Trailing-edge Population Dynamics in the Southern Appalachian Mountains

by

Heather Elizabeth Gaya

(Under the Direction of Richard Chandler)

Abstract

Trailing-edge populations at low-latitude range margins are often important components of regional biodiversity, but they face high extinction risk from climate change, and little is known about the ecological processes involved in climate-induced population declines. I used count data and individual-level demographic data to understand the spatio-temporal dynamics of breeding birds in a trailing-edge hotspot in the southern Appalachian mountains. Results of a dynamic multi-species N-mixture model indicated that 33% of trailing-edge species declined in abundance and occupancy, while 69% of species at the core of their range increased in abundance over the ten-year study period. To understand the causes of these declines, I developed a novel Markov point process to investigate the effects of abiotic climate variables and individual-level biotic interactions on a cool-adapted species at the trailing edge of its range (black-throated blue warbler, *Setophaga caerulescens*) and a warm-adapted species in the core of its range (hooded warbler, *Setophaga citrina*). Despite coarse spatial segregation and many ecological similarities between the two species, I found minimal evidence of individual-level interactions and spatial competition. Abiotic climate variables exerted much stronger influence on spatial and temporal variation in abundance and distribution. I next used a spatial Cormack-Jolly-Seber model to test the hypothesis that black-throated blue warblers will be able to track optimal climate conditions via directional dispersal. Natal dispersal tended to be directed away from warm and dry locations while adults exhibited strong site fidelity between breeding seasons, suggesting that dispersal may drive climate tracking. Finally, I developed an individual-based modeling framework that allows for inference on the effects of traits on population-level demographic processes. Parentage is modeled as a partially observed process, making it possible to link age-dependent dispersal, survival, and reproduction within a unified spatio-temporal model. The framework performed well under simulation and recovered parameters with minimal bias, and it should be broadly applicable to numerous systems. Overall my results demonstrate that trailing-edge populations in the southern Appalachian mountains are declining due to abiotic factors affecting survival and dispersal. Future work should investigate the impacts of predation, food availability and long-distance dispersal on the dynamics of trailing-edge populations.

Index words: [individual-based models, climate change, dispersal dynamics, range-shifts, species distributions, trailing-edge populations]

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by

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Chapter 1

Introduction and Literature Review

Biodiversity has declined rapidly in recent decades despite extensive conservation efforts (Brook *et al.*, 2008; Butchart *et al.*, 2010). Although some threats such as habitat loss and over-exploitation can be managed locally, many other threats occur at the global scale, with invasive species and climate change being among the most difficult to address (Holmes & Sherry, 2001; Parmesan & Yohe, 2003; Brook *et al.*, 2008). Climate change impacts are highly variable in space, suggesting that species-level conservation efforts may be less effective than population-level efforts targeting vulnerable population segments with distinct genetic structure (Ehrlich & Daily, 1993; Purvis & Hector, 2000). Although most conservation efforts focus on maintaining species-level diversity, there is growing recognition of the importance of within-species, population-level diversity (Purvis & Hector, 2000). Within-species trait variability can alter the frequency and strength of species' interactions (Bolnick *et al.*, 2011; Forsman, 2015; Kaiser *et al.*, 2019) and increase a population's adaptive capacity for coping with novel climate conditions (Meyer *et al.*, 2009; Bolnick *et al.*, 2011; Carlucci *et al.*, 2015). Trait diversity may also play a key role in community assembly and variation in ecosystem patterns (Carlucci *et al.*, 2015; Spasojevic *et al.*, 2016; Jones *et al.*, 2019).

Birds are one of the best studied vertebrate group (Sekercioğlu *et al.*, 2004; Rosenberg *et al.*, 2019) and often considered good indicator species for environmental change (Fraixedas *et al.*, 2020). Globally, over 20% of bird species are currently extinction-prone (Sekercioğlu *et al.*, 2004), with an estimated 2.9 billion birds lost in North America since 1970 (Rosenberg *et al.*, 2019). Birds can have diverse roles within ecological communities and the continued loss of bird diversity will have far-reaching consequences for ecosystem function (Sekercioğlu *et al.*, 2004; Whelan *et al.*, 2015; Rosenberg *et al.*, 2019). As climate change puts pressure on already stressed ecosystems, there is an urgent need for expanded research and conservation focused on avifauna.

Population-level impacts of climate change often occur through the effects of warming temperatures and extreme precipitation events (Parmesan & Yohe, 2003; Oliver & Morecroft, 2014). Rapidly warming temperatures can directly affect organisms through physiological stress and dehydration (Akesson *et al.*, 2021), or through indirect effects mediated by changes in predator-prey dynamics (Laws, 2017), phenology (Rushing *et al.*, 2015), or food availability (Both *et al.*, 2009). For example, many arthropods reproduce earlier in response to higher temperatures, causing a mismatch between peak insect and avian nestling abundance (Both *et al.*, 2009; Iler *et al.*, 2021). This mismatch may result in lower nestling weights, ultimately increasing chick mortality and driving population declines (Visser *et al.*, 2006; Iler *et al.*, 2021).

Changes in precipitation patterns can have either positive or negative effects on populations (Morrison & Bolger, 2002; Brown & Sherry, 2006; Pillar *et al.*, 2015). Increased rainfall can accelerate vegetation growth and thus prey populations (e.g., herbivorous insects) (Lister & Garcia, 2018). For example, Morrison & Bolger (2002) found that rufous-crowned sparrows (*Aimophila ruficep*) fledged six times more offspring in wet years as compared to dry years, likely due to food availability. Conversely, cooler temperatures accompanied by intense short duration rain events can reduce arthropod larvae survival and disrupt development, altering community-level interactions (Chen *et al.*, 2019). Heavy rainfall events decrease activity of flying insects (Lawson & Rands, 2019), reducing food availability for aerial insectivores and ultimately decreasing nestling body mass (Cox *et al.*, 2019). Increased rainfall may also drive downhill migration in tropical frugivores (Boyle, 2008; Hsiung *et al.*, 2018), temporarily altering local population abundance. Thus, projected increases in the variability of rainfall events (Zobel *et al.*, 2018) have important implications for wildlife populations.

At the community level, rising temperatures in cool climates are correlated with an increase in species richness, even as abundance of some species declines (Lemoine & Böhning-Gaese, 2003; La Sorte *et al.*, 2009; Davey *et al.*, 2012). Increases in warm-adapted and generalist species may drive increased richness if expansions outpace the declines of cold-adapted species (Hampe & Petit, 2005; Robinson *et al.*, 2015). Differential rates of immigration and extinction can create biased estimates of short-term trends of species richness, masking signs of long-term biodiversity loss and extinction debt (Tilman *et al.*, 1994; Ewers & Didham, 2006). As temperatures continue to rise, communities with a high proportion of cold-adapted species may transition to communities dominated by warm-adapted species.

Among the most vulnerable populations to climate change are those occurring near low latitude range margins. These populations are often sensitive to changes in temperature and precipitation and therefore face a high risk of extinction. Loss of these peripheral populations would have negative species-level and ecosystem-level effects because they often harbor high genetic diversity, and they can comprise large fractions of regional biodiversity (MacArthur, 1984; Cahill *et al.*, 2014; Rushing *et al.*, 2020). Trailing-edge populations may experience novel climates and competitive interactions not present in the center of species' ranges (McDonald *et al.*, 2012; Cahill *et al.*, 2014), or display differences in ecological and evolutionary traits from individuals at the range core (Brown *et al.*, 1996; Gaston, 2009). Previous research has proposed rear-edge population may be better adapted to warmer climates than their counterparts in the range-core, but most trailing-edge populations are predicted to decline as temperatures warm (Møller *et al.*, 2008; Merker & Chandler, 2020).

Early work on biogeography predicted that the first stage of species-level declines should be characterized by declines of peripheral populations, resulting in geographical range contraction (Brown *et al.*, 1996). Biogeography theory also predicts that population densities at range margins should be low relative to the core of the range (Gaston, 1996; Brown *et al.*, 1996), but recent work has demonstrated that fragmented pockets of high-quality habitat can sustain dense populations at range peripheries (Channell & Lomolino, 2000). Warm-edge range limits are often driven by biotic interactions (Schemske *et al.*, 2009; Hargreaves *et al.*, 2014), but populations of trailing-edge species can be influenced by both abiotic variables and biotic interactions (Vilà-Cabrera *et al.*, 2019; Merker, 2021). Assessing the strength of abiotic and biotic interactions is complicated by problems of scale-dependence (Clark *et al.*, 2014; Ovaskainen *et al.*, 2016; König *et al.*, 2021), and the development of a modeling framework allowing for individual-level interactions and population-level inferences remains an ongoing challenge (Wisz *et al.*, 2012; Poggiato *et al.*, 2021).

Species' responses to climate change depend on life history traits (Williams *et al.*, 2008). While many species are predicted to shift to higher latitudes and elevations in response to rising temperatures (Parmesan & Yohe, 2003), future climate conditions will disproportionately threaten cold-adapted species by reducing available habitats and fragmenting populations into isolated islands (Habibzadeh *et al.*, 2021). Conversely, for warm-adapted species, increases in temperature at the cold-edge of their range may represent an opportunity to expand into areas that were previously unsuitable (Lehikoinen *et al.*, 2004; Melles *et al.*, 2011). For instance, hooded warblers (*Setophaga citrina*) have expanded the northern edge of their breeding range into southern Ontario in response to rising temperatures (Melles *et al.*, 2011), with further expansions predicted over the next 50 years (Naujokaitis-Lewis *et al.*, 2013).

Small variations in individual traits can disproportionately affect survival and fecundity, but this heterogeneity was mostly ignored in classical population models, which often focused exclusively on a single source of variation such as age or size (Harper, 1977; Lomnicki, 1978). However, a consequence of removing individual identity is the loss of information about mechanisms that might shape population growth (Sprague *et al.*, 2021). A fundamental challenge is that unrelated individual-level interactions and behaviors can produce similar population-level patterns but suggest entirely different management approaches (Knudsen *et al.*, 2011; Hertel *et al.*, 2020). To advance knowledge of the drivers of population change, mechanistic models are needed that link individual-level behaviors and abiotic influences to population-level demographic processes.

Population dynamics are also dependent on spatial structure. Foundational work on island biogeography (MacArthur, 1972), predator-prey systems (Huffaker, 1958), and dispersal dynamics (Skellam, 1951) demonstrated the importance of space and habitat configuration on species interactions and population dynamics. For computational reasons, most early models incorporated space implicitly, capturing broad environmental relationships while averaging over species interactions and individual movements (Patterson *et al.*, 2008; Morales *et al.*, 2010). However, models that ignore individual-level interactions can sometimes yield incorrect inferences (Sherry & Holmes, 1988), especially if fine-scale interactions are the drivers of population-level patterns (Perry & Enright, 2007). While spatially implicit models can be powerful approximations of ecological processes (Morales *et al.*, 2010), there remains a need for spatially-explicit models that can develop our understanding of spatial and temporal dynamics at both the individual and population level.

The outline of this dissertation is as follows. In chapter 2, I assessed hypotheses about the effects of climate on a breeding bird community in the southern Appalachian Mountains. The southern Appalachian mountains are a hotspot for trailing-edge population diversity (Merker & Chandler, 2020). I fit a dynamic N-mixture model (Alldredge *et al.*, 2007; Dail & Madsen, 2011; Sollmann *et al.*, 2015) to quantify the changes in abundance and spatial distribution of species using data on unmarked birds collected from 10 years of point counts. I assessed differences in trends between trailing-edge species and those at the core of their range, and evaluated the effect of migratory strategy on population trends.

In chapter 3, I presented a hierarchical species distribution model with a Markov point process to evaluate how an individual's location is jointly affected by abiotic conditions and the locations of individuals of another species. Both abiotic and biotic factors are potential drivers of trailing-edge range limits, but are difficult to model together due to issues of scale and imperfect detection (Belmaker *et al.*, 2015). I demonstrated the approach using 4 years of data on hooded warbler and black-throated blue warbler in the southern Appalachian Mountains. I investigated the relative role of climate (based on temperature and precipitation) and hooded warbler presence on black-throated blue warbler activity centers.

In chapter 4, I fit a dispersal model to the locations of black-throated blue warblers banded in the southern Appalachian Mountains. Species that cannot track optimal climatic conditions via dispersal are likely to experience increased extinction risks (Hoffmann & Sgrò, 2011; Mota *et al.*, 2018). I used a discrete-time, discrete-space Bayesian Cormack-Jolly-Seber (CJS) (Lebreton *et al.*, 1992) model to describe natal and adult dispersal, restricting my analysis to birds that returned to the study area. I tested the hypotheses that natal dispersal distances are greater than adult dispersal distances, and natal dispersal is directed towards locations with colder and wetter climate conditions than conditions at hatch locations.

In chapter 5 I presented an individual-based modeling framework that can be used to jointly estimate spatially-varying individual-level demographic parameters in both theoretical and applied ecological settings. Many of the advancements in individual-based modeling have been focused on agent-based simulations that use behavioral 'rules' to simulate populations and individual actions. These models are rarely confronted with data using formal inference methods. I proposed a general inference framework that incorporates individual-level traits such as age, sex, and location and links these characteristics to population-level demographic processes. The model includes parent-offspring linkages and an age-based movement model to describe how individual heterogeneity in demography arises from local environmental effects and individual traits.

In chapter 6, I summarized the major findings of chapters 2–5. I discussed trailing-edge population trends in the southern Appalachian mountains and connected my findings to the broader literature of avian population declines. I also emphasized the importance of mechanistic individual-based models for conservation and population management. Finally, I suggested future directions for research on trailing-edge species experiencing climate change and discussed the need for individual-level approaches when modeling population dynamics.

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CHAPTER 2

SPATIO-TEMPORAL COMMUNITY DYNAMICS IN A HOTSPOT OF TRAILING-EDGE POPULATION DIVERSITY [1]

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Abstract

Mounting evidence indicates that populations at the warm edge of geographic ranges are declining in response to climate change, but most studies have focused on trailing-edge population dynamics of single species, and little is known about community-level impacts of trailing-edge population declines. Community-level assessments are particularly needed in regions where proportional richness of trailing-edge populations is high. We used ten years (2014–2023) of avian point count data from the southern Appalachian Mountains, USA, to assess changes in abundance and spatial distribution of 9 trailing-edge populations and 16 populations at the core of their range. Three (33%) of the nine trailing-edge populations decreased in abundance over the 10 year period whereas six (67%) species had no change. For species near the core of their ranges, one of 16 (6%) populations decreased in abundance, 11 (69%) increased, and 4 (25%) exhibited no change. Species richness increased at the majority of sites, especially at high elevations. Our results indicate that community composition in a trailing-edge hotspot has become increasingly dominated by warm-adapted species, and increases in species richness may be temporary if declines of cool-adapted species continue.

2.1 Introduction

Population-level extinction risk from climate change is predicted to be highest at low-latitude range margins (Hampe & Petit, 2005; Sekercioğlu *et al.*, 2008; Rushing *et al.*, 2020; Stevens *et al.*, 2023b) where species frequently occur near their thermal tolerances and experience increased competition and predation pressure from warm-adapted species encroachment (MacArthur, 1984; McDonald *et al.*, 2012; Sunday *et al.*, 2012; Akesson *et al.*, 2021). Trailing-edge populations are often genetically distinct from populations at the core of their range and can be important components of regional biodiversity (Gaston, 2009; Rehm *et al.*, 2015; Ferrari *et al.*, 2018; Merker & Chandler, 2020). However, most research on trailing-edge populations has involved single-species studies, making it difficult to assess community-level consequences of population declines.

Community structure in regions with large proportions of trailing-edge species could be impacted by climate change in numerous ways. If cool-adapted species at the edge of their range decline precipitously, complete community turnover could be possible (Hampe & Petit, 2005; Sunday *et al.*, 2012). Alternatively, if invasion by warm-adapted species happens faster than the retreat of cool-adapted species, rising temperatures could lead to increased species richness, even as abundance of trailing-edge populations declines (Lemoine & Böhning-Gaese, 2003; La Sorte *et al.*, 2009; Davey *et al.*, 2012). Under this scenario, species richness might increase, but species composition will be severely altered.

The speed of community encroachment by warm-adapted species, and the rate of decline of cool-adapted species, may depend on species-level traits other than thermal tolerance. For instance, the ranges of short-lived species often shift upwards in elevation faster under climate change than long-lived species (Couet *et al.*, 2022). In avian communities, long-distance neotropical migrants shift their cold-edge range boundaries slower than short-distance migrants or resident species (Rushing *et al.*, 2020; Välimäki *et al.*, 2016; Stevens *et al.*, 2023a). Many migratory species have a slower phenological response to ongoing climate warming than resident species, which may translate to a reduced competitive advantage on the breeding ground (Wittwer *et al.*, 2015; MacLean & Beissinger, 2017). Thus, population-level extinction risk may be higher for trailing-edge populations of migratory species than resident species.

We used 10 years of avian survey data from a hotspot of trailing-edge population diversity (Merker & Chandler, 2020) in the southern Appalachian Mountains to (1) assess the generality of trailing-edge population declines, and (2) determine the consequences for community structure. We predicted species-specific shifts in abundance and occupancy would depend on range-position, migratory strategy and temperature preferences. We predicted that cool-adapted trailing-edge populations would decrease in abundance and become increasingly restricted to high elevations. In contrast, we predicted that warm-adapted species near the center of their geographic ranges would increase in abundance and expand their distributions upwards in elevation. We further predicted long-distance migratory species would have slower rates of local range shifts than short-distance migrants or residents.

2.2 Methods

Study Area

The Nantahala National Forest in the southern Appalachian Mountains contains a high diversity of species at the trailing-edge of their breeding range (Merker & Chandler, 2020). Elevation within the region ranges from 660–1590 m (Figure 2.1), with drier conditions found on the steeper, more exposed slopes in the eastern portion of the study area. High elevation sites are cooler than those at lower elevations, with an average May temperature of 10.5 °C above 1300 m, compared to 14 °C at 700 m. During the breeding season (May – July), sites above 1300 m receive an average 26.4 cm of precipitation in comparison to only 18.2 cm of precipitation at the lowest elevations in the study area.

Dominant and subdominant tree species include oaks *(Quercus spp.)*, hickory *(Carya spp.)*, yellow poplar *(Liriodendron tulipifera)*, birch *(Betula spp.)* maple *(Acer spp.)*, fraser magnolia (*Magnolia fraseri*), and common buckeye (*Aesculus flava*). Serviceberry (*Amelanchier spp.*) and witchhazel (*Hamamelis virginiana*) are common in the mid-story. Following declines of American chestnut (*Castanea dentata*) and Eastern hemlock (*Tsuga canadensis*), rhododendron *(Rhododendron maximum)*, mountain laurel *(Kalmia latifolia)*, and huckleberry (*Vaccinium spp.* and *Gaylussacia spp.*) have become more common in the understory and in forest gaps (Elliott & Swank, 2008).

Environmental Data

We calculated total annual precipitation for each year (2013–2022) based on nine USDA Forest Service (USFS) climate stations (Miniat *et al.*, 2022), and we used interpolations of PRISM data (Daly *et al.*, 2008) to create smoothed precipitation layers spanning the study area. We standardized each year's spatial data by subtracting all values by the mean across all years and dividing by the standard deviation. To represent the heat accumulation during the breeding season, we calculated growing degree-days (Lany *et al.*, 2016; Cesaraccio *et al.*, 2001) in May of each year (2013–2022). For many species in the southern Appalachian Mountains, May represents a critical part of the breeding season when birds build nests and begin provisioning fledglings (Lumpkin & Pearson, 2013; Lewis *et al.*, 2023). Temperature data were collected hourly from 34 temperature loggers (Onset Computer Corp., Bourne, MA, model number UA-002-64) distributed throughout the study area, as well as at 5 US Forest Service (USFS) climate stations (Miniat *et al.*, 2022). May mean minimum and maximum temperatures (2014–2022) were 0.43 °C and 33.6 °C, respectively, with a mean annual precipitation of 230.6 cm.

Soil moisture and stream frequency in the study area follow an east-west gradient, with eastern slopes receiving and retaining less moisture. To account for the east-west gradient of soil moisture in the study area, we included the standardized easting coordinate of the site as a proxy for watershed moisture.

Surveys

Point count surveys were conducted by trained technicians from 2014 to 2023. Seventy-one points were surveyed in 2014 and 2015, with 38 additional locations added in 2016 and surveyed each year thereafter. Each location was surveyed once per year during the breeding season (May to July). All surveys were conducted between sunrise and 5 hours after sunrise. Observers recorded the distance of all singing birds heard in a 10-minute session split into four consecutive 2.5-minute intervals. Observers also recorded noise level, wind, precipitation and starting time for each survey.

Process Model

We analyzed point count data using dynamic multi-species N-mixture models (Alldredge *et al.*, 2007; Dail & Madsen, 2011; Amundson *et al.*, 2014). These models allow for the assessment of environmental effects on spatial and temporal variation in population growth rates while accounting for demographic stochasticity, serial correlation, and observation error arising from variation in detection probability. We categorized each species by migratory strategy (resident, short-distant migrant, or long-distance migrant) and range position (trailing-edge or core) to assess differences between groups. We restricted analyses to species detected at least 50 times over the 10 years of sampling because data on rare species provide little information about population trends.

We modeled abundance of each species in year 1 (2014) as a function of degree days, annual precipitation, and soil moisture at each site in the previous year (2013). To account for soil moisture, we included the standardized easting coordinate of the site as a proxy for watershed moisture. The model for the first time period was:

$$N_{i,k,1} \sim \text{Poisson}(\psi_{i,k,1}) \tag{2.1}$$

$$\log(\psi_{i,k,1}) = \beta^{\psi}_{0,k} + \beta^{\psi}_{1,k}\text{DegreeDays}_{i,1} + \beta^{\psi}_{2,k}\text{Precip}_{i,1} + \beta^{\psi}_{3,k}\text{SoilMoisture}_{i} \tag{2.2}$$

where $N_{i,k,1}$ is the abundance of species k at site i in year 1. The species-specific coefficients in Eq. 2.2 were modeled as normally-distributed random effects on the log scale.

$$\begin{bmatrix} \beta^{\psi}_{0,k} \\ \beta^{\psi}_{1,k} \\ \beta^{\psi}_{2,k} \\ \beta^{\psi}_{3,k} \end{bmatrix} \sim \text{Normal}\left(\begin{bmatrix} \bar{\beta}^{\psi}_{0,k} \\ \bar{\beta}^{\psi}_{1,k} \\ \bar{\beta}^{\psi}_{2,k} \\ \bar{\beta}^{\psi}_{3,k} \end{bmatrix}, \begin{bmatrix} \sigma_{\beta^{\psi}_0} & 0 & 0 & 0 \\ 0 & \sigma_{\beta^{\psi}_1} & 0 & 0 \\ 0 & 0 & \sigma_{\beta^{\psi}_2} & 0 \\ 0 & 0 & 0 & \sigma_{\beta^{\psi}_3} \end{bmatrix} \right) \tag{2.3}$$

The expected values were described by an intercept and fixed effects of range position and migratory strategy to assess the possibility that species with similar traits have more similar responses to the environment.

$$\bar{\beta}^{\psi}_{q,k} = \alpha_{q,0} + \alpha_{q,1}\text{Range}_k + \alpha_{q,2}\text{Migration}_k \tag{2.4}$$

with $q = 0, \ldots, 3$ being the coefficient index.

For years $t > 1$, abundance of each species at each site was determined by the annual growth rate, $\lambda_{k,t}$. We modeled the yearly growth rate as a function of the prior breeding season's degree days and the previous year's annual precipitation.

$$\begin{gathered} N_{i,k,t} \sim \text{Poisson}(\psi_{i,k,t}) \\ \psi_{i,k,t} = \lambda_{i,k,t}\psi_{i,k,t-1} \\ \log(\lambda_{i,k,t}) = \beta^{\lambda}_{0,k} + \beta^{\lambda}_{1,k}\text{DegreeDays}_{i,t} + \beta^{\lambda}_{2,k}\text{Precip}_{i,t} \end{gathered} \tag{2.5}$$

Here again, the coefficients were modeled as random effects determined by guild structure, using the same formulation as in Eq. 2.3 and 2.4. We modeled yearly abundance as a function of the previous year's expected abundance (ψ), rather than realized abundance (N), to allow for the possibility of local colonization (Hostetler & Chandler, 2015).

Species richness at site i in year t was calculated as the realized number of species present at the site: $S_{i,t} = \sum_{k=1}^{K} I(N_{i,k,t} > 0)$. For each location, we also calculated the proportion of richness attributable to trailing-edge species.

Observation Model

Conventional distance sampling assumes perfect detection at zero distance from the observer (Buckland *et al.*, 2001), an assumption that is easily violated if an animal does not vocalize during the survey window (Laake & Borchers, 2004). To address this potential bias, we followed Amundson *et al.* (2014) and modeled the observation process as the product of availability (probability of an individual singing during the sampling period), p_k^a, and distance-based detection probability (probability of observing an individual given it was present and available), $p_{i,k,t}^d$. We modeled the total number of individuals of each species observed at each site as the outcome of a binomial distribution: $n_{i,k,t} \sim \text{Binomial}(N_{i,k,t}, p_k^a p^d)$. We modeled p_k^a as a random effect following a logit-normal distribution: $\text{logit}(p_k^a) \sim \text{Normal}(1, \kappa)$.

To calculate distance-based detection probability, we truncated observations to a 100 m radius (Buckland *et al.*, 2001) and grouped all detections into 10, 10-m distance bins (b in $b = 1, \ldots, B$). To estimate the effect of distance on detection, we used a half-normal detection function with scale parameter δ.

$$\log(\delta_{i,k,t}) = \beta_{0,k}^d + \beta_{1,k}^d \text{noise}_{i,t}$$

$$p_{i,k,t}^d = \sum_{b=1}^{B} \int_{10(b-1)}^{10b} e^{\frac{-x^2}{2\delta_{i,k,t}^2}} dx$$

We fit models using Bayesian methods in NIMBLE (v. 0.10.1) via the 'rnimble' package in R (de Valpine *et al.*, 2017; NIMBLE Development Team, 2019; R Core Team, 2019). Prior to analysis, we standardized each continuous covariate by subtracting the mean and dividing by the standard deviation. We ran 100,000 MCMC iterations using three parallel chains with a burn-in of 90,000, resulting in 10,000 posterior samples. We assessed convergence of Markov chains using the Gelman-Rubin statistic (Gelman & Rubin, 1992) and visual inspection.

2.3 Results

Across 10 years of sampling, we detected 33,125 birds representing 92 species, of which 25 species had at least 50 detections (Table 2.1). The majority (16) of these species were at the core of their breeding range (hereafter, "core species"), whereas 9 species were at the trailing-edge of their ranges (hereafter, "trailing-edge species"). Each core species was detected at an average of 88 sites (range 47 – 108), with a mean 43 (range 10 – 157) detections per species per year. Trailing-edge species were detected at an average of 65 sites (range 22 – 109), with a mean 43 (range 7 – 91) detections per species per year.

Temperatures were highest in 2017 with an average May temperature of 16.1 °C at the lowest elevations and 12.6 °C at the highest elevations. Temperatures were lowest in 2018 with average temperatures ranging from 12.1 °C to 8.7 °C across the elevational gradient. Low temperatures coincided with heavy rains, with a total precipitation of 12.6 cm at elevations above 1300 m and 8.7 cm at sites below 800 m in 2018. However, there was no correlation between temperature and precipitation over time ($r = -0.07$, $p = 0.84$). The driest year was 2016, with total precipitation ranging from 4.8 cm at the highest elevations to 3.3 mm at the lowest elevation. Annual precipitation steadily increased in the study area over the past 30 years (Figure A.1). There was no trend in May degree days during the study period, though prior to 2020, average May temperature showed a positive trend (Lewis *et al.*, 2023).

We used the average percent change in abundance between years to classify each species as decreasing, stable or increasing in abundance (Table 2.1). Of the 25 species in our study, 21 species had stable or increasing populations (Figure 2.2). Declines were more common in trailing-edge species than those in the core of their range. Three trailing-edge species declined in abundance during the study period, compared with 1 core-species. There were no trailing-edge species with increasing abundance or occupancy (Figure 2.3). For species at the range core, 11 species increased in abundance, with all but 3 species (eastern towhee, eastern wood-pewee and wood thrush) also increasing in site occupancy.

To avoid the binary classification of species as "warm-adapted" and "cool-adapted", we used the species-specific coefficients in Eq. 2.2 as a proxy for each species relationship to temperature and precipitation.

Species with a positive relationship to temperature and a negative relationship to precipitation were more likely to have stable or increasing populations (Figure 2.4). By migratory strategy, the largest declines in abundance were seen in long-distance migrants, with stable or increasing abundances associated with short-distance migrants and resident species (Figure 2.4).

Species richness ranged from 11–19 species/ha and was lowest above 1300 m (Figure 2.5). At sites above 1300 m, species composition was initially dominated by trailing-edge species (up to 61% trailing-edge species at some locations in 2014), transitioning to a majority of core species in later years (average 40% trailing-edge species in 2023). At mid elevation (1000 – 1300 m) sites, trailing-edge species contributed an average of 38% of species richness in 2014 compared to 27% by 2023 (Figure 2.6).

2.4 Discussion

Almost all models of climate change impacts on species distributions predict shifts towards higher elevations and latitudes (Parmesan & Yohe, 2003). Populations occurring near low latitude range margins and at the highest elevations are expected to experience stronger negative effects of climate change than populations near the core of the range, subjecting them to increased risk of extinction (Razgour *et al.*, 2013; Habibzadeh *et al.*, 2021). Consistent with these predictions, cold-adapted species at the trailing-edge of their range were more likely to exhibit population declines than warm-adapted species. Extirpation of trailing-edge species from lower elevation sites was slower than colonization by core-species, leading to increased species richness coupled with declining trailing-edge abundance.

Continued declines of trailing-edge populations will likely result in complete reorganization of community composition and decreased species richness. Ecosystem-level impacts of species turnover are difficult to predict, but many ecological processes, such as nutrient cycling and predator prey dynamics, are a direct result of functional diversity within community assemblages (Chapin III *et al.*, 2000; Sekercioğlu *et al.*, 2004). For example, nuthatches, blue jays and other seed-caching species can play a critical role in oak and pine tree dispersal (Sekercioğlu *et al.*, 2004). Loss of trailing-edge species may also decrease genetic diversity (Harrison, 2020). Trailing-edge populations often harbor genotypes that are better adapted to climate extremes relative to their counterparts in the core of the range (Hampe & Petit, 2005; Rehm *et al.*, 2015). Therefore the loss of locally adapted populations may not only alter local community composition, but further threaten the range-wide adaptive capacity (Rehm *et al.*, 2015).

Consistent with previous research, the negative impacts from increasing temperatures were most pronounced for species associated with cool climates (Rodenhouse *et al.*, 2008; Pearce-Higgins *et al.*, 2015). Species with a wide thermal tolerance may be less immediately affected by warming temperatures, in part because climate generalists (i.e. species without a strong association to temperature) are often habitat generalists (Davey *et al.*, 2013; Godet *et al.*, 2015; Sweeney & Jarzyna, 2022). Though low-latitude, peripheral populations can demonstrate high degrees of local adaptation and resilience to less favorable conditions (e.g., high temperatures) (Hampe & Petit, 2005; Bennett *et al.*, 2015), these adaptations are unlikely to prevent population declines. In addition to increasing temperature, latitudinal range shifts of warm-adapted species may introduce novel competitive interactions (McDonald *et al.*, 2012; Gibson-Reinemer & Rahel, 2015), which invading warm-adapted species are more likely to win (Urban *et al.*, 2012). As temperatures continue to rise, communities with a high proportion of trailing-edge species will likely transition to communities dominated by warm-adapted species.

In the early years of the study, the majority of species present at high elevation sites were at the trailing-edge of their range, but this proportion decreased in later years. Combined with the increases in species richness observed at almost all sites, these results suggest a pattern of homogenization of the bird community across the elevation gradient. Previous research suggests within-community variation in preferred temperatures (e.g. a mix of cold- and warm-adapted species) increases the capacity of a community to respond to climate change (Akesson *et al.*, 2021), but no equivalent research exists regarding community composition of trailing-edge and core species. Homogenization can increase vulnerability to environmental disturbance (Catano *et al.*, 2020; Olden & Poff, 2004), especially if members of the homogenized community compete for food or habitat resources (Davey *et al.*, 2012). In the southern Appalachian mountains, a high proportion of trailing-edge populations are composed of cold-adapted species. Thus, it is difficult to separate the homogenization of preferred temperature from the homogenization of population range position. While none of the species in our study declined to local extinction, the ecosystem ramifications of increased prevalence of species in the core of their range remains an open question.

Climate change may also threaten cold-adapted species by reducing available habitat and fragmenting populations into isolated habitat patches (Abeli *et al.*, 2018; Habibzadeh *et al.*, 2021). Many trailing-edge populations are already confined to fragmented high-elevation habitat (Habibzadeh *et al.*, 2021), and thus latitudinal range shifts would require long distance dispersal to other suitable 'sky islands'. Long-distance dispersal is notoriously difficult to study, but there is scant evidence that long-distance neotropical migratory passerines disperse more than a few kilometers between breeding sites (Faaborg *et al.*, 2010; Årevall *et al.*, 2018; Vilà-Cabrera *et al.*, 2019). Though not investigated here, dispersal limitations may prevent climate tracking even after habitat quality declines below optimal conditions (Hampe & Petit, 2005; Bennett *et al.*, 2015; Robinson *et al.*, 2015), concentrating populations into small habitat patches and temporarily increasing population densities and species richness (Collinge, 1998).

Although trailing-edge populations declined during the ten years of investigation, none of the species in our study declined to local extinction. Thus, as warm-adapted species shifted upward in elevation, species richness increased, particularly at high elevations. Differential population growth rates of cool and warm-adapted species can create short-term trends of increasing species richness (Urban *et al.*, 2012), masking signs of long-term biodiversity loss and extinction debt (Tilman *et al.*, 1994; Ewers & Didham, 2006; Urban *et al.*, 2012). However, elevated levels of species richness are usually temporary (Tilman *et al.*, 1994; Hampe & Petit, 2005; Habibzadeh *et al.*, 2021), suggesting subsequent reductions in species abundance and richness in the near future (Ewers & Didham, 2006; Halley & Pimm, 2023).

In contrast to the congruence of our results with predictions of climate change impacts, several studies have found unexpected latitudinal and elevational changes in species distributions (Tingley *et al.*, 2012; Rubenstein *et al.*, 2023; Freeman *et al.*, 2018a). There are several possible explanations for the agreement of our findings with predictions from climate change models. Firstly, numerous studies suggest the strength of climate-induced range shifts is strongly species and region specific (La Sorte & Jetz, 2012; Thompson & Fronhofer, 2019). For instance, several passerine species in California have demonstrated counter-intuitive downhill movements as increasing precipitation pulled species downslope while rising temperatures pushed species in the opposite direction (Tingley *et al.*, 2012). Species with limited dispersal options due to fragmented habit may showed delayed responses to environmental changes (Ewers & Didham, 2006; Platts *et al.*, 2019). Finally, the southern Appalachian Mountains harbor a high proportion of neotropical migrants, which tend to have shorter life spans than resident species (Soriano-Redondo *et al.*, 2020), and short-term range shifts are more likely to be observed in species with short life expectancy (Tingley *et al.*, 2012; Couet *et al.*, 2022).

Modeling the direction and velocity of range shifts remains a difficult task and most trait-based range forecasts have poor predictive power (Angert *et al.*, 2011; Auer & King, 2014; Hovick *et al.*, 2016). Research on the dispersal capacity of different migratory strategies has been mixed. Some studies have demonstrated no difference between migratory strategies (Sekercioğlu, 2007; Angert *et al.*, 2011; Hovick *et al.*, 2016), while others have noted significantly reduced range expansion in long-distance migrants (Laaksonen & Lehikoinen, 2013; Rushing *et al.*, 2020). We found migratory status was a poor predictor of range shifts; however, when used in concert with range position, long-distance migrants had lower average percent change in abundance than resident species. However, all but one of the studied long-distance trailing-edge species had a negative relationship with temperature, while the reverse was true for range-core species. These results suggest migratory status may play a role in a species's capacity for climate-induced range shifts, but the effects are less pronounced than the effect of individual species' range position and life history traits.

Although air temperatures have generally increased over the last decade, there was no trend in May degree days during the study period. However, prior to 2020, there was a positive trend in average daily May temperature (Lewis *et al.*, 2023), suggesting several years of cold temperatures obscured the otherwise positive trend. Increased climate variation may pose a greater threat to species persistence than increased mean temperature (Vasseur *et al.*, 2014), but there is often a delay between temperature change and changes in species composition (Godet *et al.*, 2011; Devictor *et al.*, 2012; Lindström *et al.*, 2013). Many species are resilient to occasional fluctuations in climate, only moving uphill or adjusting behaviors after repeated exposure to extreme conditions (Cohen *et al.*, 2020). While several species appeared to be responding to changing temperatures, longer-term data sets ($>$ 10 years) may be necessary to fully reveal the connection between breeding season climate and yearly abundance for many species. With additional years of data, we expect the connection between abundance and yearly temperature variability will become more apparent, especially as yearly temperature differences become more extreme (IPCC, 2022).

The high proportion of stable or increasing species in our study may in part be the result of our inability to model the dynamics of rare species. We only modeled species with ≥ 50 aural detections to ensure the model had a reasonable sample size for estimating yearly changes (Buckland *et al.*, 2001). By focusing only on species detected by sound, we removed a source of variability in our detection model, but also removed all raptors, owls, and most female individuals, who are less likely to vocalize. Moreover, we likely excluded lower abundance species that may have shown declines during our study. For instance, Acadian flycatcher (*Empidonax virescens*) and Chestnut-sided warbler (*Setophaga pensylvanica*) are both present at the study site and declining in the southern Appalachian Mountains (Sauer *et al.*, 2017), but were excluded from the study due to low detection.

Our study reinforces growing concerns that climate change is driving trailing-edge population declines. As temperatures increase in the near future, food and habitat resources may move uphill or decline (Parmesan & Yohe, 2003; Lehikoinen *et al.*, 2014) putting further pressure on trailing-edge communities. However, without a mechanistic approach, we cannot effectively predict the long-term consequences of range shifts. If range shifts are driven by directional dispersal, trailing-edge genetic diversity may persist as individuals move towards core populations (Hargreaves & Eckert, 2014). In contrast, if uphill movements represent an 'escalator to extinction' (Sekercioğlu *et al.*, 2008; Freeman *et al.*, 2018b), then trailing-edge range retractions may signal impending extinctions. Future studies should focus on the specific drivers of abundance and species composition within trailing-edge communities and assess the conservation implications of trailing-edge range shifts.

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Table 2.1: Species with at least 50 detections from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA. Trend values > 0 indicate the population is increasing, whereas values of < 0 indicate the population is declining. Trends with 95% CIs excluding zero are indicated by an asterisk (*).

Range	Common Name	Scientific Name	Species Code	Migratory Strategy	Abundance Trend
Core	Black-and-white Warbler	*Mniotilta varia*	BAWW	Long-distance	0.03 (0.01 – 0.06)*
	Blue Jay	*Cyanocitta cristata*	BLJA	Resident	0.07 (0.03 – 0.12)*
	Carolina Chickadee	*Poecile carolinensis*	CACH	Resident	0.03 (-0.02 – 0.08)
	Eastern Towhee	*Pipilo erythrophthalmus*	EATO	Short-Distance	-0.04 (-0.07 – 0.00)*
	Eastern Wood-Pewee	*Contopus virens*	EAWP	Long-distance	-0.04 (-0.11 – 0.04)
	Hairy Woodpecker	*Leuconotopicus villosus*	HAWO	Resident	0.11 (0.01 – 0.25)*
	Hooded Warbler	*Setophaga citrina*	HOWA	Shrub-level	0.04 (0.01 – 0.07)*
	Northern Parula	*Setophaga americana*	NOPA	Short-Distance	0.11 (0.06 – 0.20)*
	Ovenbird	*Seiurus aurocapilla*	OVEN	Long-distance	0.02 (0.00 – 0.04)*
	Pileated Woodpecker	*Dryocopus pileatus*	PIWO	Resident	0.09 (0.04 – 0.16)*
	Red-eyed Vireo	*Vireo olivaceus*	REVI	Long-distance	0.06 (0.03 – 0.10)*
	Scarlet Tanager	*Piranga olivacea*	SCTA	Long-distance	0.01 (-0.02 – 0.04)
	Tufted Titmouse	*Baeolophus bicolor*	TUTI	Resident	0.03 (0 – 0.07)*
	White-breasted Nuthatch	*Sitta carolinensis*	WBNU	Resident	0.11 (0.02 – 0.23)*
	Worm-eating Warbler	*Helmitheros vermivorum*	WEWA	Long-distance	0.10 (0.02 – 0.22)*
	Wood Thrush	*Hylocichla mustelina*	WOTH	Long-distance	-0.01 (-0.05 – 0.02)
Trailing	Blue-headed Vireo	*Vireo solitarius*	BHVI	Short-Distance	0 (-0.03 – 0.04)
	Blackburnian Warbler	*Setophaga fusca*	BLBW	Long-distance	-0.04 (-0.12 – 0.07)
	Black-throated Blue Warbler	*Setophaga caerulescens*	BTBW	Long-distance	-0.06 (-0.08 – -0.03)*
	Black-throated Green Warbler	*Setophaga virens*	BTNW	Long-distance	-0.01 (-0.05 – 0.05)
	Canada Warbler	*Cardellina canadensis*	CAWA	Long-distance	-0.1 (-0.13 – -0.06)*
	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR	Long-distance	0.01 (-0.05 – 0.07)
	Slate-colored Junco	*Junco hyemalis*	SCJU	Short-Distance	-0.03 (-0.06 – 0.01)
	Veery	*Catharus fuscescens*	VEER	Long-distance	-0.08 (-0.12 – -0.05)*
	Winter Wren	*Troglodytes hiemalis*	WIWR	Short-Distance	0.03 (-0.07 – 0.24)

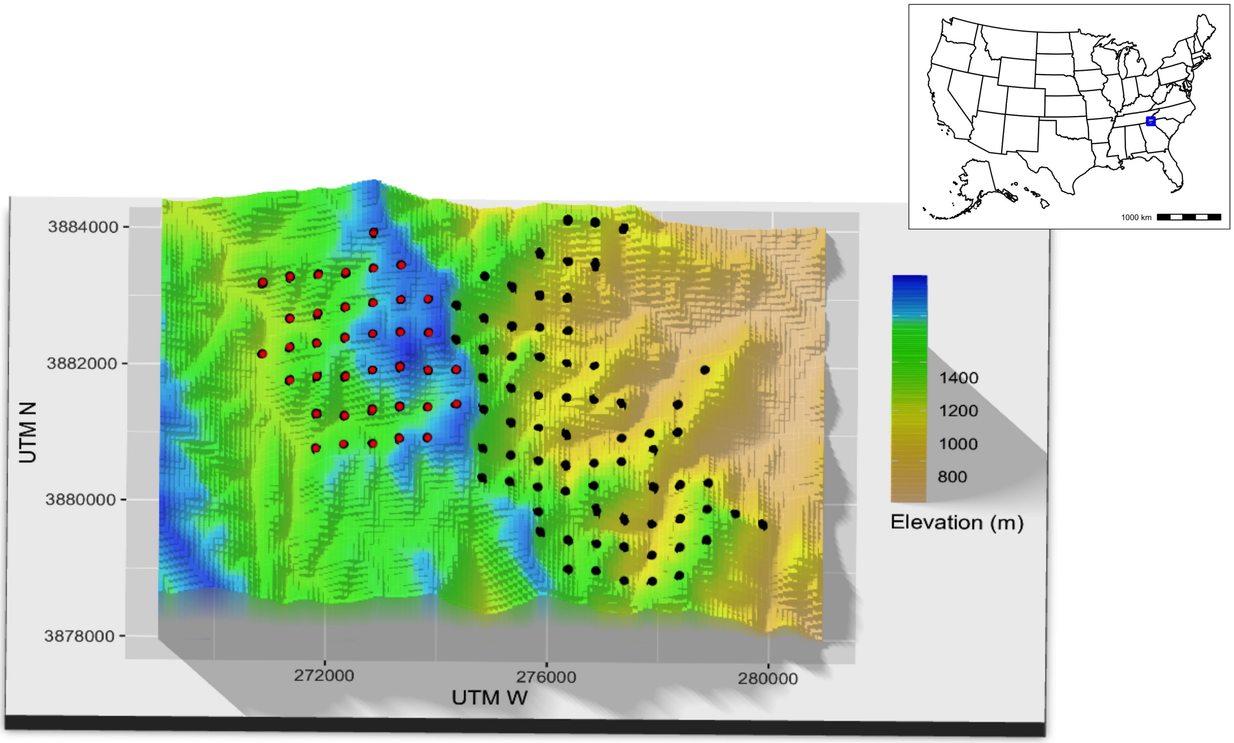

Figure 2.1: Map of point count locations in the Nantahala National Forest, North Carolina, USA. Points in black (right side) were surveyed from 2014-2023. Locations in red (left side) were surveyed starting in 2016.

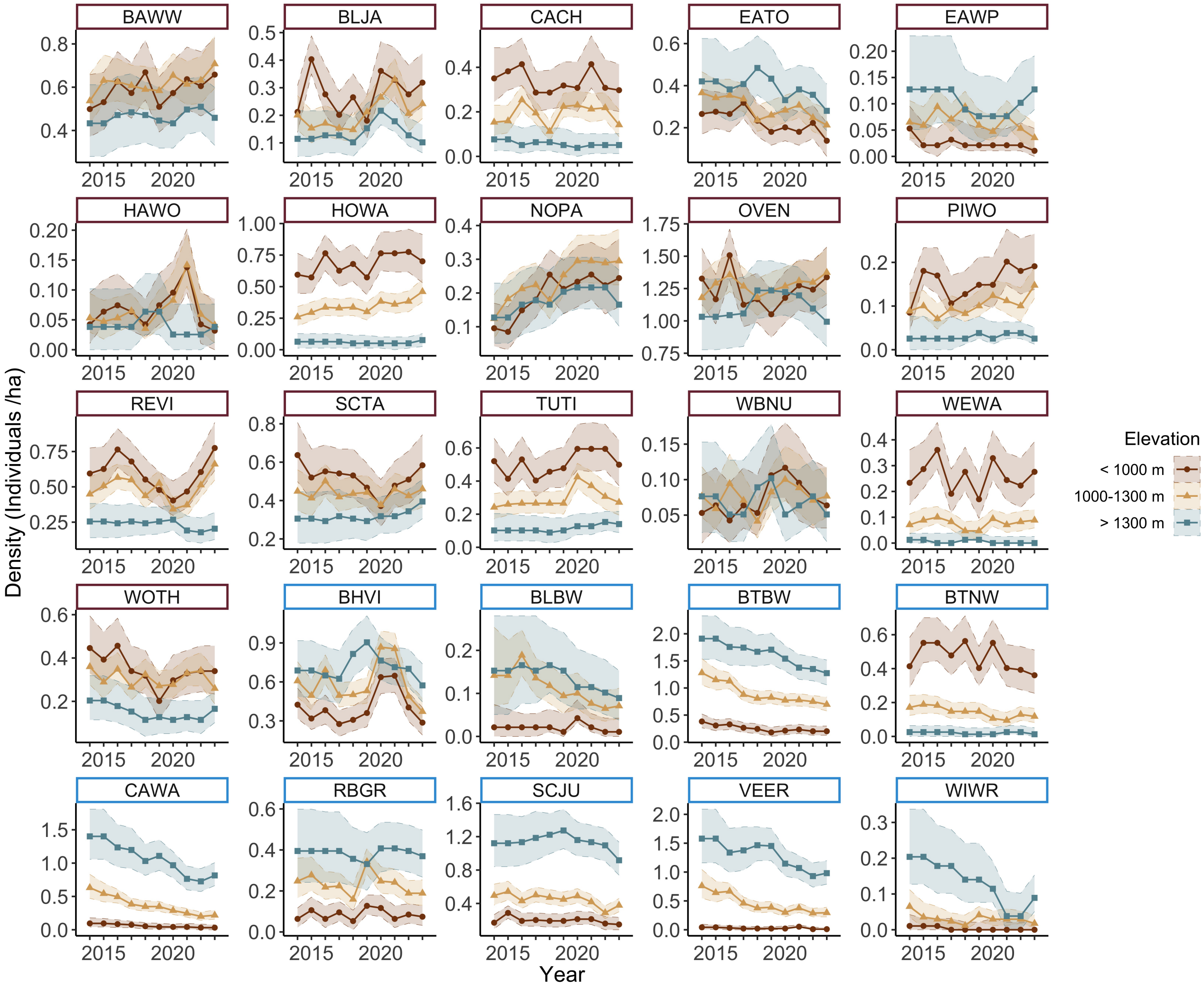

Figure 2.2: Average density (individuals per hectare) in the study area at high, medium and low elevations. Estimates are the realized values of density averaged across all monitored sites within each elevation category. Point estimates are posterior means shown with 95% CIs. Species are sorted by range position. Populations at the trailing-edge of the species' range are outlined in blue and populations in the core of their range are outlined in red. The scale of the y-axis varies between species.

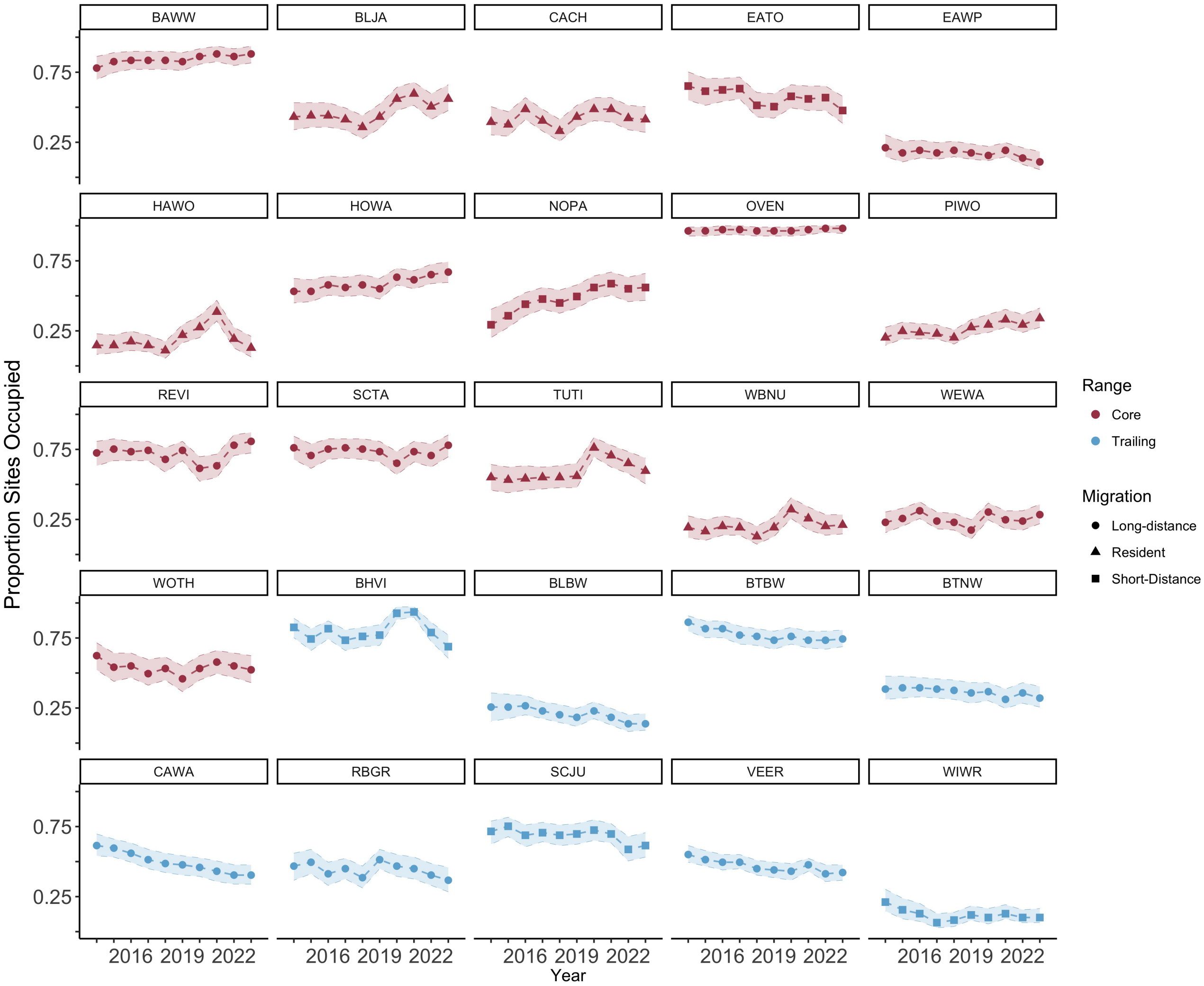

Figure 2.3: Site occupancy for species in the Nantahala National Forest, North Carolina, USA from 2014 to 2023. Estimates are posterior means (points) and 95% CIs. Species are sorted by range position with trailing-edge species in blue and core species in red. Point shapes indicate if a species is a long-distance migrant (circles), short-distance migrant (squares) or resident species (triangles).

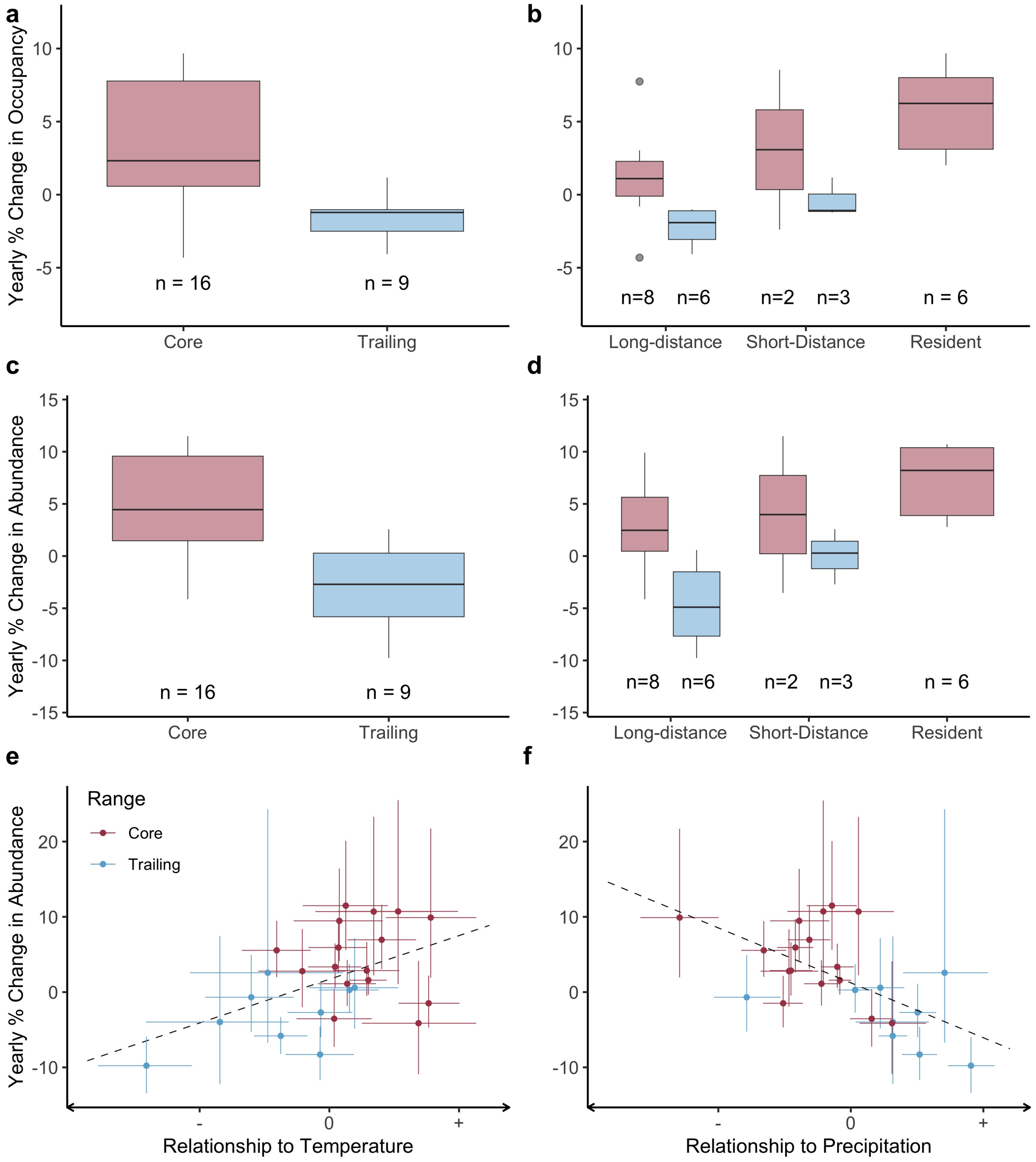

Figure 2.4: Average percent yearly change in abundance and occupancy from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA with species grouped by range position (a and c), migratory strategy (b and d), relationship to temperature (e) and relationship to precipitation (f). For all panels, trailing-edge populations are shown in blue, with core populations shown in red. Relationship to temperature and precipitation are shown as the estimated effects of temperature and precipitation on species abundances in the first year of the study (2014). Scatterplots display posterior means (points) with 95% credible intervals, while boxplots are based on posterior means for each species. The dashed lines in panels (e) and (f) display a simple linear model between coefficients and change in abundance.

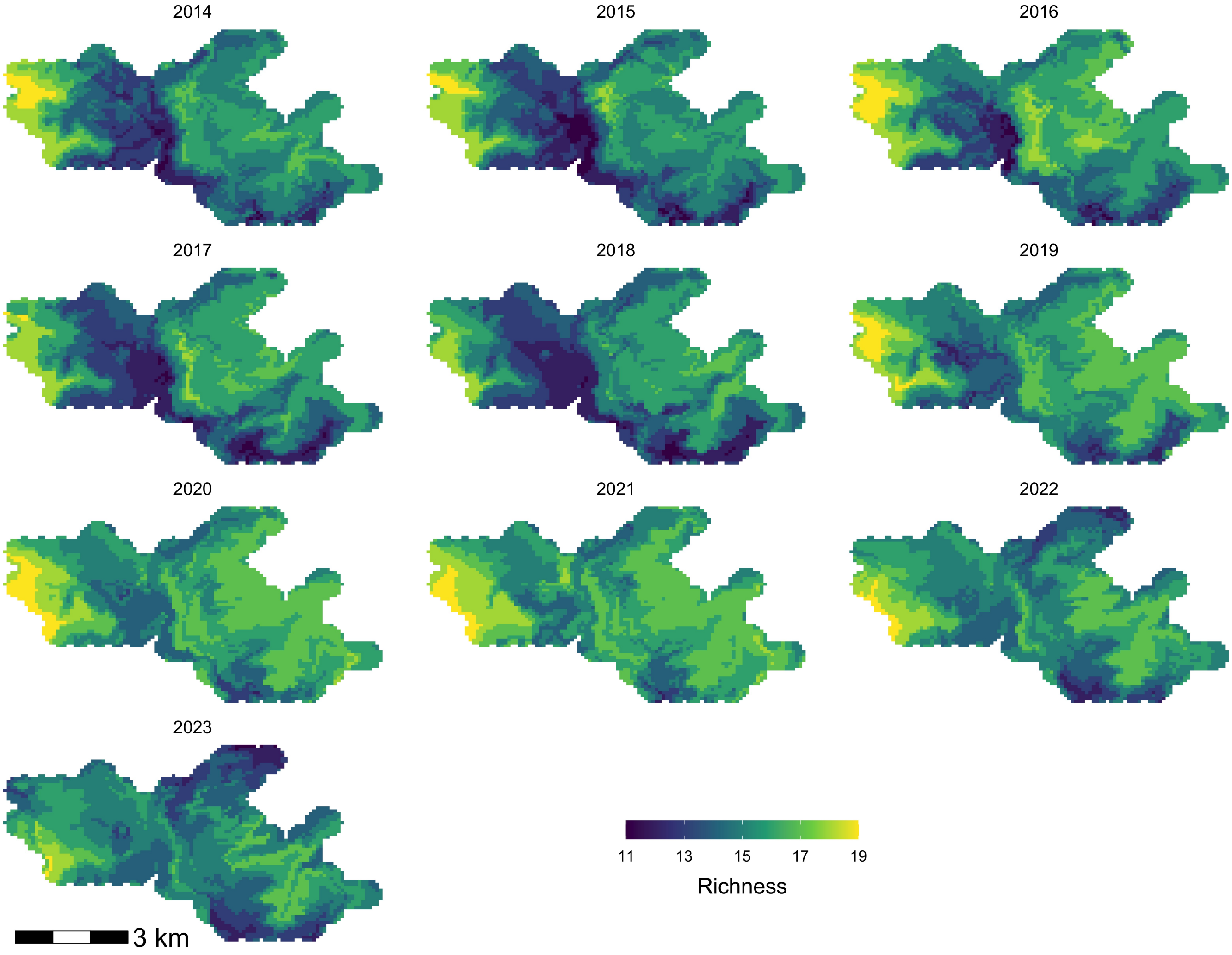

Figure 2.5: Species richness in the Nantahala National Forest, North Carolina, USA from 2014 to 2023. Richness is shown at the 1 km^2 pixel level.

Consider reversing this color ramp, so that the hot colors are at lower elevations.

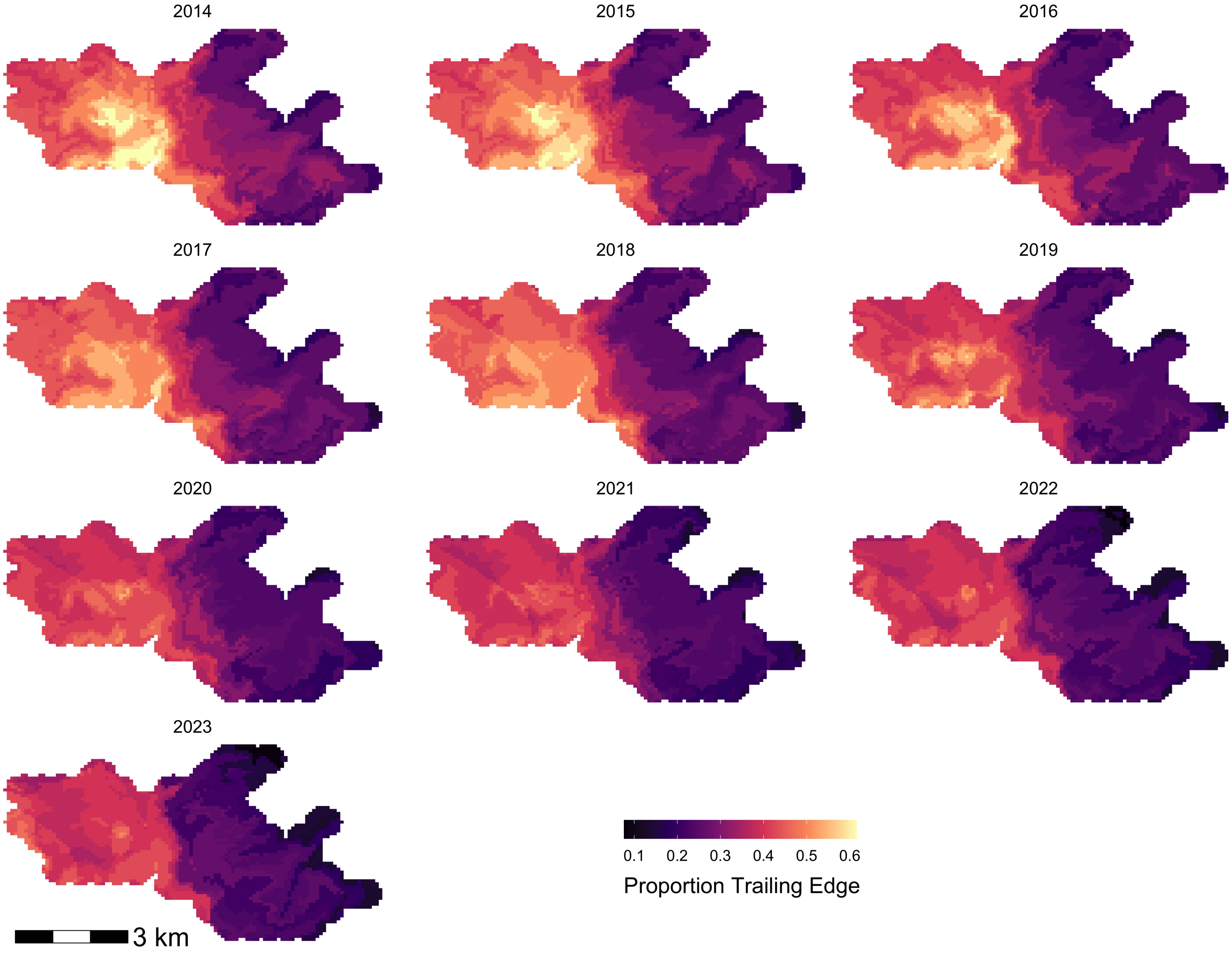

Figure 2.6: Proportion of species richness contributed by trailing-edge species in the Nantahala National Forest, North Carolina, USA from 2014 to 2023. Estimates are shown at the 1 km^2 pixel level.

CHAPTER 3

INDIVIDUAL-LEVEL BIOTIC INTERACTIONS AND SPECIES DISTRIBUTION MODELS [1]

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[1] Gaya, H.E. and Chandler, R. B. Submitted to *Ecography*, September 13, 2023

Abstract

Species interactions and abiotic factors are important determinants of abundance and distribution, but accounting for biotic interactions is complicated by the fact that interactions occur at the individual-level at unknown spatial scales. Ignoring individual-level interactions can yield incorrect conclusions about biotic interactions when analyzing aggregated count data or presence-absence data. We present a hierarchical species distribution model that includes a Markov point process in which an individual's location is dependent upon both abiotic variables and the locations of individuals of another species. The model can be regarded as a thinned point process in which encounter probability is a function of the distance between individual activity centers and survey locations. We applied the model to spatial capture-recapture data on two ecologically similar songbird species – hooded warbler (*Setophaga citrina*) and black-throated blue warbler (*Setophaga caerulescens*) – that segregate over a climate gradient in the southern Appalachian Mountains, USA. In spite of coarse spatial segregation and many ecological similarities between the two species, we found minimal evidence of spatial competition. There were strong, and opposing effects of climate on spatial variation in population densities, but spatial competition did not influence their distributions. A small simulation study indicated that the model can identify the distinct effects of environmental variation and biotic interactions on co-occurring species distributions. Unlike previous statistical models that attempt to infer competition from species-level co-occurrence data, the framework proposed here can be used to investigate how population-level patterns emerge from individual-level processes, while also allowing for inference on the spatial scale of biotic interactions. Our finding of minimal spatial competition between black-throated blue warbler and hooded warbler adds to the growing body of literature suggesting that, contrary to early theory from biogeography, abiotic factors may be more important than competition at low-latitude range margins.

3.1 Introduction

Species distributions are influenced by both biotic and abiotic factors, but most species distribution models focus exclusively on abiotic effects because of numerous challenges associated with drawing inferences on biotic interactions (Belmaker *et al.*, 2015; Dormann *et al.*, 2018). Biotic interactions can shape range boundaries (Hardin, 1960; Case & Gilpin, 1974) and contribute to climate-driven range shifts (Araújo & Luoto, 2007; Jankowski *et al.*, 2010; Lumpkin *et al.*, 2012; McDonald *et al.*, 2012; Warren *et al.*, 2016), but the relative contributions of biotic versus abiotic factors in most systems remains unclear. Abiotic factors such as temperature and precipitation often appear to limit species' distributions, but can produce similar spatial patterns to those produced by strong biotic interactions (Terborgh & Weske, 1975; Diamond, 1978; Camarota *et al.*, 2016).

A fundamental challenge is that most biotic interactions occur at the individual level, and a mechanistic understanding of the interactions of individuals is often lost when analyzing aggregated information such as local abundance or species occurrence data (Cody, 1974; Clark *et al.*, 2014; Harms & Dinsmore, 2016; Poggiato *et al.*, 2021). An example of the loss of information arising from aggregation can be seen in competing species that partition space at fine spatial scales, yet at broader scales, share similar geographic ranges (Jaeger, 1971; Suhonen *et al.*, 1994; Belmaker *et al.*, 2012). Models that ignore individual-level interactions and instead focus on local abundance or occurrence can yield incorrect inferences suggesting that the two species exhibit mutualistic rather than competitive associations (Sherry & Holmes, 1988; Harms & Dinsmore, 2016; König *et al.*, 2021). This is an example of the modifiable area unit problem in which different scales of aggregation lead to different conclusions about the system (Laymon & Reid, 1986; Jelinski & Wu, 1996). The implications of scale dependence for accurately assessing the strength of abiotic and biotic interactions have been well documented in the literature on joint species distribution models (Clark *et al.*, 2014; Ovaskainen *et al.*, 2016; König *et al.*, 2021), but the development of a modeling framework allowing for individual-level interactions and population-level inferences remains a fundamental challenge (Wisz *et al.*, 2012; Dormann *et al.*, 2018; Poggiato *et al.*, 2021; König *et al.*, 2021).

Populations at trailing edges of shifting species distributions provide unique opportunities for simultaneously examining both biotic and abiotic causes of range limits. Trailing-edge populations may experience novel climates and competitive interactions not present in the center of species' ranges (McDonald *et al.*, 2012; Cahill *et al.*, 2014), or display differences in ecological and evolutionary traits from individuals at the range core (Brown *et al.*, 1996; Gaston, 2009). Early theory predicted that the strength of biotic interactions should decrease with latitude because climate conditions are typically harsher and species richness is often lower at high latitudes (Schemske *et al.*, 2009; Hargreaves *et al.*, 2014). Similarly, abiotic factors were proposed as the main source of poleward range limits (Darwin, 1859; Dobzhansky, 1950; MacArthur, 1972; Louthan *et al.*, 2015; Paquette & Hargreaves, 2021). In contrast, Cahill *et al.* (2014) found that abiotic factors were often the primary drivers of warm-edge range limits, but few of the reviewed studies simultaneously investigated abiotic and biotic factors. Even at range boundaries most strongly limited by biotic interactions, abiotic factors often influence distribution (Martin, 2001), reproductive success (Matías & Jump, 2012) and density dependence (Merker & Chandler, 2021).

Here we present an approach for learning about the influence of individual-level interspecific interactions and abiotic conditions on species distributions, characterized in terms of species-specific abundance and spatial variation in density. The core of the modeling framework is a spatial point process observed imperfectly through the lens of capture-recapture data on two potentially interacting species. The approach is demonstrated using four years of data on two warbler species—one near the trailing-edge of its range and one near its range center—to determine the relative roles of abiotic conditions and competition for space in shaping local species distributions over a strong climate gradient in the southern Appalachian Mountains, USA.

3.2 Methods

Point process models

A species distribution can be described in terms of abundance (N) and distribution ($\boldsymbol{s}_1, \ldots, \boldsymbol{s}_N$), where the point $\boldsymbol{s}_i$ represents the spatial coordinates of individual i, typically in a two dimensional region $\mathcal{S} \in \mathbb{R}^2$. Spatial point process models can be thought of as species distribution models (SDMs) that predict both abundance and distribution (Baddeley, 2007; Renner *et al.*, 2015). As such, point process models are clearly connected to clearly-defined ecological state variables and may provide richer insights than SDMs focusing solely on occupancy or relative abundance (Warton & Shepherd, 2010; Yackulic *et al.*, 2013; Renner *et al.*, 2015; Gelfand & Schliep, 2018).

One of the simplest and most important classes of spatial point process models is the inhomogeneous Poisson point process defined by an intensity function $\mu(\boldsymbol{s})$, which is the expected value of density at location $\boldsymbol{s} \in \mathcal{S}$. The intensity function, or density surface, can be modeled as a function of spatially-referenced environmental variables to learn about the influence of abiotic variables on species distributions (Warton & Shepherd, 2010; Nightingale *et al.*, 2015). The area under the density surface, given by the two-dimensional integral over $\mathcal{S}$, defines the expected value of abundance. Realized abundance is typically modeled as an outcome of a Poisson distribution, and the points ($\boldsymbol{s}_1, \ldots, \boldsymbol{s}_N$) are also stochastic, distributed according to the density surface (Fig. 3.1 panel II).

One reason why standard point process models have not been more widely adopted in studies of species distributions is that they require coordinates of *all* individuals in the region of interest. Ecological applications of conventional point process models have therefore been limited primarily to studies of sessile organisms in small geographic extents (Rathbun & Cressie, 1994; Illian *et al.*, 2008; Nightingale *et al.*, 2015). Recently, however, hierarchical point process models have been developed that allow for inference from data on a subset of the individuals in the spatial region. Spatial distance sampling and spatial capture-recapture (SCR) can be viewed as thinned point process models that describes the probability of detecting (or capturing) an individual as a function of the distance between sampling locations and individuals (Johnson *et al.*, 2010; Royle *et al.*, 2013).

Existing hierarchical point process models have focused on the abundance and distribution of a single species (Hefley & Hooten, 2016). We present an expanded framework describing the abundance and distribution of two interacting species using a Gibbs point process model. The observation process is the same as used in SCR models—a thinning process determined by encounter rates—although it could be generalized to other types of individual-level ecological data.

Interspecific individual-level interactions

We define $\boldsymbol{s}_i$ as an individual's activity center—its average spatial location—which could be a territory center or a home range center during a specified time interval. Assume that all individuals have constant activity centers during the time period of interest. Let A and B represent two sympatric and potentially interacting species. Activity centers for species A are governed by an inhomogeneous point process with intensity $\mu^A(\boldsymbol{s})$ that describes the expected density of individuals of species A at spatial location $\boldsymbol{s}$ with environmental variables denoted by the vector $\mathbf{x}(\boldsymbol{s})$. The intensity can be modeled by using any function suitable for non-negative continuous variables, including a basis function approach or a log-linear function which we employ: $\log(\mu^A(\boldsymbol{s})) = \mathbf{x}'(\boldsymbol{s})\boldsymbol{\beta}^A$, where $\boldsymbol{\beta}^A$ represents a vector of coefficients. The expected value of abundance is given by:

$$\Lambda^A = E(N^A) = \int_{\mathcal{S}} \mu^A(\boldsymbol{s})\, d\boldsymbol{s}$$

Realized abundance is treated as an outcome of a Poisson distribution: $N^A \sim \text{Pois}(\Lambda^A)$. Conditional on N^A, the probability density of an activity center is given by the intensity at location $\boldsymbol{s}_i^A$ divided by the expected number of individuals of species A in $\mathcal{S}$:

$$p(\boldsymbol{s}_i^A | N^A) = \frac{\mu^A(\boldsymbol{s}_i^A)}{\Lambda^A}$$

Biotic interactions between individuals of species A and B are modeled using a Gibbs point process—a type of Markov point process model characterized by a pairwise interaction function (Ripley, 1981). Several types of Gibbs point process models exist, including hard-core Strauss point processes (Matérn, 1960; Strauss, 1975) with a radius parameter r controlling the minimum distance between interacting points. Hard-core processes have been used to study a wide variety of biological phenomena including the spatial distribution of forest fires (Turner, 2009), landslides (Das & Stein, 2016), and territory locations of small mammals (Reich & Gardner, 2014).

A generalized approach to hard-core process models can be obtained by a distance-dependent pairwise interaction function that modulates intensity surface such that the probability of occurring at location $\boldsymbol{s}$ depends on the distance to all other points (individuals) in the spatial region of interest (Teichmann *et al.*, 2013; Nightingale *et al.*, 2015). These approaches are often referred to as soft-core point process models (Huber & Wolpert, 2009; Teichmann *et al.*, 2013). In the absence of species A, abundance and distribution of species B is modeled as an independent Poisson point process. When species A is present, abundance and distribution of species B may be influenced by both abiotic interactions and the abundance and distribution of species A.

$$\mu^B(\boldsymbol{s}) = \exp(\mathbf{x}'(\boldsymbol{s})\boldsymbol{\beta}^B)\,\underbrace{h(\boldsymbol{s}|\boldsymbol{s}_1^A,\ldots,\boldsymbol{s}_{N^A}^A)}_{h(\boldsymbol{s})} \tag{3.1}$$

The interaction function $h(\boldsymbol{s}|\boldsymbol{s}_1^A,\ldots,\boldsymbol{s}_{N^A}^A)$ describes the effect of species A on the density of species B at location $\boldsymbol{s}$. The expected value of abundance of species B is $E(N^B) = \Lambda^B = \int_{\mathcal{S}} \mu^B(\boldsymbol{s})d\boldsymbol{s}$. The interaction function could be a hard-core inhibition process or it could approximate a soft-core inhibition process, allowing for weaker interactions than total inhibition within a fixed radius. We express the interaction function in the form of the product of Gaussian kernels with scale parameter ω^2:

$$h(\boldsymbol{s}|\boldsymbol{s}_1^A,\ldots,\boldsymbol{s}_{N^A}^A) = \prod_{i=1}^{N^A}\left\{1-\exp\left(\frac{-\|\boldsymbol{s}_i^A-\boldsymbol{s}\|^2}{2\omega^2}\right)\right\} \tag{3.2}$$

where $||\boldsymbol{s}_i^A - \boldsymbol{s}||$ is the Euclidean distance between the ith activity center of species A and location $\boldsymbol{s}$. Thus, as the density of species A increases in the vicinity of location $\boldsymbol{s}$, the probability of species B occurring at that location decreases. The parameter ω^2 determines the scale of repulsion between the two species. An illustration of the model is presented in Fig. 3.1.

Observation Model

The model is designed for data on uniquely identifiable individuals, such as mark-recapture data or even data on sessile organisms. We proceed with the case of spatial capture-recapture data, in which encounters of each individual are referenced by space and time. Typically, an array of traps is used to capture, mark, and release individuals. For a model with two species, the data are denoted by y_{ijk}^A, which indicates if individual i of species A was captured at trap j on sampling occasion k. The same data structure is used for species B. An obstacle in this situation is that many individuals go undetected because they are elusive or because the traps only effectively sample a subset of the region of interest. Thus, both N^A and N^B are unknown, which poses problems when performing Bayesian inference because the dimensions of the parameter space are not known.

To facilitate inference, we used a data augmentation approach for the capture-recapture data (Royle, 2009). Data augmentation fixes the dimensions of the parameter space by introducing an upper bound on abundance (M). Rather than putting a prior directly on N, the goal becomes one of estimating the proportion of the M individuals that were alive during time interval. Specifically, in this case, binary latent variables are introduced, with $z_1^A, \ldots, z_{M^A}^A$ indicating if individual i was part of the population of species A. The binary variables are modeled as Bernoulli outcomes $z_i^A \sim \text{Bern}(\psi^A)$ where ψ^A is the proportion of the M^A individuals that are part of the population, which is related to the expected value of abundance via $E(N^A) = M^A\psi^A$. The data can then be modeled conditional on the latent binary indicators: $y_{ijk}^A \sim \text{Bern}(p_{ijk}^A z_i^A)$. For this to work, the observed data must be padded with $M^A - n^A$ 'all zero' encounter histories, where n^A is the number of individuals of species A that were captured. We describe the model for capture probability p_{ijk} after discussing the observation model for species B.

For species B, the expected number of individuals in the spatial region $\mathcal{S}$ depends on the abundance and distribution of individuals of species A, and thus ψ^B must be modeled as a function of species A. Specifically, we have $\psi^B = \Lambda^B / M^B$. Note that M^B should be large enough to ensure that ψ^B is a probability. We can determine the appropriate size of M^B by inspection of the posterior chains after model convergence. Data augmentation also requires that we modify the pairwise interaction model (Eq. 3.2). Only individuals of species A that are alive and in the population of interest are included in the process model's inhibition function. This is accomplished by multiplying the Gaussian kernel in Eq. 3.2 by z_i^A. Thus, individual with $z_i^A = 0$ have no effect on the intensity of species B.

Capture probability can be modeled using a Gaussian detection function that depends on the distance between activity centers and traps. For example, the probability that individual i of species A is captured at trap j on survey occasion k is given by:

$$p_{ijk}^A = p_0^A \exp\left(\frac{-\|\boldsymbol{s}_i^A - \mathbf{x}_j\|^2}{2\sigma_A^2}\right) \tag{3.3}$$

where $\mathbf{x}_j$ denotes the coordinates of capture location j, and $\boldsymbol{s}_i^A$ represents the activity center of species A.

The detection parameters p_0^A and σ_A determine the baseline capture probability and the decay in capture probability with distance, respectively. An equivalent model was used for capture probability of species B. Following standard SCR assumptions, home ranges of both species are assumed to follow a bivariate normal distribution, as implied by the Gaussian capture probability function (Royle & Young, 2008; Royle *et al.*, 2013).

Simulation study

We explored the performance of the two-species model under five scenarios: (1) Repulsion between species and no relationships to environmental variables; (2) Repulsion between species and inverse relationships to environmental variables; (3) Repulsion between species with species A, but not species B, influenced by the environment; (4) Repulsion between species and both species positively associated with the environment; and (5) No repulsion between species and inverse relationships to the environmental gradient (Table B.1). We simulated a 5 occasion, 10 by 10 trapping array in a spatially autocorrelated environment. Trap detection was modeled from a Gaussian detection function as shown in Eq. 3.3, with a baseline capture probability,p_0, of 0.3 and a σ of 0.05 for both species. Additional information on simulation parameters can be found in the data archive for this manuscript.

We evaluated bias of the posterior median, coefficient of variation (CV), root-mean-square error, and 95% credible interval coverage for all β coefficients and the repulsion parameter ω. For each scenario, we simulated 96 datasets. The number of simulations was chosen to facilitate efficient computations across computing clusters with 16 cores. We used Markov chain Monte Carlo (MCMC) to draw posterior samples in JAGS 4.3.0 with the 'rjags' package in R 3.6.3 (Plummer, 2003, 2022; R Core Team, 2019). We ran 1 chain for 8,000 iterations with 1,000 burnin iterations.

Case Study

We collected mark–recapture data on hooded warblers *(Setophaga citrina)* and black-throated blue warblers *(Setophaga caerulescens)* in the Nantahala National Forest, North Carolina, USA (35.1°N, 83.4°W) from May to June 2018–2021. The two species are ecologically similar in foraging behavior, nest site selection, and size and have overlapping ranges in the Southern Appalachian Mountains (Ogden & Stutchbury, 1996; Weeks, 2001; Holmes, 2011). For the black-throated blue warbler, the Southern Appalachian mountains represent the warm edge of their breeding range which extends to the boreal shield in Canada. Abundance of black-throated blue warblers is declining at the southern edge of the breeding range, whereas hooded warbler populations are stable or increasing in many parts of their range, including at our study site (Merker, 2017; Sauer *et al.*, 2017; Lewis *et al.*, 2023).

Birds were captured and banded at 19 sites, each with an array of 20 nylon mist nets (32 mm mesh, 12 m long) arranged in 4 rows of 5 nets (Fig. 3.2). Nets were spaced on a 50 m grid with the inner row skipped to create 2 rows of 10 nets, a gap of 100m, and 2 more rows of 10 nets. Ten of the 20 nets (2 rows per day) were operated on each day beginning approximately 30 minutes before sunrise from May 7 to June

28. Each net was open for 2 consecutive days with each site sampled for 4 consecutive days, except when weather interfered. Each captured individual was marked with a US Geological Survey aluminum band and a unique combination of three color bands. Species, age, sex and morphological measurements were recorded for all captured individuals. The use of animals in this study was approved by the University of Georgia's Animal Care and Use Committee (Permit A2022 11-007-Y1-A0).

For each year, we modeled abundance and distribution of both species as a function of yearly climate c_t, represented as the first principal component (Jolliffe, 2005) of the average May temperature and cumulative precipitation in the study area at each site. High values of the climate variable represented cold and wet sites with low values representing hot and dry locations. Temperature data was collected hourly from 34 temperature loggers (Onset Computer Corp., Bourne, MA, model number UA-002-64) across the study area, as well as at 5 U.S. Forest Service climate stations (Miniat *et al.*, 2017). Precipitation was calculated as the total precipitation between May–June of each year (2018–2021) based on Daymet's 1-km x 1-km daily precipitation data (Thornton *et al.*, 2022).

Elevation of the sampling locations ranged from approximately 600 m to 1600 m (Fig. 3.2), with higher elevations being colder and wetter than low elevation sites. Data from the four years were modeled jointly. We assumed the strength of the interspecific repulsion was constant across years, but allowed abundance and individual activity center locations to vary between years. For computational efficiency, we modeled climate as constant at each site within a given year. We defined the spatial region $\mathcal{S}$ by placing a 100-m buffer around each set of 20 nets, based on our knowledge of both species's territory sizes. We assumed each population was geographically and demographically closed within a year. We did not model survival, recruitment, or movement among years because these processes were beyond the scope of the study.

We used Markov chain Monte Carlo (MCMC) to draw posterior samples in NIMBLE 0.9.0 with the 'rnimble' package in R 3.6.3 (de Valpine *et al.*, 2017; NIMBLE Development Team, 2019; R Core Team, 2019). We ran 3 chains for 50,000 iterations each with 30,000 burnin iterations and a thinning rate of 10. We assessed convergence using the Gelman-Rubin statistic (Gelman & Rubin, 1992) and visual inspection of the chains. We used the Watanabe–Akaike information criterion (WAIC) to determine the influence of the inhibition parameter on model fit.

3.3 Results

Parameters were recovered with low bias for all simulated scenarios (Fig. 3.3). For scenarios with simulated repulsion (Scenarios 1–4), median bias in estimates of ω (the repulsion parameter) ranged from -0.006 to -0.003, with 95% credible intervals capturing the true value 94–98% of the time (Table C.1). When points were simulated without repulsion (Scenario 5), the model correctly identified that repulsion was low, with lower estimates of repulsion approaching 0.

We captured 274 black-throated blue warblers and 151 hooded warblers across 4 breeding seasons. Individuals captured per year ranged from 58 to 87 black-throated blue warblers and from 33 to 52 hooded warblers (Fig. E.1). Most individuals (79%) were only captured once in a given year, with a maximum of 3 captures within the same year. The average elevation was 1064 m (SD = 155 m) for hooded warblers and 1250 m (SD = 134 m) for black-throated blue warblers. One site at 1216 m had no captures of either species across the 4 breeding seasons. No hooded warblers were captured at one of the highest sites (1224 m), and no black-throated blue warblers were captured at four sites, most of which were at low elevations (744, 942, 994, and 1216 m). The remaining 13 sites recorded captures of both species at least once. We captured black-throated blue warblers and hooded warblers in the same net at only 2% of the net locations.

There was a strong effect of climate on spatial variation in density of both black-throated blue warblers and hooded warblers, with only moderate annual variation in abundance (Figs. 3.4 - 3.5). Abundance of hooded warblers was highest at drier and hotter sites, though hooded warblers were predicted to occur at all sites. Black-throated blue warblers were an average of 11 times more abundant at the coldest and wettest sites than hooded warblers and were rarely detected at sites below 950 m. Abundance of both species was lowest in 2019, with very few black-throated blue warblers captured at the driest and hottest sites (Fig. 3.4).

The inhibition parameter ω was estimated to be 2.31 (95% CI: 0.084–6.58) (Table D.1), suggesting a weak repulsion between the two species at fine scales (Fig. G.1). Repulsion between activity centers was strongest when activity centers were at the same location, with almost no repulsion at distances greater than 5 meters. There were almost no changes in abundance estimates of both species when the model was run with and without the interaction function (Fig. F.1). The WAIC was 4378 when the interaction function was included and 4362 when removed, suggesting the interaction function did not improve model fit.

3.4 Discussion

Understanding both the abiotic and biotic drivers of species distributions is critical for predicting responses to environmental change. Species distributions are often dependent upon the distribution of other species, but uncertainty in the distribution of one or both species greatly complicates efforts to model spatial variation in density. Further complications arise because the spatial scale of biotic interactions is unknown. We have presented a model that overcomes these challenges and allows for joint modeling of spatial variation in density of two potentially interacting species. By formulating the spatially-explicit model at the individual level, it is possible to learn about population-level processes that emerge from the combination of individual-level interactions and abiotic influences.

Although we present our model in the context of spatial competition, the framework could be applied to other types of biotic interactions that result in patterns such as attraction and clustering. While numerous methods exist for estimating clustering of individuals within a single species, relatively little attention has been given to interspecific attraction at the individual level (Keil *et al.*, 2021). By using an alternative interaction function, the model can formally test the strength of repulsion or attraction interactions between co-occurring species. For instance, this model could be applied to co-occurring plant species with facilitative interactions (He *et al.*, 2013) or to the locations of marine birds and whales sharing the same food resources (Gostischa *et al.*, 2021). The flexibility of the framework to accommodate a wide range of interaction functions further underscores its potential use in joint species distribution models (Wilkinson *et al.*, 2021).

The model of interspecific interactions is conditional, with the distribution of species B depending on the distribution of species A. However, this the interaction function is symmetrical, meaning that the labeling of the two species as Species A or Species B in the model has no effect on the resulting abundance estimates or estimated strength of the inhibition parameter. As a result, predicting the spatial distribution of two species in a new location does not require knowledge of their arrival times to the site, allowing the model to be used even when temporal data is not readily available. Although not explored here, SCR models can be expanded to include movement processes (McClintock *et al.*, 2022; Theng *et al.*, 2022), allowing for estimation of instantaneous location, rather than activity centers. Expanding these models to include species interactions may allow for inference on complex animal movements and space use in the presence of competition. Combined with behavioral observations, this approach could be used to determine dominance relationships between two species, and their population-level consequences.

Another benefit of the conditional structure of the pairwise interaction function is that it avoid the computational problems associated with most Gibbs point process models. Gibbs process models for a single species during a single time period involve a normalizing constant that cannot be computed easily, not even with MCMC (Ripley, 1981; Reich & Gardner, 2014; Nightingale *et al.*, 2015). The probability density of the point pattern is intractable because every point depends on every other point such that the joint distribution cannot be factored into simpler conditional distributions. However, by conditioning one species' abundance and distribution on the other, the problem becomes tractable and standard MCMC software can be used.

The simulation study revealed that the model successfully distinguished true repulsion from random variation in individual locations or inverse species relationships to habitat characteristics. However, within a defined area, strong repulsion could lead to the complete exclusion of one species from a habitat even if the area is suitable for both species when competition is not present. For small sampling areas and highly abundant species, the packing density of individual activity centers may be too high to allow for any additional individuals from a competing species (Dolby & Solomon, 1975; Norberg, 1988). Thus, the model is naturally only applicable in cases where evidence exists of individual-level interactions between sympatric species.

In spite of seemingly strong competition between black-throated blue warblers and hooded warblers, our results indicate that spatial segregation of these two species is primarily due to abiotic effects of climate rather than biotic interactions. While the distributions of these two populations appear to be inversely correlated at the scale of the study area, this pattern is most likely the product of niche partitioning. While historic competition could have produced the current pattern of spatial segregation (Price & Kirkpatrick, 2009), our results suggest competitive interactions are not currently driving the distribution of these two species. In other words, if hooded warblers were removed from this ecosystem, our results indicate there would be no immediate effect on the distribution of black-throated blue warblers. This finding appears to contrast with the traditional view that biotic interactions are the main drivers of species distributions at warm-edge range limits (Paquette & Hargreaves, 2021), but our results are consistent with previous research on trailing-edge species of birds in the southern Appalachian Mountains (Merker & Chandler, 2020). However, there are other biotic interactions that could be at play, and black-throated blue warblers may be competing with other species not included in our study, or they may be shifting their range in response to pathogens, predation or changes in habitat structure (Paquette & Hargreaves, 2021).

One concern with individual-based models is how best to predict abundance and spatial density for entire ranges when individual-based data is only available in a small subset of the range. In our model, we link observed individual activity centers to site abundance through an observation process that accounts for imperfect detection. For range-wide prediction, we could include an additional observation process linking count data to abundance with an integrated model conditioned on an individual-level process model (Chandler & Royle, 2013; Chandler *et al.*, 2018). Although we applied the model to spatial capture-recapture data from a subset of the species' ranges, the model could be generalized to accommodate multiple data types covering broader spatial scales. For instance, activity centers may be inferred from mark-resight studies on banded birds, GPS locations from animals with radio tags, or direct information on sessile species (Sollmann *et al.*, 2013; Christiansen *et al.*, 2015; Berberich *et al.*, 2016), all of which could be easily accommodated by our model. Count data or presence-absence data could be linked to the process model (Zipkin *et al.*, 2021) to expand results beyond the study area. It may also be possible to apply our framework to intraspecies interactions, expanding on work done by Reich & Gardner (2014) to account for territoriality or clustering. The flexibility of the model will allow for analysis of a wide range of systems where understanding individual-level interactions is critical to accurate inference on population-level processes.

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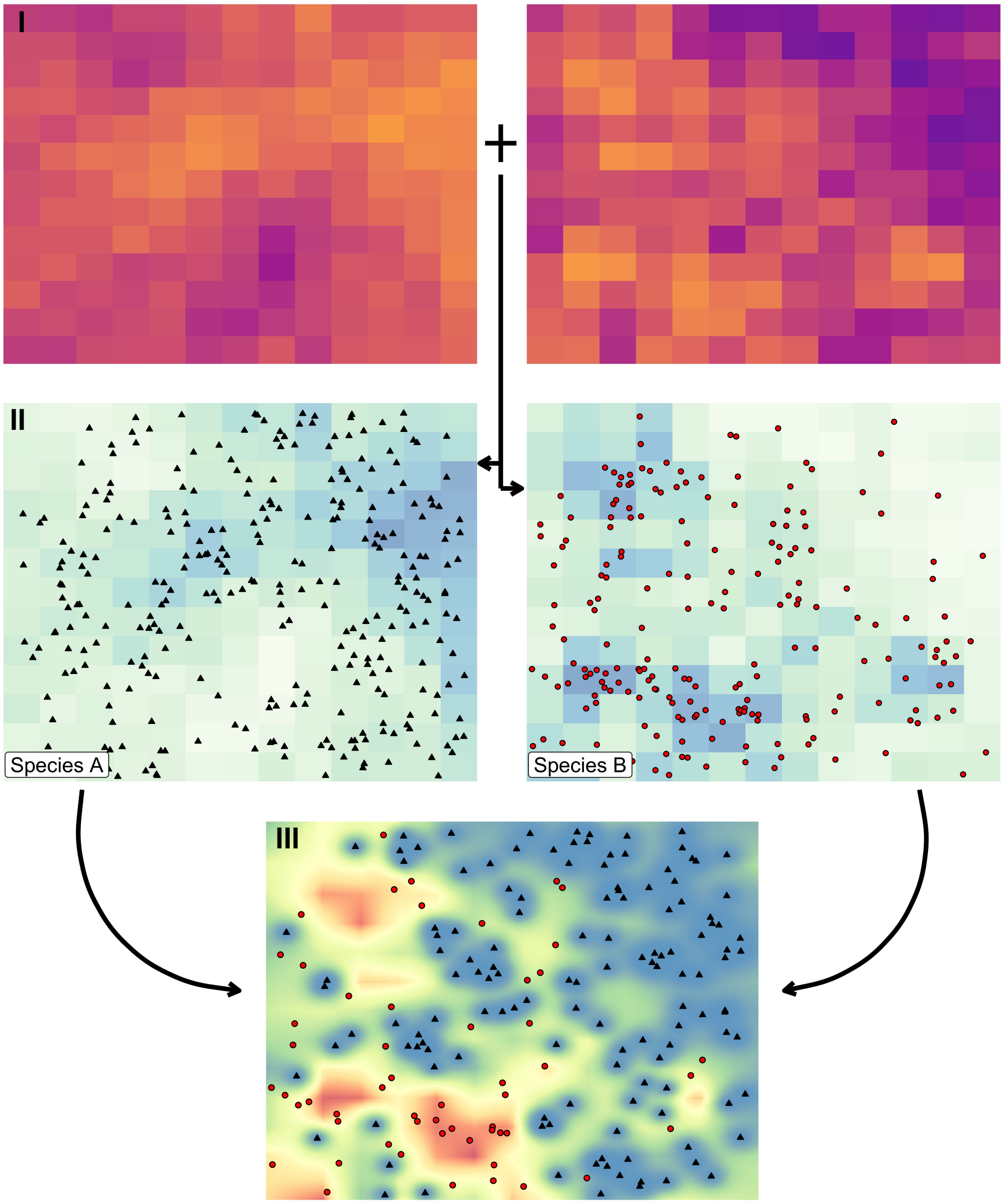

Figure 3.1: Conceptual depiction of the point process model for two interacting species. Top panels (**I**) *Abiotic conditions*. Environmental variation in this example is described by two spatial layers depicted as raster images. Middle panels (**II**) *Realized distribution with no biotic interaction*. The abundance and distribution of individuals that in the absence of biotic interactions are drawn from an inhomogeneous Poisson process. The relationship to the environmental variables may be different for each species. Background color indicates the expected density (intensity) at each pixel, given the abiotic conditions. Bottom panel (**III**) *Distribution with both abiotic effects and biotic interactions*. The realized distribution of both species is thinned by an interaction function, resulting in a final distribution that accounts for both abiotic variables and biotic interactions.

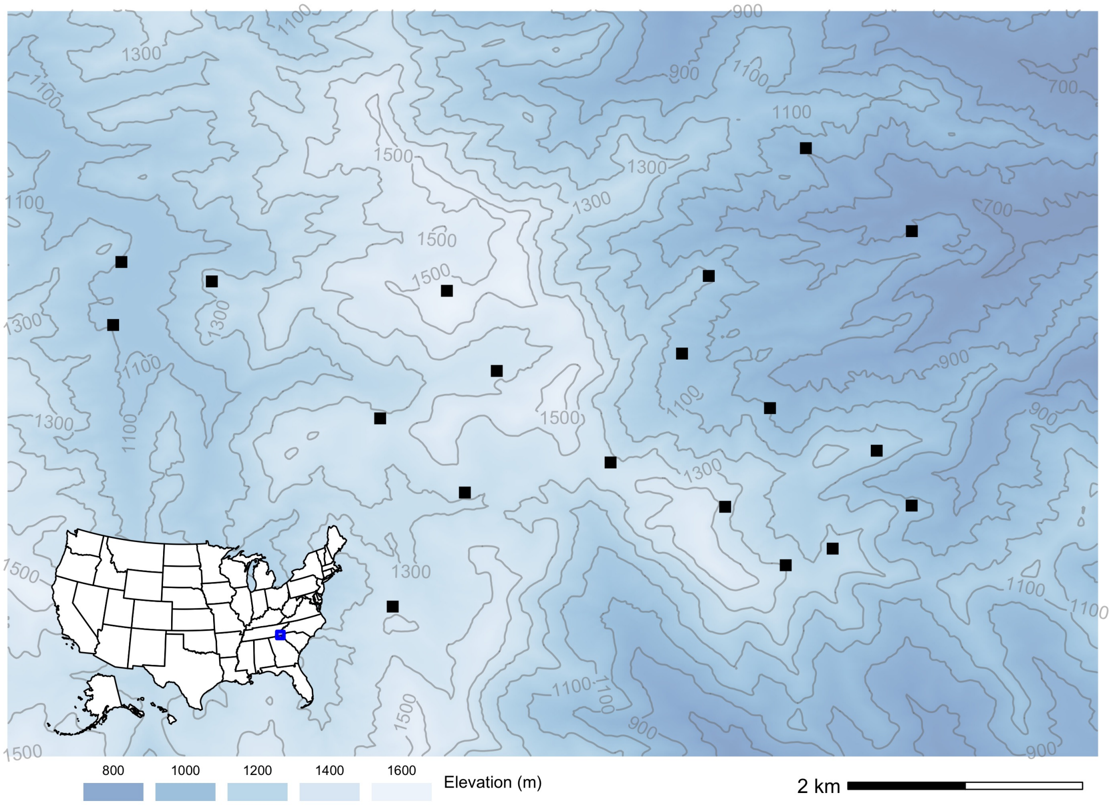

Figure 3.2: Capture-recapture sites in the Nantahala National Forest, North Carolina, USA. Each site had 20 net locations in 4 rows of 5 nets, with nets spaced 50 m apart. Sites were sampled from May to June 2018–2021.

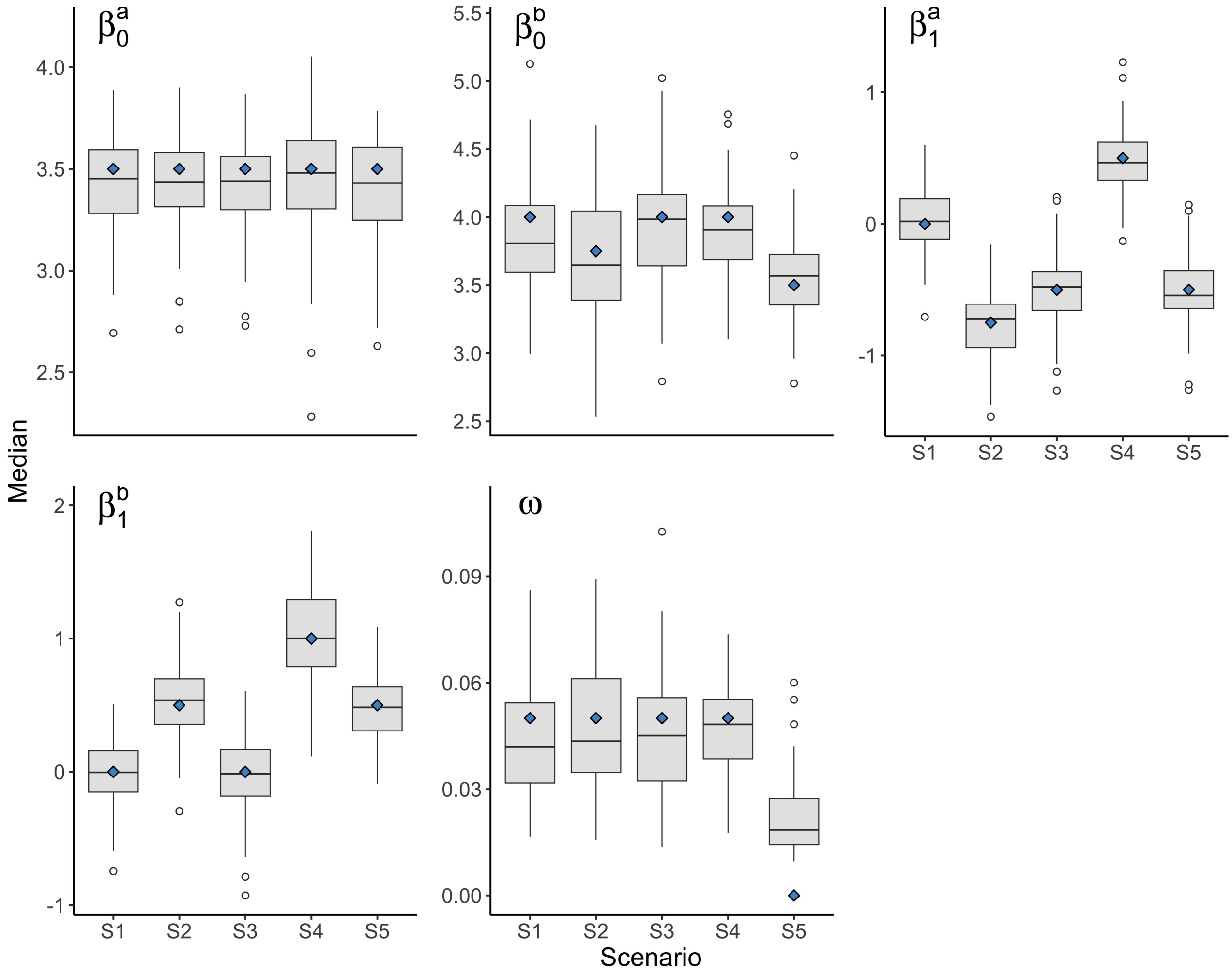

Figure 3.3: Simulation study results for 5 scenarios, each with 96 simulated datasets. The posterior mode was used as a point estimator. Blue dots represent the true data generating values.

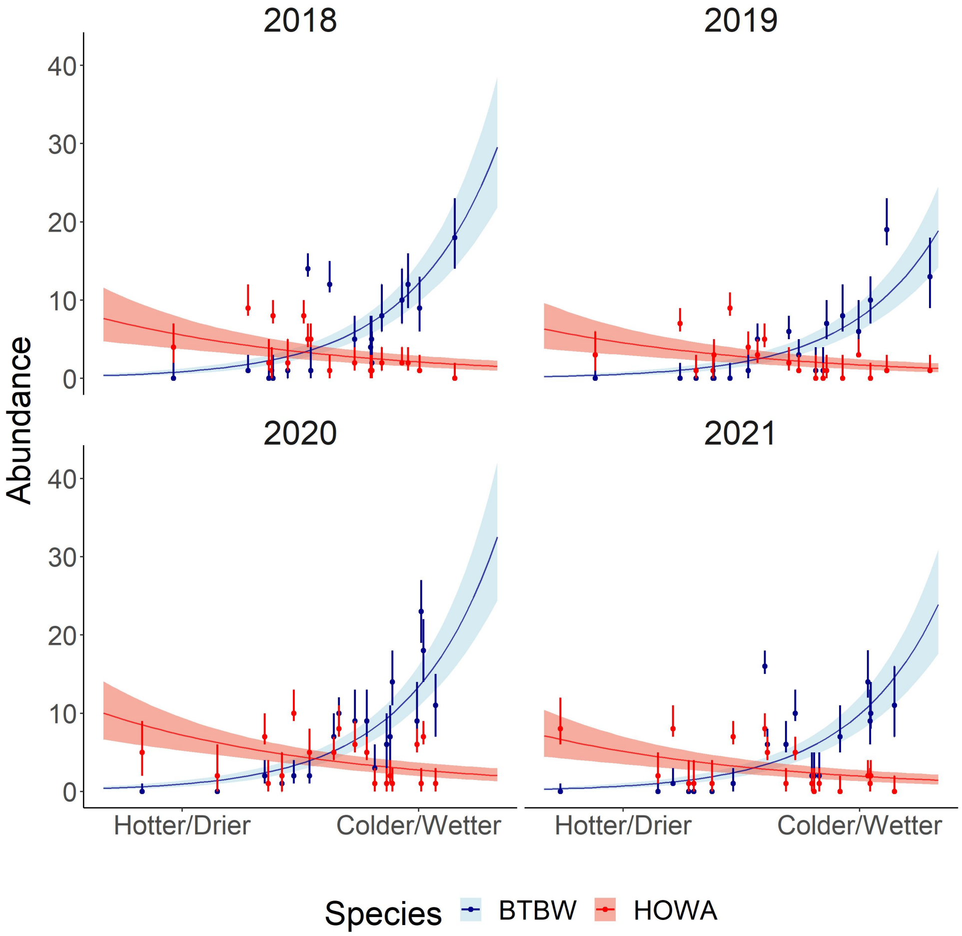

Figure 3.4: Abundance and 95% CIs for black-throated blue warbler (*Setophaga caerulescens*) and hooded warbler (*Setophaga citrina*) from 2018 to 2021 in the Nantahala National Forest, North Carolina, USA. Trend lines show the expected values of abundance for each species when only abiotic relationships are considered.

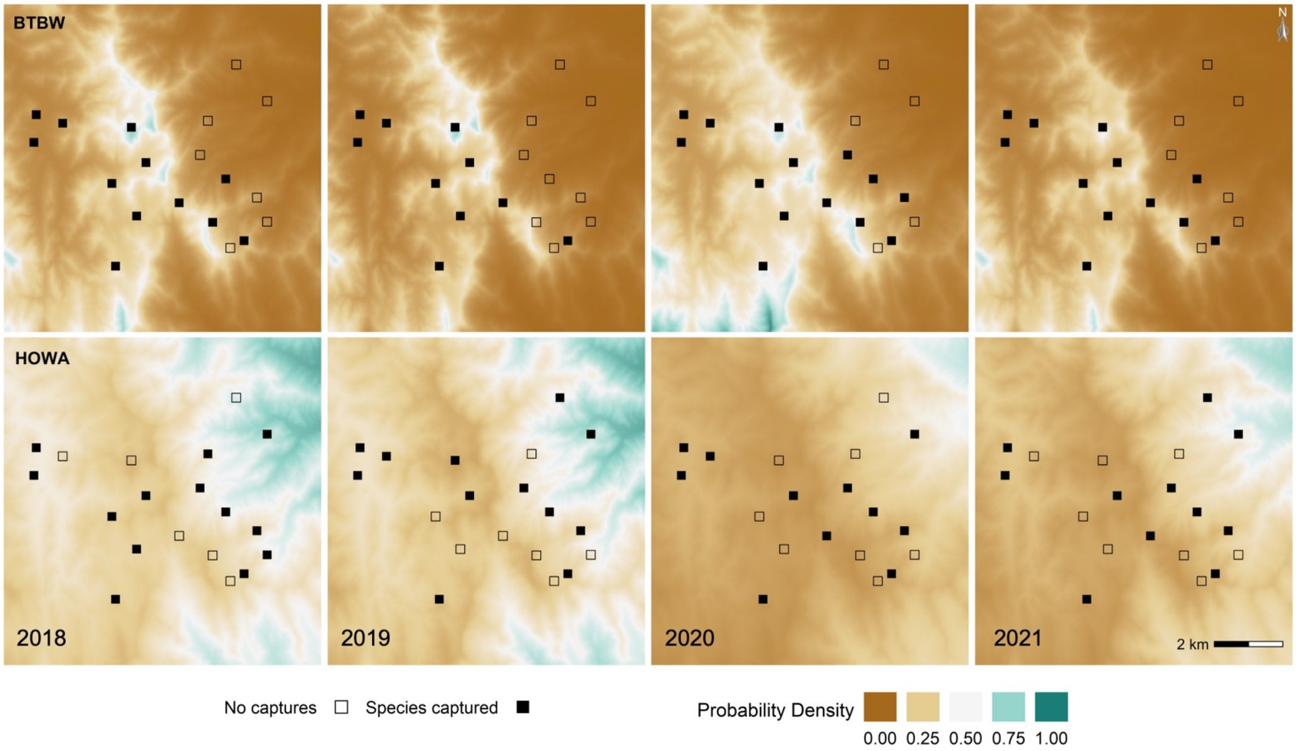

Figure 3.5: Annual density surfaces of black-throated blue warbler (*Setophaga caerulescens*) and hooded warbler (*Setophaga citrina*) from 2018 to 2021 in the Nantahala National Forest, North Carolina, USA.

CHAPTER 4

CLINGING TO THE TOP: NATAL DISPERSAL TRACKS CLIMATE GRADIENT IN A TRAILING-EDGE POPULATION OF A MIGRATORY SONGBIRD

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[1] Gaya, H. E., Cooper, R. J., Delancey, C. D., Hepinstall-Cymerman, J., Kurimo-Beechuk, E. A., Lewis, W. B., Merker, S. A., and Chandler, R. B. Submitted to *Movement Ecology*, September 23, 2023

Abstract

Purpose: Trailing-edge populations at the low-latitude, receding edge of a shifting range face high extinction risk from climate change unless they are able to track optimal environmental conditions through dispersal.

Methods: We fit dispersal models to the locations of 3,165 individually-marked black-throated blue warblers (*Setophaga caerulescens*) in the southern Appalachian Mountains in North Carolina, USA from 2002 to 2023. Black-throated blue warbler breeding abundance in this population has remained relatively stable at colder and wetter areas at higher elevations but has declined at warmer and drier areas at lower elevations.

Results: Median dispersal distance of young warblers was 917 m (range 23 – 3200 m), and dispersal tended to be directed away from warm and dry locations. In contrast, adults exhibited strong site fidelity between breeding seasons and rarely dispersed more than 100 m (range 10 – 1300 m). Consequently, adult dispersal kernels were much more compact and symmetric than natal dispersal kernels, suggesting adult dispersal is unlikely a driving force of declines in this population.

Conclusion: Our findings suggest that non-random natal dispersal may mitigate fitness costs for trailing-edge populations by allowing individuals to track changing climate and avoid warming conditions at warm-edge range boundaries.

4.1 Background

Theoretical models of spatial population dynamics suggest that the effects of climate change on population viability and gene flow will depend on dispersal capacity (Clark *et al.*, 2001; Schloss *et al.*, 2012). Species that cannot track optimal climatic conditions via dispersal are likely to experience increased extinction risk from reductions in survival and reproduction (Hoffmann & Sgrò, 2011; Rushing *et al.*, 2015; Mota *et al.*, 2018). However, studying dispersal in natural populations is notoriously difficult, especially for mobile species, and few empirical studies have investigated the degree to which dispersal is directed towards optimal climate conditions (Penteriani & Delgado, 2011; Stillman *et al.*, 2021).

Populations at the trailing edge of a shifting range provide many opportunities for investigating dispersal responses to climate change. Trailing-edge populations are often near their physiological thresholds (Deutsch *et al.*, 2008; Habibzadeh *et al.*, 2021) and are therefore likely to be sensitive to novel abiotic conditions (Cahill *et al.*, 2014; Schierenbeck, 2017; Mota *et al.*, 2018). Suitable habitat is often more fragmented at the trailing edge than at the core of the range, constraining the available area for dispersal (Graves, 1997; Hampe & Petit, 2005; Habibzadeh *et al.*, 2021). As a result, dispersal capacity is especially critical for trailing-edge populations facing climate-based extinction (Hargreaves *et al.*, 2015).

Dispersal capacity can vary with age, sex and other individual traits (Greenwood & Harvey, 1982; Martínez-Pérez *et al.*, 2022). Natal dispersal is typically greater than adult dispersal within vertebrates (Greenwood & Harvey, 1982; Paradis *et al.*, 1998; Fonte *et al.*, 2019), suggesting that natal dispersal could be a key driver of climate-induced range shifts (Greenwood & Harvey, 1982; Clobert *et al.*, 2001; Norkko *et al.*, 2001). For adults, site fidelity offers numerous advantages such as increased mating success (Hanski *et al.*, 2006) and familiarity with available food resources (Greenwood, 1980; Broderick *et al.*, 2007), whereas dispersal represents a risky trade-off (Fleischer *et al.*, 1984; Bonte *et al.*, 2012, but see Merkle *et al.*, 2022). For young individuals, dispersal serves as a mechanism to seek higher-quality habitat (Bonte *et al.*, 2012; Cline *et al.*, 2013), avoid competition or inbreeding with relatives (Kokko & López-Sepulcre, 2006;

Cline *et al.*, 2013), escape parasites (Shaw, 2020), and increase mate availability (Clarke *et al.*, 2008; Hargreaves & Eckert, 2014).

Migratory species face unique challenges from climate change, which can impact phenology, physiology, and demography at non-breeding and breeding sites throughout the annual cycle (Nathan, 2006; Møller *et al.*, 2008; Sanderson *et al.*, 2006; Wilson *et al.*, 2011; Zurell *et al.*, 2018). Studying these effects is complicated because changes in either survival or breeding site selection can make it difficult to observe dispersal events (Winkler *et al.*, 2005; McKim-Louder *et al.*, 2013). Long-term studies of marked individuals occurring over strong climate gradients provide one of the few options for advancing knowledge of climate change impacts on demography and dispersal (Holmes, 2007; Clutton-Brock & Sheldon, 2010).

We used 21 years of mark-recapture data from a trailing-edge population of black-throated blue warblers (*Setophaga caerulescens*) to test the hypothesis that a key mechanism underlying climate-induced range shifts of trailing-edge populations is natal dispersal. We predicted that natal dispersal would be greater than adult dispersal, and natal dispersal would be directed towards locations with colder and wetter climate conditions than conditions at birth locations. Because individuals hatched at the coldest and wettest sites cannot disperse to better conditions, we further predicted that natal dispersal distance would be positively correlated with availability of colder and wetter conditions in the surrounding landscape.

4.2 Methods

The black-throated blue warbler is a Neotropical migratory bird that winters in the Caribbean and Central America and breeds in the eastern United States and southeastern Canada. The southernmost breeding populations occur in the southern Appalachian Mountains. Black-throated blue warblers have been heavily studied in the core of their breeding range (Holmes, 2011; Cline *et al.*, 2013), but less is known about trailing-edge populations (Conroy *et al.*, 2011). Within the trailing edge, breeding abundance has remained relatively stable at colder and wetter areas at higher elevations but populations have become extirpated at the warmest and driest sites at lower elevations (Sauer *et al.*, 2017; Lewis *et al.*, 2023).

In the core of the range, adult black-throated blue warblers exhibit strong site fidelity during the breeding season, and dispersal is influenced by both habitat structure and sex (Sillett & Holmes, 2002; Cline *et al.*, 2013). Adult black-throated blue warblers rarely disperse from their chosen patch except in response to habitat disturbance (Betts *et al.*, 2006, 2008). As with most Neotropical migratory songbirds, little is known about natal dispersal, but natal dispersal distances >1 km are thought to be common in the core of the range (Holmes *et al.*, 2020).

Field Methods

From 2002 to 2022, we monitored black-throated blue warblers in the Nantahala National Forest in western North Carolina (35.1°N, 83.4°W), at the trailing edge of the range. The southern Appalachian Mountains are characterized by steep topography ranging from 500–1600 m above sea level. Historically, both eastern hemlock (*Tsuga canadensis*) and American Chestnut (*Castanea dentata*) were common, especially in riparian areas (Day & Monk, 1974). The study site is now composed of mixed oaks (*Quercus* spp.), tulip poplar (*Liriodendron tulipifera*), hickories (*Carya* spp.), and maples (*Acer* spp.). Yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), black cherry (*Prunus serotina*) and black gum (*Nyssa sylvatica*) are also common throughout the area. Understory foliage is dominated by rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*), with some dry sites lacking any shrub or mid-canopy layer. The coldest and wettest sites are found at the highest elevations. Mean annual precipitation increases from 1868 mm year^{-1} at 600 meters to 2514 mm year^{-1} at 1400 meters above sea level. Mean May air temperatures decrease from 17.5 °C at the lowest elevations to 13.9 °C at the highest elevations (Daly *et al.*, 2008).

We surveyed 19 study plots (each plot covering about a 12 ha area) ranging in elevation from 600 m to 1500 m above sea level (Figure 4.1). The study began with one intensively-surveyed (henceforth ‘intensive’) plot in 2002, with a second intensive plot added in 2003 and 17 auxiliary plots added between 2014 and 2018. Each intensive plot was surveyed approximately every 2 days during the breeding season to map black-throated blue warbler territories, assess breeding density, find nests, and monitor nesting success.

Once found, nests were monitored until failure or successful fledging of chicks. All surviving nestlings were banded with a U.S. Geological Survey aluminum leg bands 6 days after hatching. Nestlings were not sexed during initial banding.

We attempted to capture, sex, and age all adult black-throated blue warblers on our intensive plots every year through targeted and constant-effort mist-netting. At the 17 auxiliary plots, we performed constant effort mist-netting for 4 days during the breeding season to band birds and monitor nests found during banding operations. In some years, nest searching and re-sighting surveys were also performed at some of these plots. Nest searching on these auxiliary plots was not exhaustive. All captured adult individuals were banded with a U.S. Geological Survey aluminum leg band and a unique combination of colored leg-bands.

We used PRISM's 30-year climate normals (1991–2010) (Daly *et al.*, 2008) at an 800 m resolution to estimate the average May precipitation and temperature across our study area. After standardization, we conducted a principal component analysis (Jolliffe, 2005) to create a single variable that represented the dominant climate gradient of the region. Higher values of this variable represented hotter and drier locations, with lower values representing wetter and colder sites.

Modeling Framework

We analyzed dispersal events of individuals recaptured at least once between 2002 and 2022. We used the distance between nestling location and first year capture location to calculate natal dispersal distance. For adult birds, dispersal distance was calculated as the distance between capture locations in consecutive years. We used a discrete-time, discrete-space extension of the Cormack-Jolly-Seber (CJS) (Lebreton *et al.*, 1992; Schaub & Royle, 2014) model to describe natal and adult dispersal. We divided the study area into $N = 320$ grid cells with each cell covering a 800 x 800 m area and snapped all locations to grid cell centers. Following the framework of Schick *et al.* (2008), we defined $z_{i,t}$ as a vector of length N, indicating the location of individual i in year t. Each location $z_{i,t}$ was modeled as the outcome of a multinomial distribution over all possible locations in the study area, conditional on the individual's location and age (nestling or adult), a, in the previous year.

$$z_{i,t,a(t)} | z_{i,t-1,a(t-1)} \sim \text{Multinom}(1, \boldsymbol{\theta}_{i,t,a(t)})$$

The probability $\theta_{i,k,t,a}$ of dispersing to location k, conditional on surviving and returning to the study area, is found by normalizing the dispersal kernel:

$$\theta_{i,k,t,a(t)} = \frac{h_{i,k,t,a(t)}}{\sum_{k'=1}^{N} h_{i,k',t,a(t)}}$$

The dispersal kernel describes the relative probability that individual i with age a selects location k in year t given the available climate conditions and the distances from the origin at location j.

$$h_{i,k,t,a(t)} = e^{-\beta_{1,a(t)} X_{i,k} + \beta_{2,a(t)} c_k}$$

The variable $X_{i,k}$ is the distance in kilometers between the individual's location at time $t-1$ and location k, and c_k is the climate at location k. For black-throated blue warblers, we modeled movements between years as dependent on the precipitation and temperature at location k, combined into a single standardized climate variable.

To account for the uneven spatial and temporal distribution of survey effort across our study area, we modeled the detection of an individual, $y_{i,k,t}$, as a Bernoulli outcome with detection probability p_k. To differentiate between intensive and auxiliary plots, we assumed detection was dependent on plot type. To account for variation in effort, we included a binary variable, $s_{k,t}$, that represented if grid cell k was sampled in year t.

$$p_k = \begin{cases} p_1 s_{k,t} & \text{if intensive plot} \\ p_2 s_{k,t} & \text{if auxiliary plot} \end{cases}$$

We conditioned detection on survival using a discrete-time Bernoulli model,

$$w_{i,t} \sim \text{Bern}(\phi_a w_{i,t-1})$$
$$y_{i,k,t} \sim \text{Bern}(p_k w_{i,t})$$

where ϕ_a is survival probability based on age (nestling or adult) and $w_{i,t}$ indicates if individual i was alive in year t.

We analyzed data from natal and adult birds together. Because we were unable to study long-distance dispersal (i.e., dispersal beyond our study area), we set priors on the dispersal distance parameter $\beta_{1,a}$ to constrain inference to short-distance dispersal within the study area. For this, we used an exponential distribution, $\beta_{1,a(t)} \sim \text{Exponential}(0.1)$, which puts $<$ 0.05 prior probability on dispersal distances $>$30 km. Consequently, we acknowledge that dispersal outside the study area was indistinguishable from mortality, and thus the resulting survival estimates are the probability of surviving and returning to the study area.

Analysis was performed in JAGS via the 'rjags' package in Program R (R Core Team, 2019; Plummer, 2022). Convergence was assessed using visual inspection of three chains and the Gelman-Rubin statistic (Gelman & Rubin, 1992). Each Markov chain was run for 15,000 iterations, resulting in 45,000 posterior samples.

4.3 Results

We banded 2,072 nestling black-throated blue warblers from 2002 to 2022. Of the nestlings banded, 24 were re-captured in the study area (1.2% return rate) —19 as first-time breeders (second-year birds, SYs) and 5 as adults (after-second-year birds, ASYs). Recaptured birds were slightly male biased, with 16 males and 8 females recaptured. The median distance between nest location and first-year location was 917 m (range 23 – 3200 m) (Figure 4.2). Median dispersal distance was slightly farther for females (1092 m, range 356 – 3200 m) than males (812 m, range 235 – 2800 m). The majority (18 of 24) of the recaptured nestlings were born at the coldest and wettest sites above 1300 m elevation, where black-throated blue warbler density was highest. Two of the recaptured nestlings were born in the same nest, but established first-year territories 800 m apart. Yearly survival, conditional on returning to the study area, was estimated to be 10% (6 – 14%) for yearlings.

We banded 1,093 black-throated blue warbler adults (451 females, 632 males, and 10 with sex not recorded). We recaptured 190 individuals (114 males, 76 females) in subsequent years (17.4% return rate). Most recaptured birds were observed in two years, which were not always consecutive. One individual was observed in seven different years. The median distance between territories in consecutive years was 79 m (range 10 – 1300 m) for adults, with females moving a median distance of 112 m (range 10 – 1300 m) compared to 71 m (range 10 – 1300 m) for males. Only 5 adults (3 SY females, 1 SY male, and 1 ASY male) were recorded moving $>$500 m between years. Yearly survival, conditional on returning to the study area, was 55% (50 – 61 %) for adult birds.

For nestlings, dispersal was more likely to be directed towards cooler and wetter locations relative to available conditions surrounding hatch locations (Figure 4.3). Natal dispersal distances were shortest for individuals born at the highest elevations. For these individuals, there were no cooler climates available within the study area, and there were no observations of dispersal to low elevation sites with warmer, drier climates (Figure 4.4). In contrast, natal dispersal distances were greater, and more directional, for yearlings hatched in the warmer, drier conditions at lower elevations. Overall, the effect of climate (β_2) on natal dispersal was -0.41, with a 95% credible interval that did not include zero (-0.74 – -0.13) for nestlings.

Adult dispersal was more restricted and less directional than natal dispersal. Average adult dispersal distance was 79 m, compared to 917 m for recaptured nestlings. The estimated effect of climate on adult dispersal (β_2) was 0.18 with a 95% credible interval including zero (-0.06 – 0.54). Consequently, adult dispersal kernels were much more compact and symmetric than natal dispersal kernels (Figure 4.3).

4.4 Discussion

Trailing-edge range shifts can result from reduced vital rates or directional dispersal. Although both processes can cause local population declines, reduced survival and reproduction can lead to reductions in population-level fitness and the loss of genetic diversity. In contrast, directional dispersal can mitigate the effects of changing environmental conditions by allowing individuals to track optimal conditions. Our results, coupled with previous findings on demography (Lewis *et al.*, 2023), suggest that directional natal dispersal away from warmer and drier climate conditions may explain the local range shift towards higher elevations. Though small, our study represents some of the first direct observations of natal dispersal in a migratory species whose natal dispersal patterns are largely unknown.

In a long-term study of female black-throated blue warbler demography, Lewis *et al.* (2023) found that population declines were greater at the trailing edge of the range than at the range core. At both range positions, population density was highest, and trends were most stable, at higher elevations characterized by cooler and wetter climates. Because their study used non-spatial mark-recapture data at six independent sites, they were unable to separate mortality from dispersal. However, consistent with our results, they found declining return rates at lower elevations near the trailing-edge of the range.

Within our study, natal dispersal was more sensitive to climate and occurred over greater distances than adult dispersal. In contrast to first-year birds, adult black-throated blue warblers exhibited strong site fidelity between years. The dispersal distances seen in our study are consistent with those found in the core of the breeding range (Cline *et al.*, 2013; Holmes *et al.*, 2020) and suggest population movements will largely be driven by natal dispersal. However, few birds hatched at the highest elevation sites were observed selecting territories at lower elevations. This non-random natal dispersal, combined with minimal dispersal of adult individuals, suggests low elevation populations will continue to decline.

The nestling return rates in our study area were substantially higher than those seen in the core of the breeding range. Holmes *et al.* (2020) reported that only 22 (0.44 %) of >5000 nestlings are known to have returned to the range core between 1986 and 2016. Of these returning birds, the closest return was 300 m from the individual's natal site, with most birds dispersing more than 500 m, including several dispersal events >2 km from their natal sites. In our study, we observed 24 nestlings returning to the study area, despite having approximately half the sample size of banded nestling black-throated blue warblers and 10 fewer years of data. The high return rate at our study is potentially attributable to the lack of suitable habitat at the trailing-edge where the species is restricted to fragmented high elevation forests.

The availability of cold, high elevation sites in the study area appeared to play a major role in natal dispersal outcomes. Individuals at the highest elevations that returned to the study area had no available colder climate to disperse into and had no choice but to establish territories at the same elevation or lower than their natal location. Importantly, though more than double the number of nestlings were banded at the highest elevation plot compared to the lower elevation intensive plot, none of these individuals were ever observed establishing territories at the low elevation intensive plot, though conditions at this site are suitable for black-throated blue warblers. The lack of movement downhill to the lowest elevation intensive site strongly suggests a pattern of non-random natal dispersal.

Movements to higher latitude mountains may not represent a significant barrier to black-throated blue warblers and other long-distance migrants that already annually migrate thousands of kilometers (Wiens, 1995), but this theory is largely untested. Intraspecific competition or non-thermal abiotic conditions such as habitat quality can prevent individuals from tracking changing climate, even when population movements as a whole trend towards cooler locations (Lenoir *et al.*, 2010; Gibson-Reinemer & Rahel, 2015). While the young birds in our study showed flexibility in dispersal distance, it remains unclear if these local movements will translate into long-distance movements between fragmented patches of high elevation habitat. Due to the logistical challenges of studying long-distance movements (Koenig *et al.*, 1996), we chose to restrict our analysis to birds that returned to the study area, but future research should attempt to understand the extent and direction of long-distance dispersal in trailing-edge populations and its role in maintaining population viability under future climate conditions.

Conclusions

For many species, trailing-edge populations act as reservoirs for genetic diversity (Hampe & Petit, 2005; Assis *et al.*, 2013) which can confer higher resistance to environmental change (Willi *et al.*, 2006; Jump *et al.*, 2009; Schierenbeck, 2017). Previous studies of climate change and dispersal predict an increase in dispersal distances under future climate conditions and more frequent long-distance dispersal events (Travis *et al.*, 2013; LaRue *et al.*, 2019). Our findings suggest that the negative effects of climate change on trailing-edge populations can be mitigated by directional natal dispersal, provided that sufficient connectivity exists between high-quality habitat at the edge and core of the range.

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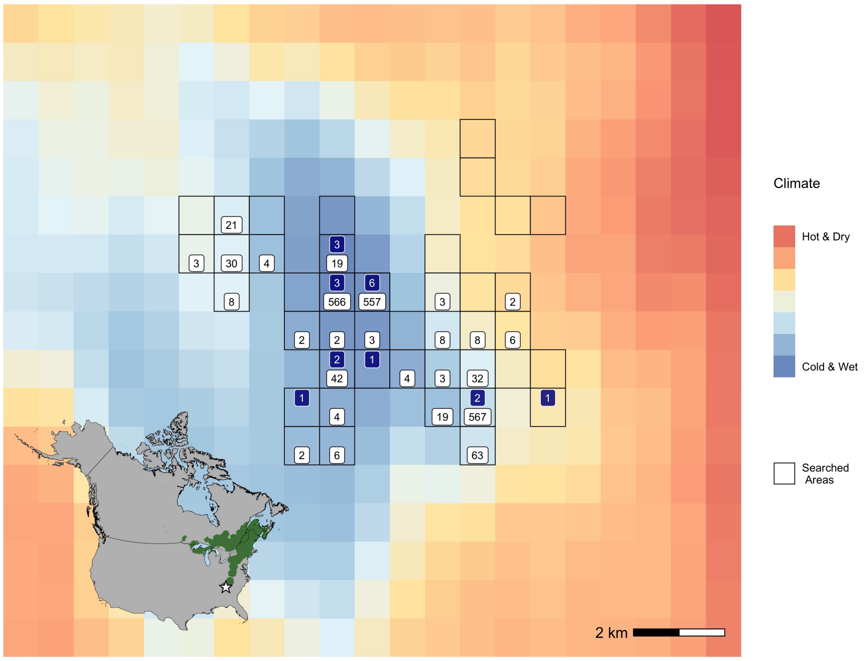

Figure 4.1: Locations of black-throated blue warblers banded as nestlings in the Nantahala National Forest, North Carolina, USA. From 2002 to 2022, 2,072 nestling black-throated blue warblers were banded and released, of which 19 were recaptured as second-year birds. White squares represent the total number of nestlings banded in each grid cell. Blue boxes show the number of nestlings that were recaptured as second-year birds in that grid cell. Nestlings recaptured as after-second-year birds are not included in the figure. Some study plots span more than one grid cell. The inset shows the breeding range of the black-throated blue warbler in green, with a star marking the study site location.

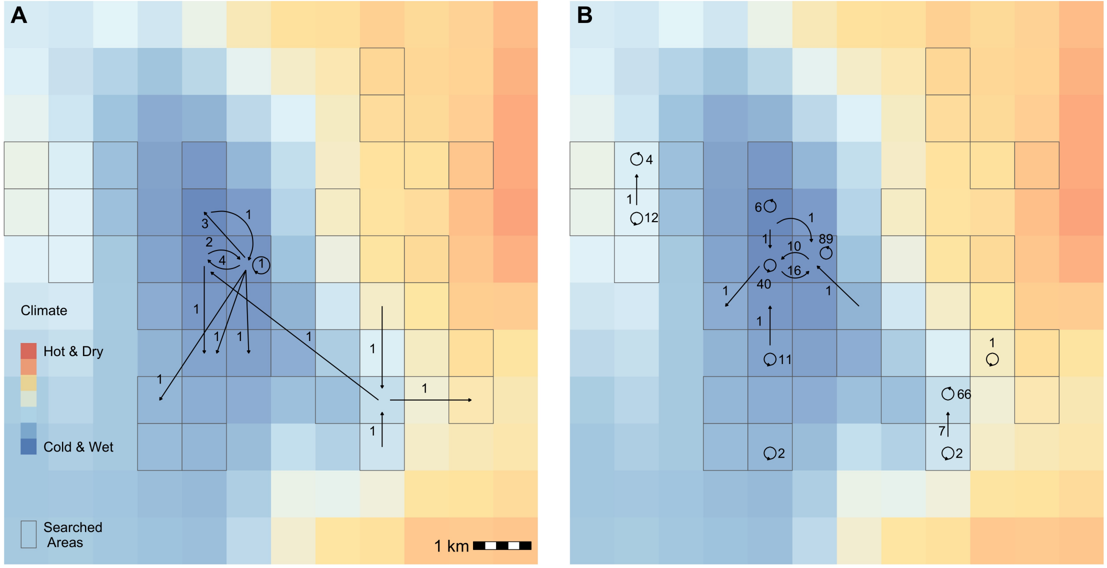

Figure 4.2: Dispersal events for black-throated blue warblers between consecutive years for (A) 19 nestlings and (B) 190 adult birds in the Nantahala National Forest, North Carolina, USA from 2002 to 2022. Arrows depict the number of individuals that dispersed between locations. Panel (A) only shows nestlings encountered the year after hatching.

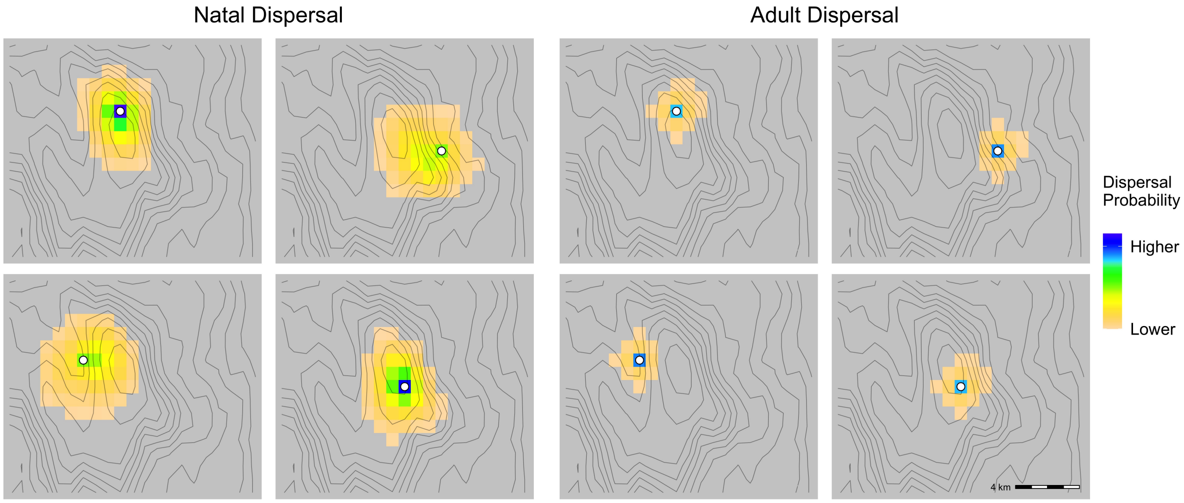

Figure 4.3: Dispersal kernels of black-throated blue warblers at 4 locations in the Nantahala National Forest, North Carolina, USA. White circles represent origin of dispersal. Grid cell colors represent the probability of dispersing to a location from the origin. Climate contours are shown as grey lines.

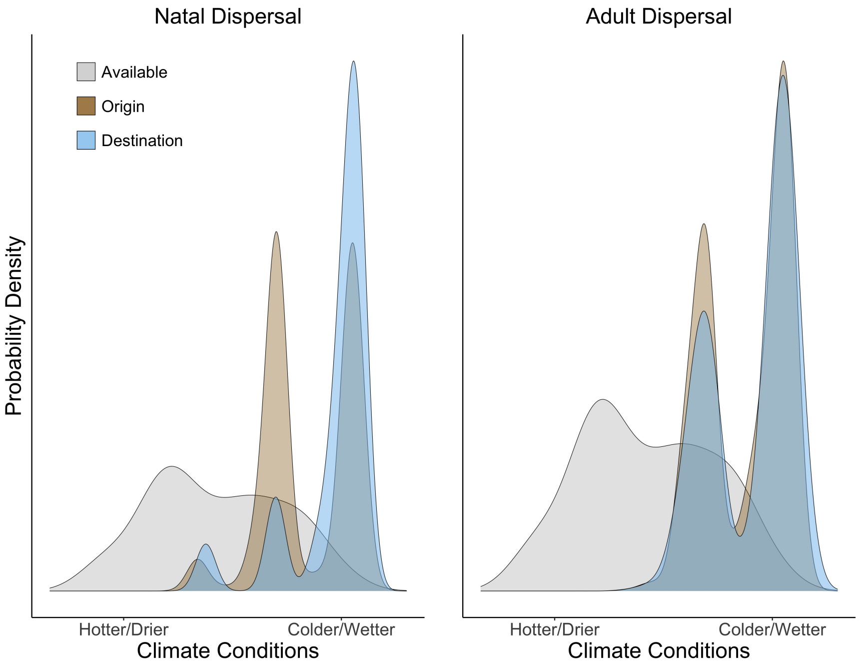

Figure 4.4: Climate conditions at dispersal destinations (blue distributions) compared to available climate conditions (grey distribution) for dispersal events of black-throated blue warblers banded in the Nantahala National Forest, North Carolina, USA. Conditions where black-throated blues were first banded at any age (nestlings or adults) is shown in brown. Nestlings recaptured more than one year after hatching are excluded from the nestling destination distribution.

CHAPTER 5

AN INDIVIDUAL-BASED MODELING FRAMEWORK FOR INFERENCE ON POPULATION DYNAMICS [1]

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[1] Gaya, H. E., and Chandler, R. B. To be submitted to *Trends in Ecology and Evolution*

Abstract

There are two general frameworks for modeling the dynamics of spatially-structured populations characterized by high levels of individual heterogeneity in demographic rates. The classical and most widely used framework employs reaction-diffusion models, integrodifference models, or metapopulation models—depending on whether space and time are treated as continuous or discrete—to describe spatio-temporal variation in the density of individuals. Individual identity is not preserved over time in these models and differences are described by evolving probability distributions or transitions among discrete categories. The second framework involves individual-based models (a type of agent-based model) in which individuals are tracked over time as they are move, grow, reproduce, and die. Although both approaches have proven valuable in theoretical contexts, neither class of models is routinely confronted with data using formal inference methods. By ignoring individual identity, the classical approach makes it difficult to confront with longitudinal data on marked individuals—the very type of data required to estimate the fundamental demographic parameters underlying population dynamics. We present an individual-based modeling framework that combines the mathematical rigor of classical models with the high degree of flexibility in modeling individual heterogeneity afforded by agent-based methodologies. The framework is spatially explicit, making it possible to study how reproduction, growth, movement, and mortality rates depend on location, as well as other individual-level traits, including age, size, and sex. Inference on kinship and pedigrees is made possible by treating parent-offspring relationships as a latent or partially-observed network process. The framework subsumes the strengths of classical and agent-based modeling frameworks without loss of generality and with the added benefits of accommodating numerous sources of data to inform the parameters and providing insights about the factors governing spatio-temporal population dynamics and population viability.

5.1 Introduction and a brief history of classical models

Population dynamics is one of the oldest, and still most active, focal points of ecology. An understanding of the demographic responses of organisms to their environment and to one another is critically important to both theoretical and applied ecologists (Leslie, 1945; Lomnicki, 1978; Grimm, 1999). Models of population dynamics are necessary to understand the causes of local and global scale ecological phenomenon including biological invasions, population cycles, and range shifts (Lotka, 1910; Levins, 1969; Matías & Jump, 2012). Moreover, models of population dynamics are required to advance knowledge about the effects of environmental change and conservation actions on past, current, and future abundance and distribution of threatened and endangered species (Ehrlich & Daily, 1993; Channell & Lomolino, 2000). However, in spite of its long history and progress towards accurate and broadly applicable predictions, major obstacles continue to hinder efforts to learn about the drivers of population dynamics in rapidly changing environments. Two of the biggest challenges are accounting for individual heterogeneity and the limited ability to confront theoretical models with observed data.

Classical population models provided the foundation for understanding how populations should behave under a set of simplifying assumptions. Early ecologists were inspired by the generality of the laws of physics, seeking to use deterministic equations such as exponential growth, logistic growth, and other ordinary differential equations to explain general patterns seen in nature (Lotka, 1910; May, 1974). These models captured several fundamental truths about population dynamics – environments cannot support infinitely large populations, the number of individuals in a population can limit the growth, reproduction and survival of other individuals, and the interactions between species can have dramatic effects on their population dynamics.

Central to the study of population dynamics is an argument over the importance of individual-level complexity in model structure. Does individual variation create noise that blocks the identification of universal ecological patterns (Lawton, 1999; Berryman, 2002) or are individual-level behaviors and demographic differences fundamentally important in their own right (Huston *et al.*, 1988; DeAngelis &

Rose, 1992)? This argument has been flourishing since the mid-1950s (McIntosh, 1985; Lawton, 1999; Judson, 1994), with both sides bemoaning the failure of mathematical models to realistically reproduce complex dynamics in ecology (Judson, 1994). This discussion, along with further debate over the existence of general rules of ecology, spawned the earliest agent-based models, referred to as individual-based configuration models (Caswell & John, 1992). Since their inception, the scientific community has realized the potential of agent-based models to represent complex individual stochasticity (Huston *et al.*, 1988; DeAngelis & Rose, 1992), but questioned their generality and legitimacy (Lomnicki, 1992; Berryman, 2002), leading to two largely separate approaches to models of population dynamics.

As ecological models progressed, additional attention was given to the impact of temporal and trait-based variation in vital rates. The first discrete trait-based models focused on differences between age classes in the context of natural selection (Sharpe & Lotka, 1911; Fisher, 1930; Leslie, 1945). Particular interest was given to age-varying fecundity and the estimation of stable age-structures and growth rates (Sharpe & Lotka, 1911). In formative spatial models of population dynamics such as reaction diffusion models, similar questions were explored in continuous time and space (Skellam, 1951; Gilligan, 1995). Though simple, age-structured models allowed ecologists to model populations as a distribution of discrete states that collectively interact with the environment to produce stochastic population dynamics.

By grouping individuals by phenotypic traits (and later, environmental conditions), the dynamics of different subsets of the population could be studied and quantified. For instance, under the framework of Metz & Diekmann (1986), individuals can be classified both by a physiological trait (for example, age class) as well as by a location (perhaps a site or a habitat type). Changes in survival, reproduction or movement affect abundance in each trait-location category (state) by altering the probabilities of transitioning between states. Matrix population models such as those described by Metz & Diekmann (1986) and Caswell (2008) explore population dynamics using both traits and time as discrete categories; integrodifference equations (Kot *et al.*, 1996; Turchin, 1998) explore the same questions, but describe states as continuous, while time is discrete. Such frameworks acknowledge the inherent variation between demographic components of a population and paved the way for more complex state-based approaches with multi-dimensional states (Heckman & Singer, 1982; Caswell, 2008; Roth & Caswell, 2016). Moreover, structured population models can be easily fit to observational data (Caswell, 1978; Ellner & Rees, 2006; Caswell, 2008), which may explain their wide adoption amongst population ecologists (Ellner & Rees, 2006).

Individual heterogeneity and inference in classical models

Classical spatio-temporal models focused on population structure and the role of specific life stages in shaping population dynamics. These models characterize the dynamics of population structure through population-level state transition, while ignoring the individual-level transitions that characterize actual populations. While computationally efficient, many classical models are 'mean field approximations' of the underlying individual-level demographic processes (Pascual *et al.*, 2001; Melbourne & Chesson, 2005), averaging across individuals in an effort to focus on broad system patterns (Wallhead *et al.*, 2008; Morozov & Poggiale, 2012). However, as a consequence of removing individual identity these models often struggle to effectively tease apart interactions between mechanisms that might shape population growth (Sprague *et al.*, 2021). For example, schools of ocean fish may be composed of many 'follower' members and a small number of 'leader' individuals (Conradt & Roper, 2005). During migration, the navigation ability of the 'leader' fish contributes disproportionately to the survival of other group members (Conradt & Roper, 2005; del Mar Delgado *et al.*, 2018). Without individual identity, the impacts of these behaviors on population vital rates may be impossible to fully explore.

Individual-level interactions are perhaps the biggest obstacle in classical spatio-temporal models. Spatially inhomogeneous populations with diverse individual traits produce numerous numerical difficulties (Gurney *et al.*, 2001; Kooi & Kelpin, 2003), particularly when vital rates are influenced by local interactions (Sprague *et al.*, 2021). A fundamental challenge is that disparate individual-level interactions and behaviors can produce similar population-level patterns but have vastly different conservation or management implications (Knudsen *et al.*, 2011; Hertel *et al.*, 2020). For instance, species distributions limited by strong biotic interactions can produce similar spatial patterns to the range limits produced by abiotic factors such as climate (Camarota *et al.*, 2016). In a management context, biotic interactions may be managed by population culling or displacement of an undesired species from the area (Srivastava *et al.*, 2019) whereas patterns driven by abiotic drivers may suggest habitat alteration as a viable management solution (Johnston *et al.*, 2019). Thus, the ability to differentiate between possible mechanisms is critical for effective population management.

Without individual identity, questions of kinship, family structure or inbreeding cannot be effectively investigated (Moore *et al.*, 2014; Peyran *et al.*, 2022). Kinship analysis is possible in structured population models (Goodman *et al.*, 1974; Coste *et al.*, 2021), but hinges on the assumption that the dynamics of the population has been at the steady state for an extended period of time (Caswell & Song, 2021; Coste *et al.*, 2021). There are currently no formulations of kinship models that can account for density dependence and environmental stochasticity (Coste *et al.*, 2021). However, kinship dynamics can alter demographic vital rates (López-Sepulcre & Kokko, 2002) and may be of interest when estimating population viability. One compelling example is the study of conspecific brood parasitism in waterfowl, first described by Leopold (1951). Brood parasitism is a common female breeding tactic in ducks (Yom-Tov, 1980; Andersson & Åhlund, 2000). Parasitic females lay eggs in the nests of other members of the same species and the host mother raises the offspring as her own (Yom-Tov, 1980). Previous studies demonstrate that the host and parasitic females are often related, with female ducks parasitizing the nests of their sisters and mothers more often than chance (Andersson & Åhlund, 2000). Moreover, survival of parasitic offspring is correlated with the degree of relatedness (López-Sepulcre & Kokko, 2002) , suggesting kinship can have direct impacts on population abundance.

Inference for both Eulerian and Lagrangian population models has proven difficult, and population modeling and parameter estimation have too often been viewed as separate endeavors. Traditionally, population growth rates and demographic parameters were estimated separately (Schaub *et al.*, 2004; Merow *et al.*, 2014), often using independent datasets collected at different scales. Following estimation, the importance of particular demographic parameters on population growth were assessed with a sensitivity analysis (van Groenendael *et al.*, 1988). However, this method tends to under-represent uncertainty in estimation (Clark, 2003; Elderd & Miller, 2016), which is further compounded when vital rates are estimated in isolation from population growth rates (Schaub & Abadi, 2011; Merow *et al.*, 2014). An additional concern is the problem of quantifying covariance between demographic parameters that are derived independently (Fung *et al.*, 2022). Correlations between growth, survival and reproduction can alter demographic conclusions (Fay *et al.*, 2022; Fung *et al.*, 2022), but are not easily incorporated into classical estimation frameworks, especially when vital rates are estimated independently. Thus, it is difficult to formally draw inferences from data, creating a disconnect between classical models of population dynamics and models used to estimate parameters in real-world scenarios.

Agent-based Simulations

A second framework for studying population processes is agent-based models, with a focus firmly on individual heterogeneity. There are several arguments for the use of individual-based models. First, almost all individuals have unique genotypes, experience unique environments, or both (Huston *et al.*, 1988). Secondly, interactions between individuals take place locally (Pacala & Silander, 1985; McCauley *et al.*, 1993). In classical stage-structured models, individuals in the population possess a 'global' knowledge of the system as a byproduct of model structure (Hogeweg & Hesper, 1990), leading to potentially improbable outcomes of biotic interactions. All individuals within a given stage are assumed to experience the environment equally – an assumption that cannot hold true if local interactions only include specific individuals (Caswell, 2008). By focusing on individuals, these local interactions are much easier to model. Finally, selection often happens at the level of the individual (Mayr, 1997) – it is therefore logical to study it using individual-level models.

Agent-based models use behavioral 'rules' to simulate individual movements, behavior, and vital rates (Grimm, 1999; Smouse *et al.*, 2010; Railsback & Grimm, 2019). Individuals and their respective traits are followed through time as individuals move, reproduce, grow and die (Grimm, 1999). Simulations are often loosely based on real data, with parameter ranges informed by previous studies when available, and emergent patterns from these simulations are then compared to observed patterns to propose how individual-based actions result in population-level outcomes (Railsback & Grimm, 2019). Due to their unique structure, agent-based models can easily accommodate non-linear responses (Railsback & Grimm, 2019), which can formulate chaotic and intrinsically unpredictable behaviors (May, 1974). Under certain scenarios, particularly when deterministic models are computational impractical using currently available software, agent-based models can provide valuable insight into the potential drivers of population dynamics (Caswell & John, 1992; DeAngelis & Grimm, 2014).

In classical models, stochasticity plays a fundamental role in the realization of abundance. Traditionally, demographic stochasticity is estimated through branching process or diffusion approximations (May, 1974; Lande, 1993; Engen *et al.*, 1998). In an individual-based model, stochasticity is incorporated through probability distributions, which produces stochastic outcomes even with fixed demographic rates. Thus, different realizations of an individual's alive/dead state can produce stochastic population trajectories.

An alternative but similarly focused approach to agent-based models is cellular automata models (Hedlund, 1969). As with agent-based approaches, population patterns arise by aggregating the results of many individual actions (Clarke, 2014). Cellular automata models typically consist of a series of grid cells, each with a 'neighborhood' of 4 or 8 cells with which each cell can interact, and a series of rules governing interactions. In contrast to agent-based models, where individuals can either be mobile or sessile, the modeled entities are cells that remain static. Cellular automata models are most often applied to questions of forest dynamics (Lett *et al.*, 1999), vegetation succession (Hogeweg, 1988), and land-use change (Torrens & O'Sullivan, 2001; Clarke, 2014).

However, individual-based models built from either simulation framework are often criticized as *ad hoc* for their lack of transparency and mathematical rigor compared to traditional analytical models (Wennergren *et al.*, 1995; Ruckelshaus *et al.*, 1997; Müller *et al.*, 2014). Improvements in standardization have mitigated some of these issues (Grimm *et al.*, 2006), but rigorous validation of model findings is relatively uncommon (Wallentin, 2017; Troost *et al.*, 2023). Agent-based models can also easily become over-parameterized (Radchuk *et al.*, 2016, 2021). When models start to increase in complexity, there may be little or no data on which to base parameter values (Wallentin, 2017; Tonelli *et al.*, 2023). Over-fitting also leads to poor out-of-sample predictive performance, and hence lack of reproducibility and generality (Hooten *et al.*, 2020; Zhang & DeAngelis, 2020; Srikrishnan & Keller, 2021). Though well-suited for site-specific questions of population management, individual-based simulation frameworks often struggle to "link between the problem at hand and the issues of theoretical population biology" (Grimm, 1999).

In this paper, we present a class of individual-based models of population dynamics that we argue is more general than the classical approach, yet firmly rests on a mathematical foundation from point process theory that allows it to be transferable to any system. Moreover, the individual-based framework greatly enhances the ability to draw inferences on individual-level demography from empirical observations subject to observation error. We demonstrate how this modeling framework can be formulated and fitted to various data streams to draw inferences on spatial, temporal, and individual-level sources of variation in demography that govern changes in population abundance and distribution (Figure **??**).

5.2 A general framework for individual-based models

Point process models (PPMs) are a class of stochastic processes that can be used to describe the abundance, spatial distribution, and temporal dynamics of collections of points (Diggle, 1983; Stoyan, 2006; Illian *et al.*, 2008). In the context of population dynamics, the points are individual organisms. Analysis of PPMs focuses on the correlations and dependencies between observations (Illian *et al.*, 2008). The flexibility of these models for detecting and describing patterns makes them ideal tools for analyzing population processes. Past applications of PPMs to ecological data include studies of survival dynamics in pine forests (Rathbun & Cressie, 1994), predation rates of turtle nests (Burke *et al.*, 1998), and range shifts in marine mammals (Mäkinen & Vanhatalo, 2018).

One of the simplest classes of spatial PPM is the Poisson point process, defined by an intensity function $\mu(\boldsymbol{s})$ which describes the expected value of density at location $\boldsymbol{s}$ within some finite region $\mathcal{S}$. There are many options for the intensity function. In a homogenous landscape where individuals are randomly distributed, we could describe $\mu(\boldsymbol{s})$ as a constant across the entire region. More often, the relationship between location and environmental conditions $\mathbf{x}(\boldsymbol{s})$ is of interest. For instance, we can describe the expected density of individuals at any location using a log-linear relationship: $\log(\mu(\boldsymbol{s})) = \mathbf{x}(\boldsymbol{s})\boldsymbol{\beta}$. Other options include basis functions (Wikle & Hooten, 2010) or spatial random fields (Cox & Isham, 1980), depending on the spatial patterns of interest. Intensity functions can also describe interactions with other points, leading to patterns such as clustering or repulsion (Matérn, 1960; Cox & Isham, 1980; Dereudre, 2019), though the complexity of these interactions can lead to significant computational challenges (Illian *et al.*, 2008; Dereudre, 2019).

The spatial distribution of individuals ($i = (1, 2, \ldots, N)$) is proportional to the density surface $\boldsymbol{s}_i \propto \mu(\boldsymbol{s})$. The probability density for the location of a single point is:

$$p(\boldsymbol{s}_i) = \frac{\boldsymbol{s}_i}{\Psi}$$

where $\Psi = \int_{\mathcal{S}} \mu(\boldsymbol{s}) d\boldsymbol{s}$. Consequently, the expected value of abundance in time 1 is Ψ.

PPMs can also incorporate points (individuals) with marks (traits or states) that persist over time. However, there are many computational challenges associated with tracking traits across a non-constant a number of individuals (Royle *et al.*, 2007; Royle & Dorazio, 2009b). One solution is to fix the dimensions of the parameter space through data augmentation (Royle *et al.*, 2007), such that the alive/dead state of an individual is modeled as a trait and all individuals have a location regardless of their alive/dead state. Let M be some large integer much greater than the total number of individuals that were alive during the study period. An individual is alive at time $t = 1$ with probability $\psi = \Psi/M$, and the realized alive/dead state is given by:

$$z_{i,1} \sim \text{Bernoulli}(\psi)$$

Consequently, the realized value of abundance in time $t = 1$ is binomial: $N_1 \sim \text{Binomial}(M, \psi)$. Individuals can have additional traits, such as age, sex, or size. Traits can be continuous or discrete and may change over time. For instance, the sex and initial age of individual i might be:

$$\text{sex}_i \sim \text{Bernoulli}(\omega)$$
$$\text{age}_{i,1} \sim \text{Poisson}(\eta)$$

Dynamics in time ≥ 2

An individual's alive/dead state $z_{i,t}$ depends on their state in the previous time period. If the individual was previously alive ($z_{i,t-1} = 1$), their state in time t depends on survival. For individuals not yet alive, their future state depends on recruitment.

Survival and Recruitment

Survival can be modeled as constant, time varying or a combination of individual traits and environmental conditions. Consider a discrete-time survival model that relates individual survival to age and spatial location in the previous time period. As is the case for both integral projection models and simple regressions, survival for some ages or locations may be unknown and must be inferred based on the available data (Easterling *et al.*, 2000). We can describe survival probability, $\phi_{i,t-1}$, from time $t-1$ to time t as a function of age in the previous time period ($\text{age}_{i,t-1}$) and spatial location at time $t-1$ ($\boldsymbol{s}_{i,t-1}$). In the absence of reproduction, an individual's alive/dead state $z_{i,t}$ is a binomial draw of survival probability. Naturally, individuals can only survive to time t if they were previously alive in time $t-1$.

$$\text{logit}(\phi_{i,t-1}) = \mathbf{x}(\boldsymbol{s}_{i,t-1}, \text{age}_{i,t-1})\boldsymbol{\beta}^{\phi}$$

To indicate if an individual is available to be recruited (has never been alive previously), we define the variable a as follows:

$$a_{i,1} = 1 - z_{i,1} \quad \text{for } t = 1$$

$$a_{i,t} = a_{i,t-1}(1 - z_{i,t}) \text{ for } t > 1$$

At t, the expected number of recruits depends on the fecundity $\gamma_{i,t-1}$ of all members of the population. Here we consider a pre-reproductive model, where individuals entering the population in time t are produced in time $t-1$. We define fecundity as the expected number of surviving offspring produced by an individual in time $t-1$. Fecundity may depend on individual characteristics or be affected by density dependence.

$$log(\gamma_{i,t}) = \beta_0^\gamma - \beta_1^\gamma N_{t-1}$$
$$E(R_t) = \sum_{i=1}^{M} \gamma_{i,t-1} z_{i,t-1}$$

Note that when $\beta_1^\gamma = 0$, fecundity is no longer density dependent. Let the number of individuals available to be recruited be: $A_t = \sum_{i=1}^{M} a_{i,t-1}$. The entrance probability $\tilde{\gamma}$ is just the expected number of recruits divided by the number of available to be recruited:

$$\tilde{\gamma}_t = E(R_t)/A_t$$

The individual's dead/alive state in time t, $z_{i,t}$ is then defined as a probabilistic draw based on either ϕ or $\tilde{\gamma}$, depending on the individual's previous state. Individuals that have previously been recruited ($a_{i,t-1} = 0$) cannot be recruited again. Similarly, individuals can only survive to time t if they were previously alive in time $t-1$. Total abundance in time t is just the sum of the dead/alive states, $N_t = \sum_{i=1}^{M} z_{i,t}$, of all possible individuals.

$$z_{i,t} \sim \text{Bernoulli}(\phi_{i,t-1} z_{i,t-1} + \tilde{\gamma}_{t-1} a_{i,t-1})$$

Parentage

Parentage plays a central role in ecology and evolution, and models that ignore it cannot be used to directly assess inheritance or fitness (Jones *et al.*, 2010; Moore *et al.*, 2014; Peyran *et al.*, 2022). For the vast majority of species, general knowledge of biology implies several aspects of reproduction. Firstly, all new recruits that join a population require a parent. Secondly, the location of an individual's birth depends on the previous location of the parent individual, as discussed in the next section.

Not all individuals in a population are equally likely to produce offspring that survive until the next time period. An individual's expected number of offspring in time t is $\gamma_{i,t-1}z_{i,t-1}$. Individuals with higher fecundities are more likely to produce more offspring. For all new recruits in the population, the expected proportion produced by each previously alive individual is $\frac{\gamma_{1:M,t-1}z_{1:M,t-1}}{E(R_t)}$. Thus the parent of a new recruit can be described as a categorical draw based on the fecundity of all living individuals in the previous time period:

$$\text{Parent}_{i,t} \sim \text{Categorical}(\frac{\gamma_{1:M,t-1}z_{1:M,t-1}}{E(R_t)})$$

Tracking the relationships between offspring and parents allows for the creation of multigenerational family trees and pedigrees of natural populations. These trees can be used to calculate reproductive success and fitness across the study period and between different traits. For instance, we can calculate the number of new recruits contributed by individual i across all time periods. The total number of recruits produced by individual i across time $t = 1 \ldots T$ is:

$$\sum_{t=1}^{T}\sum_{i=1}^{M}(\text{Parent}_{i,t} = i)$$

Movement and Dispersal

Simple random walk models describe movements as the outcome of a symmetrical bivariate gaussian distribution, with expected value $\boldsymbol{s}_{i,t-1}$ (the individual's previous location) and variance parameter κ^2.

Larger values of κ^2 indicate that larger movements away from the starting location are more common. When $\kappa^2 = 0$, individuals do not move between time periods.

$$\boldsymbol{s}_{i,t} \sim \text{Normal}(\boldsymbol{s}_{i,t-1}, \kappa^2)$$

Random walks are uncorrelated, meaning the direction of movement in time t is independent of the direction moved in time $t-1$, and unbiased, meaning the direction moved at each step is completely random. Random walks are well suited for representations of passive dispersal or overall trajectories across longer time periods (e.g. movements between years), but are unrealistic when movements are directed towards a specific destination (Kareiva & Shigesada, 1983; Morales *et al.*, 2010).

For some mobile species, movements may be motivated by environmental gradients such as climate, elevation, or distance to water. Let $\nabla c(\boldsymbol{s}_{i,t-1})$ represent a habitat gradient evaluated at an individual's location in time $t-1$. The gradient is the partial derivative of the habitat covariate in both the easting $\frac{\partial c(\boldsymbol{s}_{i,t-1})}{\partial \boldsymbol{s}_{x,i,t-1}}$ and northing $\frac{\partial c(\boldsymbol{s}_{i,t-1})}{\partial \boldsymbol{s}_{y,i,t-1}}$ directions, pointing in the direction of the greatest rate of increase (Preisler *et al.*, 2013). The magnitude of the resulting vector corresponds to the rate of increase in that direction (Dawber, 1987). For instance, if $\boldsymbol{s}_{i,t}$ is located at the base of a mountain and the environmental gradient of interest is elevation, $\nabla c(\boldsymbol{s}_{i,t-1})$ will have the largest magnitude in the direction of the mountain's peak. Let δ represent the individual's movement response to the habitat gradient. Positive values of delta suggest an attraction to areas with higher covariate values, while negative values suggest avoidance of these values. When $\delta = 0$, there is no movement response to the environmental gradient and the movement model reverts to a random walk.

$$\boldsymbol{s}_{i,t} \sim \text{Normal}(\boldsymbol{s}_{i,t-1} + \delta \nabla c(\boldsymbol{s}_{i,t-1}), \kappa^2)$$

In addition to environmental features, movement is often influenced by age. In vertebrates, natal dispersal is typically greater than adult dispersal (Greenwood & Harvey, 1982; Paradis *et al.*, 1998; Fonte *et al.*, 2019). For sessile species, passive natal dispersal away from a parent is likely the only movement an individual will make during their lifetime (Bonte *et al.*, 2012). To incorporate natal dispersal dynamics, assume first year dispersal depends on the parent's previous location, $s_{Parent,t-1}$. Thus, the location of individual i in time $t+1$ is described as:

$$\boldsymbol{s}_{i,t} \sim \begin{cases} \text{Normal}(\boldsymbol{s}_{Parent_i,t-1} + \delta \nabla c(\boldsymbol{s}_{Parent_i,t-1}), \kappa_a^2) & \text{if new recruit} \\ \text{Normal}(\boldsymbol{s}_{i,t-1} + \delta \nabla c(\boldsymbol{s}_{i,t-1}), \kappa_a^2) & \text{otherwise} \end{cases}$$

Observation Process

With few exceptions, it is rare to have perfect information on the locations and traits of all individuals in a population. More commonly, detailed information is available on a subset of individuals, potentially accompanied by broad non-demographic data sampled over a larger area. Recent advancements in hierarchical and integrated population modeling allow for the integration of multiple data sources collected at different scales of observation while accounting for observation error and stochasticity in demographic rates (Besbeas *et al.*, 2003; Royle & Dorazio, 2009a; Chandler & Clark, 2014). Below, we consider how two common types of data might be incorporated into the individual-based modeling framework presented above.

Count data

Count data is often the easiest and least expensive data to collect on natural populations. These data are collected by counting all individuals observed during a fixed survey time interval, usually within a defined spatial region. Individual identity is not retained during this process. Common examples of count data include transect walks and point counts (Plumptre, 2000; Alldredge *et al.*, 2007). Assume an observer detects individuals within a defined area D_j with constant probability p. Assume p is bound between 0 and 1; that is, observers cannot detect a negative number of individuals, nor can they perceive more individuals than are present at the survey location. The observed counts $n_{j,t}$ at each location in time period t can be defined as:

$$n_{j,t} \sim \text{Binomial}(N_{j,t}, p)$$
$$p \sim Uniform(0, 1)$$

To calculate $N_{j,t}$, the abundance of individuals within the survey spatial region, we sum up the individuals that were both alive $z_{i,t} = 1$ and located within D_j in time t:

$$N_{j,t} = \sum_{i}^{M} z_{i,t}(s_{i,t} \in D_j)$$

Mark-recapture data

A common technique for monitoring wildlife populations is capture-mark-recapture (CMR). Individuals are captured, tagged with a uniquely identifying marker, and released back into the population (McCrea, 2014). Ideally, the process is repeated over several sampling occasions during which the population is assumed to be constant. The data from CMR studies is in the form of a 'capture history' – the record of each individual's detection or non-detection in each sampling occasion (Royle & Dorazio, 2009b). For simplicity, imagine a study with 5 consecutive days of sampling, with a constant capture probability p for all individuals alive and in the population.

Each individual's capture history $y_{i,k,t}$ (the record of detection on day k in time t), is given by:

$$y_{i,j,t} \sim \text{Bernoulli}(z_{i,t} p)$$
$$p \sim Uniform(0, 1)$$

Critically, detection of individuals, $y_{i,j,t} = 1$ is only possible for live animals (where $z_{i,t} = 1$). By repeated sampling of a closed population, it is possible to separate non-detections due to observation error from true absences and estimate population abundance.

Simulation Study

To test the performance of the proposed framework, we simulated population dynamics in an inhomogeneous landscape across 4 years under two scenarios and assessed parameter recovery. In both scenarios, we used a two-category age system where newly recruited individuals were age 1 and all other individuals were age 2, similar to the aging system used in many avian studies. In our first scenario, newly recruited individuals had large dispersal distances (higher values of κ^2) and were attracted to higher landscape values while older individuals moved with a random walk ($\delta = 0$). In our second scenario, both newly recruited and older individuals had random dispersal kernels, though values of κ^2 varied between ages.

We simulated a spatial capture-recapture (SCR) observation process (Royle *et al.*, 2013). By leveraging the pattern of both capture and non-capture locations, SCR models estimate locations for all individuals in the study area, allowing for estimation of density and abundance at the population level. As with non-spatial capture-mark-recapture, individuals are captured, tagged, and released back into the population. We simulated a trapping array with 144 traps laid out in a 12 by 12 trapping array and 4 days of trapping per time period.

We modeled capture probability, the probability of an individual being detected at any given trap location, using a Gaussian detection function that depended on the individual's alive/dead state, $z_{i,t}$, and the distance between activity centers and traps. The probability that individual i was captured at trap j on survey occasion k in year t, given an activity center location of $\boldsymbol{s}_{i,t}$, is given by:

$$p_{i,j,k,t} = z_{i,t} g_0 \exp\left(\frac{-\|\boldsymbol{s}_{i,t} - \mathbf{x}_{j,t}\|^2}{2\sigma^2}\right)$$

where $\mathbf{x}_j$ denotes the coordinates of capture location j. Parameters g_0 and σ determine the baseline capture probability and the decay in capture probability with distance, respectively. For both scenarios, we simulated a baseline capture probability,g_0, of 0.5 and a σ of 0.04.

Each individual's capture history $y_{i,j,k,t}$ (the record of detection at each trap j on survey occasion k in year t), is given by:

$$y_{i,j,t} \sim \text{Bernoulli}(p_{i,j,k,t} z_{i,t})$$

If an individual was detected in time period t, we assumed perfect observation of the individual's sex, age, and number of offspring for that time period. We also assumed parent identity was known for any new recruits with a female parent captured in the previous time period. We set the fecundity of all male individuals to 0, such that only female members of the population could be chosen as parents and produce offspring. A full list of simulated parameter values can be found in Table 5.1.

We evaluated bias of the posterior median, coefficient of variation (CV), root-mean-square error, and 95% credible interval coverage for all parameters listed in Table 5.1. For each scenario, we simulated 50 datasets. We used Markov chain Monte Carlo (MCMC) to draw posterior samples in NIMBLE 1.0.1 with the 'nimble' package in R 4.1.3 (de Valpine *et al.*, 2017; R Core Team, 2019). For all simulations, we ran 3 chains for 50,000 iterations with 20,000 burnin iterations.

5.3 Results

All parameters were recovered with low bias (Fig. 5.2) with the exception of the dispersion parameter κ. Median bias in estimates of δ (the landscape attraction parameter) was especially low, ranging from -0.01 to 0.00 (Table 5.2). For scenarios with random dispersal, the model correctly identified values of δ as close to 0. Estimates of fecundity, β_0^{γ}, were biased high in the second scenario. All simulations successfully converged within 50,000 iterations.

5.4 Discussion

In both theoretical and applied ecology, there remains a need for population models that can be used for inference on demography in complex landscapes. We have presented a framework that combines the mathematical background of point process models with the individual focus of agent-based methodologies. By considering population processes at the individual level, we propose a rigorous framework to explore the mechanisms that drive demographic patterns. Historically, numerous computational difficulties of including individual variation into existing ecological models (DeAngelis & Grimm, 2014) have precluded the development of a generalizable individual-based framework that can be formally confronted with data. By proposing a general framework that can apply to a diverse array of ecological systems, we provide a solution to incorporate individual-level processes without sacrificing mathematical rigor.

The difficulties of 'marrying basic and applied ecology' (Levin, 1992) remains an ongoing struggle for population modeling (DeAngelis & Yurek, 2017). One of the major reasons for this is that few theoretical or agent-based models are designed for rigorous validation with observed data. Furthermore, there is often no clear criteria for assessing a model's realism (Augusiak *et al.*, 2014), especially for processes that are inherently unobservable. In contrast, the individual-based framework presented here is based on the solid mathematical foundation of point process models with a rich history of validation, model selection and repeatability (Neyman & Scott, 1952; Cox & Isham, 1980; Baddeley *et al.*, 2005). The wide variety of techniques available for fitting, validating and predicting from spatiotemporal point process models (Baddeley *et al.*, 2005; Cronie *et al.*, 2023) ensures that future findings can be rigorously confronted with observed data.

Dispersal is a fundamental driver of population dynamics, impacting spatial variation in density and gene flow (Wright, 1943; Hanski & Simberloff, 1997; Walters, 2000).Theoretical models of spatial population dynamics suggest that dispersal capacity plays a critical role in maintaining population viability under climate change (Clark *et al.*, 2001; Schloss *et al.*, 2012) Species with limited dispersal capacity cannot track optimal climatic conditions and are likely to experience increased extinction risk (Hoffmann & Sgrò, 2011; Mota *et al.*, 2018). However, direct observations of dispersal in natural populations is notoriously difficult, especially for mobile species (Penteriani & Delgado, 2011; Stillman *et al.*, 2021). Therefore, having a mechanistic modeling framework of dispersal dynamics across all subsets of the population is essential for capturing the complexity of demographic trends and accurately predicting species persistence.

Estimating recruitment location is often of great interest for population management, as conditions at recruitment locations can have lifelong impacts on fitness or behavior (Blödner *et al.*, 2007; Mitchell *et al.*, 2013). For instance, many evolutionary models predict increased dispersal distances when conspecific densities are high at natal locations (Matthysen, 2005). Across several taxa, rearing conditions have been shown to alter future habitat preferences (Davis & Stamps, 2004), reproductive success (Gaillard *et al.*, 2003), and survival (Van De Pol *et al.*, 2006). By explicitly modeling locations of new recruits, the framework presented here could also be used to explore the impact of recruitment locations on population viability and source-sink dynamics.

Tracking parent-offspring relationships across time can provide extensive information on kinship and inbreeding potential (Jones *et al.*, 2010; Peyran *et al.*, 2022). One barrier to incorporating parent-offspring dynamics is the need to model the location of all individuals, regardless of their alive-dead state. In common individual-based extensions of the Jolly-Seber model (Royle, 2008), newly recruited individuals probabilistically 'appear' in the world, often using spatially referenced covariates and density dependence to model the expected locations of new recruits (Chandler *et al.*, 2018). However, individuals are not born at the population-level and the individual-level traits of new recruits are not independent of parent characteristics. Moreover, by applying a mechanistic approach to recruitment and individual traits, it may be possible to model gene flow, providing direct linkage between applied ecological and eco-evolutionary theory.

The basic formulations of survival and recruitment in our framework were initially proposed by Royle *et al.* (2007) and Royle & Dorazio (2009a) for the analysis of capture-mark-recapture data. Spatial extensions were described by Saracco *et al.* (2010), though space was treated as a discrete variable. A fundamental difference between these models and the proposed framework is the implementation of a mechanism to explain individual locations in continuous space. Thus, the framework presented here can be seen as an extension of the individual-based capture-mark-recapture models, with the addition of an underlying point process.

The flexibility of this framework naturally lends itself to exploration of individual-level interactions. Investigations of these interactions has long been possible in agent-based models (Letcher *et al.*, 1998; Grimm, 1999), but implementation of these dynamics is often difficult in mean field approaches (Radchuk *et al.*, 2021). Recent movement models linking individual animal movement behavior to population dynamics have focused on the attraction or repulsion of fixed environmental features (Borchers, 2012; McClintock *et al.*, 2022). These movement models could be easily accommodated by the proposed individual-based framework or expanded to include interactions with other species (Chapter 3).

The framework presented here could be generalized to accommodate multiple data structures. For sessile species, direct information on a subset of individual locations may be readily available or estimated with distance sampling (Berberich *et al.*, 2016). Presence-absence data could be linked to the process model (Zipkin *et al.*, 2017) and combined with GPS locations from radio tagged information to infer abundance and dispersal dynamics. Though individual-based models are notoriously 'data-hungry' (Radchuk *et al.*, 2016, 2021), the framework presented here is compatible with a wide variety of data structures and systems.

In the face of changing climates, accurate predictions of population-level patterns will be critical for population management and conservation. Mechanistic models that link individual-level behaviors and abiotic influences to population-level processes are crucial to understanding the drivers of population change. Using currently available models, it remains difficult to estimate the effects of individual interactions, dynamic environmental conditions, and realistic stochasticity on population dynamics. Until we routinely confront our models with data under formal inference techniques, our predictive ability and understanding of population processes will continue to suffer.

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Table 5.1: Parameters used in two simulation scenarios. Populations were simulated 50 times for each scenario.

Parameter	Description	Value	
		S1	S2
η	Proportion adult individuals in year 1	0.35	0.35
ω	Probability of female sex	0.65	0.65
β_0^{μ}	$E(N)$ year 1 intercept	2.2	2.5
β_1^{μ}	$E(N)$ year 1 coefficient	4.5	2.5
β_0^{ϕ}	Location dependent survival intercept	-0.8	-0.8
β_1^{ϕ}	Location dependent survival coefficient	2.5	2.5
β_0^{γ}	Fecundity intercept	-1.0	-1.0
β_1^{γ}	Density dependent penalty on fecundity	0.0	0.0
ϕ_1^{γ}	Survival to age 1 for new recruits in $t = 2$	0.3	0.8
ϕ_2^{γ}	Survival to age 1 for new recruits in $t = 3$	0.3	0.8
ϕ_3^{γ}	Survival to age 1 for new recruits in $t = 4$	0.3	0.8
δ_1	Movement response (new recruits)	0.1	0.0
δ_2	Movement response (adults)	0.0	0.0
$\frac{1}{\sqrt{\kappa_1}}$	Dispersal parameter (new recruits)	0.0	250
$\frac{1}{\sqrt{\kappa_2}}$	Dispersal parameter (adults)	0.0	500
g_0	Baseline detection probability	0.50	0.50
σ	Detection parameter	0.04	0.04

Table 5.2: Root-mean-squared error, coefficient of variation, 95 % credible interval performance and bias of the posterior median for parameters simulated under 2 different scenarios. Each scenario was simulated 50 times.

param	RMSE	CV	CI	bias	RMSE	CV	CI	bias
N	5.32	0.02	0.86	0.81	1.82	0.03	0.77	-1.52
η	0.06	0.13	0.90	0.00	0.08	0.21	0.98	0.01
ω	0.05	0.07	0.96	-0.01	0.08	0.09	0.96	0.00
ψ_1	0.05	0.06	1.00	0.03	0.04	0.14	1.00	-0.01
β_0^{ϕ}	0.46	-0.54	0.98	0.08	0.55	-0.66	0.98	0.10
β_1^{ϕ}	0.66	0.22	0.98	-0.05	0.89	0.34	0.94	-0.34
β_0^{γ}	0.15	-0.13	0.98	0.01	0.20	-0.18	0.90	0.09
ϕ_1^{γ}	0.10	0.27	0.98	-0.01	0.18	0.21	1.00	-0.10
ϕ_2^{γ}	0.10	0.27	0.98	-0.01	0.18	0.21	1.00	-0.10
ϕ_3^{γ}	0.10	0.27	0.98	-0.01	0.18	0.21	1.00	-0.10
$\frac{1}{\sqrt{\kappa_1}}$	62.35	0.26	1.00	-0.28	82.34	0.24	0.86	-61.47
$\frac{1}{\sqrt{\kappa_2}}$	73.23	0.10	0.94	38.84	83.21	0.13	0.90	-26.30
δ_1	0.03	0.25	0.92	-0.01	0.03	-0.75	0.96	-0.00
δ_2	0.01	0.08	0.94	-0.00	0.01	-0.42	0.86	-0.00
g_0	0.03	0.04	0.98	-0.00	0.04	0.06	0.96	-0.01
σ	0.00	0.02	0.92	0.00	0.00	0.03	0.98	0.00

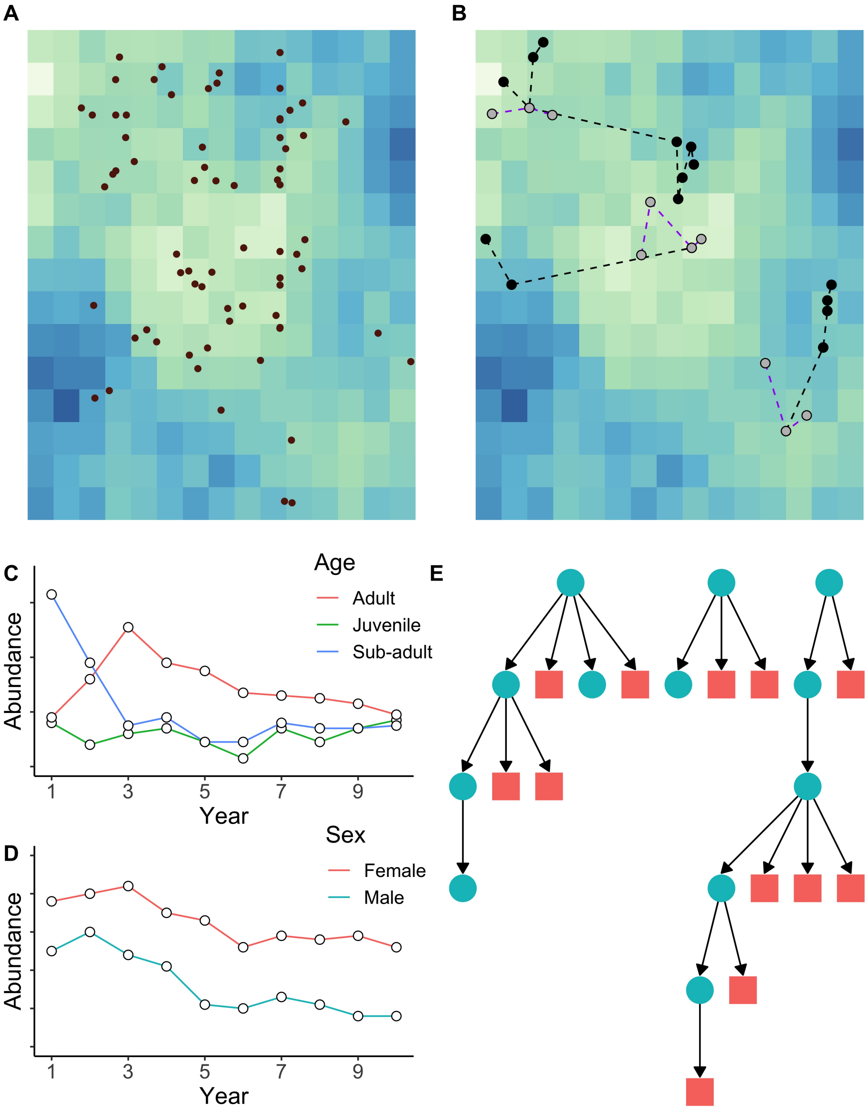

Figure 5.1: Conceptual figure showing the diversity of inference possible with an individual-based model spatial temporal point process framework . A. Estimates of locations for all individuals in the population B. Dispersal patterns and location of parent individuals. Parent locations are shown as grey points, with offspring depicted in black. Dotted lines indicate dispersal pathways. C. Population age over time for a population with 3 age categories. D. Counts of individuals of each sex across time. E. Parent-offspring lineages for a female-based reproductive model. Female individuals are shown as blue circles. Males are depicted as red squares and do not contribute to fecundity. Offspring with a shared parent are not necessarily born in the same time period.

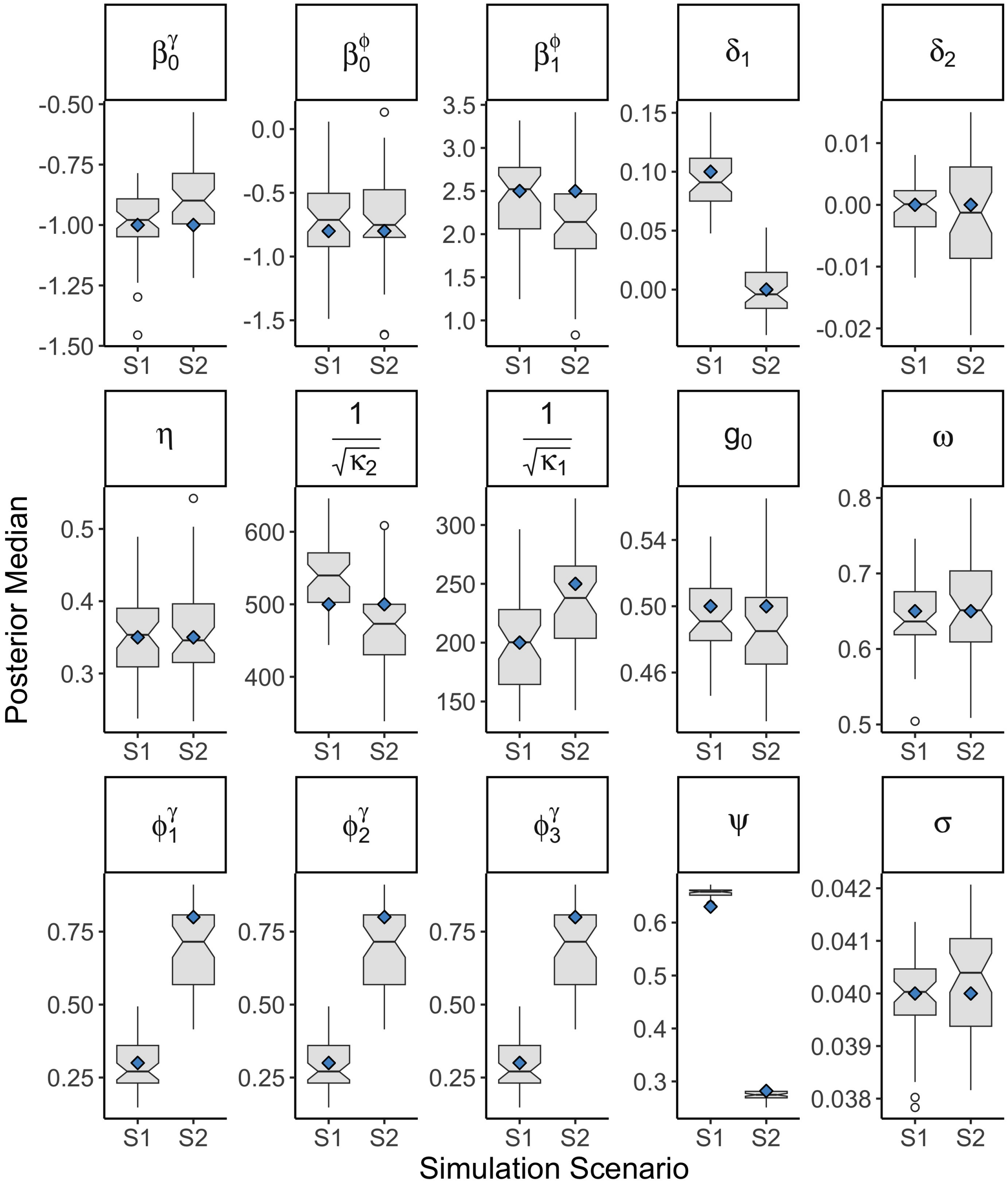

Figure 5.2: Simulation study results for 2 scenarios, each with 50 simulated datasets. The posterior mode was used as a point estimator. Blue dots represent the true data generating values.

CHAPTER 6

CONCLUSION

Almost all models of species distributions under climate change predict shifts towards higher elevations and latitudes. Populations at the low-latitude margins of ranges are expected to experience the strongest effects of climate change, with the highest risk of climate-induced extinction. Though trailing-edge populations often harbor high genetic diversity, little attention has been given to the impacts of climate change on communities with a high proportion of trailing-edge species. As global biodiversity continues to decline, there is an urgent need to understand the mechanisms that drive population dynamics of trailing-edge communities under changing climate conditions.

In Chapter 1, I assessed population trends in the avian community in the southern Appalachian mountains over the past decade. Declines were more common for trailing-edge species than for those in the core of their range, especially for cold-adapted species with long-distance migrations. Species richness increased in the majority of the study area, particularly at high elevations, suggesting that declines in cold-adapted trailing-edge species are occurring at a slower rate than uphill encroachment of warm-adapted species. I further found that species range position (trailing-edge vs. core species) and migratory strategy were both important predictor for shifts in species density, but the effects are complicated by individual species' life history traits. Though I found that species movements were related to changes in temperature and precipitation, my analysis did not provide any mechanistic explanations for how individual species traits and life histories interacted with range position to drive population trends. Thus, I was not able to estimate the impact of competition or individual-level interactions on range shifts or population declines.

In Chapter 2, I introduced an individual-level framework for estimating species abundance and spatial distribution that can accommodate both environmental and biotic relationships. In simulation, the proposed framework effectively recovered all simulated parameters with low bias, suggesting the model was able to differentiate between biotic and abiotic drivers of population patterns. I then applied the framework to spatial capture-recapture data on two potentially competing songbird species – hooded warbler (*Setophaga citrina*) and black-throated blue warbler (*Setophaga caerulescens*) – that segregate over a climate gradient in the southern Appalachian Mountains. Abundance of hooded warblers was highest at drier and hotter sites, while black-throated blue warblers were much more abundant at the coldest and wettest sites and rarely detected at sites below 950 m. I found a strong effect of climate on spatial variation in density of both black-throated blue warblers and hooded warblers, with little evidence of spatial repulsion between the two species. In Chapter 1 I found that hooded warbler abundance and occupancy increased at mid and low elevations over the past decade while the inverse was true for black-throated blue warbler. In combination, the results from Chapters 1 and 2 suggest that competition with hooded warblers is unlikely to be the main driver of declines in black-throated blue warbler abundance, contrasting with the traditional view that biotic interactions are the main drivers of species distributions at warm-edge range limits.

In Chapter 3, I explored dispersal dynamics of black-throated blue warblers in the southern Appalachian Mountains. Studying dispersal in natural populations is notoriously difficult and few empirical studies have investigated the degree to which dispersal is directed towards optimal climate conditions. I used 21 years of mark-recapture data to test the hypothesis that a key mechanism in climate-induced range shifts of trailing-edge populations is natal dispersal. For nestlings, dispersal was more likely to be directed towards cooler and wetter locations relative to available conditions surrounding hatch locations. In contrast, adult dispersal was more restricted and less directional than natal dispersal. These results suggest that directional natal dispersal away from warmer and drier climate conditions may explain local range shift of black-throated blue warblers towards higher elevations. This non-random natal dispersal, combined with minimal dispersal of adult individuals, further suggests that low elevation populations will continue to decline. Additionally, these findings highlight the need to explicitly incorporate dispersal dynamics into population models when assessing the drivers of trailing-edge range shifts.

In Chapter 4, I presented a spatially-explicit individual-based modeling framework that directly links each individual in the population to a parent individual to model natal and adult dispersal. The framework accounts for complex spatial patterns while retaining individual attributes across time, such as age, parent identity, location, and sex. By applying a mechanistic approach to recruitment and individual traits, I argued it should be possible to model gene flow, providing direct linkage between applied ecological and eco-evolutionary theory.

As discussed throughout this dissertation, accurate predictions of population-level patterns are critical for effective population management and conservation. Individual-level data allows for a mechanistic link between individual behavior and abiotic influences and is essential for capturing the complexity of demographic trends and accurately predicting species persistence. Future work on the southern Appalachian bird community at both the community and single species level, should focus on individual-level data to determine the specific drivers of abundance and species composition.

Appendix A

Temperature and precipitation conditions from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA.

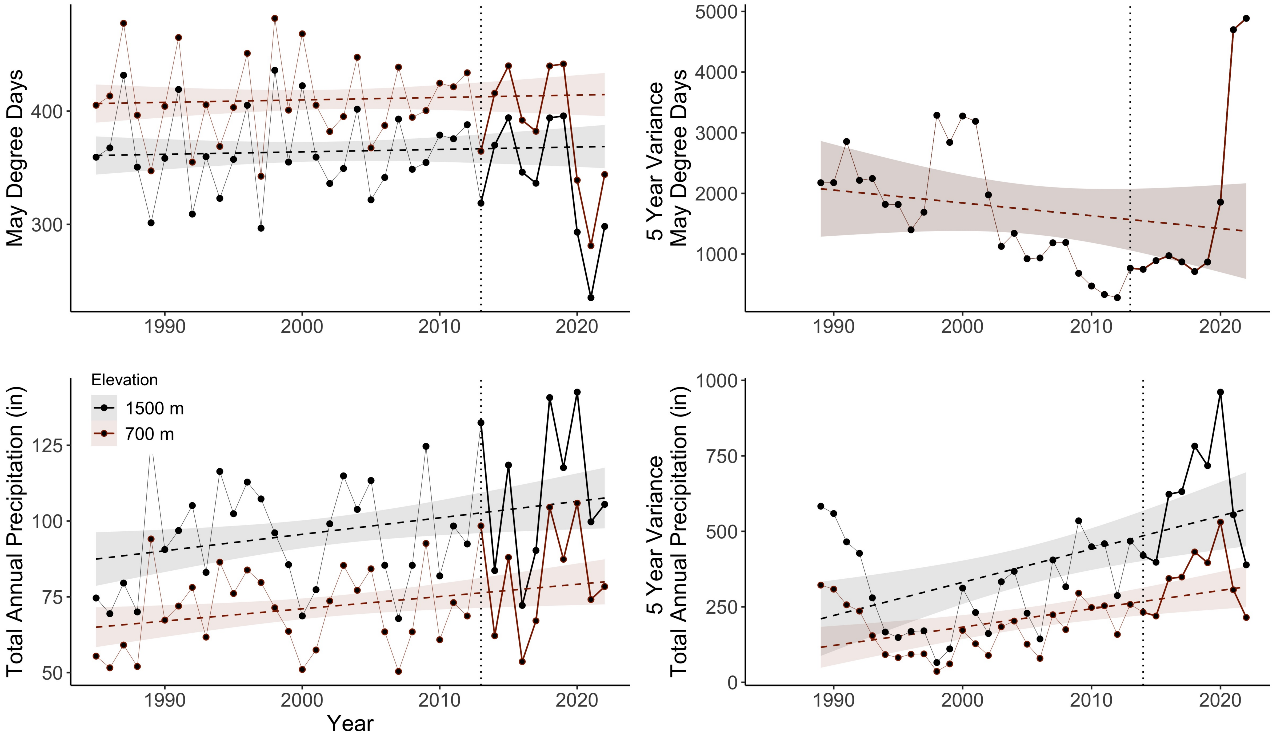

Figure A.1: Temperature and precipitation conditions from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA. Trend lines from a linear model are shown with dashed lines and shaded confidence intervals. The vertical dotted line indicates the first year of the study

APPENDIX B

PARAMETERS USED IN SIMULATION OF TWO-SPECIES BIOTIC INTERACTIONS

Table B.1: Parameters used in simulation. Populations were simulated 96 times for each scenario.

Parameter	Description	Value				
		S1	S2	S3	S4	S5
β_0^a	Species A $E(N)$ intercept	3.5	3.5	3.5	3.5	3.5
β_0^b	Species B $E(N)$ intercept	4.0	3.75	4.0	4.0	3.5
β_1^a	Species A relationship to covariate	0.0	-0.75	-0.50	0.50	-0.50
β_1^b	Species B relationship to covariate	0.0	0.50	0.0	1.0	0.50
ω	Repulsion parameter	0.05	0.05	0.05	0.05	0.0
σ	Effect of distance on detection	0.05	0.05	0.05	0.05	0.05
p_0	Detection intercept	0.30	0.30	0.30	0.30	0.30

APPENDIX C

95 % CREDIBLE INTERVAL PERFORMANCE, BIAS OF POSTERIOR MEDIAN, ROOT-MEAN-SQUARED ERROR AND COEFFICIENT OF VARIATION FOR PARAMETERS USED IN SIMULATION OF TWO-SPECIES BIOTIC INTERACTIONS

Table C.1: 95 % Credible interval performance, bias of posterior median, root-mean-squared error and coefficient of variation for parameters simulated under 5 scenarios. Each scenario was simulated 96 times.

		β_0^a	β_0^b	β_1^a	β_1^b	N^a	N^b	ω
Scenario 1	CI	0.89	0.92	0.97	0.96	0.94	0.98	0.94
	Bias	-0.076	-0.166	0.026	-0.006	0.635	-0.010	-0.006
	RMSE	0.25	0.52	0.31	0.34	4.87	5.10	0.02
	CV	0.06	0.10	0.56	0.04	0.11	0.13	0.45
Scenario 2	CI	0.90	0.98	0.95	0.97	0.97	0.99	0.97
	Bias	-0.067	-0.070	-0.003	0.034	0.052	0.979	-0.003
	RMSE	0.26	0.61	0.33	0.36	5.32	5.13	0.02
	CV	0.06	0.13	-0.37	0.55	0.13	0.10	0.44
Scenario 3	CI	0.92	0.92	0.94	0.95	0.98	0.98	0.95
	Bias	-0.083	-0.078	0.003	-0.015	0.188	0.740	-0.004
	RMSE	0.25	0.53	0.32	0.34	4.81	5.17	0.02
	CV	0.06	0.10	-0.51	0.09	0.13	0.12	0.44
Scenario 4	CI	0.92	0.97	0.93	0.96	0.97	0.98	0.98
	Bias	-0.046	-0.111	-0.019	0.015	-0.490	0.938	-0.003
	RMSE	0.26	0.45	0.28	0.39	4.82	6.37	0.02
	CV	0.06	0.09	0.44	0.29	0.09	0.11	0.27
Scenario 5	CI	0.91	0.96	0.96	0.99	0.96	0.95	0.00
	Bias	-0.104	0.048	-0.010	-0.022	-0.167	-0.281	0.022
	RMSE	0.24	0.34	0.33	0.30	4.99	4.61	0.02
	CV	0.06	0.08	-0.51	0.47	0.13	0.09	0.67

Appendix D

Posterior summary statistics describing the abundance and density of black-throated blue warbler (species A, *Setophaga caerulescens*) and hooded warbler (species B, *Setophaga citrina*) in the Nantahala National Forest, North Carolina, USA from 2018 to 2021.

Table D.1: Posterior summary statistics describing the abundance and density of black-throated blue warbler (species A, *Setophaga caerulescens*) and hooded warbler (species B, *Setophaga citrina*) in the Nantahala National Forest, North Carolina, USA from 2018 to 2021.

	Description	Mean	SD	2.5%	97.5%
$\beta^a_{0,t=1}$	Species A $E(N_1)$ intercept	1.27	0.12	1.03	1.51
$\beta^a_{0,t=2}$	Species A $E(N_2)$ intercept	0.83	0.15	0.54	1.12
$\beta^a_{0,t=3}$	Species A $E(N_3)$ intercept	1.38	0.12	1.14	1.60
$\beta^a_{0,t=4}$	Species A $E(N_4)$ intercept	1.06	0.13	0.79	1.32
$\beta^b_{0,t=1}$	Species B $E(N_1)$ intercept	1.17	0.15	0.87	1.46
$\beta^b_{0,t=2}$	Species B $E(N_2)$ intercept	0.98	0.17	0.63	1.29
$\beta^b_{0,t=3}$	Species B $E(N_3)$ intercept	1.44	0.13	1.18	1.68
$\beta^b_{0,t=4}$	Species B $E(N_4)$ intercept	1.10	0.15	0.79	1.39
β^a_1	Species A $E(N)$ relationship to climate	1.80	0.14	1.52	2.08
β^b_1	Species B $E(N)$ relationship to climate	-0.65	0.13	-0.90	-0.39
p^a_0	Species A detection intercept	0.03	0.01	0.03	0.05
σ^a	Effect of distance on detection of Species A	163.00	25.08	111.33	198.68
p^b_0	Species B detection intercept	0.07	0.02	0.03	0.11
σ^b	Effect of distance on detection of Species B	97.66	23.04	66.50	159.69
ω	Interaction parameter	2.31	1.79	0.08	6.58

Appendix E

Four years of capture data on black-throated blue warbler (BTBW, *Setophaga caerulescens*) and hooded warbler (HOWA, *Setophaga citrina*) at 19 sites in the Nantahala National Forest, North Carolina, USA.

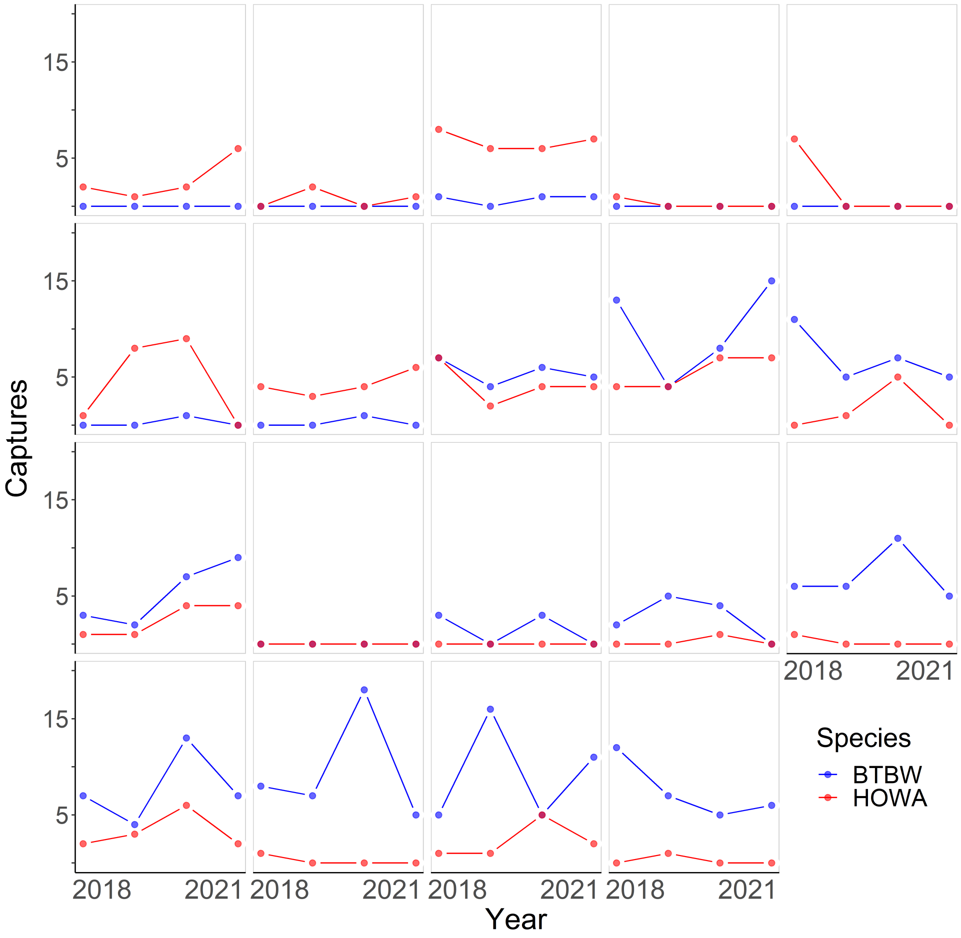

Figure E.1: Four years of capture data on black-throated blue warbler (BTBW, *Setophaga caerulescens*) and hooded warbler (HOWA, *Setophaga citrina*) at 19 sites in the Nantahala National Forest, North Carolina, USA. Sites are sorted (left to right, top to bottom) from the hottest, driest sites in the top left to the coldest, wettest sites in the bottom right.

Appendix F

Abundance estimates of black-throated blue warbler (BTBW, *Setophaga caerulescens*) and hooded warbler (HOWA, *Setophaga citrina*) when biotic interactions were or were not considered in the model.

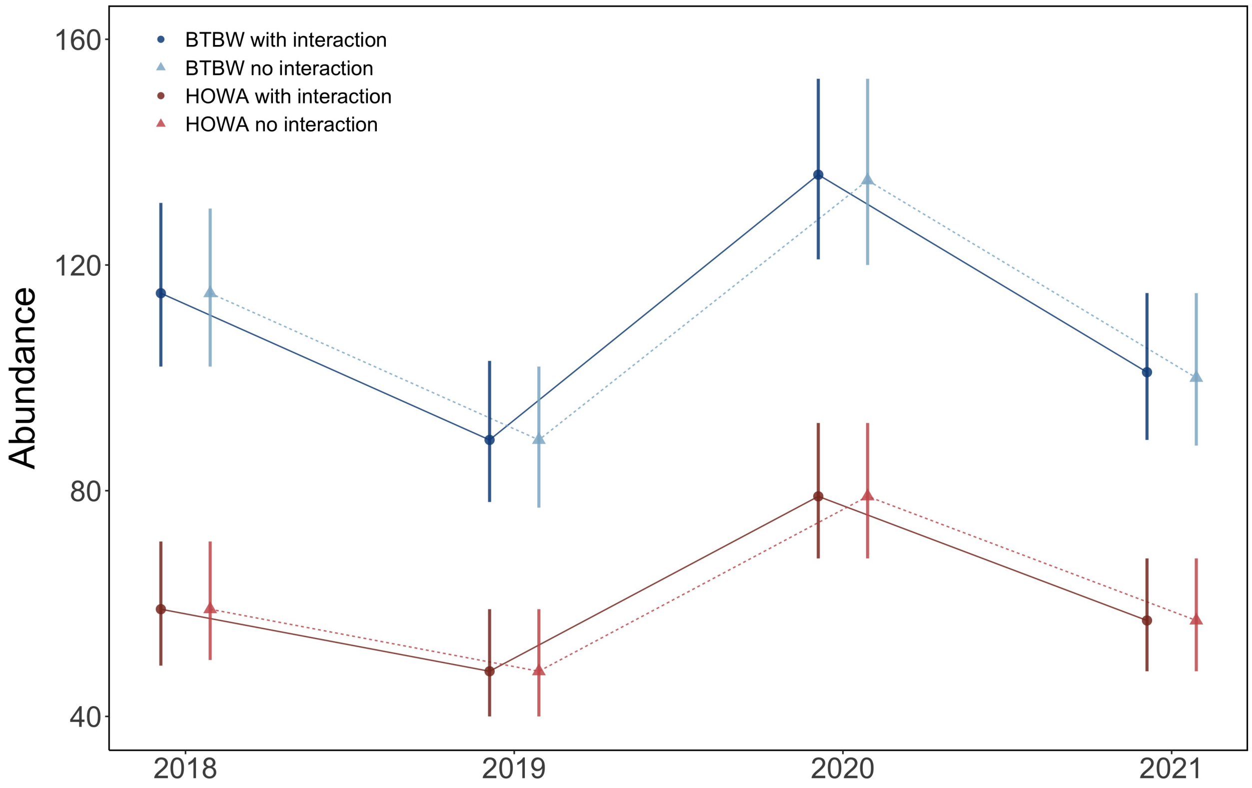

Figure F.1: Abundance estimates of black-throated blue warbler (BTBW, *Setophaga caerulescens*) and hooded warbler (HOWA, *Setophaga citrina*) when biotic interactions were or were not considered in the model. Each point represents the total yearly abundance of that species across 19 sampling sites.

Appendix G

Inhibition between hooded warbler (HOWA, *Setophaga citrina* and black-throated blue warbler (BTBW, *Setophaga caerulescens*) at fine spatial scales.

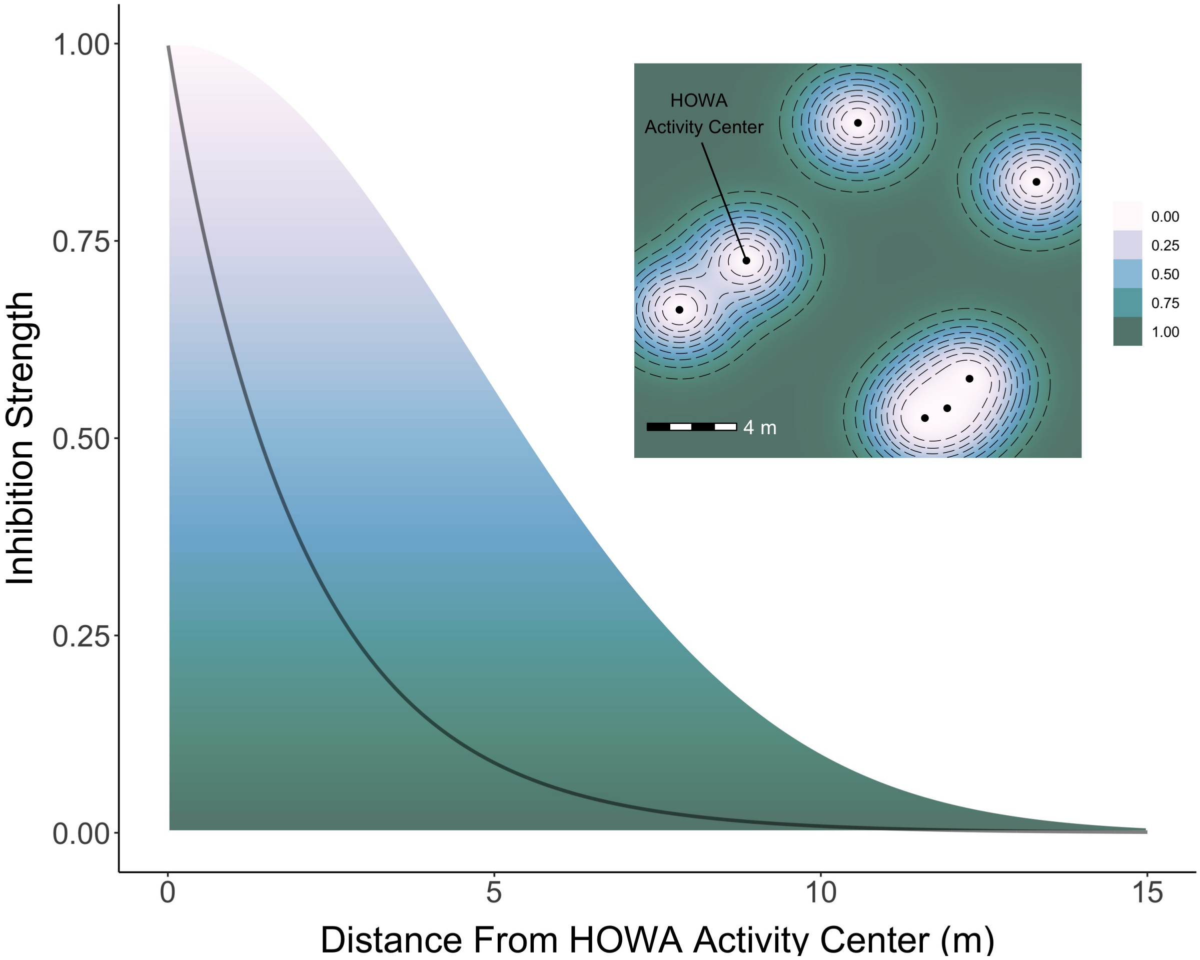

Figure G.1: Inhibition between species at fine spatial scales. The probability of hooded warbler (HOWA, *Setophaga citrina*) activity centers inhibiting black-throated blue warbler (BTBW, *Setophaga caerulescens*) activity centers changes relative to distance. Inset shows the total inhibition probability when multiple hooded warbler activity centers are present. Lighter colors suggest higher inhibition, while darker colors represent areas where hooded warbler activity centers do not impact the location of black-throated blue warbler activity centers.