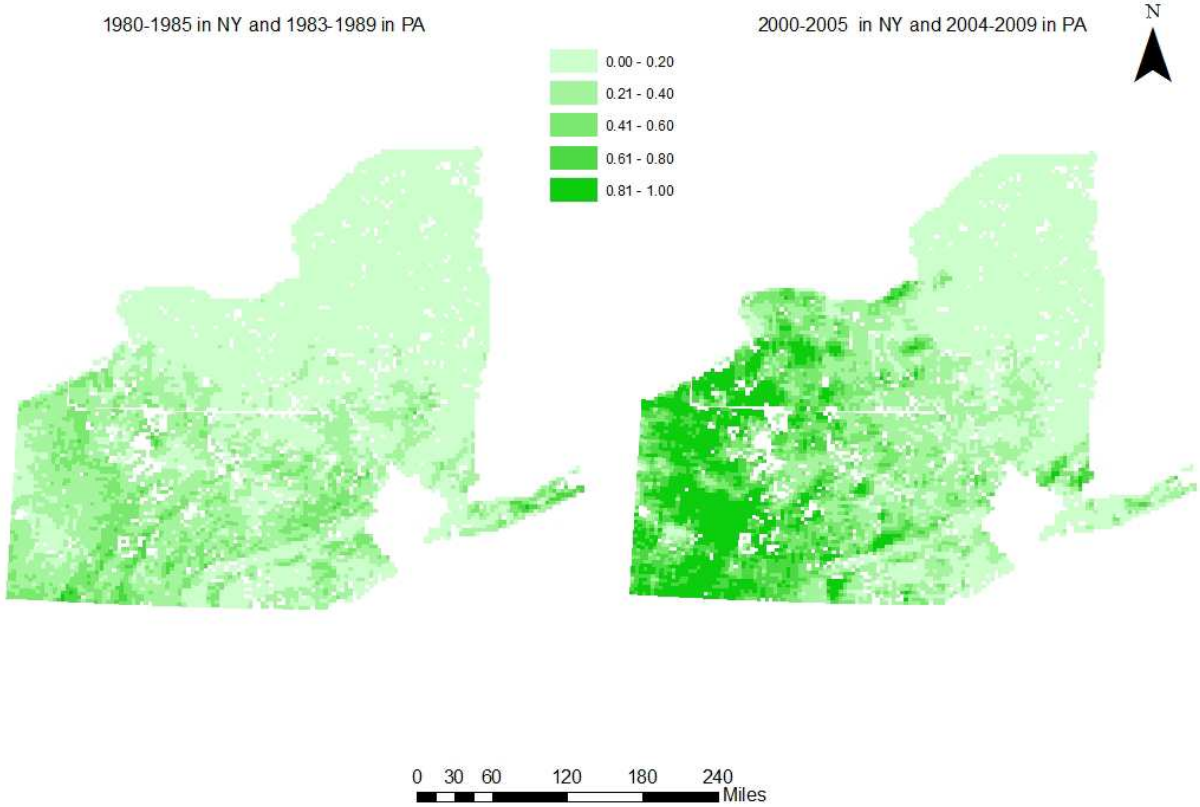
House finch (Haemorhous mexicanus) occupancy probability



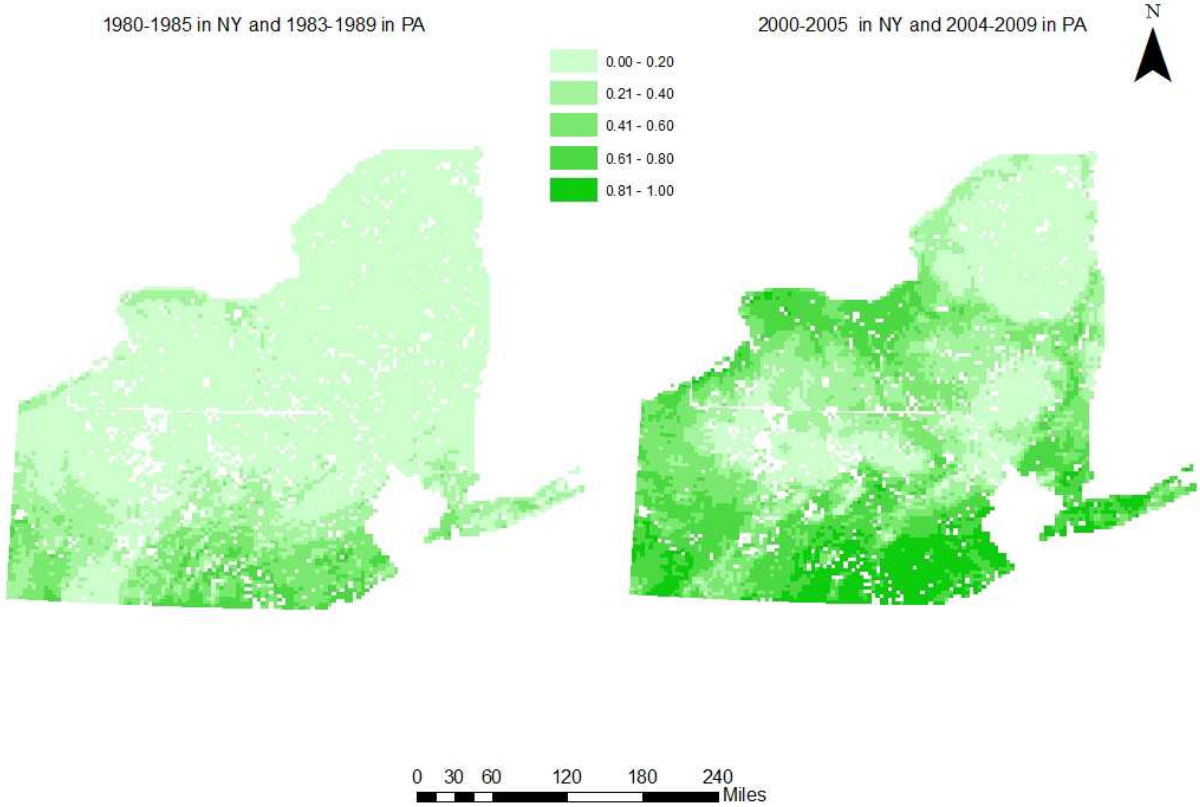
Horned lark (Eremophila alpestris) occupancy probability



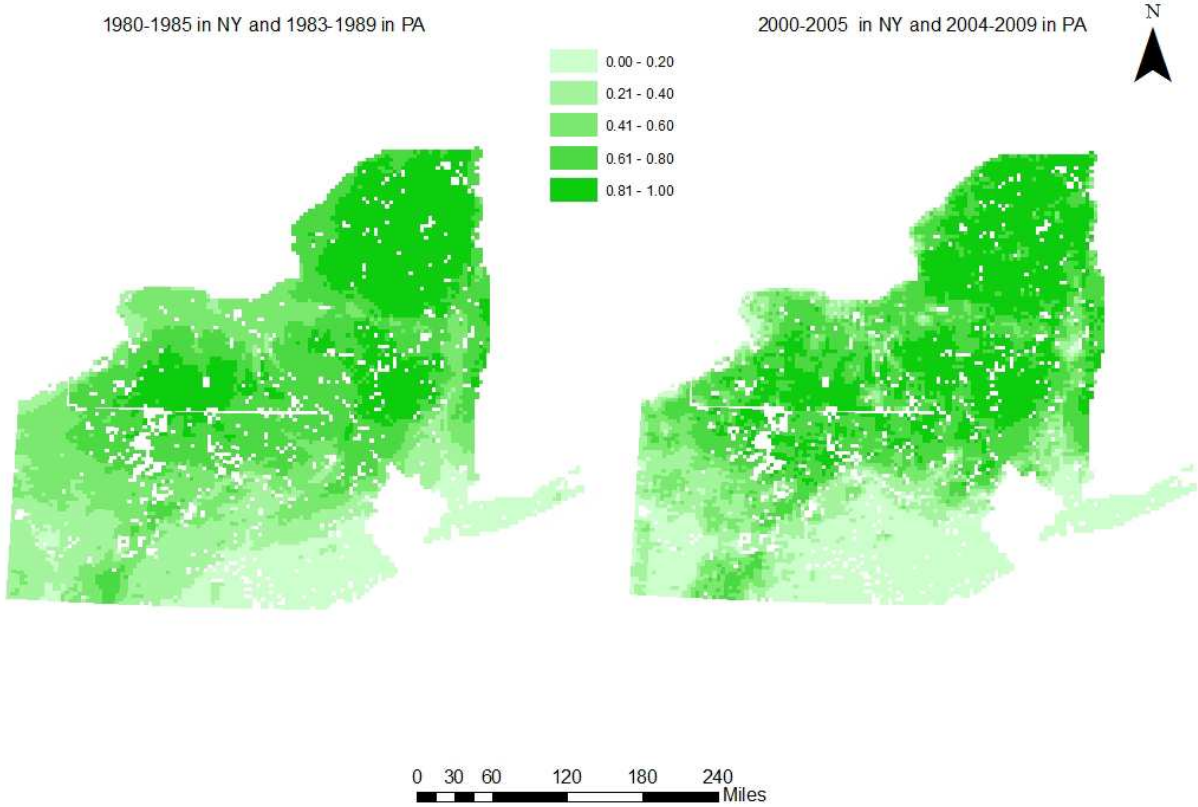
Hooded warbler (Setophaga citrina) occupancy probability



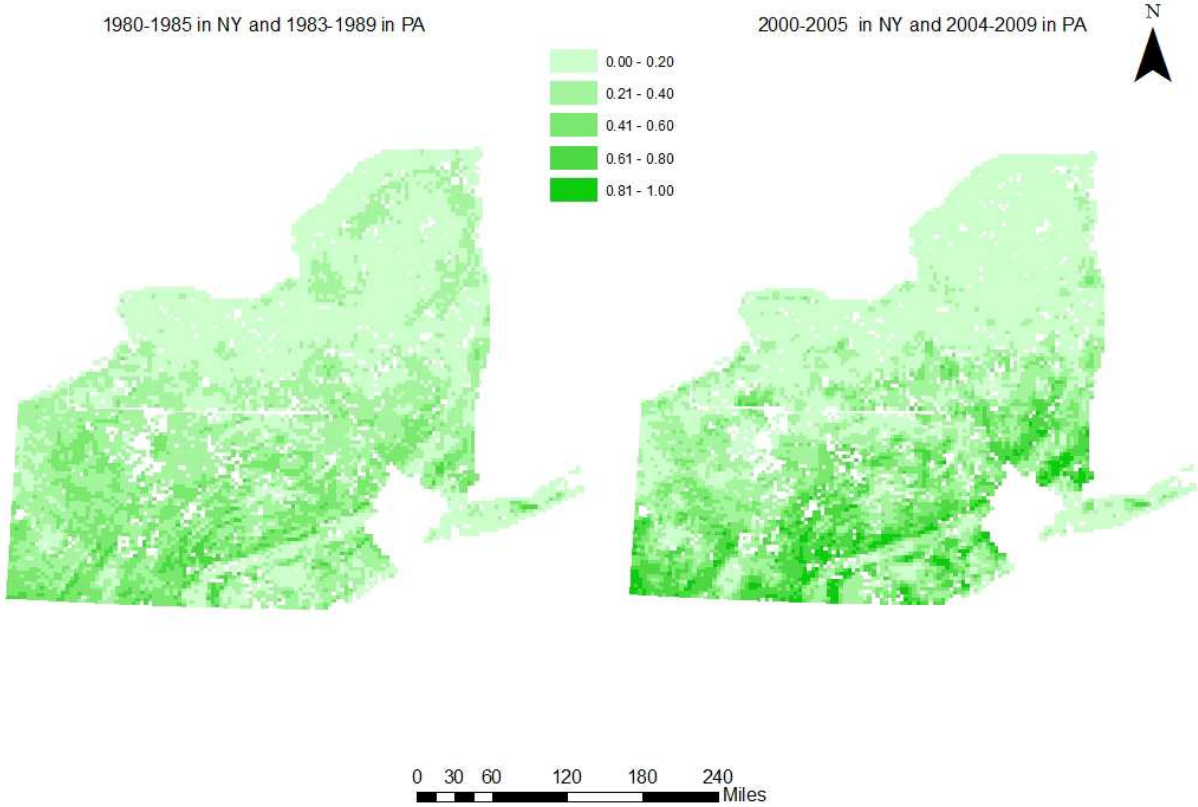
Killdeer (Charadrius vociferus) occupancy probability



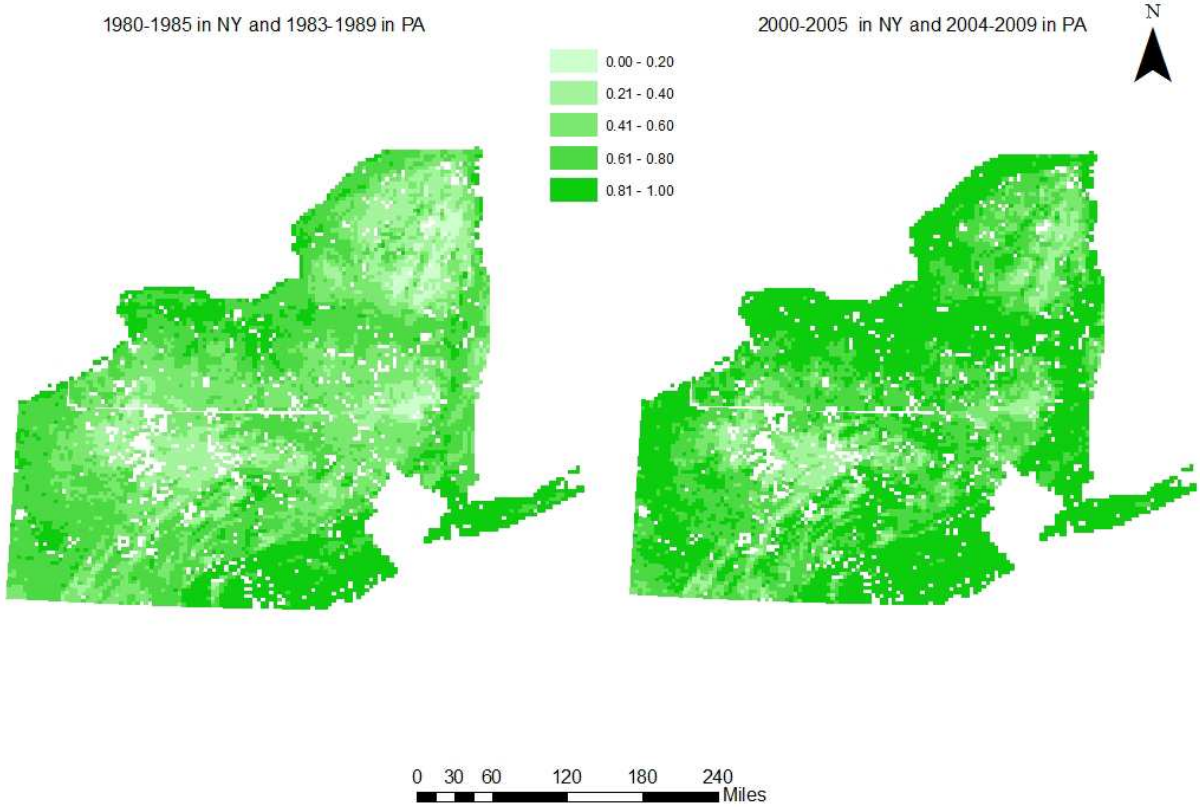
Least flycatcher (Empidonax minimus) occupancy probability



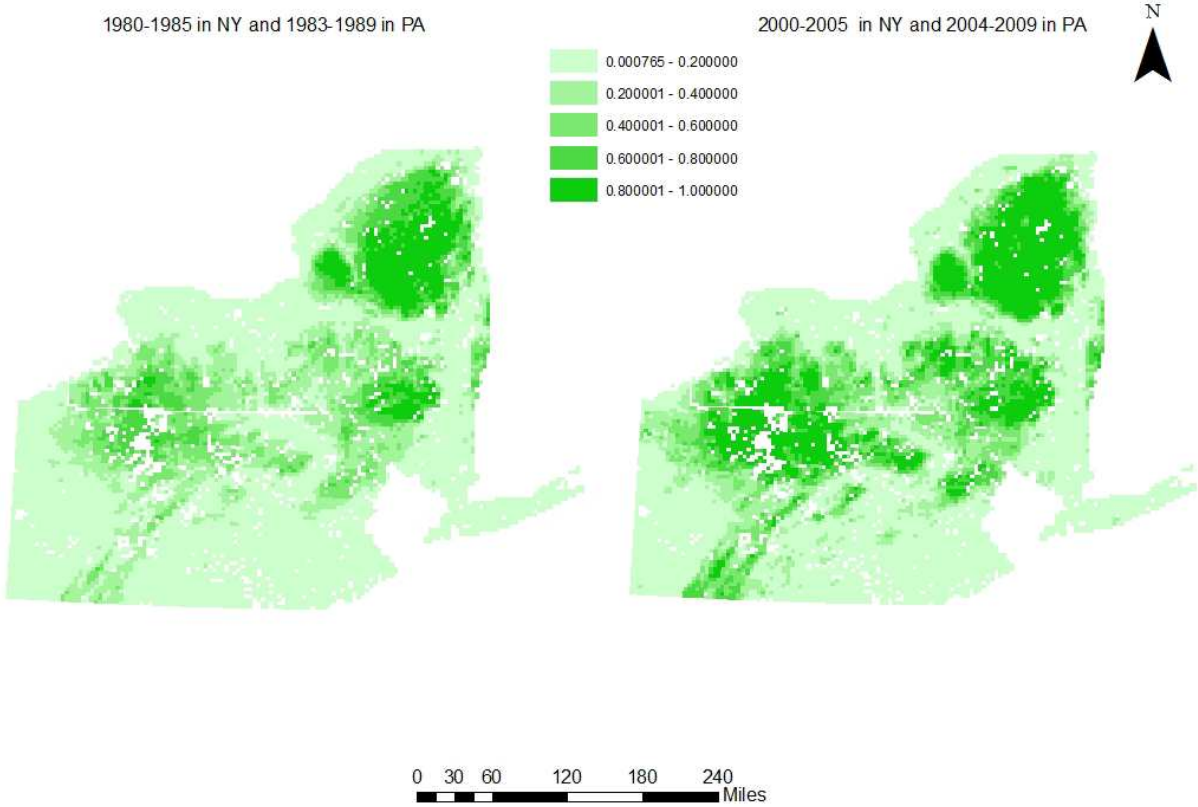
Louisiana waterthrush (Parkesia motacilla) occupancy probability



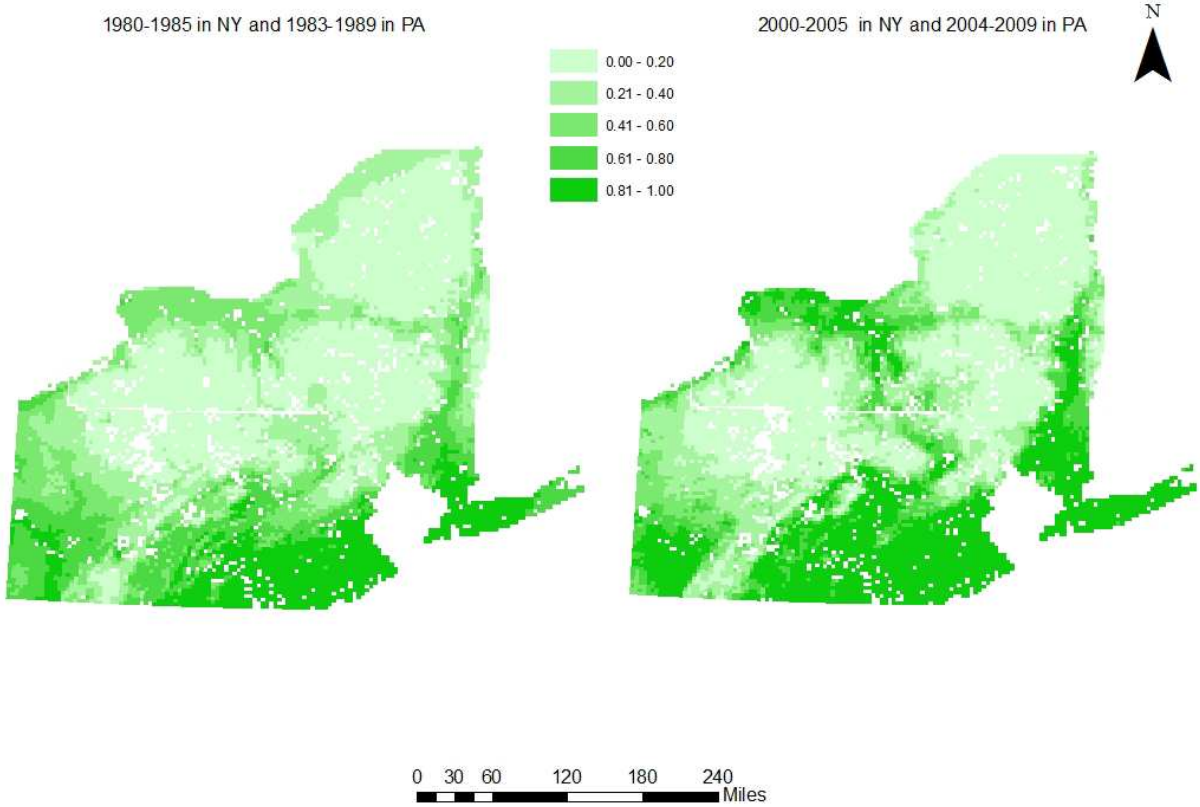
Mallard (Anas platyrhynchos) occupancy probability



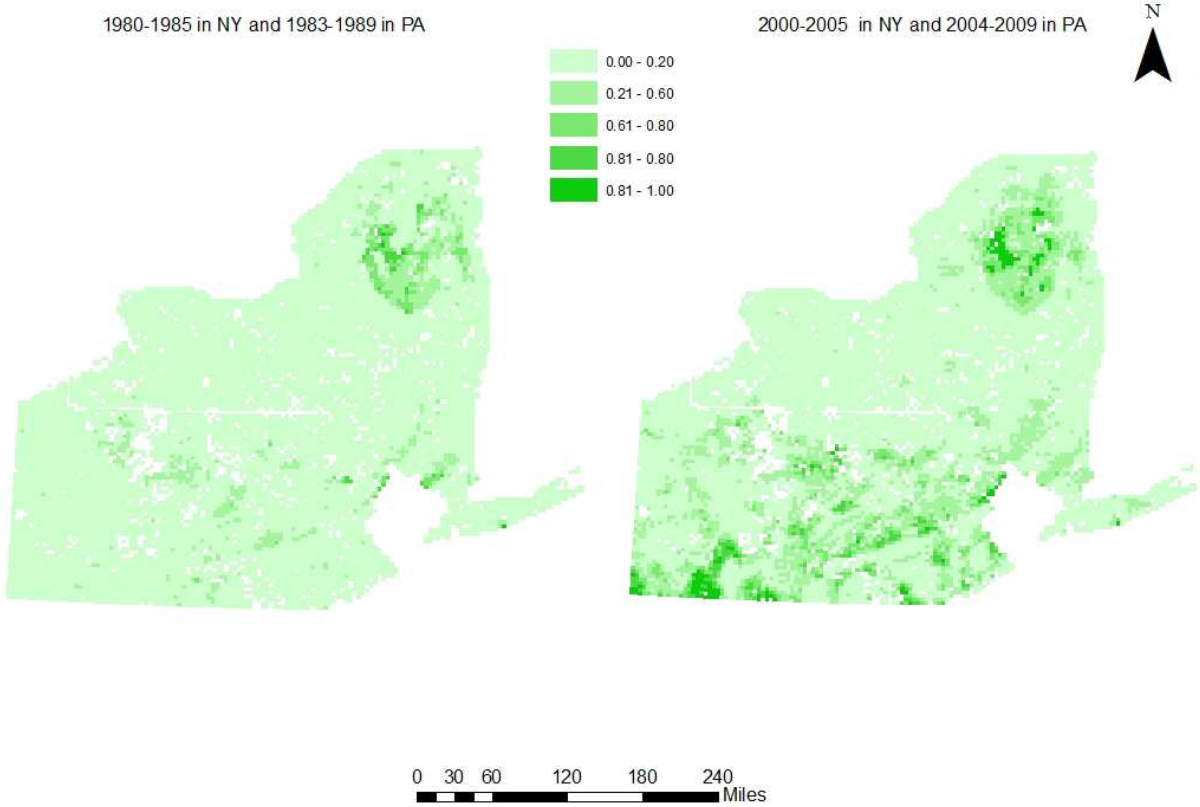
Magnolia warbler (Setophaga magnolia) occupancy probability



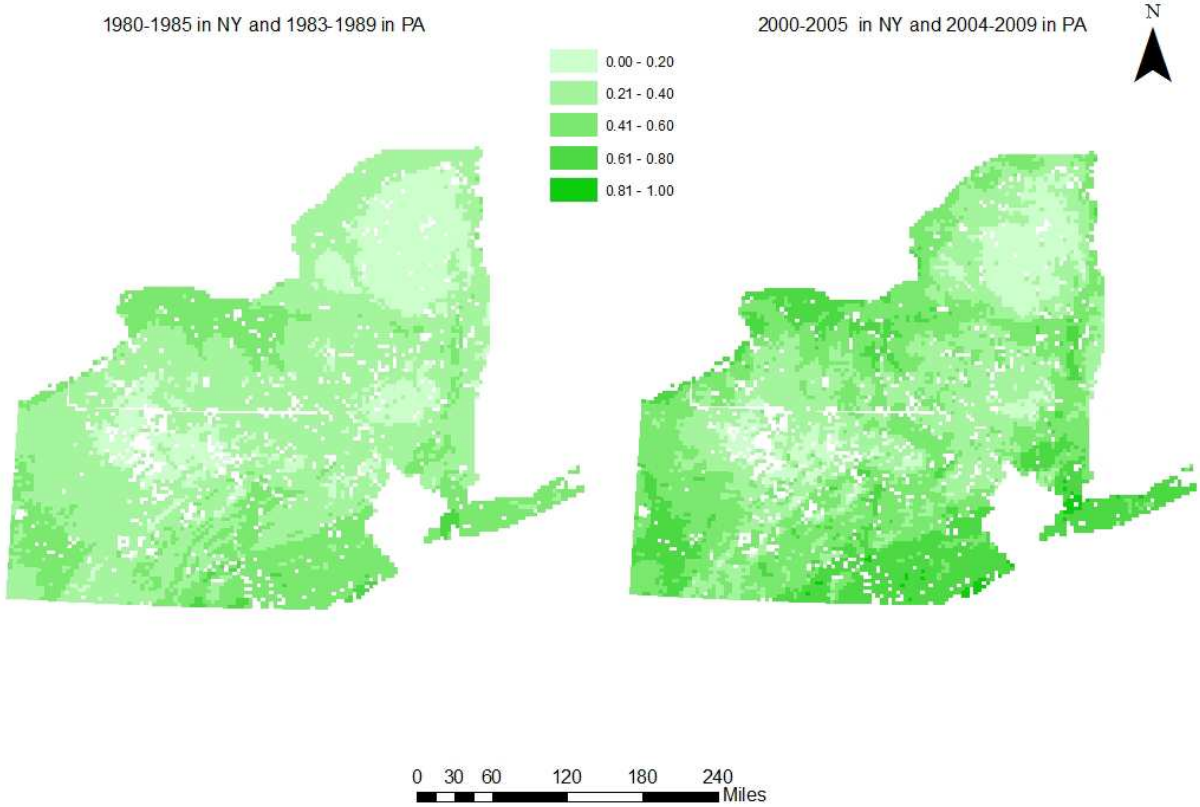
Northern mockingbird (Mimus polyglottos) occupancy probability



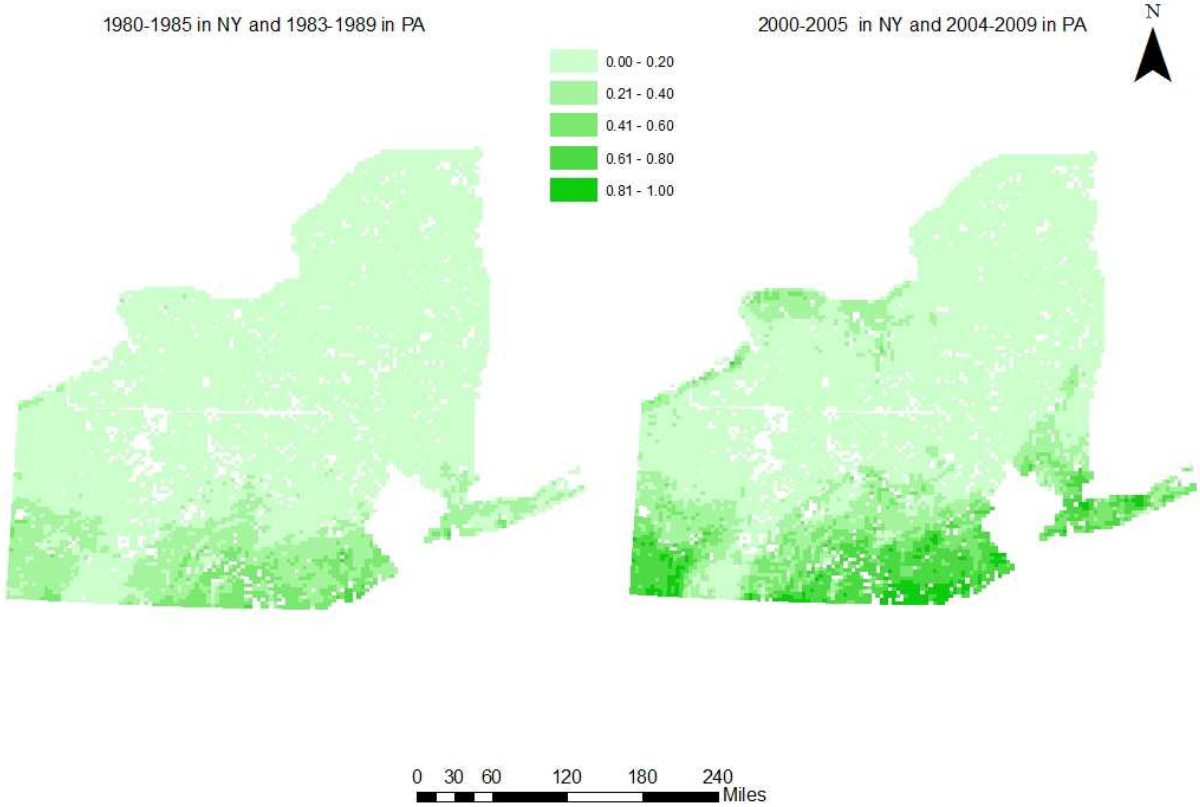
Northern parula (Setophaga americana) occupancy probability



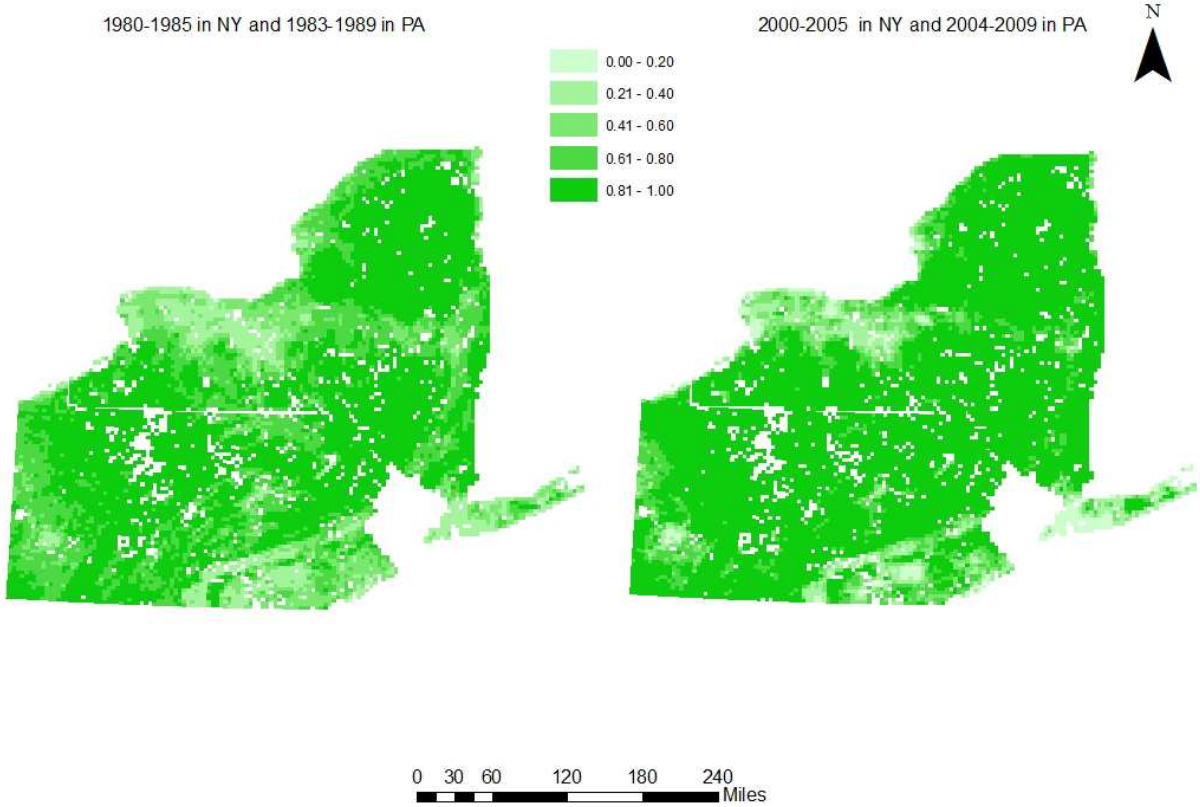
Northern rough-winged swallow (Stelgidopteryx serripennis) occupancy probability



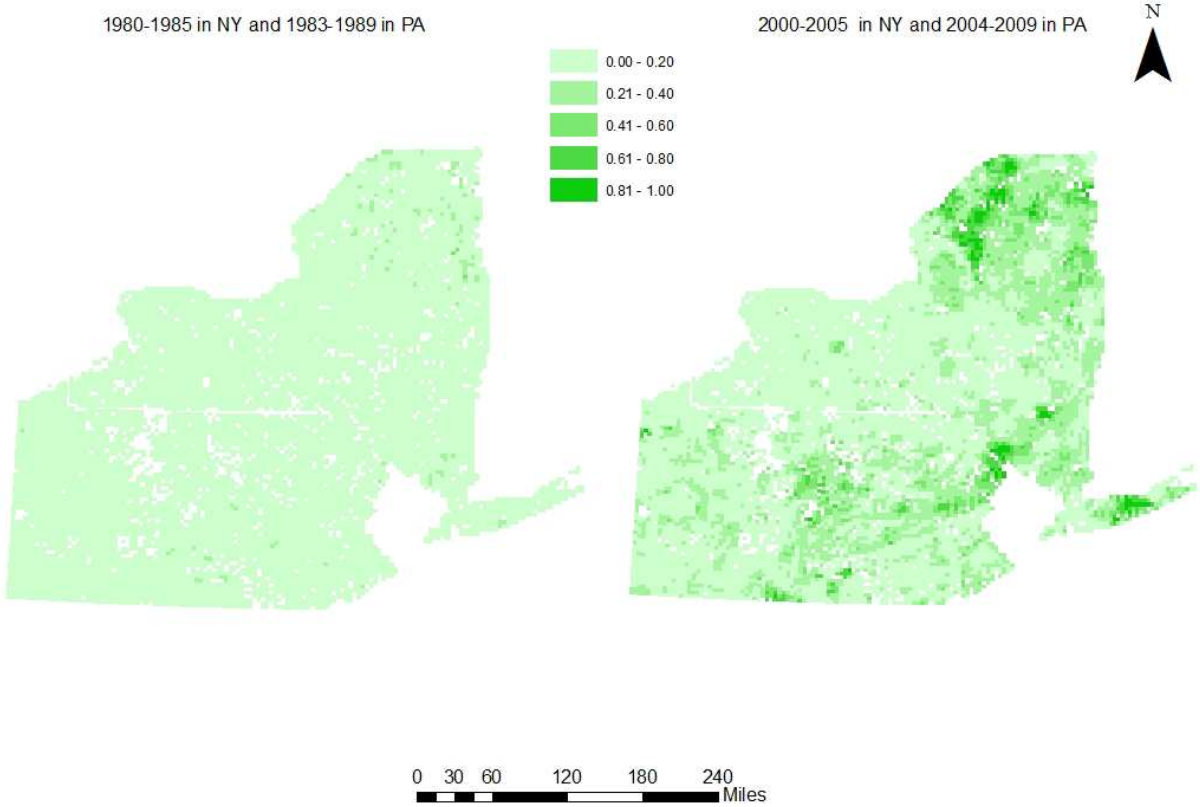
Orchard oriole (Icterus spurius) occupancy probability



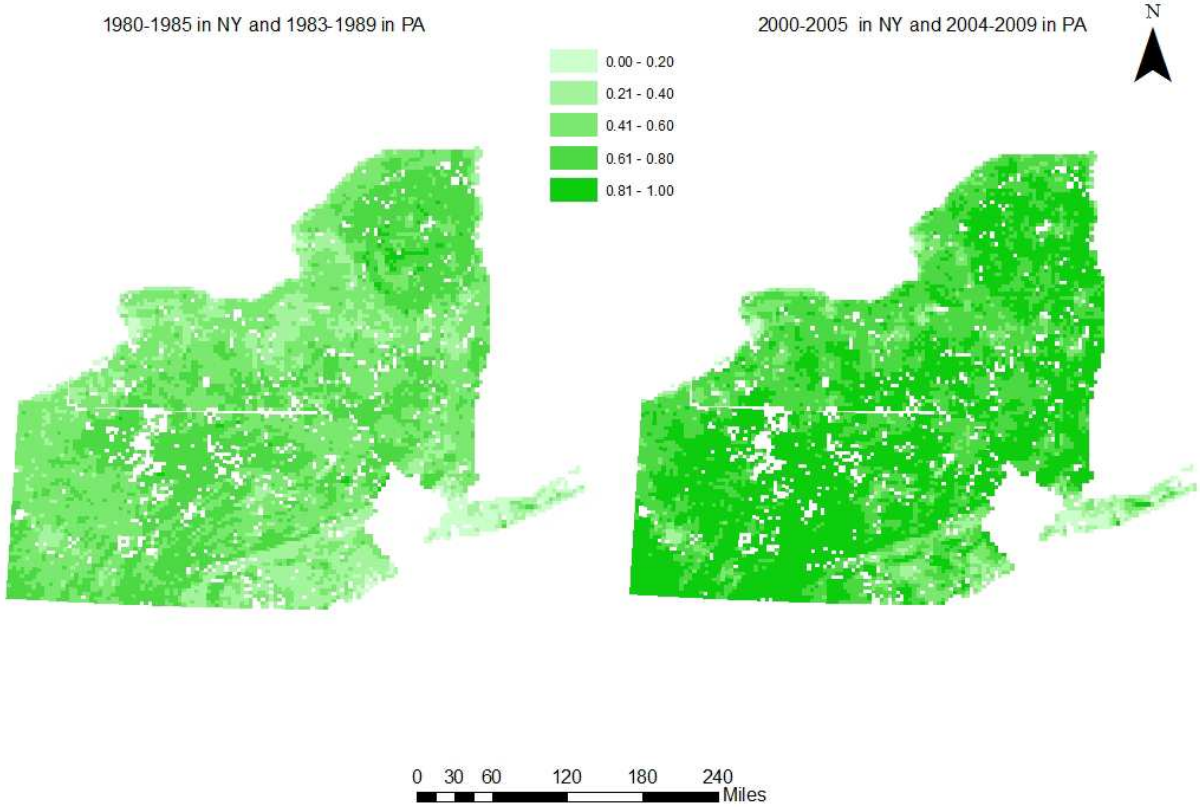
Ovenbird (Seiurus aurocapilla) occupancy probability



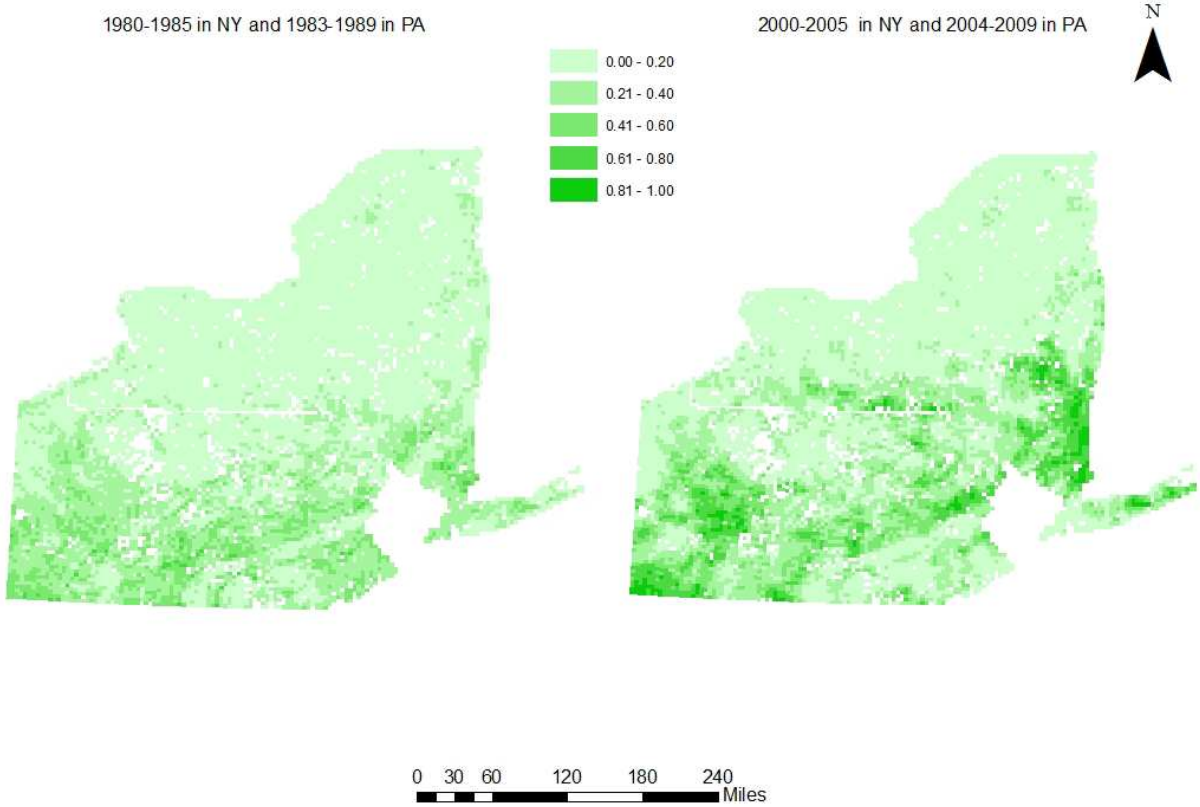
Pine warbler (Setophaga pinus) occupancy probability



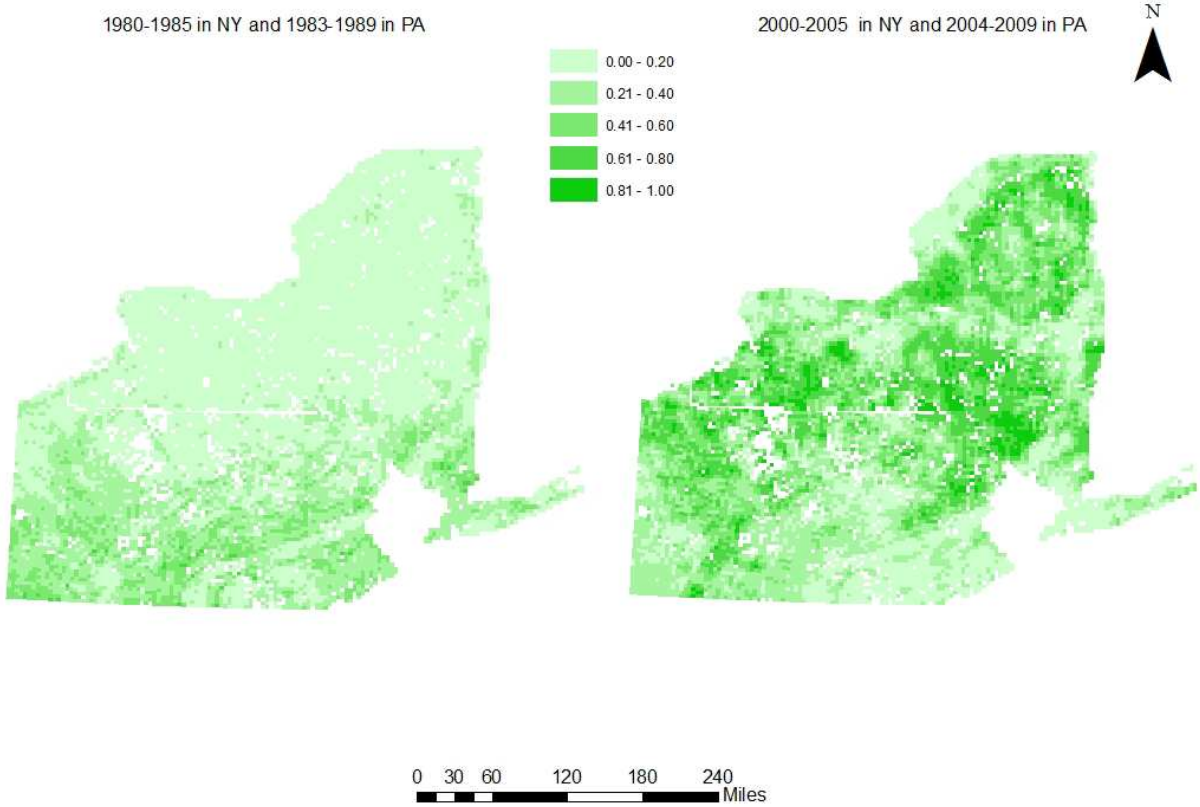
Pileated woodpecker (Dryocopus pileatus) occupancy probability



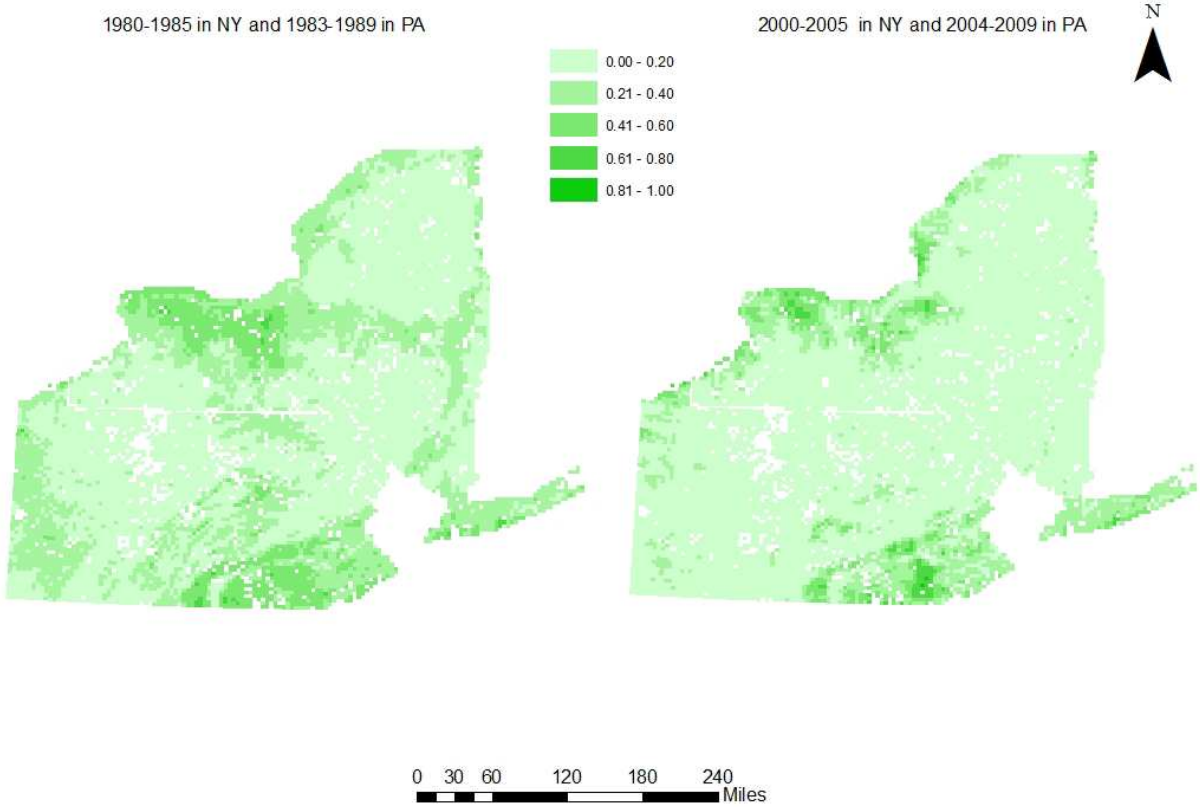
Prairie warbler (Setophaga discolor) occupancy probability



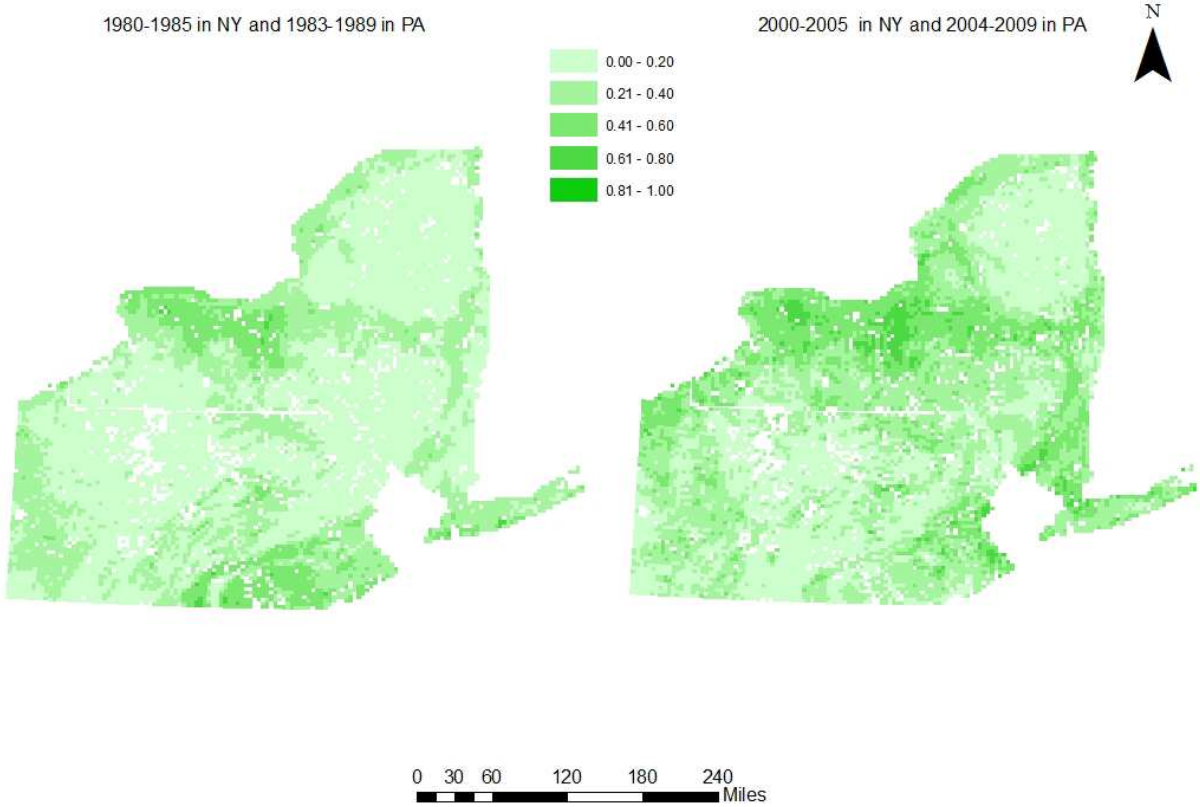
Purple finch (Haemorhous purpureus) occupancy probability



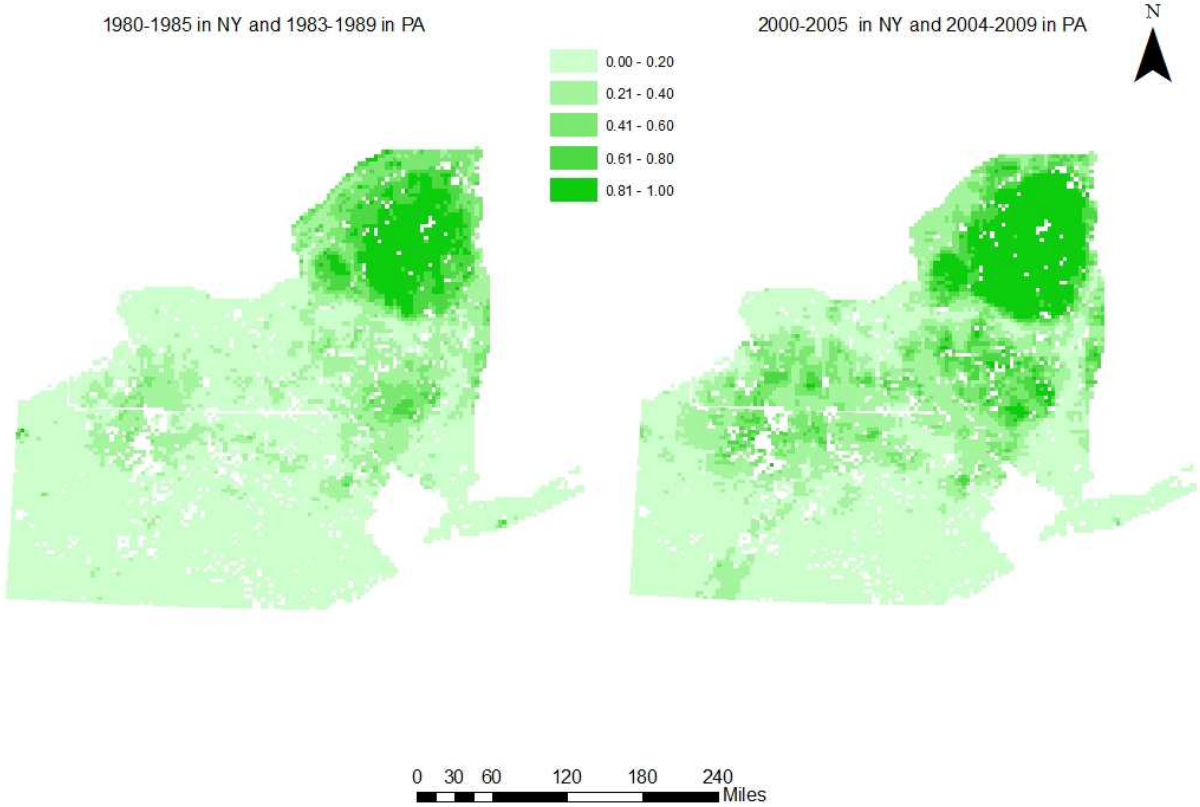
Purple martin (Progne subis) occupancy probability



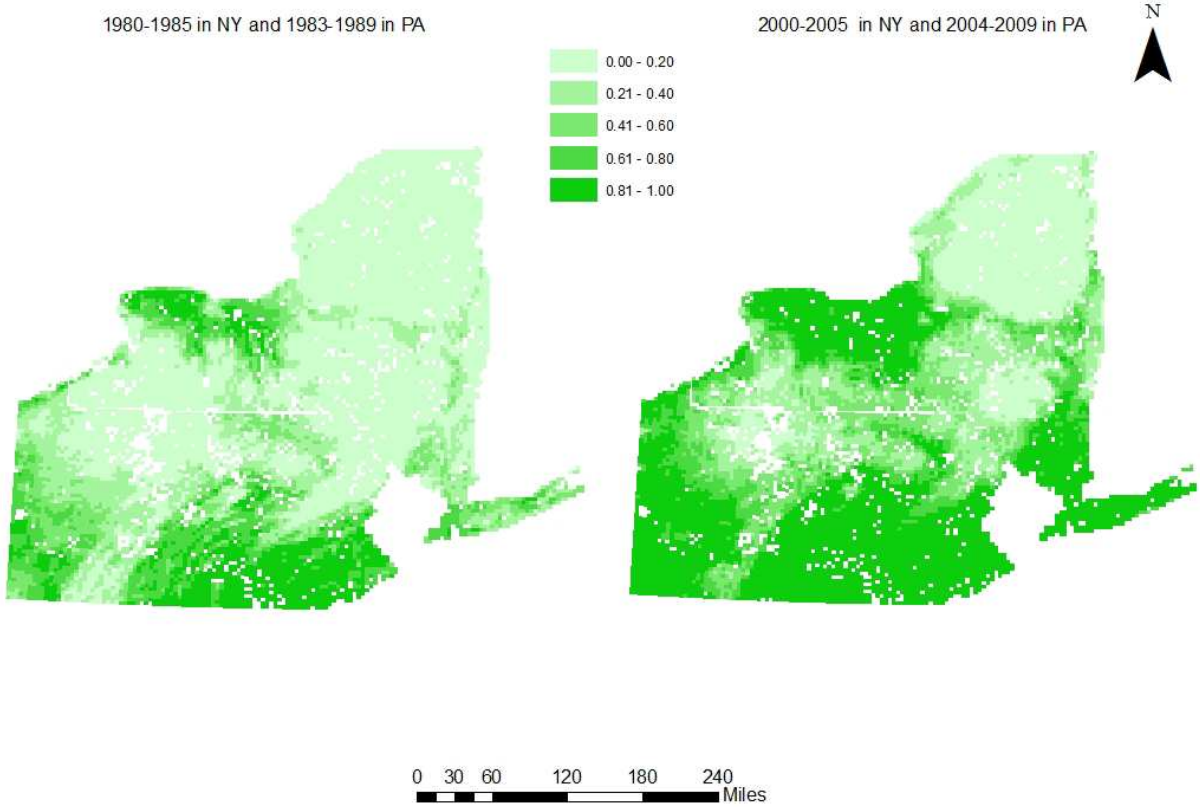
Rose-breasted grosbeak (Pheucticus ludovicianus) occupancy probability



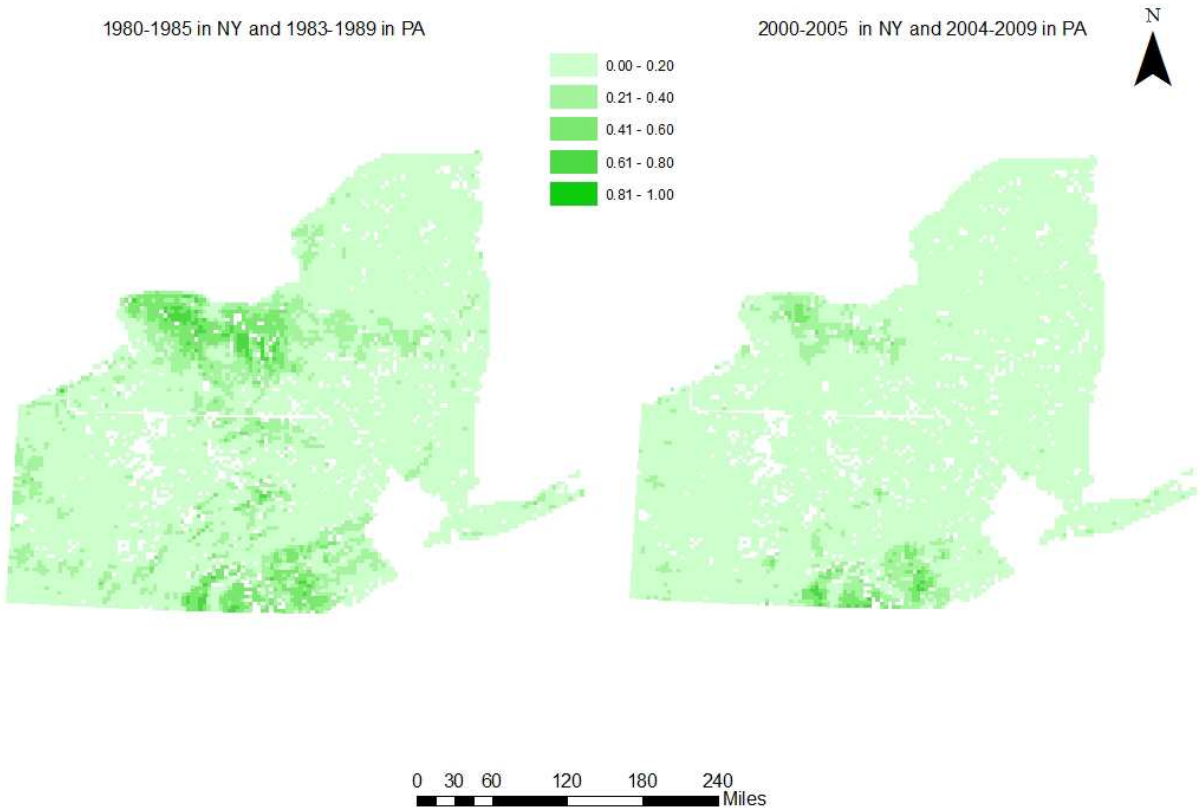
Red-breasted nuthatch (Sitta canadensis) occupancy probability



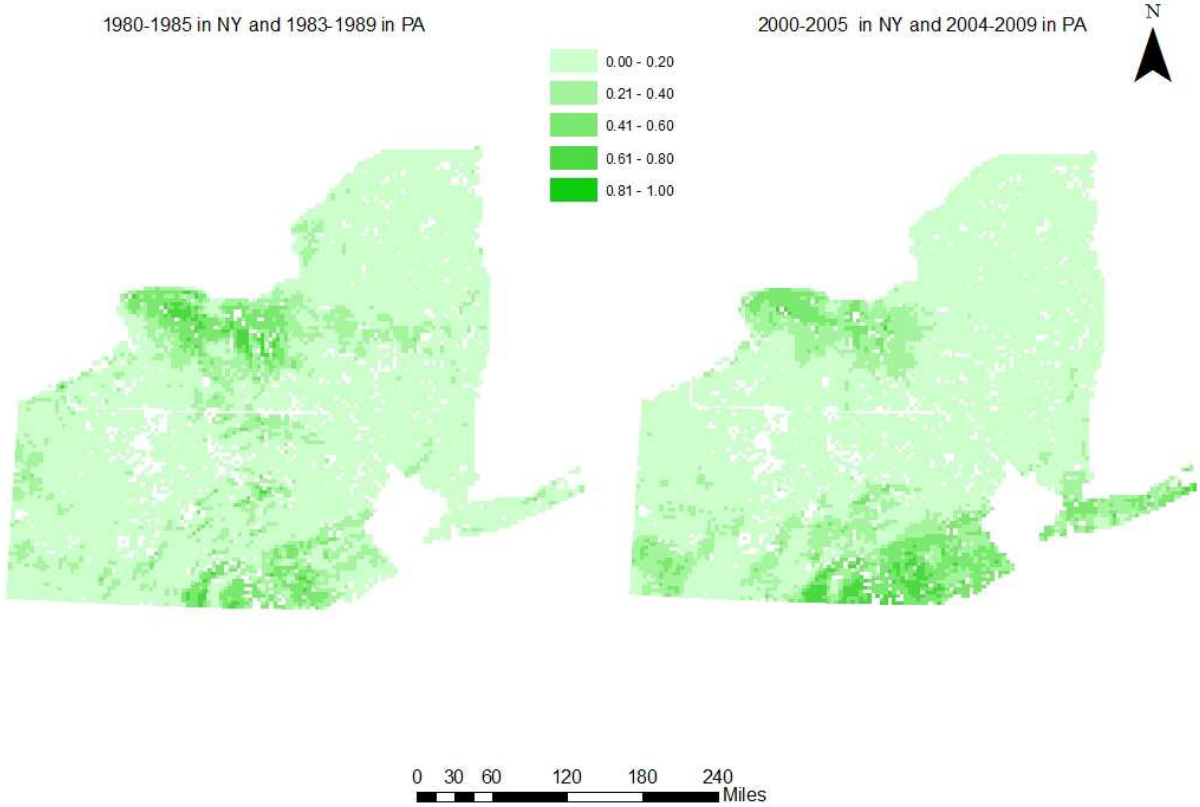
Red-bellied woodpecker (Melanerpes carolinus) occupancy probability



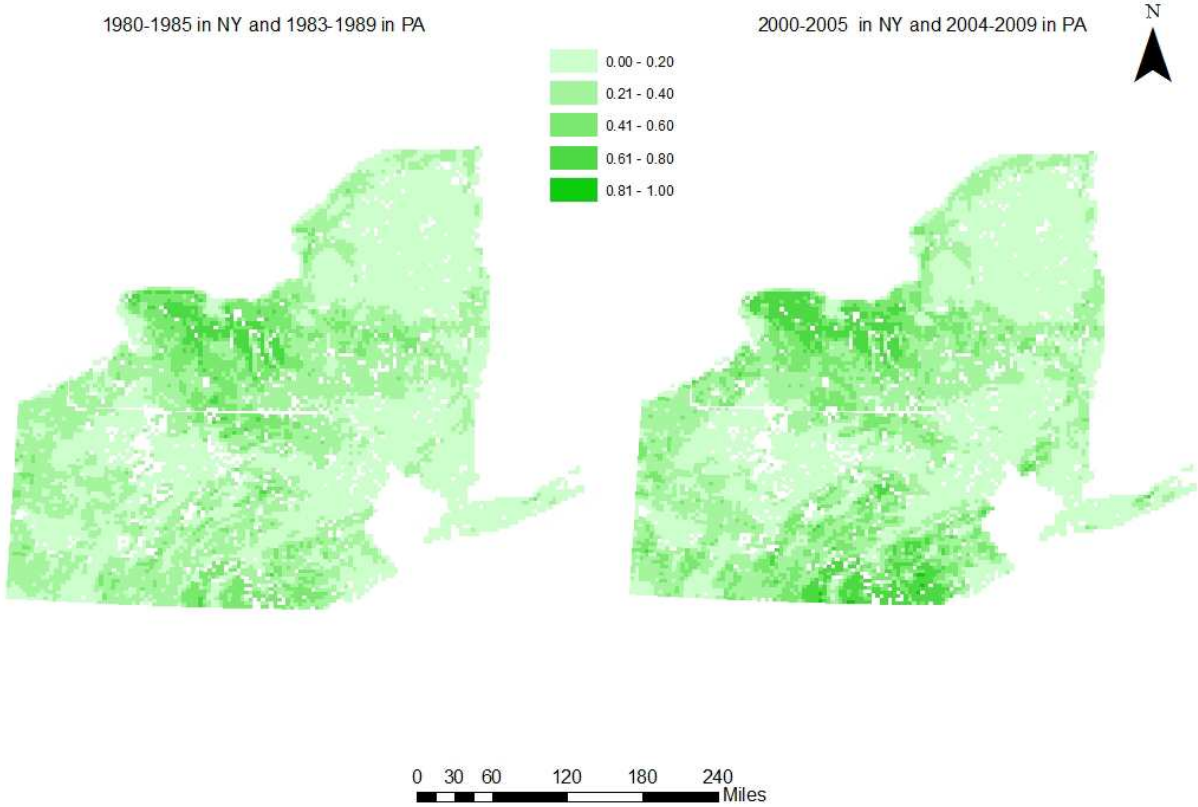
Red-headed woodpecker (Melanerpes erythrocephalus) occupancy probability



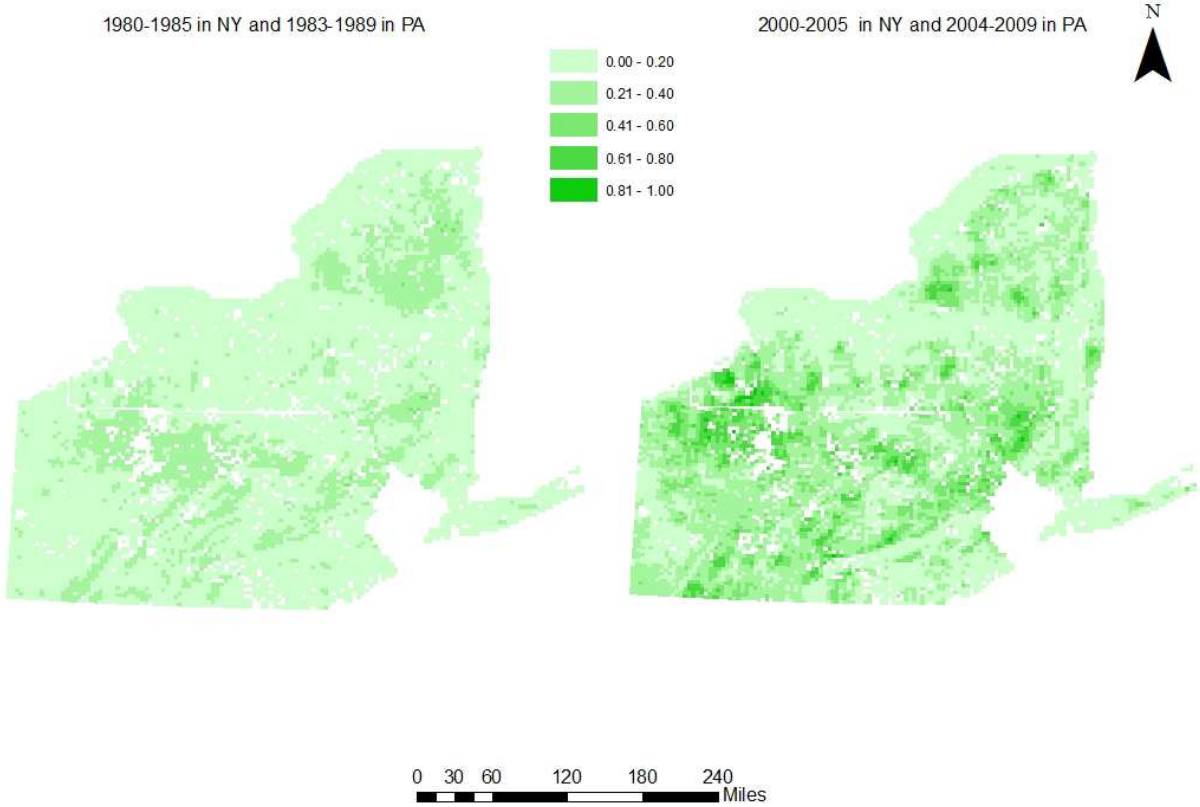
Ring-necked pheasant (Phasianus colchicus) occupancy probability



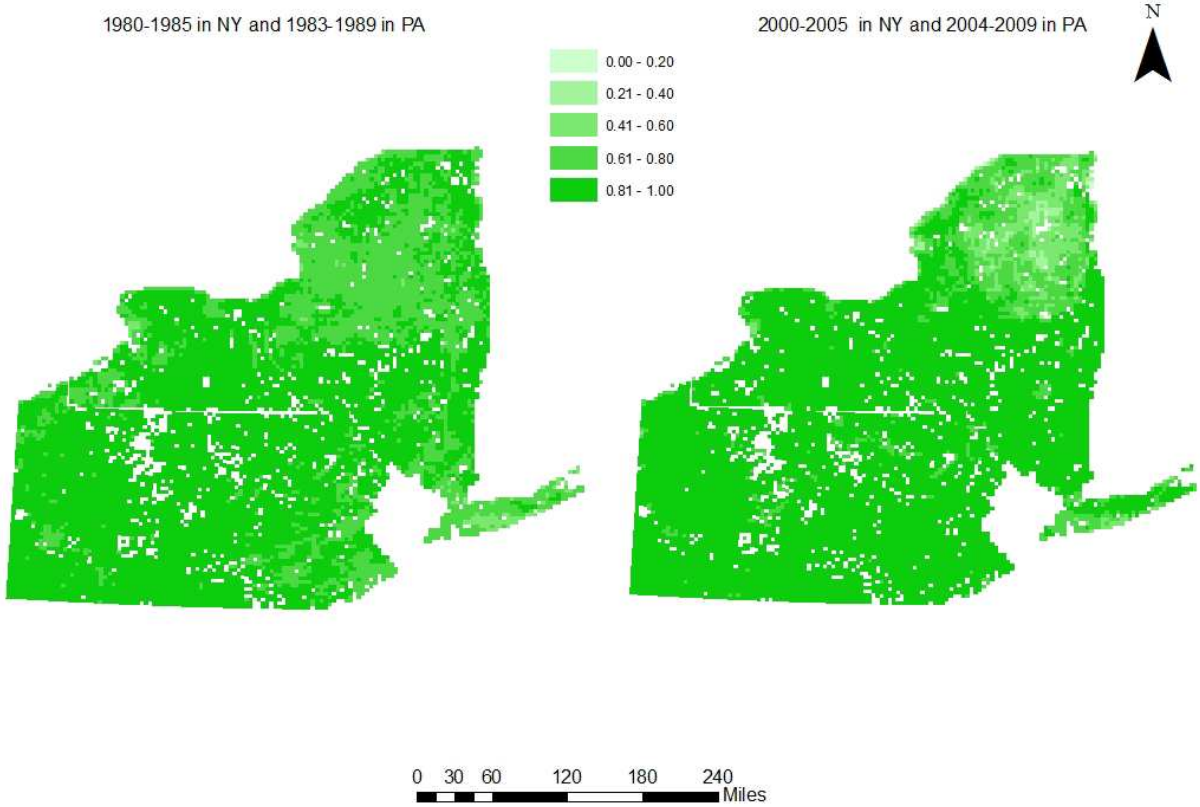
Rock pigeon (Columba livia) occupancy probability



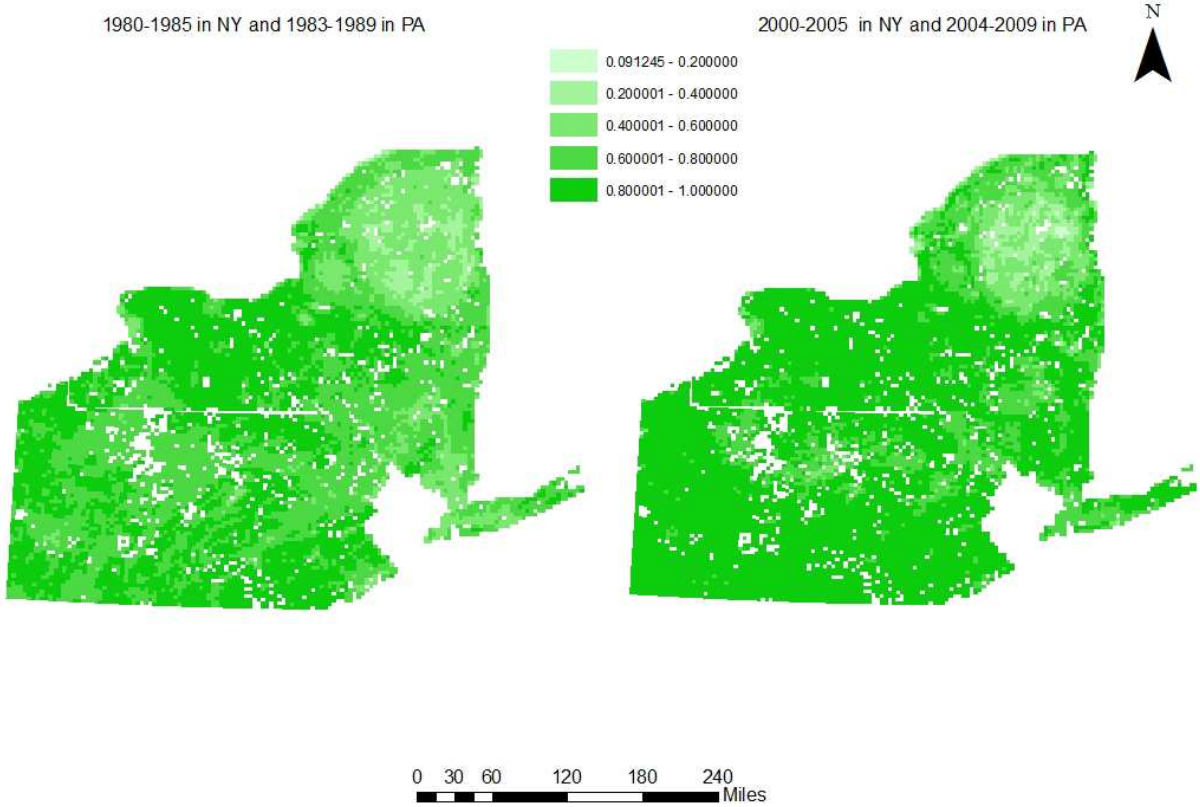
Red-shouldered hawk (Buteo lineatus) occupancy probability



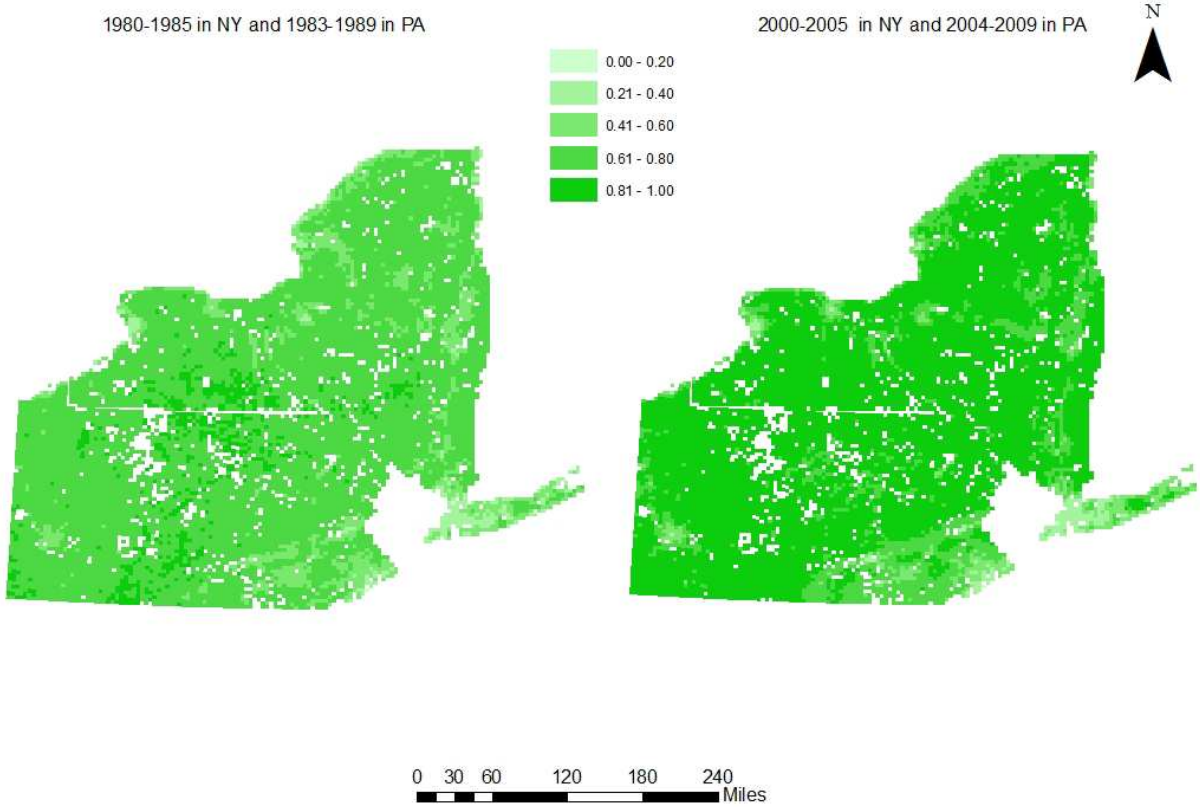
Red-tailed hawk (Buteo jamaicensis) occupancy probability



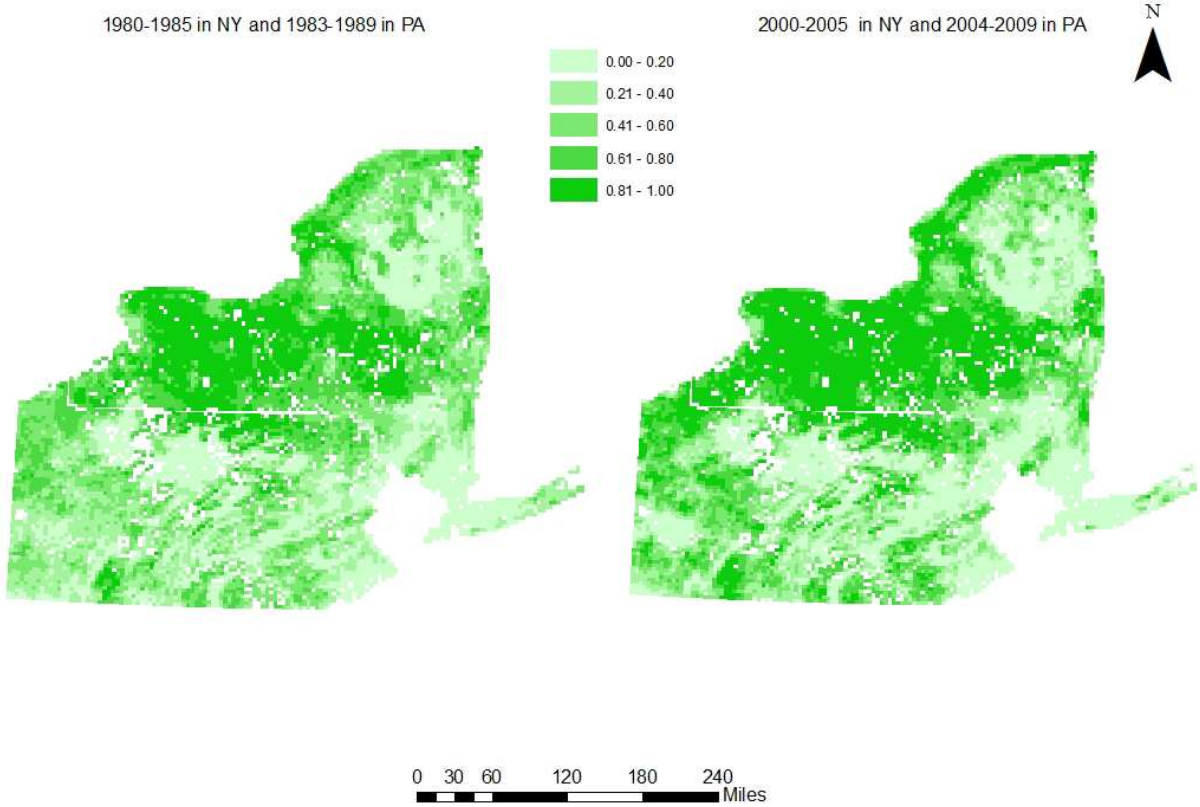
Ruby-throated hummingbird (Archilochus colubris) occupancy probability



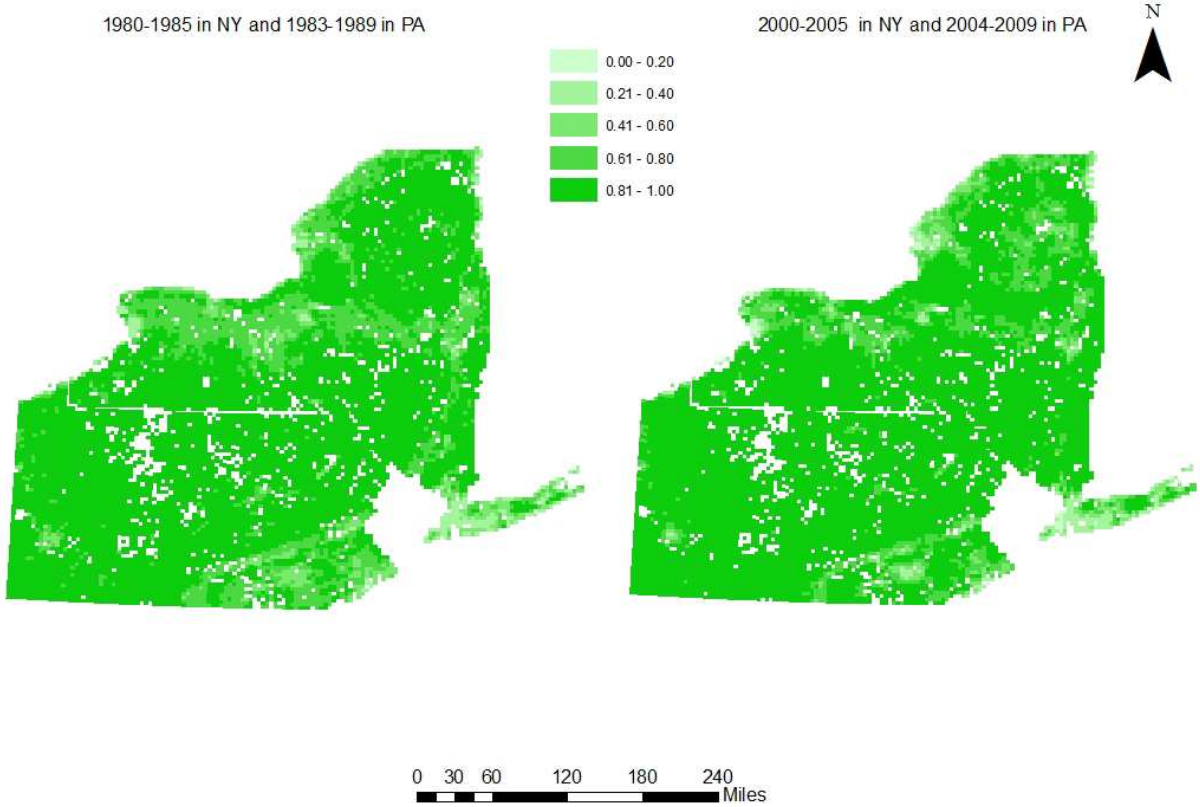
Ruffed grouse (Bonasa umbellus) occupancy probability



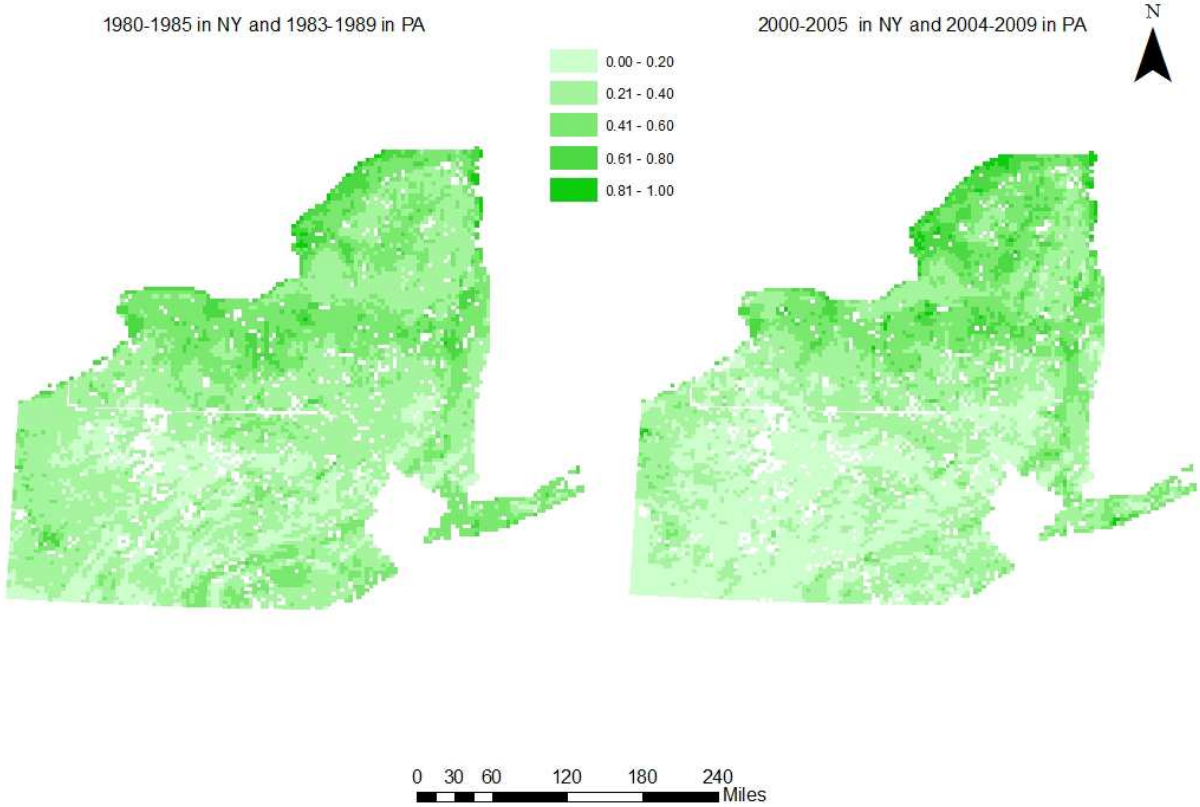
Savannah sparrow (Passerculus sandwichensis) occupancy probability



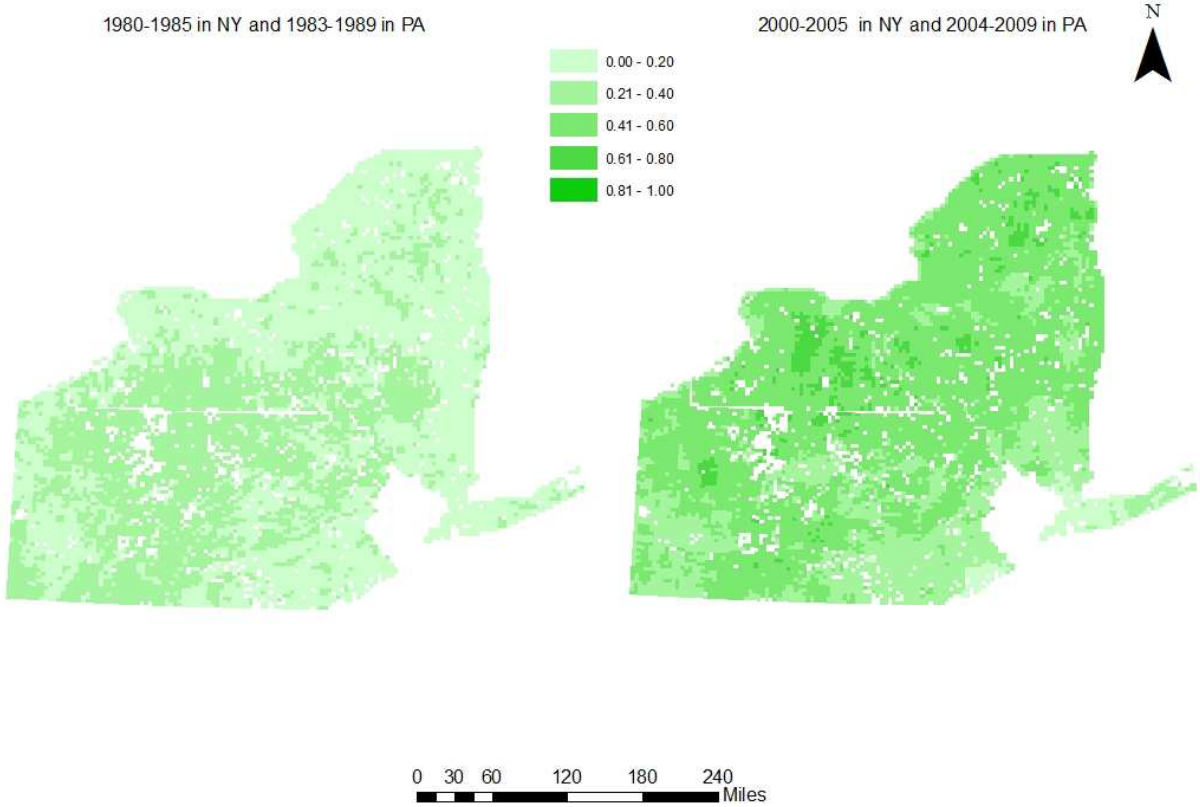
Scarlet tanager (Piranga olivacea) occupancy probability



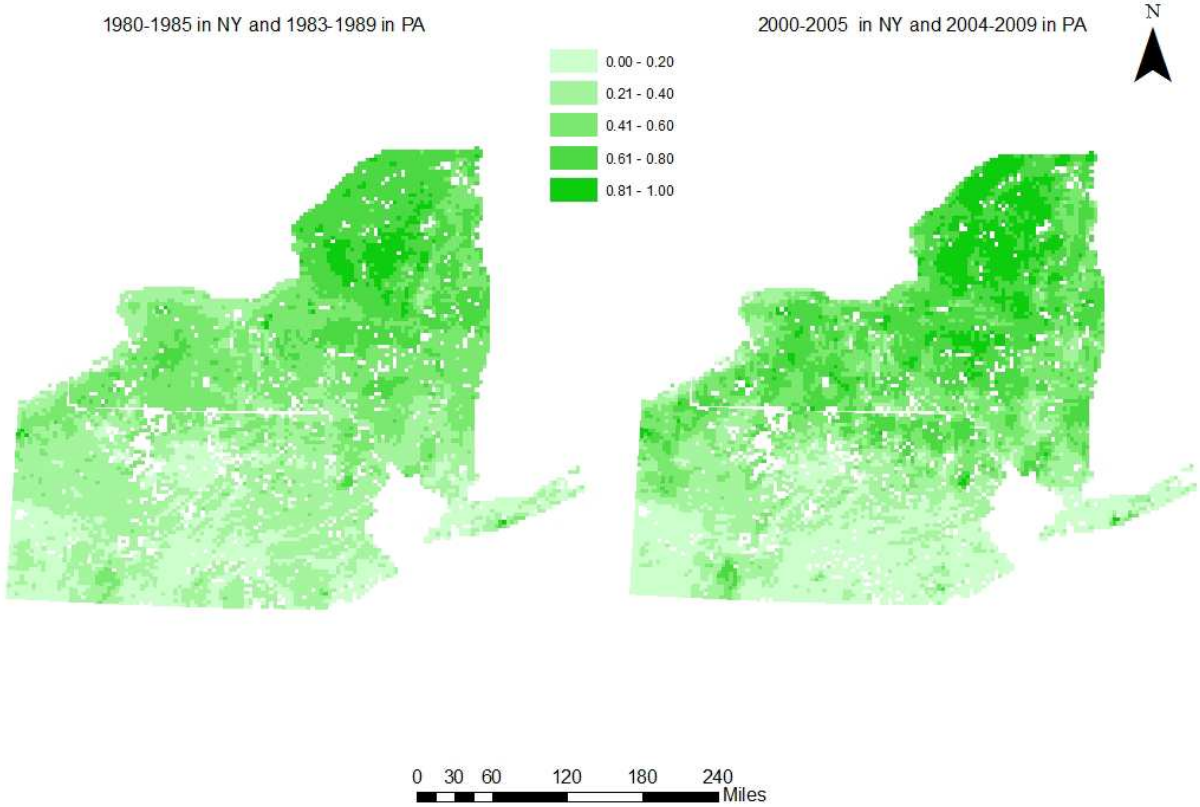
Spotted sandpiper (Actitis macularius) occupancy probability



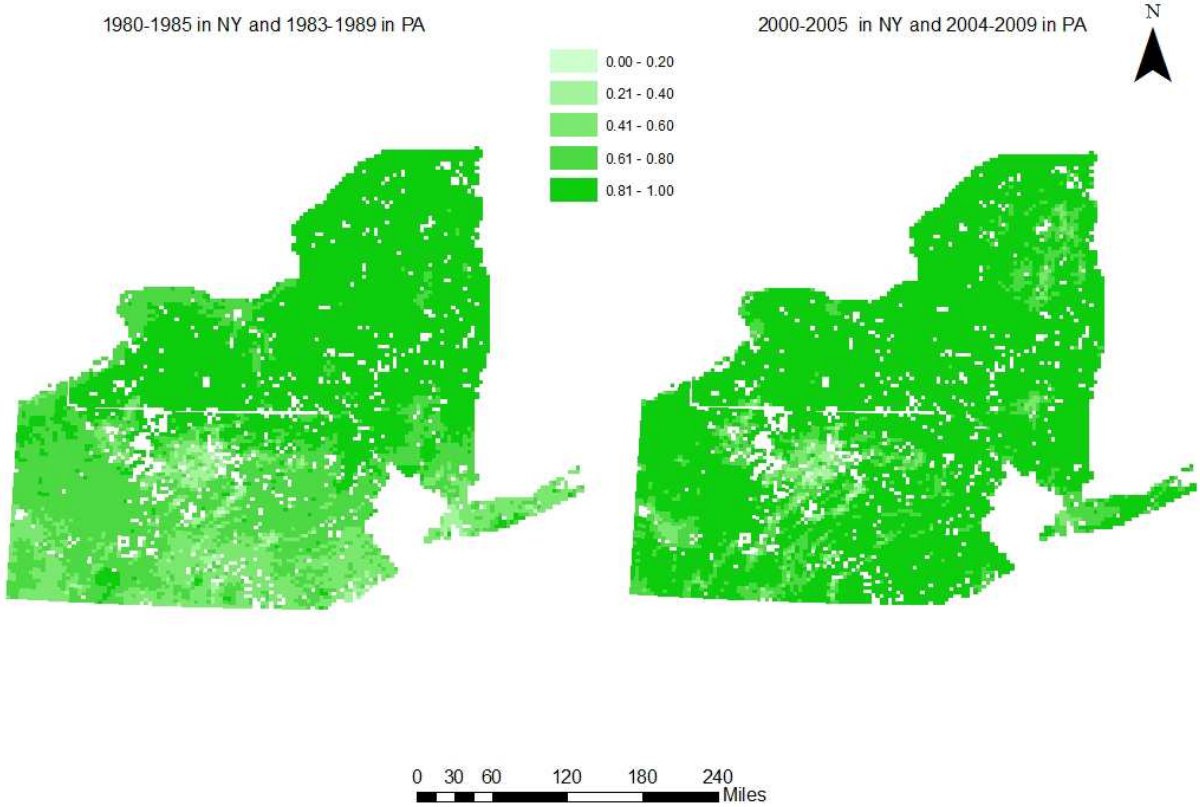
Spotted sandpiper (Actitis macularius) occupancy probability



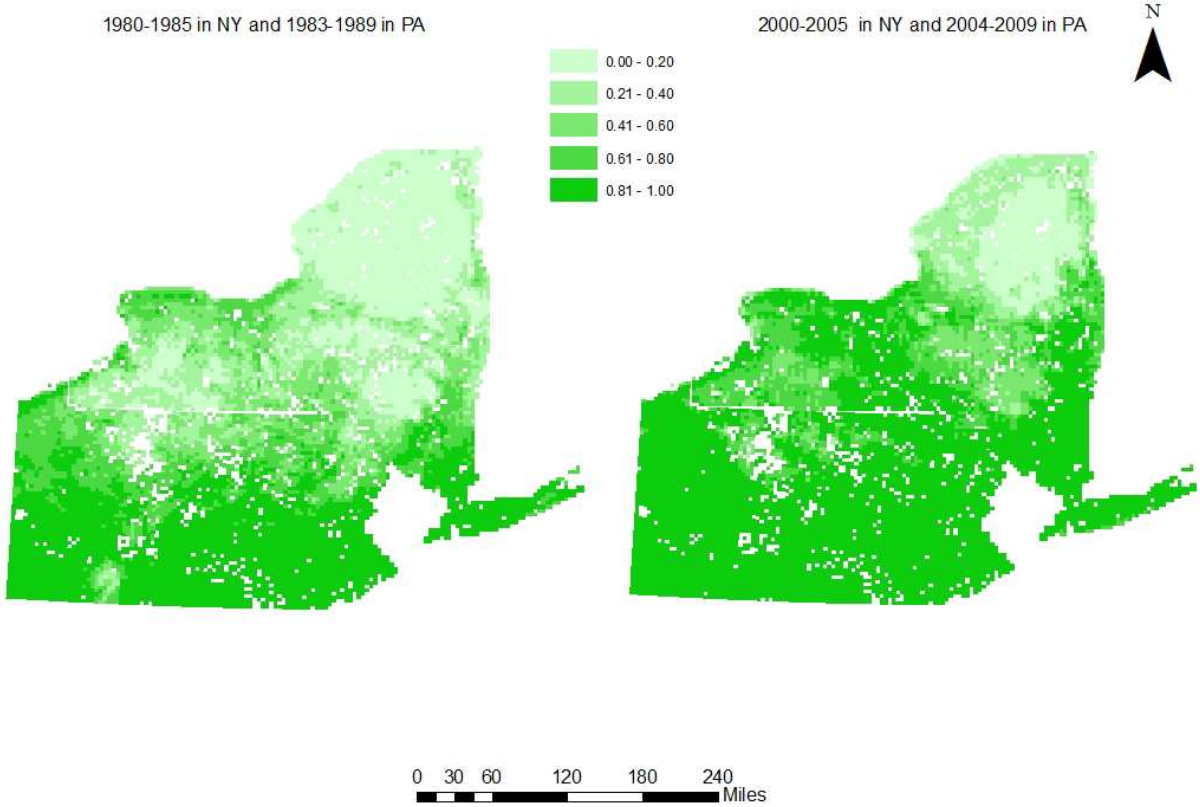
Swamp sparrow (Melospiza georgiana) occupancy probability



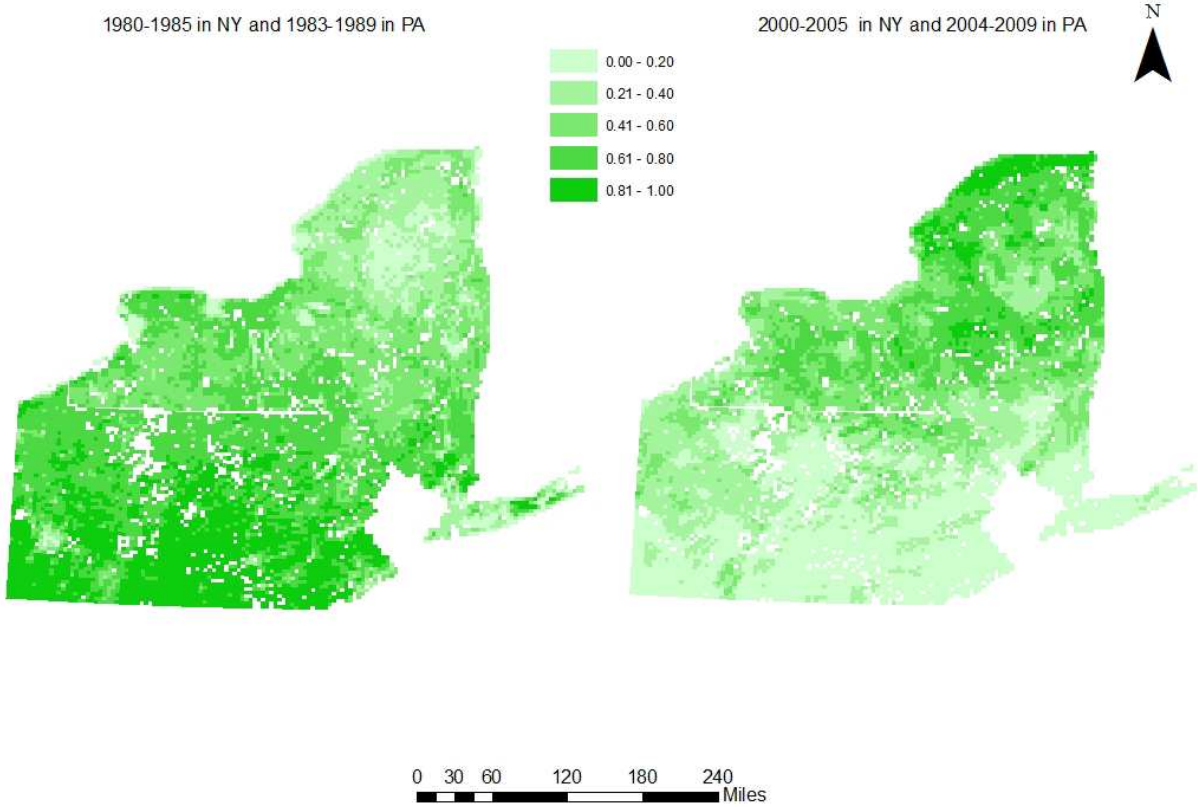
Tree swallow (Tachycineta bicolor) occupancy probability



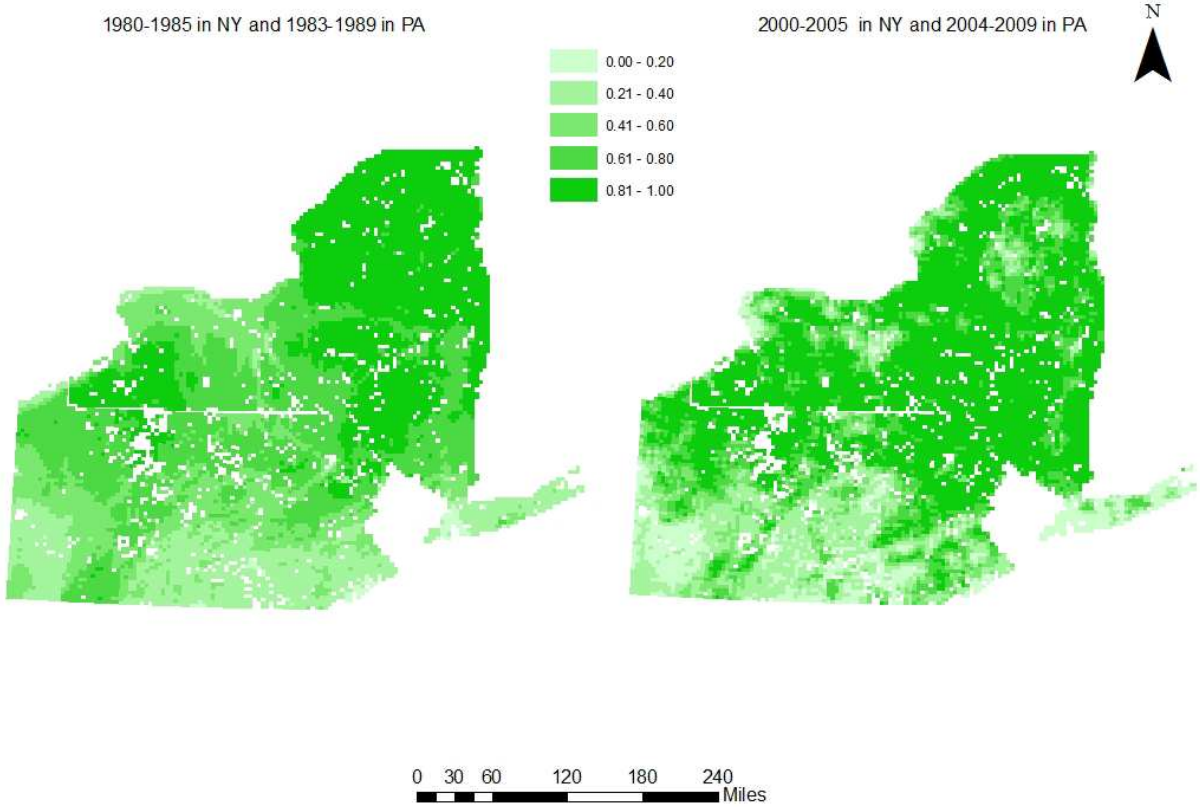
Tufted titmouse (Baeolophus bicolor) occupancy probability



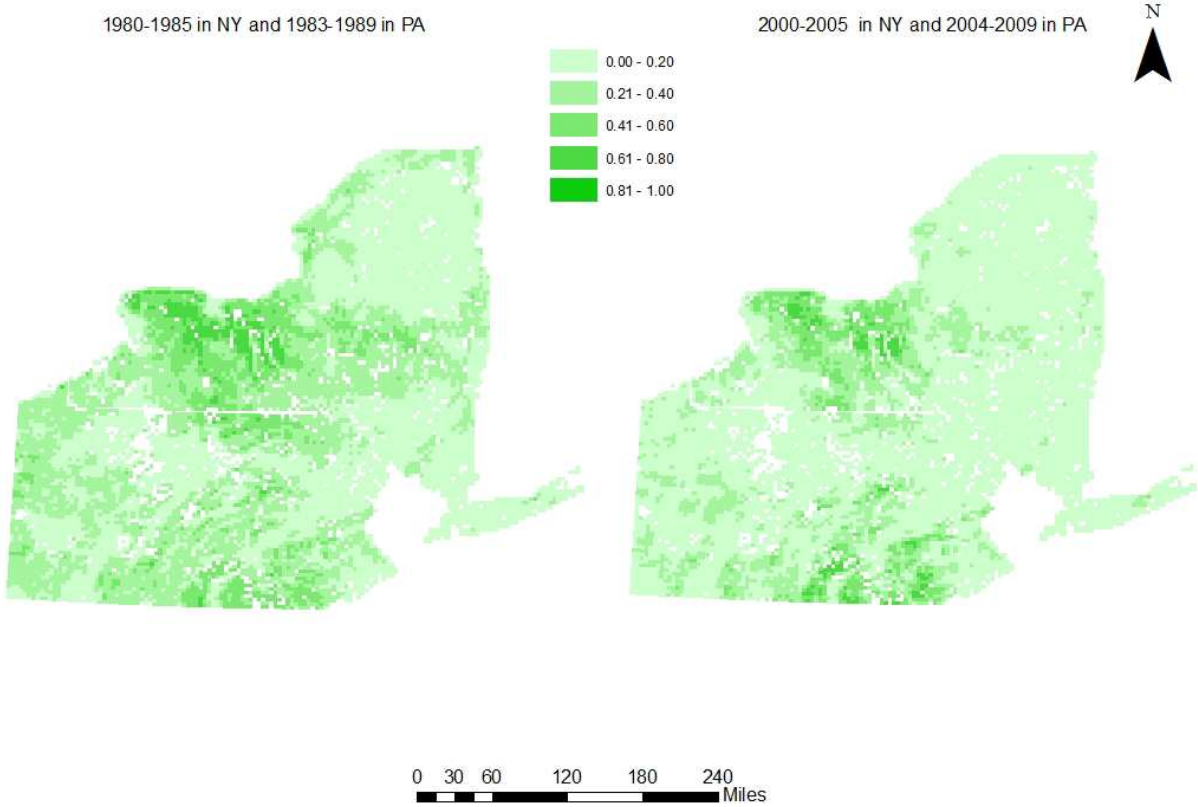
Turkey vulture (Cathartes aura) occupancy probability



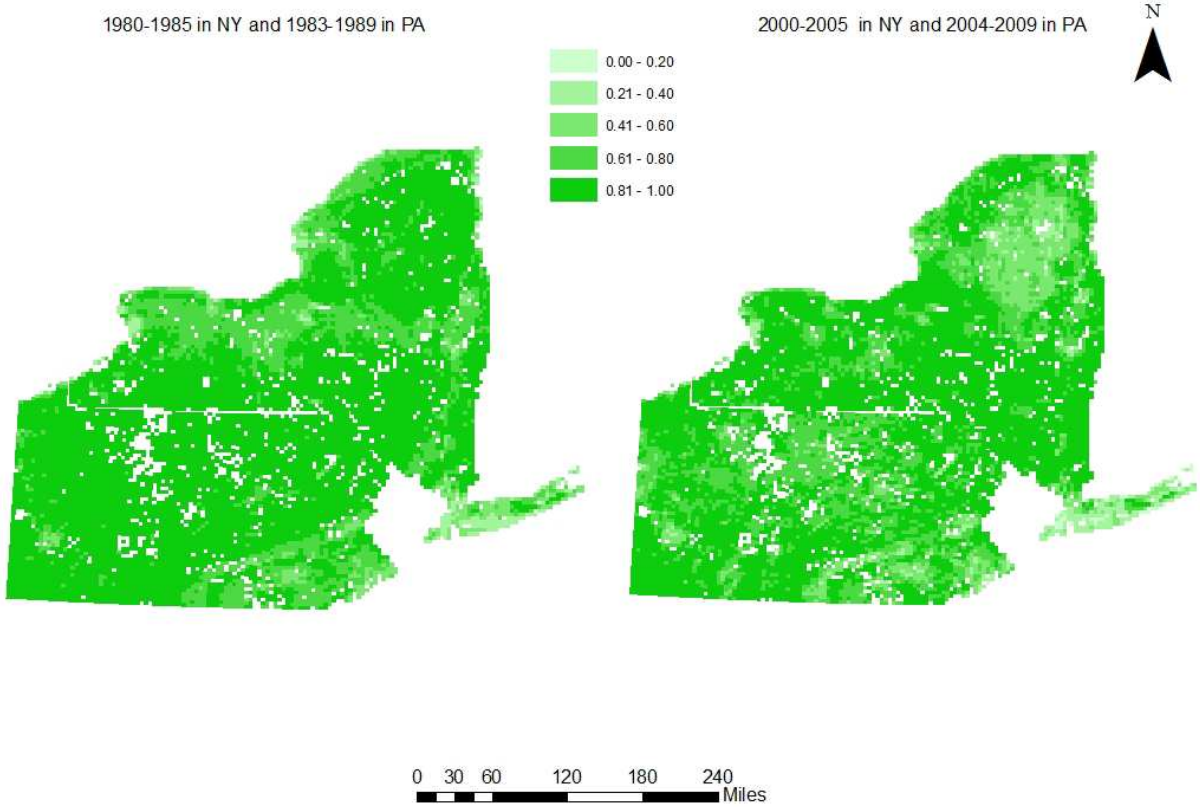
Veery (Catharus fuscescens) occupancy probability



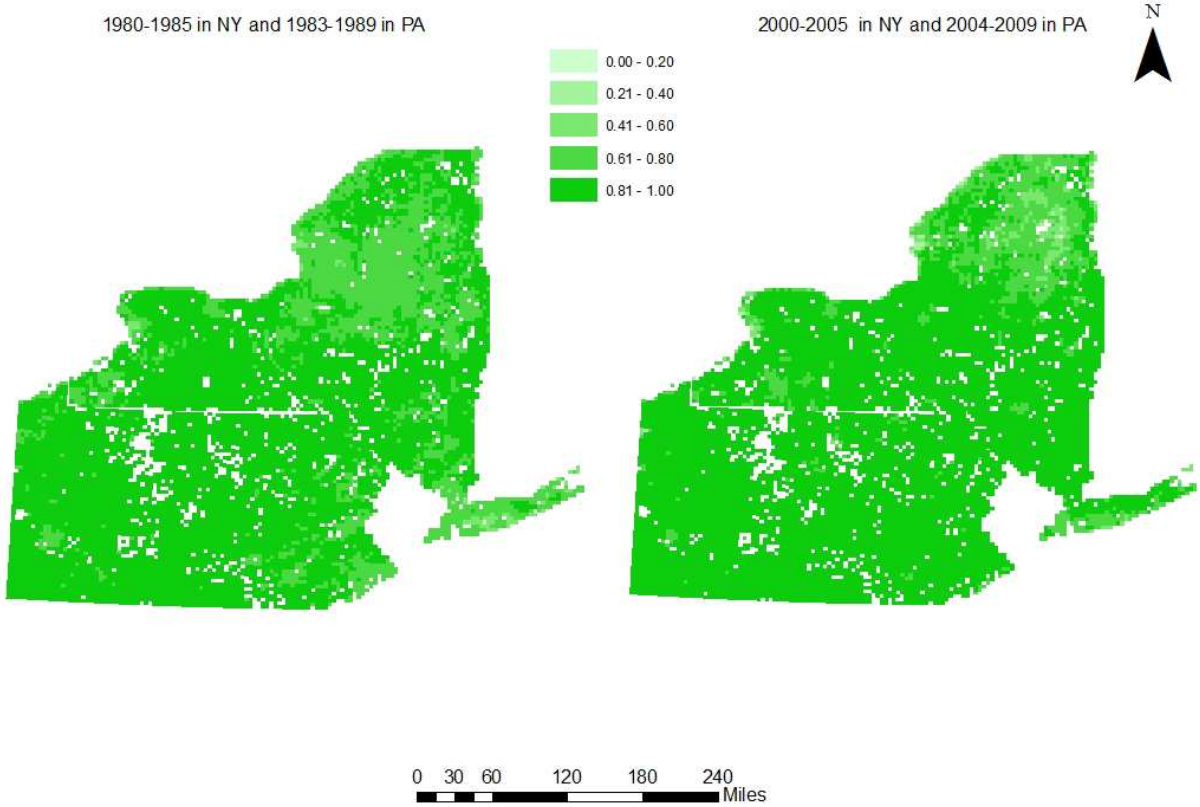
Vesper sparrow (Pooecetes gramineus) occupancy probability



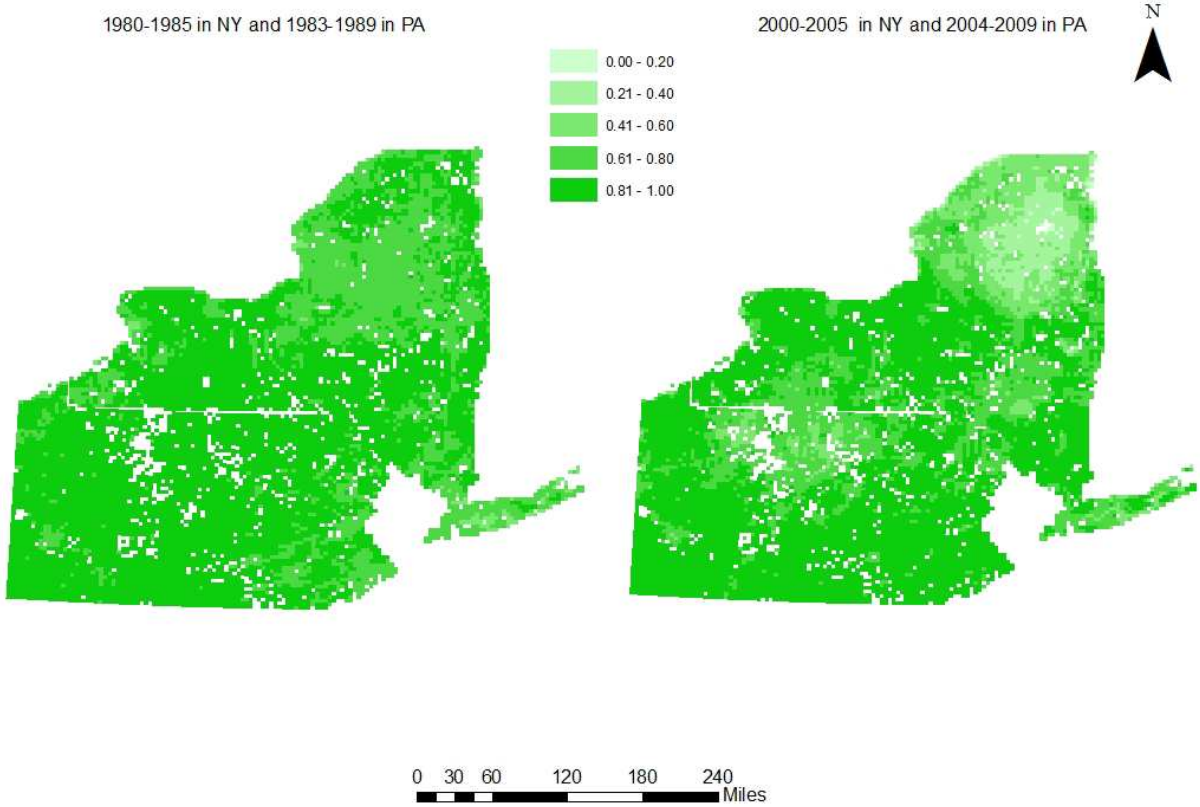
Warbling vireo (Vireo gilvus) occupancy probability



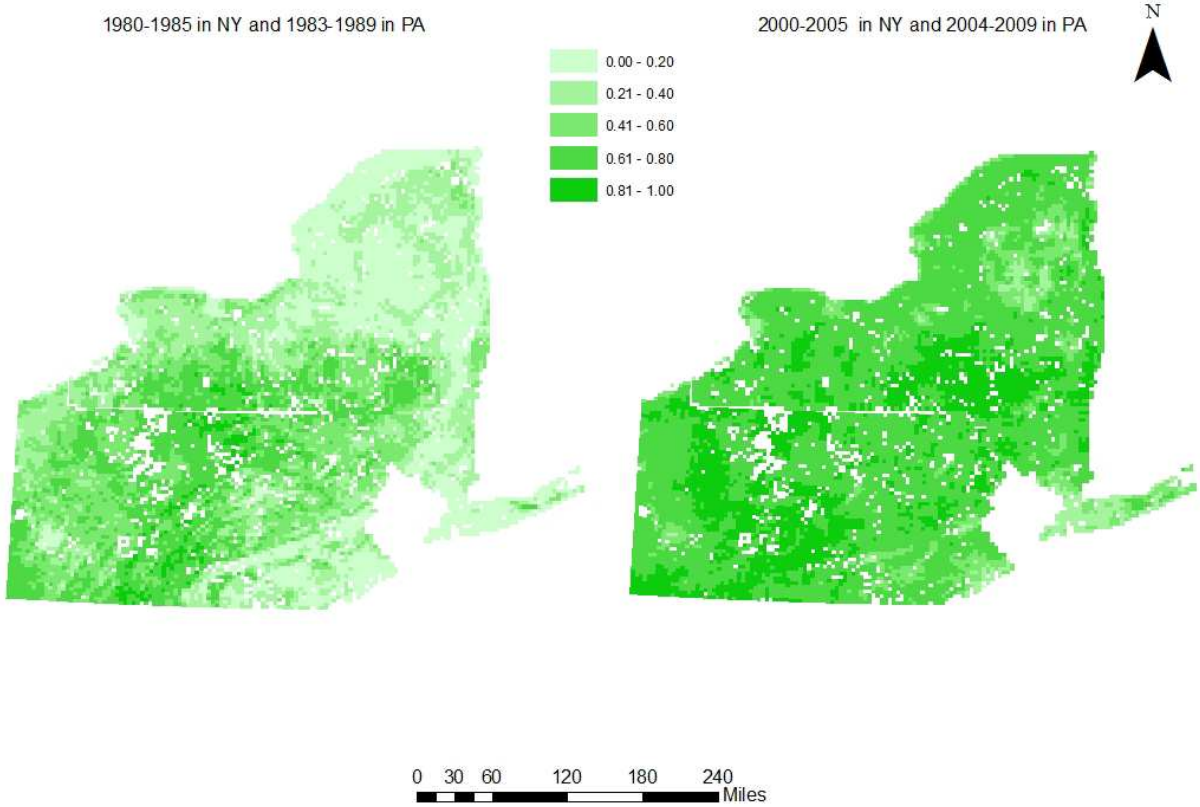
White-breasted nuthatch (Sitta carolinensis) occupancy probability



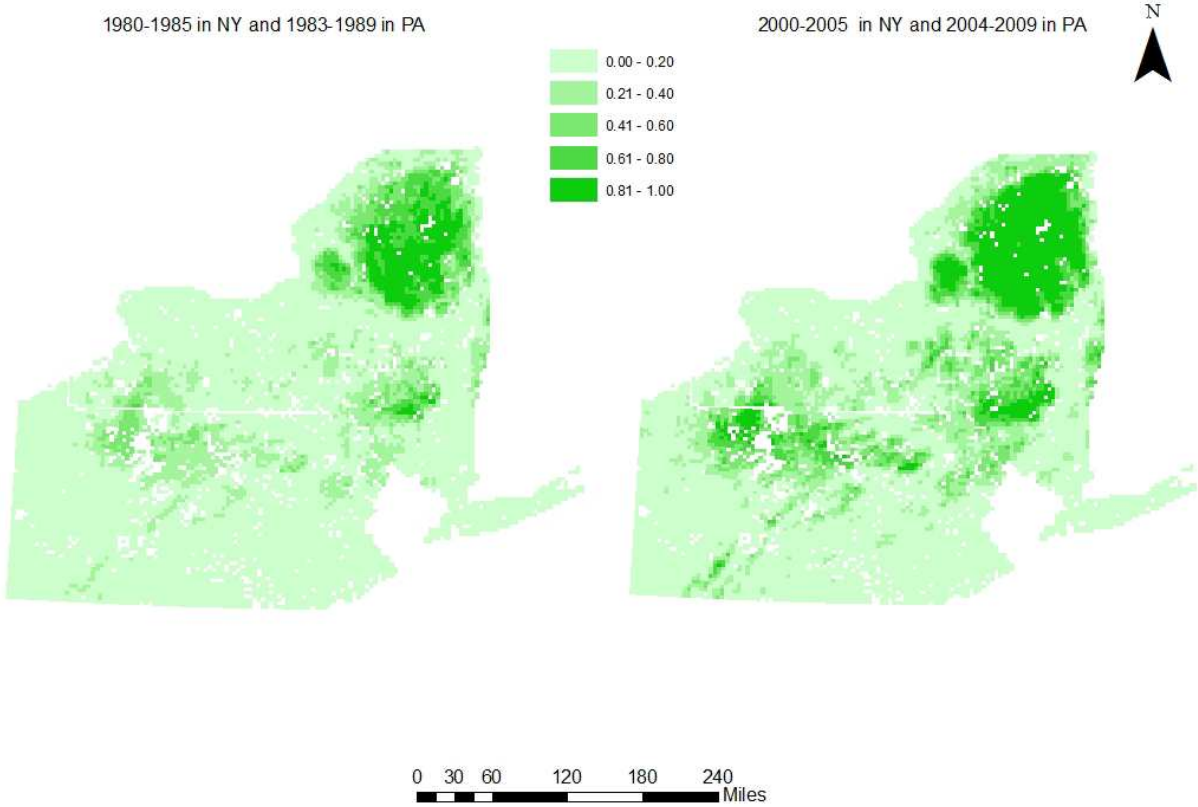
Willow flycatcher (Empidonax traillii) occupancy probability



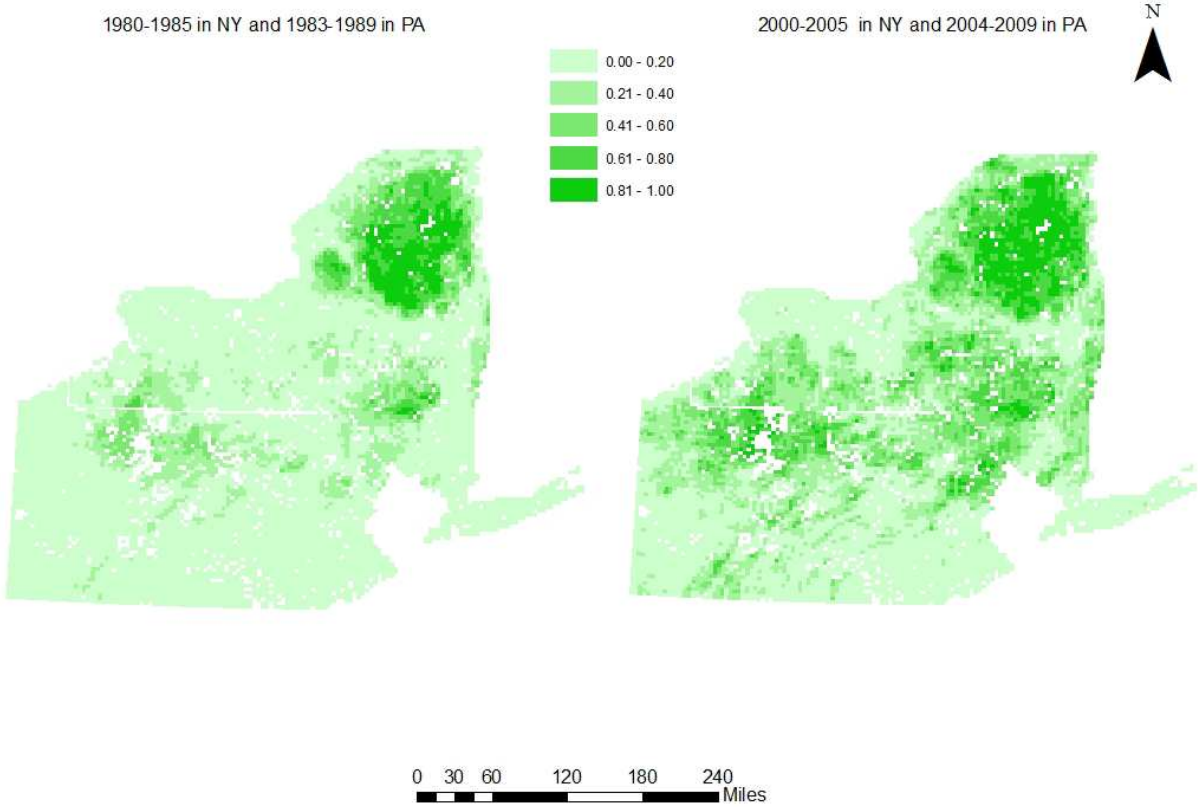
Wild turkey (Meleagris gallopavo) occupancy probability



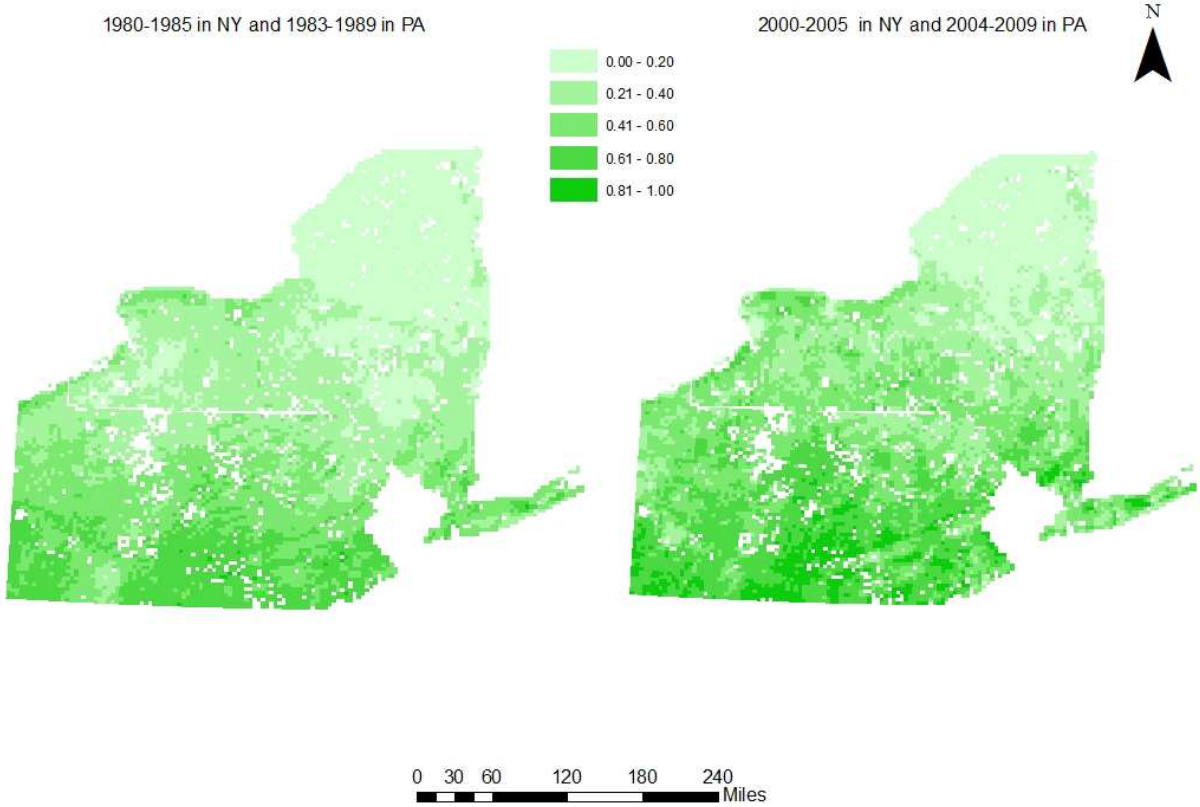
Winter wren (Troglodytes hiemalis) occupancy probability



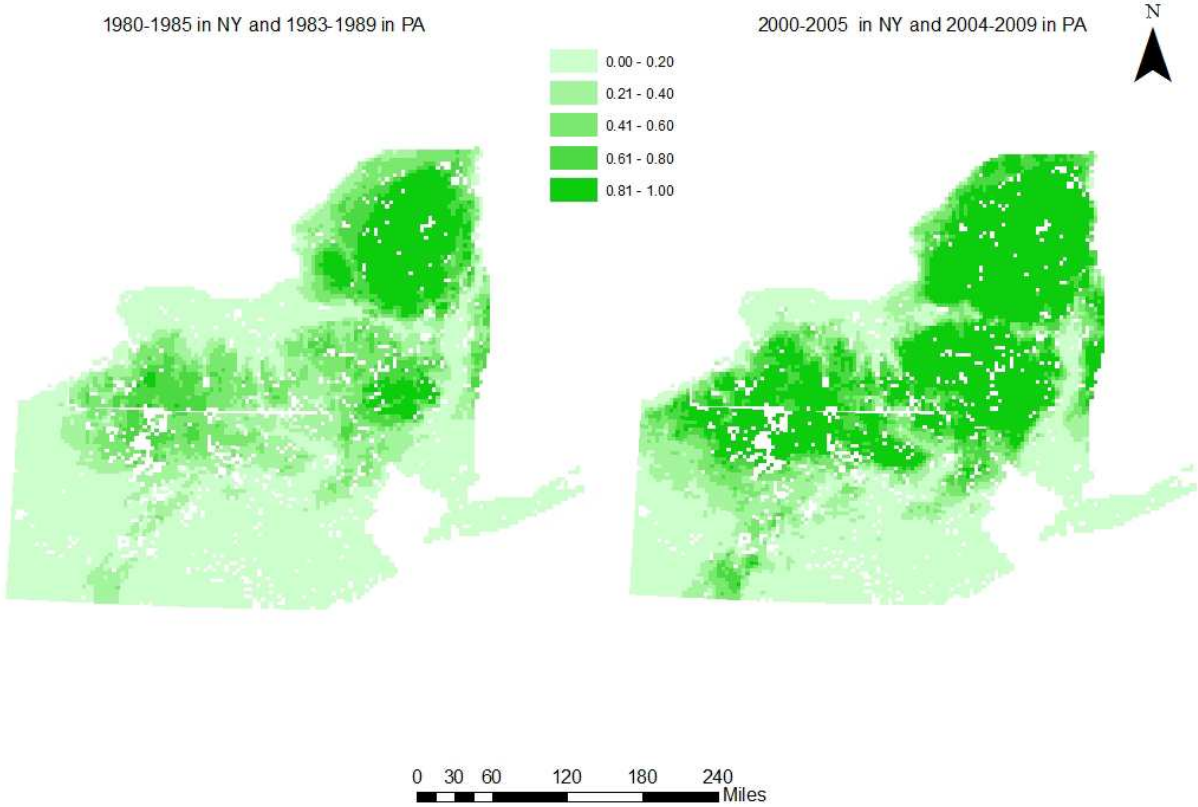
Wood duck (Aix sponsa) occupancy probability



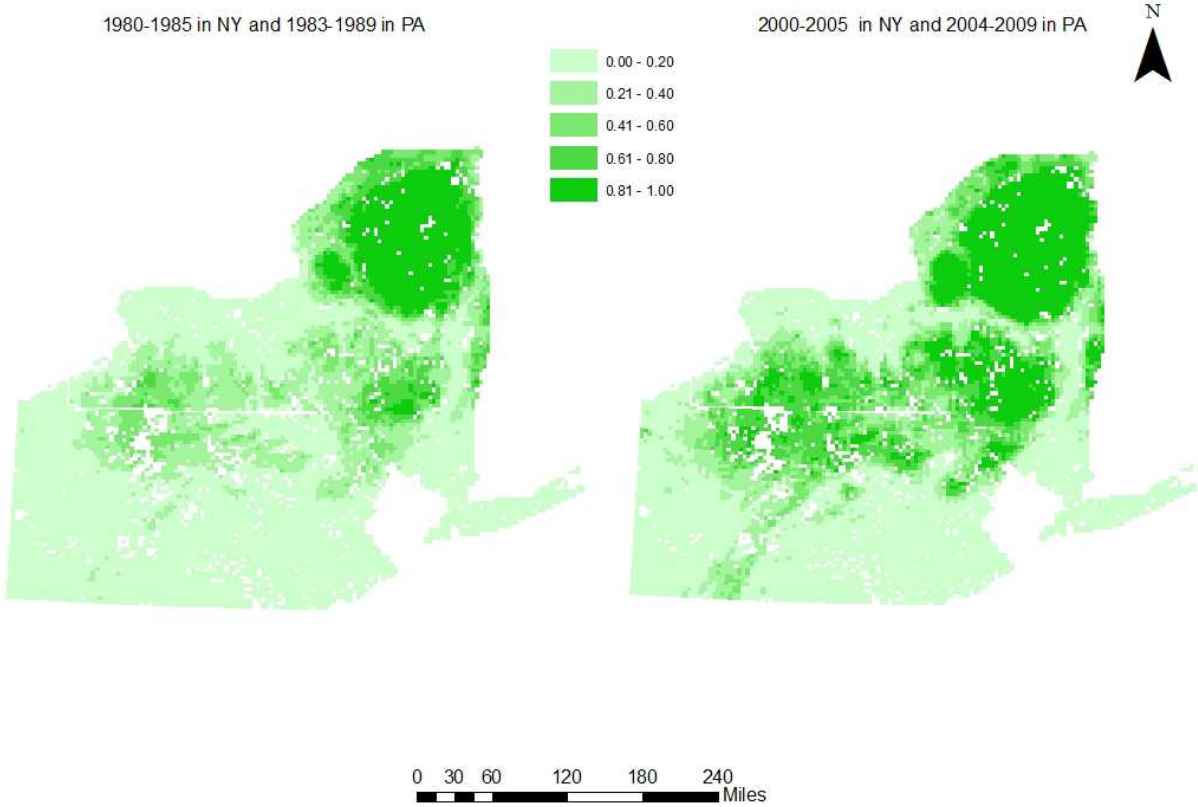
Yellow-billed cuckoo (Coccyzus americanus) occupancy probability



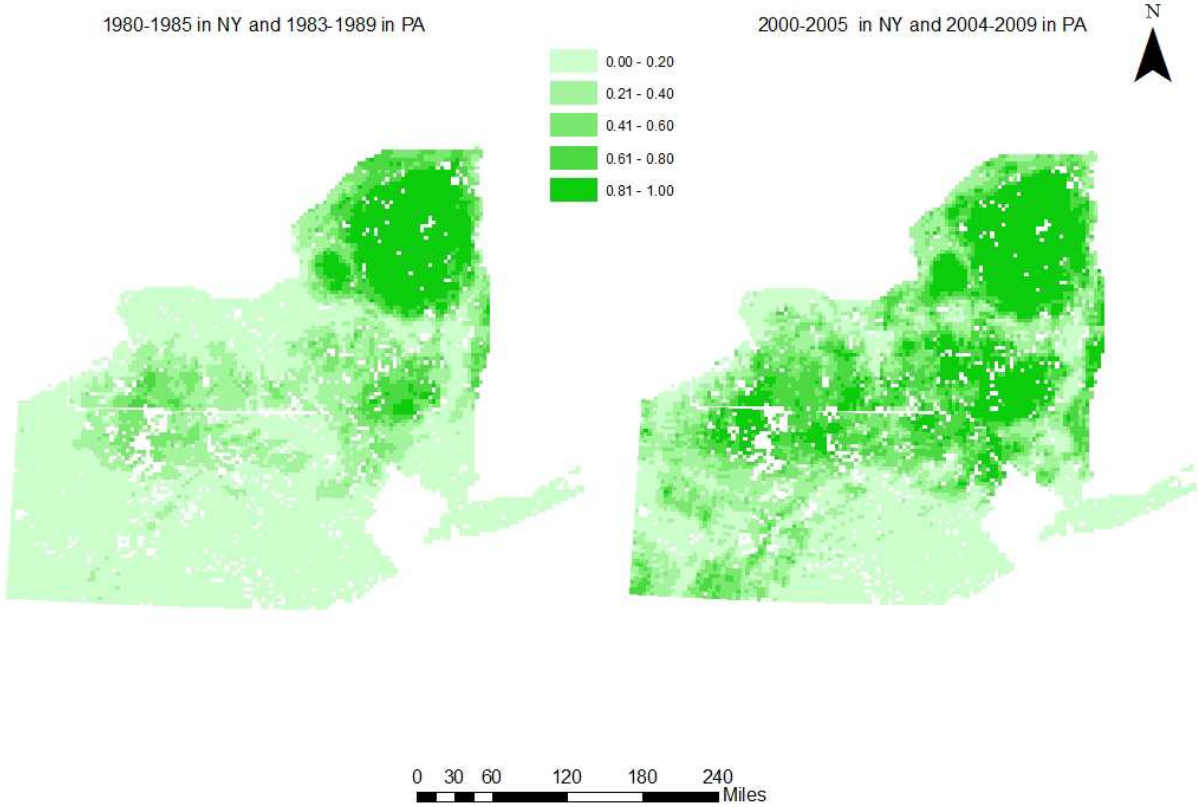
Yellow-bellied sapsucker (Sphyrapicus varius) occupancy probability



Yellow-rumped warbler (Setophaga coronata) occupancy probability



Yellow-throated vireo (Vireo flavifrons) occupancy probability



CURRICULUM VITAE

Michelle A. Peach Lang

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EDUCATIONAL BACKGROUND

Doctoral Candidate (ABD) in Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY
Dissertation: Evaluating the role of protected areas in mitigating species' responses to climate and land use change
Advisors: Dr. Jacqueline Friar and Dr. Jonathan Cohen, Department of Environmental and Forest Biology

M.S. in Land Resources, University of Wisconsin, Madison, WI 2005
Thesis: Topographic heterogeneity and sedge meadows: Ecological patterns reinforce the need for experimental approaches to wetland restoration despite social barriers
Advisor: Dr. Joy B. Zedler, Department of Botany

B.A. in Biology, magna cum laude, Carleton College, Northfield, MN 1997

TEACHING AND MENTORING EXPERIENCE

Adjunct Instructor, SUNY ESF, Syracuse, NY 2010
- *EFB 493/693 Wildlife Habitats and Populations (4 credits):* Taught capstone course for undergraduate wildlife students covering quantitative methods of habitat assessment and modeling, population modeling, management planning, and adaptive management.

Adjunct Instructor, SUNY ESF, Syracuse, NY 2010
- *EFB 202 Ecological Monitoring and Biodiversity Assessment:* Designed and taught the classroom and field-based introduction to map, compass, GPS, and GIS skills component of the course

Teaching Assistant, SUNY ESF, Syracuse, NY 2009
- *EFB 493/693 Wildlife Habitats and Populations (4 credits):* Responsible for GIS and population modeling lab instruction, mentoring students, and grading.
- *EFB 390 Wildlife Ecology and Management (4 credits):* Led discussion sections; wrote and graded exams

Guest Lecturer, Cornell University, NY, 2006
- *NTRES 601 Seminar on Selected Topics in Natural Resources:* Described The Nature Conservancy's Tug Hill conservation program and supported student led projects related to forest conservation and management

Course Coordinator, University of Wisconsin Madison, WI 2003
- *EnvSt 900 Conservation Skills and Management (1-3 credits):* Developed and facilitated graduate level course that prepared students to write and implement management plans for natural areas

Teaching Assistant, University of Wisconsin Madison, WI 2002 – 2003

- *ZOO 102 Animal Biology Laboratory (2 credits):*Team taught introduction to zoology in lab based class
- *BIOCORE 301 Evolution, Ecology and Genetics (3 credits):* Facilitated discussion sections to supplement material presented during lectures

Coordinator, Youth in Natural Resources Program, Minnesota Department of Natural Resources, Minneapolis, MN 2000
- Developed partnerships with federal, state, and non-profit natural resource agencies
- Recruited, trained, and supervised 14 high school students in natural resource internships

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- Developed partnerships with federal, state, and non-profit natural resource agencies
- Recruited, trained, and supervised 14 high school students in natural resource internships

ENVIRONMENTAL MANAGEMENT EXPERIENCE

Wetland Scientist, Rhode Island Natural History Survey, RI 2012 – 2014
- Completed wetland monitoring and assessment at forested wetlands throughout RI
- Analyzed data from 5 years of wetland monitoring and assessment to inform the RI Wetland Monitoring and Assessment Plan and State Wildlife Action Plan
- Led stakeholder outreach efforts to evaluate wetland monitoring and assessment activities in RI and to develop a new Wetland Monitoring and Assessment Plan

Tug Hill Project Director, The Nature Conservancy, Pulaski, NY 2005 – 2009

- Responsible for writing and implementing ecological and general property management plan for 14,500-acre conservation area, with a focus on forest restoration, wetland protection, and invasive species management
- Coordinated TNC responses to Tug Hill conservation opportunities and threats, such as land acquisition, conservation easements, invasive species, wind energy, public recreation, aquifer withdrawal, etc.
- Collaborated with academic institutions, government agencies, and local partners on research priorities, including atmospheric deposition, forest restoration, and landscape connectivity
- Managed regional conservation action planning process for the Salmon River watershed, including leading planning workshops, collecting expert input, GIS mapping and analysis, and outreach to local communities and land managers
- Successfully obtained grants to support invasive species mapping, control and public outreach; logger trainings on wetland and stream protection; and TNC property management

Forest Ecologist, Community Forestry Resource Center, Institute for Agriculture and Trade Policy, Minneapolis, MN 2000 - 2002

- Assisted private and public landowners with sustainable forest management and provided support to developing forest landowner cooperatives
- Developed training workshops and guidebooks to help private landowners assess the ecological and silvicultural effects of their management and to comply with forest certification requirements
- Facilitated the Lake States Working Group regional standards writing for the Forest Stewardship Council forest certification process
- Successfully obtained grants to support invasive species training for loggers and other programmatic objectives

Team Leader, Northwest Service Academy, AmeriCorps, Trout Lake, WA 1997 - 1999

- Completed watershed restoration projects, including invasive species inventory and control, riparian fencing, revegetation, bank stabilization, check dam construction, salmon stocking, and trail building
- Managed logistics, training, member development, discipline and team building for 9 employees
- Developed and taught hands-on, interactive forest ecology class based on local ecosystems that met state science standards for 3rd-5th graders

ACADEMIC PUBLICATIONS AND PRESENTATIONS

Peach, M., J. Cohen and J. Frair. 2017. Single-visit dynamic occupancy models: An approach to account for imperfect detection with Atlas data. Journal of Applied Ecology. In press.

Peach, M., J. Cohen and J. Frair. 2016. Single-visit dynamic occupancy models: An approach to account for imperfect detection with Atlas data. North American Ornithological Conference, Washington, D.C.

Peach Lang, M., Zuckerberg, B., Frair J., and W. Porter. 2010. An evaluation of the effectiveness of protected lands at maintaining avian biodiversity over time. The Wildlife Society, Snowbird, Utah.

Peach, M. and J.B. Zedler. 2006. How tussocks structure sedge meadow vegetation. Wetlands 26(2):322-335.

Zedler, J.B. and M. Peach. 2005. Increasing wetland diversity: How one plant creates habitat for others. Arboretum Leaflets 2005-02

Peach, M. 2003. Mud Castles: Why being an ecologist means never having to grow up. Madison Environmental Group Seminar, Madison, Wisconsin.

Allen, A., S. Kercher, D. Larkin, H. Morzaria-Luna, and M. Peach. 2003. Perrow, M.R., and A.J. Davy, editors. 2002. Handbook of ecological restoration. Volume 1: Principles of restoration. Volume 2: Restoration in practice. Cambridge University Press, Cambridge, UK. Conservation Ecology 7(2):4. [online] URL: http://www.consecol.org/vol7/iss2/art4

OTHER PROFESSIONAL REPORTS AND PUBLICATIONS

Kutcher, T. and M. Peach. 2014. RIRAM v.2.14 User's Guide. Draft report prepared for Rhode Island Department of Environmental Management, Office of Water Resources, Providence, RI. 36 pages.

The Nature Conservancy. 2009. Invasive species handbook: A guide to invasive plants in the Tug Hill region. The Nature Conservancy, Central and Western New York Chapter, Rochester, NY. Available at http://www.sleloinvasives.org/wp-content/uploads/2010/01/Invasive%20Species%20Tug%20Hill.pdf

Peach, M. 2007. Management Plan for the Tug Hill Conservation Area. Central and Western New York Chapter, The Nature Conservancy, Rochester, NY.

Peach, M. 2013. Developing and applying wetland monitoring and assessment protocols for wetland condition in Rhode Island. Draft report prepared for Rhode Island Department of Environmental Management, Office of Water Resources, Providence, RI. 47 pages.

Peach, M. 2013. A review of wetland indicators with recommendations for Rhode Island. Draft report prepared for Rhode Island Department of Environmental Management, Office of Water Resources, Providence, RI. 29 pages.

Peach, M. 2014. Evaluating the effectiveness of RI freshwater monitoring and assessment tools in forested wetlands. Draft report prepared for Rhode Island Department of Environmental Management, Office of Water Resources, Providence, RI. 23 pages.

ACADEMIC GRANTS, FELLOWSHIPS AND AWARDS

- Cooper Ornithological Society Board of Directors Student Paper Award for presentation at the North American Ornithological Conference
- Cooper Ornithological Society travel award to attend the North American Ornithological Conference
- Betty Moore Chamberlaine Award for outstanding female graduate student in avian ecology, SUNY-ESF, 2010
- Sussman Fellowship (to support research), SUNY-ESF, 2009
- Lois Almon Small Grants Recipient (to support research), University of Wisconsin—Madison, 2004
- Doris Duke Conservation Fellowship (to support graduate studies and develop conservation leadership skills), Doris Duke Foundation, 2003 - 2004