LARGE AND FINE SCALE DRIVERS OF INSECTIVORES IN THE SOUTHERN APPALACHIAN MOUNTAINS: USING INFERENCE REGARDING BIOLOGICAL INTERACTIONS TO BUILD A BETTER HABITAT SUITABILITY MODEL

by

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(Under the Advisement of John Maerz, Jeffrey Hepinstall-Cymerman)

ABSTRACT

We examined how spatial variation in long-term precipitation patterns and site productivity potential directly and indirectly predicted foliar C:N, caterpillar biomass, and abundance of 11 songbird species in the southern Appalachian Mountains. Our results suggested that variation in abundance was best explained by elevation. In order to understand the potential driver of elevation or mean annual precipitation at a larger scale, we compared occupancy models using land cover and elevation only to models that included finer scale climate data for trailing-edge populations of the Black-throated Blue Warbler (*Setophaga caerulescens,* BTBW). Models that included local mean annual precipitation, integrated moisture index, and heat load index predicted 4,800 - 44,776 fewer acres than models using land cover and elevation.

INDEX WORDS: Abundance, occupancy, N-mixture model, precipitation, integrated moisture index, foliar nitrogen, trophic relationships, insectivorous songbirds, caterpillar, black-throated blue warbler, species distribution models

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DEDICATION

This dedication is two-fold. First, I dedicate this thesis to my husband David Conners Jr. Without his love and support I may have never pursued my dreams and career in this field; his patience, unwavering support, and the fact that he put his life and dreams on hold so that I may accomplish mine make him someone no human deserves. With that, this thesis is a much a product of him as it is my own. I am honored, privileged, and thankful for his presence in my life, because with it I am the best version of myself. As always David, I would rather share one lifetime with you than face all the ages of this world alone. Second, I dedicate this thesis to my parents. Taken before their time, I know that they would be immensely proud of me and my efforts. Not knowing if they’ll ever know my feelings towards their encouragement, I would like to acknowledge the fact that their motivation, encouragement, and praise of my endeavors throughout my life gave me the confidence and assuredness to know I can do anything, including this master’s project. This thesis is therefore a product of their love and encouragement as much as it is a product of my own efforts.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction and literature review

Global climate change

Earth's surface temperatures are changing due to anthropogenic emissions of greenhouse gases, and such changes in temperature are expected to affect global and regional precipitation regimes. Model projections of global climate change show continued warming trends for the southeastern United States, with annual temperatures expected to increase from -15.3 to -11.9° C by 2080 (Karl et al. 2009). Rising temperature has caused significant changes to temperature and precipitation patterns in the southeastern United States (Groisman et al. 2004). Since 1970 the southeastern U.S. annual average temperature has risen -17°C (Karl et al. 2009), and there have been increases in precipitation variability (Karl and Knight 1998, Groisman et al. 2004) including more frequent and prolonged periods between rainfall events and increasing frequency and intensity of drought (Karl and Knight 1998, Groisman et al. 2004). If trends continue, future drought patterns are expected to reduce the productivity of forest ecosystems (Elliott et al. 2015).

Productivity and songbird abundance

Vegetation composition is a known driver of local songbird abundance and community composition (MacArthur 1964, Rotenberry and Wiens 1980, Cody 1981). Vegetation composition and structure often serve to benefit songbird species by providing appropriate breeding habitat (Block and Brennan 1993). For breeding songbirds, the primary factor determining habitat suitability is availability of nesting habitat Thus, within the landscape songbird species will select areas that fulfill their structural habitat requirements. However, one hypothesis for songbird habitat selection states that, once songbird habitat becomes optimal for a species, in terms of vegetative structure, slight differences in structure may no longer control total species composition; this is referred to as a structural saturation point. At a structural saturation point, one or more additional factors may influence microhabitat selection of avian species (Wiens and Rotenberry 1981).

Within optimal vegetative structure for breeding, songbirds use a hierarchical selection process based on most critical to least critical resources for survival and growth during the breeding season (Steele 1993, Matsuoka et al. 1997). For breeding songbirds, the most critical resource is food for chicks (Arcese and Smith 1988, Marshall et al. 2002). For example, Black-throated Blue Warblers (*Setophaga caerulescens*) undergo a hierarchical selection process; choosing first appropriate nesting habitat and then, within that breeding habitat, choosing territories based on prey availability (Steele 1993, Matsuoka et al. 1997).

Prey availability is likely to be directly related to ecosystem productivity (Cody 1981); which can be limited by precipitation, soil moisture, and/or available sunlight (White 1958, Churkina and Running 1998, Lieth and Whittaker 2012, Nayak et al. 2013). When soils are dry, the uptake of nitrogen and other nutrients is reduced, resulting in lower foliar nutrient concentrations and reduced photosynthetic activity (Shure et al. 2003, Rustad et al. 2003, He and Dijkstra 2014). Foliar nitrogen availability has direct impacts on insect community structure and abundance (Prestidge and McNeill 1983, Dohmen et al. 1984, Kytö et al. 1996) and nitrogen is the considered the most limiting micronutrient for herbivorous insects such as caterpillars (Mattson 1980, White 1993, McClure et al. 2013). Because of the relationship between songbird prey availability and precipitation and soil moisture, these two climatic variables are likely to be an important determinant of migratory insectivore bird distributions. Indeed, several studies have found that the abundance of breeding birds is positively correlated with precipitation (Odum 1950, Bertin 1977, Smith 1977).

In addition to variation in precipitation, slope and aspect can create steep climate gradients and heterogeneous microclimates that affect insect abundance in montane ecosystems (Rosenberg et al. 1983, Desta et al. 2004). For example, humidity can strongly affect terrestrial arthropod development, growth, and metabolic activity (Neville 1975, Horn 1976, Edney 1977); and, there are greater abundances of forest insects when humidity is higher (Whittaker 1952). It has been shown that soil moisture is a significant predictor of habitat use by some insectivorous songbirds (Kendeigh and Fawver 1981), likely because moist soils are often associated with higher prey availability.

Trailing edge populations

Populations located at the edge of their bioclimatic range play a crucial role during climate driven range shifts because, by their very nature, range shifts occur at the edges of species' ranges. Currently, range expansion and contraction are not occurring at similar rates for most species. Evidence suggests that the rate of range contraction is occurring at twice the rate of range expansion for some species (Brommer et al. 2012). The effects of climate-induced range shifts on trailing and leading edge populations is expected to be markedly different for trailing edge populations at contracting portions of a species' range because those species are likely to be increasingly dependent on more specific and fragmented habitat requirements (Thuiller et al. 2008, Anderson et al. 2009).

Trailing edge (i.e., the contracting or retreating edge) populations are valuable for conservation and preserving places that harbor such species should be a conservation priority. Trailing edge populations often exhibit high degrees of local adaptation and often contain unique genotypes. Such genotypes are of extreme importance for species persistence under current and future climatic change (Hylander et al. 2015). Theoretically, trailing edge populations should occur in areas that historically provided a wider range of suitable climatic conditions for the species and in landscapes of high environmental heterogeneity where historic climate refugia are likely to persist (Tzedakis et al. 2002). For example, the topography of mountainous regions create steep gradients of temperature and precipitation that allow many species to find suitable bioclimatic conditions across relatively short elevational shifts, on north or south facing aspects (Loarie et al. 2008), or between ridge and cove sites represented by unique or uncommon vegetation types (Lenoir et al. 2013). In these kinds of regions, trailing edge populations are typically restricted to habitat islands (microclimatic refugia) within a matrix of unsuitable climate or habitat (Hampe et al. 2005, Rull 2009, Ashcroft 2010, Hylander et al. 2015). The more fragmented nature of habitat in trailing edge landscapes affects population demography and can create strong selection for novel or compensatory traits in trailing edge populations (Hoffmann and Blows 1994, Parmesan et al. 1999, Hampe et al. 2005, Bridle and Vines 2007, Gillingham et al. 2012, Sunday et al. 2014, Varner and Dearing 2014). As a consequence, montane ecological communities are often more diverse and contain more endemic species that surrounding lowland environments (Rahbek and Graves 2001).

Research Needs

Mountainous systems are also some of the most vulnerable to climate change (Nogués-Bravo et al. 2007). These areas are of conservation concern in the face of warming temperatures and changing precipitation patterns that stand to alter current microclimates and the availability of microrefugia. Understanding how local climate drivers influence the ecology of trailing edge populations is important for forecasting biodiversity responses to climate change and to inform conservation planning. In the context of avian ecology, few studies address the potential effects of climate change on species distribution and abundance via the effects of climate on prey availability (Sillett et al. 2000, Bale et al. 2002, Staley et al. 2007). Needed are robust models that link local climate to primary production, resource quality, insect abundance, and bird population ecology.

Southern Appalachia is the southern-most breeding range for several insectivorous passerine species. Evidence of range shifts is already apparent in several passerine (Parmesan et al. 1999, Parmesan and Yohe 2003, Parmesan 2006), and further shifts are expected as shifts often lag environmental changes (Svenning et al. 2008). As microclimate refugia become more limited and fragmented, range shifts should be proceeded by local changes in demographic rates and abundance (Fang and Lechowicz 2006). Therefore, quantifying the relationships between climate, productivity, and insectivorous songbird ecology among trailing edge populations is needed.

Suitable habitat and species distribution models (SDMs) are tools that allow researchers and managers to use ecological or correlational relationships to map potential distributions of suitable habitat or species occupancy or abundance (Elith and Leathwick 2009). Generally, SDM models relate coarse scale climate or land cover features to presence or abundance data. Current SDMs or suitable habitat models are used to set regional conservation priorities and to facilitate the application of this information to land management activities (U.S.G.S. Gap Analysis Program. 2011), are correlative to expected occupancy habitat types and elevational range thresholds (U.S.G.S. Gap Analysis Program. 2011). Often these models rely on data from presence locals largely within the core of a species range. Habitat-occupancy correlations within the core of a species range are likely to over-predict available habitat or the distribution of a species, particularly when modeling areas of trailing edge populations that may have more specialized habitat requirements. The use of models that incorporate more local site variables and regional patterns and processes are needed to better forecast and manage the responses of trailing edge populations.

Study overview

The purpose of my research was to examine whether local climate and resource productivity and quality metrics could be used to model local variation in breeding songbird abundance. I used precipitation, integrative moisture index (an index of site productivity potential), vegetation structure, and caterpillar biomass to model the abundance of 11 songbird species including several trailing edge species. I then used the relationships I established for one trailing edge species, the Black-Throated Blue Warbler

(Setophaga caerulescens) to compare different model estimates of habitat availability and fragmentation across Macon County, North Carolina, USA.

Macon County, NC is a rural yet rapidly exurbanizing landscape in close proximity to several major metropolitan areas (Atlanta, GA; Charlotte, NC; Asheville, NC; and Knoxville, TN) (Gragson and Bolstad 2006). Historically, the region had extensive valley bottom agriculture, but much of the mid and upper elevations remained forested. Over a half million acres of high elevation forests occur within the Nantahala National Forest, particularly in the eastern half of the county. Over the last one to two decades, there has been a rapid increase in development of higher elevation forests into residential, second home and vacation communities (Wear and Bolstad 1998, Gragson and Bolstad 2006). As the region continues to develop high elevation forests, conservation efforts to protect the rich diversity of plants and animals including migratory songbirds will depend on rigorous habitat and population models.

Study objectives

In chapter two, I tested whether mean annual precipitation and integrated moisture index were direct predictors of foliar C:N and indirect predictors of caterpillar biomass and the abundance of 11 songbird species. I used structured equation modeling of point count data from 68 sites over two years to test the predictions that: (1) that sites with higher mean annual precipitation and integrated moisture would be negatively correlated with foliar C:N; (2) mean annual precipitation and integrated moisture would be positively correlated with caterpillar biomass, and foliar C:N would be negatively correlated with caterpillar biomass; (3) mean annual precipitation, integrated moisture index would be positively correlated with songbird abundance (Figure 2.1). I also investigated the relationship between mean annual precipitation, integrated moisture index, vegetation structure, and songbird abundance.

In chapter three, I compared models of Black-Throated Blue Warbler occupancy that did or did not include local climate measures in addition to traditional land cover and elevation data. I determined the degree to which models with additional local climate variables differed in predicted warbler occupancy across the county. I compared the extent to which more refined models predicted the abundance, distribution, and fragmentation (isolation) of occupied habitats. I used three recent data sets that provided good coverage of Macon County, North Carolina, USA (Figure 1.2).

Study Area

This study took place in the Coweeta Basin (CWT), a 1,626 hectare (ha) watershed of the USDA Forest Service Coweeta Hydrologic Laboratory and the Coweeta Long-Term Ecological Research (LTER) project that has been subject to whole-watershed manipulations since the 1930's (Day et al. 1988, Douglass and Hoover 1988) (Figure 1.1). Within the basin, elevation ranges from 677 m to 1600 m. CWT topography including steep slopes with north and south facing aspects results in steep gradients in precipitation and soil moisture over a relatively short distance (Figure 2.2 and see Daly et al. 2017). CWT is located in Macon County which is located within the eastern deciduous forest of the Blue Ridge Physiographic Province of the southern Appalachian Mountains and contains approximately 240,634 acres of forest, most of which is located within The Nantahala National Forest. Forest types within The Nantahala National Forest consist of oak-hickory, oak-pine, and northern hardwoods. Annual precipitation varies significantly in this region, from 178 cm at lower elevations to over 250 cm at higher elevations (Kohl

1990). Mean July temperatures average 21.6 °C. Most low elevation areas (lower than 700m) in Macon County are developed for residential, commercial, or agricultural use, and development of higher elevation areas has increased (Wear and Bolstad 1998, Gragson and Bolstad 2006)

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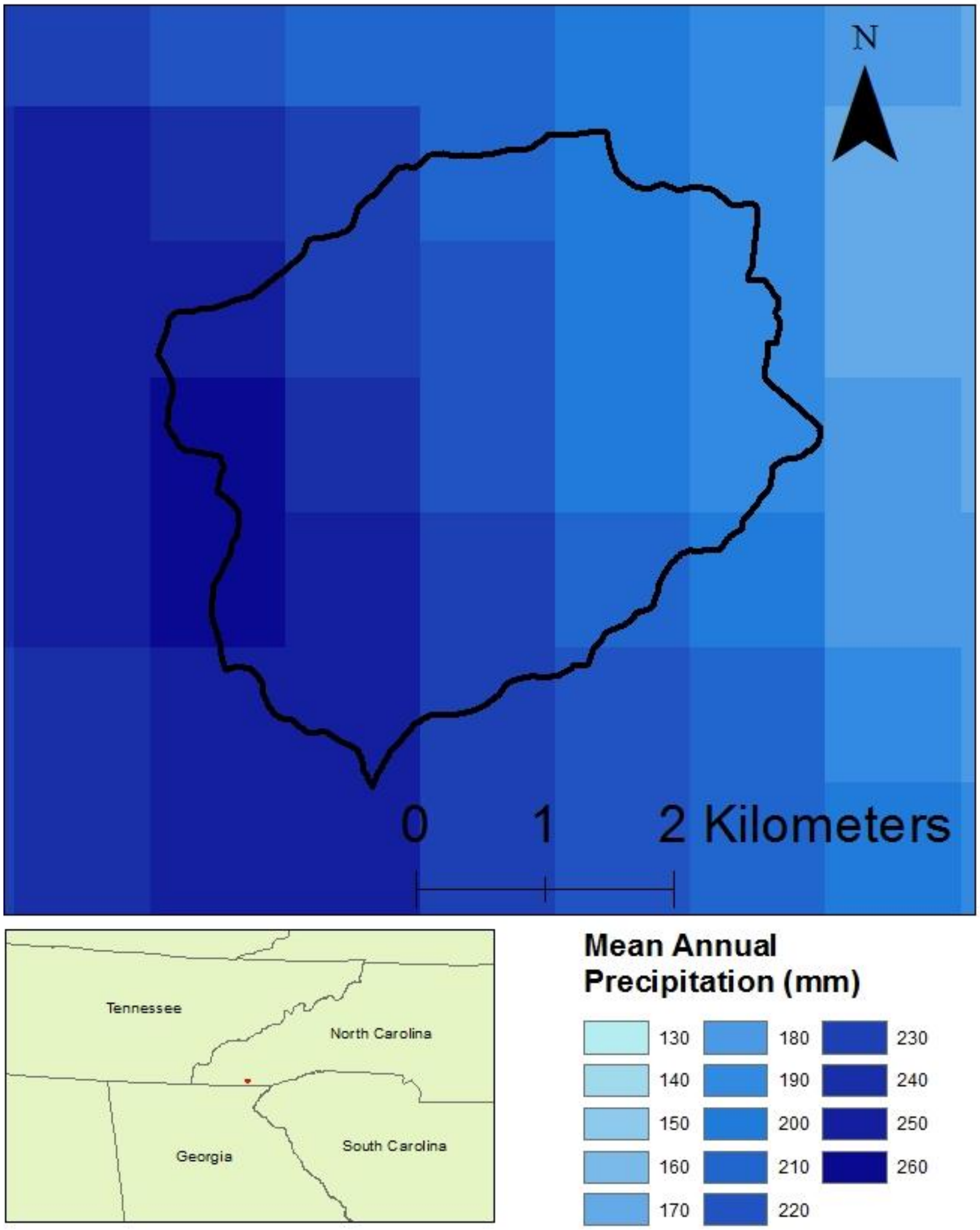

Figure 1.1. Chapter two study area, Coweeta Basin, which is located in Macon County, North Carolina across a mean annual precipitation gradient.

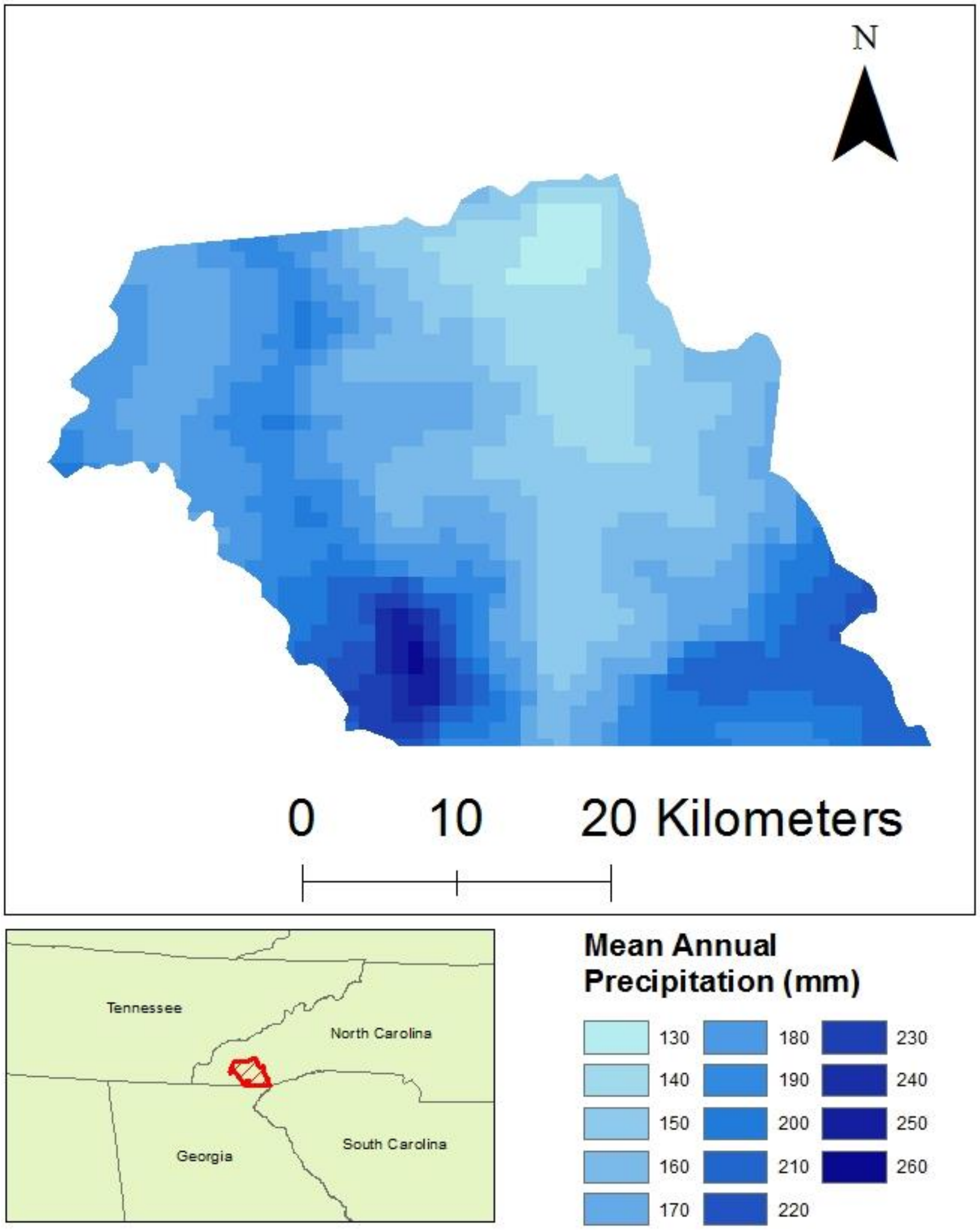

Figure 1. 2. Chapter three study area, which consists of most of Macon County, North Carolina across a mean annual precipitation gradient.

CHAPTER 2

RELATIONSHIPS BETWEEN FINE-SCALE SITE PRODUCTIVITY METRICS AND THE ABUNDANCE OF INSECTIVOROUS SONGBIRDS IN THE SOUTHERN APPALACHIAN MOUNTAINS[1]

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ABSTRACT

We examined how spatial variation in long-term precipitation patterns and site productivity potential (integrated moisture index) directly and indirectly predicted foliar C:N, caterpillar biomass, and abundance of eleven songbird species in the southern Appalachian Mountains. We found that mean annual precipitation and IMI were significant local predictors of bird abundance; however, only four of eleven species showed a positive relationship between mean annual precipitation and abundance. Consistent with our predictions, mean annual precipitation was positively correlated with lower foliar C:N; however, foliar C:N was not a significant predictor of caterpillar biomass. We also did not observe any significant direct relationship between mean annual precipitation or IMI and caterpillar biomass. Our results suggest that variation in songbird abundance was best explained by elevation, which was highly positively correlated with mean annual precipitation.

INDEX WORDS: Abundance, distribution, N-mixture model, precipitation, integrated moisture index, elevation, insectivorous songbirds, caterpillars, foliar nitrogen, southern Appalachian Mountains

INTRODUCTION

Animal distributions and abundances are driven by a variety of hierarchical influences. At larger spatial scales, organisms' range limits and regional patterns of abundance are limited by physiological tolerances, which is determined by climate (Johnson 1980, Kaspari et al. 2000a, Kaspari et al. 2000b, Porter et al. 2000, Kaspari 2001, Brown and Ernest 2002). Within that physiologically suitable climate, individuals select habitat based on features that results in local non-random distributions of individuals (Fretwell and Lucas 1970, Johnson 1980). Identifying the hierarchical nature of features related to finer-scale species abundances is important for identifying the proximate influences driving habitat selection, and for developing finer-resolution habitat suitability models to inform management.

For some species, the proximate variables generating local patterns of abundance are not known; however, it is generally assumed that the availability of food, suitable refugia or nesting sites, or predator abundance are important factors. Despite recognition of their importance, these biological factors are challenging to quantify and, therefore, usually excluded from models used by managers and planners (e.g. U.S. Geological Survey Gap Analysis Program 2011). Moreover, prey and predator abundance are likely temporally variable, therefore snapshot measurements of those factors are likely poor predictors of local abundance. A potential solution to this challenge is the identification of indirect measures of resource availability or predator abundance. In many ecosystems, high food availability is often associated with high primary productivity and resource quality (Perner et al. 2005). Therefore, local measures of primary productivity and resource quality may serve as better, finer-scale predictors of consumer abundance. In montane forest ecosystems, a suite of local drivers including local rainfall, slope, and aspect produce local variation in soil moisture and humidity that drive local variation in primary productivity, foliar nitrogen, and insect abundance (Rosenberg et al. 1983, Desta et al. 2004).

The goal of our research was to determine whether local estimates of climate and productivity were related to prey biomass and insectivorous songbird abundance in the southern Appalachian Mountains. Insect abundance, especially caterpillar abundance, is a critical resource for migratory songbirds attempting to raise chicks (Graber and Graber 1983, Graber et al. 1985, Arcese and Smith 1988, Holmes and Schultz 1988, Marshall et al. 2002, Nagy and Holmes 2005). Using field data collected in 2015 and 2016 we used structural equation modeling (SEM) to examine the relationships among mean annual precipitation, integrated moisture index, foliar nutrient quality of leaves, caterpillar biomass, and abundance of insectivorous breeding songbird, in the Coweeta Basin in western North Carolina. Further, we expected our measures of caterpillar biomass may be difficult to relate to bird abundance because caterpillar larvae is highly heterogeneous in time and space, surveying at a landscape level may be problematic (Gutiérrez et al. 1999). Instead we used foliar nitrogen (foliar N) as a proxy for caterpillar abundance. As a result we also examined the relationship among mean annual precipitation, integrated moisture index, foliar nutrient quality of leaves, and abundance of insectivorous breeding songbird in our study area.

We predicted a hierarchical relationship among songbird abundance and our predictor variables. Specifically, we predicted: (1) that sites with higher mean annual precipitation and integrated moisture would be negatively correlated with foliar C:N; (2)

mean annual precipitation and integrated moisture would be positively correlated with caterpillar biomass, and foliar C:N would be negatively correlated with caterpillar biomass; (3) mean annual precipitation, integrated moisture index would be positively correlated with songbird abundance (Figure 2.1). Further, we predicted similar relationships but removed caterpillar biomass; specifically we predicted: (1) that sites with higher mean annual precipitation and integrated moisture would be negatively correlated with foliar C:N; (2) foliar C:N would be negatively correlated with songbird abundance; (3) mean annual precipitation, integrated moisture index would be positively correlated with songbird abundance (Figure 2.2). Because habitat structure influences songbird nesting (MacArthur 1964, Johnson 1980, Rotenberry and Wiens 1980, Cody 1981), we also investigated the relationship between mean annual precipitation, integrated moisture index, vegetation structure, and songbird abundance.

METHODS

Study Site

Our study site was the Coweeta Basin (CWT), a 1,626 hectare (ha) watershed in the Nantahala National Forest of western North Carolina and site of the USDA Forest Service Coweeta Hydrologic Laboratory. CWT is located within the Blue Ridge Physiographic Province and is predominantly eastern deciduous forest. Mean July temperatures average 21.6 °C. Annual precipitation varies significantly in this region, from 178 cm at lower elevations to over 250 cm at higher elevations (Kohl 1990). Within the basin, elevation ranges from 677 m to 1600 m. Forest types within the watershed consist of oak-hickory, oak-pine, northern hardwoods, and cove hardwoods and areas have been subject to site and whole-watershed manipulations since the 1930’s (Day et al.

1988, Douglass and Hoover 1988). CWT topography including steep slopes with north and south facing aspects results in steep gradients in precipitation and soil moisture over a relatively short distance (Figure 2.3 and see Daly et al. 2017).

Plot selection

We chose 68 sampling locations at least 200 m apart and stratified among eight sub-watersheds and north and south facing aspects. Plots ranged in elevation between 900-1200 m and spanned the gradient of mean annual precipitation gradient between 150-260 mm (Figure 2.2). Mean annual precipitation was determined using 30-year, daily precipitation estimates at 1-km2 resolution (Thornton 2016). elevation of sites was determined using 10 m DEM in ArcMap 10.X (U.S. Geological Survey 2016), in ArcMap 10.X (ESRI 2011). For each site we calculated an integrated moisture index (IMI) derived from hillshade, flow accumulation of water downslope, curvature of the landscape, and soil depth (Iverson et al. 1997).

Estimating Breeding Bird Abundance

We conducted two, single observer, 10 minute, 100 m radius point count surveys (Hamel et al. 1996) between May 3 and July 10, 2015 and 2016. The first sample occurred during the early portion of the breeding season and the second sample date occurred during the middle to latter portion of the breeding season. Because songbird activity declines as the day progresses (Robbins 1981), we conducted all surveys before noon. We visited multiple sites each day, and we varied the order of site visits each time to avoid bias. Before each count we recorded variables that might affect a songbird detection such as wind and noise. We assigned noise levels to one of five categories: “no background noise (e.g., from a stream or road traffic)”, “some noise”, “more noise”, “even more”, and “heavy noise limiting ability to hear nearby birds”. We assigned wind levels to one of five categories: “no wind”, “leaves and twigs moving”, “small branches moving”, “small trees and/or branches moving”, and “strong wind”. We did not conduct counts during rain or when wind was strong enough to cause large trees to sway (Hamel et al. 1996). Our focal species were insectivorous songbirds (Table 2.1) but we recorded all songbirds detected.

Estimating Caterpillar Biomass

We conducted surveys of caterpillars within 50 m of each point count location every two-weeks between May 1st and July 9th. The repeated samples were to accommodate emergence of different caterpillar families. At each location, we selected at least two saplings of six focal tree species: *Castanea dentata, Acer rubrum, Quercus rubra, Acer pensylvanicum, Betula alleghaniensis, Amelanchier spp*. We systematically searched 50 leaves on each sapling and counted, identified to family, and their lengths measured (leaves and supporting petioles). We estimated each caterpillar’s wet mass using the length to mass regression equation of Rodenhouse (Rodenhouse 1986):

$$\textit{caterpillar wet mass} = 0.004*(\textit{caterpillar length in cm})^{2.64}$$

We summed biomass across the entire season for both years.

Estimating Vegetation Structure

We conducted vegetation surveys in a 10 m radius circular plot at the center of each point count location. We recorded diameter at breast height (DBH) for all woody species present that were ≥ 7.5 cm DBH and counted all woody saplings that were taller than one meter. From these data, we calculated mean and variance of DBH per plot. We also calculated shrub and deciduous sapling (< 7.5 cm) stem density per plot. To reduce the number of vegetation structure variables in our subsequent models, we took these four measures of structure and used a principal components analysis (Jolliffe 2002) as a data reduction technique to obtain two composite measures of habitat structure.

Estimating Foliar C:N

To estimate mean foliar C:N, we sampled leaves from two common species, *Q. rubra* and *A. rubrum*, which are known to exhibit variation in foliar C:N in response to variation in precipitation (Shure et al. 2003). Sampling occurred in July of 2016, late in the growing. From each species, we randomly sampled five leaves. For *A. rubrum*, we were able to sample individuals in three size classes (< 2.5 cm diameter at breast height (DBH), ≥ 2.5 cm to < 10 cm DBH, and ≥ 10 cm DBH) within each site. For *Q. rubra* we were only able to sample saplings (< 2.5 cm DBH). To sample leaves on larger trees, we used extension pole clippers to remove two small branches before selecting leaves from those branches. We stored leaves from each tree in individual, sterile, marked bags and placed each bag in a cooler with ice. In the lab, we stored samples in a standard freezer. For analysis, we dried leaves in a forced-air drying oven at 112°F (44.4°C), milled via a Wiley mill, and homogenized all samples by species and sample location. We measured total nitrogen and carbon using an Elemental Analyzer (Thermo-Fisher Scientific Flash 2000, P/N 31712052) at the Water and Soil Laboratory for Environmental Analysis at the University of Georgia. For each sample, we calculated the molar ratio of C:N as follows:

$$C/N = \%C / \%N * 1.17.$$

We estimated a “mean plot foliar C:N” as the average C:N of *Q. rubra* and *A. rubrum* weighted by their basal area, estimated for each site.

Statistical Analysis

We first examined correlation among our explanatory variables using correlation matrices and principal component analysis. We used this to eliminate any highly redundant variables and to guide inferences from our structured equation model. We used a general linear model to test the effects of mean annual precipitation and integrated moisture on *A. rubrum* and *Q rubra* foliar C:N.

We used gdistsamp, a hierarchical likelihood-based model (Chandler et al. 2011) in the R package Unmarked (Fiske and Chandler 2011) to examine the effects of environmental noise, observer, and time of day and of year on our ability to sample songbirds during our study; we were interested in these variables because they ultimately have the ability to impact estimated songbird abundance. Availability is the probability that a songbird would be singing at the sampling location during the 10 minute sampling period; we examined how the effects of day of year and time of survey impacted songbird availability. Detection is the probability we would be able to detect a songbird by song at the sampling location during the sampling period; we examined the effects of observer, wind, and noise on songbird detection.

For models of availability we held detection and abundance constant across sites (MacKenzie et al. 2005). We compared four availability models: (1) availability was constant, (2) availability varied among survey periods based on time of the survey, (3) availability varied among survey periods based on date of year, (4) and availability varied among survey periods based on time of survey and day of year. We used model selection (Burnham and Anderson 2002) to compare these models for each species.

We modeled detection probability for each species assuming constant abundance and availability across sites (MacKenzie et al. 2005). We compared five detection models: (1) probability of detection was constant, (2) probability of detection varied by observer, (3) probability of detection varied by noise, (4) probability of detection varied by wind, (5) and probability of detection varied by observer, noise, and wind. We used model selection (Burnham and Anderson 2002) to compare these models for each species. We included covariates that affected availability and detection in our subsequent structured equation model to account for imperfect availability and detection.

We used the lavvan package (Rosseel 2012) in R 3.2.2 (R Core Team 2015) to conduct structured equation modeling of vegetation, precipitation, and integrated soil moisture effects on foliar C:N, caterpillar biomass, and bird abundance (Figures 2.1)(Grace 2006). Because we expected our measures of caterpillar biomass may be difficult to relate to bird abundance (Gutiérrez et al. 1999), we also created a SEM without caterpillar biomass, as a proximate factor to bird abundance (Figure 2.3). We standardized all variables prior to analysis. We tested models with different covariate combinations and concluded that models with coefficients < | 0.05 | were effectively zero and, thus, chose to incorporate covariates that had estimates > | 0.05 | to minimize over-parameterization. We tested the fit of each SEM using several methods. First, we tested the absolute fit of the model to observed data versus a null model using a chi-squared test, and by checking the value of the standardized root mean square residual (SRMR), where a value of ≤ 0.08 indicates good fit (MacCallum et al. 1996). We also checked the root mean square error of approximation (RMSEA), which takes model parsimony into consideration, and where a value of 0.06 or below indicates good fit. In addition, we checked the comparative fit index (CFI), which compares model fit to a nested baseline model, and the Tucker–Lewis index (TFI), which is similar to the CFI but takes model parsimony into account. In both of these indices, a value of 0.95 or larger indicates good model fit (Brown 2006).

RESULTS

We conducted a total of 272 point counts among the 68 plots between 2015 and 2016. We detected a total of 64 species and 4,294 individual birds. In both years, we conducted 680 caterpillar surveys of 34,000 leaves and detected 625 individual caterpillars representing six families. In 2015 we conducted vegetation surveys of 68 plots and identified 4,237 individual shrubs and trees to 54 species. In 2016 we collected 1,020 leaves from *A. rubrum* and 340 leaves from *Q. rubra*.

Mean annual precipitation was highly positively correlated with elevation among our sites (R^2=68%, $p < 0.001$). Thus, we did not include elevation in any subsequent analysis. Based on our principal component analysis of our remaining environmental variables (Figure 2.4, Table 2.2) mean annual precipitation was positively correlated with the basal area of *Q. rubra* and variation in tree DBH, and negatively correlated with shrub stem density. Mean annual precipitation was also negatively correlated with foliar C:N of *Q. rubra* and *A. rubrum.* Average DBH was positively correlated with basal area of *A. rubrum* and negatively correlated with deciduous stem density. There was no significance difference in mean foliar C:N between *Q. rubra* and *A. rubrum* (Table 2.3). Mean annual precipitation and IMI were both negatively correlated with mean foliar C:N. There were no significant interactions between tree species and mean annual precipitation or IMI on mean foliar C:N (Table 2.3).

The first two principal components from our PCA of vegetation structure explain 74% of the variation among our four variables (Figure 2.5, Table 2.4). The first PC explained 42% of the variation and was driven predominantly by variation in mean DBH, DBH variance, and deciduous sapling density. Thus, the first PC largely separated forest plots with older and more variable tree size structure from younger, more homogenous forest plots. The second PC explained 32% of the variation and was determined largely by shrub stem density, deciduous sapling stem density, and variance in DBH. Therefore, the second PC separated plots with more shrub midstory versus plots with more deciduous midstory.

Mean annual precipitation was significantly correlated with estimated plot-level mean foliar C:N (Table 2.5). Mean annual precipitation was negatively correlated with habitat structure principal component one and IMI was positively correlated. For mean annual precipitation, this indicated a positive relationship between mean annual precipitation and deciduous average DBH and a negative relationship between historic precipitation and deciduous stem density, primarily driven by saplings (Table 2.5). However, for IMI, this indicated a negative relationship between IMI and average DBH, and a positive relationship between and variation in DBH deciduous stem density, primarily driven by saplings (Table 2.5). Principal component two was significantly negatively correlated with mean annual precipitation and significantly positively correlated with IMI. This indicated a negative relationship between mean annual precipitation and shrub stem density and a positive relationship between IMI and shrub stem density (Table 2.5). Caterpillar biomass was not significantly related to any variables (Table 2.5).

The effects of day of year and time of day on availability and the effects of wind and noise on detection varied among species (Tables A.1). Day of year affected availability of two of 11 species and time of survey affected availability for three of the 11 species (Table A.1). Noise affected detection for one of 11 species, wind affected four of 11 species, and observer affected three species (Table A.2). Some species detection models would not coverage and thus are not accounted for and as a result delta AIC has not been calculated for such models (Table A.2)

SEM models of bird abundance that included latent variables generally had model fit outside generally accepted thresholds. SEM models of bird abundance with latent variables excluded had substantially improved model fit. Parameters estimates were similar in models with and without latent variables (Tables 2.6 and 2.7). Therefore, we proceeded with models that did not include latent variables for detection and availability (Tables 2.6 and 2.7).

For SEM models that included caterpillar biomass, the effects of vegetation structure (PC1 and PC2), precipitation, IMI, foliar C:N, and estimated caterpillar biomass on bird abundance varied by species (Table 2.6). Abundance differed between years for six of 11 species. One species showed a significant direct, negative correlation between caterpillar biomass and abundance. Mean annual precipitation was significantly directly correlated with abundance for ten of 11 species. Mean annual precipitation was directly, significantly positively correlated with abundance for four of 11 species and significantly negatively correlated with abundance for six. IMI was directly, significantly positively correlated with abundance for four species and directly, significantly negatively correlated with two species. Vegetation structure PC1 and PC2 were significantly correlated with abundance of three and two species, respectively. Relationships between these parameters and bird abundance did not differ substantially for models where mean plot foliar C:N was substituted for caterpillar biomass (Table 2.9).

DISCUSSION

Our results showed that mean annual precipitation and IMI were significant local predictors of bird abundance. However, abundance of only two of 11 species showed a positive relationship with mean annual precipitation and IMI, as we had predicted. For three of the 11 species, the relationships were negative. We expected that the indirect, proximate mechanism linking mean annual precipitation and IMI to bird abundance would be the effects of moisture on foliar quality and subsequent effects on caterpillar biomass. Consistent with our predictions, mean annual precipitation was significantly positively correlated with lower foliar C:N for both *A. rubrum* and *Q. rubra*; however, foliar C:N was not a significant predictor of caterpillar biomass. We also did not observe any significant direct relationship between mean annual precipitation or IMI and caterpillar biomass. One potential explanation for why we had strong but, inconsistent relationship between mean annual precipitation and songbird abundance, was that mean annual precipitation was strongly correlation with elevation; therefore, songbird abundance was likely responding more to temperature gradients facilitated by elevation rather than historic precipitation. Consistent with this trend, the four species that showed positive relationships with mean annual precipitation, Blue-headed Vireo (*Vireo solitaries*), Black-throated Blue Warbler (*Setophaga caerulescens*), Canada Warbler (*Cardellina canadensis*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*), are all species known associated to be associated with high elevation habitat in the southern

Appalachian Mountains. The five species that showed negative relationships are species that are more widely distributed across the southeast U.S. and known to occur at low elevations in the southern Appalachian Mountains. Therefore, among the 11 songbirds we studied it appears more likely that temperature, driven by elevation, is the primary factor driving local abundances of songbirds. For those four species that were more abundant at higher elevation, it is not clear whether they are responding directly to the higher mean annual precipitation or whether some other factors associated with elevation are driving local abundance. However, there is evidence to suggest that one species is responding to higher mean annual precipitation. In a subsequent study, looking at the distribution of Black-throated Blue Warbler we found that models using precipitation were better than models that contained elevation (Chapter 3, Abernathy 2017).

There are many potential reasons why we failed to find a relationship between caterpillar biomass, foliar quality, and songbird abundance. One possibility is that our methods for estimate caterpillar biomass maybe too imprecise or stochastic to represent true prey availability. In our search of 34,000 leaves we only found 625 caterpillars, suggesting that caterpillar density, or detection is very low. This would suggest that significantly more sampling effort would be require to generate more reliable estimates of caterpillar biomass. Nonetheless, a number have other studies, using similar caterpillar survey methods to ours, have found positive relationships between estimated caterpillar biomass and nesting attempts, number of fledging per nest, nestling growth rates and survival (Rodenhouse and Holmes 1992, Nagy and Holmes 2004, Nagy and Holmes 2005). A second reason why we found no relationship could be that, while caterpillars are important resource, the songbird sampled in this study exhibit prey switching and we did not account for other insects present at a site. A third reason, may be that songbirds can compensate for local variation in caterpillar abundance by expanding their search area when feeding nestlings; this is because territory size is inversely related to food abundance (Stenger 1958, Pitelka 1959, Moss 1969, Clarke 1970, Holmes 1970, Watson and Moss 1970, Stimson 1973, Slaney and Northcote 1974, Gill and Wolf 1975, Simon 1975, Gass et al. 1976, Salomonson and Balda 1977, Maher and Lott 1995, Anderson et al. 2009). So it may be that caterpillar biomass would be better predicted if it was integrated across a larger sample area. Therefore, in sites with lower caterpillar biomass, songbirds could compensate for local variation in prey, by (1) expanding their diet breath or (2) expanding their search area. Further efforts might be improved by having more robust ways of estimated caterpillars or other insects at larger spatial extents. It should be noted that failing to find a relationship between caterpillar biomass, foliar quality, and songbird abundance need not be limited to the outlined reasons above; other factors such as stochastic biological processes and songbird competition could also play a role in trophic relationships.

As expected we also found evidence that habitat structure influenced the abundance of some bird species. Black-throated Blue Warbler, Canada Warbler, and Northern Parula (*Setophaga americana*) were positively associated with sites with higher mean DBH and greater variation in DBH. This indicates that they were distributed among older, more uneven forest stands. Paradoxically, Black-throated Blue Warbler abundance was negatively associated with shrub stem density. It is well known that Black-throated Blue Warbler, in their southern range, preferentially nest in shrubs (Steele 1993, Holmes 1994), and have been known to nest in *Rhododendron species* (Holmes 2005). Our measure of shrub stem density did not distinguish *Rhododendron species* from other shrub species, notably *K. latifolia*. While Black-throated Blue Warbler have shown to nest in *K. latifolia* in the southern Appalachian Mountains (Burdett and Niemi 2003), *K. latifolia* are typically found in xeric southern-facing slopes (Gleason and Cronquist 1963, Lorenz et al. 1991, McNab and Browning 1993, Blankenship and Arthur 1999, Radford et al. 2010). Therefore, we hypothesize that the negative relationship between shrub stem density and Black-throated Blue Warbler reflects the high number of mountain laurel we observed at our sites, and ultimately a negative relationship with Black-throated Blue Warbler and xeric sites. Given that Black-throated Blue Warbler have a positive relationship with mean annual historic precipitation and IMI, the negative relationship between Black-throated Blue Warbler and xeric sites is consistent with our findings. We note that *Rhododendron species* density is typically higher on sites with higher mean annual precipitation (Oosting and Bourdeau 1955, Whittaker 1962, Gleason and Cronquist 1963, Strausbaugh and Core 1978, Seymour 1982, Wofford 1989, Little 2002, Radford et al. 2010) and ideal habitat for this species is within coves (Nilsen 1986, Nilsen et al. 1987, Plocher and Carvell 1987) and on north-facing slopes (Spencer 1932, Lipscomb and Nilsen 1990, Dobbs and Parker 2004), both of which have high IMI (Iverson et al. 1997). This may be an important proximate mechanism linking high mean annual precipitation to Black-throated Blue Warbler abundance.

Our study did find evidence that local climatic variables were good predictors of variation in breeding songbird abundance. We did not find any evidence that those climatic variables serve as good indirect prey availability. Caterpillar biomass were not a significant predictor of bird abundance and foliar C:N was not a significant predictor of bird abundance. Instead, our results suggest for some species local climate variables may be a driver of vegetation structure which could affect nest site availability. The strong relationship with most species and elevation may also indicate that factors we have not considered in this study are important determinates of local songbird abundance.

One such factor could be the unique habitat associations of trailing edge populations. Within stable trailing-edge populations selection tends to favor local adaption as opposed to vagility and generalism (Dynesius and Jansson 2000); in combination with reduced gene flow from core populations this can yield individuals with unique and distinct ecotypes (Hampe and Bairlein 2000, Castric and Bernatchez 2003, Pérez-Tris et al. 2004). For example, within the age structure of *Juniperus communis* L. classes shifted from that of young dominated in the northern range to young dominated in the southern range due to lack of water availability (García et al. 1999). Thus, future studies should more rigorously consider the habitat associations of southern trailing edge insectivores may be unique compared to core populations and could explain local songbird abundance in this area.

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TABLE 2.1. This table lists the alpha code, preferred breeding food source, foraging behavior, and indicates is a species is at the southern limit of its breeding range (Rodewald 2015). Caterpillars are in boldface.

Bird	**Preferred food**	**Behavior**	**Edge species**
BHVI	**Caterpillars**, stink bugs, beetles, wasps, bees, ants, moths, tree crickets, and many others; also spiders.	foliage gleaner	yes
BTBW	**Caterpillars**, moths, and crane flies, also spiders.	foliage gleaner	yes
BTNW	**Non-hairy caterpillars** during summer, as well as beetles, true bugs, gnats, aphids, and others, also spiders.	foliage gleaner	yes
CAWA	Beetles, mosquitoes, flies, moths, and **smooth caterpillars**	foliage gleaner	yes
HOWA	Wide variety of insects, including **caterpillars**, moths, grasshoppers, beetles, flies, and many others; also eats many small spiders	foliage gleaner	no
NOPA	Small beetles, flies, moths, **caterpillars**, egg clusters, true bugs, ants, bees, wasps, and other insects, also spiders.	foliage gleaner	no
RBGR	About half of annual diet may be insects, including beetles, **caterpillars**, grasshoppers, true bugs, and others, also spiders and snails. Eats many seeds, including those of trees such as elms, and sometimes eats buds and flowers.	foliage gleaner	yes
REVI	**Caterpillars**, moths, beetles, wasps, bees, ants, bugs, flies, walking sticks, cicadas, treehoppers, scale insects; also some snails and spiders. Also eats many berries	foliage gleaner	no
SCTA	**Caterpillars**, moths, beetles, wasps, bees, aphids, and many others; also some spiders, snails, worms, millipedes. Also eats wild fruits and berries	foliage gleaner	no
TUTI	Insects make up close to two-thirds of annual diet, with **caterpillars** the most important prey in summer; also eats wasps, bees, sawfly larvae, beetles, true bugs, scale insects, and many others, including many insect eggs and pupae.	foliage gleaner	no
WEWA	Eats smooth **caterpillars**, small grasshoppers, bugs, ants, bees, walking sticks, beetles, sawfly larvae, and spiders.	foliage gleaner	no

TABLE 2.2. Summary of the results of our principal component analysis of abiotic variables used in our structured equation models.

Variables	PC1	PC2	PC3	PC4	PC5	PC6
Percentage explained	2.0425	1.7881	1.4728	1.0413	0.90694	0.83607
Average DBH	-0.40012	1.3163	-0.1079	0.070785	-0.35537	0.12268
Stem density shrubs	0.79767	0.5756	-0.5375	0.586177	0.65638	0.02099
DBH variation	-1.05981	0.68572	0.4317	0.172022	-0.31995	0.5477
Stem density deciduous	0.13132	-0.94204	0.7842	-0.2309	0.33228	0.7259
Mean annual precipitation	-0.89362	-0.54922	-0.4267	0.049009	0.06086	0.08677
IMI	-0.41671	0.11308	-0.9892	-0.00799	0.72084	0.73127
CN molar ratio RM	0.94459	-0.09773	-0.2039	0.255317	-0.78539	0.86033
CN molar ratio NRO	0.49241	0.28526	0.9404	0.93193	0.36032	0.03921
Total basal area of NRO	-1.11466	-0.39984	0.2743	0.812911	0.10407	-0.0648
Total basal area of RM	-0.02438	0.80094	0.7406	-0.81665	0.54482	0.18309

TABLE 2.3. Generalized linear model output from examining the relationship between mean annual precipitation or integrated moisture and tree species (*Q. rubra* and *A. rubrum*).

Variable	Estimate (CI)	Pr(>|t|)
Intercept	193 (101, 370)	0.000
Mean annual precipitation	0.996 (0.994, 1)	0.038
Species (*A. rubrum* and *Q. rubra*)	0.72 (0.30, 1.73)	0.462
IMI	0.99 (0.988, 1)	0.047
Mean annual precipitation *Species (A. rubrum and Q. rubra)	1 (0.998, 1.005)	0.469
Species (*A. rubrum* and *Q. rubra*)*IMI	1 (0.997, 1.013)	0.223

TABLE 2.4. Summary of the results of our principal component analysis of our vegetation metrics which will serve as habitat structure in our structured equation model.

Variables	PC1	PC2	PC3	PC4
Percentage explained	41.7	31.9	16.6	0.98
Average DBH	1.7909	-0.05828	0.2937	0.8921
Shrub stem density	0.3204	1.69651	1.0073	-0.3118
Variation in DBH	1.2745	-1.26968	0.5641	-0.7334
Deciduous stem density	-1.3764	-0.85657	1.1389	0.409

TABLE 2.5. Effects of historic mean annual precipitation and integrated moisture index (IMI) on principal components of forest vegetation structure (PC1 and PC2), foliar C:N, and caterpillar biomass. Statistically significant associations, where the 95% confidence intervals do not overlap with zero, are marked with boldface. CFI =1.0, RMSEA =0.00, SRMR =0.01.

X Variable ~ Y Variable (s)	Estimate	Standard Error	P(>|z|)
PC1 ~			
Mean annual precipitation	-0.003	0.09	0.97
Integrated moisture index	0.14	0.09	0.11
PC2 ~			
Integrated moisture index	0.18	0.08	**0.03**
30-year annual average precipitation	-0.24	0.08	**0.01**
Molar foliar C:N ~			
Integrated moisture index	-0.13	0.08	0.13
30-year annual average precipitation	-0.24	0.08	**0.004**
PC1	-0.05	0.08	0.55
Estimated caterpillar biomass ~			
Molar foliar C:N	0.02	0.09	0.84
Year	-0.20	0.17	0.23
PC1	-0.05	0.09	0.59
PC2	-0.05	0.09	0.59

TABLE 2.6. Parameter estimates, latent variables, and fit statistics of the SEM 1 for each bird species. Bold parameter estimates are significant. Species with asterisks and their corresponding parameters estimates are models that have accounted for the respective species most significant variables that impact that species detection and availability.

Species	Mean annual Precipitation	IMI	PC1	PC2	Caterpillar Biomass	Year	Date	Time	Wind	Noise	Observer	CFI	SRMR	RMSEA
BHVI	**0.49**	0.09	-0.09	-0.14	-0.12	**1.18**	-	-	-	-	-	1	0.01	0
BTBW*	**1.19**	**0.42**	**0.32**	**-0.36**	0.12	0.49					0.09	0.85	0.07	0.10
BTBW	**1.20**	**0.44**	**0.34**	**-0.36**	0.12	**0.61**	-	-	-	-	-	1	0.01	0
BTNW*	**-0.59**	0.07	-0.19	-0.21	-0.12	-0.50	-	-	**-0.22**	-	-	0.56	0.09	0.12
BTNW	**-0.74**	0.06	-0.15	-0.21	-0.11	-0.15	-	-	-	-	-	1	0.01	0
CAWA*	**0.64**	**0.24**	**0.17**	-	-	-0.22	-	-	-	-	**-0.19**	0.84	0.07	0.09
CAWA	**0.63**	**0.21**	0.15	-	-	**-0.47**	-	-	-	-	-	0.74	0.08	0.11
HOWA*	**-0.30**	**0.28**	-	0.16	-0.10	-0.15		-	**-0.24**	-	-	0.64	0.09	0.12
HOWA	**-0.46**	**0.27**	-	0.15	-0.09	0.23	-	-	-	-	-	1	0.01	0
NOPA*	-	**0.07**	**0.10**	-	-	-0.09		0.03				1.0	0.05	0
NOPA	-	**0.07**	**0.10**	-	-	-0.07	-	-	-	-	-	1	0.02	0
RBGR*	**0.35**	**-0.24**	**-0.20**	0.09	-0.06	-0.18	-	-	-		0.03	0.76	0.07	0.10
RBGR	**0.35**	**-0.24**	**-0.20**	0.09	-0.05	-0.14	-	-	-	-	-	1	0.03	0
REVI*	**-0.30**	0.08	-0.17	-0.13	**-0.21**	**-0.79**	**0.03**	-	-	-	-0.03	0.45	0.09	0.12
REVI	**-0.36**	0.07	-0.17	-0.12	**-0.21**	**-0.85**	-	-	-	-	-	1	0.02	0
SCTA*	**-0.26**	-0.10	0.08	-0.05	**0.20**	0.03	**-0.03**	**-0.40**	**-0.18**	**-0.14**	0.07	0.55	0.11	0.13
SCTA	**-0.46**	-0.16	0.06	-0.05	0.10	0.11	-	-	-	-	-	1	0.02	0
TUTI*	**-0.17**	**-0.14**	-	**0.14**	-	**0.79**	-	-0.02	-	-	-0.07	0.66	0.08	0.09
TUTI	**-0.18**	**-0.15**	-	**0.14**	-	**0.70**	-	-	-	-		1	0.02	0
WEWA*	**-0.23**	-0.08	-	-	-0.05	**-0.34**	-	-0.11	-	-	-	1	0.05	0
WEWA	**-0.25**	-0.08	-	-	-0.06	**-0.38**	-	-	-	-		1	0.06	0

TABLE 2.7. Results for each bird species of the structured equation model 2 that uses foliar nitrogen as a proxy for caterpillar biomass. Bold parameter estimates are significant. Species with asterisks and their corresponding parameters estimates are models that have accounted for imperfect detection and availability variables in the structured equation model.

Species	Mean annual precipitation	IMI	PC1	PC2	Molar C:N	Year	Date	Time	Wind	Noise	Observer	CFI	SRMR	RMSEA
BHVI	**0.50**	0.11	-0.08	-0.13	-	**1.2**	-	-	-	-	-	1	0	0
BTBW*	**1.15**	**0.39**	**0.32**	**-0.33**	-0.12	0.45	-	-	-	-	0.10	0.83	0.08	0.12
BTBW	**1.16**	**0.41**	**0.33**	**-0.34**	-0.10	**0.59**	-	-	-	-	-	1	0	0
BTNW*	**-0.60**	-	-0.18	-0.19	-0.10	-0.48	-	-	**-0.22**	-	-	0.48	0.10	0.13
BTNW	**-0.74**	-	-0.15	-0.19	-0.07	-0.13	-	-	**-**	-	-	0.84	0.06	0.06
CAWA*	**0.64**	**0.22**	**0.18**	-	-	-0.22	-	-	-	-	**-0.18**	0.79	0.08	0.13
CAWA	**0.61**	**0.18**	**0.15**	-	-0.06	**-0.47**	-	-	-	-	-	1	0.01	0
HOWA*	**-0.24**	**0.25**	-	**0.21**	0.09	-0.26	**0.03**	-	**-0.22**	-	-	0.56	0.12	0.15
HOWA	**-0.45**	**0.32**	-	0.17	0.11	-0.25	-	-	-	-	-	1	0	0
NOPA*	-	**0.08**	**0.10**	-	-	-0.09	-	0.03	-	-	-	1	0.05	0.01
NOPA	-	**0.08**	**0.10**	-	-	-0.07	-	-	-	-	-	1	0.01	0
RBGR*	**0.38**	**-0.24**	**-0.19**	0.08	0.05	-0.16	-	-	-	**-**	0.02	0.78	0.08	0.12
RBGR	**0.38**	**-0.23**	**-0.19**	0.08	0.1	-0.12	-	-	-	-	-	1	0.01	0
REVI*	**-0.33**	-	-0.17	-0.08	-0.13	**-0.90**	0.03	-	-	-	-0.03	0.44	0.10	0.15
REVI	**-0.39**	0.05	-0.17	-0.11	-0.14	**-0.81**	-	-	-	-	-	1	0	0
SCTA*	**-0.26**	-0.08	0.07	-0.07	0.10	-	**-0.03**	**-0.36**	**-0.17**	**-0.12**	0.06	0.75	0.09	0.10
SCTA	**-0.43**	-0.13	0.07	-0.06	0.17	0.09	-	-	-	-	-	1	0	0
TUTI*	**-0.17**	-0.07	-	0.12	0.12	**0.86**	-	0.01	-	-	**-0.08**	0.52	0.11	0.15
TUTI	**-0.16**	-0.11	-	0.13	0.10	**0.69**	-	-	-	-	-	1	0.01	0
WEWA*	**-0.22**	-	-	-	0.07	**-0.33**	-	-0.11	-	-	-	0.59	0.05	0
WEWA	**-0.24**	-	-	-	0.08	**-0.37**	-	-	-	-	-	1	0.01	0

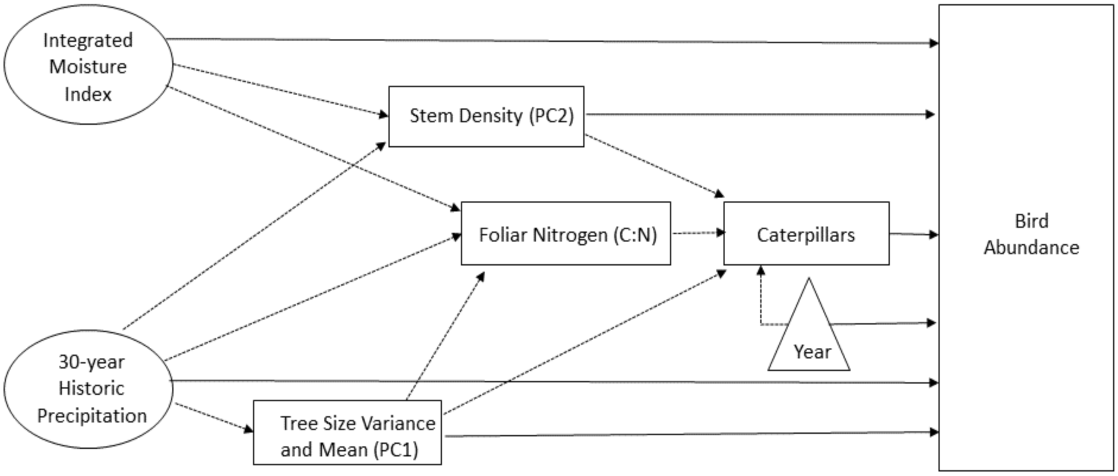

FIGURE 2.1. The structural equation model used to estimate the indirect and direct of mean annual precipitation and integrated moisture index vegetation structure, foliar C:N, caterpillar biomass, and songbird abundance. Arrows between boxes represent assumed causal associations between the mean-standardized traits, dashed lines represent indirect relationship, and solid lines represent direct relationships.

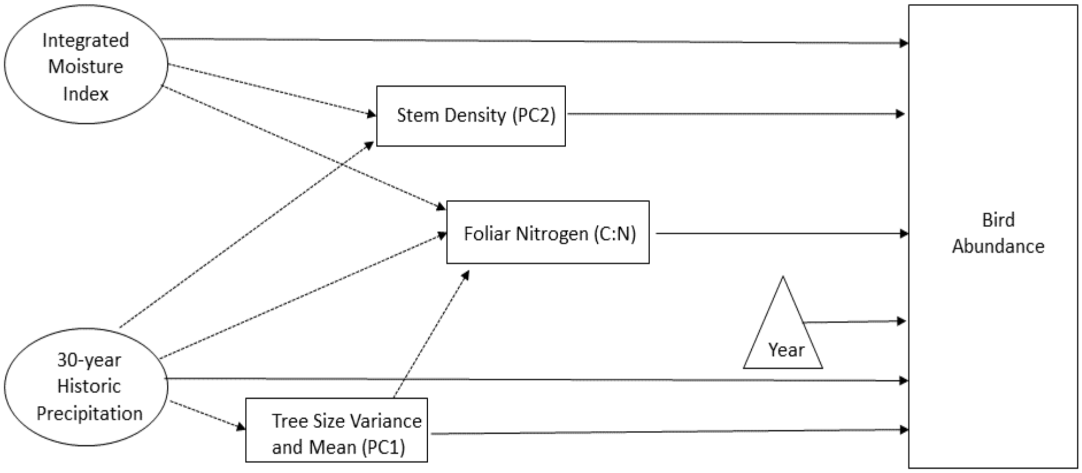

FIGURE 2.**2**. The structural equation model used to estimate the indirect and direct of mean annual precipitation and integrated moisture index vegetation structure, foliar C:N, and songbird abundance. Arrows between boxes represent assumed causal associations between the mean-standardized traits, dashed lines represent indirect relationship, and solid lines represent direct relationships.

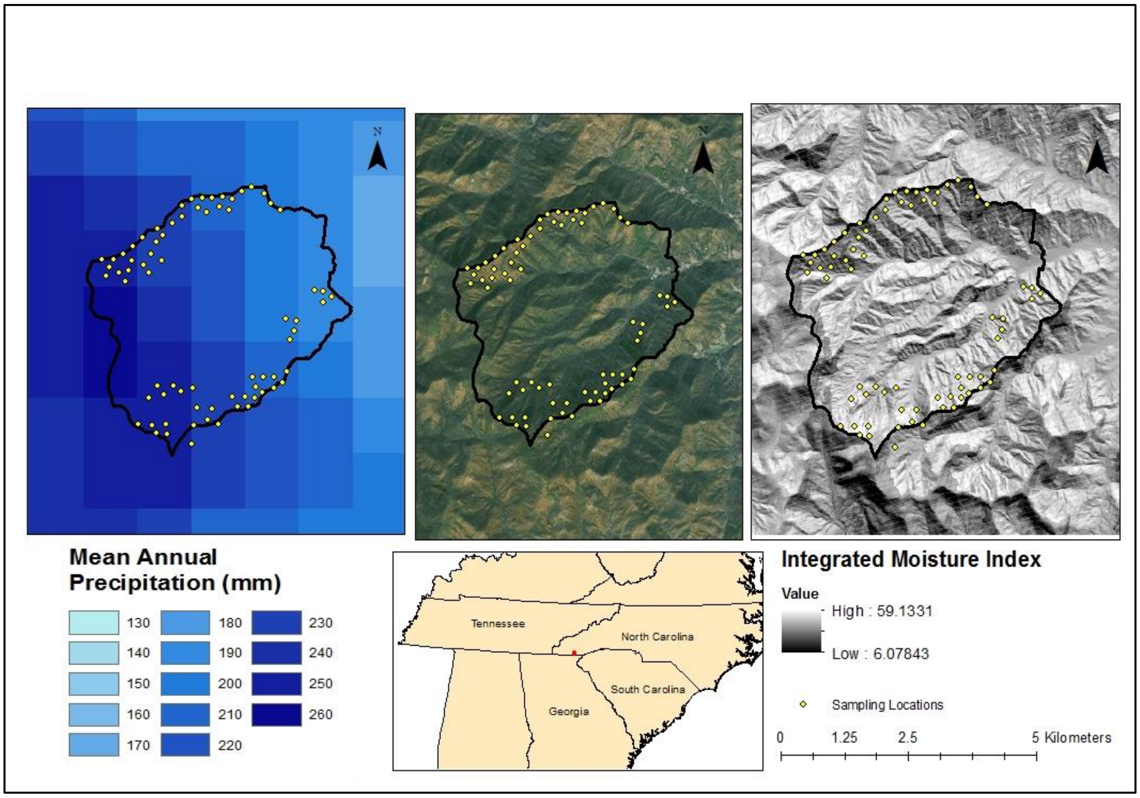

FIGURE 2.3. Coweeta Basin, Macon County, NC displayed over respective spatial data from left to right: historic precipitation, aerial imagery, and integrated moisture index.

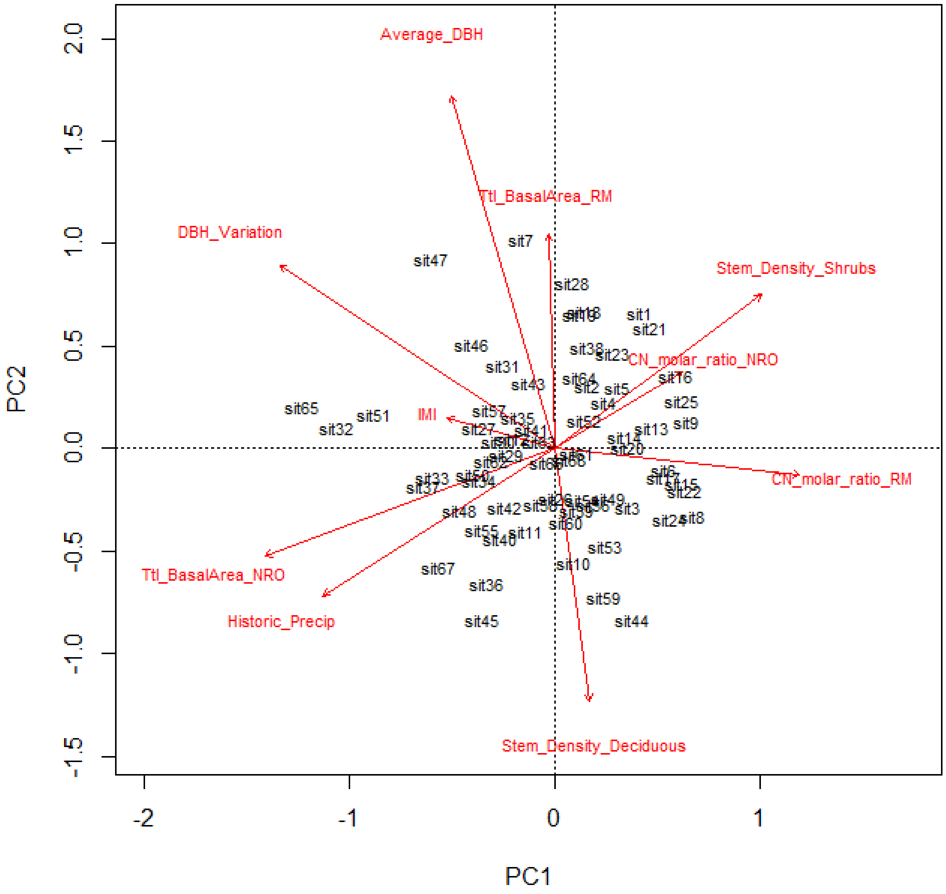

FIGURE 2.4. A 2-D representation of the principal component analysis which was used to examine the correlations between abiotic variables used in the structured equation models.

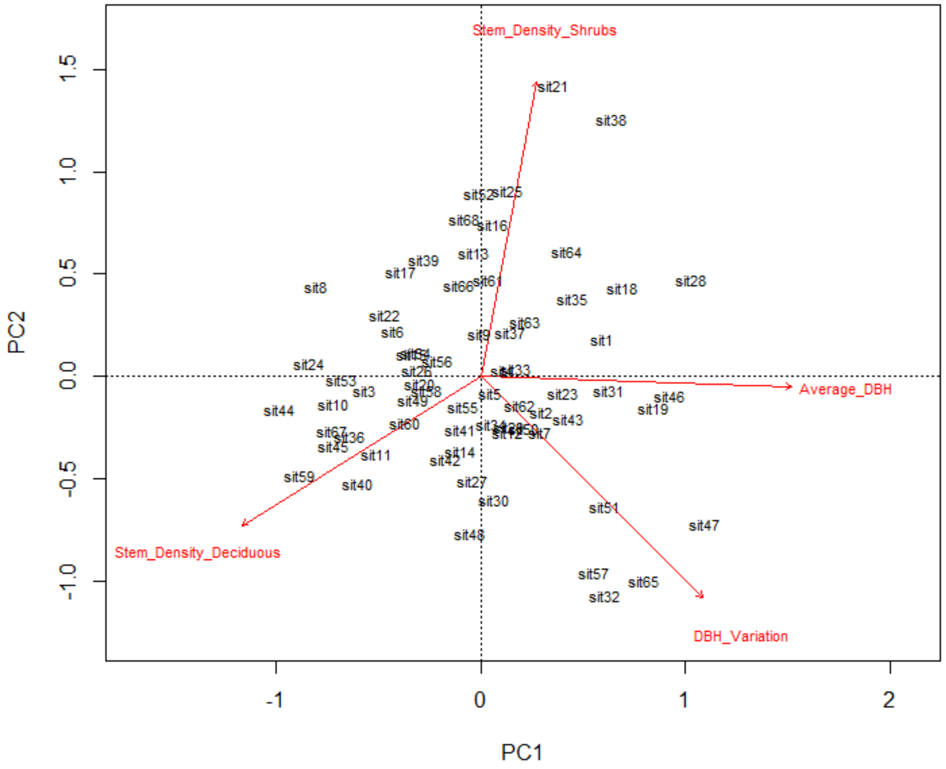

FIGURE 2.5. A 2-D representation of the principal component analysis used to reduce vegetation survey data into two variables, which represent most of the variation within our vegetation data.

CHAPTER 3

INCORPORATING FINE SCALE ABIOTIC VARIABLES TO BUILD BETTER DISTRIBUTION MODELS FOR TRAILING EDGE SPECIES[1]

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[1] Heather Abernathy, John Maerz, and Jeffrey Hepinstall-Cymerman. To be submitted to *Journal for Nature Conservation*

Abstract

Identifying areas of suitable habitat is a fundamental management need. We compared occupancy models using land cover and elevation only to models that included finer scale climate data to compare estimates of habitat availability, distribution, and fragmentation for trailing-edge populations of the Black-throated Blue Warbler (*Setophaga caerulescens*, BTBW) in western North Carolina. Models that included local mean annual precipitation, integrated moisture index, and heat load index predicted 4,800 - 44,776 fewer acres of suitable habitat than models using land cover and elevation. Further, the configuration and connectivity of Black-throated Blue Warbler trailing edge population distributions is likely more fragmented and isolated than is currently represented by widely accessible SDMs for this species. SDMs for trailing-edge populations in the southern Appalachians should re-examine habitat and occupancy correlations for such populations; this reconsideration will reduce over-predictions, enhance targeted management, and decreases the likelihood of unnecessary conflict between other land uses and habitat protection for priority management species.

INDEX WORDS: Occupancy, species distribution, N-mixture model, precipitation, integrated moisture index, elevation, Black-throated Blue Warbler, trailing edge populations, southern Appalachian Mountains

Introduction

Species Distribution Models (SDMs) are used in a variety of ways to explore ecological concepts and inform conservation and management decisions (Austin 1992, Beerling et al. 1995, Leathwick et al. 1996, Leathwick 1998, Pearce and Lindenmayer 1998, Guisan and Theurillat 2000, Anderson et al. 2002, Elith and Burgman 2002, Ferrier 2002, Vetaas 2002, Peterson 2003, Raxworthy et al. 2003, Araújo et al. 2004, Engler et al. 2004, Graham et al. 2004, Thomas et al. 2004, Thuiller 2004). SDMs are empirical models that relate field observations to environmental predictor variables to generate response surfaces (Guisan and Zimmermann 2000). In order for SDMs to produce robust predictions, sound ecological principles and mechanistic relationships should be used in a systematic manner to justify decisions made during the modeling process (Austin 2002, Huston 2002, Wiens and Scott 2002). This is particularly true when applying SDMs in marginal portions of species' ranges. Most SDMs are developed using range-wide occurrence data and species-habitat relationships that are heavily influenced by data on populations within the core of a species' range. Populations at range margins may have unique ecological relationships which may not be represented by the habitat associations of core populations. As a result, SDMs should attempt to integrate more local factors associated with occupancy patterns in range margins (Austin and Van Niel 2011).

The National GAP Analysis Program (GAP) is a program which aims to create habitat suitability models for many species to highlight areas of conservation and management. Many of the habitat suitability models that GAP creates are fundamental in conservation planning, forecasting (e.g., climate change), and research because, in most cases, such models are the most readily available and cover large spatial extents (U.S. Geological Survey Gap Analysis Program 2011). Rather than predict species probability of occupancy, GAP models predict areas of suitable habitat through the use rule-based models of species-habitat association. In GAP models and others, habitat suitability evaluates an area's suitability for a particular species. While GAP provides baseline estimates of potential habitat, these models are derived from habitat relationships for populations located predominantly within the species core range and elevational thresholds (U.S. Geological Survey Gap Analysis Program 2011). As a result, models of suitable habitat, particularly at range margins, are likely too generalized and coarse for targeted management (e.g., habitat protection), and may increase the likelihood of unnecessary conflict between other land uses and habitat protection for priority management species.

The need to consider finer resolution habitat characteristics may be particularly acute for management of trailing-edge populations. Trailing-edge populations are more likely to depend on specific bioclimatic refugia that buffer exposure to unsuitable climates (Parmesan et al. 1999, Hampe et al. 2005, Rull 2009, Ashcroft 2010, Gillingham et al. 2012, Sunday et al. 2014, Varner and Dearing 2014, Hylander et al. 2015). Interrupted gene flow between trailing edge and core populations can result in the evolution of unique and distinct ecotypes within trailing edge populations (Hampe and Bairlein 2000, Castric and Bernatchez 2003, Pérez-Tris et al. 2004) and adaptations, such as more specific habitat selection behaviors (Holt 1987, Hoffmann and Blows 1994, Bridle and Vines 2007). Therefore, it may not be appropriate to apply habitat attributes derived from core populations when predicting local distributions of trailing edge populations (Austin and Van Niel 2011).

For temperate species, montane landscapes often provide bioclimatic refugia for trailing-edge, populations at warmer latitudes. This is because montane landscape provide steeply varying elevation (Gollan et al. 2014), dramatic shifts in slope and aspect (Loarie et al. 2008), or unique vegetation types (Lenoir et al. 2013). To predict and manage changes in the distribution of trailing edge populations, models to forecast the specific locations of suitable, montane refugia should be a priority (Keppel et al. 2012, Staudinger et al. 2013, Seabrook et al. 2014, Hylander et al. 2015, Jones et al. 2016, Morelli et al. 2016).

The objectives of this study were to: (1) develop local occupancy models using local bioclimatic factors for a trailing edge species in the southern Appalachian Mountains (2) and to compare these models to a coarser model using only land cover and elevation (*sensu* GAP). We compared the predicted amounts, distributions, and degree of fragmentation and isolation of predicted occupied habitats. The southern Appalachian Mountains contain a high diversity of species at the southern limits of their range. The steep topography creates a diversity of habitats and steep climate gradients creating significant habitat heterogeneity (Thornthwaite 1953, Weiss et al. 1988, Brown 1991, Coughlan and Running 1997). The Black-throated Blue Warbler (*Setophaga caerulescens*, BTBW) is an example of a species with trailing-edge breeding populations located in the southern Appalachian Mountains. Within the region, the species is restricted to high elevation fully-forested sites (Hamel 1992); and recent evidence suggests that individuals preferentially select breeding habitat that receive more mean annual precipitation (Abernathy 2017, chapter 2), suggesting Black-throated Blue Warbler may have unique habitat associations in the southern Appalachian Mountains compared to the core of their range. We predicted that models that included relationships between occupancy and local bioclimatic variables would predict significantly less Black-throated Blue Warbler occupied habitat.

We also predicted that models that included relationships between occupancy and local bioclimatic variables would predict significantly more Black-throated Blue Warbler habitat fragmentation. To examine how fragmentation changed between models, we examined varying thresholds of predicted probability occupancy with regard to fringe versus core habitat. We predicted that occupancy of core habitat would be less fragmented in the land cover and elevation model and have lower amounts of fringe habitat at all thresholds. Further, in both models we expected total amount of both core and fringe habitat to decrease with higher thresholds of predicted portability occupancy.

Methods

Study Site

Our study area was Macon County, North Carolina, USA (Figure 3.1). Macon County is located within the eastern deciduous forest of the Blue Ridge Physiographic Province of the southern Appalachian Mountains and contains portions of The Nantahala National Forest. The Nantahala National Forest within our study area consisted of oak-hickory, oak-pine, northern hardwoods, and cove hardwoods (Day et al. 1988). Mean July temperatures average 21.6 °C. Annual precipitation varies significantly in this region, from 178 cm at lower elevations to over 250 cm at higher elevations (Kohl 1990). Most low elevation areas (lower than 700m) in Macon County are either developed for residential, commercial, or agricultural use. Much of the higher-elevation area lies within the Nantahala National Forest and is covered by relatively contiguous second-growth hardwood forest (Day and Monk 1974). Over the last few decades, remnant privately-owned, high elevation areas have recently become vulnerable to exurban development (Wear and Bolstad 1998, Gragson and Bolstad 2006).

Songbird Data

We combined three point count datasets collected between 2010 and 2016 that covered large portions of the county (Table 3.1). The surveys differed in the number of times visited to each site, the number of observers at each point, and the time spent at each point count (Table 3.1). The surveys were similar in that they all: had a sampling area of 100 m, assumed sampling independence, occurred during the breeding season, occurred approximately at the same time of day, and were visited multiple times. All point count locations were minimally 200 m apart to increase sample independence. In order to create a prediction surface for our distribution maps, we created a minimum convex polygon around all point count locations. Additionally, we added a 100 m buffer around the polygon to account for points on the periphery. All surveys took place from May 4th to July 7th day of year (Table 3.1); this time period falls within the breeding season of most songbirds in the region (Hall 1964), and because of that, we assumed population closure within each season. The first sampling date occurred early in each season and the second sampling date occurred during the middle/later portion of the breeding season. The daily sampling window for the three surveys occurred between 6:00-11:15AM, as songbird activity declines as the day progresses (Robbins 1981). Multiple sites were visited each day, varying the order of site visit for each round of counts to account for potential changes in activity throughout the morning.

GIS Data

For each point, we created 100 m buffers and calculated the mean integrated moisture (IMI) (Iverson et al. 1997), heat load index (HLI) (McCune and Keon 2002), 30-year average annual precipitation (Thornton et al. 2016), elevation (U.S. Geological Survey 2016), and 2011 land cover (Homer 2015) within each buffer.

IMI was derived from hillshade, flow accumulation of water downslope, curvature of the landscape, and soil depth (Iverson et al. 1997). It represents the change in soil moisture potential across a topographically variable landscape and is a robust indicator of site productivity (Iverson et al. 1996) and available soil nitrogen (Morris and Boerner 1998). The HLI integrates both direct incident solar radiation and temperature (McCune and Keon 2002, Evans et al. 2014). The HLI was created using the ArcGIS Geomorphometry & Gradient Metrics in ArcMap 10.X (McCune and Keon 2002, ESRI 2011, Evans et al. 2014). We derived our historic precipitation data from DAYMET, which uses thousands of weather stations to generate daily 1-km^2 maps of temperature, precipitation, humidity, and radiation over large regions of complex terrain (Thornton 2016).

We used land cover classification of preferred Black-throated Blue Warbler habitat used by GAP (U.S. Geological Survey Gap Analysis Program 2011). GAPs land cover data that was acquired in 1991 and 1992 using Landsat TM satellite imagery. First we obtained land cover classification from GAP. We followed the vegetation classification protocol as GAP; specifically, we reclassified land cover into habitat and not-habitat based on preferred habitat of Black-throated Blue Warbler used by GAP, derived from the literature (see U.S.G.S. Gap Analysis Program, 2011, for supporting literature). We calculated the percentage of habitat for Black-throated Blue Warbler within a 100 m buffer around each point. All rasters were resampled to 30 m x 30 m pixel size in order to be comparable to commonly used GAP distribution models.

Statistical Analysis

We transformed the count data to presence absence data. In order to estimate detection probability and occupancy of Black-throated Blue Warbler we used a hierarchical likelihood-based approach presented by Mackenzie et al. (2002) using the package Unmarked (Fiske and Chandler 2011). Specifically, our detection model was:

$$logit(p_i) = \alpha_0 + \alpha_1 * covariate_i 1 + \alpha_2 * covariate_i 2 + \ldots + \alpha_x * covariate_i X$$

We first modeled detection probability assuming constant occupancy across sites (MacKenzie et al. 2005). Because the songbird data was collected using three survey methods, we included survey type in our detection model. We compared three detection models: one assuming probability of detection was constant, the second assuming probability of detection varied by survey type, and the third assuming probability of detection varied by day within the season and survey type. Survey type was coded as a factor and day within the season was coded as an integer. Day of season was standardized (to mean of zero and standard deviation of one) to improve stability (Kéry 2010). We used Akaike's Information Criterion to compare detection models (Burnham and Anderson 2002), and used the best-approximating detection model in our occupancy models. Once we selected our top model, we calculated a probability of detection across all our sites.

Our occupancy model was:

$$logit(\psi_i) = B_0 + B_1 * covariate_i 1 + B_2 * covariate_i 2 + \ldots + B_x * covariate_i X$$

In our occupancy model all variables were continuous, and thus, standardized (to mean of zero and standard deviation of one) to improve stability (Kéry 2010). Our null model assumed that occupancy was constant across sites (MacKenzie et al. 2005). For our competing models, we considered combinations of the following variables: land cover, mean elevation, mean HLI, mean historic precipitation, and mean IMI. From those variables, we constructed a set of 19 candidate models to calculate occupancy (Table 3.2). It should be noted that elevation, land cover, historic precipitation were highly, positively correlated (Table 3.3). We selected the best-supported model structure, as indicated by Akaike's Information Criterion (Burnham and Anderson 2002).

Using the parameter estimates from our top model we used the Raster package (Hijmans & van Etten 2012) to predict occurrence probability across our study area. The probability of occurrence was predicted for each 30 x 30 m pixel in our convex polygon around all survey points with a 100 m buffer that served as our study area boundary. All statistical analysis was conducted in program R 3.2.2 (R Core Team 2015).

GIS Modeling for Distribution Maps

To compare our top model to our land cover and elevation model we needed to convert occupancy values to a binary "suitable" or "unsuitable" classification. In order to evaluate how fragmentation changed between models, we examined varying thresholds of predicted probability occupancy with regard to fringe versus core habitat.

We tested the effects of occupancy thresholds ranging between 0.50 and 0.90, by 0.10 unit increments to code as unoccupied or occupied, on our results. We also compared the absolute value of the pixel-by-pixel difference in probability of occupancy between our top competing and our land cover and elevation only model. We finally calculated the difference in probability of occupancy on National Forest and non-National Forest lands.

Landscape Pattern Analysis

To evaluate the pattern of occupancy in our study area at different thresholds of suitable habitat, we used FRAGSTATS 4.2 (McGarigal et al. 2002) to estimate landscape structure metrics. We used six class (i.e., suitable) metrics that represent isolation and fragmentation of suitable habitat: total area (ha), percentage of landscape, area-weighted mean patch size, patch area coefficient of variation, area-weighted Euclidean nearest neighbor distance, and mean proximity index within a 100 m radius. Total area and percentage of landscape are critical measures of landscape composition because such variables quantify how much landscape is of a particular type; such measure were used to quantity total amount and percentage at each threshold of both models.

Mean patch size is the function of the number of patches in a class and total area and represents the average size of patches. Further, this metric and the associated second order statistics, provide a measure of habitat fragmentation because progressive reduction in the size of habitat patches is a key component of habitat fragmentation. Area weighted mean patch size provides a landscape-centric perspective of patch size across the extent of the landscape because such a measure returns the average condition of a pixel chosen at random, and is therefore at better measure than unweighted-mean patch size. This variable is best used in conjunction with the variation of patch size, as focusing on first-order statistics only can loss information such as uniformity of patches across the landscape. Area-weighted Euclidean nearest neighbor distance quantifies the distance between patches and assigned more weight to larger patches. Mean proximity index measures both the degree of patch isolation and the degree of fragmentation of the probability of predicted occupancy, within 100 m of the focal patch.

Results

Collectively, 1,433 surveys were conducted among the three data sets. We detected a total of 315 Black-throated Blue Warbler across all sites. We examined the linear correlation between our occupancy model covariates and found that land cover was moderately linearly correlated with elevation (r = 0.73) and that elevation and precipitation were strongly correlated (r = 0.81) (Table 3.3).

For our detection model, survey type was our top model (Table 3.4). Mean detection probability across all sites was 0.52. For our occupancy model, our top model that included local bioclimatic variables yielded a positive relationships with percent land cover and IMI, and mean annual precipitation, and a negative relationship with the interaction of HLI and mean annual precipitation (Table 3.5). Percent land cover, mean annual precipitation, and the interaction between mean annual precipitation and HLI were statistically significant and had confidence intervals that did not overlap zero (Table 3.5).

Our land cover and elevation model and our land cover, IMI, mean annual precipitation, and HLI yielded probability of occupancy across our buffered minimum convex polygon (Figure 3.2). Our land cover and elevation model predicted occupancy for 86,882 acres at our 50% threshold, 80,188 acres at our 60% threshold, 73,711 acres at our 70% threshold, 65,443 acres at our 80% threshold, and 48,965 acres at our 90% threshold (Figure 3.3). Our land cover, IMI, mean annual precipitation, and HLI occupancy model predicted 58% less acres at our 50% threshold, 64% less acres at our 60% threshold, 65% less acres at our 70% threshold, 50% less acres at our 80% threshold, and 62% more acres at our 90% threshold when compared to our land cover and elevation model (Figure 3.4). On U.S. Forest Service property, our land cover and elevation model predicted 77,075 acres at our 50% threshold, 52,496 acres at our 60% threshold, 27,398 acres at our 70% threshold, 9,655 acres at our 80% threshold, and 922 acres at our 90% threshold. Our land cover, IMI, mean annual precipitation, and HLI occupancy model predicted 52% less acres at our 50% threshold, 59% less acres at our 60% threshold, 62% less acres at our 70% threshold, 48% less acres at our 80%

threshold, and 64% more acres at our 90% threshold when compared to our land cover and elevation model property (Figure 3.4).

In addition, the landscape configuration of suitable habitat changed at different thresholds of suitability and between our two main models. For our land cover and elevation model, area-weighted mean Euclidian nearest neighbor distance increased with increasingly stringent definitions of suitable (Table 3.6). For our land cover, precipitation, IMI, and HLI model, area-weighted mean Euclidean nearest neighbor distance remained relatively constant, whereas area-weighted mean patch area, patch area coefficient of variation, and mean proximity index all decreased (Table 3.6 and 3.7).

Discussion

The objective of this study was to estimate the difference in projected suitable Black-throated Blue Warbler habitat as predicted by models that integrate finer-resolution bioclimatic data to model occupancy of trailing edge species and compare that model to land cover and elevation models based on core range, species-habitat relationships. The latter approach is currently used in regional conservation and management decisions. The occupancy model that included the additional local factors of IMI, HLI, and mean annual precipitation out-performed the land cover and elevation model. The coarser nature of the land cover and elevation model predicted between 4,803 and 44,776 more occupied acres by Black-throated Blue Warbler across Macon Co. within the thresholds of 50 to 80% than models that included local bioclimatic variables; however, the land cover and elevation model predicted 1,528 less acres occupied acres by Black-throated Blue Warbler. Further, habitat loss, as measured by total area and/or percentage of predicted distribution across the landscape, was more severe in the model that incorporates local bioclimatic variables in all but the 90% threshold. Approximately half of over-predicted occupied habitat was on private land, which would be important for management and planning in this area as this area becomes more developed.

Our results suggest that Black-throated Blue Warbler in the southern Appalachian Mountains are selecting sites with specific local climates. Our top model showed that Black-throated Blue Warbler occupancy has a negative relationship to the interaction of HLI and mean annual precipitation. HLI represents temperature based on solar radiation. Though Black-throated Blue Warbler occupancy was higher on sites with high mean annual precipitation, occupancy declined in areas with southwest facing slopes with that receive high annual mean precipitation, likely because those areas were too warm. Further, IMI was significantly positively correlated with Black-throated Blue Warbler occupancy. IMI integrates precipitation, slope, and aspect, and is considered an index of local site productivity (Iverson et al. 1997) and has been shown to predict nitrogen availability (Morris and Boerner 1998). Areas of high productivity may be related to prey availability and vegetation structure such as midstory shrubs that serve as critical nesting habitat. Several studies have found that the abundance of breeding birds is positively correlated with precipitation (Odum 1950, Bertin 1977, Smith 1977). These studies propose songbird relationship with precipitation is indirect and that the direct relationship is with food resources. Black-throated Blue Warbler have been found to cluster in areas that meet their habitat structural requirements and within those areas select habitat with the highest food resources (Steele 1993). Black-throated Blue Warbler, in their southern range, preferentially nest in shrubs (Steele 1993, Holmes 1994), and have been known to nest in *Rhododendron species* (Holmes 2005). *Rhododendron spp.* density is typically higher on sites with higher mean annual precipitation (Oosting and Bourdeau 1955, Whittaker 1962, Gleason and Cronquist 1963, Strausbaugh and Core 1978, Seymour 1982, Wofford 1989, Little 2002, Radford et al. 2010) and ideal habitat for this species is within coves (Nilsen 1986, Nilsen et al. 1987, Plocher and Carvell 1987) and on north-facing slopes (Spencer 1932, Lipscomb and Nilsen 1990, Dobbs and Parker 2004), both of which have high IMI (Iverson et al. 1997). The presence of *Rhododendron spp.*, and consequently more nesting substrate, may be another important proximate mechanism linking high mean annual precipitation and IMI to Black-throated Blue Warbler occupancy.

Across our study site optimal land cover types, precipitation, and elevation were moderately to highly correlated. Within our study site, most high elevation areas have not been developed compared to the valleys, and thus, it is likely high elevation forest hold the only optimal habitat conditions for Black-throated Blue Warbler within our study area. It is unclear the degree to which the importance of elevation represents an important thermal refuge or is a proxy for other factors including precipitation and site productivity for Black-throated Blue Warbler. Our study occurred in montane forest where there is high orographic precipitation and elevation are tightly correlated. Elevation is considered a habitat requirement for Black-throated Blue Warbler populations located in the southern Appalachians (Hamel 1992); however, elevation only emerged in one of three of our top competing occupancy models that included local bioclimatic factors. This likely means that elevation itself is not a habitat requirement, but rather that elevation serves as a reasonable proxy for precipitation, temperature, and habitat structure. Our more refined model does identify occupied habitats below the current elevational threshold for Black-throated Blue Warbler when suitable climate exists, and discriminates among high elevation sites with suitable land cover that are more or less likely to be occupied based on local climate patterns.

In addition to differences in the amount of predicted occupied habitat, the configuration of the predicted occupied habitat changed with the inclusion of bioclimatic variables. The land cover and elevation only model and the land cover, precipitation, IMI, and HLI model had similar trends with most landscape pattern metrics with area predicted as suitable decreasing and measures of fragmentation increasing with higher thresholds of predicted probability of occupancy. An indicator of habitat fragmentation is habitat loss and progressive reduction in the size of habitat fragments (i.e. area-weighted mean patch size) is a key component of habitat loss and fragmentation. However, between the models, more fragmentation is predicted by the land cover, precipitation, IMI, and HLI model as is evidenced by overall less total area, percentage of landscape, and area-weighted mean patch size in the majority of thresholds. These variables being both lower in comparison to the land cover and elevation model, and also decreasing as the threshold becomes higher, indicate fragmentation is occurring within the predicted occupancy distribution. In addition, land cover, precipitation, IMI, and HLI model also shows less uniformity in distribution of predicted occupancy, as evidenced by higher levels of variation. Thus, not only is patch size decreasing, it is become less uniform across the landscape. Less uniformity could be related to inherent landscape processes driving the land cover, precipitation, IMI, and HLI such as the interaction of variables in our top model across the landscape. In our study area precipitation is orographic, and as a result the precipitation gradient across Macon County has a lot of variation due to the variability in topography. Thus, areas of suitable habitat may be more clustered in the landscape that is currently represented by land cover and elevation models; such a distinction has important implications for land management and land acquisition for conservation.

Our land cover and elevation only model and our land cover, precipitation, IMI, and HLI model had similar trends in isolation, specifically, as the threshold increased, isolation between occupied landscape increased; however, it appeared that more isolation is occurring in the land cover and elevation model when examining the mean proximity index and the area-weighted mean Euclidean nearest neighbor distance. This is likely related to smaller patches of suitable habitat retained in the land cover and elevation model, and in the land cover, precipitation, IMI, and HLI model those smaller patches are likely lost; the loss of more total area and percentage of landscape and less uniformity in distribution of predicted occupancy in the land cover, precipitation, IMI, and HLI model support this notion. In summary, there was more isolation in the land cover and elevation model and less total habitat in the land cover, precipitation, IMI, and HLI model. However, habitat loss and fragmentation are intertwined which makes it a complicated matter to rank the importance of such variables in relation to habitat isolation with regards the impacts on a species occupancy (Fahrig 2002, Lee et al. 2002, Neel et al. 2004, Fahrig 2013).

Based on our occupancy models, we suggest that Black-throated Blue Warbler are selecting areas with favorable microclimates and higher productivity within larger areas of suitable land cover. This is consistent with expectations for trailing edge populations Black-throated Blue Warbler, which often face increased environmental selective pressure to choose more specific habitat (Holt 1987, Hoffmann and Blows 1994, Bridle and Vines 2007, Sexton et al. 2009). The result being that trailing-edge populations are restricted to “islands” of suitability habitat within a matrix landscape of unsuitable habitat (Hampe et al. 2005), potentially resulting in more fragmented distributions not observable with coarser distribution models. Our findings for Black-throated Blue Warbler are consistent with this pattern. It is likely that selection for suitable refugia and high productivity sites may mitigate some of the environmental selective pressure these species make at their range margins. Increased fragmentation of suitable habitat has been shown to cause reduction in pairing and fecundity. Pairing success is impacted by lowering chances of attracting a potential mate (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). This in turn lowers songbird fecundity (Böhning-Gaese et al. 1993, Donovan et al. 1995, Robinson et al. 1995). Which ultimately leads to populations declines via a reduction in recruitment of individuals into the breeding population (Donovan et al. 1995).

Our findings suggest that habitat associations for trailing edge Black-throated Blue Warbler populations differ from those located in core populations. Thus, SDMs for

Black-throated Blue Warbler trailing populations need to re-evaluate the ecological assumptions and habitat relationships of such models. Species distribution maps, especially those produced by GAP and similar programs, are valuable for planners, managers, and researchers. However, if the underlying relationships between species occupancy or abundance and local habitat factors are not incorporated, models are likely to over-predict occupied habitat. This may lead to erroneous conclusions about population dynamics and the status of trailing edge populations, and could create unnecessary conflicts in conservation planning. Habitat relationships for trailing edge populations may not be known or available to conservation managers or planners. If the objectives of programs such as GAP or similar programs is to conduct regional assessments of the conservation status of native terrestrial vertebrate species to inform regional land management activities (U.S. Geological Survey Gap Analysis Program 2011), then there will be a need to complementary local models that incorporate local species-habitat relationships to guide more effective planning.

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TABLE 3.1. Table outlining the major differences in survey methods used in this study.

Author	Times visited per year	# of observers	Duration of survey	Number of points	Years surveyed	Survey start/end day of year
Barlow, Paige	3	2	8 minutes	265	2010, 2011	5/9 – 7/7
Beasley, Camille	3	2	6 minutes	73	2011, 2012	5/22 - 6/29
Abernathy, Heather	2	1	10 minutes	92	2015, 2016	5/4 – 7/2

TABLE 3.2. Set of 19 models used to estimate occupancy of Black-throated Blue Warbler.

Model	Parameters
1	Percent optimal land cover + Elevation
2	Percent optimal land cover
3	HLI*Mean annual precipitation
4	Elevation
5	Percent optimal land cover + Elevation + IMI
6	Percent optimal land cover + IMI + Mean annual precipitation
7	Percent optimal land cover *IMI
8	Percent optimal land cover + IMI* Mean annual precipitation
9	Percent optimal land cover + IMI*Elevation
10	Percent optimal land cover + IMI + HLI + Mean annual precipitation
11	Percent optimal land cover + IMI + HLI* Mean annual precipitation
12	Percent optimal land cover + IMI*HLI + Mean annual precipitation
13	Percent optimal land cover + Elevation*HLI + IMI
14	Percent optimal land cover *HLI + IMI + Mean annual precipitation
15	Percent optimal land cover + Elevation + IMI + HLI
16	Percent optimal land cover + Elevation + IMI*HLI
17	Percent optimal land cover *HLI + Elevation + IMI
18	Percent optimal land cover + HLI* Mean annual precipitation
19	Percent optimal land cover + Elevation + HLI*Mean annual precipitation

TABLE 3.3. Pearson's correlation coefficient (r) table of all variables used in the model displaying an r = 0.60 or higher.

	Elevation mean	IMI mean	HLI mean	Percent optimal land cover	Mean annual precipitation
Elevation mean	1.00	-	-	0.73	0.81
IMI mean	-	1.00	-	-	-
HLI mean	-	-	1.00	-	-
Percent optimal land cover	0.73	-	-	1.00	0.69
Mean annual precipitation	0.81	-	-	0.69	1.00

TABLE 3.4. Top competing models to account for imperfect Black-throated Blue Warbler detection with associated parameters estimates and confidence intervals. Significant parameters estimates are in bold-face.

Competing Models	Survey Type 1	Survey Type 2	Survey Type 3	Date	Δ AIC
$\text{logit}(\psi_i) = \alpha_0$	-	-	-	-	4.40
$\text{logit}(\psi_i) = \alpha_0 + \alpha_1$ * Survey Type	1.31 (0.91, 1.88)	1.43 (0.92, 2.25)	**0.26 (0.11, 0.63)**	**-**	0.00
$\text{logit}(\psi_i) = \alpha_0 + \alpha_1$ * Date	-	-	-	0.88 (0.75, 1.08)	3.36
$\text{logit}(\psi_i) = \alpha_0 + \alpha_1$ * Survey Type + α_2 * Date	1.33 (0.93, 1.92)	1.37 (0.78, 2.15)	**0.26 (0.17, 0.66)**	0.94 (0.78, 1.11)	1.31

TABLE 3.5. Top competing refugia occupancy models chosen based on a delta AIC below 2. Significant parameters estimates are in bold-face

Competing Models	% Habitat	IMI	HLI	Elevation	Precipitation	HLI*Precipitation	HLI* % habitat	Δ AIC
logit(ψ_i) = B_0 + B_1*Percent habitat + B_2*IMI + B_3*HLI*Mean annual precipitation	**1.66 (1.21, 2.28)**	**1.40 (1.05, 1.86)**	1.11 (0.79, 1.56)		**3.57 (2.51, 5.07)**	**0.71 (0.51, 0.98)**		0.00
logit(ψi) = B_0 + B_1*Percent habitat + B_2*Elevation + B_3* Mean annual precipitation*HLI	**1.45 (1.04, 2.02)**		0.92 (0.68,1.24)	**1.70 (1.07, 2.71)**	**2.39 (1.54, 3.71)**	**-**	**0.68 (0.49, 0.95)**	0.44
logit(ψi) = B_0 + B_1*Percent habitat + B_2*IMI + B_3*Mean annual precipitation	**1.68 (1.22, 2.32)**	**1.38 (1.07, 1.78)**	-		**3.73 (2.66, 5.25)**	-	-	0.76

Table 3.6. FRAGSTATS 4.2 output for land cover and elevation occupancy model.

	Threshold				
Landscape Metric	0.50	0.60	0.70	0.80	0.90
Total area	31190.94	21244.50	11087.46	3907.17	373.32
Percentage of landscape	19.85	13.52	7.06	2.49	0.24
Area-weighted mean patch area	8361.51	5893.90	2097.85	708.58	140.47
Coefficient of variation of patch area	683.50	677.39	502.99	284.04	224.06
Area-weighted mean of Euclidean nearest neighbor distance	69.74	105.06	111.14	228.01	779.38
Mean proximity index	9418.66	5016.47	830.67	45.70	4.69

Table 3.7. FRAGSTATS 4.2 output for land cover, precipitation, IMI, and HLI occupancy model.

	Threshold				
Landscape Metrics	0.50	0.60	0.70	0.80	0.90
Total area	13070.97	7637.58	3940.02	1963.71	991.62
Percentage of landscape	8.32	4.86	2.51	1.25	0.63
Area-weighted mean patch area	1673.93	1265.46	1367.12	969.80	405.06
Coefficient of variation of patch area	2009.51	1991.82	1868.39	1576.07	898.31
Area-weighted mean of Euclidean nearest neighbor distance	62.66	64.01	66.97	68.67	66.35
Mean proximity index	587.51	431.12	263.80	330.63	105.19

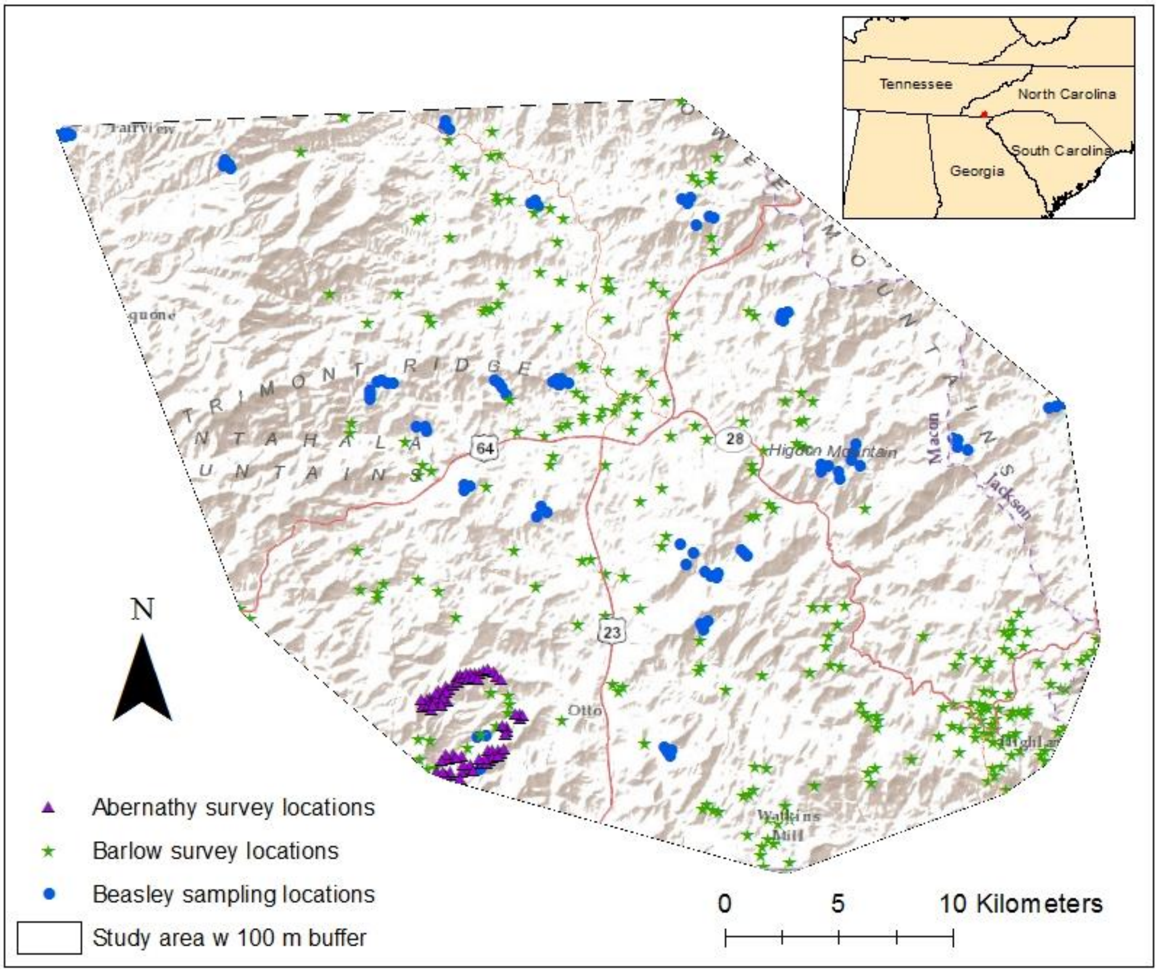


Figure 3.1. Map of our study area located in Macon County, NC. Points are differentiated with different colors and symbols and indicate survey locations.

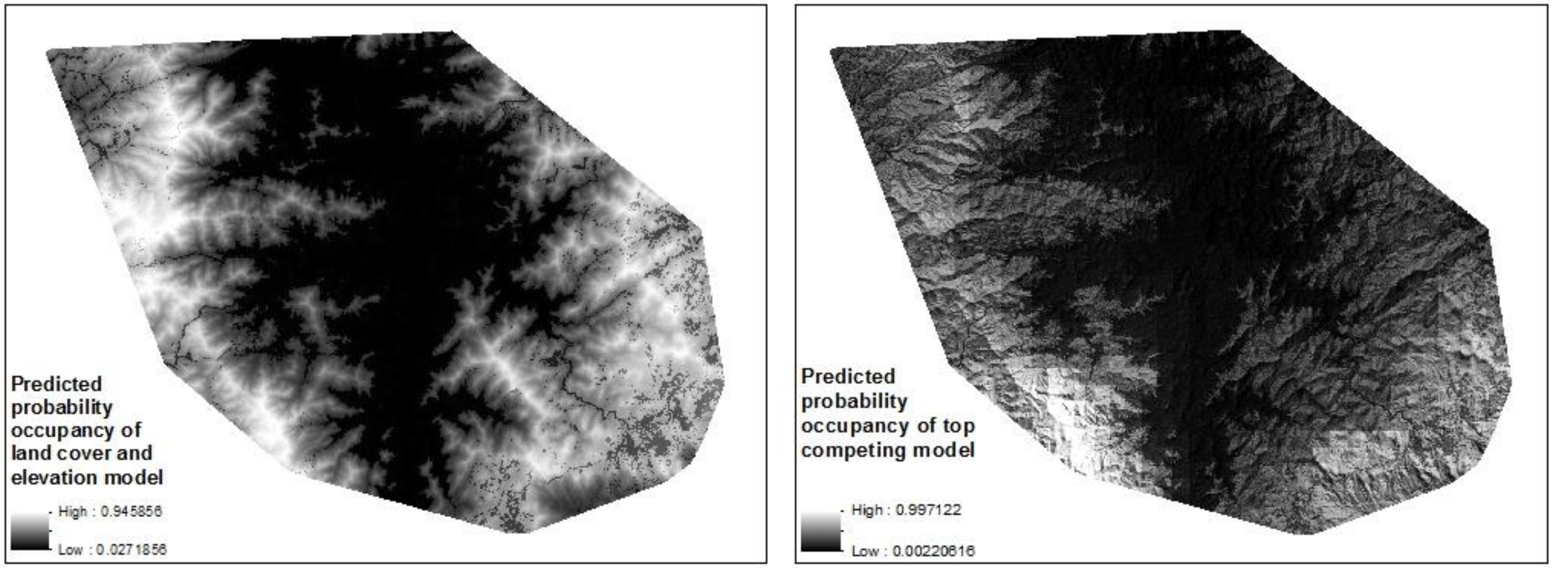


Figure 3.2. Predicted probability occupancy mapped over our study area, Macon County, NC. The left map displays the prediction of our land cover and elevation model and the right map displays the prediction of our top refugia model. Lighter colors represent a higher predicted probability of occupancy.

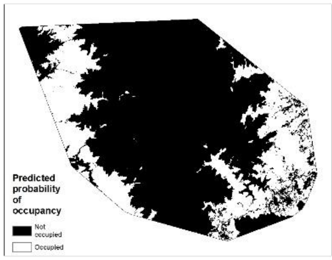
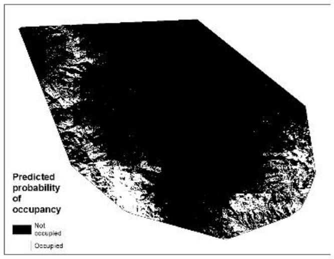
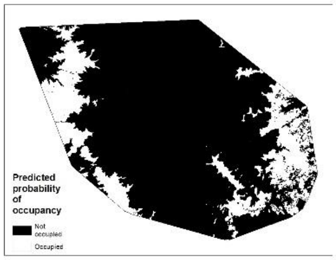
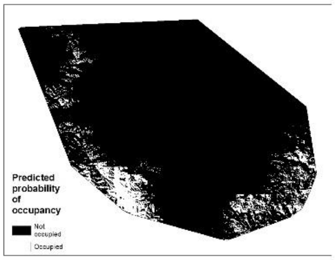
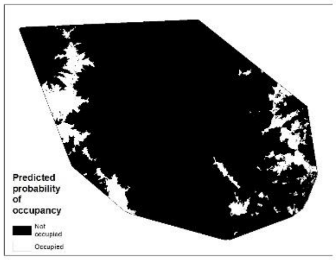
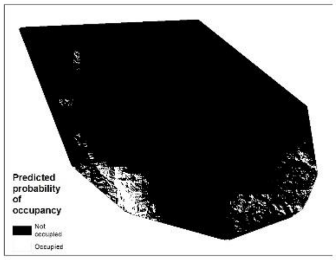
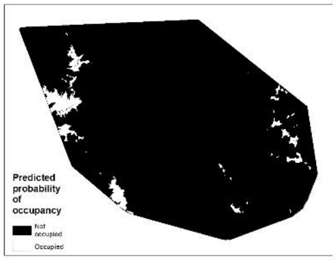
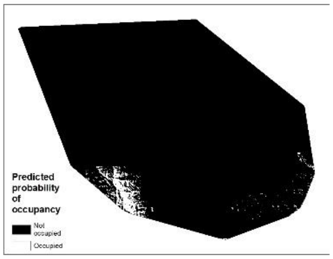
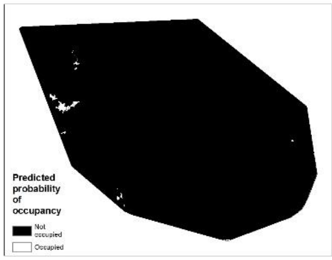
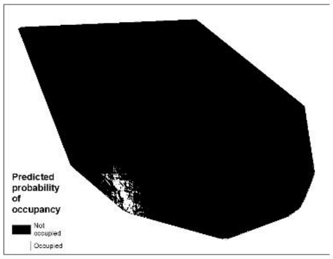
Threshold	Land cover and elevation model	Top refugia model
50%		
60%		
70%		
80%		
90%		

Figure 3.3. Suitable habitat mapped over our study area, Macon County, NC, at varying thresholds of predicted probability occupancy. The first column represents respective threshold of the probability of predicted occupancy. The middle and far right column contain predicted probability occupancy maps for the land cover and elevation and the land cover, precipitation, IMI, and HLI model at varying thresholds respectively.

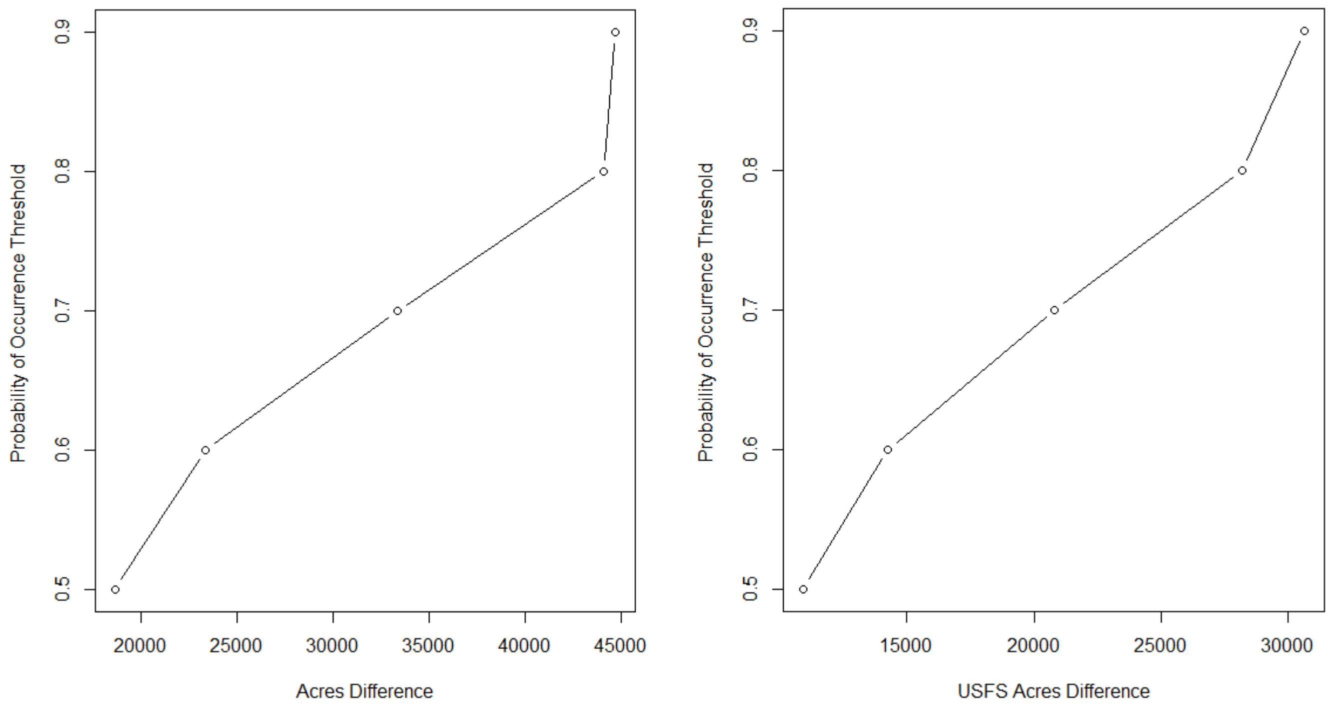


Figure 3.4. The difference in acres between land cover and elevation only and land cover, precipitation, IMI, and HLI model suitable habitat at varying thresholds of predicted probability occupancy. The graph on the left represents all property-types and the graph on the right is difference of acres on U.S.F.S. property only.

CHAPTER 4

SUMMARY AND CONCLUSIONS

Summary and conclusions

The purpose of my research was to examine whether local climate, resource productivity, and quality metrics could be used to model local variation in breeding songbird abundance. I used precipitation, integrative moisture index (an index of site productivity potential), vegetation structure, and caterpillar biomass to model the abundance of 11 songbird species including several trailing edge species. I then used the relationships I established for one trailing edge species, the Black-Throated Blue Warbler (*Setophaga caerulescens*, BTBW) to compare different model estimates of habitat availability and fragmentation across Macon County, North Carolina, USA.

In chapter two, I tested whether mean annual precipitation and integrated moisture index were direct predictors of foliar C:N and indirect predictors of caterpillar biomass and the abundance of 11 songbird species. I used structured equation modeling of point count data from 68 sites over two years to test the hypotheses that: (1) that sites with higher mean annual precipitation and integrated moisture would be negatively correlated with foliar C:N; (2) mean annual precipitation and integrated moisture would be positively correlated with caterpillar biomass, and foliar C:N would be negatively correlated with caterpillar biomass; (3) mean annual precipitation, integrated moisture index would be positively correlated with songbird abundance (Figure 2.1). I also investigated the relationship between mean annual precipitation, integrated moisture index, vegetation structure, and songbird abundance.

My results showed that mean annual precipitation and IMI were significant local predictors of bird abundance. However, only for four of 11 species showed a relationship between mean annual precipitation and IMI a positive relationship with abundance. For four of the 11 species, the relationships were negative. I expected that the indirect, proximate mechanism linking mean annual precipitation and IMI to bird abundance would be the effects of moisture on foliar quality and subsequent effects on caterpillar biomass. Consistent with my predictions, mean annual precipitation was positively correlated with lower foliar C:N although foliar C:N was not a significant predictor of caterpillar biomass. I also did not observe any significant direct relationship between mean annual precipitation or IMI and caterpillar biomass. One potential explanation for why I had strong but, inconsistent relationship between mean annual precipitation and songbird abundance, was that since mean annual precipitation was strongly correlated with elevation birds are responding to elevation, and ultimately temperature differences. For those four species that were more abundant at higher elevation, it is not clear whether they are responding directly to the higher mean annual precipitation or whether some other factors associated with elevation are driving local abundance. In chapter three, looking at the distribution of Black-throated Blue Warbler, I found that models using precipitation were better than models that contained elevation (Chapter 3, Abernathy 2017). Additionally, as expected, I also found evidence that habitat structure influenced the abundance of some bird species.

There are several potential reasons why I failed to find a relationship between caterpillar biomass, foliar quality, and songbird abundance. One possibility is that my methods for estimate caterpillar biomass maybe too imprecise or stochastic to represent true prey availability. A second reason why I found no relationship could be that while caterpillars are important resource, the songbird sampled in this study exhibit prey switching, and I did not account for other insects present at a site. A third reason, may be that songbirds can compensate for local variation in caterpillar abundance by expanding their search area when feeding nestlings.

In summary, my study did find evidence that local climatic variables were good predictors of variation in breeding songbird abundance, but I did not find any evidence that those climatic variables serve as good indirect prey availability. Caterpillar biomass was not a significant predictor of bird abundance and foliar C:N was not a significant predictor of bird abundance. Instead it may be that, for some species, local climate variables may be a driver of vegetation structure, which could affect nest site availability. The strong relationship with most species and elevation may also indicate that factors I have not considered in this study are important determinates of local songbird abundance.

In chapter three, I compared models occupancy models for Black-throated Blue Warbler included land cover and elevation only (*senu* GAP) to models that included land cover and additional abiotic variables that represent refugia. I determined the degree to which models with additional local climate variables differed in predicted warbler occupancy across the county. I compared the extent to which more refined models predicted the abundance, distribution, and fragmentation of occupied habitats. My hypothesis was that SDMs, which only consider habitat associations of core populations, would over-predict more acreage than SDMs that were built with abiotic variables, associated with refugia, for trailing edge populations. I found that occupancy models that included the additional factors of IMI, HLI, and mean annual precipitation, out-performed the habitat-only model that only included suitable land cover and elevation. My land cover and elevation only model predicted 4,803 and 44,776 more occupied acres by Black-throated Blue Warbler across Macon Co my top competing model that included additional bioclimatic variables. In addition, my top competing model yielded a distribution map that is more fragmented and isolated than is currently represented with publicly accessible distribution maps. About half of over-predicted land was on private land; this information is particularly important for management and planning in this area as this area becomes more developed.

My results suggest that Black-throated Blue Warbler in the southern Appalachian Mountains are selecting sites with specific local climates. Though Black-throated Blue Warbler occupancy was higher on sites with high mean annual precipitation, occupancy declined in areas with southwest facing slopes that received high annual mean precipitation; this is likely because those areas were too warm. Further, IMI was significantly positively correlated with Black-throated Blue Warbler occupancy. Areas of high IMI (productivity (Iverson et al. 1997)) may be related to prey availability and vegetation structure such as midstory shrubs that serve as critical nesting habitat.

Based on our occupancy models, we suggest that Black-throated Blue Warbler are selecting areas with favorable microclimates and higher net-primary productivity, via relatively more precipitation, within larger areas of suitable land cover. This is consistent with expectations for trailing edge populations Black-throated Blue Warbler, which often face increased environmental selective pressure to choose more specific habitat (Holt 1987, Hoffmann and Blows 1994, Bridle and Vines 2007, Sexton et al. 2009). It is likely that selection for suitable refugia and high productivity sites may mitigate some of the environmental selective pressure these species make at their range margins.

Across our study site, optimal habitat, precipitation, and elevation were moderately to highly correlated. Within our study site, most high elevation areas have not been developed compared to the valleys, and thus, it is likely high elevation forest hold the only optimal habitat conditions for Black-throated Blue Warbler. In addition to differences in the amount of predicted occupied habitat, the configuration of the predicted occupied habitat changed with the inclusion of bioclimatic variables. At the lowest suitability threshold, it appears there was little effect of including bioclimatic variables on the spatial pattern of predicted occupancy. Compared to the land cover and elevation-only model, we found that our top model with additional bioclimatic variables lost small patches of habitat throughout predicted distribution. Increased isolation and fragmentation of suitable habitat has been shown to cause reduction in pairing and fecundity. This could indicate that populations will decline in the coming years due to a reduction in recruitment of individuals into the breeding population (Donovan et al. 1995).

Our findings suggest that habitat associations for trailing edge Black-throated Blue Warbler populations differ from those located in core populations. Thus, SDMs for Black-throated Blue Warbler trailing edge populations need to reevaluate the ecological assumptions and habitat relationships of such models. Habitat relationships for trailing edge populations may not be known or available to conservation managers or planners. If the objectives of programs, such as GAP, is to conduct regional assessments of the conservation status of native terrestrial vertebrate species to inform regional land management activities (U.S. Geological Survey Gap Analysis Program 2011), then there will be a need to complement local models that incorporate local species-habitat relationships in order to guide more effective planning.

Overall, I found that mean annual precipitation was highly correlated with elevation and likely drove the variation in breeding songbird abundance; further, microrefugia and potentially productivity drove occupancy at the Black-throated Blue Warbler trailing edge populations sampled. This study was largely a pilot study which tried to get behind the mechanism driving insectivore songbird abundance across the landscape; because of the study's pilot-like nature, there are certainly areas of exploration in this study area. Future studies should focus on improving the methodology of Chapter 2. My findings suggest that caterpillar detection and/or abundance was very low across the landscape. This would suggest that significantly more sampling effort would be required to generate more reliable estimates of caterpillar biomass. Further, efforts might be improved by having more robust ways of estimated caterpillars or other insects at larger spatial extents. I would also suggest that researchers examine other food resources available to songbirds at a site. This is because the songbird being studied can exhibit prey switching and thus, only sampling caterpillar biomass may be insufficient to fully capture the prey available at a site. Furthermore, a wider gradient of precipitation should be examined, specifically a gradient that incorporated more high elevation dry sites. The study in chapter three can be expanded upon by modeling occupancy for other trailing edge populations in the southern Appalachian Mountains or elsewhere.

Despite possibilities for improvement, I still think the findings from this study can contribute to the field, especially the findings of chapter three. Chapter two elucidates that songbirds are responding to precipitation and those that have positive relationships could be responding to available nesting substrate. Chapter three shows the flaws with widely accessible SDMs used by managers and planners. Further because knowledge of such ecological relationships are not widely available or known to managers or planners, such information has not assisted in past and current land management. The consequence of such will likely lead to further fragmentation and population decline for the species if optimal habitat has been or is currently being reduced. This study elucidated the need for conservation planners to be aware that, because of increased environmental selective pressure, trailing edge populations are likely dependent on areas of high productivity and refugia. More broadly, researchers and managers should reconsider unique biological relationships for species on range margins. This consideration will aid in more refined distribution maps and reduce over-predictions and ultimately help in preservation of trailing edge populations in the southeast.

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APPENDIX A: ENVIRONMENTAL VARIABLES THAT IMPACTED DETECTION AND AVAILABILITY IN SONGBIRDS

Appendix A contains tables of observational covariates that impacted songbird detection and availability used in the structural equation model for Chapter 1.

Table A.1 A table of each species availability model. Model covariates that are in boldface are the covariates corresponding to species specific estimate, confidence interval, and AIC value in each respective row. Asterisks denotes significance.

Availability Model	BHVI Estimate	BHVI Δ AIC
logit($\phi_{s,k}$) = B_0	0.04* (0.14, 0.01)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.97* (1.14, 0.83)	1.88
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	1.02* (1.20, 0.88)	1.90
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**1.02 (0.88, 1.19)**, *0.97(1.14, 0.83)*	3.79
Availability Model	BTBW Estimate	BTBW Δ AIC
logit($\phi_{s,k}$) = B_0	0.73 (0.07, 7.53)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	1.09 (0.85, 1.41)	1.44
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	0.94 (0.77, 1.14)	1.58
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**0.93 (0.76, 1.15)**, *1.09 (0.85, 1.42)*	3.02
Availability Model	BTNW Estimate	BTNW Δ AIC
logit($\phi_{s,k}$) = B_0	0.09 (0.03, 0.26)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	1.06 (0.90, 1.25)	1.52
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.97 (0.80, 1.19)	1.93
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**1.06 (0.89, 1.25),** *0.98 (0.81, 1.20)*	3.49
Availability Model	CAWA Estimate	CAWA Δ AIC
logit($\phi_{s,k}$) = B_0	0.54 (0.03, 8.37)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	0.82 (0.59, 1.15)	0.54
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.84 (0.57, 1.24)	0.95
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**0.82 (0.58, 1.15),** *0.84 (0.57, 1.22)*	1.49

Availability Model	HOWA Estimate	HOWA Δ AIC
logit($\phi_{s,k}$) = B_0	1.04 (0.10, 10.5)	14.4
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	14.6* (2.82, 75.1)	0.00
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.28* (0.08, 1.00)	3.66
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**10.1 (1.26, 84.0),** *0.67 (0.38, 1.18)*	0.03
Availability Model	NOPA Estimate	NOPA Δ AIC
logit($\phi_{s,k}$) = B_0	0.01 (0, 0.27)	1.71
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	0.87 (0.51, 1.48)	3.42
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.61 (0.35, 1.05)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**0.85 (0.49, 1.48),** *0.61 (0.35, 1.05)*	1.61
Availability Model	RBGR Estimate	RBGR Δ AIC
logit($\phi_{s,k}$) = B_0	0.06 (4.72E-05, 68.9)	0.00
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	0.99 (0.70, 1.41)	2.00
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.98 (0.70, 1.37)	1.99
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**0.99 (0.70, 1.41),** *0.98 (0.70, 1.37)*	3.99
Availability Model	REVI Estimate	REVI Δ AIC
logit($\phi_{s,k}$) = B_0	0.07 (0.05, 1.07)	4.36
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	1.35 (0.90, 2.01)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.95 (0.79, 1.13)	5.96
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**1.34 (0.91, 1.97),** *0.95 (0.77, 1.18)*	1.79
Availability Model	SCTA Estimate	SCTA Δ AIC
logit($\phi_{s,k}$) = B_0	0.53 (0.16, 1.74)	14.0

logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	0.89 (0.68, 1.15)	15.2
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.60* (0.42, 0.86)	0.50
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**0.76 (0.50, 1.16),** *0.53* (0.50, 1.16)*	0.0
Availability Model	TUTI Estimate	TUTI Δ AIC
logit($\phi_{s,k}$) = B_0	0.01 (0.00, 0.05)	2.70
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	0.89 (0.70, 1.15)	3.86
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.78* (0.62, 0.98)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**0.89 (0.69, 1.14),** *0.77* (0.61, 0.98)*	1.04
Availability Model	WEWA Estimate	WEWA Δ AIC
logit($\phi_{s,k}$) = B_0	0.04 (0.01, 0.17)	3.48
logit($\phi_{s,k}$) = B_0 + B_1 * Julian Date	0.87 (0.64, 1.19)	4.68
logit($\phi_{s,k}$) = B_0 + B_1 * Survey Time	0.71* (0.52, 0.95)	0.0
logit($\phi_{s,k}$) = B_0 + B_1 * **Julian Date** + B_2 * *Survey Time*	**0.84 (0.60, 1.16),** *0.70 (0.51, 0.94)*	0.74

Table A.2. A table of each species detection model. Model covariates that are in boldface are the covariates corresponding to species specific estimate, confidence interval, and AIC value in each respective row. Significant values are denoted with an asterisk.

Detection Model	BHVI Estimate - 1	BHVI Estimate - 2	BHVI Estimate - 3	*BHVI Estimate - 4*	Δ AIC
$\log(\sigma_s,k) = B_0$	0.68 (50.8, 90.4)				0
$\log(\sigma_s,k) = B_0 + B_1$ * wind	2.60E+04 (4.43E+03, 1.53E05)	6.60E-01 (0.46, 0.95)	9.78E-01 (0.63, 1.52)	122 (1.22E-58, 1.22E+62)	13.4
$\log(\sigma_s,k) = B_0 + B_1$ * noise	8.10E+03 (0.06, 1.07E+05)	9.43E-01 (0.50, 1.73)	4.88E-01 (0.02, 1.0)	2.98E+03 (1.46E-50, 6.09E+56)	39.7
$\log(\sigma_s,k) = B_0 + B_1$ * observer	2.11E-01(4.11E-32, 1.08E+30)	3.38E-01(9.31E-20, 1.23E+18)	1.66 (3.82E-54, 7.23E+53)	10.8 (3.79E-04, 3.08E+05)	50.5
$\log(\sigma_s,k) = B_0 + B_1$ * **noise** + B_2 * *observer* + B_3 * wind	**1.5E+03 (9.1E-10, 2.4E+15),** *1.10 (4.3E-11, 1.2E+14),* 1.2 (0.72E-01, 1.84)	**0.93 (0.63, 1.37),** *1.03 (0.71, 1.49),* 1.15 (0.72, 1.84)	**0.56 (0.19, 1.70),** *0.71 (4.3E-11, 1.2E+14),* 0.52 (1.25, 1.38)	**0.02 (1.7E-158 2.3E+160),** *4.3E+03 (2.6E-09, 7.0E+15),* 0.52 (2.2E-11, 1.2E+14)	64.6
Detection Model	Null / BTBW Estimate -1	BTBW Estimate - 2	BTBW Estimate - 3	BTBW Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	41.56 (37.8, 45.7)				6
$\log(\sigma_s,k) = B_0 + B_1$ * wind	1.09 (0.94, 1.27)	1.02 (0.87, 1.21)	1.13 (0.92, 1.39)	0.97 (0.67, 1.41)	10
$\log(\sigma_s,k) = B_0 + B_1$ * noise	2.72 (9.6E-18, 7.7E+17)	2.72 (6.6E-26 1.1E+26)	7.39 (7.6E-16 7.2E+16)	7.39 (6.4E-87 8.5E+87)	144

$\log(\sigma_s,k) = B_0 + B_1$ * observer	1.05 (0.74, 1.11)	1.29 (0.89, 1.20)	1.29 (1.10, 1.51)	0.99 (0.81, 1.21)	0
$\log(\sigma_s,k) = B_0 + B_1$ * **noise** + B_2 * *observer* + B_3 * wind	**2.72 (2.6E-18, 2.8E+18),** *1.03 (3.1E-11, 1.6E+12),* 2.71 (1.2E-60, 6.0E+60)	**2.71 (2.2E-12, 3.3E+12),** *1.0 (1.6E-10, 6.2E+09),* 2.71(1.1E-116 8.8E+115)	**7.39 (3.0E-11, 1.8E+12),** *1.00 (4.7E-26, 2.1E+25),* 1.0 (5.2E-75, 1.9E+74)	**7.39 (3.1E-11, 1.7E+12),** *1.0 (3.2E-57, 3.1E+56),* 1.0 (1.7E-77, 6.0E+76)	157

Detection Model	Null / BTNW Estimate -1	BTNW Estimate - 2	BTNW Estimate - 3	BTNW Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	57.9 (47.5, 70.6)				1.22
$\log(\sigma_s,k) = B_0 + B_1$ * wind	1.27 (0.84, 1.51)	0.83 (0.58, 1.17)	0.58* (0.41, 0.83)	0.86 (0.43, 1.75)	0
$\log(\sigma_s,k) = B_0 + B_1$ * noise	8.12E+03* (10.3, 6.40E+06)	2.18 (0.55, 1.19)	0.38* (0.18, 0.83)	2.98e+03 (8.07E-218, 1.10E+224)	48.91
$\log(\sigma_s,k) = B_0 + B_1$ * observer	3.97E+05 (1.86, 8.46E+10)	18.1 (8.42E-05, 3.87E+06)	2.71 (3.80E-05, 1.94E+05)	7.38 (1.14E-05, 4.78E+06)	33.16
$\log(\sigma_s,k) = B_0 + B_1$ * **noise** + B_2 * *observer* + B_3 * wind	**2.72 (3.35E-64, 2.2E+64),** *1.36 (0, inf),* 1.00 (1.59E-231, 6.27E+230)	**2.72 (4.12E-16, 1.80E+16),** *2.72 (0, inf),* 2.72 (8.58E-199, 8.62E+198)	**2.27 (3.06E-39, 2.41E+39),** *0.10 (1.87E-92 5.33E+91),* 2.27 (0, inf)	**2.72 (0, inf),** *7.39 (3.33E-101 1.64E+102),* 2.72 (0, inf)	48.91

Detection Model	Null / CAWA Estimate -1	CAWA Estimate - 2	CAWA Estimate - 3	CAWA Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	47.0 (38.4, 57.4)				0.75
$\log(\sigma_s,k) = B_0 + B_1$ * wind	1.37 (1.0, 1.88)	1.33 (0.94, 1.90)	1.49 (0.99, 2.26)	0.74 (0.39, 1.40)	15.93
$\log(\sigma_s,k) = B_0 + B_1$ * noise	7.39 (2.37E-72, 2.03E+80)	7.39 (1.19E-72, 4.59E+73)	7.39 (2.97E-60, 1.84E+61)	7.39 (0, inf)	51.81

$\log(\sigma_s,k) = B_0 + B_1$ * observer	0.60* (0.49, 0.87)	0.68* (0.51, 0.92)	0.51* (0.37, 0.70)	0.67 (0.43, 1.05)	0
$\log(\sigma_s,k) = B_0 + B_1$ * **noise** + B_2 * *observer* + B_3 * wind	**2.71 (1.49E-04, 4.97E+04),** *5.42 (0, inf),* 2.72 (0.01, 1.13E+03)	**7.51 (8.98E-03, 6.29E+03),** *7.42 (0, inf),* 2.72 (2.62E-04, 2.82E+04)	**20.3 (0.01, 2.91E+04),** *2.77 (0.10, 75.9),* 20.6 (0.15, 2.93E+03)	**7.39 (1.23E-16 4.44E+17),** *1.00 (1.53E-05, 6.54E+04),* 20.1 (2.68E-07 1.51E+09)	65.71
Detection Model	Null / HOWA Estimate -1	HOWA Estimate - 2	HOWA Estimate - 3	HOWA Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	41.1 (36.1, 46.7)				16.58
$\log(\sigma_s,k) = B_0 + B_1$ * wind	0.96 (0.80, 1.18)	0.73* (0.57, 0.93)	0.51* (0.36, 0.72)	1.57 (0.66, 3.72)	0
$\log(\sigma_s,k) = B_0 + B_1$ * noise	19.5 (0.06, 6.93E+03)	17.8 (0.05, 6.76E+03)	20.3 (0.08, 5.39E+03)	54.6 (9.58E-03, 3.13E+05)	96
$\log(\sigma_s,k) = B_0 + B_1$ * observer	0.95 (0.77, 1.15)	0.89* (0.72, 1.09)	1.25 (1.02, 1.53)	0.79 (0.55, 1.14)	12.58
$\log(\sigma_s,k) = B_0 + B_1$ * **noise** + B_2 * *observer* + B_3 * wind	**19.0 (6.16E-06 5.87E+07),** *9.6 (1.97, 56.4),* 7.60 (2.44, 23.7)	**8.03 (2.62E-06 2.46E+07**), *7.43* (1.12, 49.4)* , 2.7 2* (0.20, 38.0)	**55.4 (1.71E-05 1.80E+08**), *21.0 (0.73 605),* 7.47* (1.31 42.5)	**20.1 (4.52E-06 8.92E+07),** *20.0* (1.09, 364),* 7.35* (1.86 29.0)	109.78
Detection Model	Null / NOPA Estimate -1	NOPA Estimate - 2	NOPA Estimate - 3	NOPA Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	46.2 (31.7, 67.5)				0
$\log(\sigma_s,k) = B_0 + B_1$ * wind	0.10 (0.52, 1.89)	0.83 (0.40, 1.70)	1.26 (0.49, 3.22)	1.10E+03 (1.00E-189 1.20E+195)	8.83
$\log(\sigma_s,k) = B_0 + B_1$ * noise	-	-	-	-	N/A

log(σ_s,k) = B_0 + B_1 * observer	4.07E+02 (1.37E-35, 1.45E+39)	4.03E+02 (1.41E-31 1.15E+36)	4.04E+02 (7.99E-43 2.04E+47)	4.35 (8.64E-291 1.88E+295)	13.62
log(σ_s,k) = B_0 + B_1 * **noise** + B_2 * *observer* + B_3 * wind	-	-	-	-	N/A
Detection Model	Null / RBGR Estimate -1	RBGR Estimate - 2	RBGR Estimate - 3	RBGR Estimate - 4	Δ AIC
log(σ_s,k) = B_0	60.3 (40.2, 90.5)				9.7
log(σ_s,k) = B_0 + B_1 * wind	20.08 (4.49E-160, 8.98E+161)	20.1 (6.12E-160, 6.59E+161)	20.1 (4.36E-160, 9.24E+161)	20.1 (1.37E-108, 2.94E+110)	23.7
log(σ_s,k) = B_0 + B_1 * noise	7.39 (1.32E-27, 4.14E+28)	7.39 (1.07E-93, 5.42E+94)	20.1 (6.16E-51, 6.55E+52)	7.39 (0, INF)	23.83
log(σ_s,k) = B_0 + B_1 * observer	1.30 (0.70, 1.76)	1.24 (0.62, 2.52)	0.48* (0.26, 0.83)	0.31* (0.12, 0.82)	0
log(σ_s,k) = B_0 + B_1 * **noise** + B_2 * *observer* + B_3 * wind	**7.42 (7.07E-18, 7.79E+18),** *2.95 (0.79, 80)*, 7.30 (2.03E-17, 2.63E+18)	**7.30 (3.79E-18, 1.41E+19),** *2.70 (0.03, 210)*, 7.51 (2.07E-17, 2.73E+18)	**18.6 (1.76E-17, 1.98E+19),** *2.50 (0.14, 44.7)*, 18.2 (4.75E-17, 6.98E+18)	**7.35 (8.61E-18, 6.26E+18),** *2.79* (1.50, 5.22)*, 20.2 (5.18E-17, 7.87E+18)	37.7
Detection Model	Null / REVI Estimate -1	REVI Estimate - 2	REVI Estimate - 3	REVI Estimate - 4	Δ AIC
log(σ_s,k) = B_0	47.18 (41.2, 54.0)				11.17
log(σ_s,k) = B_0 + B_1 * wind	1.15 (0.93, 1.43)	1.60 (0.90, 1.50)	0.77* (0.60, 0.99)	0.79 (0.49, 1.28)	8.17
log(σ_s,k) = B_0 + B_1 * noise	1.26 (1.03, 1.54)	1.29 (0.99, 1.68)	0.92 (0.56, 1.50)	1.10E+03 (2.24E-252, 5.36E+257)	13.92

$\log(\sigma_s,k) = B_0 + B_1 *$ observer	0.95 (0.48, 1.07)	0.72* (0.59, 0.88)	0.83 (0.67, 1.03)	0.57* (0.41, 0.80)	0
$\log(\sigma_s,k) = B_0 + B_1 *$ **noise** $+ B_2 *$ *observer* $+ B_3 *$ wind	-	-	-	**-**	N/A
Detection Model	Null / SCTA Estimate -1	SCTA Estimate - 2	SCTA Estimate - 3	SCTA Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	51.9 (44.2, 61.0)				7.22
$\log(\sigma_s,k) = B_0 + B_1 *$ wind	0.87 (0.69, 1.11)	0.68* (0.52, 0.88)	0.77 (0.58, 1.01)	0.91 (0.50, 1.67)	4.02
$\log(\sigma_s,k) = B_0 + B_1 *$ noise	0.98 (0.79, 1.23)	0.74 (0.58, 0.95)	0.64 (0.40, 1.02)	392.79 (3.87E-165, 3.99E+169)	5.12
$\log(\sigma_s,k) = B_0 + B_1 *$ observer	0.91 (0.76, 1.23)	0.80* (0.65, 0.99)	1.22 (0.94, 1.59)	1.15 (0.76, 1.73)	3.18
$\log(\sigma_s,k) = B_0 + B_1 *$ **noise** $+ B_2 *$ *observer* $+ B_3 *$ wind	**0.96 (0.75, 1.24),** *0.83 (0.60, 1.05),* 0.86 (0.65, 1.137)	**0.81 (0.61, 1.08),** *0.70 (0.55, 0.91),* 0.68* (0.50, 0.93)	**0.64 (0.38, 1.09),** *1.06 (0.82, 1.38),* 0.76 (0.56, 1.03)	**58.9* (1.21E-35, 2.86E+38),** *1.07 (0.71, 1.62),* 0.92 (0.51, 1.67)	0
Detection Model	Null / TUTI Estimate -1	TUTI Estimate - 2	TUTI Estimate - 3	TUTI Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	263 (0.99, 7.04E+04)				57.83
$\log(\sigma_s,k) = B_0 + B_1 *$ wind	7.39 (5.33E-69, 1.02E+70)	20.1 (6.91E-50, 5.84E+51)	7.39 (8.34E-51, 6.549E+51)	7.39 (2.84E-72, 1.92E+73)	65.33
$\log(\sigma_s,k) = B_0 + B_1 *$ noise	7.38 (3.35E-23, 1.63e+24)	20.1 (8.13E-29 4.96E+30)	7.39 (1.55E-95, 3.51E+96)	7.39 (0, INF)	65.89
$\log(\sigma_s,k) = B_0 + B_1 *$ observer	12.3 (8, 340)	7.01 (0.18, 280)	506 (1.19E-47, 2.16E+52)	0.79 (0.40, 1.52)	0

$\log(\sigma_s,k) = B_0 + B_1$ * **noise** + B_2 * *observer* + B_3 * wind	-	-	-	-	N/A

Detection Model	Null / WEWA Estimate -1	WEWA Estimate - 2	WEWA Estimate - 3	WEWA Estimate - 4	Δ AIC
$\log(\sigma_s,k) = B_0$	40.5 (33.9, 48.8)	-	-	-	5.07
$\log(\sigma_s,k) = B_0 + B_1$ * wind	1.19 (0.88, 1.62)	0.72 (0.50, 1.05)	0.92 (0.65, 1.30)	0.81 (0.37, 1.76)	1.07
$\log(\sigma_s,k) = B_0 + B_1$ * noise	-	-	-	-	N/A
$\log(\sigma_s,k) = B_0 + B_1$ * observer	0.78 (0.56, 1.50)	0.63 (0.46, 0.85)	0.81 (0.61, 1.10)	0.62 (0.36, 1.05)	0
$\log(\sigma_s,k) = B_0 + B_1$ * **noise** + B_2 * *observer* + B_3 * wind	-	-	-	-	N/A