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METHOD

Individual-level biotic interactions and species distribution models

Heather E. Gaya | **Richard B. Chandler**

Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA

Correspondence
Heather E. Gaya, Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green St, Athens, GA 30602, USA.
Email: heather.e.gaya@gmail.com

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Abstract

Aim: Accounting for biotic interactions in species distribution models is complicated by the fact that interactions occur at the individual-level at unknown spatial scales. Standard approaches that ignore individual-level interactions and focus on aggregate scales are subject to the modifiable aerial unit problem (MAUP) in which incorrect inferences may arise about the sign and magnitude of interspecific effects.

Location: Global (simulation) and North Carolina, United States (case study).

Taxon: None (simulation) and Aves (case study).

Methods: We present a hierarchical species distribution model that includes a Markov point process in which the locations of individuals of one species are modelled as a function of both abiotic variables and the locations of individuals of another species. We applied the model to spatial capture-recapture (SCR) 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.

Results: A simulation study indicated that the model can identify the effects of environmental variation and biotic interactions on co-occurring species distributions. In the case study, there were strong and opposing effects of climate on spatial variation in population densities, but spatial competition did not influence the two species' distributions.

Main Conclusions: Unlike existing species distribution models, the framework proposed here overcomes the MAUP and 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 abiotic factors may be more important than competition at low-latitude range margins. The model can be extended to accommodate count data and binary data in addition to SCR data.

KEYWORDS
biotic interactions, competition, individual-based models, modifiable areal unit problem, point process, spatial capture-recapture, species distribution model

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 (Case & Gilpin, 1974; Hardin, 1960) 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 (Camarota et al., 2016; Diamond, 1978; Terborgh & Weske, 1975).

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 analysing aggregated information such as local abundance or species occurrence data (Clark et al., 2014; Cody, 1974; 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 (Belmaker et al., 2012; Jaeger, 1971; Suhonen et al., 1994). 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 (Blanchet et al., 2020; König et al., 2021; Sherry & Holmes, 1988). This is an example of the modifiable area unit problem (MAUP) in which different scales of aggregation lead to different conclusions about the system (Jelinski & Wu, 1996; Laymon & Reid, 1986). 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; König et al., 2021; Ovaskainen et al., 2016), but the development of a modelling framework allowing for individual-level interactions and population-level inferences remains a fundamental challenge (Dormann et al., 2018; König et al., 2021; Poggiato et al., 2021; Wisz et al., 2012).

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 centre of species' ranges (Cahill et al., 2014; McDonald et al., 2012) 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 (Hargreaves et al., 2014; Schemske et al., 2009). Similarly, abiotic factors were proposed as the main source of poleward range limits (Darwin, 1859; Dobzhansky, 1950; Louthan et al., 2015; MacArthur, 1972; 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, characterised in terms of species-specific abundance and spatial variation in density. The core of the modelling 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 4 years of data on two warbler species—one near the trailing-edge of its range and one near its range centre—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.

2 | MATERIALS AND METHODS

2.1 | Point process models

Spatial point process models can be thought of as individual-level species distribution models defined in terms of abundance (N) and distribution ($\mathbf{s}_1, \dots, \mathbf{s}_N$), where the point $\mathbf{s}_i \in \mathcal{S}$ represents the spatial coordinates of individual i, typically in a two dimensional planar region $\mathcal{S} \subset \mathbb{R}^2$ (Baddeley, 2007; Renner et al., 2015). In many ecological applications, $\mathcal{S}$ is synonymous with the study area or geographic region of interest. It is a spatial region where the N individuals occur. Because they are formulated in terms of clearly defined ecological state variables (i.e. abundance and spatial variation in density), point process models provide more direct insights about populations than SDMs focusing on relative abundance (Gelfand & Schliep, 2018; Renner et al., 2015; Warton & Shepherd, 2010; Yackulic et al., 2013). For instance, popular SDM modelling approaches such as MAXENT (Renner & Warton, 2013) and some forms of logistic regression (Baddeley, 2007) can be equivalently described as Poisson point processes, with additional flexibility not available using other methods (Matthiopoulos et al., 2023). One of the simplest and most important classes of spatial point process models is the inhomogeneous Poisson point process defined by an intensity function $\mu(\mathbf{s})$, which is the expected value of density at location $\mathbf{s} \in \mathcal{S}$. The intensity function, or density surface, can be modelled as a function of spatially referenced environmental variables to learn about the influence of abiotic variables on species distributions (Nightingale et al., 2015; Warton & Shepherd, 2010). The area under the density surface, given by the two-dimensional integral over $\mathcal{S}$, defines the expected value of abundance within the spatial region $\mathcal{S}$. Realised abundance is typically modelled as an outcome of a Poisson distribution, and the points ($\mathbf{s}_1, \dots, \mathbf{s}_N$) are also stochastic, distributed according to the density surface (Figure 1 panel II).

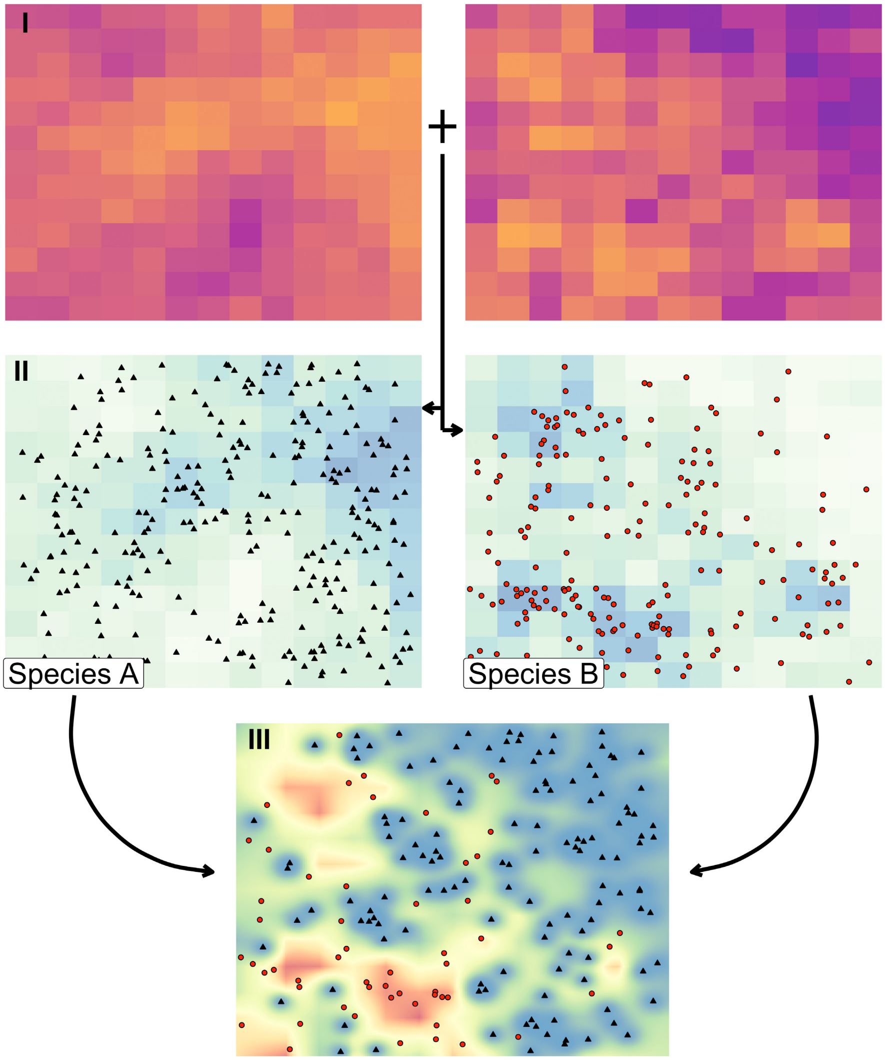


FIGURE 1 Conceptual depiction of the point process model for two interacting species. Top panels (I): *Abiotic conditions*. Environmental variation in this example is described by two spatial layers depicted as raster images. Middle panels (II): *Realised distribution with no biotic interaction*. The abundance and distribution of individuals, 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 colour indicates the expected density (intensity) at each pixel, given the abiotic conditions. Bottom panel (III): *Distribution with both abiotic effects and biotic interactions*. The realised distribution of both species is thinned by an interaction function, resulting in a final distribution that accounts for both abiotic variables and biotic interactions.

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 (Illian et al., 2008; Nightingale et al., 2015; Rathbun & Cressie, 1994). 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 (Efford, 2004; 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 Markov 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 generalised to other types of individual-level ecological data.

2.2 | Interspecific individual-level interactions

We define $\mathbf{s}_i$ as an individual's activity centre—its average spatial location—which could be a territory centre or a home range centre during a specified time interval. Focusing on activity centres instead of instantaneous locations simplifies the model by avoiding the need to describe how individuals move during short time periods (McClintock et al., 2022; Royle et al., 2013).

Assume that all individuals have constant activity centres during the time period of interest. Let A and B represent two sympatric and potentially interacting species. Activity centres for species A are governed by an inhomogeneous point process with intensity $\mu^A(\mathbf{s})$ that describes the expected density of individuals of species A at spatial location $\mathbf{s}$ with environmental variables denoted by the vector $\mathbf{x}(\mathbf{s})$. The intensity of the point process, for example the expected density of species A, can be modelled by using any function suitable for non-negative continuous variables, including a basis function approach or a log-linear function which we employ: $\log\left(\mu^A(\mathbf{s})\right) = \mathbf{x}'(\mathbf{s})\boldsymbol{\beta}^A$, where $\boldsymbol{\beta}^A$ represents a vector of coefficients. Below, we describe this process in terms of continuous space, though in practice the spatial region is discretised into pixels to match the resolution of available environmental data. The expected value of abundance is given by:

$$\Lambda^A = E(N^A) = \int_{\mathcal{S}} \mu^A(\mathbf{s})d\mathbf{s}. \tag{1}$$

In other words, the expected abundance within the spatial region $\mathcal{S}$ is the area under the intensity surface. Realised 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 centre is given by the intensity at location $\mathbf{s}_i^A$ divided by the expected number of individuals of species A in $\mathcal{S}$:

$$p(\mathbf{s}_i^A | N^A) = \frac{\mu^A(\mathbf{s}_i^A)}{\Lambda^A}. \tag{2}$$

Biotic interactions between individuals of species A and B are modelled using a Gibbs point process—a type of Markov point process model characterised 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 generalised approach to hard-core process models can be obtained by a distance-dependent pairwise interaction function that modulates the intensity surface such that the probability of occurring at location $\mathbf{s}$ depends on the distance to all other points (individuals) in the spatial region of interest (Nightingale et al., 2015; Teichmann et al., 2013). 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, the abundance and distribution of species B is modelled as an independent Poisson point process. When species A is present, the abundance and distribution of species B may be influenced by both abiotic interactions and the abundance and distribution of species A.

$$\mu^B(\mathbf{s}) = \exp(\mathbf{x}'(\mathbf{s})\boldsymbol{\beta}^B)\ \underbrace{h(\mathbf{s}|\,\mathbf{s}_1^A, \ldots, \mathbf{s}_{N^A}^A)}_{h(\mathbf{s})}. \tag{3}$$

As with species A, the expected value of abundance of species B is $E(N^B) = \Lambda^B = \int_{\mathcal{S}} \mu^B(\mathbf{s})d\mathbf{s}$, but for species B the intensity includes the interaction function $h\left(\mathbf{s}|\,\mathbf{s}_1^A, \ldots, \mathbf{s}_{N^A}^A\right)$, describing the effect of species *A* on the density of species B at location $\mathbf{s}$. Under strong competition with species A, we would expect fewer individuals of species B to choose activity centres where species A is present, even if the abiotic conditions at location $\mathbf{s}$ are suitable for species B. Thus, strong competition will lead to lower abundance of species B at location $\mathbf{s}$. 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:

$$h(\mathbf{s}|\,\mathbf{s}_1^A, \ldots, \mathbf{s}_{N^A}^A) = \prod_{i=1}^{N^A}\left\{1 - \exp\left(\frac{-\left\|\mathbf{s}_i^A - \mathbf{s}\right\|^2}{2\omega^2}\right)\right\}, \tag{4}$$

where $\|\mathbf{s}_i^A - \mathbf{s}\|$ is the Euclidean distance between the *i*th activity centre of species A and location $\mathbf{s}$. Thus, as the density of species A increases in the vicinity of location $\mathbf{s}$, the probability of species B occurring at that location decreases. The parameter ω^2 determines the scale of competition between the two species. Note that the distributions of the two species will become independent as ω approaches zero. In this case, the interaction function is unity, and thus the intensity of species B does not depend on species A. By estimating ω, we can learn about the degree to which individuals of species A influence the distribution of individuals of species B. An illustration of the model is presented in Figure 1.

One 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 normalising constant that cannot be computed easily, not even with MCMC (Nightingale et al., 2015; Reich & Gardner, 2014; Ripley, 1981). 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.

2.3 | Observation model

The problem with using standard point process models is that they assume that all points (i.e. individuals) can be observed, whereas in empirical studies, some individuals usually go undetected. Ignoring imperfect detection can result in underestimation of abundance and density, and incorrect inferences about the scale of individual-level interactions. Fortunately, this form of observation error can be accounted for using a hierarchical model describing how the observed data arise conditional on the partially observed state process (Royle & Dorazio, 2009). The observation model proposed here is designed for data on uniquely identifiable individuals, such as mark–recapture data or 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 (Royle et al., 2013). 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. Individuals may go undetected because they are elusive or because the traps only effectively sample a subset of the region of interest, and thus both N^A and N^B are unknown. In addition to complicating efforts to study abundance and distribution, unknown values of N pose problems when performing Bayesian inference because the dimensions of the parameter space is not fixed.

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) that is much greater than the true number of individuals in the population. Let M^A represent the upper bound on abundance for species A. Additionally, let the binary latent variables $z_1^A, \ldots, z_M^A$ indicate if individual i was part of the population of species A. As mentioned in Equation 1, the expected number of individuals in the population of species A is Λ^A. Therefore, the expected proportion of M^A individuals that are part of the population is just $\psi^A = \Lambda^A / M^A$. The binary variables are modelled as Bernoulli outcomes $z_i^A \sim \text{Bern}(\psi^A)$. Since individuals can only be detected if they are part of the population ($z_i^A = 1$), the data can then be modelled conditional on the latent binary indicators: $y_{ijk}^A \sim \text{Bern}\left(p_{ijk}^A z_i^A\right)$.

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. As with species A, we introduce an upper bound on abundance, M^B, that is much larger than the true number of individuals in the population of species B. Data augmentation also requires that we modify the pairwise interaction model (Equation 4). 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 Equation 4 by z_i^A. Thus, individual with $z_i^A = 0$ have no effect on the intensity of species *B*. As with species A, $y_{ijk}^B = 0$ for the $M^B - n^B$ individuals not observed during sampling.

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

$$p_{ijk}^A = \alpha_0^A \exp\left(\frac{-\left\|\mathbf{s}_i^A - \mathbf{x}_j\right\|^2}{2\sigma^A\sigma^A}\right), \quad (5)$$

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

The detection parameters α_0^A and σ^A determine the baseline capture probability and the decay in capture probability with distance, respectively. An equivalent model is 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 et al., 2013; Royle & Young, 2008).

2.4 | Simulation study

We explored the performance of the model under 5 conditions: (1) Spatial competition between species and no relationships to environmental variables; (2) Spatial competition between species and opposite effects of environmental variables; (3) Spatial competition between species, with species A, but not species B, influenced by the environment; (4) Spatial competition between species and both species positively associated with the environment; and (5) No spatial competition between species and opposite relationships to the environmental gradient (Table S1). We simulated a 10 by 10 square trapping array in a spatially autocorrelated environment with traps spaced 10 units apart. For all scenarios, we simulated 5 sampling occasions, with $\sigma = .05$ and $\alpha_0 = 0.30$ for both species. We tested the model under each of the 5 conditions when species density was moderate (median density 0.35 individuals per unit squared, Scenarios 1–5) or low (median density 0.17 individuals per unit squared, Scenarios 6–10). Simulated species density ranged from 0.04 individuals per unit squared to 0.76 individuals per unit squared.

We evaluated bias, coefficient of variation (CV), root-mean-square error, and 95% credible interval coverage for the posterior medians of all β coefficients and the competition 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 2 chains for 15,000 iterations with 5000 burnin iterations.

2.5 | 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 behaviour, diet, nest site selection and size and have overlapping breeding ranges in the southern Appalachian Mountains (Holmes, 2011; Ogden & Stutchbury, 1996; Weeks, 2001). The encroachment of warm-adapted species, such as the hooded warbler, into historically cooler and wetter areas has been proposed as an explanation for declines of cool-adapted species such as the black-throated blue warbler (Merker, 2017). 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 (Lewis et al., 2023; Merker, 2017; Sauer et al., 2017).

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 four rows of five nets (Figure 2). Nets were spaced on a 50 m grid with the inner row skipped to create two rows of 10 nets, a gap of 100 m and two more rows of 10 nets. Ten of the 20 nets (2 rows per day) were operated for 5 hours on each day beginning approximately

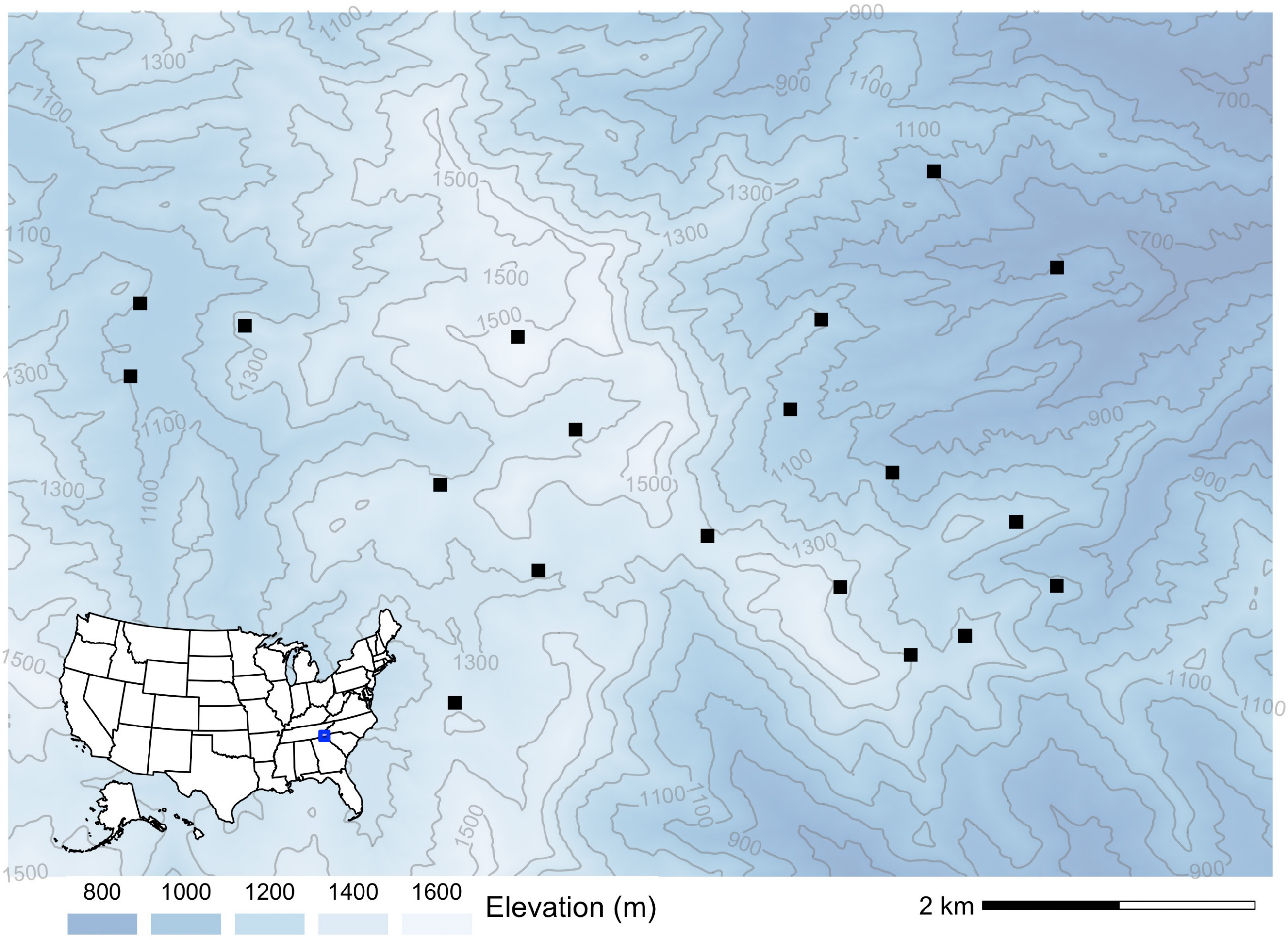


FIGURE 2 Capture-recapture sites in the Nantahala National Forest, North Carolina, USA. Each site had 20 net locations in 4 rows of 5 nets, with nets spaced 50 m apart. Sites were sampled from May to June 2018–2021.

30 min before sunrise from May 7 to June 28. Each net was open for two consecutive days with each site sampled for four consecutive days, except when weather interfered. Each captured individual was marked with a US Geological Survey aluminium band and a unique combination of three colour 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 modelled 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 five 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 × 1-km daily precipitation data (Thornton et al., 2022). Note that we did not model temporal dynamics explicitly. The scope of our work was to develop a spatially explicit individual-based species-distribution model, and thus we did not include birth, growth, movement or mortality processes. Instead, each year of data was modelled independently.

Elevation of the sampling locations ranged from approximately 600 m to 1600 m (Figure 2), with higher elevations being colder and wetter than low elevation sites. Data from the 4 years were modelled jointly. We assumed the strength of the interspecific spatial competition was constant across years, but allowed abundance and individual activity centre locations to vary between years. For computational efficiency, we modelled 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 territory sizes. We did not consider vertical partitioning in space (MacArthur, 1972), as behavioural observations suggest similar foraging and nesting heights between species. 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.

For some species, the process of being captured and banded can result in temporary avoidance of the capture location, a process known as 'trap-shyness' (Williams et al., 2002). To account for this behaviour, we allowed baseline capture probability, α_0^A and α_0^B to change between the first capture and subsequent captures of an individual at each net location.

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). Though we analysed our simulation data in JAGS, we chose to use NIMBLE for the case study to improve computation speed. 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 | RESULTS

Parameters were recovered with low bias for all simulated scenarios, even when sample sizes were below 10 individuals per species (Figure 3). For the moderate density scenarios with simulated competition (Scenarios 1–4), bias in the posterior median of ω (the competition parameter) ranged from −0.006 to −0.003, with 95% credible intervals capturing the true value 93%–100% of the time (Table S2). Point estimates of ω were slightly positively biased (range −0.002–0.020) for the low density scenarios with simulated competition (Scenarios 6–9), with 95% credible intervals capturing the true value 94%–98% of the time. Credible interval coverage was lowest for β_0^A (the intercept for abundance of species A), capturing the true value in 79%–92% of simulations. When points were simulated without competition (Scenarios 5 and 10), the model correctly identified that competition was low, with lower estimates of the competition parameter approaching 0.

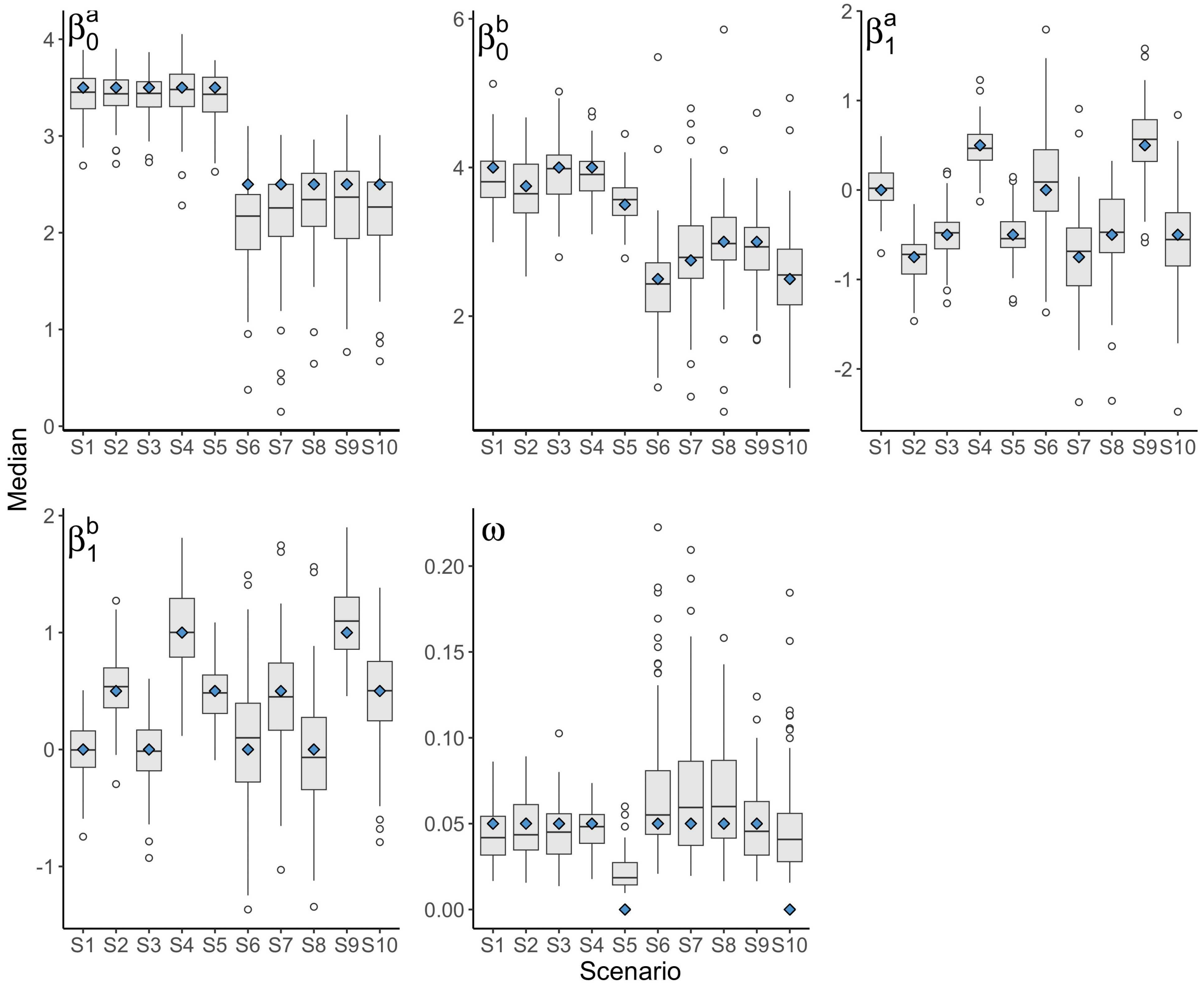


FIGURE 3 Simulation study results for 10 scenarios, each with 96 simulated datasets. The posterior mode was used as a point estimator. Blue dots represent the true data generating values. Median abundance was 35 individuals per species for scenarios 1–5 and 15 individuals per species for scenarios 6–10.

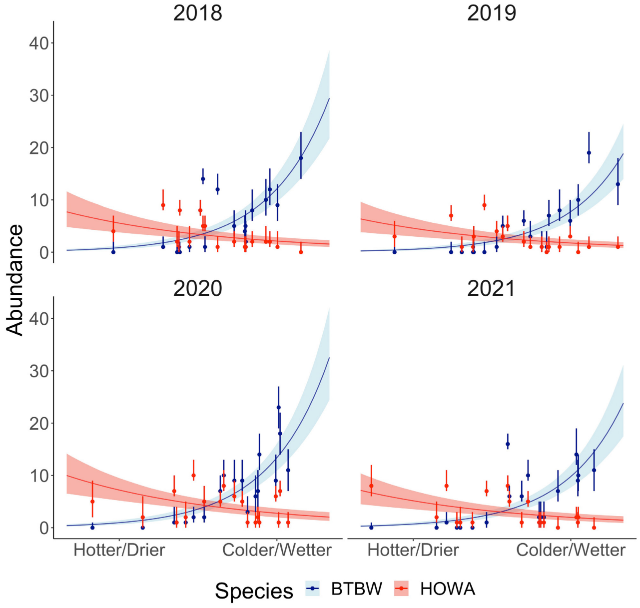


FIGURE 4 Abundance and 95% CIs for black-throated blue warbler (*Setophaga caerulescens*) and hooded warbler (*Setophaga citrina*) from 2018 to 2021 in the Nantahala National Forest, North Carolina, USA. Trend lines show the expected values of abundance for each species when only abiotic relationships are considered.

We captured 274 black-throated blue warblers and 151 hooded warblers across four breeding seasons. Individuals captured per year ranged from 58 to 87 black-throated blue warblers and from 33 to 52 hooded warblers (Figure S1). 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 (Figures 4 and 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 (Figure 4).

The competition parameter ω was estimated to be 2.31 (95% CI: 0.084–6.58) (Table S3), suggesting weak competition between the two species at fine scales (Figure 6). Spatial competition between activity centres was strongest when activity centres were at the same location, with no competition at distances greater than 10 meters. There were no changes in abundance estimates of both species when the model was run with and without the interaction function (Figure S2). The WAIC was 4578 when the interaction function was included and 4481 when removed, suggesting the interaction function did not improve model fit.

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 presented a model that overcomes these challenges and allows for joint modelling of spatial variation in density of two potentially interacting species. The simulation study revealed that the model successfully distinguished true competition from random variation in individual locations or inverse species relationships to habitat characteristics. 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.

In spite of seemingly strong competition between black-throated blue warblers and hooded warblers, our results indicate that spatial segregation of these two species in the southern Appalachian Mountains 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 result 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 stands in contrast with the traditional view that biotic interactions are the main drivers of species distributions at warm-edge range limits (Paquette & Hargreaves, 2021), yet, our results are consistent with previous research on trailing-edge species of birds in the southern Appalachian Mountains (Merker & Chandler, 2020). Nonetheless, 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).

The model of interspecific interactions is conditional, with the distribution of species B depending on the distribution of species A. However, the interaction function is symmetric, meaning that the labelling of the two species as species A or species B in the model

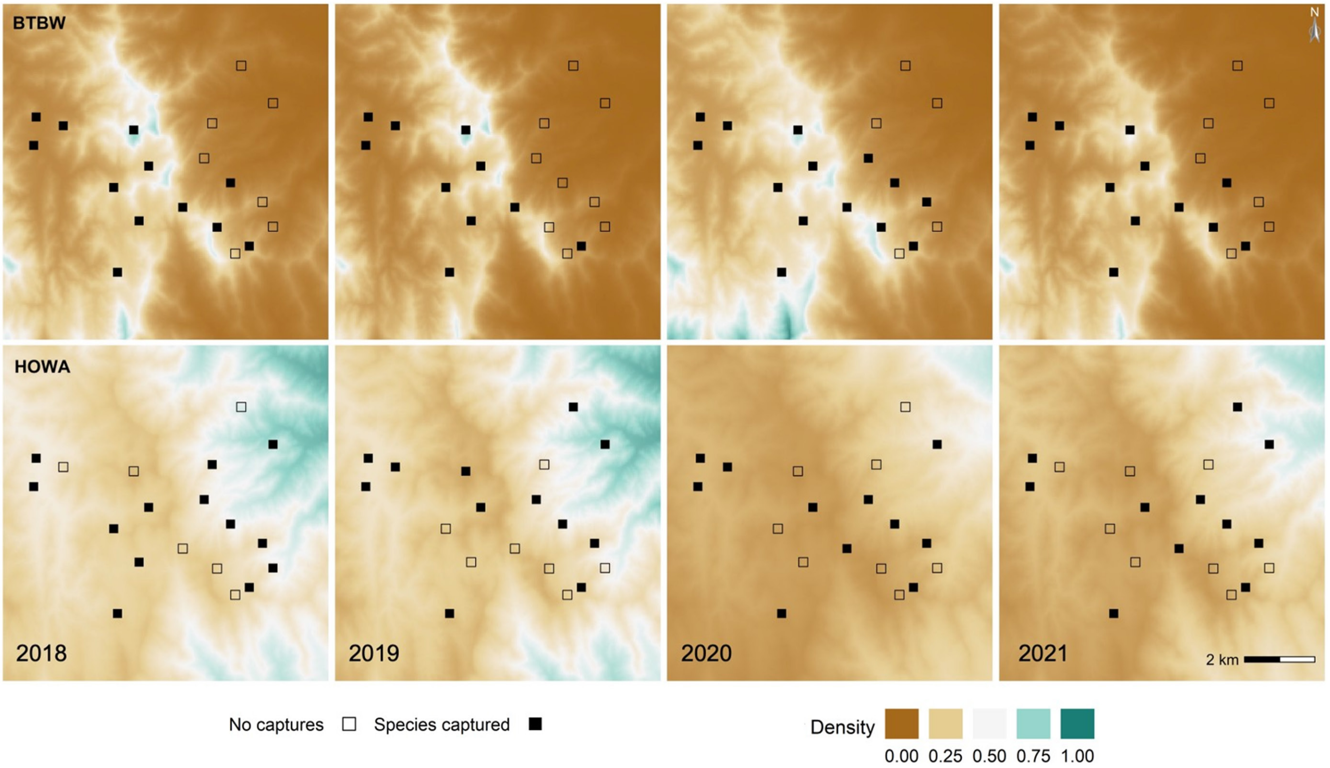
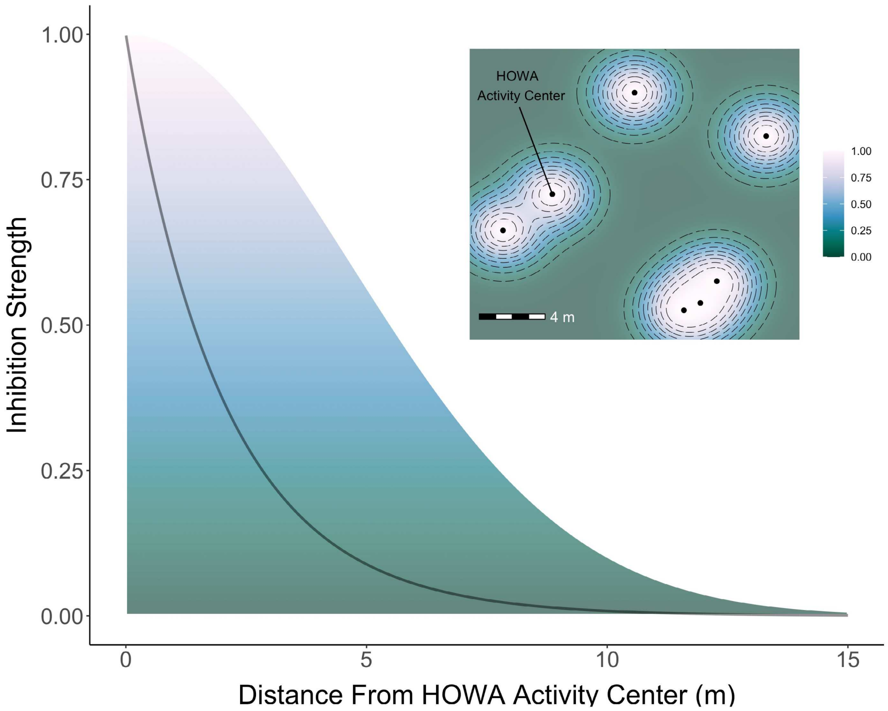


FIGURE 5 Annual density surfaces of black-throated blue warbler (*Setophaga caerulescens*) and hooded warbler (*Setophaga citrina*) from 2018 to 2021 in the Nantahala National Forest, North Carolina, USA.

FIGURE 6 Inhibition between species at fine spatial scales. The probability of hooded warbler (HOWA, *Setophaga citrina*) activity centres inhibiting black-throated blue warbler (BTBW, *Setophaga caerulescens*) activity centres changes relative to distance. Inset shows the total inhibition probability when multiple hooded warbler activity centres are present.



has no effect on the resulting abundance estimates or estimated strength of the inhibition parameter. Thus, interactions between two species can be studied even when there is no clear reason to view one species as dominant over the other.

Although not explored here, this model could be expanded to include temporal demographic processes (McClintock et al., 2022; Theng et al., 2022). By accounting for demographic processes, it should be possible to model temporal variation in biotic interactions to more accurately reflect seasonal changes in biotic relationships. With instantaneous locations, it may also be possible to consider a non-symmetric interaction between the two species. Currently available open-population joint species distribution models often quantify associations between species at relatively course spatial scales (Doser et al., 2022; Tikhonov et al., 2020). Combining these pre-existing frameworks with the individual-level model presented here should allow for inference on the demographic consequences of competition. Combined with behavioural observations, this approach could be used to determine dominance relationships between two species, and their population-level consequences.

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 competition 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 species 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).

Although we applied our model to data from a relatively small subset of the species' geographic ranges, and we used intensive capture-recapture data for inference, range-wide applications could be achieved by combining individual-level data with count data in an integrated model (Chandler & Royle, 2013; Schaub & Kéry, 2022; Zipkin et al., 2021). Other sources of information such as GPS location data could be incorporated to provide even more information about movement and distribution (Berberich et al., 2016; Christiansen et al., 2015; Sollmann et al., 2013). It may also be possible to apply our framework to intraspecies interactions, expanding on work done by Reich and 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, which is not possible with conventional species distribution models.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All code to reproduce analysis is publicly available on Zenodo: https://doi.org/10.5281/zenodo.7615731.

ORCID

Heather E. Gaya https://orcid.org/0000-0003-3573-6694

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BIOSKETCKHES

Heather E. Gaya is an ecologist and biostatistician and current Postdoctoral Researcher at the Warnell School of Forestry and Natural Resources, University of Georgia, United States. Her research interests focus on understanding the individual-level mechanisms that shape population dynamics and demography.

Richard B. Chandler is the Daniel B. Warnell Professor of Forestry and Natural Resources at the University of Georgia, United States. His research interests include spatial population dynamics and wildlife conservation.

Author contributions: Heather E. Gaya and Richard B. Chandler jointly conceived the model. Coding and data analysis were performed by Heather E. Gaya, with supervision from Richard B. Chandler. Both Heather E. Gaya and Richard B. Chandler contributed to manuscript writing and interpretation of results.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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